JURASSIC[1]

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INTRODUCTION[2]

Zoogeographic differentiation is the result of ecologic interaction of numerous regionally effective causes, such as dynamics of dispersal, struggle for existence, climate, topographic links and barriers, salinity, water depth, currents, and supply of nutrients. Yet there is no fundamental limitation in regard to the many special facies conditions that exist in small areas, even down to the occupation of cracks in the seafloor

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[2] A brief general view on the Jurassic Period (except for zoogeography) was published by the author in *Encyclopaedia Britannica* (1974, p. 354-360).

by ammonites, or of sponges by foraminifers.

Benthonic dwellers of shallow seas are generally strongly differentiated regionally as well as locally. On the other hand, nektonic and planktonic animals, as well as inhabitants of the deep sea, may be widely distributed unless restricted by climatic zones, physical barriers, or ocean currents. In many faunal descriptions insufficient checks are being made, however, and new species are being established which may be no more than varieties of known species or genera in distant areas. "Splitters," as well as "lumpers," render difficult the interpretation of zoogeographically important differences. Also, the literature has not been sufficiently searched for widely disseminated zoogeographical data. For these and some other reasons, regional comparison of Jurassic invertebrate faunas is still in its infancy.

Most conclusions pertaining to Jurassic zoogeography are based on ammonites, which, therefore, take up the major part of this discussion. SPATH, in the course of his lifelong work on ammonites, became increasingly skeptical as to their suitability as zoogeographic indices. He defended the old view of worldwide postmortem drifting of ammonite shells. Where regional zoogeographic differences were undeniable, he attempted to explain them as due to gaps in the stratigraphic record (SPATH, 1952).

Recent research, however, has confirmed the conclusions, reached by NEUMAYR (1883), that certain ammonite communities are characteristic of certain marine realms. The crossing of abyssal depths by ammonite larvae or by floating shells certainly was not the rule. Distribution patterns and lithological data suggest that climatic zones, depths of the sea, and the nature of migratory routes, may be the most important factors in explaining regional restrictions. The distribution of coral reefs also indicates climatic zonation during the Jurassic Period. The distribution of some benthonic clams (e.g., *Buchia, Inoceramus*) supports the conclusions based on studies of ammonites and makes it seem probable that the ammonites were epibenthonic and are preserved in their natural habitat to a greater extent than generally believed.

It may be assumed with confidence that the Arctic and Pacific oceans existed in the Jurassic, whereas the Atlantic and Indian oceans were probably still partly closed, and they gained their present configuration and position only through later continental drift. Deep-ocean and pelagic faunas are becoming known through studies related to the Deep Sea Drilling Project. The oldest sediments discovered to date in the present North Atlantic are presumably of Oxfordian age. We know more about rapidly subsiding geosynclinal areas that reached oceanic depths only where the influx of sediment or volcanic material was small (GARRISON & FISCHER, 1969). Jurassic shelf and littoral sediments preserved on present continents and islands are best known.

Projected on the present globe, the following major units of Jurassic marine zoogeography may be recognized (Fig. 1) following NEUMAYR (1883), UHLIG (1911), HAUG (1927), TERMIER and TERMIER (1952), and ARKELL (1956):

1) Tethys in the widest sense, subdivided into:
    a) a Mediterranean-South Asiatic center (area of alpine mountain chains with several subareas);
    b) a probable continuation westward to Mexico and to the southeast to the Malayan-New Zealandian geosyncline whose extension surpassed that even of the Tethys;
    c) epicontinental areas and inland seas (North Africa without the Rif Mountains, East Africa, peninsular India, central Arabia, Indonesia, southern China, southern Soviet Union, south-central Europe).
2) The Arctic-Boreal area (recent coastal lands of the Arctic Ocean, with strong influences in northern Europe and central Russia).
3) The Jurassic areas surrounding the Pacific Ocean lacking faunistic uniformity.

Presently known facts do not permit reconstruction of an individual Antarctic Ocean during Jurassic time (STEVENS, 1967b).

The number of genera and species decreases from the marginal areas of Tethys toward the north, thus indicating cooling

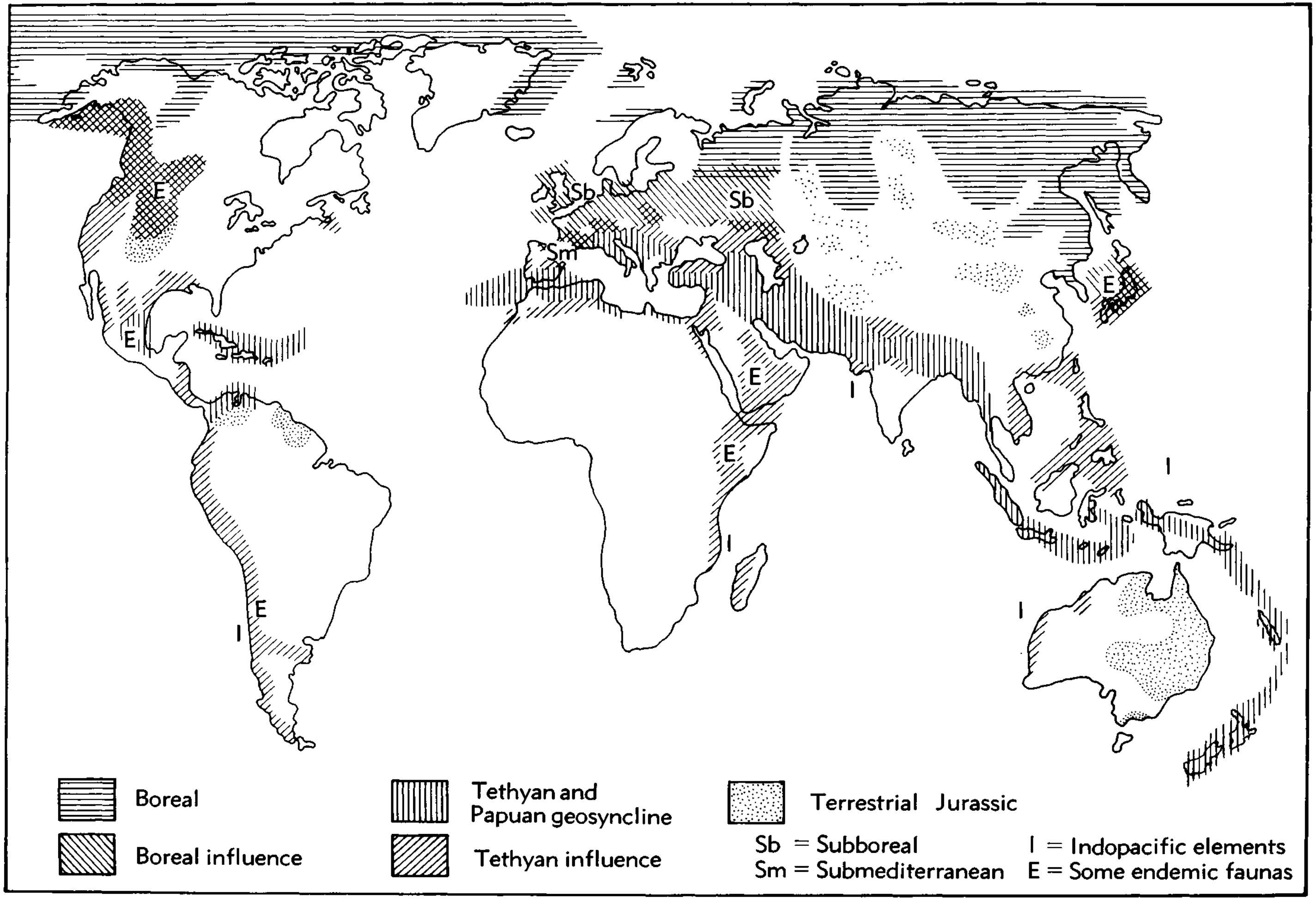

FIG. 1. Present distribution of zoogeographic realms and provinces of the Jurassic (Hölder, n).

climate in that direction (A. G. Fischer, 1961; de Lattin, 1967; B. Ziegler, 1967). It should be remembered, however, that the number of taxonomic units is also fewer in the bathyal areas of Tethys just as is true for recent faunas in deeper parts of the oceans.

In the northern hemisphere, and probably on the entire earth, the climate during Jurassic time was warmer than now. Vegetation covered areas that are now near the poles. Saks and Nalnyaeva (1966) used the term "Arctic" for the central Boreal realm during times of wider distribution of the Boreal faunas. In the changing pattern of the borders between the Boreal and non-Boreal faunas, perhaps the chemico-physically important 15°-isotherm of the sea has played a role (Ager, 1956).

PROTOZOA

The first flagellates were the Coccolithophorida and the Dinoflagellata (Peridinina) in the Early Jurassic. The coccoliths (calcareous skeletons of coccospheres, flagellates) are found in geosynclinal, as well as epicontinental sediments, for example, in oil shale of the upper Liassic and in fine-grained limestone of the Upper Jurassic of southern Germany (Flügel & Franz, 1967).

Among the Rhizopoda, the radiolarians were on the increase. The lime-secreting foraminifers, after their eclipse following the Permian, underwent a new strong development. Among these are the benthonic Lituolidae (Henson, 1949), including the large foraminifer *Orbitopsella* in the Mediterranean Lias, and the first appearance of the pelagic globigerinids *(Protoglobigerina)* in the Tethys. These appeared first in the Bathonian and became rock builders in the Oxfordian. In the Swabian Jura, *Globigerina?* appears at the Callovian-Oxfordian boundary (Seibold & Seibold, 1960).

The Ciliata appeared with the calpionellids, which have a calcified shell wall (lorica). In the Alpine-Mediterranean Tithonian and in Late Jurassic sediments from the Atlantic Ocean, they attained stratigraphic importance (le Hegarat & Remane, 1968).

PORIFERA

During the Jurassic, sponges were of greater importance than ever before in the history of the phylum. Calcareous sponges occur, as in the Triassic, in coralliferous and other sediments deposited in very shallow water. The siliceous sponges, which began to diversify in the Jurassic, preferred somewhat deeper water. In the Lower and Middle Jurassic of the Alps, spiculite rocks are composed of disassociated needles of disintegrated Monaxonida. The "gaize" of the Oxfordian of France is such a spiculite.

Hexactinellida and Lithistida formed meadows such as the Hexactinellida horizon in the Middle Liassic of Portugal and in the Callovian of La Voulte in southeastern France. With the help of blue-green algae (stromatolites), and if the supply of calcareous sediment was sufficient, they built hummock-like reefs that were preserved as massive sponge limestone. Minor occurrences of this kind are known from the Middle Jurassic of southern England, northern France, Spain, and Chile. During the Late Jurassic, a large sponge-reef belt, unique in earth history, bordered the central European Tethys from the Swiss Jura eastward through southern Germany as far as the Upper Vistula (Cracow-Kielče) (Roll, 1934). In the south German Jura, hexactinellids prevailed in the late Oxfordian, and tetraxon and monaxon lithistids in the Kimmeridgian (Schrammen, 1924). Calcareous sponges and corals generally inhabited the tops of dead siliceous sponge reefs.

ANTHOZOA

Single corals (ahermatypic, without zooxanthellae) existed throughout Jurassic time. *Chomatoseris (=Anabacia)* is important in the marly facies of the Middle

Jurassic. Reef-building (hermatypic) corals played only a minor role in the Early Jurassic. Their most important occurrence is in the massive limestones of Domerian age in the Djebel Bou-Dahar in Morocco, in the epicontinental Jurassic south of the Tethys. Facies and associated faunas are reminiscent of those of the Upper Jurassic coral limestone of Europe (Dubar, 1948). "Meadows" of colonial corals occur in the Liassic of Scotland (Hebrides) and southern Alaska. In the Middle Jurassic, hermatypic corals are strongly represented in the Tethys, with appearance of new families and development of numerous independent faunal provinces such as in eastern Iran (Flügel, 1966, comparing different coral faunas of the Tethys and East Africa) and Madagascar (Alloiteau, 1958). Collignon (1959) has interpreted the coral facies of the Bathonian of Madagascar as a barrier reef with atolls.

In western Europe the coral facies is distributed throughout France and farther north. In England it shows three main developments: in the Inferior Oolite (Bajocian), in the Great Oolite (Bathonian), and in the Corallian (Oxfordian). All three coral faunas differ greatly in the spectrum of their species; however, in southern areas where the number of genera and species is greater, the coral faunas also include many long-ranging forms with diminished stratigraphic value (Geyer, 1958). In the lower Kimmeridgian of Great Britain, two species of redeposited reef corals of possibly Oxfordian age have been found as far north as Helmsdale on the northeast coast of Scotland, which is the northernmost occurrence (58° N) of Jurassic reef corals in Europe. Only a few reef corals are known in the Oxfordian of northern and central England. Their number increases rapidly toward the south (south coast of England, Boulonnais of northern France, northwestern Germany). In the Upper Jurassic coral limestones of southern Germany and Switzerland, the number of reef coral species reaches 100 to 200 (B. Ziegler, 1964). This increase is probably due to climatic conditions; however, Arkell (1935; 1956) thought that because of the relatively short distances involved, a topographic barrier would better explain these differences. In eastern Africa, Upper Jurassic coral reefs extend as far as 5° S., which is not quite as far south as in the Middle Jurassic.

In the Kimmeridgian, coral reefs of central Europe, with the exception of a few outposts, again retracted to the northern edge of the Tethys where they shifted even farther to the south, as for instance in the Swiss Jura (M. A. Ziegler, 1962); however, in the Tethys and on the Pacific coast of southern Honshu, Japan, they are widely distributed. In South America, major reefs are lacking in the Jurassic. Individual reef complexes of the Tethys and adjacent areas are composed of only a part of the total Upper Jurassic fauna. As a rule, one-third of the genera and two-thirds of the species of adjacent areas are absent. (See comparison of Stramberg beds and the Upper Jurassic of southern Germany by Geyer, 1958.)

Excellent examples of reef-front and back-reef facies in the Jura Mountains were described by M. A. Ziegler (1962) and Enay (1965). Open colonies of hermatypic corals existed also in marly facies such as the Oxfordian of the Swiss Jura (M. A. Ziegler, 1962, p. 40).

HYDROZOA

In places, *Ellipsactinia* is an important member of Upper Jurassic reef communities of the Tethys, especially in the Carpathians and in the Balkans. Hydrozoan faunas of changing composition have recently been reported from southern Slovenia (Turnšek, 1966) and from the eastern calcareous Alps (Fenninger & Hötzl, 1965). The latter fauna shows close faunistic relationships along the entire Tethys as far east as Japan, whereas the relationships toward the west (Switzerland, France, Portugal) are far less pronounced.

BRACHIOPODA

After the decline of brachiopods in the Triassic, a new surge followed. The Thecideidae and the Terebratellaceae are known with certainty only since the Early Jurassic.

Survivors from the Paleozoic are the helicopegmatoid *Spiriferina* (until early Bajocian) and *Koninckina.* The last chonetoid brachiopod *Cadomella* (Pliensbachian-Toarcian, epicontinental Europe) acquired a helicopegmatoid brachiophore independently from the Helicopegmata (COWEN & RUDWICK, 1966).

The inarticulate brachiopods *Lingula, Discinisca,* and *Craniscus* are of almost cosmopolitan occurrence. Zoogeographical comparisons with other areas are rendered difficult by the fact that until now the study of Jurassic Articulata has been practically restricted to Europe, and in other areas there has been a tendency to establish independent taxonomic units. *Furcirhynchia,* until recently known only from Europe, has lately been found in Canada (AGER & WESTERMANN, 1963). In many cases, however, provincialism is a fact. Even in the English-Scottish Jurassic, several brachiopod provinces can be distinguished (AGER, 1956). *"Terebratula" joassi* DAVIDSON and the large *Rhynchonella sutherlandiae* DAVIDSON are endemic in the Kimmeridgian of northeastern Scotland.

The genera *Somalirhynchia, Daghanirhynchia, Septirhynchia, Bihenithyris, Somalithyris, Striithyris,* and *Trigonithyris* are restricted to the general area of East Africa and southern Asia. Multicostate Terebratulidae, which are rare in epicontinental beds of northwestern Europe, predominate along with multicostate Zeilleriidae in the reef facies of the Lower Jurassic of Morocco (DUBAR, 1942). ROUSSELLE (1968) and ROUSSELLE and BISCH (1967) have described some Rhynchonellidae and Orthotomidae that are endemic in the Moroccan Lias. The Early Jurassic brachiopods of Japan show closer affinities with those of the west than with those of North America (KOBAYASHI, 1961).

AGER (1965) offered the following ecological observations and conclusions: articulate brachiopods are almost exclusively stenohaline; *Kallirhynchia* penetrates also into the estuarine environment of the English-Scottish Middle Jurassic, elsewhere sandy and oolitic littoral environments are preferred; Rhynchonellidae tend to appear in pockets, large asymmetric forms like *Septoliphoria astieriana* were adapted to near-reef environments; *Terebratula moravica* with its long beak anchored in muddy bottom sediments is found in backreef facies, other adaptations are found on hard grounds, algal mats, and sponges; sulcate forms may be interpreted as adaptations to oxygen- and nutrient-deficient depths. Such conditions existed, for example, at the bottom of the Tethys in the Alpine-Carpathian area, which was by no means everywhere an open ocean. Here, a specially adapted form is *Pygope,* which in many places represents the only benthonic form in the Mediterranean Tithonian.

VOGEL (1966) interpreted the central perforation of the shell of *Pygope* as a means to remove used water, in the nutrient-poor bathyal region, as fast as possible from the interior of the mantle and to prevent its being mixed with water sucked into the inhalant canal. The occurrence in East Greenland of the related *Antinomia* indicates connections to the Arctic during Portlandian and Valanginian times (DONOVAN, 1953; MUIR-WOOD, 1953).

BIVALVIA, GASTROPODA

The epicontinental bivalve faunas of the Lower and Middle Jurassic comprise many widely distributed elements. The Ostreina first appeared in the Late Triassic, but did not evolve rapidly until the Jurassic. *Cardinia* is especially common in lower Liassic rocks and locally also in somewhat younger shallow-water strata from Japan to Canada. *Plagiostoma* probably has a similar distribution. The group of large-sized *Oxytoma scanica* and *O. cygnipes* is known in the lower and middle Liassic from northern Europe as far as the Alps, as well as in the Sinemurian Fernie Group of Canada (HÖLDER, 1953; FREBOLD, 1957). *Weyla alata* and related forms are common members of the western American Liassic faunas and extend as far as Portugal and southern Spain in Europe. Presence of the smaller *Weyla ambongoensis* in the Toarcian of East Africa and Madagascar caused DACQUÉ (1915) to postulate close relationships of this area with South America. Later, however, this species was also reported from Morocco and India (Cox, 1965). Leanza (1942) described several hundred species of bivalves from the Liassic of Neuquen in Argentina, two-thirds of which are indigenous. The rudist-like *Plicatostylus,* which forms biostromes, is known exclusively from the Liassic of Oregon (Lupher & Packard, 1930) and Peru (Geyer, 1973). *Gryphaea* retreated from the Arctic areas after the Liassic (Imlay, 1965). Imlay (1964a) described a bivalve fauna from the Middle Jurassic of Utah, containing a number of new, probably endemic, species. From the Middle Liassic and into the Bajocian, *Lenella* and *Arctotis* (Pteriina) are endemic in the Arctic marine Jurassic of Siberia (Saks, Mesezhnikov, & Shulgina, 1964). *Retroceramus* and *Arcticeramus* join in the Middle Jurassic. The inoceramids advanced repeatedly far to the south (Imlay, 1965), as did the buchiids in somewhat later times.

As early as the Liassic, restriction of certain bivalves caused regional biofacies. In the Liassic, reef limestone was restricted to a few areas of the Tethys, thus creating faunal associations rather similar to those that were more widely extended to the north during later Jurassic times. Examples are the already-mentioned middle Liassic reef limestones of the southern High Atlas of Morocco (Dubar, 1948), which contain, in addition to calcareous algae, abundant corals, brachiopods, gastropods, echinoderms, and bivalves such as *Perna* (length 60 cm, width 6 cm), *Pachyrisma, Durga, Pachymegalodon, Pachymytilus, Opisoma,* and *Lithiotis.* Some of these (*Opisoma, Durga, Pachymegalodon, Lithiotis,* and the related *Cochlearites*) are found in banks and reefs in the somewhat different argillaceous facies of the gray limestone of the southern Alps, which have many analogues as far east as Timor (Wanner, 1910).

Pseudomonotis tends to occur in shallow-water limestone; similarly, *Posidonia* occurs in deposits of clay and calcareous quiet-water rocks of geosynclinal and epicontinental areas. Among the posidoniids, *Bositra buchi* is widely distributed, in places as the only fossil in shaly and argillaceous rocks from the Toarcian to the Oxfordian, generally in geosynclinal facies. A pelagic-nektonic mode of life, which was inherited from the old Paleozoic root-stocks of the Limacea and Pectinacea, can be assumed because of lack of other benthonic life, other ecologic indicators, as well as from the shell morphology (Jefferies & Minton, 1965). On infrageosynclinal rises and plateaus, coquinas of *Bositra* shells accumulated, locally associated with remains of the rich benthonic life of these hard grounds (Sturani, 1967). *Silberlingia* is endemic in California (Imlay, 1963).

With the help of a number of "faunal spectra," B. Ziegler (1967) illustrated the depth dependence of bivalves in relation to other marine fauna.

Trigonia, known from the Middle Triassic onward, is richly represented in the lower Liassic of the southern Andes and of Japan. It probably originated in the Pacific area, and first reached Europe from the west during middle Liassic time. At the transition from the Lias to the Dogger, costate and clavellate trigonias spread rapidly. Trigonias are mostly found in great masses in sandy and ferruginous, more rarely in argillaceous, rocks. Their habitat is the shallow shelf at depths from 10 to 50 meters. Their abundance in epicontinental areas is in strong contrast to their absence in the Tethys. In the Upper Jurassic of East Asia and the west coast of Japan, *Nipponitrigonia* predominates, whereas *Myophorella (Haidaia)* predominates on the Pacific coast of Japan (Maeda, 1962). Occurrences of *Indotrigonia* and *Opisthotrigonia,* though represented by different species, correlate the Upper Jurassic of peninsular India with that of East Africa (Cox, 1965).

Buchia, which ranges from the Oxfordian to the Neocomian, spread repeatedly from its original Arctic-Boreal habitat far into the south where the number of its species increased. This genus is an especially important indicator for marine connections between Boreal, Pacific, and Tethys areas (Imlay, 1959, 1965). By late Oxfordian, a first advance was made southward along the American west coast reaching, in the Kimmeridgian, as far as Mexico where a *Buchia* deposit contains numerous species. Another *Buchia* invasion occurred during the Portlandian. From Mexico and possibly also from southeastern Asia, the genus reached the southern Andean geosyncline of Peru, Chile, and Argentina.

Buchiids, especially the genus *Malayomaorica* JELETZKY (1963), are known from the Spiti Shale of the Himalayan geosyncline, from the islands of Roti, Misol, and Buru of the Indo-Malayan geosyncline, and also from northwestern Australia. Their occurrence indicates that a direct connection to the Arctic via eastern Asia existed. *Buchia mosquensis* and *B. volgensis* are also found in the *Nerinea* limestones of Mangyshlak, which they may have reached by way of a Late Jurassic marine connection east of the Urals, but possibly also from the Russian area farther west. Toward the west, these forms advanced from the central Russian basin by way of Poland and Pomerania into England and the Boulonnais of northern France. In the south German Jura, *Buchia* appears in the upper Oxfordian (BRINKMANN, 1929; MAYNC, 1947).

Times of regression were characterized by euryhaline and brackish bivalve associations such as *Corbula, Eomiodon, Protocardia, Pseudotrapezium,* and *Eligmus.*

Rocks containing brackish and fresh-water molluscan faunas are known from the Estuarine Series of the Middle Jurassic of England and Scotland (HUDSON, 1963a,b), the East African-Indian area (*Eligmus* fauna), from the Purbeckian of Europe (HUCKRIEDE, 1967), the Morrison Formation of the United States, and the Tetori Group of Japan (SATO, 1961; MAEDA, 1961). On the other hand, supersalinity influenced the marine life. JORDAN (1974) interpreted the northwest German Upper Jurassic rocks as sediments of a supersaline and temporarily oil-soiled sea.

The continental Liassic fauna of central Asia consists solely of some surviving Triassic bivalves. *Pseudocardinia* appears in the upper Liassic and becomes abundant in the Middle Jurassic, whereas the fresh-water gastropod *Bithynia* appears in the Middle Jurassic. *Arguinella, Limnocyrena, Corbicula,* numerous Unionidae, and gastropods of the prosobranchiate families Viviparidae, Valvatidae, Micromelanidae, Hydrobiidae, and of the pulmonate families Planorbidae and Limnaeidae appear in the Upper Jurassic (MARTINSON, 1964). The pulmonate forms were presumably the first immigrants from land into fresh water in the history of the gastropods.

Among marine gastropods, *Discohelix* was one of the last survivors of the Paleozoic Euomphalacea. This genus is known mainly from the Lower and Middle Jurassic of the Mediterranean area, where its species serve as guide fossils (WENDT, 1968). In the oil shales of the European Toarcian, the small genus *Coelodiscus* (Euomphalacea?) is found frequently congregated around saurian carcasses.

Among mesogastropods, the Naticacea, which had their beginning in the Jurassic, the Strombacea with *Harpagodes* of Middle Jurassic to Late Cretaceous age, and *Columellaria,* a reef inhabitant of the Late Jurassic, should be mentioned. Among neogastropods the thick-shelled Nerinacea *(Nerinella, Nerinea, Itieria),* which were adapted to shallow-water facies between coral reefs, play an important, commonly rock-forming, role. They are restricted to the Jurassic and Cretaceous.

AMMONOIDEA

According to SCHINDEWOLF (1961-68), most Jurassic Ammonitina originated from *Psiloceras,* whose origin has to be looked for in the Upper Triassic Lytoceratina. WIEDMANN (1973b) considered *Phyllytoceras* from the Norian to be the ancestor of *Psiloceras.* According to KRYSTYN (1974), however, *Phyllytoceras* is based on an indeterminable inner whorl of *Rhacophyllites.* Therefore, the origin of the Neoammonoidea remains uncertain.

THE GEOSYNCLINAL-EPICONTINENTAL CONTRAST

In general, the Phylloceratacea and Lytoceratacea show a conservative evolution. During the Jurassic they mainly occupied the Tethys and, to a lesser extent, its peripheral and radiation areas. This may indicate a preference for greater ocean depth, and perhaps may also indicate climatic influences. Thus, these groups are absent from the shallower areas of the Tethys (Lemes beds of the Upper Jurassic of Yugoslavia, B. Ziegler, 1963; the shallow-water Jurassic of the Georgian block between deeper sedimentation basins of Caucasus and Anticaucasus, Zesashvili, 1964). This distribution indicates a more or less benthonic mode of life and generally an autochthonous mode of emplacement. Phylloceratacea and Lytoceratacea are also absent in the epicontinental Callovian and Oxfordian of the western basins of the conterminous United States (Imlay, 1967), but they are abundant in the geosynclinal areas as far as Alaska. Dwarfed phylloceratids have been found in deep cracks in eastern Alpine Triassic limestone filled with Liassic sediment. At the same time, other ammonoid genera lived on the higher sea bottom above the cracks. Dwarfed ammonites from such submarine cracks have also been mentioned from the Jurassic of Sicily (R. Fischer, 1967; Wendt, 1971).

Some genera of the Psiloceratacea, the oldest "Ammonitina," are known only from Europe, whereas others spread more or less widely through the Tethys and adjacent area. *Psiloceras* is known from northeastern Asia (Saks, 1964), New Zealand, and Laos, northward in western Europe as far as the island of Mull (western Scotland), and also from Canada, Peru, and Chile (Cecioni & Westermann, 1968). Because Hettangian faunas are unknown in Mexico, the direction of migration of *Psiloceras* to western America is still in doubt. A "Panama-strait" probably existed in Liassic time at the western end of the Tethys *(sensu lato)*, and may be assumed to have extended westward from Europe between the former land areas of Gondwana and Laurasia (Geyer, 1973).

Frebold (1967) described *Psiloceras* sp. ex aff. *P. planorbis* as the oldest known Jurassic ammonite in British Columbia. Above it follows the ribbed *P. canadense* Frebold (1951) associated with additional genera of the Psiloceratidae, *Phylloceras* and *Eolytoceras*. Differentiation of *P. planorbis* on the subspecific level is evident in Peru (Schindewolf, 1957). *Curviceras* Blind (1963) *(=Waehneroceras auct.)*, and later *Schlotheimia*, are known from New Caledonia, and also from Japan to the east, and as far as western North America. *Schlotheimia* is also known from Alaska and Peru. In the western part of the Americas, the Arietitidae extend as far as Alaska to the north *(Arietites, Coroniceras)*, and Peru and Chile to the south *(Arietites, Vermiceras)*.

In comparison with its epicontinental equivalents in central Europe, the lower Liassic of the Alpine-Mediterranean area contains a greater abundance of forms of Psiloceratidae, Schlotheimiidae, and Arietitidae (Wähner, 1882-98; Lange, 1952; Blind, 1963); however, the lower Liassic faunas of the Helvetic nappes of eastern Switzerland have an entirely central European aspect. This shallow-water sedimentation area on the southern side of the "Alemannic Land," which is the Aar Massif of today, must have been closely connected with the Jurassic sea of central Europe. The strong Mediterranean affinities of the faunas in the Liassic "Allgäu-Schichten" of the eastern Alps, as in the Lower Jurassic of the Romanic Préalpes, indicate tectonic transportation of these units from a sedimentation area much farther to the south.

The epicontinental Jurassic of central Europe and elsewhere represents not merely an area of immigration of faunal elements from the Tethys, but it was also an independent center of evolution. Although the degree of endemism reached by the ceratites in the Germanic Muschelkalk was not repeated in the Jurassic, many endemic genera and species evolved. *Saxoceras,* with many species, is almost endemic in the upper Hettangian of central Europe (Lange, 1951).

Curviceras, Schlotheimia, and the arietitids *Vermiceras, Arnioceras,* and *Asteroceras* extend as far as the North African Rif and Atlas (Arkell, 1956; Donovan, 1967). This is also true for *Oxynoticeras,* which exhibits especially well the striking contrast between paucity of species in the epicontinental facies and the wealth of species in the Alpine area (Pia, 1914). *Echioceras* and *Paltechioceras* appear in northwestern Europe, and the latter genus is also found in the Tethys.

Some species of *Gagaticeras* found in the upper Sinemurian of northwestern Germany are also present in Lorraine, the northern Alps, and in Yorkshire (northeast England), but are absent in southern England. A barrier to distribution appears to have existed, therefore, at least on the western side of the sea surrounding the Ardennes-London Island (HOFFMANN, 1941).

According to SCHINDEWOLF's (1961) investigation of the early stages of ammonoid sutures, the Eoderocerataceae evolved from Psiloceratáceae, not directly from the Lytoceratina, as indicated in *Treatise on Invertebrate Paleontology,* Part L, figure 150 (1957). In the lower Pliensbachian, their area of distribution is practically the same as that of their ancestors. Among Eoderocerataceae the differences between epicontinental and geosynclinal faunas are small and are indirectly noticeable only in the preeminence of the phylloceratids and lytoceratids. An example is the fauna of the Ak Dag of northern Turkey (PIA, 1913).

From the lower Liassic to the Middle Jurassic the northern Balkans and the Caucasus belonged to the epicontinental facies belt, and the southern Balkans belonged to the Mediterranean belt (KOVACS, 1942; DONOVAN, 1967). SAPUNOV (1973) distinguished between the European Caucasian and the Mediterranean provinces by comparing the ammonite genera and species, common or uncommon, to both these provinces in the Pliensbachian and the Toarcian. The Toarcian and Bajocian beds near Kerman in Iran have mainly northwestern European faunal elements, and the Aalenian additionally has some central European elements (SEYED-EMAMI, 1967). *Epideroceras* is restricted to the northern margin of the European Tethys, and extends eastward as far as Turkey (SAPUNOV & STEPHANOV, 1964).

BEGINNING OF THE TETHYAN-BOREAL CONTRAST

Marine rocks of early Liassic age containing Arietitinae, as well as *Oxynoticeras* and *Echioceras,* are known from northern Alaska (IMLAY, 1955) and Arctic Canada (FREBOLD, 1960). Nowhere else does it appear that the Early Jurassic Arctic Sea extended over present land areas. In East Greenland the oldest Jurassic ammonites are *Beaniceras* and *Uptonia* (Eoderocerataceae). *Amaltheus* is the earliest genus having a range from northern Canada to northeastern Asia and northern Siberia, and is the only ammonite genus of the upper Pliensbachian in this area (DAGIS & ZAKHAROV, 1974, map p. 23). *Amaltheus* also predominates in Great Britain, where HOWARTH (1958) found restriction of certain species, and in Germany it indicates an open connection between the Arctic Sea and central Europe.

Farther south the situation is different. Although *Amaltheus* does occur as far as the Caucasus and in the Middle (not High) Atlas of North Africa (COLO, 1961), it is far outnumbered by the great host of the Hildocerataceae, *Arieticeras, Canavaria, Fontannelliceras, Fuciniceras,* and *Protogrammoceras.* In Spain a sharp faunal division existed in the late Pliensbachian between the north (Cantabrian and Iberian ranges) where *Amaltheus* occurs, and the south (from the southern Keltibericum in the Province Teruel onward) where *Amaltheus* is absent (BEHMEL & GEYER, 1966). In the Alps and southern France typical mixed faunas occur. *Amaltheus* and *Canavaria* occur together also in Japan (SATO, 1960). Thus, I suggest a climatically determined reduction in the diversity of ammonite faunas from south to north similar to faunal conditions of the present day. HALLAM (1969) suggested, however, that climate during the Jurassic was too uniform to cause zoogeographic differentiation, and he therefore assumed that nearshore shallow seas with strong terrigenuous sedimentation and reduced salinity existed in boreal regions to which the boreal fauna was adapted.

The Dactylioceratidae, probably deriving from *Microderoceras* and commencing with *Coeloceras* and *Coeloderoceras* in the late Sinemurian, expanded during several advances from their Mediterranean center of evolution: *Prodactylioceras* in the Pliensbachian, and *Dactylioceras* since the Domerian (SCHMIDT-EFFING, 1972). *Dactylioceras* dominated the Arctic-Boreal region during the early Toarcian nearly as exclusively as did its predecessor *Amaltheus* in the Pliensbachian. In addition, *Harpoceras* and some other Hildoceratidae occurred, but were rare (FREBOLD, 1958, 1960; DAGIS & ZAKHAROV, 1974). In northern Siberia, *Zugodactylites* with endemic species appeared in the middle Toarcian. Outside the Arctic *Dactylioceras* is widely distributed in association with abundant *Harpoceras* and *Hildoceras*. During the late Toarcian and early Bajocian, the Arctic was somewhat more abundantly populated by species of *Pseudolioceras, Grammoceras, Erycites,* and *Ludwigia*. At the same time, a far greater abundance of forms occurred to the south in the Tethys and its peripheral regions as far as Japan, where *Dumortieria, Pleydellia, Leioceras, Graphoceras,* and *Hyperlioceras* occurred together with the above-mentioned genera. More research in the Arctic could possibly lead to a lessening of these differences, however. For instance, *Leioceras opalinum* has recently been found on Prince Patrick Island in Arctic Canada (Frebold, 1958). *Mercaticeras* and the small Bouleiceratinae *Frechiella, Paroniceras,* and *Leukadiella* form a group that is restricted to the Mediterranean. *Haplopleuroceras* ranges from Italy to England.

In addition, the Hammatoceratidae are widely spread throughout the Tethys and its peripheral regions as far as Japan, but are not entirely absent from the boreal region.

ARABIAN-MADAGASCAN EPICONTINENTAL SEA

The sea in the south of the Iran-Afghanistan part of the Tethys area transgressed in a westerly direction during the Toarcian toward the Nubian shield, where it formed the shallow Central Arabian Embayment, sediments of which are now exposed in the terraced sides (escarpment) of the Jebel Tuwaiq. The fauna consists of *Bouleiceras, Nejdia, Hildaites,* and *Protogrammoceras* (Arkell, 1952), and shows affinity to that of the western Tethys (Baluchistan to Portugal; Geyer, 1965), but is very impoverished and contains endemic species. It also shows affinities with the faunas along parts of the East African coast and Madagascar. Thus, a shallow arm of the sea must have extended in the direction of the present Strait of Mozambique, which was bordered on the west by the African continent, and on the east, according to present ideas, by the Madagascan-Indian ("Lemurian") continent (Dacqué, 1910). During Bajocian, *Ermoceras* and *Thamboceras* predominated in the Central Arabian Embayment, although they also occur in the Sinai Peninsula. In the Bathonian, when a new transgression occurred, these genera were joined by additional members of the Thamboceratidae and Clydoniceratidae (Arkell, 1952). The distribution of Clydoniceratidae reached as far as Madagascar and Europe.

In the Bajocian, the above-mentioned strait that separated East Africa from Madagascar extended farther over the continent and harbored a considerably richer ammonite fauna than that found in the obviously rather restricted central Arabian Embayment. This fauna consists of Tethyan genera, including lytoceratids and phylloceratids, but also of European elements, indicating the existence of connections across the Tethys. Conditions in the Callovian were similar, and during this time the East African-Madagascan sea spread northeastward to peninsular India (Kutch).

From the Callovian to the early Tithonian, Ethiopia was covered by a peripheral shallow sea. Besides endemic and some Indian elements, its ammonite fauna has numerous forms known from southern Germany. Conditions essential for life probably were equally favorable to the north and south for emigrants from the Tethys (Cariou, 1965; Zeiss, 1971). The northern fauna (highland of Harar) in the Ethiopian Jurassic consisted mainly of perisphinctids and aspidoceratids. It was replaced to the southeast by a fauna containing additional oppeliids and hybonoceratids, and finally also phylloceratids and lytoceratids. According to B. Ziegler (1967), this indicates an increase in water depth.

ISOLATION OF ARCTIC JURASSIC SEA AND THE "ARCTIC TRANSGRESSION"

During the Bajocian the Arctic-Boreal region developed its own faunistic characteristics to a far greater extent than during the middle Liassic. Increasing isolation through regression or rise of shoals has been suggested by Arkell (1956) as a cause for this phenomenon. These events took place at the time of the greatest evolutionary development of the Jurassic ammonites. The oldest element in this Arctic endemic fauna is the stephanoceratid *Arkelloceras* FREBOLD (1957) in the middle Bajocian of Arctic Canada (FREBOLD, 1967). This was followed by the Cadoceratinae *Cranocephalites, Arctocephalites,* and *Arcticoceras* in the late Bathonian, and in the Callovian by *Kepplerites* and *Cadoceras,* forming the root of the Kosmoceratidae, and by the Cardioceratidae (CALLOMON, 1963), the earliest representative of which is *Quenstedtoceras.*

The Kosmoceratidae and Cardioceratidae penetrated in varying degrees toward the Tethys. TERMIER and TERMIER (1952) have described this penetration, which is not restricted to the ammonites, as the "Arctic transgression" that follows the above-mentioned regression of the sea. Among the Kosmoceratidae, *Seymourites* reached Japan, *Kosmoceras* Portugal, and some genera the Caucasus. The center of distribution of the Kosmoceratidae is found in the Russian boreal area and in the central and western European regions, rather than in the Arctic (BRINKMANN, 1929). TINTANT (1963) has published distribution maps of *Kepplerites (Kepplerites), K. (Gowericeras),* and of *Zugokosmoceras* in Europe, concluding that geographical isolation was responsible for evolution of some of the species. *Cardioceras* advanced to the northern edge of the Tethys and mingled there with Mediterranean forms, as near Cetechowitz (outer Carpathian cliff zone), in the Helvetian and Savoyan Alps, the French Préalpes, and the Préalpes Maritimes; it did not, however, reach the inner Carpathian cliff zone nor the Préalpes Romandes (NEUMANN, 1907).

FAUNAL MOSAIC OF THE PACIFIC OCEAN

The Pacific Ocean, in contrast to the presumably younger Atlantic, is surrounded by a continuous belt of Jurassic sediments. The sedimentation areas in this belt were partly geosynclines, partly epicontinental shelves and inland seas; however, no uniform Pacific faunal realm exists because this sedimentation area crossed many climatic zones. Connections with the Tethys to the east and west, and with the Arctic Sea to the north, led to the same faunal contrasts that characterize the Tethys-Boreal region. Moreover, because of the size of the area and the differences in relief and facies prevailing there, special faunas composed of endemic forms developed. Only a few ammonite genera restricted to the Pacific succeeded in establishing themselves on both its eastern and western side; however, the scarcity of such forms suggests that already at that time this great ocean played an important role as an ecologic barrier.

Noteworthy and puzzling are the circum-Pacific genera *Pseudotoites, Zemistephanus, Neuqueniceras,* and *Epicephalites,* which did not penetrate into the Tethys area. It has been suggested that these genera belonged to a specialized Pacific fauna, which is little known only because it moved so rarely out of the area of the Pacific Ocean. More abundant are ammonite genera that occur on both sides of the Pacific as well as along the Tethys Ocean. To explain this distribution pattern the assumption of trans- or circum-Pacific connections cannot be excluded, but is not strictly necessary.

The Jurassic faunas of southern Alaska were separated from those of northern Alaska, and contained a rich ammonite fauna, especially in Middle Jurassic time (IMLAY, 1952). In the early Bajocian (Aalenian), *Tmetoceras* and *Erycitoides* occurred with a number of endemic species along with other genera (WESTERMANN, 1964). In the late Bajocian, representatives of widely spread Stephanocerataceae probably migrated into the area from the south along the Cordilleran geosyncline. In the Callovian, Arctic-Boreal forms (*Cadoceras, Kosmoceras,* and others) predominated, as may be expected, considering the general advance of the boreal fauna at that time, but *Phylloceras* was also present. *Arcticoceras* was absent.

Another macrocephalitid, *Lilloetia,* belongs to the northeast Pacific faunal province, some members of which also lived in the shallow sea of interior Canada and the United States ("Logan Sea"). In this epicontinental sea, southern and Arctic elements mingled with endemic species, which show only slight morphological specialization (FREBOLD, 1951; 1957; 1959; IMLAY, 1948; 1952). Endemic forms of the late Bajocian (Imlay, 1967) are *Sohlites* (Stephanoceratidae?) and *Eocephalites* (Cadoceratinae), which occur with the more widespread *Spiroceras*. In the Bathonian, *Warrenoceras* replaced *Arctocephalites* as the endemic form (Frebold, 1963). In the Callovian, *Kepplerites* and *Arcticoceras*, the latter not found in southern Alaska, were joined by the endemic genus *Imlayoceras* (Macrocephalitidae). The genera *Choffatia, Parareineckeia,* and *Pseudocadoceras,* known from southern Alaska (*Pseudocadoceras* from southwestern British Columbia also), seem to be missing. The occurrence of *Arcticoceras* seems to suggest a direct connection with the Arctic Sea via the Yukon area, though corresponding sedimentary rocks have not been found (Frebold, 1957). That suggestion was supported by Saks and Nalnyaeva (1966) on the basis of the occurrence of belemnites of boreal affinities in the Logan Sea.

The generic composition of the Mexican Middle and, especially, Late Jurassic fauna is much like that of the Tethyan of southern Europe. Predominating are Perisphinctidae *(Idoceras, Nebrodites, Sutneria),* Aspidoceratidae, and Oppeliidae *(Ochetoceras, Taramelliceras, Streblites, Glochiceras),* as well as a few lytoceratids and phylloceratids, indicating a partly geosynclinal facies; however, there are endemic genera such as *Mazapilites* (Oppeliidae) and, of course, numerous endemic species. Endemic genera are also found in Cuba: *Vinalesphinctes* (Oxfordian) and *Dickersonia* (Himalayitinae, Tithonian). On the basis of so much endemism, Arkell (1956) thought it hardly probable that the Central American-Mexican sedimentation area was situated any closer to the Jurassic sedimentation areas of Europe than it is today.

The resemblance of the lower Liassic Mexican ammonite fauna with that of Europe has already been mentioned above.

Hillebrandt (1970) has given a precise introduction to the biostratigraphy of ammonites of the South American Andes. Up to the Sinemurian, the ammonite succession resembles that of epicontinental Europe. From the Pliensbachian upward it also contains numerous Mediterranean elements. Amaltheids are absent, as surprisingly are also the later graphoceratids, parkinsoniids and taramelliceratids. In the predominantly shallow Jurassic seas of South America, phylloceratids and lytoceratids were rare. Boreal ammonites advanced far to the south in the western part of North America, but are rarely seen in South America.

Connections between Europe and South America certainly existed, but did not allow for all genera to pass through.

A few genera, whose occurrences are restricted to areas near the Pacific Ocean, are of special interest. Apart from some circum-Pacific genera, *Xenocephalites* (Callovian) is, except for Greenland, restricted to the east coast of the Pacific, where it has a surprisingly extensive latitudinal distribution from South America through Mexico to southern Alaska. During the Bajocian, *Megastephanoceras* and *Eocephalites* also appear to be restricted to the western part of North and South America.

The characteristic Tethyan influence on Late Jurassic faunas of Mexico is also noticeable in the northern part of the South American Andean geosyncline as well as farther north in California and Oregon, where boreal elements were met along a borderline that shifted from time to time (Imlay, 1952; 1963; 1964b; B. Ziegler, 1971). In the southern (Argentinian) Andean geosyncline, many endemic genera occur within the Berriasellidae (e.g., *Hemispiticeras* and *Andiceras*).

The Ellsworth Mountains of the Antarctic (Quilty, 1970) have a noteworthy Middle to Upper Jurassic (Bajocian-Oxfordian) ammonite fauna with Stephanocerataceae of European character, which, in contrast to that of the Arctic, seems not to represent an independent zoogeographical region.

The Jurassic of Japan has some boreal genera such as *Amaltheus, Kepplerites,* and *Seymourites,* but more generally shows the influence of Tethyan and marginally Tethyan faunas (Sato, 1960; 1962). In addition, a number of important endemic genera and species are present. The connection with the New Zealand-Sumatra geosyncline and with the Tethys may have been across Taiwan where the occurrence of Jurassic was first described by Lin (1961), and across the epicontinental shallow seas which extended from the south coast of China towards Indonesia, though documented thus far only for the Liassic.

JURASSIC TETHYAN AMMONITE FAUNAS

Having discussed the extra-Tethyan regions, we now return to the Tethys. The families Parkinsoniidae and Morphoceratidae, are mainly restricted to the Eurasian region. *Garantiana* reached Transbaikalia via Japan. In the Callovian, the Reineckeiidae were found almost throughout the Tethyan area and its peripheral regions; *Reineckeia* itself extended outside Tethys into Madagascar, South America, and northern Alaska (IMLAY, 1955), but not to northwestern Germany. The Macrocephalitidae and Pachyceratidae occurred in Tethys and its connected regions of South America, East Africa, southeastern Asia, and as far as New Guinea. *Pleurocephalites* reached Greenland. The Perisphinctidae first appeared during the Bajocian and, together with the Aspidoceratidae, Haploceratidae, and Oppeliidae, constitute the bulk of the Upper Jurassic Ammonitina. Of these families, only the Perisphinctidae invaded the boreal region. Groups originally inhabiting the Tethys penetrated far into its peripheral seas both to the north and south. According to B. ZIEGLER (1963, 1967), in central and southern Europe the perisphinctids preferred shallow water, and, therefore, with increasing depth, were replaced in succession by the Aspidoceratidae, the Oppeliidae, and finally the lytoceratids and phylloceratids. This sequential replacement may explain the often-discussed substitution of *Gregoryceras* and *Epipeltoceras* (Aspidoceratidae, Peltoceratinae) in the middle and upper Oxfordian of southern Europe by Perisphinctidae as time-equivalent index fossils in northwestern Europe (GYGI, 1966).

The Asiatic and Mediterranean mountain ranges disclose cross sections of the Tethys in structural, though tectonically disturbed, connection. Thus, in the Pamir, Early Jurassic epicontinental sediments of the northern margin of Asiatic Tethys are known (ANDREEVA & DRONOV, 1964). North of the Pamir the marine facies changes into terrestrial sediments of the Jurassic basins of the immense Siberian region. In the Himalayas there are indications of a fauna rather similar to that of the Alpine geosyncline of the Tethys. This occurs in blocks of allochthonous wildflysch containing phylloceratids and lytoceratids of Liassic age and in the tectonic klippen of the Kiogars, which consist of *Calpionella* limestone of Tithonian age. The greater part of the Himalayan Tethys, however, was probably occupied by shallow seas, as indicated by the wide distribution, from the western Himalayas to southern Tibet, of the Spiti Shale and of sandy and marly shales in northwestern Pakistan, which contain a rich ammonite fauna of Late Jurassic age (UHLIG, 1903-1910; 1910; FATMI, 1972). The Tithonian fauna is especially rich:

Upper Tithonian—contains *Corongoceras, Micracanthoceras, Aulacosphinctes, Protacanthodiscus, Blanfordiceras, Kossmatia, Himalayites,* and in addition *Haplophylloceras strigile* (BLANFORD) and *Paraboliceras* occur as far as the Malayomaorican geosyncline.

Lower Tithonian—contains *Virgatosphinctes* and *Aulacosphinctoides,* in addition to *Hildoglochiceras* (Oppeliidae).

Tithonian faunas, in spite of similarities exhibited throughout the Tethys and as far as Japan and South America, do show a certain amount of regional differentiation, being due in part to ecologic factors, and in part by incompleteness of the stratigraphic record.

In a western direction, toward the Mediterranean, the Tithonian of the Tethys can be subdivided in greater detail than in the Himalayas (BARTHEL *et al.,* 1966). Here, middle Tithonian is discernible with *Pseudolissoceras, Semiformiceras* (Streblitinae), *Simoceras volanense,* and the unrolled *Protancyloceras.* From Kurdistan SPATH (1950) described a middle Tithonian fauna with some endemic Virgatosphinctinae, the endemic *Oxylenticeras* (Streblitinae, with closed umbilicus) and an unrolled small *Cochlocrioceras,* to date also known only from this locality. WIEDMANN (1973a) reported on the Tithonian heteromorph ammonites *Protancyloceras, Cochlocrioceras, Vinalesites,* and *Bochianites,* and their dis-

Stages	Tithonian	Kimmeridgian	Oxfordian	Callovian	Bathonian
OTHER REGIONS	S AMERICA Proniceras and Substeueroceras Corongoceras Windhausenice ras MEXICO Torquatisphinctes and Mazapilites Hybonoticeras		WESTERN INTERIOR USA Cardioceras	Quenstedtoceras Kepplerites Gowericeras Arcticoceras	Warrenoceras C ARABIA, IN PART N AFRICA Dhrumaites Micromphalites Tulites Thambites Bramkampia
ARCTIC, N CANADA GREENLAND	Chetaites Craspedites and Virgatosphinctes Epivirgatites and Laugeites Dorsoplanites, Pavlovia Pectinatites, Subplanites, and Eosphinctoceras	Streblites and Amoeboceras Aulacostephanus Rasenia Pictonia	Amoeboceras Cardioceras	Cadoceras	Arcticoceras Arctocephalites Cranocephalites Boreiocephalites
VOLGA REGION	Craspedites Kachpurites Epivirgatites Virgatites Zaraiskites, and Gravesia	Virgatoxioceras	Ringsteadia	Quenstedtoceras Peltoceras Erymnoceras Kosmoceras Kepplerites	Clydoniceras Tulites Gracilisphinctes
NW EUROPE	Craspedites Titanites Glaucolithites Zaraiskites Pavlovia Pectinatites Virgatosphinctoides Gravesia	Aulacostephanus Aulacostephanus Rasenia Pictonia baylei	Ringsteadia Decipia Perisphinctes Cardioceras	Quenstedtoceras Peltoceras Erymnoceras Kosmoceras jason Sigaloceras and Kepplerites Macrocephalites	Clydoniceras Oxycerites aspidoides Prohecticoceras retrocostatum Morrisiceras Tulites Gracilisphinctes Zigzagiceras
EUROPEAN TETHYS, SOUTHERN, MIDDLE AND SW EUROPE	Berriasella Semiformiceras, Pseudolissoceras, Lemencia, Pseudovirgatites, and Glochiceras lithographicum Hybonoticeras	Hybonoticeras beckeri and Virgatoxioceras Enosphinctes subeumela Aspidoceras acanthicum Katroliceras divisum Ataxioceras Sutneria platynota	Sutneria galar Idoceras planula Epipeltoceras bimammatum and Amoeboceras Gregoryceras transvers.		

FIG. 2. Ammonite biostratigraphy of some important Jurassic regions (Hölder, n).

tribution throughout the Tethys and neighboring areas.

ENAY (1973) critically reviewed the zoogeography of Tithonian ammonite faunas, and mentioned the difficulties in taxonomic distinction of the Perisphinctaceae.

South of the Himalayas lies peninsular India, a part of the old Gondwana continent, where terrestrial rocks of Jurassic age occur in the upper part of the Gondwana Series. In the northwestern region, in the well-known Jurassic area of Kutch, nearshore

Stages	Bajocian	Aalenian	Toarcian	Pliensbachian	Sinemurian	Hettangian
C ARABIA, IN PART N AFRICA	Ermoceras Thamboceras Sohlites and Eocephalites Stemmatoceras		Hildaites Nejdia Bouleiceras			
ARCTIC, N CANADA GREENLAND	Arkelloceras Tugurites	(Leioceras)	Pseudolioceras Zugodactylites Dactylioceras and Harpoceras	Amaltheus	Echioceras Oxynoticeras oxynotum Arctasteroceras	
VOLGA REGION						
NW EUROPE	Parkinsonia parkinsoni Garantiana Strenoceras Teloceras Stephanoceras Otoites Sonninia —	Hyperlioceras Ludwigia Tmetoceras Leioceras —	Pleydellia Dumortieria and Grammoceras — Haugia Hildoceras Harpoceras Dactylioceras —	Amaltheus Prodactylioceras Tragophylloceras ibex Uptonia —	Echioceras Oxynoticeras oxynotum Asteroceras obtusum Euasteroceras turneri Arnioceras Arietites —	Schlotheimia angulata Alsatites Psiloceras —
EUROPEAN TETHYS, SOUTHERN, MIDDLE AND SW EUROPE			Dumortieria Phymatoceras and Paroniceras Mercaticeras, Frechiella and Leukadiella	Protogrammoceras, Fuciniceras and Arieticeras		

FIG. 2. *(Continued from facing page.)*

shallow-water sediments of Callovian to Tithonian age contain an unusually rich fauna of ammonites (SPATH, 1927-33) and bivalves (COX, 1940). This fauna probably originated at the southern margin of the Tethys. As may be expected, the Tithonian faunas exhibit strong relationships with faunas of the Spiti Shale, although in Kutch, the phylloceratids, strangely, are somewhat more abundant, with the exception of *Haplophylloceras,* which is not represented. Furthermore, close relationships exist between the early Late Jurassic ammonite faunas of Kutch and those of southern Europe, including southern Germany. These can be demonstrated from the Callovian up to and including the *Hybonoticeras* Zone of the Kimmeridgian, the lowest zones of which are missing. *Phlycticeras, Paraspidoceras,* and *Hemihaploceras* are among genera that as yet are known only from Europe eastward as far as Kutch. The Kutch section shares many other genera with Europe and with wide areas of the Tethys. SPATH (1927-33), however, pointed out that more than two-thirds of the approximately 550 described ammonite species of the Kutch area are known only from there. It is possible that extravagant taxonomic splitting may be partly responsible for this picture.

The Jurassic of Kutch belonged to the East African-Madagascan-peninsular Indian epicontinental sea (Ethiopian biogeographical province), which had evolved since Callovian time from the Arabian-Madagascan seaway, and presumably was bordered on the southeast by the then still-existing Lemurian portion of Gondwanaland.

In the upper Oxfordian, the Mayaitidae, which were homeomorphic with, and even indistinguishable from, the older and more widely distributed Macrocephalitidae, are confined strictly to the East African-Indonesian region. In the Kimmeridgian, *Katroliceras,* occurring also from Europe to Japan, and *Torquatisphinctes* are especially abundant in Madagascar. Other very important European genera include *Taramelliceras, Streblites, Glochiceras, Aspidoceras, Physodoceras,* and *Hybonoticeras.* We even find identical stratigraphic index species such as *Aspidoceras acanthicum* and *Hybonoticeras hybonotum.*

The Tithonian of Madagascar, having a fauna composed almost exclusively of cephalopods, can be subdivided as follows:

Upper Tithonian—*Aulacosphinctes hollandi, Berriasella privasensis, Micracanthoceras micracanthus, Blanfordiceras* sp., *Lytohoplites* sp., and others.
Lower Tithonian—*Hildoglochiceras kobelli, Haploceras elimatum, Physodoceras avellanum,* and others.

This sequence has very close faunal relationships with Kutch, the Himalayas, Europe *(Berriasella, Hybonoticeras),* North Africa *(Djurdjuriceras, Corongoceras, Lytohoplites),* and also with Central and South America *(Corongoceras, Lytohoplites).* The following genera found in Madagascar have a distribution from eastern Asia westward to South America: *Himalayites, Micracanthoceras, Aulacosphinctes, Proniceras* (COLLIGNON, 1964b). On the other hand, *Hildoglochiceras* is only distributed eastward to Central and South America, and suggests a migration route into the peripheral area of the Pacific Ocean. For some genera even a southern migration route may be considered, which possibly could have connected the Jurassic seas of South America, southeastern Africa, and New Zealand (STEVENS, 1967a). Such a route, however, could have exerted little faunal influence compared to that of the Arctic-Boreal region. A biostratigraphical table for comparison of all Tithonian areas was given by VERMA and WESTERMANN (1973).

LATE JURASSIC FAUNAS NORTH OF THE TETHYS AND OF THE EUROPEAN INTERMEDIATE ZONE

The relatively monotonous Late Jurassic Arctic-Boreal ammonite faunas, composed of a smaller number of genera, represent a contrast to the rich contemporaneous faunas of the Tethys. Cardioceratidae are found in the Oxfordian and lower Kimmeridgian, and boreal Perisphinctidae such as *Pectinatites, Pavlovia, Dorsoplanites, Glaucolithites,* and *Craspedites* are found in the Kimmeridgian and Portlandian. In Europe, Tethyan, Boreal and endemic faunal elements met and intermingled in a large intermediate region between the Tethyan and Boreal seas. For example, the Boreal Cardioceratidae, just as the earlier Kosmoceratidae, diminished and finally disappeared toward the south in this area.

This intermediate region can be divided into a subboreal province (ENAY, 1966; ZEISS, 1968) comprising northern, western, and central Europe, and a submediterranean province (GEYER, 1961) comprising Portugal, southern Catalonia, southeastern France, southern Germany, and southern Poland.

Some of the faunal differences have already been noted in recording the absence of *Gregoryceras* and *Epipeltoceras* in the subboreal north. The submediterranean province is distinguished by the great variety of the Oppeliidae (Taramelliceratinae, Streblitinae, Ochetoceratinae); *Idoceras, Ataxioceras, Glochiceras,* and *Sutneria* are also important. This faunal pattern is reminiscent of the one found in Mexico. The strange *Cymaceras* (Ochetoceratinae, lower Kimmeridgian) is thus far known only from southern Germany, Switzerland, and southeastern France (GEYER, 1959). The perisphinctids *Pomerania* (upper Oxfordian) and *Pictonia* (lower Kimmeridgian) are abundant in the subboreal province, but are rare in the Jurassic of southern Germany where they occur together with the Tethyan *Nebrodites,* which here makes its most northerly appearance (GEYER, 1961).

To explain the faunal differences between the subboreal and submediterranean provinces the following causes may be invoked: minor climatic differences; somewhat greater depth of the sea in the submediterranean province as indicated by greater abundance of the Oppeliidae; dividing barriers such as the French Central Plateau, the Rhenish-Ardenne Island, and the Bohemian Massif; and perhaps also special ecological conditions in the vicinity of the submediterranean sponge-reef facies.

In the above-described intermediate area, especially in its submediterranean part, we also find *Rasenia* and its successor, *Aulacostephanus.* Both range far into the Boreal region and *Aulacostephanus* also as far as Mexico and Kurdistan. In northern France and southern England other species take the place of *Aulacostephanus pseudomutabilis,* which is characteristic of the southern German area. Migrations, such as along the northern edge of Scandinavia into Russia and Poland, were responsible for chronological differences in the appearance of some species (B. ZIEGLER, 1961, 1962). In the subboreal part of the intermediate region *Aulacostephanus* is represented by the index species *A. autissiodorensis,* which continued to exist here at a time when the genus had already disappeared in the submediterranean part. Here a fauna developed, which is especially well known from the south German Jurassic, containing *Hybonoticeras beckeri, Sutneria subeumela, Virgataxioceras setatum,* and *Oxyoppelia* (BERCKHEMER & HÖLDER, 1959; HÖLDER & ZIEGLER, 1959). Representatives of this fauna are also known from southeastern France, Bakony in western Hungary, Rumania, the Pienninic Klippen zone, and the Jurassic basin of Poland. *Sutneria subeumela* is also found on the middle Volga (GEYER, 1969), and *Virgataxioceras* is found in northern Siberia.

In the middle Kimmeridgian (=lower Tithonian) *Gravesia,* an Upper Jurassic homeomorph of *Stephanoceras,* is abundant in the subboreal province. Its occurrences are increasingly rare toward the south and east (Spain, Alpine margin, and central Russia), but where present, it allows correlation of the lower Tithonian with the *Hybonoticeras hybonotum* Zone and its northern equivalents. In Russia, *Subplanites* predominates instead of *Gravesia.*

Gravesia is followed higher in the section by perisphinctids of the subfamily Pseudovirgatitinae (ZEISS, 1968). Further regional differentiation took place in England *(Pectinatites)* and central Russia *(Ilowaiskya).* In the southern German Jura Mountains, on the other hand, different forms of Mediterranean Pseudovirgatitinae represented by *Usseliceras* and *Franconites* occur, accompanied by *Neochetoceras* and *Aspidoceras. Pavlovia* predominates in the uppermost Kimmeridgian (=middle Tithonian, lower middle Volgian) of the northern part of the European intermediate region, whereas in the Tethyan peripheral area the typical Tethyan *Pseudolissoceras* fauna occurs. In the Portlandian *sensu stricto* (=upper Tithonian, middle Volgian) in southern England new faunas evolved from *Glaucolithites,* which ranged as far as Greenland. In Russia forms with true virgatotome ribs evolved from *Virgatites.* In the beginning of this stage, *Zaraiskites* occurred in Russia, Poland (WILCZYŃSKI, 1962; DABROWSKA, 1967), and the submediterranean Franconian Jura, as well as southern England. ZEISS (1968) has compiled a map showing migration routes of these and other genera. *Zaraiskites* (Virgatitinae) seems to have originated from the submediterranean Pseudovirgatitinae (ZEISS, 1968; KUTEK & ZEISS, 1974).

The faunal differences between the submediterranean and the subboreal provinces, as well as within the latter, support subdivision into three subprovinces: 1) northern French-southern English province, 2) Russian, and 3) Polish (ZEISS, 1968). The subboreal province of ZEISS and others corresponds approximately to the Boreal-Atlantic region of SAKS and NALNYAEVA (1966), including an eastern European province. The Polish subprovince shows Russian, as well as submediterranean influences (KUTEK, 1962a,b,c; KUTEK & ZEISS, 1974). *Garniericeras* is endemic in the upper Volgian of Russia, and is a precursor of *Platylenticeras.* The previously mentioned *Craspedites* spreads far beyond the Arctic-Boreal zone. MEZESHNIKOV and ZAKHAROV (in DAGIS & ZAKHAROV, 1974) illustrated the differences between the Volgian ammonite faunas of the boreal-European, boreal-Russian, and arctic (north Siberian) regions. Surprisingly, a fauna of late Volgian age from Khatanga Bay in northern Siberia contains *Berriasella (Lamencia)* cf. *B. richteri* and highly specialized Virgatosphinctinae in association with *Craspedites* (SHULGINA, 1967).

NAUTILOIDEA

Only one genus of Nautiloidea *(Cenoceras)* crosses the boundary between the Triassic and Jurassic systems, reaching worldwide distribution in the early Liassic (KUMMEL, 1956). Several new types evolved in the Middle and Late Jurassic: *Eutrephoceras, Pseudonautilus, Paracenoceras, Cymatoceras, Aulaconautilus,* and others. The pointed sutural lobes of *Pseudonautilus* make this genus a homeomorph of *Permoceras* of the Lower Permian of Timor, and the two genera are hardly distinguishable.

Simultaneous crises of the ammonoids and nautiloids at the end of the Triassic indicate the presence of external influences, which affected the ectocochlian cephalopods more than other groups.

COLEOIDEA

Atractites is abundant in Lower Jurassic rocks of the geosynclinal regions of the Tethys and North America, but occurs also in smaller numbers in epicontinental areas.

Jurassic belemnites, represented by strongly dwarfed forms of the Belemnitidae (=Passaloteuthidae), first appeared during the Hettangian in epicontinental seas of Europe (SCHWEGLER, 1962). Complemented by the Hastitidae, they experienced their first great evolutionary phase during the Early Middle Jurassic. As early as the middle Liassic they spread to northern Siberia, Iran, northern Africa, and South America. The ability of the coleoids to disperse worldwide, however, was less than that of the ammonites. STEVENS (1967a), therefore, assumed their greater dependence on neritic shelves as migration routes. Thus, belemnites of the Liassic would have been prevented by deep-sea areas from reaching the eastern Tethys and New Zealand (Fig. 3), whereas ammonites of European type were able to migrate there. Only in the Toarcian-Aalenian did *Brachybelus* reach New Zealand, making it the oldest belemnite genus known in that country. At the same time the endemism of the New Zealand faunas became less pronounced.

During the Toarcian, Siberia became an important evolutionary center of belemnites (SAKS & NALNYAEVA, 1970), which before were absent there. Half of the species are identical with those of Europe, where an especially rich Toarcian fauna from the Franconian Jura Mountains has been described by KOLB (1942). *Parahastites* (Hastitidae) is endemic in Siberia. In the Middle Jurassic, belemnites, like ammonites, developed a special boreal fauna, which according to SAKS and NALNYAEVA (1966), began in arctic North America with *Cylindroteuthis* and *Pachyteuthis.* From the Callovian onward additional genera, such as *Acroteuthis* and *Lagonibelus,* as well as many subgenera and species evolved. These groups, like the boreal ammonite fauna, penetrated far southward, retaining a much higher variability in the Arctic-Boreal region proper than in its peripheral areas. In the

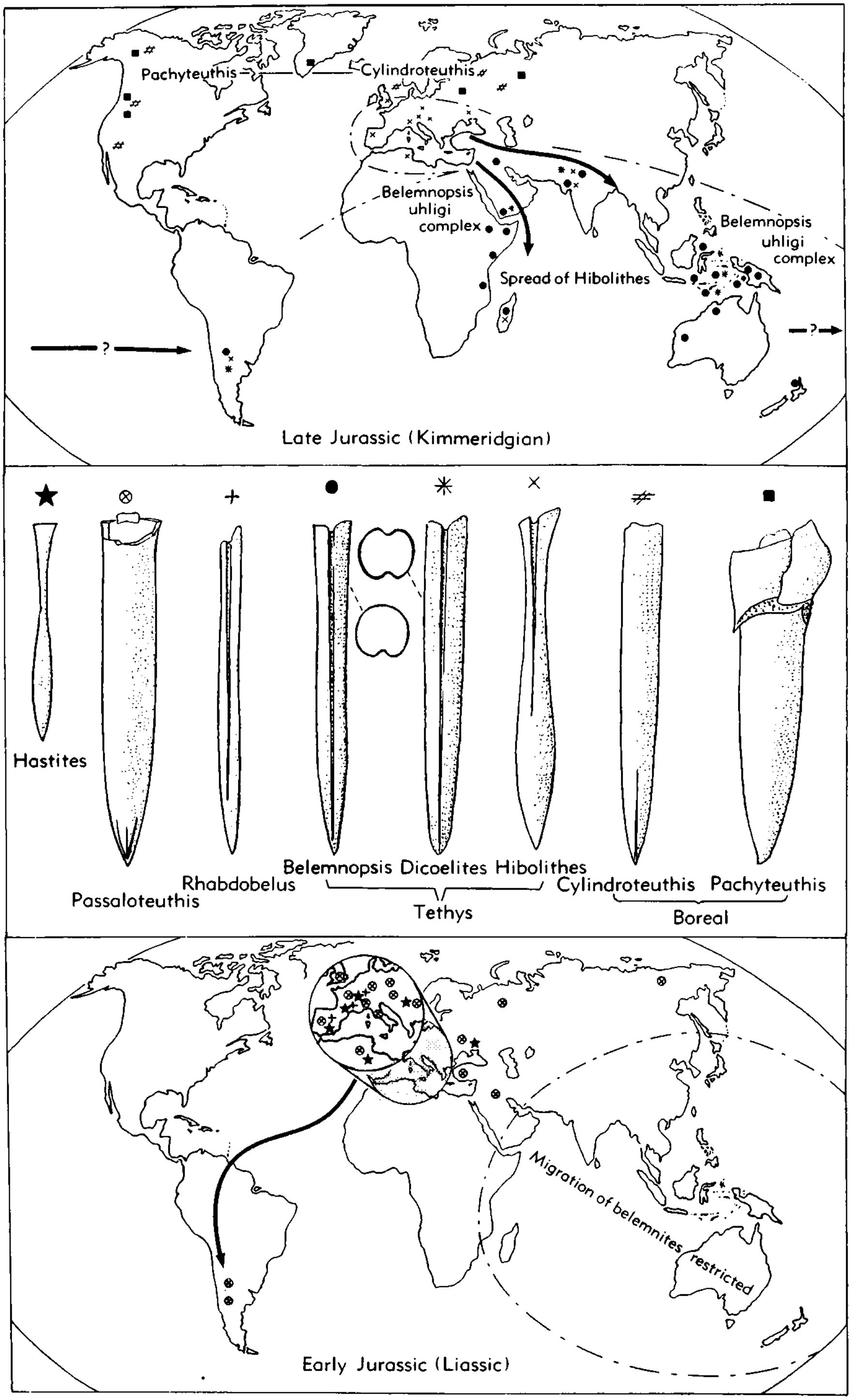

Fig. 3. Examples of the distribution of Jurassic belemnite faunas (maps after Stevens, 1965).

Callovian, *Cylindroteuthis* and *Pachyteuthis* reached Spain, California, and the southern Logan Sea. *Cylindroteuthis* even invaded Argentina, and perhaps, along a southern latitudinal route, also reached New Zealand (Stevens, 1963; 1965).

In the Aalenian, Belemnopsidae with guards having a characteristic ventral groove evolved from the European Hastitidae quite independently of the boreal fauna. *Hibolithes, Duvalia,* and *Conobelus* spread across the Mediterranean region; *Belemnopsis, Conodicoelites, Dicoelites,* and in the Tithonian *Hibolithes,* also spread across the Indo-Pacific Province. Here, differentiation into a *Belemnopsis orientalis-gerardi* fauna took place in the East African-Madagascan-peninsular Indian epicontinental sea, and a *Belemnopsis uhligi* fauna in the Himalayan-Indomalaysian area. The latter probably also reached Argentina along a southern Pacific route (see *Cylindroteuthis* mentioned above).

Like the ammonite fauna, the belemnite fauna of Madagascar shows strong affinities with Europe, especially from the Bathonian to the late Oxfordian. In the Tithonian, *Hibolithes* is important in the entire area from Madagascar to the Indomalaysian geosyncline, and was joined in the late Tithonian by *Duvalia.*

The paucity of belemnites in the Upper Jurassic of southern Germany is in striking contrast to the wealth of ammonites in these rocks. *Hibolithes* is almost the only belemnite found there.

RHYNCHOLITES

Cephalopod mandibles (rhyncholites) are common in some Jurassic clays and limestone beds of the Mediterranean Tethys, where they are known today as far east as the Crimea and the Caucasus with the exception of sporadic occurrences in the European epicontinental seas. The more important Jurassic genera are *Rhynchoteuthis, Palaeoteuthis, Hadrocheilus, Leptocheilus, Akidocheilus,* and *Gonatocheilus.* "The known facts are best accommodated by the interpretation that rhyncholites were formed by unknown cephalopods, some of which probably belong to the Nautilida" (Teichert, Moore, & Zeller, 1964, p. *K*476).

CRUSTACEA

The Ostracoda are important as index fossils and occasionally render possible finer stratigraphic zonation than the ammonites (Plumhoff, 1963). They are especially helpful in correlation of the Purbeckian and Wealden of northwestern and central Europe, as well as for determination of the Jurassic-Cretaceous boundary (Bartenstein, 1959; Wolburg, 1959). Along with some widely distributed species, many strictly localized ones occur.

Isopoda, known since the Triassic, have been described from the middle Liassic of Württemberg, from the reef and lagoonal limestones of the Tithonian, and in abundance from the Purbeckian.

During Jurassic time the Decapoda evolved more rapidly than ever before. Among the macruran Trichelida, swimmers of worldwide distribution are found, for example, *Eryma* (Förster, 1966). The degree of dependence on a benthonic mode of life determines distribution. Among the Anomura, *Gastrodorus,* which has an unprotected abdomen, represents the first of the Paguridae (hermit crabs). From the gastralids, through *Pemphix,* were derived 1) the macruran Palinuridae and 2) the Brachyura, which reached their acme in the Cretaceous. Important Brachyura are the Dromiaceae *Eocarcinus* in the Liassic, *Goniodromites* since the Liassic, and *Pithonoton,* and *Prosopon.* Close relatives of the Jurassic Anomura and primitive Dromiaceae are found in the present deep seas (Beurlen, 1931; Glaessner, 1933).

OTHER INVERTEBRATES

Zoogeographical data for other Jurassic invertebrates are poor, though adaptability of the Crinoidea and Echinozoa was remarkable. *Seirocrinus subangularis* with floating arms became the largest crinoid of earth history. The stemless, freely mobile genera *Antedon* and *Saccocoma* spread during the Late Jurassic, the latter especially in the Tethys, although the late Triassic *Osteocrinus* Kristan-Tollmann (1970) is the oldest planktonic microcrinoid known in the Tethyan. Among the Jurassic reef-dwellers are *Apiocrinus, Millericrinus, Eugeniacrinites,* and the stemless, bowl-shaped *Cotylederma* (Liassic), which has much reduced and fused calyx plates.

Within the Jurassic echinoids, the Cidaroidea acquired their final shape with rigid skeletons. The gnathostome Holectypida *(Pygaster, Holectypus),* with tests covered by densely spaced spines, are the first typical "Irregularia." Also the atelostome, sediment-eating Cassidulidae *(Hypoclypeus, Galeropygus, Echinobrissus, Clypeus, Pygurus)* and the Holasteridae (*Collyrites* since the Liassic, *Dysaster* with dissected upper region) appeared. Today the Holasteridae are almost entirely restricted to deep seas.

Conodonts hitherto seemed to be absent in the Jurassic, but recently *Gladigondolella* and *Hindeodella,* known from the Upper Triassic, were found in the Upper Jurassic of Japan (Nohda & Setoguchi, 1967); however, Müller and Mosher (1971) opposed the interpretation of these fossils and pointed to the possibility of reworking and to the uncertainty of the stratigraphic position.

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CRETACEOUS[1]

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CONTENTS

INTRODUCTION

The Cretaceous marks one of the most varied and active periods in the evolution of marine organisms and their ecological interactions. From Late Triassic and Jurassic rootstocks, the ancestry of most modern biotas is to be found in a series of spectacular Cretaceous radiations in which many of the higher taxonomic groups and adaptive strategies that characterize living marine invertebrate assemblages were developed and refined. Of particular importance in this respect was evolutionary diversification among foraminifers, radiolarians, scleractinian corals, cheilostome bryozoans, neogastropods, infaunal and epifaunal bivalves, and irregular echinoids. At the same time, the Cretaceous invertebrate faunas developed a unique character through the broad radiation of several im-

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portant groups that became extinct, or nearly so, at the end of the period. Among the Foraminiferida, these include the Rotaliporidae, Globotruncanidae, Schackoinidae, and many genera of larger tropical benthonic foraminifers; among the Bivalvia are the Inoceramidae, Trigoniidae, and "reef"-forming rudistids. In addition, several families each of scleractinian corals, cheilostome bryozoans, gastropods, ammonites, and irregular echinoids characterized the Cretaceous (see HARLAND *et al.,* 1967; appropriate volumes of this *Treatise*).

Taxonomic diversification among Cretaceous invertebrates was accompanied by an equal increase in complexity of ecological interactions within the Cretaceous biota, and by major evolutionary advances in the structure and diversity of ecological units at all levels—from symbioses to paleobiogeographic units. Many types of ecological interactions that characterize modern faunas are first expressed without question in the Cretaceous fossil record. Benthonic marine paleocommunities, which are taxonomically and structurally comparable to modern communities in the same environments, developed widely for the first time in the Cretaceous.

Marine paleobiogeographic units similarly show marked increase in numbers and complexity during the Cretaceous Period, more than doubling in number those described from the Triassic and Jurassic (compare papers in HALLAM, 1973). Each biogeographic unit further had its own complex Cretaceous evolutionary history that reflects climatic, oceanographic, and paleogeographic changes linked to plate tectonism (KAUFFMAN, 1973a,b). By the end of the Cretaceous, paleobiogeographic differentiation similar to that of modern seas had been achieved and marine climatic zones (exclusive of cold-water zones) had become well established as climates generally became cooler.

The Cretaceous-Tertiary boundary represents one of the major extinction episodes in the history of life, with the disappearance of such characteristic Mesozoic groups as dinosaurs, most gymnosperms, ammonites, and numerous families of scleractinian corals, bivalves, gastropods, and echinoids. For some Cretaceous groups, especially those of the warm-water plankton (foraminifers and coccoliths) and tropical to subtropical benthos (for example, rudist bivalves), this event was near-catastrophic and characterized by massive extinctions within a short period of time, occurring at or near the apex of their evolutionary diversification.

Against this backdrop, the Cretaceous has become one of the key periods from which concepts in evolution, paleoecology, paleobiogeography, and biostratigraphy have been developed from the fossil record. Cretaceous faunas and associated paleoenvironments have been well studied in many parts of the world. The mass of data available from these studies has in turn encouraged detailed interpretation of the interrelationships between organisms and their environments and has led many scholars to utilize the Cretaceous fossil record as a testing ground for biological, ecological, and stratigraphic theories.

In part, the spectacular evolution of Cretaceous invertebrates can be attributed to achievement of a certain structural, behavioral, or ecological grade as a result of a long pre-Cretaceous history, which allowed rapid and widespread radiation into new ecological niches. For example, Mesozoic development of siphons among bivalves allowed extensive Cretaceous exploitation of benthonic infaunal habitats. Similarly, an apparent relationship exists between extensive diversification of Cretaceous invertebrate groups and commensurate diversification and increasing structural complexity in Cretaceous ecological units. Whereas the number and kind of marine habitats probably did not change appreciably between the Late Triassic and Cretaceous, the diversity of organisms and adaptive strategies changed dramatically during Cretaceous radiations. Niche partitioning within already occupied marine habitats and exploitation of new habitats resulted.

In part, the evolution of Cretaceous organisms was also strongly affected by large scale, geographically widespread, and often rapid changes in global environment, and thus in diverse natural selective forces acting on invertebrate evolution in the marine realm. The Cretaceous was one of the periods of most active plate movements, sea floor spreading, and continental drift. The

Atlantic opened as a new major ocean basin during the Cretaceous with final separation of Africa and South America, attaining approximately 75 percent of its present size by the end of the period. Large new areas of deep ocean floor were formed, and colonization and initial ecological structuring of this vast marine basin was largely a Cretaceous event. As a result of Atlantic spreading, new oceanic current systems (including the proto-Gulf Stream) were formed and played a major role in the redistribution of fauna and the evolution of Cretaceous biogeographic units. Opening of the South Atlantic, large scale breakup of Gondwanaland, and the development of major deep marine connections between the North Atlantic and the "circumboreal" seaway allowed cool temperate-zone waters to enter the Atlantic and South Pacific basins on a large scale for the first time. This resulted in changes of lateral and vertical oceanic temperature gradients leading to a cooling trend during the Late Cretaceous, with expansion of temperate climatic zones, and a great constriction of the tropical Tethyan seaway. This in turn caused a major restructuring of Cretaceous biogeographic units, the evolution of new faunas in the broadening cool- to mid-temperate marine zones, and increased competition and niche partitioning within the Eurasian arm of Tethys.

Late Jurassic and Cretaceous plate tectonics also resulted in the first major opening of the tropical Caribbean Sea with broad Pacific and Atlantic connections, linking tropical faunas of the eastern Pacific and Eurasian Tethys for the first time. The Caribbean became a new tropical sea in which shallow-water invertebrate organisms were introduced, largely through westward drift of their planktonic stages, and radiated rapidly. It is here that the rudists reached their greatest development and levels of endemism (KAUFFMAN & SOHL, 1973; KAUFFMAN, 1974).

Cretaceous plate tectonics had an even more direct effect on the evolutionary history of diverse marine organisms (KAUFFMAN, 1973a). Physical barriers to migration and gene flow were constructed (as in the closing of the Mediterranean Tethys) and broken down (as in opening of the Caribbean) on a large scale. Periods of rapid sea-floor spreading widened the Atlantic in sufficiently short periods of geologic time to create a major isolating mechanism for many shallow-water marine invertebrates as the transatlantic distance exceeded the drift potential of their planktonic larvae. Such genetic isolation permitted independent radiation of shallow-water biotas on both sides of the Atlantic basin during the Cretaceous. Similarly, the breakup of Pangea and drifting apart of India, South America, Australia, New Zealand, and Antarctica effectively isolated shelf biotas of these areas to varying degrees, resulting in accelerated rates of faunal and biogeographic differentiation.

Plate tectonics during the Cretaceous also brought whole ecosystems, developed originally in isolation from one another, into contact. This was accomplished by impinging their effective zones of larval drift, as happened with partial "closing" of the North Pacific, or by direct "collision" of ecosystems (as in the collision of India with Eurasia during the Cenozoic). Such events created major competition between highly structured marine biotas, resulted in widespread extinction, niche partitioning and specialization among surviving organisms, and provided a stimulus for new pulses of radiation during the period when these competing ecosystems were unstructured.

An additional control by Cretaceous plate tectonics on the evolutionary history of marine invertebrates and their ecological structure was that of numerous large scale eustatic fluctuations that appear to have resulted from the emplacement and subsidence of major topographic features on the ocean floors of the world. Eustatic rise of several hundred feet may have been produced by uplift of large areas of ocean floor, or continental subsidence, or both, resulting in: 1) widespread marine transgression onto world cratons (Fig. 1); 2) interconnection of formerly isolated water bodies and their biotas; 3) broad faunal mixing; 4) development of widespread, equable maritime climates, broadening of thermal gradients, and thus greater climatic stability for long periods of time; 5) greater spread of tropical waters onto continents, in some cases rapidly, and resultant temperature increase in formerly

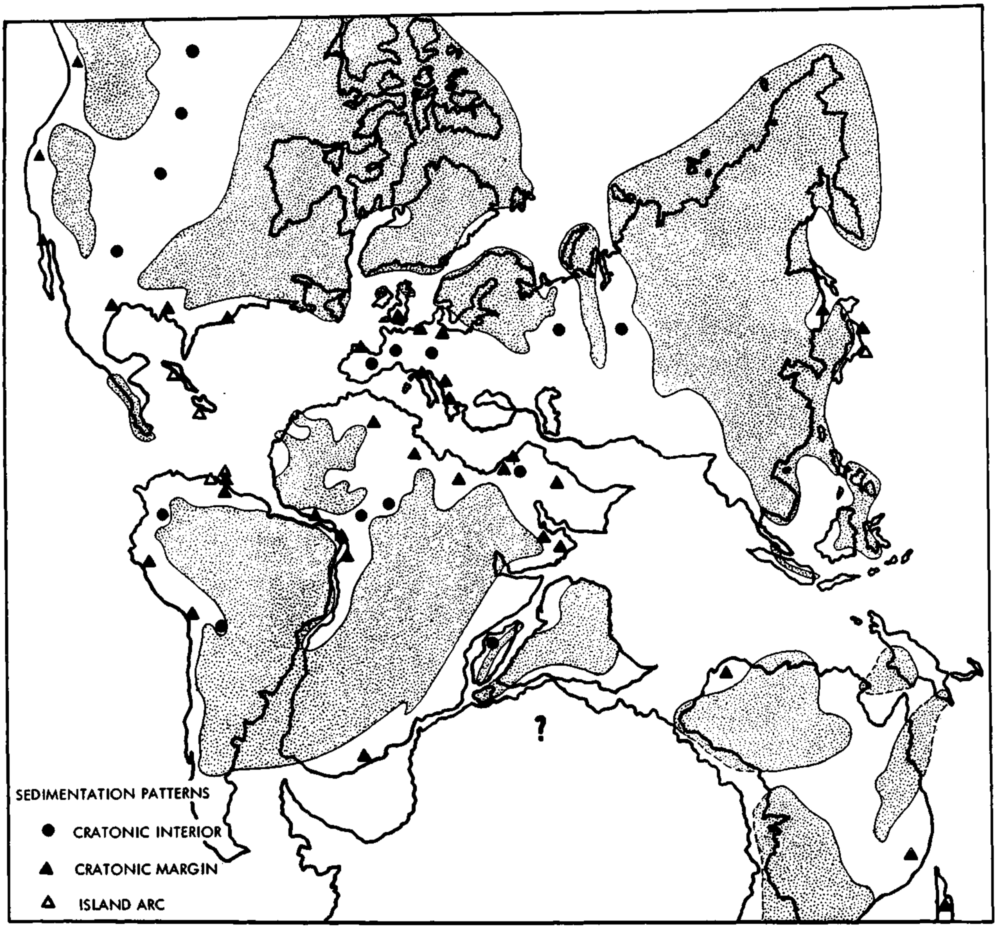

FIG. 1. Generalized world map of Late Cretaceous (Cenomanian-Santonian) maximum transgressions showing extent of epicontinental seas (white; generalized for all transgressions), land areas (stippled), continental arrangements (Dietz & Holden, 1970; Smith, Briden, & Drewery, 1973), and data points from which interpretations of transgressive-regressive history and sedimentation patterns are drawn. Where almost continuous data exist for an area (e.g., Western Interior of North America, Western Europe), data points represent regional centers where facies and faunas are distinct from those of adjacent regions (Kauffman, n).

temperate areas; 6) restriction of deep oceanic circulation and expansion of anaerobic conditions in the oxygen-minimum zone; and 7) considerable increase in the primary ecospace of marine invertebrates, the photic shelf and shallow epicontinental zones, and upper pelagic zone of the open ocean. Tremendous opportunities for radiation were presented by these episodes, yet physically controlled pressures of natural selection were low.

On the other hand, eustatic lowering of sea level greatly constricted many prime habitats, eliminated others, increased competition, increased seasonality, decreased stability in the marine climate, and generally increased the acuteness of natural selective forces acting on the evolution of Cretaceous organisms. This was especially true when such changes were very rapid, as in the Middle Turonian[1] regression. This in

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[1] Substages are used as formal stratigraphic units (KAUFFMAN, COBBAN, & EICHER, 1977) in this chapter.

turn provided the format for widespread extinction of some groups, and greatly accelerated evolutionary rates for others.

Of particular importance to understanding the evolutionary history of Cretaceous organisms is the fact that environmental "stability" over long periods of time did not generally exist, nor were there many gradual long-term changes. Plate tectonic events and their resultant climatic, oceanographic, and geographic effects were of considerable magnitude and were irregularly fluctuating between "active" and "quiet" intervals. As many as ten distinct global transgressions and regressions are recorded, which represent eustatic fluctuations during the Cretaceous (Fig. 2). It is important to consider the chain of paleoenvironmental events that resulted from each of these plate tectonic pulses—geographic changes in continents, shallow seas, and ocean basins, and thus rearrangement of water masses, their current systems, chemistry, temperature gradients, and the biogeographic units that characterized them; major eustatic changes in sea level and resultant global climatic changes; changes in available habitats and ecospace, and in stress factors of natural selection; and as a result of all of this, constantly altering patterns of gene flow.

Superimposed on these factors is the unusual character of the Cretaceous marine environment in both the open ocean and in epicontinental seas when compared to modern counterparts. Tropical to cool-temperate waters predominated over virtually the entire globe; without cold polar waters the vertical temperature differential over large ocean basins was small. Bottom waters were considerably warmer than at present, and the oceanic thermocline, to the extent that it existed, was probably of small magnitude and broadly graded during much of Cretaceous history. There is evidence that deep to midwater oceanic circulation may have, as a result, been periodically much more sluggish, producing less oxygenation, than at present. Tremendous areas and thicknesses of well-laminated, dark organic-rich shale and pelagic carbonate, and of glauconitic sand characterize Cretaceous marine rocks. Many intervals contain, at most, a sparse benthonic epifauna and virtually no infauna, suggesting periodically broad areas of chemically inhospitable substrate and oxygen depletion both in the sediment and the overlying water column (Fischer & Arthur, 1977). These conditions strongly affected biotic diversity and ecological structure in benthonic and pelagic habitats of the world's oceans. High planktonic diversity and productivity, and maximum complexity in pelagic ecological structure coincided with more uniform oceanic temperatures, eustatic rise, widespread anaerobism in deep marine basins, heavy carbon isotopic values in marine organisms, and formation of organic-rich sediment. Low pelagic diversity was associated with lowering of global sea level, regression, cooling of temperatures, intensification of temperature gradients and current systems, oxygenation of the deep ocean and light-carbon isotopic values (Fischer & Arthur, 1977).

Carbonate compensation depth may have fluctuated widely during the Cretaceous

Fig. 2. Summary of Cretaceous radiometric time scales (MYBP), magnetostratigraphy (M.S.; Van Hinte, 1976), transgressive-regressive history (T-R Cycles), and paleotemperatures. Geochronology (MYBP) columns represent (left, single asterisk) K-Ar dating of sanidine and biotite from bentonite and ash beds in the Western Interior of North America (Obradovich & Cobban, 1975; Gill & Cobban, 1966; Kauffman, 1978, and references in each) compared to the global standard of Van Hinte (1976; double asterisk). Transgressive (T, peak right) and regressive (R, peak left) pulses of Cretaceous marine cycles are interpreted from global patterns of sedimentation (Kauffman, 1973a,b; modified) represented by solid line and T_1-T_{10}, R_1-R_{10} designations; compared with generalized eustatic curve (dashed line) of Schlanger & Jenkyns (1976) for Cretaceous. Oxygen isotopic temperature curves (at right) plotted against C scale (at base) for typical Cretaceous organisms. Generalized composite temperature curve shown by heavy line in mid-graph (FA, from Frerichs & Adams, 1973). Other curves, from left to right are: BF-benthonic foraminifers (Saito & Van Donk, 1974), BE-belemnites (Lowenstam & Epstein, 1954), DS-whole rock analysis of pelagic sediments (Lower Maastrichtian and older) and planktonic foraminifers (Middle, Upper Maastrichtian) in central North Pacific (Douglas & Savin, 1973), BR-brachiopods (Lowenstam & Epstein, 1954), and PF-planktonic foraminifers, DSDP site 171, central North Pacific (Douglas & Savin,

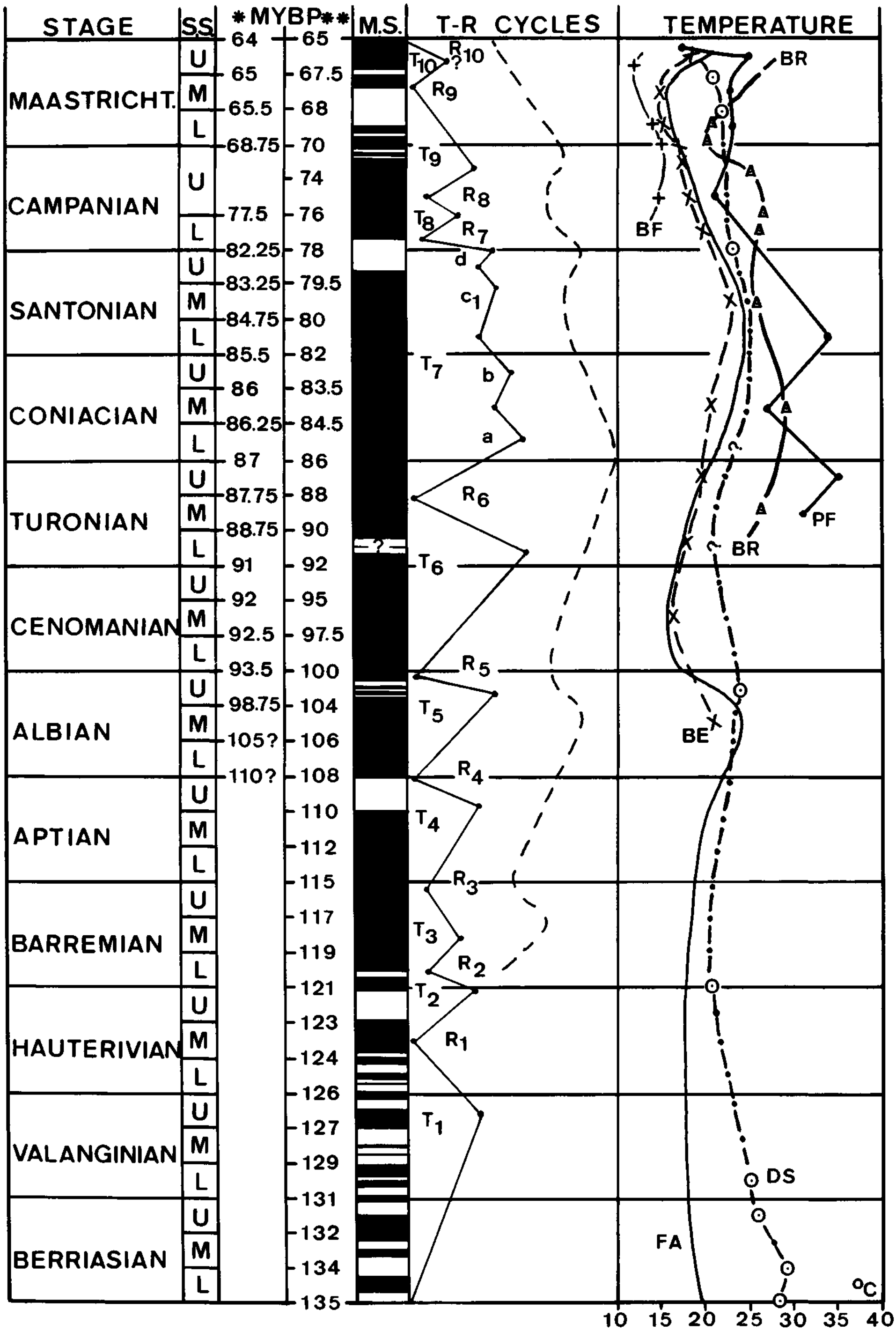

FIG. 2. *(Continued from facing page.)*

1973, fig. 3). [Explanation: S.S. = Substages.] [From Kauffman, 1977f; used with permission of Rocky Mountain Assoc. Geol., Denver.]

with a predictable effect on the planktonic biota. Low-diversity invertebrate faunas from many epicontinental seas further suggest large areas of slightly brackish surface waters (Kauffman, 1975) and possibly entire brackish seaways. As evidenced by carbon and oxygen isotopic analyses and the succession of marine biotas, these conditions fluctuated broadly and irregularly during the Cretaceous, and may have been related to plate tectonic events.

Interpretation of the intricate relationships that must have existed between the evolutionary history of Cretaceous organisms, their ecological structure, and the many varying factors of the global environment during the period is a challenge of the highest magnitude to the paleobiologist. This review will, at best, allow broad insights into these problems. It is the purpose of this general introduction to show that the Cretaceous was a dynamic time of considerable physical, chemical, and biological activity on earth, and it was a pivotal time in the evolution of the modern biota.

SURVEY OF CRETACEOUS MARINE ENVIRONMENTS

The evolutionary and ecological history of Cretaceous invertebrates is intricately related to many changing factors of the Mesozoic marine environment, such as large-scale natural selective forces linked to plate tectonic activity, eustatic changes in sea level, major changes in aquatic chemistry, temperature and circulation patterns, and broader variations in the global climate. These interrelationships were highly complex and reflect forces and evolutionary response of a magnitude several times greater than was envisioned only two decades ago. For example, Kauffman (1972, 1973a,b, 1976, 1977a) and Fischer and Arthur (1977) have proposed direct relationships between plate tectonic activity, resultant eustatic fluctuations, epicontinental transgression or regression, fluctuating salinity, marine temperatures and climatic gradients, marine oxygenation, diversity and ecological complexity of the marine biota, distribution and history of biogeographic units, and evolutionary rates in a variety of marine mollusks.

TEMPERATURE

The Cretaceous marine system was generally characterized by comparatively warm bottom and surface temperatures without cold-temperate to cold polar conditions, and with broad vertical and horizontal temperature gradients. Bottom temperatures, determined mainly from oxygen and carbon isotopic analyses of benthonic invertebrates, ranged from 10°C to 17°C (Lowenstam & Epstein, 1959; Bowen, 1966). Surface temperatures ranged from 15°C (polar) to 35°C (equatorial). Temperature gradients were broad, involving low temperature differential from pole to equator. Bowen (1966, p. 169) noted a differential of only 15°C (at 75° latitude) to 24°C (at 25° latitude) during the Albian temperature maximum, of 17°C (at 75° latitude) to 24°C (at 45° latitude) at the Santonian temperature maximum, and only a 13°C to 14°C difference between the Santonian polar and equatorial waters. Major temperature minima during the Cretaceous had only slightly more disparate ranges, for example, 10°C (at 75° latitude) to 25°C (at 25° latitude) for the Cenomanian, and an 18°C difference between the Cenomanian poles and equator. Cretaceous isotherms were 10° to 20° of latitude closer to the poles than in modern seas. Water temperatures gradually cooled during the Cretaceous, leading to breakup of equable maritime climates with terminal Cretaceous regression.

Bowen (1966) reviewed and summarized massive paleotemperature data, obtained through oxygen and carbon isotopic analyses of a variety of shelled mollusks, foraminifers, brachiopods, worms, and whole biogenic carbonate rock samples. Widely disparate analyses for the same time interval or stratigraphic unit were noted among diverse organisms. This reflects 1) variation in shell chemistry of diverse organisms, 2) cooler benthonic and warmer pelagic water temperatures in the same area, and 3) latitudinal paleotemperature gradients. Average temperature curves drawn indiscriminately for all organisms gives a general picture of Cretaceous fluctuations (Frerichs & Adams, 1973, text-fig. 4) with important temperature maxima in the Middle Albian and Santonian, and significant minima in the Neocomian, Late Cenomanian, and Maastrichtian. More precise analyses based on temporally closely spaced points, separation of benthonic and pelagic data, and consideration of latitudinal gradients (see especially Lowenstam & Epstein, 1959; Bowen, 1966; Douglas & Savin, 1973; Saito & Van Donk, 1974; and references therein), however, suggest a more complex Cretaceous temperature history (Fig. 2), with a Berriasian peak, a decline from Valanginian through Barremian time, rising Aptian temperatures, culminating in a Middle Albian high, and dropping abruptly again to a low from Middle Cenomanian to earliest Turonian time. This last fluctuation is puzzling because the Late Cenomanian to Early Turonian temperature minimum correlates with the peak of one of the greatest Cretaceous transgressions, when isotopic and faunal evidence indicate poleward migration of tropical Tethyan waters and biotas. Marine climates warmed again during the Turonian, peaked in the Coniacian to Santonian, then declined gradually through the Campanian with a small rise near the end of the stage. Early and Late Maastrichtian temperatures were low, with a slight Middle Maastrichtian rise. Evidence suggests that shallow epicontinental seaways may have warmed more quickly, and to somewhat higher levels, than did open oceanic environments.

During principal transgressive maxima, tropical to warm-temperate marine climatic zones covered much of the globe and even cool-temperate zones disappeared in the polar regions. At peak transgressions (e.g., Late Albian, earliest Turonian, Coniacian to Santonian, early Late Campanian, Middle Maastrichtian) subtropical waters spread for short periods of time over many cratonic areas previously occupied by shallow warm-temperate seas, and the warm-temperate zones shifted poleward. These incursions produced abrupt temperature rises and caused massive, rapid extinction of stenotopic warm-temperate marine taxa, and caused their replacement by mixed Tethyan and warm-temperate eurytopic faunas in poorly structured paleocommunities. Warm-temperate biotas replaced tropical to subtropical elements in marginal Tethyan areas during initial phases of regression and restriction of Tethyan marine climates.

Throughout the Cretaceous, there is no evidence for a well-defined oceanic thermocline or for cold bottom waters. Broad vertical thermal gradients persisted, becoming more accentuated during regression and general cooling of the oceanic water masses, and more gradational during transgression, warming, and amelioration of the marine climate.

Fischer and Arthur (1977) have linked broad Cretaceous temperature fluctuations to changes in deep ocean circulation, water and sediment chemistry, and diversity in both benthonic and pelagic biotas. Eustatic rise and transgression were associated with warming and amelioration of the surficial marine climate, warming of polar waters, and consequently a lower horizontal thermal gradient. As a result, polar waters did not sink as rapidly or move as readily across the deep ocean floor. Stagnation and expansion of oxygen-deficient zones in bottom waters and sediments resulted, producing finely laminated, organic-rich sediments supporting a greatly depleted benthonic biota. At the same time photic pelagic environments were optimal for high productivity and development of complex pelagic communities. Regressive pulses, representing eustatic lowering, were characterized by lower marine surface temperatures, accentuation of horizontal temperature zonation, return of cool- and possible cold-temperate climatic zones to polar areas, and thus more rapid sinking and deep ocean circulation of polar waters. This produced cooling of bottom waters, accentuation of the vertical thermal gradient, active bottom currents, widespread benthonic erosion, oxygenation of the deep ocean floor, and diversification of the benthonic biota. Pelagic biotas were coincidently depleted, and had lower productivity and simplified communities rich in opportunistic taxa during cooling pulses.

Fischer and Arthur (1977) noted two major fluctuations of oceanic temperature, biotas, and chemistry during the Cretaceous.

Early Cretaceous temperatures were relatively low, reaching a minimum in the Barremian; pelagic biotas were correspondingly depleted (oligotaxic) and characterized by opportunistic species during Berriasian to Hauterivian time (126 MYBP low point). Increases in temperature and pelagic diversity (polytaxic) reached a first peak during the Albian transgressive maximum. Lower temperatures and oligotaxic pelagic biotas were again characteristic at 94 MYBP, the Cenomanian-Turonian boundary according to the time scale of VAN HINTE (1976), but the Albian-Cenomanian boundary zone according to OBRADOVICH and COBBAN (1975) and KAUFFMAN (1978). The Albian-Cenomanian boundary coincided with a regression and best fits the FISCHER-ARTHUR interpretation. A second polytaxic interval with warming marine climates was the Late Santonian and Early Campanian, and final cooling and onset of oligotaxic conditions characterized the latest Cretaceous regressive pulse (Maastrichtian) and the Cretaceous-Paleocene boundary zone (FISCHER & ARTHUR, 1977). The FISCHER-ARTHUR hypothesis generally, but not precisely, fits independently derived Cretaceous transgressive-regressive and temperature histories.

The net effect of Cretaceous temperature distributions on the evolution of the biota was profound. Broad temperature gradients promoted widespread biogeographic mixing of faunas at indistinct marine climatic zone boundaries. The faunal overlap zone between warm-temperate and mid- to cool-temperate biotas of the Western Interior of North America during the Cretaceous was as much as 1,600 km (SOHL, 1967; KAUFFMAN, 1973a, 1975). Similarly, vertical zonation of the biota across the shelf-depth and slope-depth zones of the Cretaceous seas was very broad and nowhere near that found today off the Atlantic, Gulf (PARKER, 1960, references therein), and Californian-Mexican coasts (PARKER, 1964). These more stable regional Cretaceous climates, especially during warming trends and epicontinental transgressions, may have engendered evolution of less temperature-tolerant organisms, which in turn were severely stressed, producing high levels of extinction in some types and rapid evolution in others, by unpredictable perturbations in the global climate.

WATER CHEMISTRY

Cretaceous biotas and geochemistry suggest that water chemistry in open marine systems was similar to that of modern seas, but there were periodic variations in salinity, oxygen, carbon dioxide and carbonate content, dissolved nutrients, and carbon isotopes, especially in epicontinental seaways. These fluctuations of marine water chemistry largely reflect plate tectonic activity, related changes in sea level, changes in marine current systems, oceanic circulation and temperature distribution, variations in introduced organic and inorganic compounds from continental sources, the effectiveness of fluvial systems in transporting these materials to marine areas, and consequent changes in productivity.

The most obvious changes in water chemistry involved salinity and oxygen. HALLAM (1975) noted a decrease in invertebrate diversity northward from the European Tethys into the "Boreal" (North Temperate) Realm in the Jurassic and accounted for this, in part, by lower salinities in shallow epicontinental seas to the north, which received considerable fresh water from internal drainage of river systems. Similar paleogeographic situations existed throughout the Cretaceous, associated with Tethyan to temperate-zone decline in invertebrate diversity. But poleward decrease in diversity by itself is not good evidence for salinity decrease. SCHOLLE and KAUFFMAN (1977) have shown from oxygen and carbon isotopic analyses of associated carbonates (whole-rock analyses) and *Inoceramus* shells that subnormal salinities periodically characterized the Western Interior basin of North America throughout its middle Cretaceous history except for periods near peak transgression (latest Cenomanian to earliest Turonian, Coniacian and parts of the Santonian). Equivalent analyses of the English chalk (open shelf) sequence for the same interval, showed consistently near normal salinities in open marine facies. European epicontinental basins show faunal depletion northward, suggesting periodically less than normal salinity.

Paleocommunity analyses of the Western Interior seaway of North America by Sohl (1967), Scott (1970, 1974), Kauffman (1967, 1969) and Kauffman, Hattin, and Powell (1977), record a predominance of low diversity assemblages compared to contemporaneous open marine communities and their modern counterparts. The scarcity or exclusion of sponges (other than *Cliona*), bryozoans, corals, articulate brachiopods, echinoids, many normal-marine gastropods and bivalves, and diverse pelagic microbiotas suggests less than normal salinity in part of the water column. Yet the abundance of ammonites, normal-marine mollusks, and fishes during Cretaceous time suggests mixing with normal-marine water layers. It would appear that this situation was typical of most widespread Cretaceous epicontinental seas.

To account for mixing of normal-marine organisms with depauperate and seemingly more brackish water benthonic communities in Cretaceous temperate epicontinental seas, Kauffman (1975, fig. 3) proposed a model of stratified epicontinental seas, especially those with constricted or silled apertures. A surficial layer of slightly to (near peak regression) moderately brackish water spread across much of the seaway, generated by internal river drainage. Near normal surface salinity was associated only with periods near peak transgression. A denser, normal-marine layer occupied deeper portions of the basins. Lack of a well-defined thermocline and broadly graded vertical temperature zonation, coupled with possibly sluggish currents and low levels of wave activity, prevented extensive mixing of brackish surface water and deeper normal-marine water in this model. Seasonal or longer term overturn would not occur. In epicontinental seas with restricted apertures a Baltic Sea model might be further invoked, in which tidal exchange would mainly involve outflow of surficial waters (brackish) and inflow of deeper, more saline waters in a density stratified system. The net effect of this situation might be restriction in colonization of epicontinental seas by stenohaline pelagic organisms and pelagic larvae of many normal-marine benthonic groups; both are mainly dispersed in the upper photic zone of the water column, envisioned here as being partially brackish during much of the Cretaceous. Thus it is the more euryhaline marine and brackish water organisms, more normal marine forms with larvae distributed on deeper water currents, and organisms without stenohaline pelagic larval stages or with short-lived ones (including ammonites, marine fishes, reptiles, many mollusks) that would be able to colonize temperate epicontinental seas. This model would account for depauperate pelagic microbiotas and shallow-water benthonic paleocommunities that characterize many Cretaceous epeiric seas, and yet permit abundant, more normal marine organisms to be mixed with them. The recent discovery by Scholle and Kauffman (1977) that benthonic inoceramid shells and pelagic carbonates yield similar isotopic values suggests that much of the epicontinental water column may have been subsaline, except during peak transgression, and introduces the possibility that some Cretaceous ammonites were euryhaline.

A second major chemical variable that strongly affected the biota of Cretaceous seas was dissolved oxygen. Offshore decrease in benthonic diversity (Kauffman, 1967); the depauperate nature of many deeper water paleocommunities; large areas lacking in benthonic microfauna; widespread development of evenly and finely laminated, nonbioturbated, organic-rich clay and carbonate mud; and thick glauconite deposits during Cretaceous time have all been cited as evidence for widespread development of oxygen-depleted zones in world oceans and epicontinental seas. Schlanger and Jenkyns (1976) and Fischer and Arthur (1977) proposed that the deep ocean basins were largely oxygen depleted during major periods of Cretaceous warming, global eustatic rise, and epicontinental transgression (Late Aptian, Albian, parts of the Cenomanian-Turonian, and Coniacian-Santonian). Deep ocean circulation slowed considerably during warming of surface waters in polar regions, and lessening of horizontal and vertical temperature differentials. Organic-rich, finely and evenly laminated, generally nonbioturbated deep ocean sediments developed widely. Benthonic microfaunas were almost wholly absent and macrofaunal associations were greatly depleted. Little evidence is known for marine erosion or active bottom currents. Coincidentally, high pelagic productivity and diversity greatly increased the organic rain to the deep oceans, enhancing development of anaerobic benthonic conditions and organic-rich sediments. Oxygenation of the deep ocean occurred during Neocomian, Late Cenomanian to Early Turonian (according to FISCHER & ARTHUR, 1977, but *not* SCHLANGER & JENKYNS, 1976), and Campanian-Maastrichtian times, with global climatic cooling, eustatic lowering of sea level, epicontinental regression, cooling of polar areas, accentuation of both horizontal and vertical temperature zonation, and reestablishment of deep ocean currents. Similarly, FRUSH and EICHER (1975) proposed widespread development of oxygen-minimum zones related to oceanic oxygen depletion during the Late Cenomanian to Turonian in the Western Interior and Gulf Coast seaways of North America. Their interpretation is based on essential lack of benthonic microfauna and reduction of benthonic macrobiota with near exclusion of infaunal elements. These proposed times of oxygen depletion seem to correspond to periods of late (but not peak) transgression and early regression (late Middle and Late Cenomanian, Middle Turonian, and by analogy of similar sediments, latest Turonian and Santonian times).

Two models are possible for this type of event in epicontinental seas. The first, as suggested by FRUSH and EICHER (1975) for the North American Cretaceous, and by SEILACHER and WESTPHAL (1971, figs. 1,4) and BARTHEL (1970) for the European Jurassic, involves periodic development of a widespread low-oxygen to anaerobic zone through much of the lower water column in basinal parts of epicontinental seas, excluding nearly all infaunal and epifaunal benthonic organisms, and pelagic-nektonic organisms of the lower part of the water column, and leaving a biota that is predominantly upper pelagic to nektonic in aspect. Associated benthonic organisms are interpreted as having an epiplanktonic habitat on floating vegetation, logs, shells, or on living pelagic organisms. Exceptional preservation of articulated skeletons and soft parts in these rocks are cited as supporting evidence for widespread oxygen-minimum zones, and burial of dead organisms below the aerobic-anaerobic boundary with low levels of bacterial decay and scavenging.

KAUFFMAN (1977c) proposed an alternative model for these types of epicontinental deposits based on detailed study of normally benthonic invertebrates associated with them. He found that epiplanktonic associations of normally benthonic organisms with floating wood or other objects are rare in ancient and modern situations (KAUFFMAN, 1975), and cannot account for the numbers and diversity found with these deposits. *In situ,* low-diversity benthonic communities actually occur at many levels, in moderate abundance, with these "anaerobic" deposits. In the Cretaceous, these benthonic communities are commonly built upon thin-shelled, colonizing Inoceramidae that may reach three meters in diameter, or on shells of dead ammonites, or on molluscan mass-mortality surfaces. Initial colonizing benthonic bivalves of many oxygen-poor Mesozoic substrates show adaptations for expanded oxygen absorption, and apparent tolerance for low oxygen levels, but subsequent members of these epibiont-endobiont communities are typically more normal marine taxa representing groups less tolerant of low oxygen levels. Cemented and byssate epifaunal bivalves, cranioid brachiopods, boring and gooseneck barnacles, algal-grazing gastropods (and thus algae), bryozoans, boring and cemented tube-building worms, encrusting foraminifers, boring and encrusting sponges, and rarely other taxa comprise the communities that colonized live and dead inoceramid shells and the up-facing flanks of dead ammonites and other mollusks in these anaerobic or oxygen-depleted environments. The common occurrence of these inoceramid "island" communities on Jurassic and Cretaceous sea floors characterized by nonbioturbated, finely laminated, organic-rich sediment lacking a benthonic microfauna or infauna does not support the anaerobic-basin model with a widely spread oxygen-minimum zone. Instead, it suggests that chemically inhospitable conditions and oxygen depletion occurred mainly near the sediment-water interface (at or a few centimeters above it) and higher marine waters were sufficiently oxygenated to support a more normal marine biota. Most black shale and carbonate rocks of Phanerozoic "anaerobic" marine epicontinental basins may represent this situation instead of extensive oxygen-minimum zones. Widespread occurrence of inoceramid shells in Deep Sea Drilling Project (DSDP) cores (Theide & Dinkelman, 1977) further suggests that careful restudy of Cretaceous "oceanic anaerobic events" is warranted.

Several authors have suggested variations in carbonate content in Cretaceous oceans, broad fluctuations in CO_2, the lysocline, and carbonate compensation depth (CCD). These are thought to be related to major biotic changes. Berner (1974) defined chemical properties, interactions, and distribution patterns for carbonates in modern open marine systems, and presented detailed discussion of the lysocline and CCD, and their relation to carbonate saturation and dissolution. These principles can be applied to Cretaceous systems with consideration for temperature and circulation differences, variations in nutrient and inorganic-compound supply, and marine productivity. Widespread fluctuations in the Cretaceous marine environment, including major eustatic changes, should have strongly affected the CCD level in the world's oceans. Considerable disagreement exists as to the magnitude of these fluctuations (see papers in Hay, 1974), their timing, and causes for the establishment and migration of the CCD and lysocline.

Worsley (1971, 1974) suggested a marked decrease in $CaCO_3$ input from continental sources with erosional lowering of Late Cretaceous continents and decrease in runoff prior to early phases of the Laramide orogeny, coupled with temperature decline and CO_2 increase in cool shelf and basinal waters. Without terrestrial replenishment, Late Cretaceous periods of high productivity among shell-forming calcareous plankton (foraminifers and coccoliths) further depleted the supply of available carbonate in sea water; Worsley (1971) believed that much of this carbonate was "lost" in the deep ocean as dead plankton skeletons dissolved below the lysocline and CCD. These factors combined to cause the CCD to rise near to, or reach, the oceanic surface during latest Cretaceous time, further causing widespread dissolution of biogenic carbonate, pelagic extinctions, and collapse of the global food chain at the time of terminal Cretaceous extinction (see also Tappan, 1968).

Ramsay (1974, fig. 2) predicted that periods of oceanic surface warming were accompanied by high pelagic productivity, increased supply of carbonate skeletons to the deep ocean, decrease in available carbonate in surface waters, increase in subphotic CO_2 content brought about by increased levels of bacterial decay of the pelagic rain, greater levels of carbonate dissolution at shallower depths, and thus rise of CCD. Conversely, cool periods produced lower amounts of pelagic carbonate, less free CO_2 in subphotic zones, slower dissolution, and depressed CCD. Ramsay (1974, figs. 3, 4) calculated that the CCD fluctuated between about 5 km during the Late Cenomanian(?) to Turonian temperature minimum, and again during the latest Maastrichtian decline, to about 4.5 km during the Late Santonian to Campanian temperature decline, and to about 4 km during the Late Albian and the Late Coniacian to Santonian temperature maxima.

Tappan (1968) developed a stimulating theory on the relationship between ocean chemistry, phytoplankton production, and large-scale extinctions in the marine realm, which is applicable to the Cretaceous. Large phytoplankton blooms seem to have occurred, especially during Aptian-Albian time, near the Cenomanian-Turonian boundary (debated by some), during the Coniacian and Santonian, and during the Middle to early Late Maastrichtian. Phytoplankton blooms are closely related to the O_2-CO_2 balance in the atmosphere (Tappan, 1968). Tappan theorized that oceanic phytoplankton maxima are coincident with: 1) times of continental rejuvenation and increased input of continental nutrients and (or) initial phases of epicontinental transgression, 2) marked vertical and horizontal climatic gradients in the world's oceans, 3) active bottom currents, and 4) widespread upwelling and nutrient replenishment. High phytoplankton productivity led to high levels of diversification, decrease in atmospheric and dissolved CO_2 and coincident increase in O_2. Heavy sulfates resulted from low levels of bacterial oxidation of sulfides and decline in sulfate content. Heavy carbon (C_{13}) isotopes in sea water resulted from selective depletion of C_{12} isotopes by the phytoplankton in photosynthetic carbon fixation. Extensive biogenic carbonate was deposited, producing marine limestone and chalk. Presumably, broad preservation of such deposits in the deep ocean reflects a depressed CCD.

According to TAPPAN (1968), phytoplankton minima result from low productivity associated with low continental configuration and low input of land-derived nutrients during maximum epicontinental transgression and early regression, climatic warming and amelioration, broadening of vertical and horizontal temperature gradients resulting in sluggish ocean circulation and lowering of deep ocean oxygen levels, and decrease in upwelling. Nutrient-depleted waters thus characterize the photic zone of world oceans; nutrient sinking into oxygen-depleted layers results in temporary "loss" of oceanic nutrients, which exceeds replenishment levels from continental sources and upwellings. Oxygen production in the atmosphere and oceans decreases and relative CO_2 increases. Lighter sulfates in solution result from bacterial oxidation and breakdown of sulfides during times of low productivity. Light carbon isotopes predominate as the relative amount of C_{12} increases because of low levels for carbon fixation by phytoplankton. These conditions lead to widespread extinction among animal taxa (TAPPAN, 1968), for example, at the end of the Cretaceous.

Thus, during the Cretaceous, many factors leading to broad and intermittently severe changes in marine chemistry—salinity, O_2 and CO_2 content, carbonate content and dissolution levels, nutrient content, and the isotopic nature of various elements and compounds—were actively destabilizing the marine system as we currently view it. These episodes produced major biologic response in regard to population density, radiation, diversification and extinction.

EUSTATIC CHANGES

Most contemporary workers accept the hypothesis that major sea-level changes occurred during the Cretaceous, but there is variety of opinion regarding the number and magnitude of these fluctuations, and the driving force behind them. Five possible causes for Mesozoic eustatic sea-level changes have been recently proposed: 1) active periods of plate movement, especially rapid seafloor spreading, lead to construction of topographically elevated areas on the ocean floor, which in turn displace sea level upward and cause epicontinental transgression (HALLAM, 1971; HAYS & PITTMAN, 1973; and KAUFFMAN, 1973a,b); 2) whole plates, or large portions of plates are uplifted, especially over crustal hot spots and mantle convection cells, and subsequently lowered to produce eustatic rise and fall of sea level, and transgressive-regressive pulses; 3) whole continents subside and rise, in harmony, to produce apparent eustatic fluctuations and coincident global transgressions and regressions (BOND, 1976); 4) volumetric change in ocean basins producing eustatic displacement results from the breakup and assembly of supercontinents (VALENTINE & MOORES, 1972); and 5) transgressive-regressive history is related to eustatic changes produced by epeirogenic movements on the ocean floor with coincident epicontinental epeirogenic events (HALLAM, 1963). Current data suggest that the first and second causes account for most Cretaceous changes in sea level.

One (HAYS & PITTMAN, 1973; BOND, 1976; SCHLANGER & JENKYNS, 1976; Fig. 2, herein) to three large-scale Cretaceous transgressions are recognized by most workers; the major one peaked in the Late Cenomanian or Early Turonian, a second one in the Late Albian, and a third one in the Coniacian to Santonian (for example, FISCHER & ARTHUR, 1977). These were among the most extensive transgressions of the Cretaceous and are obvious from paleogeographic plots. Each coincided with probable times of active, relatively rapid seafloor spreading and construction of topographically elevated areas on the ocean floor. Global Late Albian and Middle Turonian regressions separated these transgressive maxima, which were only 9 and 3 to 4 million years apart, respectively (measured radiometrically; Fig. 2).

Careful examination of global strandline fluctuations and vertical stratigraphic-paleoenvironmental relationships of marine cyclothems suggests that at least four major Cretaceous transgressions reached well onto at least 60 to 75 percent of widely scattered cratonic areas (Fig. 1), indicating eustatic rises of sea level (KAUFFMAN, 1969, 1970, 1972, 1973a,b; HANCOCK, 1975; and others). These peaks occur in the early to middle Late Albian, latest Cenomanian to Early Turonian, Coniacian to Santonian (possibly two or more separate events), and early Late Campanian. In addition, KAUFFMAN (1973a,b) has reported six lesser Cretaceous transgressive peaks that mainly involve flooding of marginal continental and more restricted epicontinental areas in many parts of the world (40 to 60 percent of world Cretaceous sections), as follows: Late Valanginian, latest Hauterivian or earliest Barremian, Middle Barremian, latest Aptian, middle Late Campanian, and Middle to early Late Maastrichtian. The irregular temporal spacing of these eustatic changes (Fig. 2) suggests that they are not cyclic, and the rapidity with which some take place (Middle Turonian regression encompasses less than two million years) strongly suggests mechanisms for regression other than simple oceanic ridge collapse through heat loss (a slow process).

Cretaceous eustatic fluctuations have strongly influenced the evolutionary history of diverse organisms and biogeographic units. Global transgression was associated with the spread of warm, ameliorating maritime climates, elimination or great restriction of cool-water zones, broadening of vertical and horizontal marine temperature gradients, and great expansion of total ecospace and individual niches, especially in shallow water habitats. Oceanic productivity and resources increased, resulting in great expansion in numbers and diversity of the planktonic microbiota and the increase in complexity of food-web relationships and pelagic communities. FISCHER and ARTHUR (1977) proposed that these were also times of restricted deep marine circulation, spread of anaerobic conditions on the deep sea floor, and depletion of deep marine benthos; however, evolutionary opportunities for photic pelagic and shallow-water benthonic marine invertebrates were expanded during transgression, allowing broad diversification and niche partitioning at low taxonomic levels (mainly genera and species), and increase in the complexity of ecological interactions. Environmental perturbations probably decreased in numbers and intensity and therefore selective stress levels were decreased (biological forces of predation and competition excepted). Without high levels of stress, evolutionary rates and the magnitude of extinctions in marine invertebrates were relatively low (KAUFFMAN, 1970, 1972, 1977a).

Periods of maximum Cretaceous transgression were characterized by relatively rapid increases in water temperature and salinity in shallow temperate-zone epicontinental and shelf areas, as determined from oxygen and carbon isotopic analyses (SCHOLLE & KAUFFMAN, 1977) and from faunal changes (KAUFFMAN, 1973a, 1975; KAUFFMAN & SCHOLLE, 1977). A rise of a few degrees in water temperature seems to have constituted the first major environmental perturbation of transgressive cycles, and resulted in widespread extinction among stenotopic warm-temperate marine organisms and their replacement by more eurytopic warm-temperate and marginal Tethyan elements. The great extinctions associated with the Cenomanian-Turonian and Turonian-Coniacian boundaries reflect this phenomenon.

Global regression reflects eustatic lowering of sea level. In shallow Cretaceous shelf and epicontinental seas this resulted in decrease in prime ecospace, restriction or elimination of many photic-zone habitats, possibly increased shallow-water turbidity and lower salinity, cooling of the oceans, increase in vertical and horizontal temperature gradients and contraction of warm climatic zones, oxygenation and reestablishment of currents in the deep sea, and decrease in maritime climatic effects producing greater seasonality (KAUFFMAN, 1973a,b, 1975; FISCHER & ARTHUR, 1977). Natural selective forces increased in magnitude, environmental perturbations were probably more common, more severe, and affected a relatively greater portion of the shallow marine biota than during transgression. Competition for basic resources increased among the marine fauna (KAUFFMAN, 1972, 1975). The effect of these deteriorating marine conditions was increasingly to stress invertebrate populations, ultimately leading to widespread extinction among many groups (especially stenotopic forms), and to increase evolutionary rates commensurate with the rate and severity of environmental decline among others (especially eurytopic forms; KAUFFMAN, 1970, 1972, 1975, 1977a). Rapid major regressions, such as that of the Middle Turonian, seem to have produced the greatest evolutionary effects in the shortest period of time.

BENTHONIC ENVIRONMENTS

The study of Cretaceous pelagic environments is essentially one of changing chemistry, nutrient supply, temperature, salinity, and pelagic productivity. Cretaceous benthonic invertebrates were subject to the same controls, though more subtle in aspect, in their evolution. In addition, they were directly subjected to the physico-chemical nature of Cretaceous marine substrates, to a fluctuating CCD, and in the shelf zone to major spatial and temporal fluctuations of their preferred niches associated with major eustatic fluctuations.

In the shallowest epicontinental zones (<30 m), some of which were more than 150 km wide (for example, Western Interior seaway of North America; KAUFFMAN, 1969), Cretaceous benthonic organisms were greatly affected by fluctuations in salinity. Brackish water probably extended as a surface layer over normally marine areas during many times of epicontinental "freshening" (KAUFFMAN, 1975). Most deeper benthonic environments may have been characterized by normal salinity; however, recent isotopic studies suggest periods when subnormal salinity reached deeper zones of epicontinental seas (SCHOLLE & KAUFFMAN, 1977; KAUFFMAN & SCHOLLE, 1977). Brackish water layers in epicontinental systems may have selected heavily against immigration and dispersal of normal marine, stenohaline plankton (food resources) and planktonic larvae of varied benthonic organisms, accounting for the relatively low diversity of many epicontinental benthonic communities that contain normal-marine taxa.

The principal environmental factor affecting Cretaceous benthonic invertebrates was the oxygen level. Broad fluctuations of oxygen content in both oceanic depths (SCHLANGER & JENKYNS, 1976; FISCHER & ARTHUR, 1977) and deep portions of epicontinental seas (FRUSH & EICHER, 1975) have been noted, with widespread oxygen depletion periodically resulting from restriction of deep water circulation associated with climatic amelioration, broadening of vertical and horizontal climatic gradients, and global warming. Coincident eustatic rise resulting in widespread transgression enhanced the effect of oxygen depletion in benthonic environments. Collectively these factors had a profound impact, causing restriction of the Cretaceous benthonic biota. This is evidenced by general offshore decrease in diversity (KAUFFMAN, 1967) (as opposed to offshore increase among macroinvertebrates today), and the simple structure of many basinal and deep ocean paleocommunities. These show heavy representation by low-oxygen tolerant, detritus-feeding, carnivorous, and nonselective filter-feeding groups, plus some opportunistic taxa. There were also broad marine areas devoid of any obvious benthos, especially infauna, during the Cretaceous. Anaerobic conditions and H_2S poisoning seem to have been the major limiting factors. Periods of oxygen renewal in deep water benthonic environments allowed reestablishment of benthonic communities many times during the Cretaceous, but long-term stability never existed, and diversification of the deep benthonic biota was limited.

Whereas wide fluctuation of pelagic microplankton productivity has been noted in the Cretaceous (TAPPAN, 1968; TAPPAN & LOEBLICH, 1972; FISCHER & ARTHUR, 1977), leading one to expect significant fluctuations in the primary food source of suspension-feeding benthonic invertebrates, there is no evidence from the Cretaceous fossil record that benthonic diversity or the ecological success of any group living in normal marine situations was seriously affected by these fluctuations, with the possible exception of the Albian-Cenomanian, Cenomanian-Turonian, and Maastrichtian-Danian boundary zones. All of these boundaries are characterized by widespread, abrupt, and nearly coincident extinctions of numerous planktonic and benthonic organisms. TAPPAN (1968), TAPPAN and LOEBLICH (1972), WORSLEY (1971, 1974), KAUFFMAN (1977b), and others have proposed a direct relationship between short-term, widespread extinctions of the pelagic microbiota (including the planktotrophic larvae of many benthonic organisms), collapse of the global marine food chain, and resultant widespread extinction or depletion of the midwater and benthonic biota. But, in general, Cretaceous benthonic invertebrate biotas were buffered from lesser planktonic fluctuations by: 1) seemingly lower density and thus resource demand in many offshore communities, occupying the bulk of the marine ecospace, as compared with those of today; and 2) the comparatively strong representation of nonselective suspension feeders and detritus feeders in many Cretaceous deeper water benthonic communities. Both groups today are able to utilize a broad variety of food, including organic detritus, and thus have a relatively more stable resource supply through time. Shallow shelf and epeiric benthonic paleocommunities of the Cretaceous are closely similar in complexity and trophic specialization to those of today and seem to have been little affected by the broad fluctuations in plankton productivity, suggesting that nutrients were continually supplied to these areas from continental sources.

Two additional factors of the benthonic environment were probably important in determining the nature of Cretaceous substrates and invertebrate biotas, especially in more offshore, deeper water facies. These are: 1) substrate chemistry and water saturation levels (reflecting "firmness" or matrix density); and 2) dissolution in carbonate-undersaturated zones, below the lysocline and CCD. Whereas Cretaceous marine sedimentary rocks reflect virtually all major environments extant in today's oceans and shelf seas, this was also a period of unique benthonic environments represented by two widespread facies, both of which suggest chemically restrictive conditions. Pelagic carbonates (especially chalk, micritic limestone, and clay-enriched shaly chalk) and glauconitic sand are exceptionally widespread in Cretaceous open marine and (to a lesser extent) epeiric systems. Together with dark shale and mudstone, they comprise the major portion of the marine benthonic facies during the Cretaceous.

The predominance of finely and evenly laminated, commonly nonbioturbated, organic-rich shale, carbonate enriched shale, and evenly bedded pelagic carbonate in offshore epicontinental, shelf, and oceanic deposits during numerous intervals of Cretaceous time suggest highly inhospitable environments for even the most tolerant benthonic invertebrates. Thick stratigraphic sequences are characterized by widespread depletion or exclusion of even polychaete worms (as evidenced by scarcity of burrows)—among the most eurytopic of benthonic invertebrates, by the depauperate nature of many benthonic microfaunas, and by an abundance of disseminated pyrite and organic carbon. This suggests that these sediments were almost totally anaerobic at times. They also probably contained high levels of H_2S. Many authors have used these data as evidence to suggest widespread oxygen-minimum or wholly anaerobic zones in the overlying water column during the Cretaceous, especially in the deep oceans. The geographic spread and stratigraphic thickness of these facies in the Cretaceous exceeds that of any other period of geologic time.

Intercalated within these same sedimentary facies, especially in epicontinental areas, are numerous intervals containing a rich burrowing ichnofauna, and simple to moderately complex epibenthonic assemblages that tend to show greater "normalcy" in composition and ecological structure where they were elevated to even a few centimeters above the sediment-water interface (KAUFFMAN, 1977c). It is difficult to imagine that these more fossiliferous intervals reflect frequent large-scale fluctuations of a broad oxygen-minimum zone. Instead this suggests a more delicately balanced system of benthonic oxygenation and H_2S levels for many Cretaceous epicontinental seas and possibly some deep ocean basins. The anaerobic-aerobic and H_2S lethal interface may have been situated at, or only a few centimeters above, the sediment-water interface during times characterized by large-scale depletion or exclusion of benthonic invertebrates. In some cases, such a boundary was possibly maintained by low levels of circulation, or within a thin zone of suspended sediment, or beneath anaerobic fungal and blue-green algal mats near the interface (as today in parts of the Black Sea and the Santa Barbara basin). This type of environmental system would exclude virtually all infauna and microscopic epifauna normally living at the depositional surface, and greatly restrict settlement of larvae of all but the epibenthonic organisms that were most tolerant of low oxygen levels (Inoceramidae in the Cretaceous, commonly). Yet, following colonization by such tolerant organisms, especially those having large or inflated shells extending well above the anaerobic boundary, the upper surfaces of these shells provided substrates for habitation by somewhat more normal-marine assemblages in more oxygenated waters. Such relationships have been widely observed in Mesozoic dark shale and carbonate supposedly deposited in basins characterized by a broad oxygen-minimum zone. More extensive colonization of widespread Cretaceous carbonate and clay substrates, as evidenced by marked increase in bioturbation and diversity of epibenthonic taxa, reflects removal or dilution of the anaerobic or toxic H_2S zone situated above the sediment-water interface, or lowering of this zone into the sediment.

Even without oxygen depletion or H_2S poisoning, water saturation levels in marine sediments seem to have imposed another important control on the nature of Cretaceous benthonic environments and invertebrate faunas. High levels of water saturation normally correspond to high levels of turbidity at the sediment-water interface, that is, development of a well-defined zone of suspended sediment above the actual depositional surface, and of a broadly gradational contact between them. Such a zone can be produced biotically through intense bioturbation, and produced physically as a balance between sedimentation rate, size of material, chemistry of the depositional surface, and the magnitude and type of water circulation near the interface. Whatever the cause, high levels of water saturation within the sediment and an overlying zone of suspended fine-grained material combined in the Cretaceous, as now, to greatly alter the benthonic environment, and the composition and structure of benthonic communities (for examples, see RHOADS, 1970; RHOADS, SPEDEN, & WAAGE, 1972; KAUFFMAN, 1974, fig. 12-4). Development of these substrate conditions first choked out selective, and later nonselective suspension-feeding organisms, changing the trophic structure of the benthonic community to one dominated by detritus-feeding organisms. Continuance of turbid benthonic conditions for long periods of time may eventually have led to further exclusion of selective detritus-feeding organisms, and finally of all infaunal and epifaunal elements.

Thus, in the Cretaceous, deep water epicontinental, marine shelf, and ocean basin fine-grained carbonate and clay dominantly represent restricted benthonic habitats, especially for infaunal organisms, characterized by low-oxygen to anaerobic conditions and possibly lethal H_2S levels within and somewhat above the sediment-water interface. In deep oceanic environments, anaerobic conditions apparently spread periodically through large portions of the water column as well, in broad oxygen-minimum layers. Times of oxygen depletion may also commonly have been times of establishment of a suspended sediment zone above, and gradational with the depositional surface, increased water saturation, and increased H_2S concentrations within, the sediment. Oxygenation periods in these environments were frequent, but never long enough for the development of complex benthonic communities so far as we now can ascertain from the fossil record. In deeper ocean basins especially, there was a direct relationship between development of broad oxygen-depleted benthonic environments and restriction of deep water circulation associated with broadening of thermal gradients.

The second unique Cretaceous sedimentary environment was associated with the widespread deposition of glauconite and glauconitic sand in open marine shelf zones. This continued on into the Tertiary in many parts of the world, but is much more restricted in scope elsewhere in the Phanerozoic. The environment of deposition of glauconite has been widely discussed (Cloud, 1955; Porrenga, 1967; and others). Cool waters of shelf depth (especially the outer shelf), with slow rates of sedimentation or large-scale sediment bypass, high levels of concentration of organic material, and a microreducing environment at and below the sediment-water interface are thought to have characterized many Cretaceous and Tertiary glauconite-forming environments; however, more widespread reducing environments, low oxygen, and other chemical factors that might have restricted benthonic community development during the Cretaceous do not seem to have been characteristic of glauconite-forming environments. Cretaceous and Tertiary glauconitic sands characteristically contain a rich benthonic invertebrate biota of normal-marine aspect, with broad representation among infaunal elements, and diverse trophic strategies.

The potential for broad fluctuations of calcium-carbonate compensation depth (CCD) and the lysocline, below which dissolution becomes severe, and thus for the development of broad marine areas with benthonic environments posing difficult conditions for calcium-secreting organisms, has previously been discussed [see also the views of Ramsay (1974) vs. Worsley (1971, 1974) for the Cretaceous]. Metastable aragonite, and ultimately more stable calcite readily go into solution as one approaches the CCD, and available carbonate for shell-building in organisms living below the lysocline is greatly diminished. Below CCD the calcite shells of dead invertebrates are almost wholly dissolved, and living organisms are characterized by small, thin shells. The deeper the environments below CCD, the sparser the living shelled fauna; above CCD, modern biotas show offshore increase in diversity (see data in Sanders, 1969); but the reverse seems true in the Cretaceous. This does not necessarily mean that aragonite-shelled organisms (most mollusks for example) cannot live below the CCD; indeed, most shelled macroinvertebrates in bathyal and abyssal environments today have aragonite shell layers that are protected from dissolution by commonly thick and (or) dense organic shields (the periostracum in Mollusca). But calcitic shells are almost wholly dissolved after death in these environments, resulting in a poor fossil record (see Kennedy, 1969, p. 462-465), or even total elimination of the record of shelled invertebrates. Thus, both primary and secondary effects of the CCD greatly restrict the biota found below this level in Cretaceous as well as recent seas.

Depletion of invertebrate diversity and ecological complexity in Cretaceous deep water deposits below CCD is not simply a matter of dissolution. In the northern and western European chalk sequences, for example, where ample evidence for dissolution of aragonitic shells exists (Kennedy, 1969) and only the calcitic shells are well preserved, it has been frequently noted that levels or local zones exist where aragonitic fossils are preserved in abundance (commonly attributed to special preservation phenomena). In these zones, however, the diversity and abundance of the calcitic shells, which are generally preserved throughout the chalk, also increases. This infers both an ecological control (substrate environment) and a secondary diagenetic control (dissolution) on the preservation of organisms with carbonate shells in deep Cretaceous marine environments.

Inherent in the entire preceding discussion has been the broad range of variations in the Cretaceous marine environment: temperature, salinity, oxygen, hydrogen sulfide and carbon dioxide content, food and nutrients, sea level, ecospace, niche diversity, CCD, sediment water saturation, rate of deposition, benthonic circulation (especially in deeper water areas), and other factors. Long-term environmental stability apparently did not exist, in respect to these factors, in even the deepest parts of the Cretaceous seas. Many habitable environments were formed and wholly eliminated several times during the Cretaceous (for example, shallow epicontinental carbonate environments); others underwent severe environmental fluctuations (for example, oxygen content); others were moved wholesale over broad geographic areas (for example, marginal marine to shallow sublittoral quartz-sand facies); others were subject to great change in size, and the amount and diversity of potential ecospace for habitation that they offered. These fluctuations were highly related to the evolutionary history of Cretaceous lineages (Kauffman, 1970, 1972) and entire paleobiogeographic units (Kauffman, 1973a).

NATURE OF INVERTEBRATE FAUNAS

The following discussion will be confined to documentation of Cretaceous invertebrates that are critical to definition of stages[1] and their boundaries, biogeographic units, and regional biostratigraphic zonation. It can generally be said that the Cretaceous fauna was characterized by turrilitacean, scaphitacean, hoplitacean, desmoceratacean, acanthoceratacean, and most groups of ancyloceratacean ammonites; by great development among rudistid, inoceramid, trigoniacean, and certain ostreacean bivalves; by marked radiation among Neogastropoda, and especially tropical Nerineidae and Actaeonellidae; by planomalinid, schackoinid, rotaliporid, and globotruncanid Foraminiferida, and by many groups of Tethyan larger benthonic Foraminiferida; by tremendous diversity among scleractinian corals, especially in the middle Cretaceous where older groups of Jurassic origin occurred with and gave rise to younger Cretaceous-Cenozoic groups; by great radiation among cheilostome Bryozoa, with many groups restricted to the Cretaceous (Myagroporidae, Otoporidae, Ctenoporidae, Thoracoporidae, Taractoporidae, Calpidoporidae, Disheloporidae, and Nephroporidae); and by equally large-scale radiation among the echinoids, with the Conulidae, Discoidiidae, Galeritidae, Archiaciidae, and Clypeolampadidae restricted to the Cretaceous. An age-by-age detailed summary of Cretaceous invertebrate faunas and environmental events affecting their evolution can be obtained by surveying references previously listed. Some broad generalizations follow.

The Berriasian and Valanginian were times characterized by low-level radiations among invertebrate groups that predominantly had their origins in the Late Jurassic, in particular diverse ammonites. No major extinction events have been recorded from either age. The Late Valanginian transgressive peak marked the initial radiation of several invertebrate lineages or families among larger foraminifers, ammonites, rudist bivalves, and irregular echinoids which became increasingly more important during the later part of the Cretaceous. The first major radiation among typical Cretaceous invertebrates occurred during the Hauterivian, primarily involving warm-water groups (Tethyan foraminifers, scleractinian corals, ammonites, and irregular echinoids). This radiation was associated with climatic warming and widespread marginal epicontinental transgression. Extinctions during or at the end of the Hauterivian were of little consequence.

The Barremian was a time of rapidly fluctuating marine environments associated with two major transgressive-regressive (eustatic) cycles (Fig. 2). Evolutionary response to broadly changing natural selective forces was marked and produced the largest radiation of invertebrates in the Neocomian, especially among tropical and subtropical groups of smaller and larger foraminifers, scleractinian corals, ammonites, and rudist and glycymerid bivalves. No important extinction events occurred in or at the end of the Barremian. During Aptian time, plate tectonic activity and marine transgression exceeded that of the Neocomian, as did related evolutionary events. Aptian radiation was of greater magnitude, and involved more groups, than any previous age in the Cretaceous; it involved predominantly Tethyan, but also temperate groups of calcareous foraminifers and radiolarians, numerous scleractinian coral families, brachiopods, belemnoids, ammonites, and diverse families of bivalves. The first major Cretaceous reefs formed during the Aptian. A marked extinction event at or near the end of the age mainly involved older Tethyan groups that were ecologically replaced by better adapted counterparts arising in the Aptian; scleractinian corals, ammonites, belemnites, and ancestral rudist bivalve groups were primarily affected.

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[1] The author prefers to use the word "stage" in a biostratigraphic sense as originally defined by d'Orbigny in 1842, and as currently followed by many geologists. Nevertheless, in compliance with editorial policy, which adheres to the Code of Stratigraphic Nomenclature (American Commission on Stratigraphic Nomenclature, 1970) and the International Stratigraphic Guide (International Subcommission on Stratigraphic Classification, 1976), "stage" and "age" are used in this paper as chronostratigraphic and geochronologic units, respectively.

Albian time was characterized by the most extensive of the Early Cretaceous eustatic fluctuations and transgressions (Fig. 2), by active plate tectonism, a major climatic warming pulse, and largely restricted deep ocean circulation. Major radiation and marine diversification occurred among planktonic and shallow benthonic invertebrates, in particular planktonic foraminifers and ammonites, giving rise to complex, polytaxic, pelagic marine communities. In addition, Albian radiations involved diverse calcareous benthonic foraminifers, scleractinian corals, cheilostome bryozoans, articulate brachiopods, many neogastropod and echinoderm families, and numerous tropical bivalve groups, including rudists. Cretaceous ammonite diversity reached its peak during Albian radiation. Deep-water invertebrates, on the other hand, seem to have been severely restricted by widespread oxygen depletion. Important extinction events occurred throughout the Albian, but especially at its end. The Late Albian extinction was the most dramatic of the Early Cretaceous, and mainly affected taxa in tropical to warm-temperate seas, probably as a result of sharp decline in oceanic temperatures during the latest Albian. This extinction involved diverse ammonites, and major groups of larger foraminifers, scleractinian corals, articulate brachiopods, belemnoids, bivalves, irregular echinoids, and crinoids. The Albian thus included the first great epicontinental transgression, and the first major extinction event (associated with terminal Albian regression and temperature decline) of the Cretaceous (Fig. 2).

The Cenomanian had an exceptional history. It included the largest marine transgression of the Cretaceous (Fig. 2), which was related to active plate tectonism, rapid seafloor spreading, and major eustatic rise. It was also the greatest Cretaceous episode of invertebrate radiation, reflecting vast new ecological opportunities that became available during the great Cenomanian transgression. Surprisingly, these events were associated with a period of low global marine temperatures, which climbed only slowly during the age. Between 50 and 60 higher taxa of invertebrates, most of them tropical to warm-temperate groups, arose during the Cenomanian, including numerous genera of larger foraminifers and diverse lower level taxa of planktonic foraminifers, 6 scleractinian coral families, phylactolaemate and diverse cheilostome bryozoans, 5 ammonite families, the Belemnitellinae, numerous groups of neogastropods as well as epifaunal and especially infaunal siphonate bivalves, 3 major arthropod groups, and 5 echinoid families. The Cenomanian-Turonian boundary lies near the peak of the transgression, and coincides with an abrupt but graded extinction event associated with major temperature and salinity fluctuations near the transgressive peak. First temperate, and finally tropical taxa were involved in the extinction. Diverse planktonic and larger benthonic foraminifers, scleractinian corals, ammonites, and irregular echinoids were principal groups affected by the extinction event.

Turonian time encompassed a major regression, early phases of the second largest Cretaceous transgression, and rising global marine temperatures (Fig. 2). The great Cenomanian transgression climaxed during the earliest Turonian, and was characterized by a short-lived invasion of marginal Tethyan taxa into temperate areas, followed by their graded extinction (middle to late Early Turonian) or restriction to Tethys proper. The Middle Turonian regression was one of the most rapid on record (less than two million years), and imposed severe stress, leading to very rapid faunal turnover and widespread extinction in epicontinental (KAUFFMAN, 1970, 1972, 1977a,b), but not oceanic, environments (FISCHER & ARTHUR, 1977). Turonian radiations were moderate, and concentrated in the Early Turonian in connection with maximum transgression and the spread of warm waters over the globe. Major evolutionary diversification took place among calcareous planktonic and benthonic foraminifers, tropical scleractinian corals, cheilostome bryozoans, temperate and tropical ammonites, rudist bivalves, and irregular echinoids. Many of these same groups show strong extinctions associated with Middle Turonian regression. The end of the Turonian was marked by sharp extinction, which correlates with a major temperature and salinity increase to near normal in epicontinental seas near peak Late Turonian to Coniacian transgression. Both

Middle and Late Turonian extinctions involved primarily warm-water groups—diverse foraminifers, scleractinian corals, major groups of rudists, inoceramid bivalves, and especially tropical ammonites. In epicontinental areas, the terminal extinction marked the abrupt replacement of temperate groups with cosmopolitan and subtropical taxa.

The great Late Turonian transgression reached its peak in the Coniacian, and remained near peak development throughout that age. Maritime climates and ameliorating marine environments persisted. An Early to Middle Coniacian temperature increase is recorded by exceptionally widespread distribution of Tethyan and marginal Tethyan faunal elements, and by isotopic analyses. Major Early Coniacian radiations primarily involved warm-water groups among smaller and larger calcareous foraminifers, cheilostome bryozoans, neogastropods, cephalopods, and echinoids. Representatives of these and other tropical taxa became gradually more restricted during the Coniacian as warm water temperatures began to wane, especially during a sharp Middle Coniacian temperature drop in oceanic and epicontinental areas (DOUGLAS & SAVIN, 1973). Warm, semistable ameliorating marine climates and widespread epicontinental seas persisted into the Santonian; as a result no major extinction event marks the stage boundary, making it difficult to define (see discussion under *Biostratigraphy*). Important extinctions during the Coniacian were limited to three ammonite families and the posidoniid bivalves; genus- and species-level changes among ammonites and bivalves, or among planktonic microbiota, are currently used to define the Coniacian-Santonian boundary.

Santonian time was characterized by several small transgressive pulses superimposed on early stages of the Campanian regression (Fig. 2), by warm water temperatures and generally equable marine climates, and by continued widespread development of epicontinental seas. A broad Late Santonian cooling trend gradually increased oceanic climatic gradients, lowering planktonic diversity (FRERICHS, 1971), and lowering the similarity between foraminifers of high and low latitudes (DOUGLAS, 1972). Low to moderate levels of radiation among calcareous foraminifers, cheilostome bryozoans, scleractinian corals, rudist bivalves, and echinoderms indicate a somewhat passive evolutionary history during this climatically stable period. Other groups showed little change. Extinction within or at the end of the age was minimal, mainly involving a few Tethyan lineages of cheilostome bryozoans, scleractinian corals, and ammonites. In many areas the Santonian-Campanian boundary is thus difficult to define and is based mainly on range-zone boundaries of ammonite and inoceramid species.

The equable marine environments of the Coniacian and Santonian declined sharply during the Campanian with major marine regression (eustatic fall), upon which are superimposed two smaller transgressive peaks (Fig. 2) in the latest Early to early Late Campanian, and the middle Late Campanian. Oceanic temperatures declined strongly through the Campanian. Collectively, these factors imposed increasing environmental stress levels on evolving marine invertebrates, and diversity generally declined. Nevertheless, the late Early to early Late Campanian transgression marked a reversal in these trends, and the last major period of Cretaceous radiation among higher taxa, in particular among warm-water foraminifers, scleractinian corals, cheilostome bryozoans, and tropical and temperate bivalves. Late Campanian extinctions were surprisingly few in light of this radiation and subsequent environmental decline, and involved only some genera of larger foraminifers, and one family each of scleractinian corals, ctenostome bryozoans, ammonites, crinoids, and asteroids. The position of the Campanian-Maastrichtian boundary is thus poorly defined and a matter of considerable debate. As a result of increasing stress levels during Campanian regression, evolutionary rates among principal Campanian ammonite and bivalve groups were rapid and form the basis for a highly refined Campanian biostratigraphy (GILL & COBBAN, 1966; KAUFFMAN, 1975).

TEMPORAL AND BIOSTRATIGRAPHIC DEFINITIONS

The global correlation and interpretation of geological and biological events is strongly dependent upon widely applicable, finely divided units of geological time (usually based on biostratigraphic zones), and sufficient radiometric data to allow "absolute" dating of such events and an accurate measure of their duration (for example, KAUFFMAN, 1970). Rarely are both systems coincidently developed to a high level of refinement in the Phanerozoic, but the Cretaceous is an exception where biostratigraphy and geochronology have been refined to a high degree and extensively integrated (for example, OBRADOVICH & COBBAN, 1975; VAN HINTE, 1976; KAUFFMAN, 1978), allowing unparalleled precision in regional correlation and dating of marine strata, their biotas, and important events in their historical development. These factors have widely attracted scholars to the Cretaceous Period as a testing ground for geological and biological concepts.

DEFINITION OF THE CRETACEOUS

The Cretaceous System, or "Terrain Crétacé," was first named by the Belgian D'OMALIUS D'HALLOY (1822) wholly on the basis of lithostratigraphic characteristics as the upper one-third of the "Secondary Rocks" of ARDUINO. The Cretaceous included "the chalk formation, such as I have determined it in a preceding memoir, i.e. comprising the tuffas, sands, and marls, which occur beneath the true chalk. . . ." (D'OMALIUS D'HALLOY, 1822, p. 368, 369; translation in BERRY, 1968, p. 69). The type area is in the Paris basin of France and adjacent parts of Belgium and Holland. BERRY (1968, p. 69-73) gave a concise history of subsequent development of the concept of the Cretaceous System. Initial definition of the typical Cretaceous biota, and a crude biostratigraphic division, resulted from MANTELL'S (1822) study of "The fossils of the South Downs" in which he recognized a lower terrestrial biota of the Wealden and a younger marine biota of the overlying greensand, marl, and chalk. Although various authors, mainly French and English, described fossils from the Cretaceous System during the next two decades, the first extensive description of characteristic Cretaceous biotas and their biostratigraphic subdivision was that of the French paleontologist, ALCIDE D'ORBIGNY (1840-44; 1849-50).

D'ORBIGNY'S contribution was outstanding. In addition to his extensive systematic treatment, D'ORBIGNY was the first to clearly define major changes in the Cretaceous marine biotas through time, many of them relatively abrupt, and the fact that these changes were irregular. D'ORBIGNY recognized that large, stratigraphically distinct segments of the Cretaceous were each internally characterized by a discrete biota displaying relatively low levels of change through time. Each biota, however, was quite different from those of adjacent sequences. The boundary zones between individual biotas were clearly defined (D'ORBIGNY, 1849-50, p. 42-49, considered them to be "catastrophic"), in most cases sharp, or occupying very narrow stratigraphic intervals. These were points of major biotic turnover that have come to be recognized as indicative of large-scale evolutionary events and (or) marine environmental changes occurring within small segments of geologic time. D'ORBIGNY (1849-50) termed these biotically discrete stratigraphic segments "étages"—or stages—and gave each a name based on the area in which its unique biota was best known at the time. Thus, *from their inception, Cretaceous stages were characterized by their fossil content,* and stage boundaries were defined at the level or narrow stratigraphic interval of maximum rate of change, or abruptness of turnover of the biota from one stage to the next. Stages were thus originally defined as large-scale biostratigraphic units; this concept has been unfortunately altered where stages have been included within systems of chronostratigraphy such as that used by the American Commission on Stratigraphic Nomenclature (1970) and others. The concept of stages in the Cretaceous has been more extensively discussed by HANCOCK (1977), KENNEDY and JUIGNET (1973), RIOULT (1969), WIEDMANN (1970), and references therein, most of whom have advocated return to d'Orbigny's original concept; I wholly concur.

In defining stages, d'Orbigny became the first to recognize the varied and irregular evolutionary history of Cretaceous organisms. Subsequent research has supported the contention that major extinction events followed by important radiations exist at several points through the Cretaceous, at or near the stratigraphic levels of faunal discordance that d'Orbigny and later authors relied on to differentiate Cretaceous stages.

CRETACEOUS BOUNDARY ZONES

Historically, both the upper and lower boundaries of the Cretaceous System have been extensively debated, in particular the Jurassic-Cretaceous boundary zone and the position of the Volgian Stage and its biota in the North Temperate Realm, and (to a lesser degree) the Tithonian Stage and its biota in tropical Tethyan to warm-temperate regions. The problem has been complicated by the lack of direct marine connections linking the two biotas in many areas, difficulty in their biostratigraphic correlation, and by the absence of a large-scale boundary extinction of characteristic Jurassic taxa. Similarly, the position of the Danian "Stage" and its biota relative to the Cretaceous-Tertiary boundary zone has been greatly disputed, especially where diagnostic ammonites, belemnites, and inoceramid bivalves are rare or absent.

It is of interest that in both cases the boundary disputes stemmed primarily from study of biotas from north-temperate areas, where the evolutionary distinctions between marine faunas above and below these major boundaries appear to be less marked than across the same boundaries in the tropical Tethyan Realm. For marine invertebrates this may be directly related to comparatively higher representation of the entire tropical biota in the oceanic plankton (including the planktotrophic larvae of most benthonic organisms), where conditions apparently leading to major extinctions have had greater impact than in cooler water, temperate-realm biotas.

The Jurassic-Cretaceous boundary problem has been most extensively discussed by various authors in Casey and Rawson (1973a) and older papers referenced therein, in particular Arkell (1956), Casey (1968), Egoyan (1971), Golbert and others (1972), Saks and others (1968), and papers in Saks (1972). The controversy centered mainly around the position of strata containing the north-temperate "Subcraspeditan" ammonite fauna, placed originally in the lowermost Cretaceous or "Infravalanginian Stage" (Neaverson, 1955, and papers cited therein), and has now been largely resolved. Current placement of the Jurassic-Cretaceous boundary at the top of the Volgian Stage (containing the Subcraspeditan fauna) of the Russian platform, and equivalent strata, is supported by most workers. The base of the north temperate Cretaceous, also defined mainly on molluscan faunas, thus becomes the base of the lower Ryazanian Substage (*Runctonia runctoni* and *Hectoroceras kochi* zones; Casey, 1973).

Even so, a major problem still exists in identifying the Jurassic-Cretaceous boundary, which stems from the lack of a clear-cut evolutionary break among higher taxa in this interval, and a relatively poor fossil record in many areas. Most higher taxa of characteristic Jurassic invertebrates became extinct well before the end of the Jurassic (for example, numerous ammonite families in the Bathonian through Oxfordian stages). The Oxfordian, Kimmeridgian and Volgian-Tithonian stages instead represent a time of major radiation among many groups of invertebrates that subsequently cross the Jurassic-Cretaceous boundary without significant change to comprise the evolutionary rootstocks of characteristic Neocomian faunas. This includes many echinoids (especially families of the Irregularia), bivalves, gastropods, arthropods, and most scleractinian corals. The ammonites underwent a major radiation at the beginning of the Late Tithonian to Late Volgian subages, and 9 of 11 latest Jurassic families ranged well into the Neocomian. The earliest Neocomian (Berriasian) radiations were in no way comparable in magnitude to those of the latest Jurassic. Few important extinction events occurred in the latest Jurassic, and most of these occurred near the end of the Tithonian, especially among ammonites (for example, the important families Perisphinctidae and Aspidoceratidae); these are the primary organisms utilized to define and correlate the Jurassic-Cretaceous on a regional basis. Thus, in defining the boundary, current workers have chosen to concentrate on the few significant ammonite extinction events of the latest Jurassic rather than the older, but more dramatic interval that marks the principal radiation of typical Early Neocomian invertebrates. Principal evolutionary changes at the Jurassic-Cretaceous boundary, so defined, are marked by genus-level turnover rather than by replacement of higher taxa as elsewhere at Mesozoic period boundaries. This change is more exaggerated in the Tethys and its margins than in the North Temperate Realm.

By contrast, the top of the Maastrichtian Stage is marked by one of the most dramatic extinction events of the Phanerozoic, with final elimination of numerous orders, superfamilies, families, and subfamilies of characteristic Cretaceous invertebrates within a few million years at most. Major invertebrate groups that became extinct include the Ammonoidea (superfamilies Phylloceratacea, Turrilitaceae, Scaphitaceae, Lytocerataceae, Acanthocerataceae, Desmocerataceae, and Hoplitaceae), many Bivalvia (for example, the Arcullaeinae, Inoceramidae, Oxytomidae, Entoliidae, *Camptonectes* group, *Neithea* group, Buchiidae, Terquemiidae, Trigonioididae, Myoconchinae, Opinae, Icanotiidae, Tancrediidae, Trapeziidae, Dicerocardiidae, Corbulamellidae, Exogyrini, and the rudists Requieniidae, Monopleuridae, Caprinidae, Hippuritidae, Radiolitinae, Biradiolitinae, Sauvagesiinae, and Lapeirousiinae), the Macluritina among gastropods, the Spinctozoa among sponges, the Hemiporitidae and Thamnasteriidae among scleractinian corals, the Dactylethrata and Rhacheoporidae among bryozoans; numerous Coleoidea (Belemnitidae, Dimitobelinae, Belemnitellinae, Belemnoteuthidae), 7 families of mostly irregular echinoids (Acrosaleniidae, Conulidae, Discoidiidae, Galeritidae, Clypeolampadidae, Holectypidae, and Nucleolitidae), stelleroids of the Uractinina, 17 genera of tropical larger Foraminifera including most orbitoids and pseudorbitoids, several major groups of calcareous foraminifers (especially the Schackoinidae, Rotaliporidae, and Globotruncanidae), and the radiolarian family Amphipyndacidae. Many of these groups became extinct "abruptly" at the peak of their radiation, or while they were still important components of the marine biota.

A major radiation, especially among warm-water bivalve and gastropod molluscs, irregular echinoids, crustacea and other arthropods, cheilostome bryozoans, and both small and large calcareous Foraminiferida followed during the Tertiary, so that clearly distinct biotas bound the major extinction event that marks the top of the Cretaceous System. Why then has there been a controversy over the position of the Danian Stage in the north temperate areas of Euramerica?

The Danian controversy evolved in areas where 1) Cretaceous-style marine deposition of chalk and marl, or glauconitic sand, continued across the boundary with little change (as in Denmark, Maryland, and New Jersey), in many cases with little evidence of a major disconformity, into Paleocene time, 2) where Cretaceous microfossils were extensively reworked into similar Paleocene sediments, 3) where strata bearing Cretaceous organisms were erroneously assigned to the Danian on other grounds, and 4) in areas where uppermost Cretaceous strata did not contain abundant ammonites, inoceramid bivalves, belemnites, or other diagnostic fossils but rather were composed mainly of groups of mollusks, echinoids, and bryozoans that showed little evolutionary differentiation and only minor genus- and species-level extinction across the Cretaceous-Tertiary boundary (for example, Denmark, Greenland, and middle to northern Atlantic coasts of the United States and western Europe). These latter groups, mainly mollusks characteristic of the North Temperate Realm, were apparently protected from environmental factors contributing to the massive Late Cretaceous extinction event by nature of their broad ecological tolerance, habitat characteristics, or the nature of their ontogenetic development (especially their larval history). It is now well documented that the dramatic Cretaceous-Danian extinction events mainly involved tropical and marginal tropical groups. The recognition that many invertebrate groups

Stage	Substage	Age Ma	TETHYAN MACROFOSSIL STANDARD (1)		NORTH TEMPERATE MACROFOSSIL STANDARD (1)	PLANKTONIC FORAM.-CALPIONELLID STANDARD (1)	
		**					
HAUTERIVIAN	U	121	Pseudothurmannia angulicostata		Simbirskites discofalcatus	"Hedbergella" hoterivica	
					Simbirskites gottschei		
			Subsaynella subsayni		Simbirskites staffi		
	M	123	Crioceras duvali		Simbirskites inversum	UNZONED	
					Endomoceras regale		
	L	124	Acanthodiscus radiatus		Endomoceras noricum		
			Lyticoceras s.l.sp.		Endomoceras amblygonium		
VALANGINIAN	U	126	Saynoceras verrucosum	Saynoceras callidiscus	Arnoldia - Astieria	Calpionellites	
				Himantoceras trinodosum	Dichotomites spp.		
	M	127		Saynoceras verrucosum	Prodichotomites polytomus		
			Kilianella roubaudi	Kilianella compylotoxus	Polyptychites middendorfi		
		129			P. bancoi, P. euomphalus		
	L			Kilianella roubaudi	Platylenticeras involutum		
				Kilianella pertransiens	Platylenticeras heteropleurum	Calpionellopsis	
					Platylenticeras robustum		
BERRIASIAN	RYZANIAN U	131	Berriasella boissieri		"WEALDEN" nonmarine		
	RYZANIAN M	132				Calpionella	Calpionella elliptica
			Berriasella grandis				
	L	134					Calpionella alpina
		135					

FIG. 3A.

FIG. 3A–F. Lower Cretaceous biostratigraphic zonation and principal zonal indices in selected areas where zonation is most refined. Principal references for data coded to numbers in parentheses are: 1) Van Hinte, 1976, Tethyan and North Temperate macrofossil and pelagic microfossil zones; 2) Jeletzky, 1970, Canadian and Arctic parts of the Western Interior seaway; 3) Kauffman, Cobban, & Eicher, 1977, Albian of the interior United States; 4) Thomel, 1964, and 5) Thieuloy & Thomel, 1964, Neocomian, southern France; 6) Young, 1967, Texas Gulf Coast; 7) Scott, 1970, Albian, southern Western Interior United States; 8) Jeletzky, 1964a, 1970, western and Arctic Canada; 9) Imlay, 1960, 10) Jones, 1967, 11) Jones & Detterman, 1966, and 12) Jones, Murphy, & Packard, 1965, northern and western Alaska, west coast of United States; 13) Matsumoto, 1963, and 14) Nakano, 1960, Lower Cretaceous, Japan; 15) Casey, 1973, Berriasian, England; 16) Owen, 1973, Middle and Upper Albian, England; 17) Casey, 1961, Aptian and Lower Albian, England; 18) Kemper, 1973, Hauterivian-Valanginian, north Germany; 19) Besairie & Collignon, 1972, Madagascar; 20) Pergament, 1969, Russian platform, Siberia, and northeast Asia; and 21) Jeletzky, 1973, Lower Neocomian, Siberia. For explanation of asterisks, see Figure 2 caption (Kauffman, n).

<table>
<tr><th>NANNO-FOSSIL STANDARD (1)</th><th colspan="2">ARCTIC AND WESTERN INTERIOR NORTH AMERICA (2)</th><th>SOUTHERN FRANCE (4, 5)</th><th colspan="5">NORTH PACIFIC PROVINCE, WESTERN NORTH AMERICA (2, 8, 9, 10, 11, 12) JAPAN (13,14)</th><th>Age Ma
**</th><th colspan="2">Substage</th><th>Stage</th></tr>
<tr><td rowspan="4">Lithraphidites bollii (lower part)</td><td rowspan="5">Acroteuthis aff. A. conoides</td><td rowspan="2">Craspedodiscus cf. C. discofalcatus</td><td>Pseudothurmannia angulicostata, Balearites balearis, Paraspinoceras pulcherrimum</td><td colspan="2" rowspan="7">Crioceras ishiharai - Shasticrioceras nipponicum (part)</td><td rowspan="7">Inoceramus colonicus</td><td rowspan="2">I. ovatoides</td><td>Shasticrioceras, Crioceras discofalcatus</td><td>121</td><td colspan="2" rowspan="2">U</td><td rowspan="7">HAUTERIVIAN</td></tr>
<tr><td>Subsaynella subsayni, Crioceratites majoricensis</td><td rowspan="4">Simbirskites cf. S. broadi,
Holisites lucasi,
Speetoniceras agnessense</td><td></td></tr>
<tr><td>Simberskites cf. S. kleini, S. (S.) ex. gr. progredicus</td><td rowspan="3">Crioceratites duvali,
Crioceratites nolani</td><td rowspan="5"></td><td>123</td><td colspan="2" rowspan="3">M</td></tr>
<tr><td rowspan="2">Acroteuthis cf. A. conoides</td><td></td></tr>
<tr><td rowspan="6">Calcicalathina oblongata</td><td></td></tr>
<tr><td colspan="2" rowspan="2">UNKNOWN</td><td>Acanthodiscus radiatus</td><td rowspan="2">Holmosomites oregonensis</td><td>124</td><td colspan="2" rowspan="2">L</td></tr>
<tr><td>Lyticoceras sp.</td><td></td></tr>
<tr><td rowspan="4">Buchia inflata, Buchia n. sp. aff. B. inflata, Buchia bulloides</td><td rowspan="2">Homolsomites cf. and aff. H. quatsinoensis</td><td>Saynoceras callidiscus</td><td colspan="2" rowspan="6">Thurmanniceras isokusense</td><td colspan="3" rowspan="2">Buchia crassicollis</td><td>126</td><td colspan="2" rowspan="2">U</td><td rowspan="6">VALANGINIAN</td></tr>
<tr><td>Himantoceras trinodosum</td><td></td></tr>
<tr><td>H. cf. H. giganteus, Euryptychites stubbendorfi</td><td>Saynoceras verrucosum</td><td colspan="3">Buchia inflata,
Buchia inflata crassa</td><td>127</td><td colspan="2" rowspan="2">M</td></tr>
<tr><td rowspan="3">Cretarhabdus crenulatus</td><td>Thorsteinssonoceras ellesmerensis, Polyptychites cf. P. keyserlingi</td><td>Kilianella campylotoxus</td><td colspan="3">Buchia pacifica</td><td></td></tr>
<tr><td colspan="2" rowspan="2">Tollia cf. T. tolli,
Temnoptychites novosemelicus,
Buchia keyserlingi, s.s.</td><td>Kilianella roubaudi</td><td colspan="3" rowspan="2">Buchia tolmatschowi</td><td>129</td><td colspan="2" rowspan="2">L</td></tr>
<tr><td>Kilianella lucensis,
Kilianella pertransiens</td><td></td></tr>
<tr><td rowspan="4">Nannoconus colomi</td><td rowspan="2">S. cf. S. payeri</td><td>Buchia volgensis</td><td rowspan="3">Berriasella (Pseudargentinoceras) boissieri</td><td rowspan="4">Buchia okensis, Buchia subokensis</td><td rowspan="4">Berriasella akiyamae</td><td colspan="3" rowspan="2">Buchia uncitoides, s.l.</td><td>131</td><td rowspan="2">U</td><td rowspan="3">RYZANIAN</td><td rowspan="4">BERRIASIAN</td></tr>
<tr><td>Buchia uncitoides</td><td></td></tr>
<tr><td rowspan="2">Subcraspedites aff. S. suprasubdites</td><td>Buchia okensis</td><td colspan="3" rowspan="2">Buchia okensis,
Berriasella sp. aff. B. gallica</td><td>132</td><td>M</td></tr>
<tr><td>?
UNKNOWN</td><td>Berriasella grandis</td><td>134</td><td colspan="2">L</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>135</td><td></td><td></td><td></td></tr>
</table>

Fig. 3B. *(Explanation on facing page.)*

cross the Cretaceous-Tertiary boundary with little change, and the discovery of sufficient ammonites, belemnites, inoceramids, and characteristic Cretaceous microfossils in the areas under question to define the boundary, have basically ended the Danian controversy. Today, Danian strata are almost universally placed in the basal Paleocene. Hancock (1967), and authors cited therein, have discussed in detail the age of the Danian and defended its placement in the Paleocene.

BIOSTRATIGRAPHY

Cretaceous biostratigraphy (Figs. 3, 4) encompasses some of the most refined and regionally applicable zonations developed anywhere in the Phanerozoic, and consti-

Stage	Substage	Age Ma	ENGLAND (15) NORTH GERMANY (18)		MADAGASCAR (19)		RUSSIAN PLATFORM (20) SIBERIA (20, 21) NORTHEAST ASIA (20)	
		**						
HAUTERIVIAN	U	121	Simbirskites (Craspedodiscus) discofalcatus, "Crioceras" strombecki	NORTHWEST GERMANY	Saynella besairiei		Simberskites decheni, S. speetonensis, Craspedodiscus discofalcatus	Inoceramus aucella
			Simbirskites (Craspedodiscus) gottschei					
			Simbirskites (Milanowskia) staffi S.(M.) ihmensis S.(M.) staffi					
	M	123	Aegocrioceras capricornu, Aegocrioceras spp.		Duvalia dilatata	UNZONED	Speetoniceras versicolor	
	L	124	Endemoceras regale, Acanthodiscus bivirgatus			Phylloceras spathi Eutrephoceras uitenhagense	Homolsomites bojarkensis	regionally absent
			Endemoceras noricum					
			Endemoceras amblygonium E. longinodum					
VALANGINIAN	U	126	Astieria sp.		Holcostephanus sp., Neocomites neocomiensis,	Hibolithes pistilliformis		Homolsomites petschorensis
			Dicostella pitrei					
			Neocraspedites complanatus, N. undulatus		Rogersites schenki, Rogersites madagascarensis, Hoplites ex. gr. teschenensis		Dichotomites spp., Polyptychites polyptychus	
			Dichotomites bidichotomus, D. tardescissus					
			Dichotomites biscissoides					
	M	127	Prodichotomites polytomus Valanginites nucleus Neocraspedites flexicosta				Polyptychites michalskii, Polyptychites keyserlingi, Astieriptychites asteriptychus	
			Polyptychites middendorfi, P. clarkei		Belemnopsis africana, Belemnopsis madagascariensis, Duvalia polygonalis, Duvalia spp.			
	L	129	Polyptychites brancoi, P. euomphalus Costamen. pumilio				Temnoptychites syzranicus, T. hoplitoides	
			Platylenticeras involutum		Hibolithes joleaudi, Neocomites teschenensis			
			Platylenticeras heteropleurum				Tollia stenomphala, Tollia tolli, Pseudogarnieria undulatoplicatilis	
			Platylenticeras robustum / Paratollia					
BERRIASIAN	RYZANIAN U	131	Peregrinoceras albidum	EAST ENGLAND	Berriasella spp.,		Surites (Surites) spasskensis	Surites (Bojarkia) mesezhnikowi
			Surites (Bojarkia) stenomphalus					
			Surites (Lynnia) icenii					Surites analogus
	M	132	Hectoroceras kochi		Spiticeras spp.		Riasonites rjasanensis	Hectoroceras kochi
			Runctonia runctoni					Chetaites sibiricus
	L	134	?					
		135						

FIG. 3C. *(Explanation on page A442.)*

tutes an important model of biostratigraphic methodology. Several factors contribute to this situation. First, the Cretaceous was a period of evolutionary overlap among some of the most useful biological groups ever applied to zonation and correlation. The first major series of radiations among the planktonic microbiota, especially foraminifers and coccolithophorids, occurred during the Cretaceous at a time when ammonites and ubiquitous bivalves of the families Inoceramidae, Ostreidae, and Buchiidae were still important components of the marine biota, belemnites were in their final radiation, and echinoids (especially irregular groups) were undergoing one of their major periods of diversification. These groups constitute the principal invertebrate components of Cretaceous biostratigraphy. Other taxonomic groups are useful in certain facies and regions, and may be the bases for local systems of zonation, but they do not compare with these primary groups in regional correlation potential or in the historical development of Cretaceous biostratigraphic systems.

Second, Cretaceous biostratigraphy historically arose by the independent development of systems based on such groups as planktonic foraminifers, ammonites, belemnites, inoceramid bivalves, and echinoids. In more recent times, however, there has been a conscious effort to develop more integrated biostratigraphic systems (for example, KAUFFMAN, 1970). This has been undertaken first through the collation of data from these primary groups into simple assemblage- and concurrent range-zones (VAN HINTE, 1976; SMITH, 1975; KAUFFMAN, HATTAN, & POWELL, 1977, and others). Subsequently, using these as a plotting base for testing the biostratigraphic utility of diverse invertebrates, modern Cretaceous biostratigraphic systems are becoming increasingly concerned with the formation of complex multitaxic assemblage-zones incorporating all elements of the biota with biostratigraphic potential as defined by their biological, biogeographic, evolutionary, and ecological characteristics (KAUFFMAN, 1970). Complex multitaxic assemblage zonation and biostratigraphic schemes being developed through graphic correlation methods (MILLER, 1977, and references therein) promise to yield the most refined levels of biostratigraphic zonation, with the broadest environmental and biogeographic application. Zonations as refined as 0.1 my/zone with intercontinental correlation potential have already resulted in the Cretaceous utilizing "composite assemblage zonation" techniques (KAUFFMAN, 1970). Composite assemblage-zones may incorporate organisms from all facies throughout the study area (for example, a Cretaceous epicontinental seaway), including marginal marine and even nonmarine facies, and even from distinct basins, allowing broad regional correlations to be made.

Third, the Cretaceous displays an extensive, well-preserved biological and stratigraphic record, widely dispersed in epicontinental areas of the world (Fig. 1) and nearly continuous across vast areas of intervening ocean basins as evidenced in DSDP core materials. Bed-by-bed collecting of populations representing diverse taxa is possible in many epicontinental areas, leading to evolutionary studies using population analysis, to taxonomic refinement, and thus to more refined biostratigraphic division of the Cretaceous sequence (for example, KAUFFMAN, 1970, text-fig. 4, and discussion).

Fourth, radiometric data for the Cretaceous exceed those for all but late Cenozoic parts of the geological column because of the abundance of volcanic ash, bentonite beds, and glauconite in global Cretaceous marine sections. These data are spread throughout most of the Cretaceous sequence, being more abundant for Albian and younger rocks. To a large extent, but especially in the Western Interior of the United States and Canada, these dates have been closely integrated with the biostratigraphic system (GILL & COBBAN, 1966; OBRADOVICH & COBBAN, 1975; VAN HINTE, 1976; KAUFFMAN, 1978). This allows "absolute" dating of the time and duration of biostratigraphic zones, and provides data for the measurement of evolutionary rates in various lineages.

Fifth, historically, the Cretaceous period has been intensely studied in regard to its fossil content and biostratigraphic zonation. Early biostratigraphic work was especially focused on ammonites and echinoids, and biostratigraphic concepts and methods have had a relatively long period of testing. As a result, Cretaceous systems of zonation and correlation have evolved rapidly to levels beyond those for many other periods of geological time.

Sixth, many Cretaceous organisms showed exceptionally rapid biogeographic dispersal (and thus regional biostratigraphic utility). Three environmental factors contributed to this: a) long periods of climatic amelioration with warm, maritime climates spread over most of the globe, low temperature gradients, and few barriers to dispersal of temperate to tropical invertebrates, which dominate Cretaceous marine biostratigraphic systems; b) broad and continuous areas of shallow marine shelf environments within single climatic zones, especially during each of the Cretaceous epicontinental transgressions (Fig. 2), reducing barriers to rapid, widespread dispersal of shelf organisms; and c) short enough distances across the opening Atlantic as not to exceed, for much of the Cretaceous, the swimming

Stage	Substage	Age Ma		TETHYAN MACROFOSSIL STANDARD (1)		NORTH TEMPERATE MACROFOSSIL STANDARD (1)	PLANKTONIC FORAM.-CALPIONELLID STANDARD (1)	
		**	*					
ALBIAN	U	100	93.5 94	Stoliczkaia dispar		Stoliczkaia dispar	Rotalipora appenninica Rotalipora ticinensis	
			96 97	Mortoniceras inflatum		Mortoniceras inflatum	Ticinella (Biticinella) breggiensis	
			98	Diploceras cristatum		Diploceras cristatum		
	M	104	98.8	Hoplites lautus, Hoplites nitidus		Hoplites lautus	Ticinella praeticinensis	
						Hoplites loricatus		
				Hoplites dentatus		Hoplites dentatus	Ticinella bejaouaensis, Ticinella primula, Globigerinelloides gyroidinaeformis	
	L	106		Douvilleiceras mammilatum		Douvilleiceras mammilatum	Ticinella bejaouaensis, Globigerinelloides gyroidinaeformis	
				Leymeriella tardefurcata		Leymeriella regularis, Leymeriella tardefurcata, Leymeriella schrammeni		
APTIAN	U	108		Diodochoceras nodosocostatum		Hypacanthoplites jacobi	Globigerinelloides ferreolensis, Ticinella bejaouaensis	
				Cheloniceras subnodocostatum		Parahoplites melchioris, Parahoplites nutfieldensis	Globigerinelloides ferreolensis, Hedbergella trocoidea	
	M	110				Cheloniceras martinoides	Globigerinelloides algerianus	
				Aconeceras nisus		Tropaeum bowerbanki	Schackoina cabri	
	L	112		Deshayesites deshayesi, (Puzosia matheroni)		Deshayesites deshayesi	Globigerinelloides blowi	
						Deshayesites forbesi		
						Praedeshayesites fissicostatus	Hedbergella sigali	
BARREMIAN	U	115		Silestes seranonis	Pulchella provincialis	Parancyloceras bidentatum		
						Simancyloceras stolleyi		
						Ancyloceras innexum		
	M	117		"Nicklesia" pulchella		Paracrioceras denckmanni		Hedbergella sp. aff. H. simplex
					Pulchella caicedi	Paracrioceras elegans		
	L	119			Pulchella didayi	Hoplocrioceras fissicostatum		
		121			Pulchella pulchella	Hoplocrioceras rarocinctum		

Fig. 3D. *(Explanation on page A442.)*

ranges of many mobile invertebrates such as ammonites, nor the drift potential of planktonic organisms and long-lived planktotrophic larvae of many warm-water benthonic taxa (Kauffman, 1975). Thus both benthonic and planktonic taxa dispersed readily to both sides of the Atlantic on Cretaceous ocean currents, and from there throughout the epicontinental seas of the Eurasian-African and the North American-South American continental systems. Oceanic separations of Africa and Eurasia, North and South America, and elements of Gondwanaland were even less than that

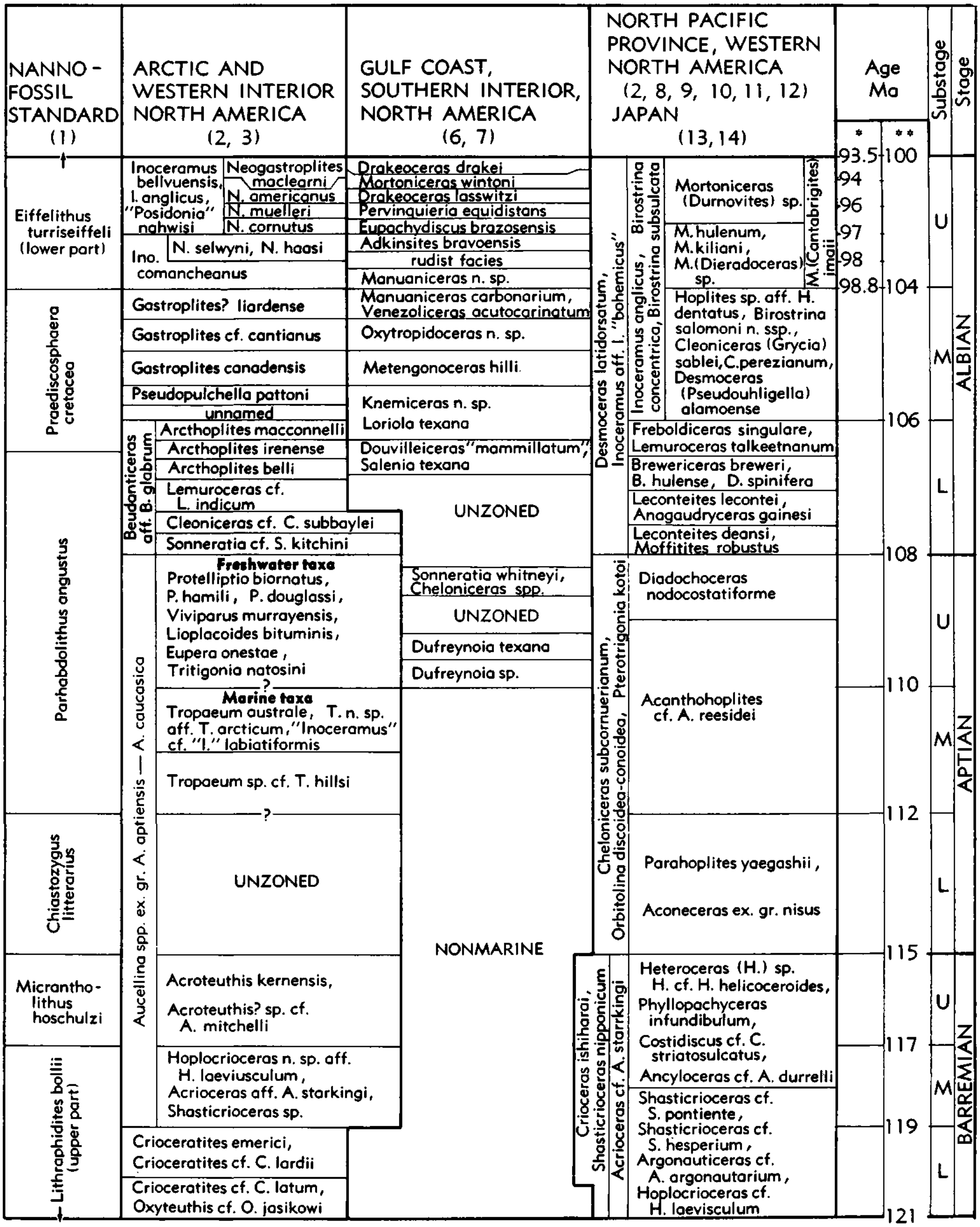
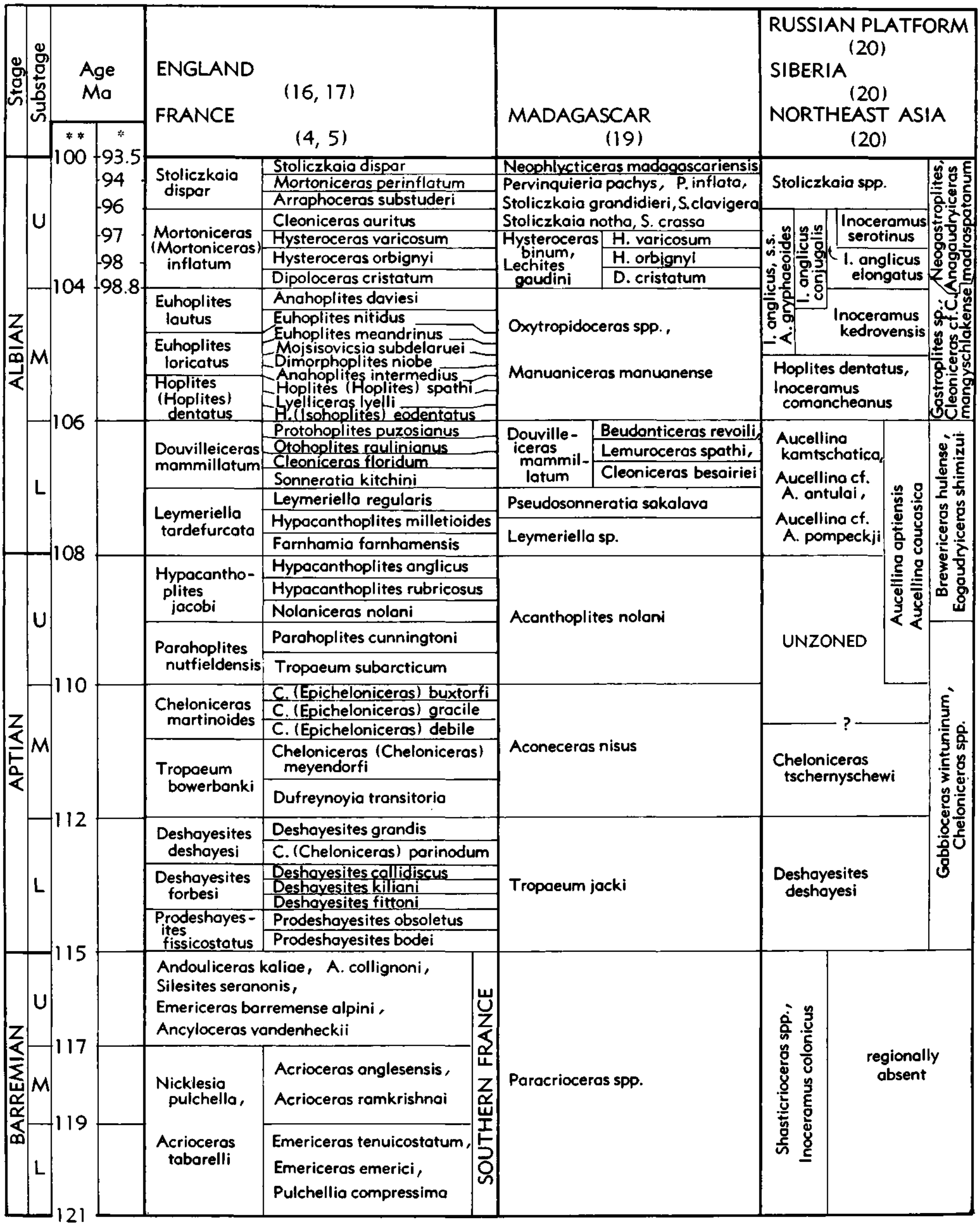


FIG. 3E. *(Explanation on page A442.)*

across the Atlantic. Therefore, precise biostratigraphic correlation over broad Cretaceous marine areas is to be expected.

Seventh, Cretaceous invertebrate taxa are related to living forms closely enough that the biostratigraphic utility of many fossil groups can be predicted from knowledge of their modern biogeographic, ecologic, and genetic characteristics. This leads to increased efficiency in the construction of complex biostratigraphic systems (KAUFFMAN, 1970, 1977a).

Eighth, evolutionary rates among Cretaceous invertebrates, especially ammonoid



Stage	Substage	Age Ma **	Age Ma *	ENGLAND (16, 17) FRANCE (4, 5)		MADAGASCAR (19)		RUSSIAN PLATFORM (20) SIBERIA (20) NORTHEAST ASIA (20)		
ALBIAN	U	100	93.5	Stoliczkaia dispar	Stoliczkaia dispar	Neophlycticeras madagascariensis		Stoliczkaia spp.		Gastroplites sp.; Neogastroplites, Cleoniceras cf. C. Anagaudryiceras mangyschlakense madraspatanum
			94		Mortoniceras perinflatum	Pervinquieria pachys, P. inflata,				
			96		Arraphoceras substuderi	Stoliczkaia grandidieri, S. clavigera				
				Mortoniceras (Mortoniceras) inflatum	Cleoniceras auritus	Stoliczkaia notha, S. crassa		I. anglicus, s.s. A. gryphaeoides I. anglicus conjugalis	Inoceramus serotinus	
			97		Hysteroceras varicosum	Hysteroceras binum, Lechites gaudini	H. varicosum			
			98		Hysteroceras orbignyi		H. orbignyi		I. anglicus elongatus	
		104	98.8		Dipoloceras cristatum		D. cristatum			
	M			Euhoplites lautus	Anahoplites daviesi	Oxytropidoceras spp., Manuaniceras manuanense			Inoceramus kedrovensis	
					Euhoplites nitidus					
				Euhoplites loricatus	Euhoplites meandrinus					
					Mojsisovicsia subdelaruei					
					Dimorphoplites niobe					
				Hoplites (Hoplites) dentatus	Anahoplites intermedius			Hoplites dentatus, Inoceramus comancheanus		
					Hoplites (Hoplites) spathi					
					Lyelliceras lyelli					
					H. (Isohoplites) eodentatus					
	L	106		Douvilleiceras mammillatum	Protohoplites puzosianus	Douvilleiceras mammillatum	Beudanticeras revoili,	Aucellina kamtschatica, Aucellina cf. A. antulai, Aucellina cf. A. pompeckji	Aucellina aptiensis Aucellina caucasica	Brewericeras hulense, Eogaudryiceras shimizui
					Otohoplites raulinianus		Lemuroceras spathi,			
					Cleoniceras floridum		Cleoniceras besairiei			
					Sonneratia kitchini					
				Leymeriella tardefurcata	Leymeriella regularis	Pseudosonneratia sakalava				
					Hypacanthoplites milletioides	Leymeriella sp.				
					Farnhamia farnhamensis					
APTIAN	U	108		Hypacanthoplites jacobi	Hypacanthoplites anglicus	Acanthoplites nolani		UNZONED		
					Hypacanthoplites rubricosus					
					Nolaniceras nolani					
				Parahoplites nutfieldensis	Parahoplites cunningtoni					Gabbioceras wintuninum, Cheloniceras spp.
					Tropaeum subarcticum					
	M	110		Cheloniceras martinoides	C. (Epicheloniceras) buxtorfi	Aconeceras nisus				
					C. (Epicheloniceras) gracile			?		
					C. (Epicheloniceras) debile			Cheloniceras tschernyschewi		
				Tropaeum bowerbanki	Cheloniceras (Cheloniceras) meyendorfi					
					Dufreynoyia transitoria					
	L	112		Deshayesites deshayesi	Deshayesites grandis	Tropaeum jacki		Deshayesites deshayesi		
					C. (Cheloniceras) parinodum					
				Deshayesites forbesi	Deshayesites callidiscus					
					Deshayesites kiliani					
					Deshayesites fittoni					
				Prodeshayesites fissicostatus	Prodeshayesites obsoletus					
					Prodeshayesites bodei					
BARREMIAN	U	115		SOUTHERN FRANCE: Andouliceras kaliae, A. collignoni, Silesites seranonis, Emericeras barremense alpini, Ancyloceras vandenheckii		Paracrioceras spp.		Shasticrioceras spp., Inoceramus colonicus	regionally absent	
	M	117		Nicklesia pulchella,	Acrioceras anglesensis, Acrioceras ramkrishnai					
	L	119		Acrioceras tabarelli	Emericeras tenuicostatum, Emericeras emerici, Pulchellia compressima					
		121								

FIG. 3F. *(Explanation on page A442.)*

and bivalve mollusks (KAUFFMAN, 1970, 1972, 1977a), are among the fastest yet recorded for marine Metazoa, attaining levels as high as one new species per .08 my within single lineages, with species durations as low as 0.12 my. This leads to zonal refinement and high resolution in correlation. These rates, measured radiometrically, were attained mainly during periods when the ecosystem was stressed either by rapid temperature and salinity changes, or by widespread regression of epicontinental seas. For many groups such as ammonites and inoceramid bivalves, rates of evolution were high even during times of climatic amelioration (transgressions) with radiation into newly developing habitats. The tremendous fluctuations in environmental and biological stress levels in the marine realm that are inherent in the environmental cycles of the Cretaceous, thus enhanced evolutionary turnover among many biostratigraphically important groups of organisms.

Despite present efforts to construct refined composite assemblage zonations for the Cretaceous throughout the world, most zonal systems in operation at this time are either based on single groups or on simple composite range-zone systems. Thus, open oceanic Cretaceous biostratigraphic systems are primarily based on planktonic foraminifers, coccolithophorids, and in cooler waters on radiolarians. Temperate-zone epicontinental systems rely heavily on ammonites, inoceramid and buchiid bivalves, belemnites, echinoids and oysters. Tethyan and marginal Tethyan systems also rely heavily on ammonites (generally distinct groups from those found in temperate zones), planktonic foraminifers, coccoliths, echinoids, and locally belemnites, rudistid, inoceramid, pectinid, trigoniid, and ostreid bivalves, and nerineid and actaeonellid gastropods.

It is commonly difficult to relate Tethyan and temperate biostratigraphic schemes in detail because they shared few organisms during much of the Cretaceous. Between the Caribbean Tethys and the North American temperate seas, for example, there was periodically less than 10 percent species similarity; however, three factors make correlation of these systems possible. First, among taxa shared between Tethyan and temperate ecosystems, especially near their juncture, are some of the most important invertebrates used in regional correlation: inoceramid and ostreid bivalves, certain echinoids, elements of the planktonic microbiota, and rarely ammonites. Both Tethyan and temperate-zone faunas show abrupt decrease in numbers and diversity where they infringe on adjacent realms. Second, basins that lie near or on the Tethyan-temperate boundary zone, for example, the Vascogotic trough of Spain (Wiedmann & Kauffman, 1977), commonly have laterally and vertically mixed cooler temperate and warmer Tethyan aquatic biotas. In these situations, especially where there is vertical stratification, the biotas are intricately mixed at many stratigraphic levels and interregional correlations can be precisely made. Third, eustatic pulses of sea level, which produced alternating transgressive and regressive events at least 10 times during the Cretaceous (Fig. 2; Kauffman, 1973a,b), also resulted in north-south migration of the temperate-Tethyan marine boundary (Coates, Kauffman, & Sohl, 1977), so that in marginal areas Tethyan and temperate biotas may retain their uniqueness but be extensively interbedded with each other, changing at points of climatic boundary migrations. These areas of interfingering of Tethyan and temperate faunas are critical to global correlation of the Cretaceous. Figures 3 and 4 show principal biostratigraphic indices for the world Cretaceous as they are currently known.

LOWER CRETACEOUS BIOSTRATIGRAPHY

In temperate and Tethyan realms, ammonites constitute the principal basis for Lower Cretaceous biostratigraphy (Fig. 3), and they are more preeminent during Early than Late Cretaceous time, when other invertebrate groups such as planktonic foraminifers, inoceramid bivalves, and belemnites had evolved to levels that allowed them to share equally in biostratigraphic zonation and regional correlation. Belemnites, which are a mainstay of temperate to cool-temperate Upper Cretaceous biostratigraphy, are of lesser importance for regional correlation of the Lower Cretaceous. They were just beginning a second major radiation from local centers of endemism (Casey & Rawson, 1973b, p. 420, 421), and were subjected to shifting biogeographic patterns (Stevens, 1973). They evolved very rapidly during the Early Cretaceous, however, and certain groups such as *Neohibolites* (Spaeth, 1971) and *Aulacoteuthis* (Rawson, 1972) allow local zonation comparable to that of the ammonites.

Bivalves have a secondary role in Lower Cretaceous biostratigraphy, except for certain groups. The Buchiidae are of primary importance in regional and intercontinental

Stage	Substage	Age Ma *	Age Ma **	TETHYAN MACRO-FOSSIL STANDARD (1)	NORTH TEMPERATE MACROFOSSIL STANDARD (1)	PLANK-TONIC FORAM. STANDARD (1)	NANNO-FOSSIL STAND-ARD (1)	CALIFORNIA (2, 3)
CONIACIAN	U	85.5	82	Parabevahites emscheri, Protexanites, Paratexanites, Texanites pseudotexanus	Magadiceramus subquadratus	Globotruncana sigali - Globotruncana concavata	Marthasterites furcatus (lower part)	Baculites schenki Texanites kawasakii, Baculites boulei, s.l. Peroniceras tehamensi, Sphenoceramus yokoyamai Baculites yokoyamai Cordiceramus cordiformis
	M	86	83.5	Barroisiceras haberfellneri	Volviceramus involutus	Globotruncana renzi - Globotruncana sigali	Micula-decussata - Tetralithus pyramidus	Prionocycloceras crenulatum Inoceramus uwajimensis
	L	86.3	84.5		Volviceramus koeneni ? ***			Barroisiceras sp., Mytiloides striatoconcentricus
*** ? TURONIAN	U	87	86	Romaniceras deverai	"Inoceramus" deformis ***	"Globotruncana" helvetica	Corollithion exiguum	Sciponoceras aff. S. bohemicum Inoceramus teshioensis, Mytiloides incertus, M. meekianus Subprionocyclus normalis Subprionocyclus neptunei
*** ?	M	87.7	88	Romaniceras bizeti, Romaniceras ornatissinum	Inoceramus "vancouverensis" Inoceramus lamarcki			Sciponoceras kossmati Inoceramus hobetsensis Collignoniceras woollgari, Romaniceras deverioide
	L	88.7	90	Mammites nodosoides, Mytiloides labiatus	Mammites nodosoides, Mytiloides labiatus	Hedbergella lehmanni		Plesivascoceras californicum, Kanabiceras septemseriatum Mytiloides opalensis, Mytiloides duplicostatus
CENOMANIAN	U	91	92	Calycoceras naviculare	Actinocamax plenus Inoceramus pictus Calycoceras cf. (C.) naviculare	Rotalipora cushmani	Lithraphidites alatus	UNKNOWN Sciponoceras baculoides
	M	92	95	Acanthoceras rhotomagense	Acanthoceras rhotomagense	Rotalipora gardolfii R. reicheli		Inoceramus crippsi, s.s. Calycoceras boulei, Calycoceras stoliczkai Calycoceras orientale, Calycoceras newboldi
	L	92.5	97.5	Mantelliceras mantelli	Schloenbachia varians Neohibolites ultimus	Rotalipora gandolfii - Rotalipora greenhornensis	Eiffelithus turriseiffeli (upper part)	Mantelliceras sp. Graysonites wooldridgei
		93.5	100					

Fig. 4A.

Fig. 4A–F. Upper Cretaceous biostratigraphic zonation and principal zonal indices in selected areas where zonation is most refined. Principal references for data coded to numbers in parentheses are: 1) Van Hinte, 1976, Tethyan and North Temperate macrofossil and pelagic microfossil zones; 2) Kauffman, 1977e, inoceramid bivalve zones, Japan; 2) Kauffman, 1977e, Inoceramidae, California; 3) Matsumoto, 1960, Upper Cretaceous ammonites, California; 4) Cobban, 1951, Scaphitidae, Western Interior, North America; 5) Cobban, 1953, Late Cenomanian ammonites, Montana; 6) Cobban, 1958, Upper Cretaceous zonation, Powder River basin; 7) Cobban, 1964, *Haresiceras*; 8) Cobban, 1969, *Scaphites hippocrepis–S. leei* lineage; 9) Cobban & Scott, 1972, Turonian ammonites, central Colorado; 10) Cobban & Scott, 1964, multinodose

WESTERN INTERIOR OF NORTH AMERICA (4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15)		WESTERN GULF COAST, U. S. A. (16, 17, 18, 19, 20, 21)		Age Ma		Substage	Stage
				**	*		
Scaphites ventricosus, Peroniceras sp., Baculites asper	Magadiceramus subquadratus, "Inoceramus" n. sp. aff. "Inoceramus" stantoni Volviceramus involutus	Prionocycloceras gabrielense, Protexanites planatus, Paratexanites sellardsi, Magadiceramus subquadratus		82	85.5	U	CONIACIAN
Forresteria forresteri, Scaphites impendicostatus, Baculites mariasensis	Scaphites preventricosus Cremnoceramus wandereri, C, inconstans (late form) Inoceramus schloenbachi Inoceramus browni	Peroniceras westphalicum, P. moureti, Prionocycloceras adkinsi, Volviceramus involutus, Cremnoceramus inconstans, etc.		83.5	86	M	
Forresteria hobsoni, Scaphites mariasensis, Scaphites frontierensis	Inoceramus deformis n. subsp. (late) Inoceramus deformis deformis I. erectus n. subsp. (late form) Inoceramus erectus erectus Inoceramus rotundatus Mytiloides fiegei, M. lusatiae	Peroniceras haasi, Coilopoceras austinense	Inoceramus deformis Inoceramus erectus Inoceramus rotundatus Mytiloides fiegei	84.5	86.3	L	
Prionocyclus quadratus, Prionocyclus reesidei, Scaphites corvensis		UNKNOWN		86	87	U	*** ? TURONIAN
Scaphites nigricollensis, I. perplexus (late form) Scaphites whitfieldi, I. perplexus s.s.	Prionocyclus wyomingensis elegans	Scaphites whitfieldi, Inoceramus perplexus					
Scaphites ferronensis Scaphites warreni	Prionocyclus wyomingensis, s.s., Inoceramus dimidius n. subsp., Lopha lugubris n. subsp. A	Prionocyclus wyomingensis	Lopha lugubris, Inoceramus dimidius				
Coilopoceras colleti, Inoceramus dimidius s.s., Lopha lugubris		UNZONED					
Coilopoceras springeri, Inoceramus howelli, Lopha bellaplicata, s. s., Lopha cunabula	Priono-cyclus hyatti	Prionocyclus hyatti, Scaphites arcadiensis, Lopha bellaplicata s.s., I. costellatus, Inoceramus apicalis, Inoceramus howelli		88	87.7	M	*** ?
Scaphites carlilensis, Lopha b. novamexicana	Inoceramus securiformis Inoceramus flaccidus	Inoceramus flaccidus					
Collignoniceras woollgari, I. cuvieri, S. larvaeformis, Mytiloides "latus"	Inoceramus aff. I. flaccidus Mytiloides hercynicus	Inoceramus cuvieri, Ostrea bentonensis	M. "latus" Collignon. woollgari				
Mammites nodosoides, Choffaticeras pavillieri	Mytiloides labiatus, M. subhercynicus Mytiloides mytiloides	M. labiatus; M. subhercynicus Mytiloides mytiloides		90	88.7	L	
Watinoceras coloradoense, Neoptychites xetriformis	Mytiloides aff. M. duplicostatus	UNKNOWN					
Watinoceras reesidei, Plesiovascoceras thomi	Mytiloides opalensis Mytiloides submytiloides	Mytiloides submytiloides					
Sciponoceras gracile, Worthoceras vermiculum, Calycoceras naviculare, Kanabiceras septemseriatum, Metoicoceras whitei, Inoceramus tenuiumbonatus	Inoceramus pictus, s.s.	Worthoceras gibbosum, K. septemseriatum Sciponoceras gracile, I. pictus, M. whitei		92	91	U	CENOMANIAN
Dunveganoceras albertense, D. conditum, Metoicoceras defordi, M. muelleri, Inoceramus ginterensis, I. flavus		Inoceramus aff. Inoceramus pennatulus, Inoceramus pictus subsp. aff. I. pictus etheridgei	Inoceramus pictus s.l. (flat broad form), Acanthoceras spp.				
Dunveganoceras pondi, Calycoceras canitaurinum, Inoceramus prefragilis, Inoceramus macconnelli ?							
Plesiacanthoceras wyomingense, Borissiokoceras orbiculatum		UNZONED		95	92	M	
Acanthoceras amphibolum, Inoceramus arvanus (late form)							
Acanthoceras alvaradoense, Tarrantoceras rotatile, I. arvanus		Acanthoceras alvaradoense, Tarrantoceras rotatile, Ostrea beloiti					
Turrilites scheuchzerianus, Acanthoceras muldoonense			I. prefragilis				
Acanthoceras bellense, Inoceramus crippsi, A. granerosense		Calycoceras leonense					
Calycoceras tarrantense, Turrilites acutus, C. gilberti		C. tarrantense, Epengonoceras dumbli, I. arvanus					
Inoceramus bellvuensis, n. subsp. "Inoceramus" dunveganensis, s.s., "I." dunveganensis n. subsp. "Inoceramus" athabaskensis (late form)		"Inoceramus" eulessanus		97.5	92.5	L	
				100	93.5		

FIG. 4B. *(Explanation continued from facing page.)*

scaphitids; 11) Gill & Cobban, 1966, Red Bird zonal sequence, Wyoming; 12) Kauffman, 1975, Western Interior bivalve zones; 13) Kauffman, Cobban, & Eicher, 1977, Cenomanian-Coniacian zonation; 14) Scott & Cobban, 1964, Coniacian-Lower Campanian zonation, central Colorado; 15) Jeletzky, 1970, Western Interior of Canada; 16) Young, 1963, Coniacian-Campanian ammonite zones, Gulf Coast; 17) Sohl, 1960, personal com., 1977, *Exogyra* zones and regional correlations; 18) E. G. Kauffman, unpub. research, Inoceramidae; 19) J. D. Powell, unpub. research, Eagle Ford Formation (Cenomanian-Turonian), Gulf Coast; 20) Stephenson, 1952, Cenomanian mollusks, Woodbine Formation, Texas; 21) Stephenson, 1941, Campanian-Maastrichtian mollusks, Navarro Group, Texas; 22-26) Seitz, 1959, 1961, 1965, 1967,

Stage	Substage	Age Ma *	Age Ma **	WESTERN AND NORTHERN EUROPE (22, 23, 24, 25, 26, 27, 28, 29 30, 31)	MADAGASCAR (32)	JAPAN (33, 34, 35, 36, 2)
CONIACIAN	U	85.5	82	Micraster cortestudinarium Magadiceramus subquadratus + subspp., Inoceramus fasciculatus, Protexanites, Paratexanites, Parabevahites emscheri Volviceramus involutus	Prionocycloceras guyabanum, Volviceramus involutus Gauthiericeras margae	Inoceramus uwajimensis Yokoyamaoceras kotoi I. hobetsensis, s.s. I. yubariensis, I. mihoensis Paratexanites orientalis, "Inoceramus" mukawaensis, Sphenoceramus yokoyamai I. naumanni (lo. part)
	M	86	83.5	Cremnoceramus inconstans Cremnoceramus koeneni "I." schloenbachi I. crassus/browni	Barroisiceras onilahyense, Kossmaticeras theobaldi Stolleyiceramus madagascariensis	Peroniceras aff. P. platycostatum Prionocycloceras aff. P. guayabanum
	L	86.3	84.5	Inoceramus deformis, Inoceramus ernsti Inoceramus erectus, s.l., I. waltersdorfensis hannovrensis I. rotundatus, I. waltersdorfensis Mytiloides fiegei, M. dresdensis, M. ? lusatiae	Peroniceras dravidicum	UNZONED Barroisiceras sp., Inoceramus uwajimensis yeharai, Inoceramus n. sp. cf. I. mihoensis
*** ? TURONIAN	U	87	86	Holaster planus, Sciponoceras bohemicum, Scaphites geinitzi, Hyphantoceras reussianum, Lewes. mantelli Inoceramus "vancouverensis" Mytiloides striatoconcentricus Inoceramus dimidius, Inoceramus lamarcki s.l. (late subspp.), I. inaequivalvis	Romaniceras deveriai, Lewesiceras masiaposense, Prionocyclus neptuni, Inoceramus humboldti	Tragodesmoceras subcostatum, Scaphites planus Yubariceras, Romaniceras I. tenuistriatus, I. pedalionoides, I. iburiensis, M. incertus Reesidites minimus Subprionocyclus normalis
*** ?	M	87.7	88	Terebratulina lata Inoceramus lamarcki (early subsp.), Inoceramus flaccidus, Inoceramus costellatus ? Collignoniceras woollgari Inoceramus cuvieri M. "latus" s.l. M. hercynicus	Prionotropis spp., Inoceramus inaequivalvis	I. hobetsensis nonsulcatus, Mytiloides teraokai Subprionocyclus neptunei Collignoniceras teshioensis, Romaniceras? otatumei, Yubariceras yubarense
	L	88.7	90	Orbirhynchia cuvieri Mammites nodosoides Mytiloides labiatus, Mytiloides mytiloides Mytiloides opalensis, Lewesiceras spp., Plesiovascoceras catinum, Fagesia pachydiscoides, Neocardioceras juddii (base) Mytiloides submytiloides	Mammites nodosoides, Mammites menabensis, Mammites hourcqi, Fagesia superstes, Fagesia rudra, Yubariceras yubarense	Kanabiceras septemseriatum, Fagesia thevestensis, Sciponoceras kossmati M.subhercynicus M. mytiloides Mytiloides opalensis M. cf. labiatus
CENOMANIAN	U	91	92	Sciponoceras gracile, Kanabiceras, Terebratella carantonensis Metoicoceras gourdoni, Actino. plenus Calycoceras naviculare, Inoceramus pictus pictus Metoicoceras geslinianum O. biauriculata, Eucalycoceras pentagonum I. pedalionoides	Acanthoceras vicinale	Acanthotrigonia dilapsa, Acanthotrigonia longiloba Acanthotrigonia agawai, Acanthotrigonia pustulosa Inoceramus yabai, Desmoceras (Pseudouhligella) japonicum, D. (Pseudouhligella) ezoanum Calycoceras naviculare, Eucalycoceras pentagonum, Inoceramus concentricus costatus, Inoceramus reduncus, Inoceramus pennatulus
	M	92	95	Acanthoceras rhotomagense Acanthoceras jukesbrownei Inoceramus ginterensis Turrilites acutus I. pictus I. n.sp. aff. I. tenuis Turrilites costatus Inoceramus flavus, s.s. I. arvanus, I. etheridgei I. crippsi, I. reachensis, I. tenuis	Calycoceras jeanneti, C. hourcqi, C. latelobatum, C. andranovoritelense Acanthoceras rhotomagense Protacanthoceras harpax, A. lymense, Eucaly. newboldi	Calycoceras stoliczkai Calycoceras orientale, Calycoceras asiaticum, Calycoceras spinosum, Acanthoceras amphibolum, I. concentricus nipponicus
	L	92.5	97.5	Mantelliceras mantelli Mantelliceras gr. dixoni I. anglicus elongata Mantelliceras saxbii I. flavus n. subsp. Hypoturrilites carcitonensis I. n. sp. aff. "I." concentrica	Mantelliceras mantelli, Mantelliceras manabense Mantelliceras martimpreyi	Mantelliceras japonicum, Sharpeiceras congo, M. cantianum Graysonites cf. G. fountaini, Desmoceras kossmati, Stoliczkaia aff. S. africana, Euhistrichoceras nicaisei, Inoceramus aff. I. crippsi
		93.5	100			

FIG. 4C. *(Explanation continued from page A451.)*

1970, Coniacian-Maastrichtian Inoceramidae, north Germany; 27) Tröger, 1967, Cenomanian-Coniacian Inoceramidae, north Germany; 28) Cox, 1967, classical British-French chalk zonation; 29) Kennedy, 1969, Late Albian-Cenomanian ammonite zonation; 30) Kauffman, 1977d, British Albian-Coniacian inoceramid zonation; 31) Kennedy & Juignet, 1973, Cenomanian-Turonian boundary-zone sequence, France; 32) Besairie & Collignon, 1972, Madagascar; 33) Matsumoto, 1959a, b; 34) Matsumoto, 1963, and 35) Noda & Matsumoto, 1976, ammonite-inoceramid bivalve zones, Japan; and 36) Nakano, 1960, trigoniid bivalves, Japan. For explanation of single and double asterisks, see Figure 2 caption. Triple asterisks designate the major area of disagreement concerning definition of the Turonian-Coniacian bound-correlations in temperate realms, especially where ammonites are rare or absent. *Buchia* is particularly useful in the Lower Neocomian of the north-temperate Euramerican region (for example, IMLAY, 1959; JONES, 1969; JELETZKY, 1964a,b, 1965; and papers cited in CASEY & RAWSON, 1973a). Because of slower evolutionary rates, they do not lead to zonation as refined as that based on ammonites; usually only 2 to 3 *Buchia* zones are recognized within each Lower Cretaceous stage in which they occur abundantly. JELETZKY (1965) discussed the limitations of *Buchia* in biostratigraphy. The Inoceramidae, biostratigraphically the most important Upper Cretaceous family of bivalves, has much more restricted application in the Lower Cretaceous. Nevertheless, whereas Buchiidae become less important above the Middle Neocomian, the Inoceramidae increase in abundance, diversity, and biogeographic spread, and become accessory biostratigraphic indices to ammonites in the Hauterivian and Barremian stages. The Inoceramidae play a major role in Albian biostratigraphy, with increasing rates of evolution and biogeographic spread almost equal to that of the ammonites (KAUFFMAN, 1977d). The Albian *Birostrina coptensis-B. salomoni* lineage, *B. concentrica-B. sulcata* lineage, *Inoceramus anglicus* lineage, and the unusual endemic groups of North American inoceramids, the *"Inoceramus"* (n. gen.) *nahwisi* and *"I."* (n. gen.) *dunveganensis* lineages are especially important (JELETZKY, 1964a). Lower Cretaceous Trigoniidae (for example, Japan; NAKANO, 1960), Pectinidae and Ostreidae (for example, Gulf Coast of the United States; STANTON, 1947) are bivalve groups that are locally important in Lower Cretaceous biostratigraphy.

Among the microbiota, Lower Cretaceous biostratigraphy is highly dependent upon planktonic foraminifers and calcareous nannofossils. Calpionellidae are important in Lower Neocomian zonation. Radiolarians and benthonic foraminifers play a minor accessory role. VAN HINTE (1976) summarized the global oceanic zonation based on microfossils (Fig. 3), a zonation that has largely arisen in the last decade through the Deep Sea Drilling Program. Lower Cretaceous microfossil zones tend to be longer in duration by 25 to 50 percent than their Upper Cretaceous counterparts, with the exception of those based on Aptian-Albian planktonic foraminifers. From Berriasian to Middle Aptian time, biostratigraphic zonation based on the microbiota is 2 to 8 times broader than that based on ammonites for the same period; beyond that point they have similar zonal durations. Calcareous nannofossil zonation is up to 4 times coarser, and radiolarian zonation up to 12 times coarser than that based on planktonic foraminifers. Biostratigraphic zonation of the Lower Cretaceous based on macrofossils is compared to that based on microfossils in Figure 3.

BIOSTRATIGRAPHICALLY IMPORTANT LOWER CRETACEOUS GROUPS

Berriasian biostratigraphy is primarily based on ammonites of the genus *Berriasella* in the marine Tethyan and temperate realms. Ammonites of the genera *Surites, Peregrinoceras, Hectoroceras, Runctonia, Chetaites, Spiticeras,* and *Raisanites* are important in the Eurasian region of the North Temperate Realm (Fig. 3). WIEDMANN (1973) noted the importance of heteromorph ammonites *(Leptoceras, Protancyloceras, Bochianites)* in Berriasian Tethyan faunas. Species of the bivalve *Buchia* are biostratigraphically important in North America (JELETZKY, 1970) and to a lesser extent in northern Europe. In the pelagic realm, species of *Calpionella,* the radiolarian assemblage of the *Sphaerostylus lanceola* Zone, and the nannofossil *Nannoconus* characterize the Berriasian. Fresh water ostracodes, in particular *Cytherelloidea* and *Cytheridea,* are mainly used in nonmarine "Wealden" facies (CASEY & RAWSON, 1973b). STEVENS (1973) noted that the

FIG. 4A-F. *(Continued from facing page.)*

ary; Europeans using Inoceramidae place the boundary above *Inoceramus deformis,* whereas ammonite specialists and American biostratigraphers place the boundary one-third of a stage lower, at the base of the *I. rotundatus-Mytiloides fiegei* Zone (Kauffman, n).

Stage	Substage	Age Ma *	Age Ma **	TETHYAN MACROFOSSIL STANDARD (1)	NORTH TEMPERATE MACROFOSSIL STANDARD (1)	PLANKTONIC FORAM. STANDARD (1)	NANNOFOSSIL STANDARD (1)	CALIFORNIA (2, 3)
MAASTRICHTIAN	U	64	65	Pachydiscus newbergicus	Belemnella casimirovensis Belemnitella junior	Globotruncanella navarroensis Globotruncana contusa Globotruncana stuarti	Micula mura Lithraphidites quadratus	Baculites rex "Inoceramus" n. sp. UNZONED
	L	65	67.5	Acanthoscaphites tridens	Belemnella occidentalis	Globotruncana gansseri		Eubaculites ootacodensis
		65.5	68		Belemnella lanceolata	Globotruncana scutilla	Tetralithus trifidus	"Inoceramus" shikotanensis Baculites columna Baculites lomaensis
CAMPANIAN	U	68.7	70	Bostrychoceras polyplocum	Belemnitella langei, Belemnitella minor Belemnitella minor	Globotruncana calcarata Globotruncana subspinosa	Broinsonia parca	Baculites sp. aff. B. anceps, Baculites occidentalis, Metaplacenticeras pacificum Baculites inornatus, Cladoceramus schmidti, Inoceramus subundatus
		71	72	Hoplitoplacenticeras vari	Belemnitella mucronata, s.s. B. mucronata, B. mucronata senior	Globotruncana stuartiformis		
		72.5	74	Delawarella delawarensis	B. mucronata senior, G. quadrata gracilis G. quadrata gracilis	Globotruncana elevata	Eiffelithus eximius	UNZONED
		75	75		Gonioteuthis quadrata, s.s.			
	L	78	76	Placenticeras bidorsatum	G. granulata, G. quadrata			Submortoniceras chicoense, Baculites chicoense, Sphenoceramus lingua?
SANTONIAN	U	82.3	78	Placenticeras syrtale,	Gonioteuthis granulata		Gartnerago obliquum	Baculites kirki Pseudoschloenbachia sp. aff. P. boulei, Baculites capensis, Sphenoceramus? orientalis ambiguus
	M	83.3	79.5	Eupachydiscus isculensis	G. westfalica, G. granulata Gonioteuthis westfalica	Globotruncana concavata, Globotruncana elevata		Baculites boulei, s.s. Cordiceramus cordiformis
	L	84.7	80	Texanites texanus	Cladoceramus undulatoplicatus		Marthasterites furcatus (upper part)	Texanites kawasakii, Baculites boulei s.l.
		85.5	82					

FIG. 4D. *(Explanation on page A450.)*

Berriasian and Valanginian may be zoned by the Cylindroteuthididae in the North Temperate Realm, and by the Duvaliidae and *Hibolithes-Curtohibolites* plexus for Tethys and the Austral-South Pacific area. *Belemnopsis* may be biostratigraphically useful in the South Temperate Realm.

In temperate realms Valanginian biostratigraphy is largely based on ammonites of the families Berriasellidae, Craspeditidae, and Olcostephanidae, and on different genera of the same families in the Tethyan Realm (Fig. 3). WIEDMANN (1973) noted restriction of the heteromorphic ammonite

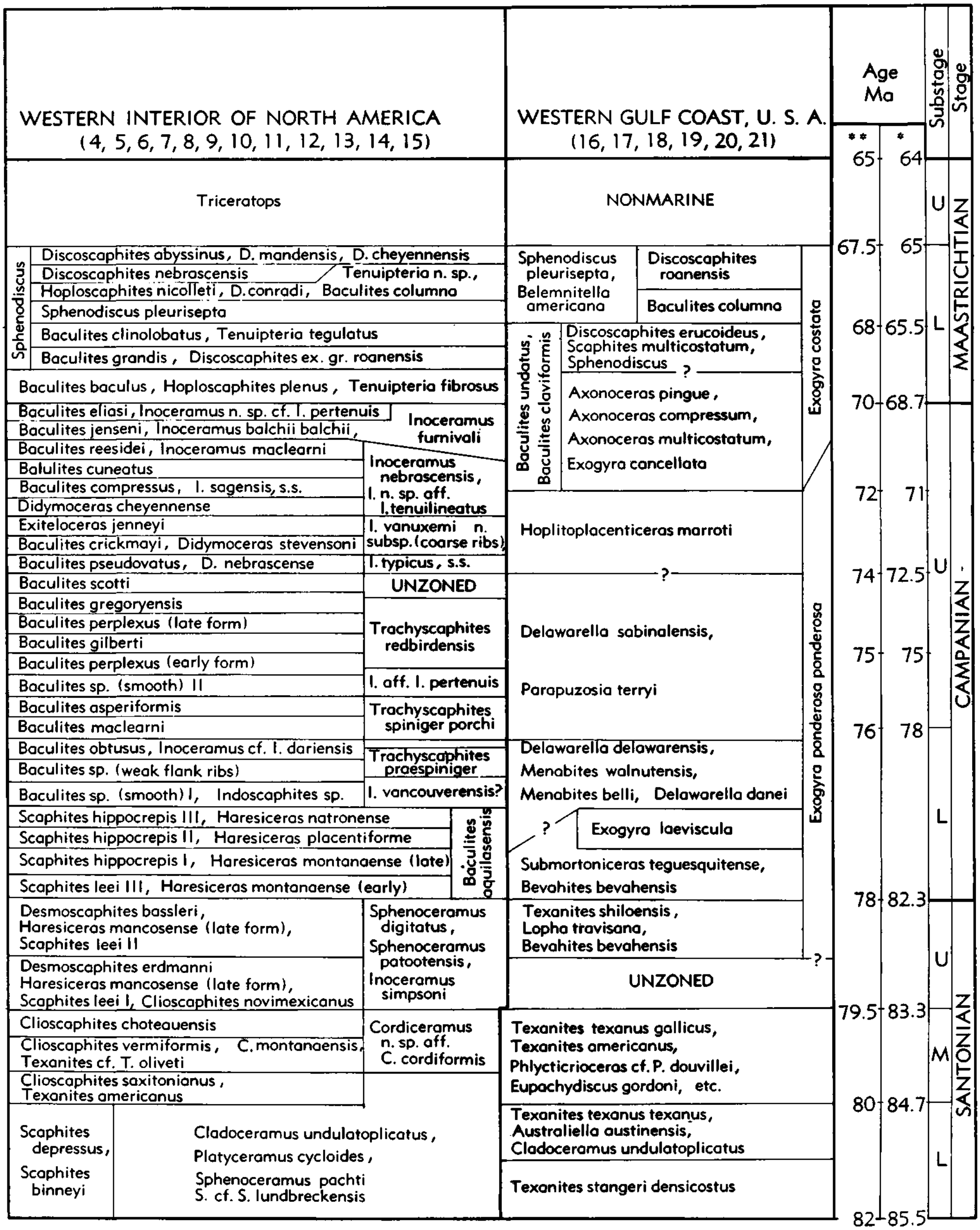


FIG. 4E. *(Explanation on page A450.)*

genera *Eocrioceratites* and *Parapedioceras* to the Tethyan Lower Valanginian, and *Juddiceras* to the Upper Valanginian (all Ancyloceratina). *Hibolithes, Duvalia,* and *Belemnopsis* are important belemnite genera in Tethys and its southern margin. Valanginian species of the bivalve *Buchia* are the main bases for zonation and correlation in temperate North America, ammonites (mainly Olcostephanidae and Craspeditidae) being less common (JELETZKY, 1970). Pelagic zonation and correlation of the Valanginian is mainly based on species of the calpionellid genera *Calpionellites* and

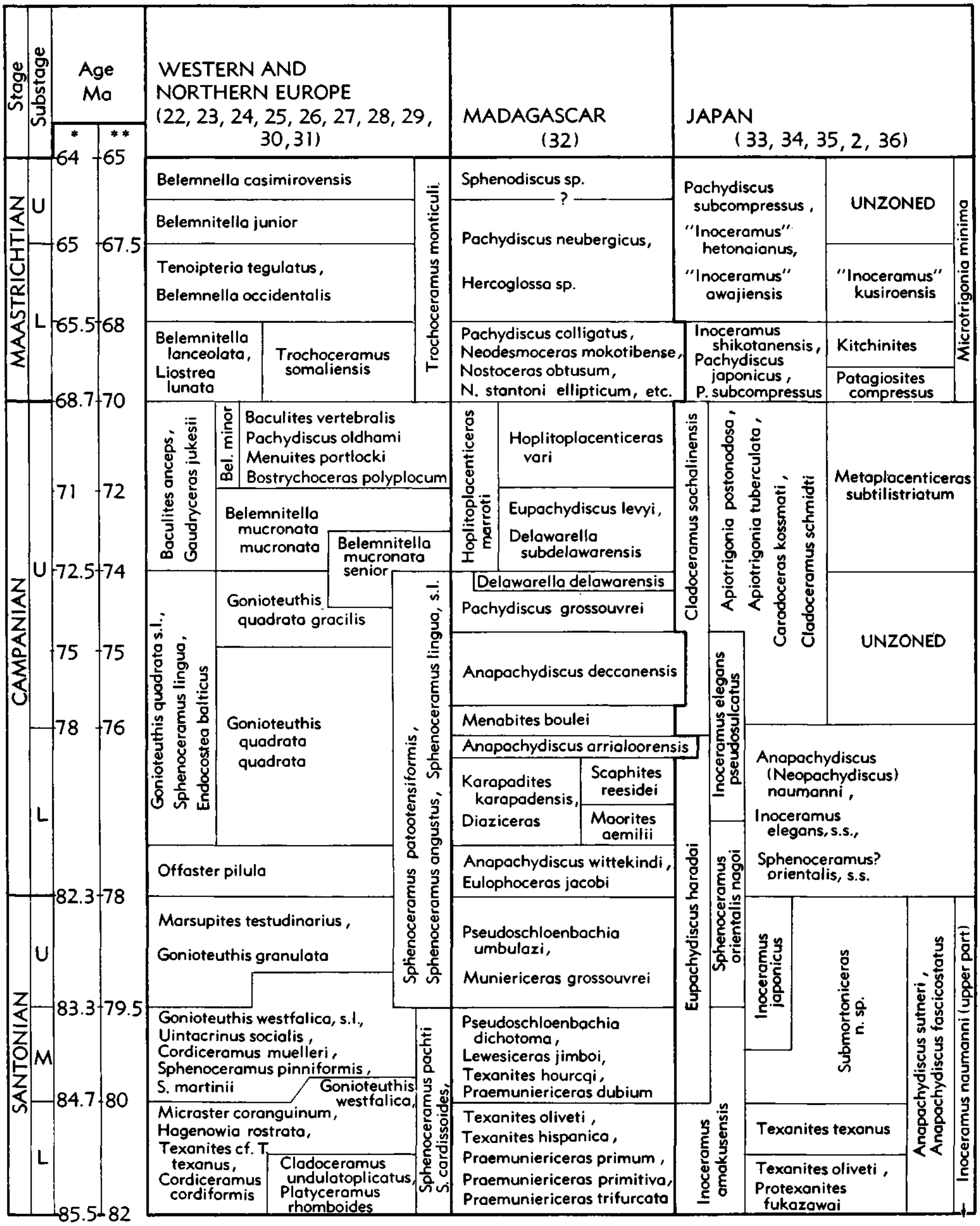


FIG. 4F. *(Explanation on page A450.)*

Calpionellopsis associated with the radiolarian fauna of the *Staurosphaera septemporata* Zone and the nannofossils *Cretarhabdus crenulatus* and *Calcicalathina oblongata* (Lower and Upper Valanginian, respectively; Fig. 3).

Hauterivian biostratigraphy draws its greatest refinement from ammonites (Fig. 3). In Tethys, the families Berriasellidae, Ancyloceratidae, Desmoceratidae, and Hemihoplitidae are of primary importance. In the temperate realms the Olcostephanidae and different genera of Ancyloceratidae are most important; species of *Simberskites* and

Endomoceras are principal zonal indices. Among belemnites, *Acroteuthis* is biostratigraphically important in temperate North America, the Cylindroteuthididae and the Oxyteuthididae throughout the North Temperate Realm, and *Hibolithes, Curtohibolites, Mesohibolites,* and the Duvaliidae in the Tethys and Austral regions. The Inoceramidae first became important as accessory index species, especially in the North Pacific Region. Among pelagic microbiota, ancestral species of *"Hedbergella,"* the last occurrence of the *Staurosphaera septemporata* radiolarian assemblage, the nannofossil assemblage of *Calcicalathina oblongata* (Lower Hauterivian), and the first occurrence of the *Lithraphidites bollii* assemblage (Upper Hauterivian) biostratigraphically characterize this stage.

Barremian biostratigraphy is as refined as that of the Valanginian and younger Cretaceous stages owing to rapid radiation among the ammonites. In Tethys, the ammonite families Pulchelliidae, Ancyloceratidae, and Silestidae are of primary importance along with the belemnites of the Duvaliidae, and the genera *Mesohibolites, Hibolithes,* and *Curtohibolites.* In the temperate realms, the Ancyloceratidae are also of principal biostratigraphic utility, based on many different genera and species from those found in Tethys. The Heteroceratidae and Lytoceratidae are of secondary utility (excepting in North America) along with belemnites of the Cylindroteuthididae and Oxyteuthididae, and the bivalves *"Inoceramus," s. l.,* and *Aucellina* (Buchiidae). In the pelagic realm, Barremian microbiotas are characterized by species of the planktonic foraminifer *Hedbergella,* by the early range of the *Stichocapsa tenuis* radiolarian assemblage, and by nannofossil assemblages of the *Lithraphidites bollii* (Lower Barremian) and *Micrantholithus hoschulzi* (Upper Barremian) zones.

The Aptian Stage is most finely zoned by ammonites, but represents the first stage where pelagic microbiotic zonation is nearly as detailed. In the Tethyan Realm, the ammonite families Douvilleiceratidae, Opeliidae, Deshayesitidae, and to a lesser extent, the Ancyloceratidae and Hoplitidae form the major bases for zonation and regional correlation. The belemnite groups Duvaliidae, *Mesohibolites,* and *Parahibolites* are of secondary importance. In the temperate realms, ammonite biostratigraphy is more refined than that of Tethys and is also centered around the Douvilleiceratidae, Deshayesitidae, and Ancyloceratidae, though based largely on different genera and species than those found in Tethys (Fig. 3; Van Hinte, 1976; Casey & Rawson, 1973b). The bivalves *Aucellina* and *"Inoceramus"* are accessory biostratigraphic indices in the Aptian. In the pelagic realm, a refined biostratigraphy based on the microbiota is centered around planktonic foraminifers belonging to the genera *Globigerinelloides, Schackoina, Ticinella,* and *Hedbergella.* Nannofossils are of lesser importance, with the *Chiastozygus litterarius* and *Parhabdolithus angustus* assemblages marking the Lower and Upper Aptian, respectively.

The Albian Stage comprises the most finely divided biostratigraphic system of the Lower Cretaceous, especially in western Europe and England (Fig. 3) where 23 ammonite subzones are recognized. This was also a time of widespread cosmopolitanism associated with the most extensive Early Cretaceous transgression; many of the same ammonites and inoceramid bivalves used in refined zonation characterize biostratigraphic zonation of the Tethyan and temperate realms. Among ammonites, Lower Albian biostratigraphy is based primarily on species of the Leymeriellidae, Douvilleiceratidae, Brancoceratidae, Hoplitidae, Lyelliceratidae, and certain Deshayesitidae. Upper Albian zonation utilizes mainly the Acanthoceratidae and Schloenbachiidae; Pachydiscidae, Engonoceratidae, and Brancoceratidae are principal zonal ammonite groups of the American Gulf Coast. Belemnites become increasingly important in Albian biostratigraphy within Tethys *(Neohibolites, Parahibolites).* In temperate North America and Europe, the Desmoceratidae and the endemic American Gastroplitinae (*Gastroplites* and *Neogastroplites*) are important ammonites in refined biostratigraphic zonation of the Albian. Among Bivalvia, cosmopolitan Inoceramidae of the genus *Birostrina* and the *"Inoceramus" anglicus* species group are important in regional correlation; the *"I." dunveganensis* and *"I." nahwisi* groups are important in

North America. *Aucellina* (Buchiidae) is locally useful in temperate biostratigraphy of the Albian; *Neithea* (Pectinidae), Ostreidae (*Texigryphaea,* Lophinae, Exogyrinae), various Trigoniidae, and rudistid bivalves are locally applied in Tethyan biostratigraphy, along with several groups of echinoids *(Epiaster, Salenia, Holectypus, Heteraster)* and gastropods (nerineids, actaeonellids). Global Albian pelagic zonation is mainly based on planktonic foraminifers of the genera *Ticinella, Globogerinelloides, Rotalipora,* and *Praeglobotruncana,* with less refined division possible from nannofossils (Fig. 3).

UPPER CRETACEOUS BIOSTRATIGRAPHY

Upper Cretaceous biostratigraphy may be the most refined and regionally applicable within the Phanerozoic. Ammonites predominate in macrofossil zonations and planktonic foraminifers and calcareous nannofossils share equal roles among the microbiota (Fig. 4). In addition, bivalves of the Inoceramidae, Trigoniidae, Ostreidae, and Hippuritacea; belemnites of the genera *Neohibolites, Parahibolites, Actinocamax, Gonioteuthis, Belemnitella,* and *Belemnella* (STEVENS, 1973); irregular echinoids such as *Holaster, Micraster, Offaster, Galeola, Echinocorys* (ERNST & SEIBERTZ, 1977); certain terebratulid and rhynchonellid brachiopods; and gastropods of the families Turritellidae, Aporrhaidae, Volutidae, Nerineidae, and Actaeonellidae (SOHL, 1977) all have been used successfully for refined zonation. This has led to widespread development of integrated biostratigraphic systems employing assemblage- and composite assemblage-zones (KAUFFMAN, 1970; VAN HINTE, 1976).

Throughout the temperate realms, ammonites and Inoceramidae share an equal role in the construction of biostratigraphic zonation of 0.25 my/zone duration or less, which is broadly applicable for precise correlation (KAUFFMAN, 1975). These two groups evolved at nearly equal rates during the Late Cretaceous, and have similarly broad biogeographic spread; Inoceramidae are consistently more cosmopolitan than ammonites at the species level. In parts of the Upper Cretaceous sequence (Turonian, Campanian-Maastrichtian), Ostreidae approach these two groups in biostratigraphic utility. Through the Cenomanian and Turonian, diverse ammonites and Inoceramidae are commonly associated and comprise simple assemblage-zones that form the north temperate standard (for example, COBBAN & REESIDE, 1952; COBBAN & SCOTT, 1972; KAUFFMAN, 1975; KAUFFMAN, COBBAN, & EICHER, 1977, for North America). In the Coniacian and Santonian, ammonites are much less common, especially in carbonate facies, and rapidly evolving inoceramids, irregular echinoids, and belemnites are the principal zonal indices. Where ammonites are abundant in clastic facies they occur with cosmopolitan inoceramids, allowing precise correlations to be made between these and ammonite-poor facies. In the Campanian and Maastrichtian, except for the chalk facies, ammonites again dominate biostratigraphic systems, and evolved more rapidly than inoceramids (KAUFFMAN, 1975, fig. 4). In the latest Cretaceous chalk facies, inoceramids and belemnites are the principal macrofossils used in biostratigraphy, with ostreid bivalves, ammonites, irregular echinoids, and floating crinoids playing an important secondary role. Planktonic foraminifers and coccolithophorids are important biostratigraphically in carbonates of the North Temperate Realm, but are commonly facies controlled in temporal and areal distribution, and have longer range zones than ammonites, bivalves, and belemnites. Their main value is in providing correlations with the Tethyan Realm and the oceanic pelagic standard.

In the Tethyan Realm, ammonites and planktonic microbiota (foraminifers, coccolithophorids) comprise the main bases for the Upper Cretaceous biostratigraphic system. Belemnites are rare, and inoceramids are much less common and less diverse in Tethys. Sufficient inoceramid bivalves are known from Tethys, however, to allow rather precise correlation with the temperate biostratigraphic standard (KAUFFMAN, 1968; WIEDMANN & KAUFFMAN, 1977). Irregular echinoids, nerineid, actaeonellid, and turritellid gastropods, and rudistid bivalves are important local supplements to Tethyan zonation. Increasing diversification and rates of evolution among planktonic foraminifers and coccolithophorids during the Late Cretaceous enhanced their biostratigraphic utility.

Detailed global correlation of the Upper Cretaceous is possible because of major epicontinental transgressions and ameliorating marine environments that characterized most of this time period and that removed barriers to broad, rapid, species-level migration of taxa with mobile adult stages (ammonites, belemnites), or with long-lived planktonic larval stages (bivalves, echinoids, and many gastropods; see KAUFFMAN, 1975, and references therein). In addition, exceptional environmental tolerance among some of the most widespread benthonic groups (for example, Inoceramidae) contributed strongly to their rapid, wide dispersal. Figure 4 outlines the major zonal schemes applied to the Upper Cretaceous for key areas of the world where refined biostratigraphic systems have been developed.

BIOSTRATIGRAPHICALLY IMPORTANT UPPER CRETACEOUS GROUPS

Cenomanian biostratigraphy places equal importance on ammonites and inoceramid bivalves throughout both temperate realms, and on similar ammonites and planktonic microbiota (especially foraminifers) in the Tethyan Realm. Belemnites *(Actinocamax, Neohibolites, Parahibolites)* are widely used in zonation of the Eurasian north temperate region. Biostratigraphically important Cenomanian ammonites belong to the Acanthoceratidae, Desmoceratidae (Pacific mainly), and Baculitidae (especially Pacific *Sciponoceras*). Biostratigraphically important temperate-zone inoceramids are the *Inoceramus pictus, "I." crippsi, I. tenuis–I. tenuiumbonatus, I. heinzi–I. ginterensis,* and *I. etheridgei–I. tenuistriatus* lineages. Trigoniidae *(Acanthotrigonia)* are useful in zoning the North Pacific Cenomanian, and species of *Rotalipora* dominate the planktonic foraminiferal zonation. Certain additional taxa are critical to zonation of Cenomanian substages. In the Lower Cenomanian, ammonites of the Mantelliceratinae, Turrilitidae, Hoplitidae and surviving Lyelliceratidae are used in Tethys; ammonites of the Schloenbachiidae, *Graysonites* (North Pacific; North America), belemnites of the *Neohibolites* group, and inoceramid bivalves of the *"Inoceramus" crippsi, "I." anglicus* and *"I." dunveganensis* (North American) lineages are used in temperate realms; and the coccolith assemblage of *Eiffelithus turriseiffeli* is used in the upper half of the substage. Middle Cenomanian zonation relies also on ammonite species belonging to the Turrilitidae, *Acanthoceras* and *Dunveganoceras* among Acanthoceratinae, late descendants of the *"Inoceramus" dunveganensis–"I." anglicus, I. rutherfordi* and *I. crippsi* lineages, and the *I. "concentricus" nipponicus* plexus (North Pacific). The Middle and lower Upper Cenomanian is characterized by coccoliths of the *Lithraphidites alatus–Staurolithites orbiculofenestrus* Zone, and echinoids of the *Holaster subglobosus* lineage (Europe). Upper Cenomanian biostratigraphy specifically utilizes ammonites of the Metoicoceratinae, certain Acanthoceratinae *(Calycoceras, Eucalycoceras),* the temperate-zone belemnite *Actinocamax,* and the North Pacific *Inoceramus pennatulus* and *I. "concentricus" costatus* plexes. The nannofossil assemblage of *Chiastozygus irregularis* marks the uppermost Cenomanian in the lower part of its range-zone (Fig. 4).

In Tethyan and temperate zones, Turonian biostratigraphy utilizes similar ammonite groups—Acanthoceratinae, Scaphitidae, Baculitidae *(Sciponoceras, Baculites),* and Muniericeratidae (North Pacific). Species of the bivalve *Sergipia,* and the belemnite *Actinocamax,* and the radiolarian assemblage of the *Dictyomitra veneta* Zone are distributed throughout the Turonian. In addition, Lower Turonian biostratigraphy employs ammonites of the Mammitinae, Acanthoceratinae *(Kanabiceras),* Vascoceratidae, late Metoicoceratinae, the brachiopod plexus of *Orbirhynchia cuvieri,* inoceramids of the *Mylitoides mytiloides–M. labiatus* lineage, planktonic foraminifers of the genera *Hedbergella* and *Praeglobotruncana,* and nannofossil assemblages of the *Chiastozygus irregularis* Zone (upper part; basal Turonian) and *Corollithium exiguum* Zone (Lower Turonian; SMITH, 1975). Middle Turonian biostratigraphy specifically utilizes certain acanthoceratid and collignoniceratid ammonites *(Collignoniceras, Romaniceras, Prionotropis)*, inoceramid bivalves of the *Inoceramus lamarcki–I. cuvieri, I. costellatus, I. hobetsensis,* and *Mytiloides hercynicus–M. "latus"* lineages, brachiopods of the *Terebratulina lata* plexus, and the oyster *Lopha.* Upper Turonian biostratigraphic systems selectively employ different Collignoniceratinae *(Reesidites, Prionocyclus)* and Pachydiscidae *(Lewesiceras)* among ammonites, inoceramid bivalves of the *Inoceramus dimidius, I. perplexus, I. teshioensis, I. kleini, Mytiloides fiegei–M. incertus, M. striatoconcentricus,* and *M. lusatiae* lineages, the ostreid *Lopha,* and echinoids of the *Holaster planus* plexus. *Globotruncana*-based zonation dominates planktonic biostratigraphy of the Middle and Upper Turonian.

Inoceramid bivalves are preeminent in Coniacian biostratigraphy of the temperate realms whereas ammonites and planktonic foraminifers remain important in Tethys. Of greatest stratigraphic value throughout the Coniacian are ammonites of the Collignoniceratidae, Kossmaticeratidae (North Pacific), Scaphitidae, Baculitidae, and Desmoceratinae, the *Inoceramus yubariensis* (North Pacific) and *Didymotis* bivalve lineages, echinoids of the *Micraster cortestudinarium* plexus (Europe), planktonic foraminifers of the genus *Globotruncana,* and radiolarians of the *Artostrobium urna* Zone (Fig. 4). In addition, the Lower Coniacian is zoned on ammonites of the Barroisiceratinae, and Peroniceratinae, inoceramid bivalves of the *Inoceramus rotundatus–I. deformis, I. ernsti, I. waltersdorfensis, "I." madagascarensis,* and, in the upper part of their range, the *Mytiloides fiegei, M?. lusatiae,* and *M. dresdensis* lineages. The nannoplankton assemblage of the *Micula decussata* and *Tetralithus pyramidus* Zone characterizes both the Upper Turonian and Lower Coniacian. Middle Coniacian zonation specifically utilizes ammonites of the Texanitinae and Peroniceratinae (Collignoniceratidae) and bivalves of the *Volviceramus involutus–V. exogyroides, Cremnoceramus inconstans, C?. koeneni–C?. wandereri, Platyceramus mantelli–P. circularis,* and *Inoceramus kleini* lineages, especially in the temperate realms. Upper Coniacian biostratigraphy relies also on additional Texanitinae and inoceramids of the *Magadiceramus subquadratus, Inoceramus mihoensis, I. yokoyamai* (North Pacific), *I. fasciculatus,* and younger parts of the *P. mantelli* and *V. involutus* lineages. The nannofossil assemblage-zone of *Marthasterites furcatus* spans the Middle and Upper Coniacian in the lower half of its range (Fig. 4).

Santonian biostratigraphy similarly depends mainly on Inoceramidae (Bivalvia), except in Tethyan areas where ammonites and planktonic microbiota predominate. Important taxa include ammonites of the Baculitidae, Texanitinae, Pachydiscidae, Scaphitidae, and Muniericeratidae; inoceramid bivalves of the *"Inoceramus" simpsoni* lineage, *Sphenoceramus lobatus–S. steenstrupi–S. pachti* lineage, *Cladoceramus undulatoplicatus* plexus, and the *Platyceramus cycloides, P. platinus,* and *I. naumanni* lineages; belemnites of the genus *Gonioteuthis*; planktonic foraminifers of the genus *Globotruncana,* and radiolarians of the upper part of the *Arctostrobium urna* Zone. Lower Santonian zonation is based further on the first occurrence of *Cladoceramus undulatoplicatus,* species of the *Mytiloides? stantoni, Cordiceramus cordiformis* and *"Inoceramus" amakusensis* lineages, the echinoids *Conulus* and *Micraster* of the *M. coranguinum* plexus, and the *Marthasterites furcatus* nannofossil assemblage. Middle Santonian zonation is characterized by the floating crinoid *Uintacrinus,* inoceramids of the *Cladoceramus cordiformis* lineage, the first common occurrences of the cosmopolitan *Endocostea balticus* lineage, and the north temperate *Cladoceramus japonicus* and *"I." (Sphenoceramus?) naumanni* lineages. The nannofossil assemblage of the *Gartnerago obliquum* Zone spans the Middle and Upper Santonian. Ammonites of the Placenticeratidae and Lenticeratinae first become important in Cretaceous biostratigraphy in the Upper Santonian, associated with the floating crinoid *Marsupites* and, in the North Pacific, with early members of the *"Inoceramus" (Sphenoceramus?) orientalis* lineage.

Campanian biostratigraphic systems utilize ammonites, inoceramid bivalves, and belemnites equally in temperate realms whereas ammonites dominate Tethyan zonation. Groups that are important throughout the Campanian include ammonites of the Nostoceratidae, Baculitidae, Placenticeratidae, Scaphitinae, and Pachydiscidae; bivalves of the *Endocostea baltica* and *Apiotrigonia* lineages; planktonic foraminifers of the genus *Globotruncana,* and radiolarians of the *Amphipyndax enesseffi* Zone. In addition, Lower Campanian zonation relies heavily on Kosmaticeratidae, Texanitinae, and Lenticeratinae in Tethys and its margins, and on other Texanitinae *(Submortoniceras),* Scaphitidae of the *Scaphites leei–S. hippocrepis* lineage, species of the belemnite *Gonioteuthis,* inoceramids of the *"Inoceramus" quadrans, "I." (Sphenoceramus?) orientalis,* and *Sphenoceramus lingua–S. lobatus* lineages, echinoids of the *Offaster pilula* plexus, and the nannofossil assemblage of the *Eiffelithus eximius* Zone. Middle and Upper Campanian zonation draws heavily from inoceramid species, especially within the *"I." (Sphenoceramus?) schmidti, I. azerbaidjanensis–I. adgjakendensis, Platyceramus sagensis–P. nebrascensis, I. convexus, I. tenuilineatus, I. subcompressus, I. barabini, I. oblongus, I. pertenuis, Platyceramus regularis,* and *Endocostea typica* plexuses in North America (KAUFFMAN, 1975, fig. 4) and their Eurasian counterparts. The genus *Belemnitella* is important for zonation of the north temperate Middle and Upper Campanian. "Middle" Campanian pelagic zonation is further characterized by coccoliths of the *Broinsonia parca* Assemblage-zone, and the Upper Campanian by those of the lower *Tetralithus trifidus* Assemblage-zone. KAUFFMAN (1967) has successfully applied the bivalve *Thyasira* to zonation of the temperate North American Middle Campanian.

Maastrichtian biostratigraphic zonation is less refined than that of preceding stages due to the evolutionary decline of many principal invertebrate groups; including the ammonites, inoceramids, and belemnites. Among ammonites, species of the Baculitidae, Pachydiscidae, Sphenodiscidae, Scaphitidae, and (Lower Maastrichtian only) the Desmoceratidae and Nostoceratidae are the main basis for zonation. Pachydiscids dominate in Tethys; the others are mainly temperate and marginal Tethyan groups. Among north temperate belemnites, *Belemnella* and *Belemnitella* are key groups. The *Tenuipteria fibrosus–T. tegulatus* lineage is the main inoceramid group used in Maastrichtian biostratigraphy; the *Inoceramus shikotaensis* (North Pacific) plexus, the *Trochoceramus helveticus* and *Platyceramus salisburgensis* lineages (north Europe), and the *P. proximus–P. subcircularis* groups (Euramerica) are secondary indices for the Lower Maastrichtian. The *I. hetonaianus–I.? awajiensis* groups are used in the Middle to Upper Maastrichtian zonation of Japan along with species of *Microtrigonia* (Trigoniidae). The pelagic realm is zoned primarily on the basis of species of *Globotruncana* and *Globotruncanella* (Upper Maastrichtian only), radiolarians of the *Theocapsoma comys* assemblage, and nannofossils of the *Tetralithus trifidus, Lithraphidites quadratus,* and *Micula mura* assemblage-zones in the Lower, Middle, and Upper Maastrichtian, respectively.

BIOGEOGRAPHY

Biogeographic units are large-scale ecological units that respond to varying environmental (niche) parameters. They are dynamic in space and time—showing major fluctuations in composition, degree of internal endemism, paleogeographic spread, and the nature of their boundaries with other units (SYLVESTER-BRADLEY, 1971; VALENTINE, 1973; KAUFFMAN, 1973a). This can be clearly demonstrated in the Cretaceous, where the development and evolution of biogeographic units was closely tied to sea-floor spreading, plate collision, and the emplacement or destruction of orogenic belts acting as paleobiogeographic barriers. These processes resulted in large-scale isolation of segments of formerly associated biotas on the one hand, and massive competition between formerly isolated biotas on the other (KAUFFMAN, 1973a). In addition, the effect of large-scale Cretaceous eustatic fluctuations (Fig. 2) on the spatial extent of marine climatic zones, the severity of environmental gradients across their boundaries, and on the development of migratory pathways across epicontinental areas, strongly contributed to dynamic changes in paleobiogeographic units.

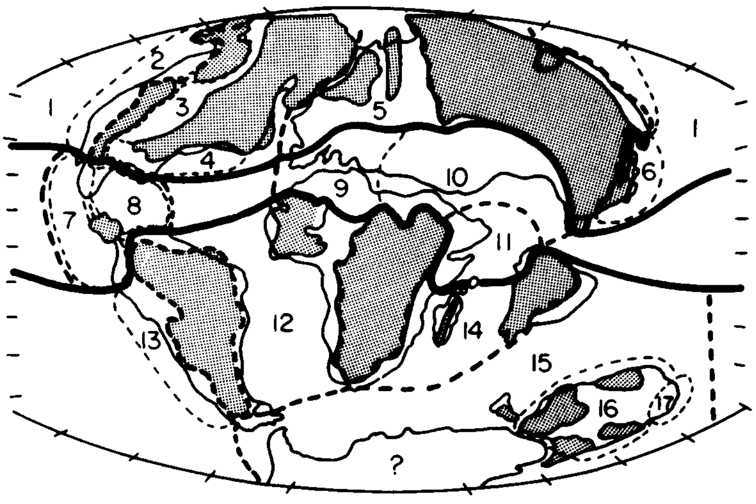
Specifically, some of the major events that most strongly influenced the evolution of paleobiogeographic units during the Cretaceous were as follows (Kauffman, 1973a): 1) opening of the Atlantic to distances that exceeded normal invertebrate larval drift or adult mobility, and which genetically isolated the warm-temperate and tropical invertebrate faunas of Eurasia from those of the Americas by Late Cretaceous time; 2) opening of the Caribbean by separation of North and South America and establishment of a tropical (Tethyan) seaway through this area which, for the first time during the Cretaceous, linked eastern Pacific with Euramerican tropical biotas; this tropical seaway effectively separated north and south temperate biotas of the Americas with a major temperature barrier; 3) closing of the North Pacific to the extent that marine biotas established separately in eastern and western Pacific shelf zones were brought into large-scale competition through overlapping larval drift ranges; 4) partial closing or restriction of the Mediterranean Tethys by Barremian time, subsequently resulting in increased isolation of Tethyan biotas of the eastern and western Mediterranean (Kauffman, 1973a, p. 360-366, fig. 3); 5) establishment of north-south marine connections between the temperate to cool-temperate Circumboreal ("Boreal") Seaway (biotas) and the warm-temperate waters (biotas) of the proto-Atlantic and Tethyan margin through initial opening of the North Atlantic and establishment of shallow epicontinental seas across Eurasia and North America during major Cretaceous transgressions; 6) opening of the South Atlantic during the Cretaceous, thus providing a pathway for mixing of south temperate "Gondwanan" marine faunas with those of the Euramerican Tethyan and North Temperate realms; Late Cretaceous separation progressively isolated segments of characteristic South Atlantic temperate faunas; 7) establishment of marine epicontinental connections between the Mediterranean Tethys and the South Atlantic seaways and biotas across north-central and northwestern Africa during major Cretaceous transgressions; 8) final breakup of Gondwanaland with isolation of Australia, New Zealand, India, Antarctica, and South America to the extent that major endemic centers became established in East Africa and Australia by the Neocomian, and in New Zealand by the Cenomanian (Kauffman, 1973a); 9) establishment of oceanic ridges and island systems as biogeographic stepping stones for migration of marine invertebrates, largely through larval drift, along the Mid-Atlantic Ridge, the island arc systems of the Caribbean, and the largely volcanic islands of the western Pacific and Indian oceans; and 10) as a result of plate tectonic activity, 9 to 10 major transgressions of epicontinental seaways onto the world's cratons, reflecting eustatic rise of sea level of up to several hundred feet; ameliorating and warming marine climates resulted, prime ecospace for marine invertebrates greatly expanded and diversified, major marine connections were established between formerly isolated areas (biotas), and climatic gradients became less severe. This resulted in breakdown of major temperature barriers to widespread dispersal of marine invertebrates. Interspersed regressions produced climatic decline, increased temperature gradients and environmental stress, and removal of many epeiric marine connections. This in turn resulted in isolation of biotas, and decrease in size but increase in number of latitudinally expressed marine climatic zones. The net stress effect of these alternating transgressive and regressive Cretaceous environments on the marine ecosystem was one of the principal dynamic forces leading to changes in Cretaceous paleobiogeographic units (Kauffman, 1973a).

Cretaceous biogeography has been viewed by different authors largely from the standpoint of distribution patterns among individual groups of organisms. Examples are ammonites (Jeletzky, 1971; Casey, 1971; Matsumoto, 1973; Owen, 1973; Wiedmann, 1973; Kennedy & Cobban, 1976), bivalves (Kauffman, 1973a), brachiopods (Ager, 1971, 1973), foraminifers (Dilley, 1971, 1973), belemnites (Stevens, 1973), corals (Coates, 1973), gastropods (Sohl, 1971), and sponges (Reid, 1967). Consequently, interpretations of the composition and distribution of biogeographic units, and their Cretaceous histories, are diverse and inconsistent. KAUFFMAN (1973a) has pointed out that this monotaxic technique is in contrast with the more holistic approach of the marine ecologist and biogeographer. A holistic approach to biogeography has the advantages of 1) presenting a consistent set of biogeographic unit concepts for each stage, which is comparable to recent data, and 2) allowing definition of ecological structure within biogeographic units.

Not only are the bases for defining Cretaceous paleobiogeographic units widely discrepant (that is, different groups may have distinct ecological response to the same general sets of changing environmental parameters and thus yield different distribution patterns in time), but so are the methods used in their construction; for example, compare papers cited in ADAMS and AGER (1967), MIDDLEMISS and RAWSON (1971), HALLAM (1973), CASEY and RAWSON (1973a), and HUGHES (1973), the principal modern compilations containing Cretaceous paleobiogeographic data. VALENTINE (1973), and KAUFFMAN (1973a), among others (see references cited in each), have reviewed this problem and discussed the means and importance of equating modern and ancient biogeographic unit concepts.

Neontologists apply two principal methods in defining biogeographic units: 1) delineation of unit boundaries by biotic discordance, that is, zones where there are numerous teil-province terminations (VALENTINE, 1961); and 2) by percentage endemism within biogeographic units (EKMAN, 1967; KAUFFMAN, 1973a). Both allow definition of biogeographic units in objective terms and their ranking within the biogeographic heirarchy. Because of the incomplete preservation of the stratigraphic record, teil-province boundaries are commonly difficult to ascertain for fossil taxa and the endemic percentage method is best applied to the definition of paleobiogeographic units. KAUFFMAN (1973a) discussed criteria for determining percent endemism, and applied a quantitative standard to the definition of Cretaceous paleobiogeographic units based on genera of Bivalvia: realm = 75 to 100 percent endemism, region = 50 to 75 percent endemism, province = 25 to 50 percent endemism, subprovince = 10 to 25 percent endemism, and endemic center = 5 to 10 percent endemism, in each case among noncosmopolitan organisms. Most past attempts at Cretaceous paleobiogeography have used a nonquantitative and inconsistent approach to the definition of units. Thus, one finds the Tethyan biota variously described as comprising a realm, a region, or a province during the Cretaceous.

The nonquantitative approach to Cretaceous paleobiogeography has had three unfortunate consequences: 1) inconsistency in classification of paleobiogeographic units; 2) lack of a consistent equation between Cretaceous and well-studied modern biogeographic units—a key to interpretation of ancient biogeography, and 3) in most studies, only a gross biogeographic division of the Cretaceous at the realm and region level has resulted, as compared to modern systems that utilize the province and subprovince as working units, and that recognize many more divisions of the global marine biota. Some Cretaceous workers have made finer biogeographic divisions to the province-subprovince level on nonquantitative treatment of diverse taxa (for example, JELETZKY, 1971; SOHL, 1971). Others have done the same by utilizing only well-studied taxa such as ammonites (MATSUMOTO, 1973; KENNEDY & COBBAN, 1976) and belemnites (STEVENS, 1973). Though they are more refined than most published biogeographic divisions of the Cretaceous, these still do not equate with modern provincial-subprovincial marine systems (for example, HALL, 1964) nor with those established for the Cretaceous utilizing the quantitative approach to definition of paleobiogeographic units (for example, KAUFFMAN, 1973a, for Bivalvia). In these nonquantitative analyses based on few taxa, the illusion is created that Cretaceous biogeographic systems were much simpler and less highly evolved than those of today, even taking into account the more severe climatic gradients of modern oceans and the predictable increase in the numbers of modern biogeographic divisions. KAUFFMAN'S (1973a) analytic treatment of Cretaceous bivalve genera, utilizing percent endemism to define and classify paleobiogeographic units, provides an alternative method that depicts



KEY

1 NORTH PACIFIC PROVINCE
2 NORTHEAST PACIFIC SUBPROVINCE
3 NORTH AMERICAN INTERIOR SUBPROV. } NORTH AMERICAN PROVINCE } EURAMERICAN REGION
4 GULF- ATLANTIC COAST SUBPROVINCE
5 NORTH EUROPEAN PROVINCE
6 JAPANESE-EAST ASIAN SUBPROVINCE
7 WEST-CENTRAL AMERICAN SUBPROVINCE } CARIBBEAN PROVINCE
8 ANTILLEAN SUBPROVINCE
9 WESTERN MEDITERRANEAN SUBPROVINCE } MEDITERREANEAN PROVINCE } INDO-MEDITERRANEAN REGION
10 EASTERN MEDITERRANEAN SUBPROVINCE
11 NORTH INDIAN OCEAN SUBPROVINCE
12 SOUTH ATLANTIC SUBPROVINCE
13 ANDEAN SUBPROVINCE
14 EAST AFRICAN PROVINCE
15 AUSTRAL PROVINCE } INDO-PACIFIC REGION
16 AUSTRALIAN SUBPROVINCE
17 NEW ZEALAND SUBPROVINCE

---- SUBPROVINCE BOUNDARIES
– – – PROVINCE-REGION BOUNDARIES
━━ REALM BOUNDARIES

Fig. 5. Generalized distribution of Cretaceous paleobiogeographic units of subprovince and higher rank (after Kauffman, 1973a, fig. 2), based primarily on molluscan distribution patterns, and plotted against slightly modified version of Dietz and Holden's (1970) reconstruction of the Cretaceous globe. Land areas not inundated during Cretaceous transgressions are stippled. Units 1 to 6 comprise the North Temperate Realm ("Boreal Realm" of authors), units 7 to 11 the Tethyan Realm, and units 12 to 17 the South Temperate Realm. [Used with permission of Elsevier Scientific Publishing Co., Amsterdam.]

the Cretaceous as being only slightly less diverse in terms of biogeographic division than modern seas (Fig. 5), and within the range predictable from the different climatic gradients that mark these two times in geological history. In the following analysis, Kauffman's units are therefore applied to biogeographic division of the Cretaceous, and the principal taxa that form the basis for biogeographic units of other specialists are fitted to this system with little difficulty.

Most biogeographic reconstructions that predate the widespread acceptance of plate tectonic theory dealt with static or near static units for each period without consideration of spatial and temporal change. Modern reconstructions recognize the dynamic nature of biogeographic units—their constantly changing composition and spatial distribution through time. Casey and Rawson (1973b, p. 418) argued the need for stage by stage evaluation of Cretaceous paleobiogeography as a mechanism for studying the dynamics of the units; Kauffman (1973a) successfully applied this method to Cretaceous bivalve biogeography. To the extent that it is possible here, the evolution of Cretaceous paleobiogeographic units is documented by stages and the observed changes in structure and distribution of the units are interpreted in light of plate tectonics and oceanic history.

NORTH TEMPERATE REALM

This realm incorporates biotas between the northern margin of tropical Tethyan biotas and the Cretaceous north pole (Fig. 5). The term "Boreal" has been widely applied to the same biotas (Matsumoto, 1973; Stevens, 1973; and others), but as explained by Kauffman (1973a, p. 367), this is an unfortunate misnomer as used by paleobiogeographers and should be abandoned. The North Temperate Realm was well established by the beginning of the Cretaceous and persisted to the end, becoming evolutionarily less unique with decreasing overall endemism but increasing subdivision into smaller paleobiogeographic units (Fig. 6). At no time during the Cretaceous is there unquestioned evidence in this realm for marine climates colder than the cool-temperate zones of modern oceans (sub-Boreal of modern zonation). The southern (Tethyan) boundary of the realm was very sharply defined early in the Cretaceous, as it was in the Jurassic, but became somewhat more diffuse through the period allowing greater precision in biostratigraphic correlation of the North Temperate and Tethyan realms.

Several schemes for paleobiogeographic division of the North Temperate Realm have been proposed (papers cited in Casey & Rawson, 1973a; Jeletzky, 1971; Sohl, 1971; Kauffman, 1973a; Matsumoto, 1973; Stevens, 1973; and others); these have been based on different organisms and result in somewhat conflicting systems. The following is a compromise, utilizing the most detailed system (Kauffman, 1973a) as a base (Figs. 5, 6). The two principal divisions of the realm, recognized by most workers, are the North Pacific Province (Jeletzky, 1971; Kauffman, 1973a; Owen, 1973), and the Euramerican Region (Fig. 5; Kauffman, 1973a; "Boreal" realm or province of many authors, in part or whole).

The North Pacific Province is clearly divisible on bivalve endemism into Northeast Pacific and Japanese-East Asian subprovinces (Kauffman, 1973a), reflecting the great breadth of the Cretaceous Pacific Ocean acting as a major water barrier to larval exchange between these areas. The North Pacific Province is characterized by: 1) bivalves such as *Apiotrigonia (Heterotrigonia), Steinmanella (Yeharella), Meekia,* and the middle Cretaceous *Inoceramus pennatulus* and *I. hobetsensis* lineages (Kauffman, 1973a); 2) Tethyan-style ammonites (phylloceratids, lytoceratids, tetragonids, desmoceratids, and kossmoceratids) during the Albian (Owen, 1973); 3) Upper Cretaceous ammonite groups that are most common in, but not restricted to the Indo-Pacific (Cenomanian and younger Desmoceratidae, Tetragonitidae, Phylloceratidae; Coniacian and younger Kossmaticeratidae and Pachydiscidae; Jeletzky, 1971; Matsumoto, 1973); 4) weak Lower Neocomian endemism among belemnites (Stevens, 1973); 5) an endemic assemblage of small benthonic foraminifers, especially agglutinated forms (Dilley, 1971); and 6) a unique North Pacific gastropod assemblage, especially in the Northeast Pacific Subprovince (Sohl, 1971). Compared to other major provinces in the Cretaceous, the North Pacific Province shows relatively weak endemism, as it did throughout the Jurassic.

Although the Northeast Pacific and Japanese-East Asian subprovinces (Fig. 5) are defined wholly on Bivalvia at this time (Kauffman, 1973a, p. 371, provided taxonomic lists), literature on other mollusks, especially gastropods, indicates that they show similar provincialism. Kauffman reported 21, mainly Lower Cretaceous, genera and subgenera of bivalves endemic to the Japanese-East Asian Subprovince, and 8 endemic genera in the northeast Pacific subprovince.

The evolutionary history of the North Pacific Province (Fig. 6) was detailed by Kauffman (1973a) using bivalves; other groups such as belemnites (Stevens, 1973) seem to support these observations. Figure 6 suggests that there was a marked decrease in endemism throughout the province and within individual subprovinces from Berriasian through Maastrichtian time, with the most abrupt change having come in the Cenomanian—a period of major plate movement. Kauffman (1973a) has attributed this decline to: 1) partial closing of the

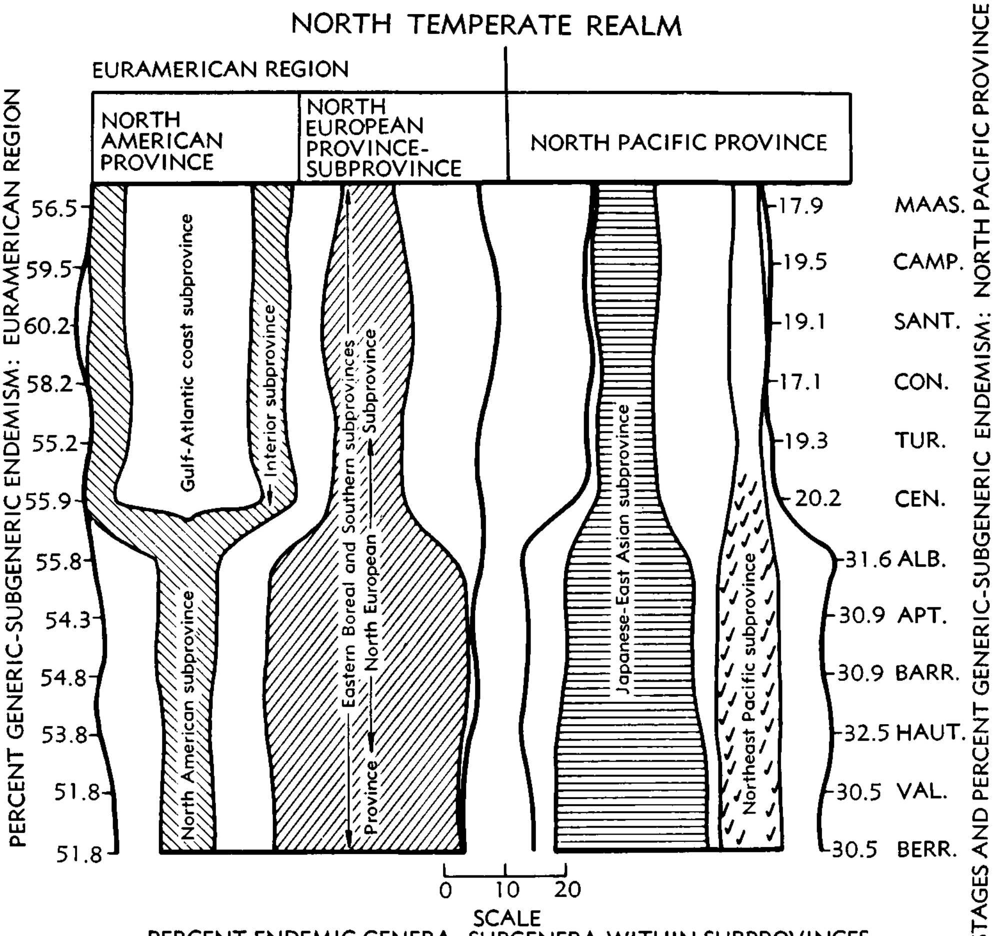


FIG. 6. Evolution of Cretaceous paleobiogeographic units in the North Temperate Realm, based mainly on bivalve Mollusca (after Kauffman, 1973a, fig. 4). Graphs show percent endemism of bivalve genera and subgenera within each unit, exclusive of cosmopolitan taxa. Scales for percent endemism of Euramerican Region and North Pacific Province are shown on left and right of graph, respectively. Patterned areas within outline for major regions or provinces represent distinct biogeographic subdivisions (provinces, subprovinces), as labeled. Different subdivisions have different patterns. The cumulative width of any patterned area at any time represents the percent endemism within it, as measured from scale at base of figure. Lack of pattern within any province or subprovince indicates reduction of endemism to less than 10 percent for that time. Unpatterned areas between patterned provincial or subprovincial graphs collectively depict that percent of endemism within the major biogeographic divisions represented by taxa shared between all subdivisions of the major unit. [Used with permission of Elsevier Scientific Publishing Co., Amsterdam.]

North Pacific, especially as a result of large-scale Cenomanian plate movements, to the point that the distinct eastern and western Pacific bivalve assemblages developed massive levels of competition for the same shallow-water niches as they came within larval drift range of each other, which resulted in a large-scale extinction and lowering of endemic diversity; 2) major epicontinental transgressions during the Late Cretaceous that opened marine pathways to migration of invertebrates in and out of the North Pacific, resulting in wider biogeographic spread of taxa and decreased local endemism as indicated by ammonites and gastropods (MATSUMOTO, 1973; SOHL, 1971) as well as inoceramid bivalves (KAUFFMAN, 1977e); and 3) climatic deterioration of the North Pacific marine environment through the Cretaceous with progressive cooling and increasing environmental gradients, resulting in lowering of North Pacific invertebrate diversity and endemism.

Biogeographic division of the Cretaceous Euramerican Region has been more inconsistent. Most authors have recognized a twofold, latitudinally (temperature) controlled division of this region, which extends from Siberia to Western Interior North America (Fig. 5), and which draws its faunal similarity from the many avenues of migration open to Eurasian and North American invertebrates through the "Circumboreal" Seaway and across the still narrow northern proto-Atlantic during much of the Cretaceous. The two proposed divisions consist of a northern cool-temperate zone and a southern warm-temperate to subtropical zone fronting on Tethys. The biogeographic treatment of the faunas characterizing these climatic zones has been diverse. Many authors have recognized two latitudinal divisions of the entire Euramerican Region. These are the northern "Boreal Province" and southern "Intermediate Latitude" zone of MATSUMOTO (1973; on ammonites), the Lower Cretaceous "Arctic" and (to the south) "Boreal Atlantic" provinces and the Upper Cretaceous "Northern" and "Southern" provinces of STEVENS (1973; based on belemnites).

KAUFFMAN's quantitative analysis of Cretaceous bivalve endemism revealed similar north-south division of the Euramerican Region independently in Eurasia and North America, but greater endemic differentiation across the proto-Atlantic in an east-west direction. He therefore recognized provincial boundaries approximately parallel to longitude, and subprovincial boundaries in both areas parallel to latitude in order to reflect the temperature-controlled faunal differentiation. This system is applied here (Figs. 5, 6), resulting in recognition of a North European Province and a North American Province, each with north-south differentiation into subprovinces or endemic centers.

The North European Province (Fig. 5) is very well defined at the base of the Cretaceous but shows decreasing endemism throughout the system for bivalves (Fig. 6) and other groups, especially after the Cenomanian. KAUFFMAN (1973a) attributed this to: 1) extensive epeiric flooding of the North American craton after the Middle Albian allowing, for the first time, widespread sharing of invertebrate taxa between Europe and America (and thus decreasing endemism in western and central Europe); the oceanic distances between Europe and North America were still within the range of larval drift for many invertebrate groups; and 2) east to west exchange of taxa that was probably greater than west to east exchange because the main surface currents of the middle proto-Atlantic gyre, representing the pelagic zone in which most planktonic invertebrates and larvae of marine benthos are carried, flowed to the west (KAUFFMAN, 1975, fig. 2); deeper countercurrents flowed east, but probably carried fewer organisms, as today. Resultant sharing of taxa would consequently have been greater from east to west, decreasing European endemism faster than American endemism in the process.

The North European Province is characterized by a strongly endemic Albian ammonite assemblage based on Hoplitidae (OWEN, 1973) and many other taxa. Late Cretaceous ammonite faunas were geographically more widespread than those of the Early Cretaceous, with broad Euramerican distribution of Acanthoceratidae, Collignoniceratidae, Placenticeratidae, Scaphitidae, Baculitidae, and Nostoceratidae being more notable than endemism within the provinces. Nevertheless, MATSUMOTO (1973) noted an endemic grouping of warm-temperate ammonite lineages common to southern Europe, East Africa, Madagascar, and the Coastal Plain of the United States, and a second group of endemics in the North American interior. Belemnites (STEVENS, 1973) show significant endemism in the North European Province (including Greenland) throughout the Lower Cretaceous (for example, the *Acroteuthis* and *Boreioteuthis* lineages of STEVENS' "Boreal Atlantic Province") and to a lesser extent in his Upper Cretaceous "Northern Province" (*Belemnella* fauna). KAUFFMAN (1973a, p. 369) reported more than 40 genera and subgenera of Cretaceous bivalves to be endemic to North Europe, and a weak endemic differentiation between eastern and western portions of the province. This is also shown by belemnites in STEVENS' (1973) "Boreal Northern" and "Southern" provinces of central and western Europe, and his eastern Crimean-Caucasian Province. AGER (1971) noted that the brachiopod group *Uralella* is restricted to the North European Province, and DILLEY (1971) recorded an endemic benthonic (especially agglutinated) foraminiferal assemblage in his temperate "Old World" Province.

North-south division of the Cretaceous North European Province into warm- and cool-temperate zones is difficult because of the diffuse climatic and biogeographic boundary between them. Bivalves and belemnites allow differentiation of a more southerly (warm temperate) "Western European Endemic Center" (KAUFFMAN, 1973a) or "Southern Province" (STEVENS, 1973; on *Belemnitella*) and a North European (KAUFFMAN, 1973a) or a "Northern Province" characterized by Late Cretaceous *Belemnella* and several bivalve genera. Brachiopods such as *Rhynchonella* and *Peregrinella* occur in warm-temperate to subtropical Euramerican zones but not to the north. MATSUMOTO (1973) reported major lowering of Upper Cretaceous ammonite diversity to the north; CASEY (1973) and MATSUMOTO (1973) documented differences between northern and southern European ammonite successions in the Lower and Upper Cretaceous, respectively; characteristic north European taxa are *Schloenbachia*, certain scaphitid groups, and certain species of *Lewesiceras*. Thus, collectively there seems to be sufficient evidence for division of the North European province into northern and southern subprovinces. Using modified terminology of others, these divisions are here named the Eastern Boreal *(s.s.)* and Southern subprovinces.

The North American Province was poorly defined (subprovincial rank) at the beginning of the Cretaceous, and showed a major increase in endemism after the Cenomanian, when it developed distinct northern and southern subprovinces (Figs. 5, 6). The Cenomanian increase in endemism reflects primarily initial establishment of the Western Interior seaway during the Late Albian, its early population by widespread Euramerican stocks introduced from Europe by westward larval drift across the then narrow proto-Atlantic, and from latest Albian to Cenomanian onward, partial isolation of the middle part of the seaway, leading to high levels of endemism among mollusks of all types. Rapid Cenomanian spreading of the middle Atlantic, magnified by later Cretaceous movements, enhanced the potential for endemism within the interior seaway. Widespread genetic isolation resulted from separation of European and interior North American populations as Atlantic spreading exceeded the limits of larval drift and adult mobility, and as the widening Caribbean arm of Tethys became more effective as a temperate barrier to immigration of temperate organisms at the south end of the Western Interior seaway.

Despite a broad zone of faunal mixing between southern warm-temperate and northern cool-temperate organisms in the North American Province (KAUFFMAN, 1970; SOHL, 1971), a clearly defined Gulf-Atlantic Coast Subprovince and North American Interior Subprovince developed by Cenomanian time and remained well defined until the end of the Maastrichtian. The diffuse biogeographic boundary reflected a broad temperature gradient within the seaway. Molluscs that characterize the North American Interior Subprovince include Albian Gastroplitidae (especially *Neogastroplites*), Turonian species groups of *Prionocyclus,* Turonian-Maastrichtian endemic ammonite lineages of the Scaphitidae *(Scaphites, Clioscaphites, Desmoscaphites),* and *Irenicoceras,* bivalves of the *"Inoceramus" dunveganensis* and *"I." nahwisi* lineages (KAUFFMAN, 1973a), certain corbiculids, *Crassatellina,* and lineages of Lower Cretaceous Buchiidae (JELETZKY, 1970). SOHL (1971) listed numerous gastropod genera and species groups restricted to his "California and Northern Western Interior Region," a term emphasizing biogeographic relationships between Upper Cretaceous gastropods of the two areas and suggesting brief marine connections across the Cordilleran geanticline. Gastropod genera with endemic species groups in this subprovince include *Closteriscus, Pseudobuccinum, Serrifusus, Vanikoropsis, Trachytriton,* and selected lineages of *Drepanochilus* and *Graphidula.* The North American Interior Subprovince is further characterized by a discrete assemblage of benthonic, especially agglutinated, foraminifers, and among planktonic species, by a distinct *Heterohelix-Hedbergella* assemblage (Dilley, 1971).

The warm-temperate to subtropical Gulf-Atlantic Coast Subprovince (Fig. 5) extends from Massachusetts south to Texas and northern Mexico and shares many invertebrate taxa with interior North America. The subprovince has few endemic ammonites, except in the Aptian-Albian of the subtropical Gulf Coast among the Deshayesitidae *(Dufreynoyia),* Douvilleiceratidae *(Hypacanthoplites),* Mojsisovicziinae *(Oxytropidoceras, Manuaniceras, Venezoliceras), Drakeoceras,* and the Cenomanian *Budaiceras* among Lyelliceratidae (Young, 1972). This is thought to be related to genetic isolation behind major barrier-reef systems during several Aptian-Cenomanian intervals. Otherwise, the Gulf-Atlantic Coast Subprovince is primarily differentiated on the basis of gastropods, bivalves, and certain echinoids. Sohl (1971) selected such genera as *Carota, Cassiope, Turritella* (*whitei* group), *Lispodesthes, Eunaticina,* and the *Fusus veneratus* groups as typical of Cenomanian-Turonian faunas, and genera such as *Sargana, Tuba, Belliscala, Confusiscala, Anchura, Stantonella, Liopeplum, Anomalofusus, Creonella, Morea,* and *Calliomphalus* as being characteristic of younger Cretaceous biotas in the Gulf-Atlantic Coast Subprovince. Kauffman (1973a) added 36 endemic bivalve genera and subgenera (for example, *Paranomia, Periplomya, Postligata, Sexta, Brachymeris, Uddenia, Scambula, Aenona, Nelttia, Tenea, Fulpia* and *Pharodina*), and suggested possible division into a mid-temperate Atlantic coastal endemic center and warm-temperate to subtropical Gulf coastal endemic center. The bivalves *Anadara, Costellacesta, Tellinimera, Larma,* and *Cyclorisma* are endemic to the Atlantic and eastern Gulf Coast, and *Linter, Lycettia, Etea, Pollex, Sinonia,* and *Terebrimya* to the western Gulf Coast (Kauffman, 1973a, p. 369).

TETHYAN REALM

The Tethyan Realm includes all tropical to subtropical waters and biotas of the Cretaceous equatorial zone and South Pacific (Fig. 5). It is the most diverse and mature of Cretaceous paleobiogeographic units, and seems to reflect time-stability evolution in a relatively uniform environment (see discussion in Kauffman, 1973a). The Tethys Sea, restricted to Mediterranean Europe and the Indo-Pacific Ocean prior to the Cretaceous, spread westward across the tropical proto-Atlantic to the Americas with opening of the Caribbean Seaway (Late Jurassic, Early Cretaceous) and linked up with the tropical East Pacific at the present site of Central America to form a circumglobal tropical marine belt. This encouraged broad distribution of tropical invertebrates. These then became progressively isolated with Late Cretaceous tectonic constriction of both the Mediterranean and Caribbean arms of Tethys, and spreading of the Atlantic Ocean to widths that exceeded the extent of larval and mobile adult species dispersal from Eurasia and North Africa to America. High levels of Late Cretaceous endemism resulted, and biogeographic differentiation was great (Fig. 7). Diversity among many groups, especially bivalves (Kauffman, 1973a, fig. 7), gastropods, corals (Coates, 1973), and pelagic microbiota, increased throughout the Cretaceous in pulses that were tied to eustatic rise, transgressive peaks, and expansion of Tethyan influence north and south over epicontinental areas formerly occupied by warm-temperate seas (Coates, Kauffman, & Sohl, 1977).

In the Early Neocomian (Fig. 7), only the Indo-Mediterranean Region of Tethys was clearly defined by endemism; the poor faunas of the early Caribbean Sea were largely of Mediterranean affinities. Valanginian through Barremian time was characterized by high levels of faunal differentiation within the region, with formation of a North Indian Ocean Subprovince in the Valanginian, and Eastern and Western Mediterranean subprovinces in the Barremian (Fig. 7), which persisted to the end

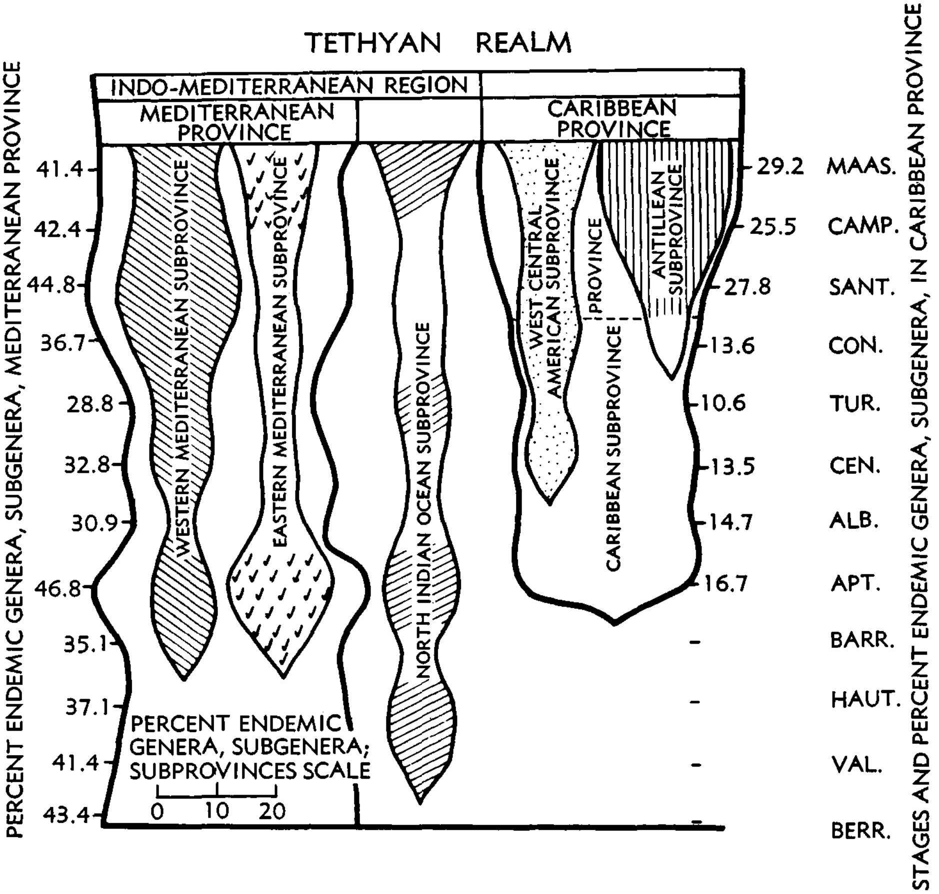


FIG. 7. Evolutionary trends in Cretaceous paleobiogeographic units of the Tethyan Realm, based mainly on bivalve Mollusca (after Kauffman, 1973a, fig. 3). Graphs show percent endemism of bivalve genera and subgenera within each unit, exclusive of cosmopolitan taxa. Scales for percent endemism in provinces (heavy lines) are shown on sides of graph. Scale for subprovinces (light lines) is shown in lower left. Origin point for each unit depicts the time at which endemism reached subprovincial rank (10-25 percent). For explanation of patterns, see Figure 6 caption. [Used with permission of Elsevier Scientific Publishing Co., Amsterdam.]

of the Cretaceous. These periods of differentiation apparently correlate with eustatic rises of sea level that produced moderate transgressions at continental margins. KAUFFMAN (1973a) called on two mechanisms to produce these Indo-Mediterranean subprovinces: 1) partial constriction of the Mediterranean Tethys during plate activity associated with closing of Tethys in Eurasia, producing barriers to east-west migration of marine organisms (sills?) and genetic isolation; and 2) "diversity pump" enrichment of local faunas (VALENTINE, 1967) resulting from isolation and differentiation of marginal Tethyan biotas in tropical epicontinental extensions of the sea during transgression, subsequent equatorial migration of these local biotas into specific regions of Tethys during regression, and their accommodation through niche partitioning among resident Tethyan faunas.

High levels of provincialism in the Caribbean first developed during the Middle Aptian (Fig. 7), associated with a moderate transgressive pulse reflecting global eustatic rise. The Caribbean Subprovince was formed and expanded to provincial rank by the Santonian. KAUFFMAN (1973a) suggested that this sudden jump in endemism might mark the point at which the middle tropical proto-Atlantic opened sufficiently to prohibit many pelagic larvae of benthonic taxa and mobile adults from regularly crossing this ocean barrier, resulting in widespread genetic isolation of similar stocks on both sides. High levels of niche specialization and radiation, especially within the rudist "reef" environment, also enhanced endemism in the Caribbean. Subsequently, partial isolation of Antillean and West-Central American Caribbean faunas occurred between Cenomanian and Coniacian times (Fig. 7), producing discrete subprovinces, and probably reflecting either early emplacement of marine barriers to migration in the present site of Central America or shifting current systems. The mid-Pacific Tethyan biotas are still poorly studied from dredge samples and cores drilled on atolls and other islands. The known biotas are generally Tethyan in aspect, containing rudist bivalves, but are of low diversity, and are most closely related to those of the West-Central American Subprovince (especially of Baja California). However, a distinct biogeographic unit may lie in the Cretaceous mid-Pacific.

Typical of the entire Tethyan Realm are rudist bivalves (Hippuritacea) (KAUFFMAN, 1973a; COATES, 1973), hermatypic corals (COATES, 1973), most larger benthonic foraminifers (DILLEY, 1971, 1973), highly diverse pelagic microbiotas, selected families of gastropods (SOHL, 1971), brachiopods (AGER, 1973), Lower Cretaceous belemnites (STEVENS, 1973), sponges (REID, 1967), echinoids, and numerous diagnostic ammonites.

Among the ammonites, WIEDMANN (1973) documented widespread heteromorphs (Ancycloceratina) in Tethys during the Early Neocomian (especially *Bochianites, Protancyloceras, Leptoceras,* and *Karsteniceras*); OWEN (1973) described his Albian "Tethyan-Gondwana Ammonite Province" as characterized by widespread lyelliceratid, brancoceratinid, mojsisovicsiinid, and mortoniceratinid ammonites. KENNEDY and COBBAN (1976) and CASEY (1971) noted that pseudoceratites such as *Parengonoceras* and Lower Cretaceous Berriasellidae are widespread in Tethys. In the Upper Cretaceous, according to MATSUMOTO (1973), Tethys is characterized by *Neolobites* ammonite faunas in the Cenomanian of Europe; by Desmoceratidae, Tetragonitidae, and Phylloceratidae in the Cenomanian-Turonian of the Indo-Pacific; by Turonian, Vascoceratidae and Tissotiidae with distinct southern and northern Tethyan assemblages of genera in the Mediterranean area; by Coniacian-Santonian, genera of Tissotiidae and Coilopoceratidae, with emphasis in warm water areas of the Indo-Pacific on genera such as *Kossmaticeras, Anapachydiscus, Damesites, Tetragonites, Gaudryceras, Hyphantoceras,* and *Scalarites*; and by local endemic groups of Campanian-Maastrichtian ammonites. STEVENS (1973) noted the spread of belemnites belonging to the genera *Hibolithes, Duvalia,* and *Conobelus* through much of the Tethys until the Barremian, when provincialism began (as in Bivalvia).

Among brachiopods, AGER (1973) noted wide Tethyan distribution, mainly within the Indo-Mediterranean Region, for Pygopiidae *(Pygope)* and *Septirhynchia.* COATES (1973) statistically documented strong similarities in hermatypic corals throughout the Lower Cretaceous Tethys, but development of strong post-Albian endemism between the Mediterranean and Caribbean provinces. Actaeonellid and nerineid gastropods characterize the Cretaceous Tethys virtually everywhere (SOHL, 1971), as do benthonic larger foraminifers, especially Lituolacea (including *Orbitolina* and associated genera such as *Dictyoconus, Choffatella, Cuneolina,* and *Pseudocyclammina*) and the "orbitoidal" foraminifers in the Upper Cretaceous (DILLEY, 1971, 1973). Many pelagic Globigerinacea were confined to circumglobal Tethyan and warm-temperate waters.

The Indo-Mediterranean Region has a marked endemic fauna, including Early Cretaceous ammonites of the Ancycloceratina such as *Hamulinites* and *Juddiceras* (WIEDMANN, 1973), genera of the Berriasellidae, and Late Cretaceous genera of the Vascoceratidae (for example, *Nigericeras, Paravascoceras, Fagesia*) (MATSUMOTO, 1973). Among Bivalvia, KAUFFMAN (1973a) listed nine genera that are endemic to the region, including *Trichites, Callucina (Callucinopsis), Pterolucina, Psilotrigonia, Arctomytilus,* and the rudist *Lapeirousia.* A similarly unique gastropod assemblage occurs, centered around genera and species groups of Nerineidae and Actaeonellidae. STEVENS (1973) noted Indo-Mediterranean restriction of several Lower Cretaceous belemnite groups belonging to the genera *Hibolithes, Duvalia, Neohibolites, Mesohibolites,* and *Parahibolites*; species groups of some of these genera show provincialism within the region. The *Neohibolites-Parahibolites* assemblage continued to characterize the region into the Cenomanian. DILLEY (1971) described a distinct larger foraminiferal assemblage from the Indo-Mediterranean region (his "Old World" Tethyan Province) centered around the Alveolinidae.

Subprovincial division of the Indo-Mediterranean Region is presently based on bivalves, Lower Cretaceous belemnites, and larger foraminifers. From the Valanginian onward the North Indian Ocean Subprovince (Fig. 5) became weakly to moderately well defined (Fig. 7) on the basis of endemic rudistid, cardiid, trigoniid, and eligmid bivalves such as *Dechaseauxia, Hardaghia, Stefaniniella, Collignonicardia, Libyaconchus, Praecardiomya, Bouleigmus,* and *Malagasitrigonia,* and larger foraminifers of the genus *Loftusia.* Early Cretaceous Ancyloceratina such as *Eocrioceratites, Menuthiocrioceras,* and *Parapedioceras* in Madagascar and Upper Cretaceous taxa detailed in the work of COLLIGNON (in BESAIRE & COLLIGNON, 1972) were endemic to the province up to the point that Madagascar became part of the temperate East African Province. STEVENS (1973) recorded an early Cretaceous split in Tethyan belemnite faunas into endemic groups, one of which *(Belemnopsis)* ranged through the Indo-Pacific during the Berriasian, with endemic species plexuses in the North Indian Ocean Subprovince.

The Tethyan Mediterranean Province (Fig. 5) was well established at the beginning of the Cretaceous and by Barremian time split into eastern and western subprovinces, each with strong endemic centers (Fig. 7). A suite of rudist, cardiid, and eligmid bivalves ranges throughout, but not beyond the province (KAUFFMAN, 1973a); this includes *Pseudoheligmus, Gonilia, Polyconites, Sabinia, Integricardium, Filosina,* and *Schiosia.* Endemic belemnites (STEVENS, 1973) appeared after earliest Cretaceous time and are mainly members of the Duvaliidae, and species plexuses of *Hibolithes, Conobelus, Mesohibolites,* and *Neohibolites.* COATES (1973) reported high levels of Late Cretaceous coral endemism in the Mediterranean. Certain groups of vascoceratid ammonites are likewise restricted to the province (MATSUMOTO, 1973). Among Foraminifera, DILLEY (1971, table 2) listed numerous endemic taxa in his "Old World Tethyan Province" among Late Cretaceous Lituolacea and Alveolinidae (especially most Alveolininae).

Eastern and Western Mediterranean subprovinces (Fig. 5) were exceptionally well defined after the Barremian on the basis of bivalves, belemnites, and larger foraminifers. The Western Mediterranean Subprovince, extending across southern Europe to the Balkans, and across North Africa to Egypt, is mainly characterized by a diverse suite of endemic rudistid bivalves such as *Bayleia, Matheronia, Valletia, Caprotina, Sphaerulites, Praelapeirousia, Orthoptychus, Roussleia, Medeela, Radiolitella,* and *Synodonites,* by belemnites of the Duvaliidae, and by certain larger foraminifers of the Alveolinidae (for example, latest Cretaceous *Murciella*; DILLEY, 1973, fig. 9).

The Eastern Mediterranean Subprovince (Fig. 5) is even more clearly defined by endemism in the same groups. Among larger foraminifers, species of *Loftusia* (Lituolacea) are largely restricted to the subprovince as are species of the alveolinid *Sellialveolina* (DILLEY, 1973, fig. 8), belemnite species of *Conobelus* and *Pseudobelus* (pre-Barremian), *Mesohibolites* and *Curtohibolites* (Barremian), *Parahibolites* (Cenomanian), and at the warm-temperate to subtropical margin, the Campanian *Belemnitella praecursor* group (STEVENS, 1973), and a small group of endemic bivalve genera, including *Agapella, Asiatotrigonia, Corbiculopsis, Vautrinia* and *Turkmenia* (KAUFFMAN, 1973a).

In both the Eastern and Western Mediterranean subprovinces, local endemic centers based on bivalve genera (mainly rudists) are defined by KAUFFMAN's (1973a) quantitative biogeographic method. In the west these include a strong southern French center (including the rudists *Retha, Offneria, Fossulites, Robertella, Arnaudia*), an Italian center (rudists include *Paronella, Apulites, Colveraia, Joufia, Pileochama*), and a Yugoslavian center (including the rudists *Neocaprina, Yvaniella, Gorjanovicia, Kuehnia, Neoradiolites, Pseudopolyconites, Milanovicia*). In the Eastern Mediterranean Subprovince these include a well-defined Syrian-Lebanese Endemic Center with *Arcullaea, Xenocardia, Syrotrigonia, Megalocardia, Nemetia,* and *Paracaprinula,* and a weakly defined Iranian Endemic Center with *Rostroperna, Dictyoptychus,* and *Osculigera.* Causes for local genetic isolation and resultant endemism of these bivalve assemblages are thought to center around collapse of the Mediterranean carbonate platform during Cretaceous closing of Tethys, and formation of numerous isolated "microcontinents" or large islands in the northern Mediterranean Tethys.

The Caribbean Province (Fig. 5) first developed during the Aptian and differentiated into West-Central American and Antillean subprovinces by the Coniacian (Fig. 7). Rudistid bivalves primarily serve to differentiate this province and the two subprovinces, but strong endemism among gastropods and larger foraminifers is also known, and ongoing studies of the hermatypic corals also indicate numerous endemic groups (COATES, 1973). Characteristic rudists of the Caribbean Province include *Amphitriscoelus, Caprinuloidea, Coalcomana, Planocaprina, Titanosarcolites, Barrettia, Praebarrettia, Chiapasella, Tampsia,* and *Tepeyacia*; the infaunal *Glycymeris (Glycymeris)* is similarly restricted. Endemic middle Cretaceous ammonites of the genera *Dufreynoyia, Hypacanthoplites, Drakeoceras, Budaiceras,* and numerous Mojsisovicziinae evolved in isolated basins behind barrier-reef tracts in the northern subtropical margin of the Caribbean Province (YOUNG, 1972). Two major groups of larger foraminifers, the pseudorbitoids and the Chubbininae, were endemic to the Caribbean Province (DILLEY, 1973). SOHL (1971) listed typical Caribbean Province gastropods, including many nerineid and actaeonellid groups, and endemic genera and species groups of fissurellids, trochids, neritids, cerithiacians, cypraeids, and strombids.

Division of the Caribbean Province into subprovinces has been made exclusively on analysis of Bivalvia, mainly rudistids and cardiids (KAUFFMAN, 1973a). The Antillean Subprovince (Fig. 5) is characterized by endemic genera such as *Bayleoidea, Pseudobarrettia, Anodontopleura, Barycopites,* and *Immanitas* with a weak, Mexican Endemic Center established around species of *Palus,* a strong Greater Antilles Endemic Center based on endemic *Parastroma, Torreites, Antillocaprina,* and *Parabournonia,* and endemic species of *Kipia* restricted to Trinidad. The West-Central American Subprovince (Fig. 5) is mainly defined on *Coralliochama, Incacardium, Vepricardium (Perucardia), Tortucardia, Peruarca,* and *Pettersia.*

SOUTH TEMPERATE REALM

All temperate-zone biotas south of Tethys are grouped within this realm (Fig. 5), which is one of the least studied and most poorly defined of Cretaceous paleobiogeographic units. Factors that account for relatively low levels of temperate diversity and endemism in the South Temperate Realm include: 1) much of the South Pacific was under the influence of tropical to subtropical waters in the Jurassic and Early Cretaceous; 2) the Tethyan-South Temperate boundary shifted slowly northward through the Cretaceous and for the first time allowed an expanded temperate zone in the South Pacific; and 3) both the opening of the South Atlantic and widespread separation of the Gondwanaland continents were mainly Late Cretaceous events. In all cases, South Temperate marine faunas were in an early stage of differentiation during the Cretaceous, with predictably low diversity and low levels of endemism. The biogeographic evolution of the realm (Fig. 8) was correspondingly simple. Following initial separation of Africa and South America by, first, shallow epicontinental seas and later narrow oceanic troughs, faunas of both the Euramerican temperate region (mainly) and the Caribbean-Mediterranean part of Tethys

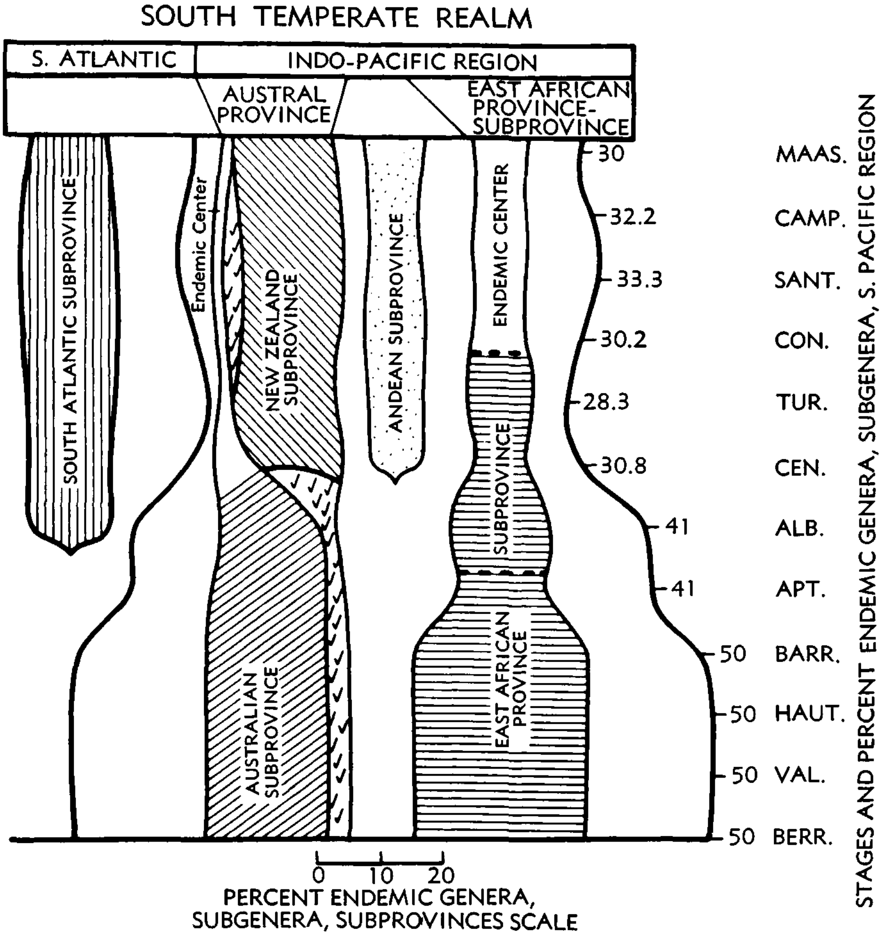


FIG. 8. Evolution of Cretaceous paleobiogeographic units in the South Temperate Realm, based mainly on bivalve Mollusca (after Kauffman, 1973a, fig. 5). Graphs show percent endemism among bivalve genera and subgenera for each area, exclusive of cosmopolitan taxa. Scale for endemism in Indo-Pacific Region at right, and scale for subprovince graphs at base of figure. For explanation of patterns, see Figure 6 caption. [Used with permission of Elsevier Scientific Publishing Co., Amsterdam.]

immigrated into the South Atlantic. Separation of the South Temperate elements from more highly evolved North Temperate biotas by the tropical Tethyan seaway led to low levels of endemism in the South Atlantic, which did not reach subprovincial grade until the Albian (Fig. 8). This corresponded with the first large-scale epicontinental transgression onto Cretaceous continents, including those bordering the South Atlantic. South Atlantic endemism did not exceed subprovincial rank throughout the Cretaceous, and due to the short distances for larval and mobile adult migration across the proto-South Atlantic, invertebrate faunas of eastern South America and West Africa remained closely related. Bivalve genera such as *Euptera, Agelasina, Anofia, Naulia, Sergipia, Pseudopleurophorus,* and *Gilbertharrisella* characterize the subprovince (KAUFFMAN, 1973a).

The biogeographic evolution of the southern Indo-Pacific Region during the Cretaceous was much more complex and involved both tectonic and climatic controls. Tectonically, the Cretaceous continuation of the breakup and dispersal of parts of Gondwanaland caused further isolation of their marginal marine shelf biotas. The east-west separation of East Africa and Australia continued, as did the early northward migration of the Indian subcontinent. Australia may have partially separated from Antarctica during the Cretaceous, moving slightly northward, and there is faunal evidence for accelerated post-Neocomian separation of New Zealand from Australia to the point where genetic isolation occurred, producing significant molluscan endemism on New Zealand. Thus, Cretaceous plate movements in some cases led to genetic isolation and endemism among South Pacific invertebrates. But based on distances between major marine shelf areas suggested by plate reconstructions such as those of DIETZ and HOLDEN (1970) and SMITH, BRIDEN, and DREWRY (1973), the degree of continental separation was not sufficient to account for the high levels of endemism observed here in the Cretaceous invertebrate faunas. KAUFFMAN (1973a) proposed an additional isolating mechanism; that is, climatic deterioration of the South Pacific resulted from a major Late Cretaceous cooling trend and northward movement of, first, the Tethyan-temperate climatic boundary (Jurassic-Early Cretaceous) followed by the warm temperate-mid temperate boundary (Lower Cretaceous) and late in the period, the cool-temperate boundary across Gondwana. Decline of tropical faunal influence from the Jurassic onward supports this (STEVENS, 1965; KAUFFMAN, 1973a). The combination of moderate tectonic separation and the differentiation and northward migration of temperate climatic zones across dispersed parts of Gondwanaland is called upon to produce isolating mechanisms and to explain observed Cretaceous endemism.

The temperate Indo-Pacific Region is characterized by widespread endemics among the bivalves (for example, *Iotrigonia, Megatrigonia, Pacitrigonia, Maccoyella*) as well as by bivalves common to the region but with limited outside distribution (for example, *Acharax, Fimbria, Freiastarte, Parapholas, Monothyra, Steinmanella,* and *Neocrassina*) (KAUFFMAN, 1973a). MATSUMOTO (1973) cited numerous genera of ammonites that have species groups typical of the Indo-Pacific Region such as Cenomanian-Maastrichtian Desmoceratidae (*Desmoceras, Puzosia, Mesopuzosia,* and *Pachydesmoceras*), Tetragonitidae *(Gaudryceras, Anagaudryceras),* Phylloceratidae *(Hypophylloceras, Neophylloceras),* and the Kossmaticeratidae (*Marshallites, Kossmaticeras, Maorites, Grossouvrites,* and *Jacobites* species plexuses). Many of these were more characteristic of tropical zones but ranged into warm-temperate areas as well. Important Lower Cretaceous Indo-Pacific ammonite groups are the Albian Lyelliceratidae, Brancoceratidae, Mojsisovicziinae, and Brancoceratinae, many of which were shared with Tethys proper. STEVENS (1973) clearly documented evolution of an endemic temperate Indo-Pacific belemnite assemblage beginning with the *Belemnopsis madagascarensis–B. patagoniensis* lineage in the Valanginian and Hauterivian, and including the Late Neocomian through Cenomanian Dimetobelidae (restricted to the Austral Province after the Cenomanian).

Two major divisions of the temperate Indo-Pacific Region were established at the beginning of the Cretaceous, an East African Province extending from South Africa to (in Late Cretaceous time) Madagascar, and an Austral Province (Figs. 5, 8). Both show marked decline in endemism in the Upper Cretaceous (Fig. 8), and this is correlative with and directly related to marine climatic decline with global cooling and northward shift of more temperate zones across the southernmost Pacific (STEVENS, 1965; KAUFFMAN, 1973a). Faunal differentiation between these two regions is thought to reflect eastward drift of Australia to distances that exceeded large-scale faunal exchange through larval drift.

The Austral Province contains two subprovinces that are basically time successive (Fig. 8), a strong Early Cretaceous Australian Subprovince that declined to a weak endemic center during the Late Cretaceous; here it was replaced by a well-defined New Zealand Subprovince that has no Early Cretaceous expression. Few taxa are endemic to the entire province, *Maccoyella* being the principal bivalve, the Dimetobelidae among belemnites, and the hoplitid ammonite *Chimbuites* (Cenomanian). Most of the Austral ammonite and bivalve fauna is comprised of widely spread Pacific and Tethyan forms.

The Australian Subprovince is most clearly defined, as presently known, by its endemic bivalves; other groups have not been similarly analyzed. Important endemic genera are *Pseudavicula, Austrotrigonia, Nototrigonia (Callitrigonia), N. (Nototrigonia), Cyrenopsis, Barcoona,* and *Tatella* in the Lower Cretaceous, and *Climacotrigonia, Actinotrigonia, Entolium (Cteniopleurium),* and *Fissiluna* in the weakly defined Upper Cretaceous Australian Endemic Center (Fig. 8). The sharp decline in endemism within the Australian Subprovince has yet to be satisfactorily explained.

The New Zealand Subprovince (Fig. 5) became sharply defined in the Cenomanian and continued as a distinct biogeographic unit through the Maastrichtian (Fig. 8). The abrupt development of New Zealand endemism is readily explained in terms of marine history. The oldest marine invasions were of Aptian age, and these were marginal transgressions characterized by low diversity faunas drawn from generalized Austral and more widely ranging Pacific stocks. Major epicontinental flooding of New Zealand first occurred in the Cenomanian and continued through the Cretaceous, producing environments for diversification and local isolation of invertebrate taxa—conditions leading to the development of endemism. KAUFFMAN (1973a) has suggested that the abrupt development of high levels of Cenomanian endemism in New Zealand might also reflect its plate tectonic separation from Australia and Antarctica to the point where faunal exchange was restricted, as well as development of climatic barriers to migration. Endemism in the New Zealand Subprovince has been defined mainly on Bivalvia, and the subprovince is characterized by genera such as *Chlamys (Mixtopecten), Electroma, Megaxinus (Pteromyrtea), Myrtea, Lahillia, Marwickia, Dosinobia,* and *Cyclorismina,* some of which have limited outside distribution.

The East African Province was well defined at the beginning of the Cretaceous (Fig. 8) but gradually declined in endemism to subprovincial rank by Albian time, and endemic center rank in the Coniacian. This decline is directly related to environmental deterioration with cooling of the South Pacific and northward migration of temperate climatic belts throughout the Cretaceous (KAUFFMAN, 1973a), eventually bringing areas as far north as Madagascar within range of temperate waters. Numerous bivalve genera are endemic to this province (for example, *Pleurotrigonia, Sphenotrigonia, Herzogina, Isotancredia, Megacucullaea,* and Madagascar lineages of *Malagasitrigonia*). COLLIGNON (in BESAIRE & COLLIGNON, 1972) has documented immense numbers of ammonites that seem to be restricted to this subprovince, and in many cases to Madagascar. The belemnite *Belemnopsis* is most abundant in this subprovince, although it ranges less commonly elsewhere.

The Andean Subprovince (Fig. 5), extending from Patagonia to southern Peru, is weakly defined; it was initiated with the first major epicontinental flooding of the west coast of South America during the Cenomanian (Fig. 8). The subprovince was isolated from western and most southern Pacific biotas by the vast water barrier of the southeast Pacific, and from north temperate faunas by the tropical Caribbean arm of Tethys. Some taxa that populated this warm-temperate subprovince were obviously drawn from the Caribbean Province, but most stocks probably came from the south through Patagonia. Population of this marine shelf area was slow after Cenomanian flooding, reflecting restriction of source areas, and endemism is consequently low. KAUFFMAN (1973a) has noted a few endemic bivalves; for example, *Anopisthodon* and *Aulacopleurum* from the Lower Cretaceous, and the same genera, in addition to *Mulinoides* and *Tellipiura,* in the Upper Cretaceous. Among other taxa, phylogenic relationships are clearly strongest southward, through Patagonia to the Austral and East African provinces.

SUMMARY AND SOME OBSERVATIONS ON EVOLUTION

A recurrent theme throughout this résumé of Cretaceous marine history and invertebrate faunas has been the dynamic relationship between major tectonic, oceanographic, and climatic changes during the period—the large scale forces of natural selection—and evolution at all levels. Thus, evolutionary rates and patterns within lineages, ecological units, and paleobiogeographic units vary tremendously in response to the rate and intensity of Cretaceous environmental changes, especially those triggered by periods of active plate tectonism. There is no long-term environmental stability or evolutionary stasis in the Cretaceous, and this demands that interpretation of invertebrate history be based on sampling intervals and analytical techniques that are designed to consistently test the dynamics of the system.

In regard to Cretaceous paleobiogeographic units, a stage-by-stage quantitative analysis of endemism yields the most detailed and consistent divisions, and allows comparison of units from relatively narrow time intervals with modern counterparts. Using this method, it becomes obvious that Cretaceous biogeographic units were nearly as complex as those of today, and showed dynamic changes—appearance and disappearance, variations in magnitude (as measured by endemism), and changes in spatial influence—throughout the period (Figs. 6-8). These variations were very closely linked to global plate-tectonic changes and climatic trends. Genetic isolation leading to significant endemism resulted from many processes: 1) sea floor spreading and progressive separation of marine shelf areas; 2) dispersal of microcontinents or pieces of supercontinents through plate tectonic events; 3) isolation of biotas through point collision of plates, as in the Mediterranean, or by tectonic emplacement of biogeographic barriers; and 4) isolation of biotas in epicontinental seaways during transgressive-regressive pulses (reflecting eustatic fluctuations) that themselves were generated by plate tectonism. Rates of faunal differentiation, leading to development and modification of paleobiogeographic units, are directly correlative with rates and intensity of the isolating mechanisms.

The decline of Cretaceous paleobiogeographic units was similarly related to 1) mass competition among distinct biotas brought into contact through plate movements or the flooding of epicontinental seas during eustatic rise, and 2) environmental decline resulting from lowering global temperatures and equatorward migration of progressively cooler temperate climatic zones. With the possible exception of the Late Cretaceous decline in Australian endemism, all evolutionary changes in Cretaceous paleobiogeographic units can be directly related to these tectonic, climatic, and biological factors. Figures 6-8 summarize the dynamic evolutionary trends within Cretaceous paleobiogeographic units.

Similarly, marine diversity during the Cretaceous increased in an irregular manner for most prominent groups between Berriasian and Campanian time (Fig. 9), with diversity fluctuations closely tied to major eustatic fluctuations (SOHL, 1967; TAPPAN, 1968, 1971; TAPPAN & LOEBLICH, 1971, 1972; KAUFFMAN, 1973a; FISCHER & ARTHUR, 1977; among others). Some Cretaceous groups continued their evolutionary diversification through the Maastrichtian and into the Paleogene, whereas others show marked decline and even total extinction at the Cretaceous-Tertiary boundary. Thus, TAPPAN and LOEBLICH (1972, p. 205) noted that "most protistan groups had coincident evolutionary bursts and declines, with similar fluctuations in their evolutionary rates" and were ". . . . intimately related to the selective pressures of the changing global environment. Advancing and retreating epicontinental and shelf seas and changes in continental position and height affected atmosphere and oceanic circulation and the climatic regime, causing variations in nutrient supply and fluctuations in productivity and food resources." They noted greatly increased diversity among protists of various types in the Upper Cretaceous associated with environmental stability and climatic amelioration produced by major periods of transgression, and great decline in latest Cretaceous protistan diversity associated with climatic deterioration and the

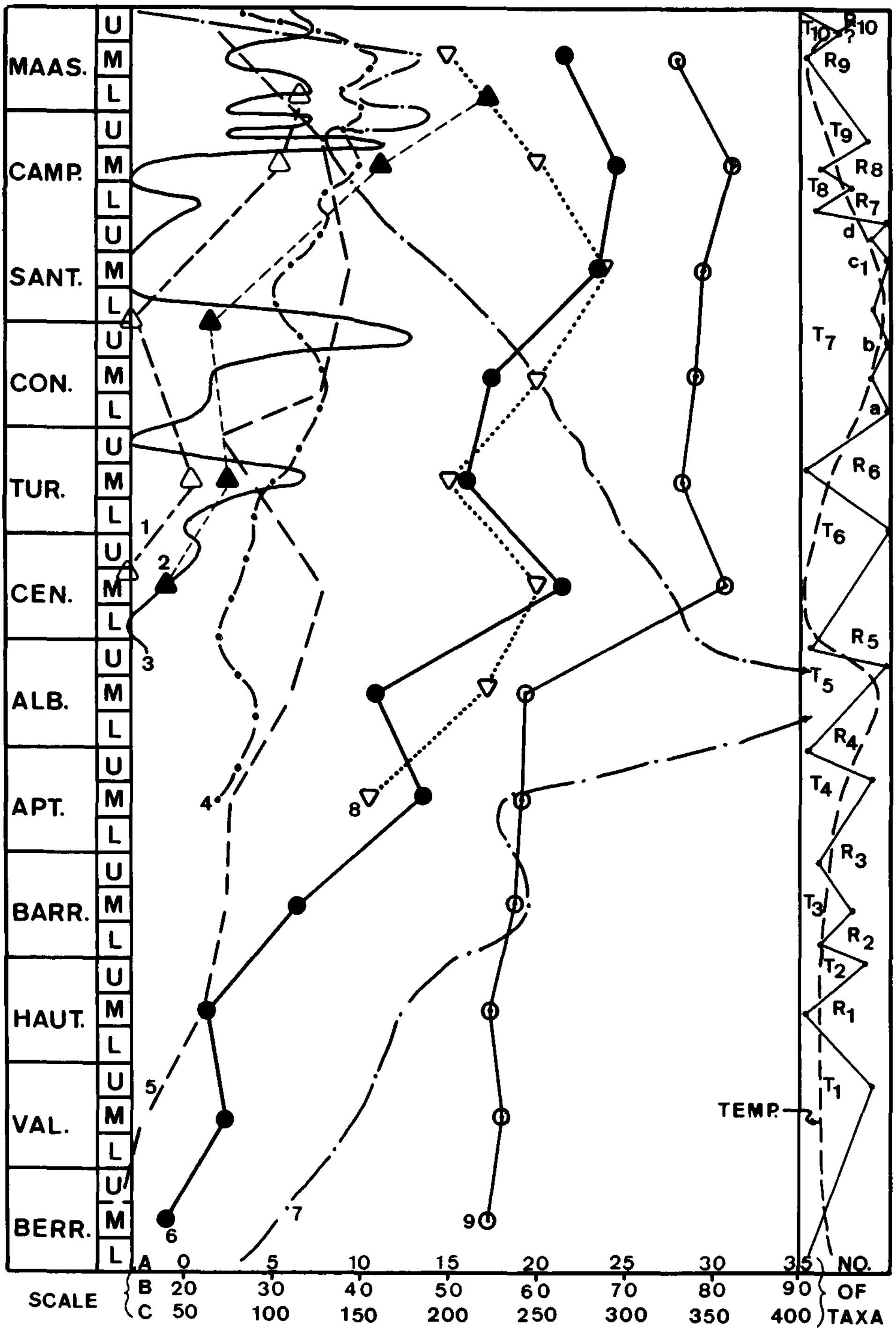


FIG. 9. Selected diversity curves for the Cretaceous. Curve 5 is plotted to scale A (bottom of chart), curves 1-3 and 6-8 to scale B, and 4 and 9 to scale C. Numbers and information for each curve are:

time of the major Maastrichtian regression (Fig. 9). Of particular interest is the close correlation of high dinoflagellate diversity with several Cretaceous transgressive maxima (Fig. 9) and low diversity with regression (TAPPAN & LOEBLICH, 1971, fig. 6). FISCHER and ARTHUR (1977) broadly analyzed pelagic Cretaceous diversity and concluded that protistans, ammonites, and marine reptiles, as well as pelagic ecological structure, increased significantly in conjunction with Albian and Coniacian-Santonian eustatic rise, epicontinental transgression, temperature rise, and climatic amelioration. SOHL (1967) has shown high diversification among gastropods of the North American Interior Subprovince to be associated both with transgressive maxima (Turonian, Coniacian, Late Campanian) and with regressive pulses near their stress maxima (Lower and Middle Campanian, Maastrichtian). Selected diversity curves from these sources are shown in Figure 9.

Some of the most detailed analyses of diversity and its relationship to Cretaceous environmental fluctuations have been made on Bivalvia (KAUFFMAN, 1973a, figs. 6-10; summarized here in Fig. 9). Diversity of bivalve genera and subgenera increased throughout the Cretaceous, with a small decline at the Maastrichtian regression and Cretaceous-Tertiary boundary. The rate of increase was irregular; diversity increased in pulses that are correlative with several of the eight transgressive maxima, reflecting eustatic rise generated through plate tectonism. Specifically, diversity increases were associated with Valanginian (Fig. 2; T_1), Aptian (T_4), latest Cenomanian (T_6), Coniacian-Santonian (T_7), and Middle Campanian (T_8) transgressive peaks. The most dramatic increase in diversity was during the great Cenomanian transgression, an extremely active period of sea floor spreading, genetic isolation, and probably the greatest epicontinental flooding during the Cretaceous. Most of the diversity increase occurs in Tethys; increase in temperate bivalves is low but more steady, and cosmopolitan bivalves retained a constant diversity level during the Cretaceous. In the overall trend toward increasing diversity of bivalves, reversals in the trend were also associated with eustatic fluctuations and peaked at times of maximum regression for the most part (Fig. 2; Hauterivian $= R_1$; Late Albian $= R_5$; Middle Turonian $= R_6$; and Late Maastrichtian $= R_8$ of KAUFFMAN's, 1973a, transgressive-regressive sequence).

Thus, many groups of Cretaceous invertebrates show diversity patterns that are primarily tied to transgressive-regressive marine epicontinental cycles, representing tectonically generated eustatic fluctuations. High marine shelf and pelagic diversity peaks were closely tied to major transgressive episodes characterized by increasing ecological space and niche opportunities, decreasing environmental stress, temperature increase and climatic amelioration. Lower diversity was associated with environmental decline, lowering of marine temperatures, decrease in ecospace and niche diversity, and epicontinental regression. Figure 9 records data for several invertebrate groups that document these relationships at various levels of refinement.

Similarly, the variable evolutionary history of lineages and higher taxonomic cate-

FIG. 9. *(Continued from facing page.)*

1–Pacific Province planktonic foraminiferal species, excluding Guembelitriinae (Douglas, 1972); *2*–Tethyan planktonic foraminiferal species, excluding Guembelitriinae, North America (Douglas, 1972); *3*–gastropod species, Western Interior North America (Sohl, 1967); *4*–planktonic globigerinid species, worldwide (Fischer & Arthur, 1977); *5*–dinoflagellate species, worldwide (Tappan & Loeblich, 1971); *6*–Tethyan bivalve genera, worldwide (Kauffman, 1973a); *7*–ammonite genera, worldwide (Fischer & Arthur, 1977); *8*–total phytoplankton species/10 (Fischer & Arthur, 1977); *9*–total bivalve genera (Kauffman, 1973a). Detail of transgressive-regressive history and generalized temperature curve (dashed line) shown in right-hand column (for sources see Fig. 2). Note relationship between large-scale transgression, warming of oceanic climates, and diversity increase among varied organisms in the Albian and Coniacian-Santonian stages. Also, diversity peaks among certain groups correlative with transgressive maxima in the Middle to Late Valanginian, Middle Barremian, Middle Aptian, Cenomanian to Early Turonian, Middle Campanian, and late Middle to Late Maastrichtian (from Kauffman, 1977f; used with permission of Rocky Mountain Assoc. Geol., Denver).

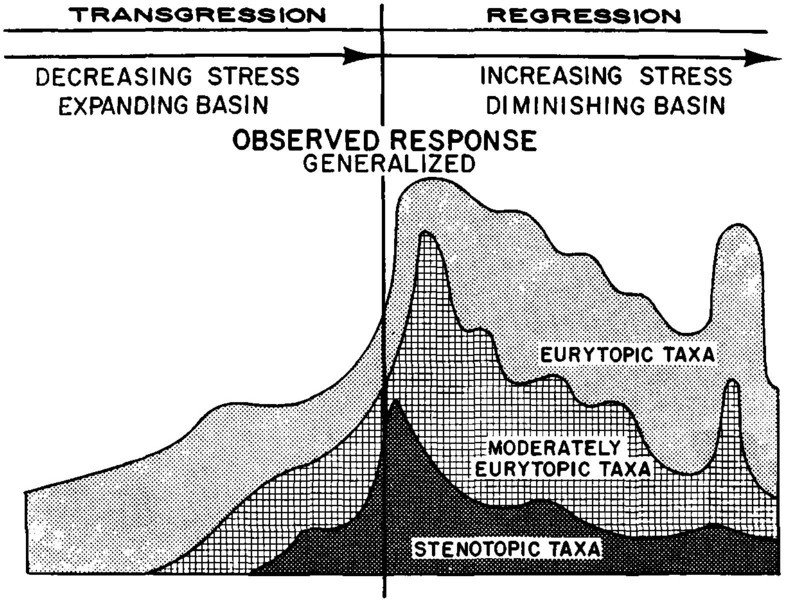


FIG. 10. Generalized model of evolutionary response by Cretaceous mollusks to eustatic changes of sea level (from studies of North American lineages; Kauffman, 1972). Graph implies increasing rates of evolution with expanding ecological opportunities during transgression, but highest evolutionary rates during regression and onset of stress conditions associated with decreasing ecospace, restriction of habitats, and increased competition. Times of maximum evolution differ for different lineages and adaptive strategies depending on degree of ecological specialization and habitat.

gories during the Cretaceous seems to show strong correlation with tectonic, oceanographic, and climatic changes. For example, evolutionary rates and patterns within single lineages, or classes, or ecological strategies of Cretaceous marine invertebrates are complex, and appear to vary primarily in response to eustatic changes in sea level, transgressive-regressive pulses, and correlative changes in physical environments, temperature, and climatic equitability (Figs. 9, 10). In other words, evolution rates vary with the intensity and rate of change of environmental stress factors (KAUFFMAN, 1970, 1972, 1977a). Global transgressions represent ameliorating marine environments and low physical stress periods, with expanding ecospace, niche opportunities, resources, and decreasing biological competition. Maritime climates predominate, reducing seasonality and increasing annual temperatures. Rates of evolution for most invertebrates are relatively low during transgression and are mainly controlled by the amount of new ecospace and niche opportunities into which "preadapted" groups can radiate rapidly. The most rapid evolutionary rates during transgression seem to be among two distinct groups: 1) early colonizing taxa that are subjected during later transgression to severe biological stress through widespread competition by the stenotopic specialists that replace them; and 2) taxa with new or modified adaptive strategies that give them a major competitive advantage within their potential niches and enhance their rapid radiation, as in rudist bivalves (KAUFFMAN, 1977a). Thus, although Cretaceous transgressions were times of marked increase in invertebrate diversity, they were not necessarily correlative with rapid evolutionary rates for most organisms until peak transgression.

KAUFFMAN (1970, 1972, 1977a) found high rates of molluscan evolution associated with peak transgression and the regression immediately following it. TAPPAN and LOEBLICH (1971, 1972) suggested the same for planktonic organisms, and SOHL (1967) in part for North American gastropods. Groups that underwent rapid evolution at or near peak transgressions were largely pelagic and offshore benthonic stenotopes responding to two types of increased stress situations: 1) relatively abrupt increase in surface water temperature and epicontinental salinity in temperate Cretaceous seas associated with major transgressive peaks (as determined isotopically, SCHOLLE & KAUFFMAN, 1977; and faunally KAUFFMAN & SCHOLLE, 1977), and 2) the initial shock of epicontinental regression associated with a concomitant lowering of temperate epicontinental water temperatures and salinities following peak transgression. Environmentally sensitive stenotopic organisms and microplankton were the groups most affected by these shifting environments. Among the benthos, gastropods especially were stressed by these changes and show strong increases in rates of evolution and extinction associated with peak transgression and earliest regression (SOHL, 1967; KAUFFMAN, 1972, for North America).

The most rapid rates of evolution documented for Cretaceous invertebrates (North American interior mollusks) were associated with later phases of marine regressions, increasing physical stress and biological competition, and diminishing ecospace, niches, and resources (KAUFFMAN, 1970, 1972, 1977a). Extinction was also high during these periods so that total diversity decreased. Among diverse North American Cretaceous molluscan species, representing most adaptive strategies and levels of environmental tolerance, a graded series of speciation peaks occurred during regression, with offshore stenotopes and many pelagic taxa peaking during early regression, moderately stenotopic shallow-water taxa peaking during mid-regression, and more eurytopic organisms as well as some nearshore stenotopes peaking near terminal regression and maximum environmental stress levels. Varied levels of extinction characterized peak regression. These studies clearly indicate an intimate relationship between evolutionary rates and patterns, environmental tolerance (stenotopy vs. eurytopy), and stress factors associated with eustatic global fluctuations and transgressive-regressive pulses in epicontinental seas. KAUFFMAN (1977a) has further shown a close correlation between evolutionary rates and ecological strategies among American Cretaceous mollusks. In a preliminary test it was found that under the same general sets of environmental changes: 1) feeding specialists evolved faster than feeding generalists; 2) epifaunal and some pelagic organisms evolved faster than semi-infaunal taxa, and these in turn faster than shallow and deep infaunal taxa; and 3) shallow-shelf taxa (especially epifaunal forms) evolved faster than either deep-water taxa on the one hand, or very shallow sublittoral, intertidal, brackish water, and freshwater taxa on the other. In each case, rapid evolutionary rates were related to ecological strategies that subjected the organism to high chance of unpredictable environmental perturbations through geological time. No relationship was found between morphological complexity and evolutionary rate among the Cretaceous organisms tested.

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TERTIARY[1]

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CONTENTS

GENERAL TRENDS

The Tertiary Period is well known as the Age of Mammals and Angiosperms. Because many richly fossiliferous sediments are still soft and little-altered diagenetically, it is possible to analyze all inorganic and biologic events recorded by them in much more detail than for older periods. The duration of the Tertiary is approximately 70 million years (Papp, 1959).

During Tertiary time, conditions developed that determined the nature of present continents, together with the make-up of their faunas and floras. Whereas Early Tertiary paleogeography differed considerably from that of the present, Late Tertiary conditions gradually approached those that exist now. The hypothesis of continental drift postulates that it was only during Tertiary time that the earth's continents reached their present positions.

During the Tertiary, the worldwide orogenies of the Alpidic Era occurred. They include numerous orogenic phases that had their origins in the Mesozoic. In connection with these crustal movements, widespread intense vulcanism, to which many presently active volcanoes owe their origin, took place. Pacific granite intrusions, vast basalt extrusions, and plateau deposits of volcanic rocks are witnesses of Tertiary volcanism. Examples are found in the volcanic belt stretching from Greenland across

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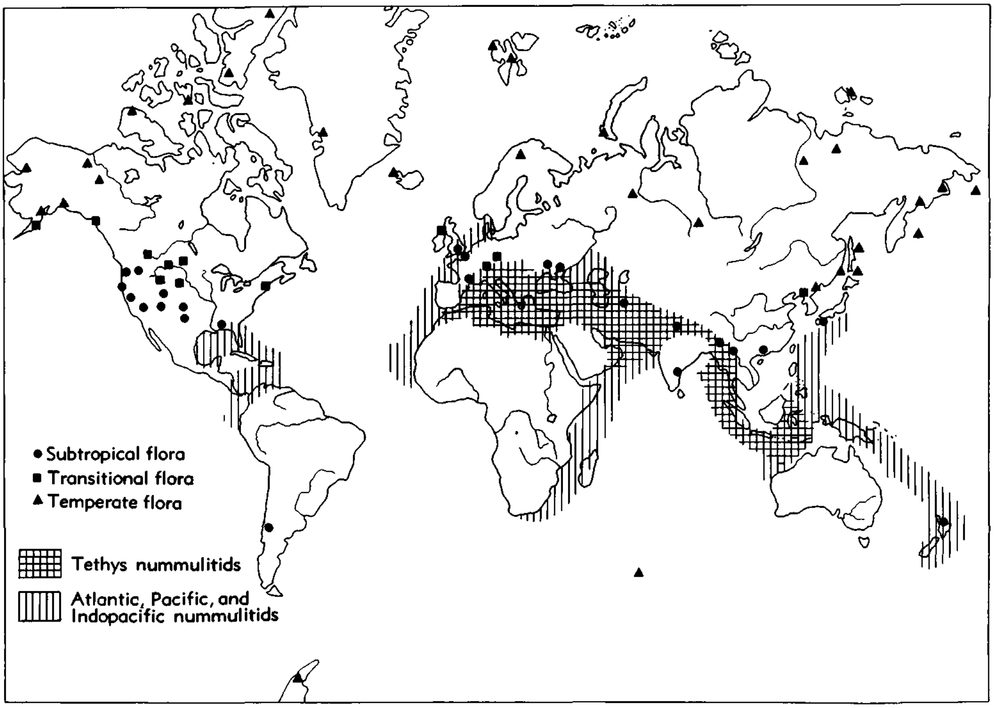

FIG. 1. Distribution of nummulitids and flora in the Early Tertiary (after Brinkmann, 1966).

Iceland to Scotland, the basalt flows of the Columbia and Colorado plateaus of North America, and the Deccan traps of peninsular India, which cover 100,000 sq km in considerable thickness.

The climate, assessable through numerous indications, was influenced by poleward shift of tropical and temperate zones during the Early Tertiary (Fig. 1). During the middle Eocene temperatures reached their optimum. The flora of the Paris basin, for example, has a tropical character. From the Eocene onward a continuous deterioration of the climate is noticeable, leading through a subtropical and warm temperate to a temperate climate, presaging the coming Ice Age. The belt of carbonate sediments became narrower. Measurements of 0^{16}-0^{18} indicate that during the Miocene the temperature at the bottom of the deep sea dropped from 10° C to 7° C, and later to the present 1.5° C. At the same time the northern limit of coral reefs receded toward the equator. During the Miocene northern Pacific mollusks reached the North Atlantic and the North Sea basin by way of the Arctic region.

On the Eurasian continent and in North America the development of savannas and bush steppes can be noted. Gradually, the distribution pattern of faunas and floras of the holarctic region developed into its Holocene picture. The disappearance of Tethys caused a division of this faunal region into three separate units: the Indo-Pacific, the Mediterranean, and the Caribbean faunal provinces. With the beginning of glaciation in the polar regions, especially the Antarctic, the scene was set for beginning of the Pleistocene and Quaternary.

The basis of paleogeography is recent geography, and all that can be done is to map the present distribution of Tertiary sediments. Tectonic processes in separate mountain ranges, and even in their individual parts, are often very complicated. Because of limitations of allotted space here, only their most important features can be outlined.

Undoubtedly, climate influences the evolu-

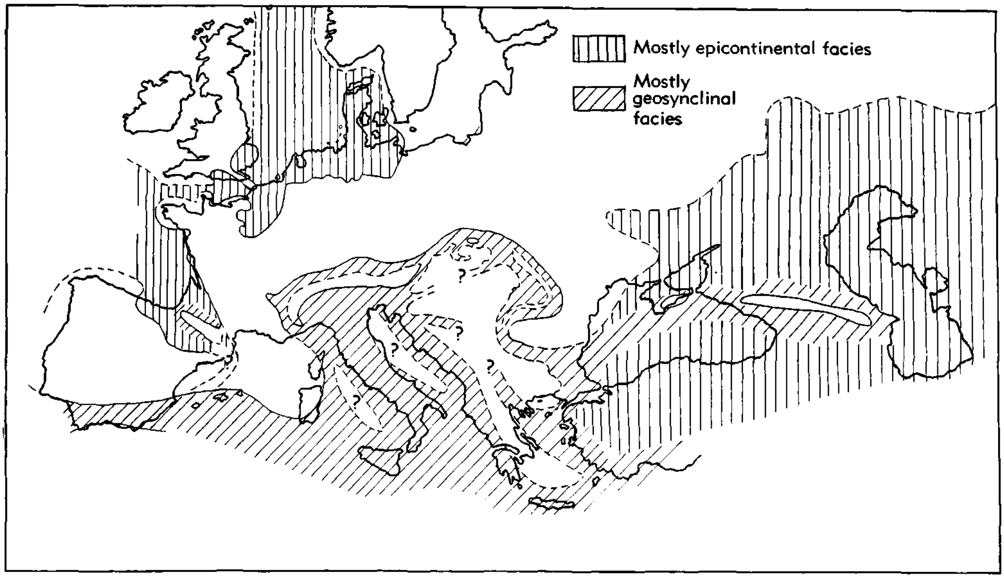

FIG. 2. Distribution of Eocene sediments in Europe (after Papp, 1959).

tion of organisms. Biostratigraphy in the Tertiary also is based on the evolution of organisms and has to be given special prominence in the present contribution.

DISTRIBUTION OF TERTIARY SEDIMENTS

EUROPE

The Paleogene of western Europe is developed in marine-epicontinental facies interbedded with brachyhaline and limnic-fluviatile sediments. The thicknesses of these sediments are relatively small. The facies changes caused by repeated marine transgressive and freshwater cycles facilitate stratigraphic subdivisions. All type sections of the stages of the Paleogene and most of the classical localities belong to this area (PAPP, 1959).

Epicontinental facies in western Europe are developed in the following areas: the Paris basin, with rich and typical faunas; Belgium; Great Britain (in the London and Hampshire basins); connecting with these toward the east, the northwest German, and Danish Paleogene (Fig. 2).

The Paleogene of the Aquitaine basin in the area of the Pyrenees is seen already to have developed characteristics of the nearby geosynclinal facies. The mountain ranges of the Alpidic area in southern Europe (southern Spain, Italy, Greece), and likewise the area of the Alps, Carpathians, Balkans, Crimea, and Caucasus, exhibit the Paleogene in geosynclinal facies. Its characteristic sediment, the Flysch, shows a repeated interbedding of sandstone (turbidites) and marl.

The primary area of flysch-type sedimentation has been destroyed by orogenic processes, nappe structures, and by narrowing of the geosynclinal space, especially in the Alps and Carpathians. A paleogeographic reconstruction of the Paleogene is therefore extremely difficult.

The Molasse zone of the outer edge of the Alps and Carpathians was introduced in the Oligocene (Fig. 2).

The distribution of the Neogene in Europe is far less than that of the Paleogene. In the north, the Neogene sequences of sediments of the northwestern European region can be delineated, with their characteristic Nordic faunal elements, which are different from those of the Atlantic-Mediterranean region. This could be explained

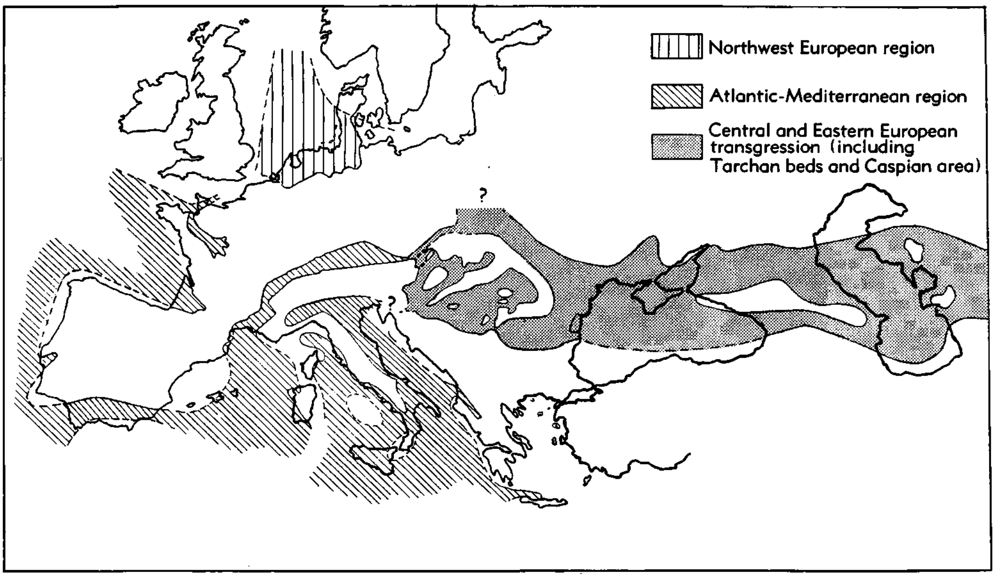

FIG. 3. Extent of the middle Miocene sea in Europe (after Papp, 1959).

by the assumption of a land barrier extending from Great Britain to Iceland.

In central Europe, continental sediments with noteworthy brown-coal occurrences were laid down. Marine sequences of the Atlantic region are developed in Brittany and Aquitaine. In southern Spain, a connection of the Atlantic with the Mediterranean existed for some time (Fig. 3).

The Mediterranean province, especially in the area of the plain of the River Po, shows classical highly fossiliferous sequences; the Pliocene began with a transgressional fauna. Connections existed between the eastern Mediterranean and the South Pacific area.

The Molasse zone along the outer edge of the Alps belongs to the Neogene. Neogene sediments cover the space from the eastern edge of the Alps to the Euxinic-Caspian area, and, farther east, to Lake Aral. The sedimentary series of the upper Miocene and of the Pliocene between the eastern Alpine edge and Lake Aral show an evolution of endemic families unique in their abundance. In the course of the Pliocene, the configuration of shore lines approached more and more that of the present. During the Quaternary the Black Sea became connected with the Mediterranean, whereas the Caspian was isolated.

ASIA

From east of the Ural Mountains, Paleogene epicontinental facies extend northward, separating Siberia from Europe. In the south they are well developed in the Tarim basin. Limnic and terrestrial Neogene strata cover wide areas of Siberia and Mongolia (Fig. 4).

Paleogene and especially Eocene deposits follow the strike of young mountain chains in Anatolia and Iran. They are widespread in Baluchistan and the Punjab and extend into the Himalayas where in places they form the lower plates of Alpine-type nappes. In the Near East, Syria, Iraq, and on the Arabian Peninsula, Paleogene and more so Eocene deposits are widely distributed as carbonate facies. Neogene sediments are confined to coastal areas.

Tertiary formations are widely distributed in Assam and Burma, as well as in Indonesia (Sumatra, Java, Borneo), the Philippines, Formosa, and Japan (Honshu, western Hokkaido). West of Kamchatka an arm of the Pacific penetrated deeply into eastern Siberia.

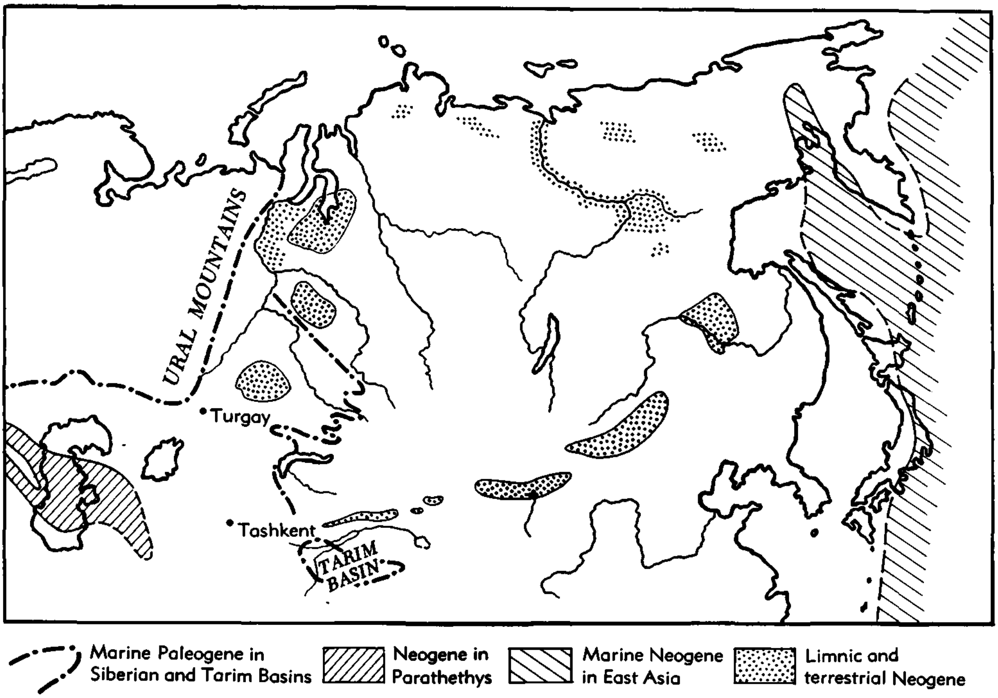

Fig. 4. Distribution of Tertiary sediments in north and central Asia (after Papp, 1959).

AUSTRALIA, NEW GUINEA, AND SOUTH PACIFIC ISLANDS

Along the west coast of Australia, Tertiary is developed in relatively narrow strips (Perth and Carnarvon basins). In the south it is found along the Australian Bight, in the Murray basin, southwestern Victoria, and Gippsland. In New Zealand, marine Tertiary is widely distributed, occurring in several basins around the centers of Mesozoic mountain ranges.

In western and central New Guinea the Tertiary begins with Eocene foraminiferal limestone facies, in the east in geosynclinal facies. The Neogene is developed in elongated basins and in great thickness.

In the South Pacific area Glaessner (in Papp, 1959) distinguished between an inner and an outer Melanesian zone. The outer one comprises the Solomon Islands, New Hebrides, Fiji, and Tonga, with pelagic Tertiary. The inner zone corresponds to southeast New Guinea and New Caledonia.

NORTH AMERICA

In North America, marine Tertiary sediments are mostly restricted to the periphery of the continent and are found in the following areas:

1) Pacific Coast: western Washington, western Oregon, California, the northeast coast of Queen Charlotte Island, on the southern tip of Vancouver, and elsewhere. Farther north, nearshore occurrences mainly of Paleogene are known: Mackenzie Bay, Banks Island (northeast of Victoria Island), and on Baffin Island.

2) Atlantic Coast: from New Jersey in the north through Maryland, Virginia, the Carolinas, and Georgia to Florida.

3) Gulf Coast: Tertiary sediments in North America are found most extensively in the Gulf province, extending from Florida across Alabama, Mississippi, Arkansas, Louisiana, to south Texas, and along the east coast of Mexico to Yucatan. In the Mississippi embayment they penetrate far

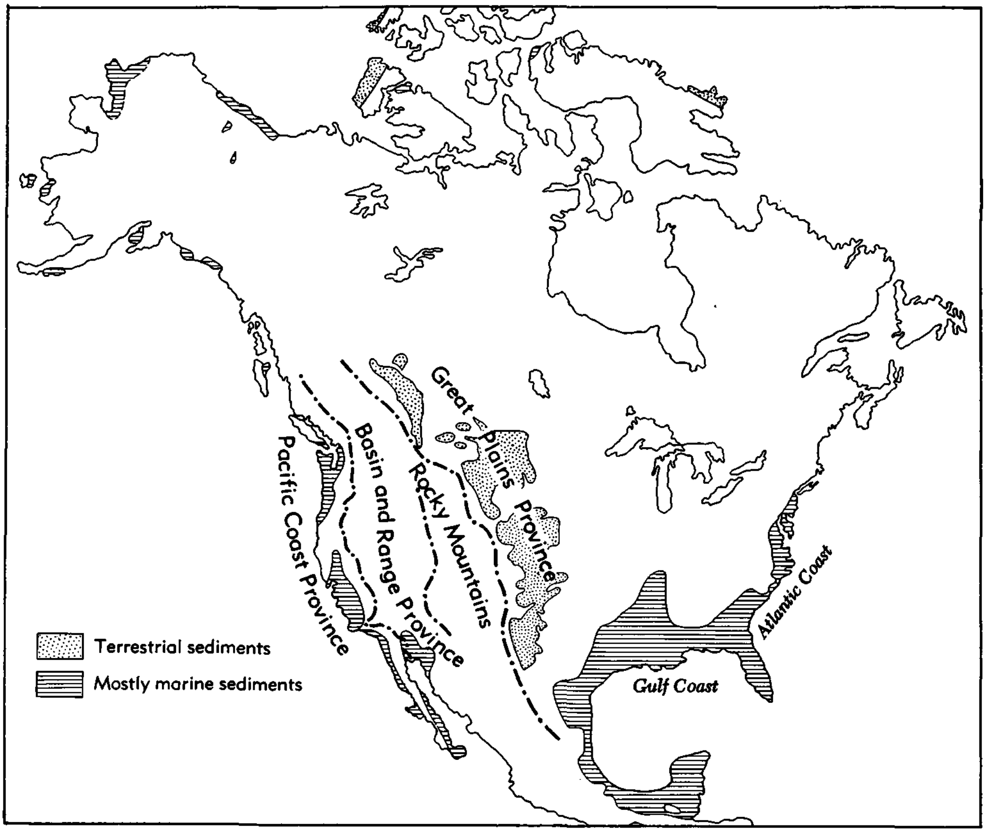

FIG. 5. Distribution of Tertiary sediments in North America (after Papp, 1959).

northward into the continent (Fig. 5).

The Tertiary fauna of the Pacific Coast has a special significance and is therefore designated as the Californian Faunal Province. It has few relationships with the Tertiary of the east coast, which may be called the West Atlantic Faunal Province. Deposits of the Gulf Coast have close relationships with the Caribbean Faunal Province.

The Tertiary nonmarine sediments of western North America with their mammalian faunas are of paramount biostratigraphic importance. They show that middle North America was a center of mammalian evolution during the whole of Tertiary time. From this area of origin, several waves of immigration reached Eurasia by way of the Bering Strait. Such mammalian invasions play an important part in stratigraphy of the nonmarine Tertiary sediments.

In North America nonmarine Tertiary deposits can be grouped in the following way (from west to east): 1) Pacific Coast Province, 2) Great Basin and Range Province, 3) Rocky Mountains Province, and 4) Great Plains Province.

CENTRAL AND SOUTH AMERICA

At the turn of the Mesozoic to the Cenozoic Era, Central America played an important role as a land bridge in the migration of mammals between the two American continents. During Tertiary time the continents were separated, and only a few faunal elements (e.g., marsupials, rodents, and notoungulates during the Oligocene) drifted into South America. Only at the end of the Tertiary, near the middle of the Pliocene, a land passage for mammals emerged.

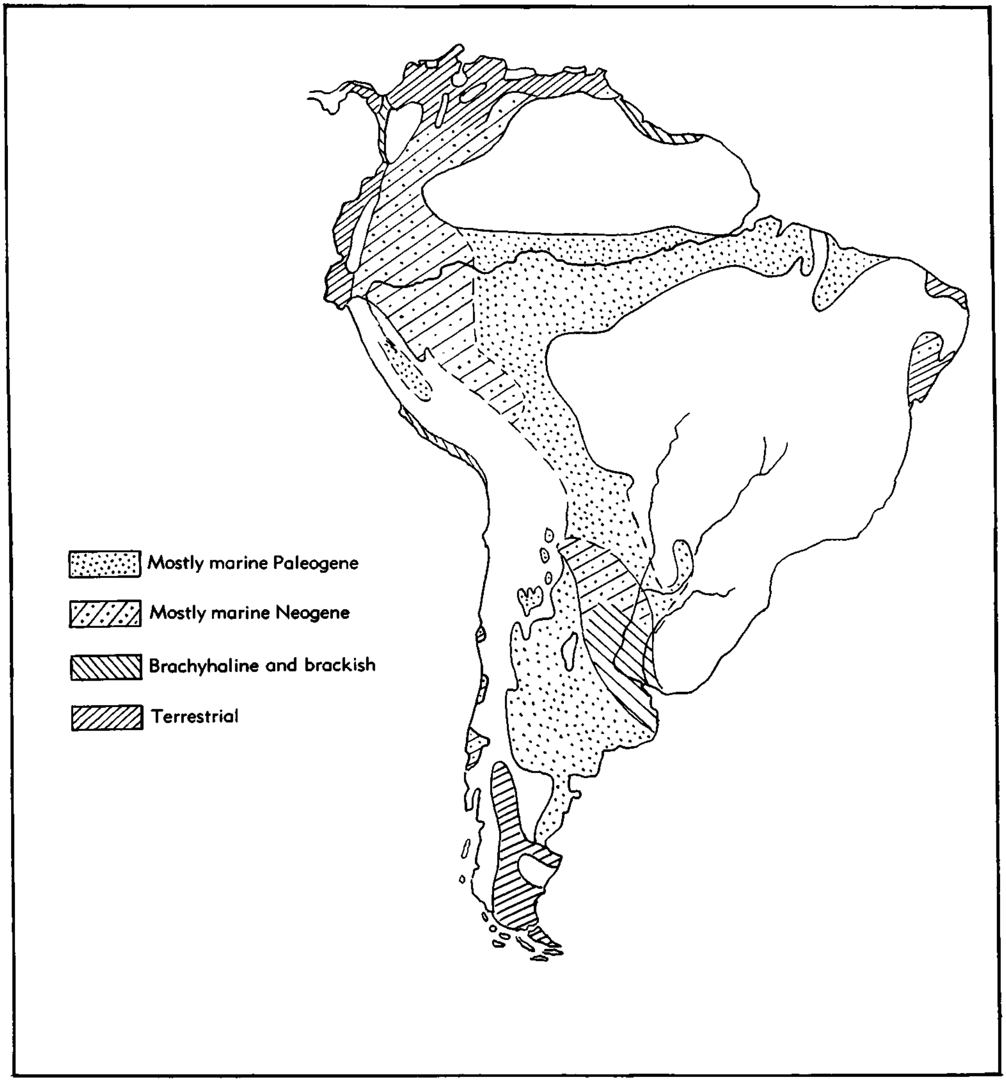

FIG. 6. Distribution of Tertiary sediments in South America (after Papp, 1959).

Sea connections crossing today's Central America facilitated faunal exchange between the Atlantic and Pacific oceans. Eocene sediments have been found at several localities in Central America, especially on the Isthmus of Tehuantepec and in Panama. Throughout Oligocene time a land connection continued to exist between the Central American region and the Greater Antilles, where outcrops of Neogene sediments also occur. In the West Indies the Tertiary naturally shows only incomplete development, with most complete sections described from Cuba, Haiti, the Dominican Republic, Puerto Rico, Jamaica, and Barbados.

In South America, marine Neogene sediments are restricted to marginal areas, but because of size of the continent, they are very extensive all the same. In the north (Trinidad, Venezuela, Colombia), close relationships to the Caribbean Faunal Province can be observed. Farther south, marine Tertiary, separated by great land masses, is found only in the La Plata basin, in

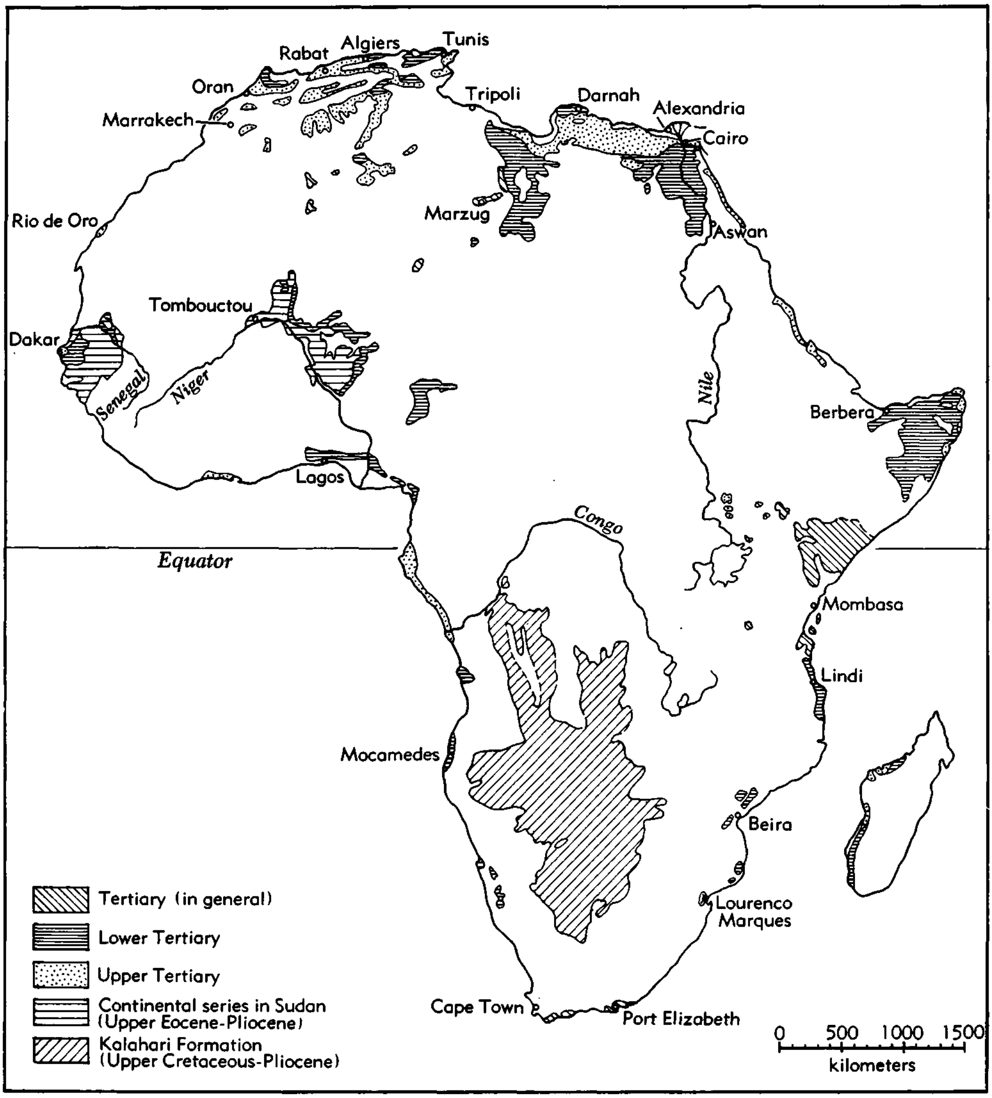

FIG. 7. Tertiary sediments in Africa (after Tollmann in Papp, 1959).

Patagonia, and in Tierra del Fuego. In central South America only terrestrial-limnic and brackish-brachyhaline sediments have been found (Fig. 6).

During the Paleogene, as well as Neogene, a zone with brachyhaline sediments extended in a syncline from northern South America southward along the east side of the Andes. Along the west coast, outcrops of Tertiary deposits worthy of mention are found in Ecuador, northwestern Peru, and central Chile.

In southern Patagonia and in the La Plata basin, marine transgressions took place at the boundaries of the Cretaceous and Tertiary, Oligocene and Miocene, and Miocene and Pliocene, facilitating a natural subdivision of the terrestrial sediments.

AFRICA

At the time of optimal transgression in

the latest Cretaceous (Maastrichtian), the Mediterranean was connected with the Gulf of Guinea across the Sahara. Only during the early Eocene and, increasingly, during the middle Eocene were seas again transgressive. During the middle Eocene orogenic movements occurred in the Atlas region, late Eocene records being incompletely developed in the east and marked by a flysch facies in the west. Nearing the Neogene, we find evidence for fault movements and vulcanism. In the Early Neogene, marine transgression at the margins of the continent attained its maximum (Fig. 7).

Individual developments of the several areas show the following characteristics:

1) In the eastern Mediterranean, gradual regression of the sea during the whole of the Tertiary.

2) In the Atlas area, continued existence of old deep trenches (South Riff trench and South Tell trench).

3) In the Sudan and Upper Guinea, emergence at the end of middle Eocene time.

4) In the East African coastal belt, Indo-Pacific characteristics.

5) In South Africa, continental series of the Kalahari Formation are prevalent.

Of more general interest are the well-known Eocene outcrops with nummulitids in Egypt, which already were mentioned in classic times.

OUTLINE OF INVERTEBRATE EVOLUTION DURING TERTIARY TIME

By far the greatest number of fossils of Tertiary age are derived from marine sediments. The boundary between the Cretaceous and Tertiary systems in the marginal facies of wide areas is marked by a characteristic phase of regression. Although the climate of the Eocene does not seem to have differed much from that of the Late Cretaceous, as indicated by the rather similar distribution of Cretaceous hippuritids and Tertiary nummulitids, Neogene temperatures steadily dropped, with consequent influence on the organisms. During the early Quaternary (i.e., Pleistocene), the temperature sank to its minimum. These climatic changes influenced the fauna and flora in wide areas in Eurasia and North America and furnish the basis for determining the boundary between Tertiary and Quaternary (Papp, 1959).

The Mesozoic-Tertiary boundary is marked by a reduction, or extinction, of numerous groups of Mesozoic (i.e., Late Cretaceous) organisms. Extinction of the great dinosaurs, plesiosaurs, mosasaurs, and flying saurians, which dominated the Mesozoic, is the most obvious change.

Among the mollusks, important faunal groups of the Mesozoic also became extinct: the ammonites and true belemnites, as well as typical groups of the Late Cretaceous, including hippuritids, acteonellids, and nerineids. Noteworthy is the decline of brachiopods during the Tertiary.

Evolution of the Foraminiferida offers the most useful definition of the Mesozoic-Tertiary boundary. Especially the planktonic foraminifers, collectively known as globotruncanas, which constituted an important faunal element of the Late Cretaceous, became extinct at the end of the Maastrichtian, as did characteristic forms of large Foraminiferida such as *Orbitoides* and *Lepidorbitoides*. The extinction of Cretaceous planktonic Foraminiferida can be traced in continuous stratigraphic sections distributed throughout the world and is thus a stratigraphic criterion of the first order. Directly above the boundary is a narrow zone with small, uncomplicated globigerinids from which typical forms of the Paleogene evolved. The *Globigerina* assemblage is generally correlated with the Danian. In classical paleontology, this was considered the uppermost stage of the Mesozoic and grouped with the Cretaceous. Increasingly important micropaleontological investigations now have led to transfer of equivalents of this stage into the Paleocene, that is, the Tertiary.

The Tertiary-Quaternary boundary is recognizable by biological criteria of climatic origin. The Cretaceous-Tertiary boundary may have like causes, but these cannot be defined by means of glaciations or similar phenomena. It is remarkable that especially such groups that had already passed their optimal development or were biologically overspecialized became extinct.

NATURE OF TERTIARY ORGANIC GROUPS

Following is a generalized discussion of the evolution of important groups of organisms that determine the specific faunal makeup of the Tertiary.

FORAMINIFERIDA

Numerous genera and species of Mesozoic Foraminiferida pass into the Tertiary. The many benthonic species showed an increasing tendency to develop new forms in the Paleocene, when large tests of complicated structure appeared. This evolution reached an optimum in the middle Eocene (Lutetian). These are the most prominent fossils of the shallow-water limestone formations and their evolutionary rates have parallels in the Tertiary only among the vertebrates.

The early Paleocene pillar-bearing rotaliids are widely distributed. The Discocyclinidae may have evolved from Cretaceous forms like *Hellenocyclina.* These cyclic foraminifers reached their optimal development in the Eocene and became extinct at the end of this epoch.

The nummulitids, *sensu lato,* include spirally coiled, multichambered foraminifers with a canal system in the spiral cord. The late Eocene *Heterostegina* and *Spiroclypeus* were derived from *Operculina,* and likewise the Oligocene *Cycloclypeus.* This latter genus developed during the Neogene in tropical seas into giant forms that died out in the Quaternary.

Small radiate forms of nummulitids appeared in the late Paleocene (Ilerdian, according to SCHAUB in KAPELLOS & SCHAUB, 1973). In the lower Eocene we find genera with definite pillar structure; in the middle Eocene very big forms with complicated suture lines. Nummulitids belong to the most abundant and, because of their size, most conspicuous Foraminiferida of the Paleogene. In the upper Eocene a pronounced decrease in size is observed, and small radiate forms predominate. In Europe they died out in the late Oligocene.

The evolution of *Assilina* is very clear, beginning with small forms in the late Paleocene, medium-sized ones in the early Eocene, and big ones in the middle Eocene, when this group became extinct. *Ranikotalia* of the Paleocene may be considered as the root form of the Nummulitidae. (In my opinion, genera of the Nummulitidae should be retained.)

Alveolinids were represented by small globular forms during the early Paleocene. They developed through several evolutionary sequences in the late Paleocene and early Eocene into the big, narrow alveolinids of the middle Eocene. *Borelis* and *Alveolinella* extend from the Oligocene and middle Miocene, respectively, into the Holocene.

In the Caribbean Province *Amphistegina* developed during the middle Eocene into *Eulinderina* and from this into *Lepidocyclina.* This cyclic foraminifer of complicated structure showed a clearly nepionic evolution in the Oligocene and Miocene, also leading to giant forms. *Miogypsina,* which was derived during the Oligocene from rotaliid foraminifers, underwent a pronounced nepionic evolution as far as the Miocene. This group can be considered as well known taxonomically and offers important indications for regional correlation of sediments of the marginal facies of the Oligocene and lower Miocene. In addition to the mentioned groups, quite a number of other benthonic Foraminiferida evolved noticeably during the Tertiary.

Investigations on planktonic foraminifers during recent years have become of greatest importance for stratigraphy. The era of the globigerinas in the oldest Paleocene (Danian) was followed by evolution of Paleogene plankton, which offers the foundation for biostratigraphic zonation of the Paleocene and Eocene. During the Oligocene a worldwide reduction in the abundance of forms occurred; in general, only simple forms of globigerinas persisted. During the Miocene the characteristic genus *Globigerinoides* developed, and during the middle Miocene *Praeorbulina* and *Orbulina.* The Miocene-Pliocene boundary is defined with the help of species of *Globorotalia.*

Because of the deterioration of climate and its influence on the composition of the several faunal provinces, common factors have to be employed for correlation of sedimentary series, especially in the Neogene. Planktonic Foraminifera provide useful indices for regional and intercontinental stratigraphy and offer the best foundation for zonation of the Neogene.

COELENTERATA AND MOLLUSCA

The number of coral genera changed little during the Tertiary, but their distribution varied greatly. The occurrence of reef-forming corals, because of the climatic gradient, became more and more restricted to warm seas.

Mollusks are the classical organisms of Tertiary time, though the importance of cephalopods diminished in comparison with the Mesozoic. The Nautiloidea persisted and are worthy of more detailed investigation. The gastropods and bivalves were the most varied molluscan groups during the Tertiary. Among marine gastropods, most families were already developed in Cretaceous time. During the Tertiary, the evolution of numerous genera and species followed. Typical is the development of the Caenogastropoda, among which siphonostome forms evolved rapidly.

Also typical for the Tertiary is the development of terrestrial gastropods. We know only relatively few and mostly small forms from the Cretaceous. Within the Tertiary we observe their differentiation into genera and families, especially among Papillaceae, Clausiliaceae, and Helicacea.

The bivalves, like the gastropods, showed a considerable increase of genera and species. Similar to a tendency among marine gastropods, the increase in burrowing forms is noteworthy. The development of sinuate forms commonly was paralleled by a reduction of the hinge. As already mentioned, the relative immobility of bivalves and gastropods led to differentiation of faunal provinces, especially in the Neogene. In the north, a boreal province developed, bordered by the North Atlantic Faunal Province on the south. Next to the latter followed the Northwest European Faunal Province. The Mediterranean area, between Atlantic and Indian oceans (Red Sea), is called the Mediterranean Province.

Along North America is the Caribbean and, along the West Coast, the Californian Faunal Province. Separated from these by the equatorial regions is the Patagonian Faunal Province along South America. The similarities of these provincial faunas with that of New Zealand are greater than with the Caribbean. Therefore, this region is called the South Pacific-Antarctic Faunal Province. The Indo-Pacific region, in spite of its great extent, has a relatively uniform faunal association that forms the Indo-Pacific Province.

In the Neogene, the northern part of disintegrating Tethys, extending from central and southeastern Europe to central Asia, became separated from the oceans through rising young mountain chains. Into these areas, collectively known as Paratethys, faunas related to those of the Indo-Pacific Faunal Province migrated during the Early Neogene, and marine faunas from the Mediterranean Province during the middle Miocene. Especially characteristic are the Sarmatian (Late Miocene) molluscan faunas found between the eastern edge of the Alps and Lake Aral. This molluscan fauna shows traits of an impoverished marine fauna with clear tendencies of endemic evolution. Also, the younger faunas are of endemic character, though in the Maeotian and Akchagylian, marine influences are noticeable. The diversity of endemic groups among the Limnocardiidae, *Congeria* and related forms, Melanopsidae, Limneidae *(Valenciennesia),* and others reached an optimum, offering excellent examples of extreme forms resulting from endemic evolution.

Mollusks used to be regarded as main index fossils for division of the Tertiary into epochs and stages. Recognition that differentiation into faunal provinces strongly influenced the composition of molluscan faunas, especially in the Neogene, has reduced their adjudged importance. Special studies of the evolution of marine genera or groups of genera are few. Nevertheless, mollusks still offer a valuable basis for local subdivisions of sedimentary series within a faunal province or a more narrowly defined sedimentary area. The evolution of endemic molluscan faunas, especially in Paratethys, offers unsurpassed biostratigraphic indicators for local stratigraphic subdivisions.

ARTHROPODA

Considering the abundance of recent arthropods, one might expect Tertiary forms to be varied and rich. Terrestrial groups may be fossilized only under most favorable conditions, however, as when they are preserved in amber. For example, the best-known material shows that among insects many younger Paleocene genera are identical with recent ones. The ostracodes have a special place among arthropods, and show a strong evolutionary tendency toward differentiation.

BRYOZOA, BRACHIOPODA, AND ECHINODERMATA

Bryozoan faunas of the Tertiary are richly differentiated and many Bryozoa are rock-formers. Cheilostomes dominated in the Tertiary.

Number of genera and distribution of brachiopods decreased considerably during Tertiary time as compared with the Cretaceous. The brachiopod faunas of the marginal facies usually contain only a few genera; locally abundant are beds with *Terebratula*. Representatives of other groups are restricted to basinal facies. In Tertiary seas brachiopods played only a subordinate role.

Remnants of echinoderms demonstrate that these invertebrates were relatively abundant in the Tertiary, though most of the dominant groups of the Paleozoic and Mesozoic were on the decline. Crinoids, for instance, were mainly represented by planktonic forms, such as *Discometra (Antedon)*. Echinoids on the other hand, were plentiful. Like the bivalves and gastropods, echinoids showed a tendency for their progressive evolution in the Late Cretaceous to continue into the Tertiary, resulting in the appearance of many new genera. Especially characteristic was the flourishing of irregular echinoids and the prevalence of burrowing forms (Spatangidae). Faunas of the Miocene and Eocene differed greatly. Representatives of the Conoclypeidae are especially characteristic of the lower and middle Eocene; Scutellidae and Clypaeastridae of the younger Tertiary.

BIOSTRATIGRAPHIC DIVISIONS

Subdivision of the Tertiary has been attempted according to different principles, that is, by utilizing different groups of organisms as guides. LYELL (1832) divided the Tertiary into three divisions or epochs according to the percentage of their contained Holocene molluscan taxa:

1) Eocene, 3.5 percent; 2) Miocene, about 20 percent; 3) Pliocene, 35-50 percent. Later, the Oligocene (BEYRICH, 1853-56) and Paleocene (SCHIMPER, 1874; KOENEN, 1885) were separated from LYELL's Eocene. HOERNES (1856, 1870) combined the two faunistically similar younger epochs, Miocene and Pliocene, as Neogene, whereas the older epochs Paleocene, Eocene and Oligocene, were grouped together as Paleogene.

These divisions are based mostly on fossil contents, especially molluscan faunas of western, southern, and central Europe, including the Oligocene Northwest European Faunal Province.

When division of the Tertiary into epochs was proposed, a division into stages was also made. First suggestions in this respect were made by MAYER-EYMAR (1857-58). The system of stages later was improved frequently and adapted to requirements of the times. Originally, molluscan faunas were used to differentiate individual stages. Undoubtedly, in Europe it was possible to define Tertiary stages paleontologically with the help of mollusks, but such attempts must have caused difficulties even then. For delineation of the relatively short period of a stage, mollusks proved mostly insufficient.

For areas outside of Europe, Tertiary molluscan faunas could not be used for correlation with European stages, because the evolutionary tendencies of individual faunal provinces differ from the European ones.

Since the first attempts at subdivision of the Tertiary, evolution of mammals has been used for this purpose. Their rapid evolutionary differentiation, with its wealth of morphological detail, offers decisive biostratigraphic keys. But the fact that most vertebrate remains occur in sediments of terrestrial origin commonly makes their correlation with marine sediments extremely difficult. For this reason, biostratigraphic units based on evolution of the vertebrates have been defined mainly in North America.

The appearance of creodonts and Condylarthra in the Paleocene is significant. In the late Paleocene the appearance of the perissodactyls, which in the Eocene and earliest Oligocene split into several evolutionary lines, is of significance. In the Oligocene, introduction of rhinoceratids in Europe and of anthracotheriids in North America is important.

In the early Miocene, *Mastodon* and other faunal elements migrated from Africa to Europe. Later, *Hipparion* and its accompanying fauna reached Eurasia from North America. This very marked immigration is often considered as a stratigraphic criterion of first order and used to define the boundary between Miocene and Pliocene. But according to contemporary opinion, the Miocene-Pliocene boundary should be drawn higher and the arrival in Eurasia of *Hipparion* would therefore have taken place in the late Miocene. In Europe the boundary between Tertiary and Quaternary is usually determined by the appearance of *Equus, Archidiscodon,* and other genera. The evolution of rodents allows a refined subdivision of zones, especially in the Neogene, though their correlation with marine zones is difficult. Therefore, it is better to divide the terrestrial-limnic deposits of Eurasia into units based on paleontological criteria indicated by mammalian evolution.

The origins of the Tertiary flora are found in development of the angiosperms in the Late Cretaceous. In the Paleocene, Cretaceous floral elements persisted and woody plants predominated. In the Eocene, the distribution of tropical floras reached an optimum. In the Oligocene a retreat of the tropical floras was paralleled by an increase in herbaceous plants. In the temperate zone older Tertiary relicts became extinct during the early Quaternary. Tertiary floras of the temperate zones are useful for evaluation of stratigraphic sequences, but have to be used with caution because of their lack of true evolutionary lines. Also, as in the case of mammals, correlation with marine deposits encounters difficulties.

Finally, tectonic phases should be mentioned as important criteria because they show special intensity during certain intervals of the Tertiary. The evaluation of such processes must be based on their effects, as the processes themselves cannot be observed. But refined stratigraphic methods have shown that the idea of worldwide, short tectonic phases cannot be upheld in its original concept. Nevertheless, tectonic processes, at least in young mountain chains, fall into definite time periods:

1) At the Cretaceous-Tertiary boundary: Laramide phase.
2) In upper Eocene-lower Oligocene: Pyrenaic phase.
3) Around the Oligocene-Miocene boundary: Savic phase.
4) From middle to upper Miocene: old and young Steiric phase.
5) the Pliocene: Rhodanic phase.
6) Around the Pliocene-Pleistocene boundary: Wallachian phase.

As already mentioned the Tertiary System has been divided into series which are subdivided into stages. The following European divisions are presently in use:

Pliocene:	Astian-Piacenzian
	Tabanian-Zanklian
Miocene:	Messinian
	Tortonian
	Serravallian
	Langhian
	Burdigalian
	Aquitanian
Oligocene:	Chattian
	Rupelian
	Lattorfian
Eocene:	Wemmelian
	Lutetian
	Cuisian
Paleocene:	Ilerdian
	Thanetian + Montian
	Danian

In recent years, stage names have been

Planktonic Foraminiferal Zones		
N 3 / P 22	Globigerina angulisuturalis	GLOBIGERINA ASSEMBLAGE
N 2 / P 21	Globigerina angulisuturalis Globorotalia opima opima	
N 1 / P 20	Globigerina ampliapertura	
P 19	Globigerina sellii Pseudohastigerina barbadoensis	
P 18	Globigerina tapuriensis	
P 17	Globigerina gortani Globorotalia centralis	HANTKENINA ASSEMBLAGE
P 16	Cribrohantkenina inflata	
P 15	Globigerapsis mexicana	
P 14	Truncorotaloides rohri Globigerinita howei	
P 13	Orbulinoides beckmanni	
P 12	Globorotalia lehneri	
P 11	Globigerapsis kugleri	
P 10	Hantkenina aragonensis	
P 9	Acarinina densa	GLOBOROTALIA ASSEMBLAGE
P 8	Globorotalia aragonensis	
P 7	Globorotalia formosa	
P 6	Globorotalia subbatinae	
P 5	Globorotalia velascoensis	GLOBIGERINA ASSEMBLAGE
P 4	Globorotalia pseudomenardi	
P 3	Globorotalia pusilla Globorotalia angulata	
P 2	Globorotalia uncinata Globorotalia spiralis	
P 1	Globocanusa daubjergensis Globigerina pseudobulloides	

Calcareous Nannoplankton Zones		EPOCH
NP25	Sphenolithus ciperoensis	OLIGOCENE
NP24	Sphenolithus distentus	
NP23	Sphenolithus predistentus	
NP22	Helicopontosphaera reticulata	
NP21	Ericsonia subdisticha	
NP20	Sphenolithus pseudoradians	EOCENE
NP19	Isthmolithus recurvus	
NP18	Chlasmolithus oamaruensis	
NP17	Discoaster saipanensis	
NP16	Discoaster tani nodifer	
NP15	Chiphragmalithus alatus	
NP14	Discoaster sublodoensis	
NP13	Discoaster lodoensis	
NP12	Marthasterites tribrachiatus	EOCENE PALEOCENE
NP11	Discoaster binodosus	
NP10	Marthasterites contortus	
NP 9	Discoaster multiradiatus	
NP 8	Heliolithus riedli	
NP 7	Discoaster gemmeus	
NP 6	Heliolithus kleinpelli	
NP 5	Fasciculithus tympaniformis	
NP 4	Ellipsolithus macellus	
NP 3	Chlasmolithus danicus	
NP 2	Cruciplacolithus tenuis	
NP 1	Markalius inversus	

FIG. 8. Paleogene zones based on planktonic Foraminiferida and calcareous nannoplankton (Papp, n).

introduced for the Tertiary on a regional basis such as for the Neogene of the central and eastern Paratethys. The terminology of the stages has been treated differently in the literature of different countries and faunal provinces. In the Paleogene, the middle Eocene (i.e., Lutetian), which is easily recognizable by optimal development

Planktonic Foraminiferal Zones		
N 23	Globigerina calida	Globorotalia truncatulinoides
N 22	Globorotalia truncatulinoides	
N 21	Globorotalia tosaensis tenuitheca	
N 20	Globorotalia multicamerata Pulleniatina obliquiloculata	Globorotalia miocaenica
N 19	Sphaeroidinella dehiscens Globoquadrina altispira	
N 18	Globorotalia tumida tumida	Globorotalia margaritae
N 17	Globorotalia tumida plesiotumida	
N 16	Globorotalia acostaensis Globorotalia merotumida	Globorotalia menardii
N 15	Globorotalia continuosa	
N 14	Globigerina nepentes Globorotalia siakensis	
N 13	Sphaeroidinellopsis subdehiscens, Globigerina druryi	Orbulina s.l.
N 12	Globorotalia fohsi fohsi	
N 11	Globorotalia praefohsi	
N 10	Globorotalia peripheroacuta	
N 9	Orbulina suturalis Globorotalia peripheroronda	
N 8	Globigerinoides sicanus Globigerinatella insueta	Globigerinoides trilobus
N 7	Globigerinatella insueta Globigerinoides trilobus	
N 6	Globigerinatella insueta Globigerinita dissimilis	
N 5	Globigerina dehiscens	Globigerinita dissimilis
N 4	Globigerinoides primordius Globorotalia kugleri	

Calcareous Nannoplankton Zones		EPOCH
NN 21	Emiliana huxleyi	PLEISTOCENE
NN 20	Geophyrocaspa oceanica	
NN 19	Pseudoemiliana lacunosa	
NN 18	Discoaster brouweri	PLIOCENE
NN 17	Discoaster pentaradiatus	
NN 16	Discoaster surculus	
NN 15	Reticulofenestra pseudoumbilica	
NN 14	Discoaster asymetricus	
NN 13	Ceratolithus rugosus	
NN 12	Ceratolithus tricorniculatus	
NN 11	Discoaster quinqueramus	MIOCENE
NN 10	Discoaster calcaris	
NN 9	Discoaster hamatus	
NN 8	Catinaster coalitus	
NN 7	Discoaster kugleri	
NN 6	Discoaster exilis	
NN 5	Sphenolithus heteromorphus	
NN 4	Helicopontosphaera ampliaperta	
NN 3	Sphenolithus belemnos	
NN 2	Discoaster druggi	
NN 1	Triquetrorhabdulus carinatus	

FIG. 9. Neogene zones based on planktonic Foraminiferida and calcareous nannoplankton (Papp, n).

of the Foraminifera, especially nummulitids and discocyclines, can be readily traced over wide areas of Eurasia and the Americas. But such easily recognized characteristics are lacking in the early Paleogene and in the Neogene. This has resulted in different usage of stage names in different countries and has led to discrepancies in usage of such names in the Paleocene, Oligocene, and Miocene, since the same stage names have been used for beds of different ages. Therefore, in recent symposia the avoidance of customary stage terminology altogether has been suggested.

New ways must be found to establish subdivisions that satisfy the requirements

Table 1. *Relationship between succession of species of* Miogypsina *and some European stratotypes.*

	M. mediterranea *M. cushmani*	
M. burdigalensis	*M. intermedia* *M. globulina*	Stratotype Burdigalian
	M. tani *M. gunteri*	Stratotype Aquitanian
M. bantamensis *M. formosensis* *M. complanata*	*M. septentrionalis*	Stratotype Chattian

of biostratigraphy. Groups of organisms employed for biostratigraphy should be worldwide in distribution and relative abundance. They should also reflect rapid and clearly recognizable evolution. The plankton of the Tertiary fulfills these demands best. For this reason, division of the Tertiary into biozones on the basis of planktonic Foraminifera has been advanced during recent years.

A second group of organisms useful in stratigraphic correlation within the Tertiary is the nannoplankton. The biostratigraphic zonation on the basis of nannoplankton is more or less equivalent to that worked out for planktonic Foraminifera. A comparison of these two schemes is shown in Figure 8 for the Paleogene and Figure 9 for the Neogene; after Berggren (1971), Blow (1969), Bolli (1966), Kapellos and Schaub (1973), and Martini (1971).

At present, the Danian, with its globigerinid fauna, is regarded as basal Paleocene.

The base of the Eocene fluctuates, depending upon which stages are employed. If the Ypresian Stage is employed as the base, then the boundary is drawn in the lower third of the planktonic foraminiferal zone P6. If the Cuisian Stage is used, then the boundary is at the base of the stratigraphically higher planktonic foraminiferal zone P8 *(Globorotalia aragonensis)* or in the lower third of the nannoplankton zone NP12 *(Marthasterites tribrachiatus)*. In this concept, the Cuisian Stage is used.

The lower boundary of the Oligocene is generally drawn at the base of zones P18 or NP21. The Oligocene encompasses, essentially, the "*Globigerina* region."

The base of the Miocene is, at present, considered to be at the base of zones N4 or NN1.

The Pliocene encompasses zones N18 to N21.

The appearance of *Globorotalia truncatulinoides* defines the Pliocene-Pleistocene boundary and, thus, the boundary between the Tertiary-Quaternary.

Following the suggestion of the Comité du Néogène Méditeranéen, at its 1967 meeting in Bologna, the Neogene should be divided into four "supraétages" on the basis of planktonic zones and it is proposed that these should be designated by the numerals I to IV. Such division is the first attempt at an exact correlation of equatorial sedimentary areas with the Mediterranean and the South Pacific-Antarctic regions.

Additional stratigraphically important groups have already been discussed: nummulitids, discocyclinids, and alveolinids in the Paleogene; lepidocyclinids and miogypsinids in the upper Oligocene-Miocene. The miogypsinids are of particular importance for definition of the Oligocene-Miocene, or Paleogene-Neogene, boundary. Drooger (1966) worked out the evolution of *Miogypsina* in great detail. As the concepts of Oligocene and Miocene originally were based on knowledge of the marginal facies, the degree of specialization of miogypsinids in stratotypes of the Chattian, Aquitanian, and Burdigalian gains special importance. The main line of miogypsinid evolution is shown in Table 1.

Following suggestions of the Comité du Néogène Méditerranéen made in 1964 and 1967, the boundary between Neogene and Paleogene should be defined by stratotypes based on occurrences of *Miogypsina*, together with the appearance of *M. gunteri*. The more primitive species, *M. septentrionalis* and *M. complanata*, indicate Chattian, and therefore, Oligocene. On the basis of planktonic zones, the lower boundary of the Neogene lies at the base of the zone containing *Globigerinoides primordius*.

The summary offered here makes no attempt to include the commonly used stage names. As mentioned before, these concepts have been used so variably that it is preferable to use local terms for beds, sequences, or formations, which are then to be correlated with the biozones.

Knowledge of the evolution of additional groups, especially of such foraminifers as *Uvigerina, Heterostegina,* and others, is essential for more precise correlation of sections within one faunal province. These would provide a basis for better understanding of molluscan faunas, and thus offer a broader foundation for biostratigraphical analysis, especially in the Neogene.

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QUATERNARY[1]

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INTRODUCTION: CONCEPT OF THE QUATERNARY

The Quaternary spans the last 1.5 Ma.[1] By any conservative standard of comparison it has been a time unique in earth history, even if we refrain from the anthropomorphic temptation of according hominid evolution undue significance.

Its individual recognition began with ARDUINO, who in 1759 proposed a Primary ("basement") and Secondary (lithified and folded) organization of formations in the crust, based on the geology of the Apennines. He also informally noted a third subdivision, that of "low mountains and hills of sand and gravel," and a fourth, final subdivision of "earth and rocky materials and alluvial debris." The third subdivision subsequently became Tertiary (or *tertiaire*) as first used in 1810 by BRONGNIART to describe strata younger than the massive Late Cretaceous chalks of the Paris basin. This was followed by the formalization of the fourth of ARDUINO's subdivisions initially as *quatrième formation d'eau douce* by MARCEL DE SERRES (in CREUZE DE LESSER, 1824, p. 174). DE SERRES later (1830) used the term Quaternary *(quaternaire)* for the same interval and subsequently (1855) claimed to have invented it, but the honor goes, somewhat unjustly, to DESNOYERS (1829).

In his study of the geology of the lowlands of western France DESNOYERS (1829) suggested that the sea had receded earlier from the Seine basin than from the regions of Touraine and Languedoc. He therefore proposed to call the nearly horizontal, relatively unconsolidated younger strata of the latter region *Quaternaire ou Tertiaire récent,* and divided them as follows:

3. *Récent*
2. *Diluvium*
1. *Faluns de Touraine, la molasse suisse, le Pliocène marin de Languedoc*

The first use of the term Quaternary itself, therefore, refers to strata that span the interval between lower Miocene and recent! This was partly because *tertiaire* in France was initially applied only to the Lower Cenozoic strata in the Paris basin, and perhaps also because the southern French Miocene to which DESNOYERS referred was less indurated or deformed than the time-equivalent Italian Miocene which ARDUINO placed in his third subdivision. However, the earlier usage of DE SERRES, which he restated (1830) in confining *quaternaire* to "diluvium" only, was more in line with that of ARDUINO, and it established the modern meaning of the term. It is interesting to note that the lithological concept of Quaternary is still a very strong tradition in geology, and many pre-Quaternary formations are included in such map units as "Quaternary terrace" or "Older Quaternary alluvium" simply because they are poorly indurated, and lack determinative fossils.

DE SERRES (1830) also affirmed that early man had lived contemporaneously with deposition of Quaternary "diluvium." This was the basis of very early and persistent attempts to define the period anthropocentrically. The first major treatise on the *Terrain quaternaire ou diluvien* (REBOUL, 1833) proposed that this time interval be considered as the *Période anthropienne.* Other writers called it the *Période homozoique* (VEZIAN, 1865), *Terrain humaine* (MERCEY, 1874-77) or *Psychozooique* (LE CONTE, 1887, in MEUNIER, 1908). It was at the International Geological Congress of 1888 in Great Britain that GAUDRY, with the approval of PRESTWICH and DE LAPPARENT, made the proposal that mankind —represented in particular by artifacts— was the characteristic element of the Quaternary, which justified its separation from the Tertiary. As we shall see, this early concept is also still very much alive, even though the geological range of artifacts, if not that of *Homo sapiens,* has since been shown to extend back nearly to the base of the Pliocene.

A third concept, that of the Quaternary as a paleontological feature, was outlined by the work of LYELL although he did not

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[1] The abbreviations Ma (Mega-annum) refers to units of yr $\times 10^6$ measured from the present (1950 A.D. by international agreement) pastward. It means the same as the cumbersome "millions of years before present" and is a fixed chronology analogous to the calendars tied to historical events. The abbreviation my (million years) is used to express simple duration in units of yr $\times 10^6$ in any given past interval.

use the term himself. Instead, he formalized the term Pliocene (already in use as a general descriptive word for beds containing fossils of relatively young age, e.g., DESNOYERS, 1829) as the latest part of Tertiary time, subdivided into two parts (LYELL, 1833, p. 61):

New Pliocene—formations containing mollusk species 90-95 percent surviving to the present time, and correlative beds.
Older Pliocene—formations containing more than 50 percent surviving species, and correlative beds.

In 1839, LYELL suggested *Pleistocene* in place of his Newer Pliocene period; BUTEUX (1843) likewise proposed *Pliostène* as a name for the brief post-Pliocene interval. The equivalence of Quaternary and Pleistocene was simply taken for granted in the literature of the time, with the former generally referring to unconsolidated continental rocks and the latter to beds with marine fossils. Today, the Pleistocene is recognized as an epoch of the Quaternary Period—with or without the Holocene or "Recent" subdivision—and its base defines the base of the Quaternary.

Thus, the basis for recognizing the Quaternary System was in various degrees lithological, archeological, and paleontological according to the earliest definitions; that of the Pleistocene was explicitly paleontological. Nevertheless, only nine years after AGASSIZ (1838) had first boldly suggested that the European continent had recently been invaded by great lowland glaciers, FORBES (1846) concluded that the molluscan faunas to which LYELL had referred in setting up the Pleistocene were the representatives of a colder climate than those of the Pliocene, and he proposed to redefine the period as ". . . the time distinguished by severe climatal conditions throughout the great part of the northern hemisphere" (p. 402). FORBES' statement is an accurate generalization, valid today and startlingly correct for its time. Nevertheless, it is no longer possible to use the "onset of glaciation" or some similar climatic criterion to distinguish the Pleistocene from the Pliocene, or the Quaternary from the Tertiary, because we can now see a much more complex and gradational record than that known to FORBES. In modern studies a limit such as "the first glaciation" is no more acceptable than other criteria with equal or better historical validity, such as "the earliest human," "the oldest artifact," "the oldest fauna with 90 percent survivors," or "the oldest unconsolidated alluvium."

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LOWER LIMIT OF THE QUATERNARY

Because of the wide variety of relatively unrelated disciplines in Quaternary research, each specialism has contended over the years that the base of the Quaternary should be marked by some auspicious event in its own field. By the middle of this century the various lower defining criteria in advocacy were perceived as follows:

Paleoanthropologists: first evidence of man or tools.
Paleoclimatologists: first (major) global cooling or glacial advance.
Vertebrate paleontologists: first joint oc-

currence of *Equus, Leptobos,* and *Elephas* (in Eurasia).

Marine invertebrate paleontologists: first occurrence of cold-water species in late Neogene sediments of Mediterranean basin (e.g., *Hyalinea baltica, Arctica islandica*).

Paleobotanists: first "glacial" floral association, or exclusion of certain southern elements from European floras.

Most of this special pleading was countered, if not silenced, at the 18th International Geological Congress. At this Congress, the Temporary Committee for the Study of the Pliocene/Pleistocene Boundary recommended (*Internatl. Geol. Congr.,* Repts. 18th Sessions, Great Britain 1948, Pt. 9, 1950, p. 6) that the boundary ". . . should be based upon changes in marine fauna, since this is the classical method of grouping fossiliferous strata." The Committee simply pointed out that the Quaternary, with the Pleistocene as its lower, major portion, was nothing more or less than the youngest period and uppermost system in the geological record.[1]

If the Committee had done no more than this it would have earned its laurels; however, it made a step onto new ground that can be seen, in retrospect, to have made the boundary accessible to modern techniques used in biostratigraphy, magnetostratigraphy, and geochronology. This was to propose that the boundary be typified in an appropriate marine section, and to recommend for this purpose that ". . . the Lower Pleistocene should include as its basal member in the type-area the Calabrian Formation (marine) together with its terrestrial (continental) equivalent the Villafranchian." Aside from the egregious and, as it turned out, mistaken inclusion of the Villafranchian, which seems to have been a sop to the nonmarine specialists on the panel, this proposal cleared the way toward establishing a single, visible, unambiguous physical feature as the key element in defining this elusive boundary.

The new definition superseded the various "model" criteria of the past, including the one based on climate-induced changes in the marine invertebrate fauna, although this fact was not clear to everyone at the time. In fact, the Committee itself justified its proposal by pointing to changes in the marine and continental faunas that were understood to indicate major climate change coincident with the proposed physical boundary in Italy. Nevertheless, their proposal established a limiting criterion that existed in physical space apart from any theoretical model of past events. In so doing, they made the record of climate, fauna, or flora, irrelevant to the definition of the boundary, although more significant than ever (because of the greater precision demanded by reference to a single geographic point) in its correlation (Fig. 1).

Numerous, detailed observations of the Calabrian Pleistocene were stimulated by the 1948 IGC proposal and the 1965 INQUA amendment (see below), but these observations together with a flood of data from other sources have not ended the controversy between those who still cling to a definition of the base Pleistocene founded on a climate model and those who would correlate from a fixed physical reference point, or "golden spike" (AGER, 1973), in the Calabrian Stage.

The fundamental assumption of the climate-model school of thought is that the base of the Pleistocene is defined by a recognizable deterioration in global climate. In this view the base of the Calabrian should correspond with this sudden, global climate change, and, if it does not, then the boundary must be moved to a more suitable level. The underlying philosophy of the second group is that once a fixed, physical reference point or "golden spike" representing a given boundary is adopted the boundary immediately takes on a real existence independent of the arguments that caused it to be placed where it is. In other words, if the establishing arguments should prove erroneous (as so often happens in geology), the definition embodied in the

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[1] *Neogene* originally denoted relatively modern faunas—those of Miocene, Pliocene, and recent strata *sensu* LYELL (1833, 1839, *et seq.*)—in contrast to the Paleogene faunas of older Tertiary strata (HOERNES, 1856; DENIZOT, 1957). Whether or not the modern Neogene includes Quaternary faunas (*fide* GIGNOUX, 1950; 1955), it is a paleontological-biochronological concept that has no place in the stratigraphic hierarchy. It is completely incorrect to speak of a "Neogene-Quaternary" boundary in place of Tertiary-Quaternary or Pliocene-Pleistocene boundary.

TERM		CRITERION (A)	AGE (Ma)	RESULT/REMARKS
ANTHROPOGENE		FIRST ADVANCED "HOMINIDS" (AUSTRALOPITHECUS)	~5-6	ELIMINATE PLIOCENE
ANTHROPOGENE		FIRST TRUE "HOMINIDS" (RAMAPITHECUS)	~14	ELIMINATE MIDDLE AND UPPER MIOCENE AND PLIOCENE
QUATERNARY (=PLEISTOCENE)		FIRST VILLAFRANCHIAN MAMMAL FAUNA	~3.3	MEANINGLESSLY SHORT PLIOCENE (5.0-3.3 Ma)
QUATERNARY (=PLEISTOCENE)		FIRST HOMO, FIRST CONTINENTAL GLACIATION IN EUROPE, FIRST BIHARIAN MAMMAL FAUNA	~0.7-0.5	EXTREMELY SHORT PLEISTOCENE (<1 Ma)
PLIOCENE/ PLEISTOCENE BOUNDARY	BANDY (1972)	FAD G. truncatulinoides LAD Discoasters	~1.8 (base Gilsa=Olduvai)	PLIOCENE OF BANDY (2.8-1.8 Ma) = LOWER PLEISTOCENE (2.8-1.8 Ma) of LAMB & BEARD
	BEARD & LAMB (68) — LAMB & BEARD (72)	LAD G. altispira FIRST CONTINENTAL GLACIATION IN NORTH AMERICA	~2.8	
MIOCENE/ PLIOCENE BOUNDARY	BANDY (1972)	LAD Prunopyle titan FAD S. dehiscens s.s.	~2.8-3.0	MIOCENE/PLIOCENE BOUNDARY OF BANDY = PLIOCENE/PLEISTOCENE BOUNDARY OF LAMB & BEARD AT ca. 2.8 Ma
	BEARD & LAMB (68) — LAMB & BEARD (72)	FAD G. margaritae	~5.0	
QUATERNARY = PLEISTOCENE		FIRST GLACIATION	~40 (ANTARCTICA)	ELIMINATE OLIGOCENE, MIOCENE & PLIOCENE
QUATERNARY = DILUVIUM		UNCONSOLIDATED CONTINENTAL ALLUVIUM	VARIABLE	Qal = Qt, etc. (on maps) = PLEISTOCENE ON LITHOLOGIC GROUNDS ONLY

FIG. 1. Stratigraphic problems associated with the position of the Pliocene-Pleistocene boundary using criteria of definition other than the "golden spike." See Figure 6 for generic names that are abbreviated on this figure (Berggren & Van Couvering, n). [Explanation: *FAD,* First Appearance Datum; *LAD,* Last Appearance Datum.]

physical reference point is not thereby invalidated. Furthermore, the proposal of a "golden spike" to define (or, if necessary, redefine) a boundary is treated as a practical matter unconnected with the fulfillment of geological ideology.

CALABRIAN DEFINITION

The Calabrian Stage is recognized in widely separated parts of Italy, so it was natural to refer the proposed definition of the base of the Pleistocene (and Quaternary) to the nominative section as described by Gignoux (1913) at Santa Maria di Catanzaro, Calabria, and which subsequently received support as the stage stratotype (Bayliss, 1969; Blow, 1969; Selli, 1971). The basal strata are not well exposed here, however, and at the 7th INQUA Congress (Denver, 1965) it was proposed to further fix the base of the Pleistocene explicitly to the base of the Calabrian Stage where it was exposed about 40 km distant from the putative stratotype at Le Castella, Calabria. This was approved by a vote of the Congress and was subsequently adopted by international geological bodies (see Emiliani, 1967, p. 410).

At Santa Maria di Catanzaro, a prominent, resistant marker (Bed G-G′) is formed by a calcarenite unit at the base of the Calabrian Stage as described by Gignoux (1913, Fig. 5). This contact was made the base of the Calabrian stratotype in the definition of Selli (1971). Inordinate emphasis has been placed, however, on the first occurrence of the bivalve *Arctica islandica* in the calcarenite unit G-G′ (Fig. 2), which arises because *A. islandica* is an indicator of cold climate and is also a principal index fossil for the Calabrian. For this reason, some have considered this level to represent the actual base of the Quaternary (e.g., Ruggieri, 1971, 1972; Ruggieri *et al.,* 1976) despite the fact that its isolated appearance in the stratotype, according to paleobathymetric interpretations (Bandy & Wilcoxon, 1970; Selli, 1967, 1977), is evidently due to slumping from a shallow-water environment. *Hyalinea baltica,* the other classic index fossil for Calabrian, is present throughout the stratigraphic section at Santa Maria di Catanzaro and ranges to at least 76 m below Bed G-G′ (Bayliss, 1969). This taxon is part of the invertebrate assemblage *(nordische Gäste)* whose initial appearance in the Mediterranean is generally considered by Mediterranean geologists to have been climatically controlled and that can serve as definitive criteria in the definition of the Pliocene-Pleistocene boundary. Thus, although Bed G-G′ at Santa Maria di Catanzaro (with *Arctica islandica*) has served as the base of the Calabrian (= base Pleistocene) for many Mediterranean geologists, the presence of *Hyalinea baltica* to the base of the section at Santa Maria di Catanzaro has led other geologists (e.g., Lamb & Beard, 1972; Bandy & Wilcoxon, 1970), to include the lower part of the section (below Bed G-G′) in the Pleistocene as well.

A description of the Le Castella section by Emiliani *et al.* (1961) showing that the sequence here was more uniformly fossiliferous, was the main basis for the 1965 INQUA amendment to the 1948 proposal. The first appearance of *Hyalinea baltica* in the 1961 sample traverse at Le Castella was said to occur between samples 50 and 51, where a thin intercalation of sand (called simply "the marker bed") crops out in the otherwise clayey sequence. (It has since been found in samples examined at Woods Hole by Bremer, Briskin, & Berggren, 1977, that the initial appearance of *H. baltica* occurs some 25 m below the marker bed at Le Castella where it already constitutes 17 percent of the total benthonic population.) On the basis of the earlier observation, however, Emiliani (1961) convincingly proposed to correlate the sandy "marker bed" to Bed G-G′ (= base of the Calabrian stratotype) at Catanzaro, even though 40 km separates the nearest outcrops of the two beds. The action of the 1968 INQUA Congress has the effect of making the intersection of this bed with Emiliani's traverse line the physical reference point defining the base of the Pleistocene. By general agreement, rather than by further official action, this point is now the "golden spike" at the origin of correlations to the beginning or bottom of the Quaternary, for those who approve of this method of definition.

Figure 2 graphically summarizes the outstanding paleontological and lithological features of the Catanzaro sequence, and Figure 3 those of the Le Castella sequence.[1]

SANTA MARIA DI CATANZARO

Gephyrocapsids (*Gephyrocapsa aperta, G.*

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[1] Figure 2 and the accompanying discussion of the Santa Maria di Catanzaro section, which provide graphic clarification of several problems relating to the stratotype Calabrian, were originally communicated in written correspondence (12 and 22 November 1974) by A. R. Edwards, New Zealand Geological Survey. We would like to thank Dr. Edwards for permission to utilize these data.

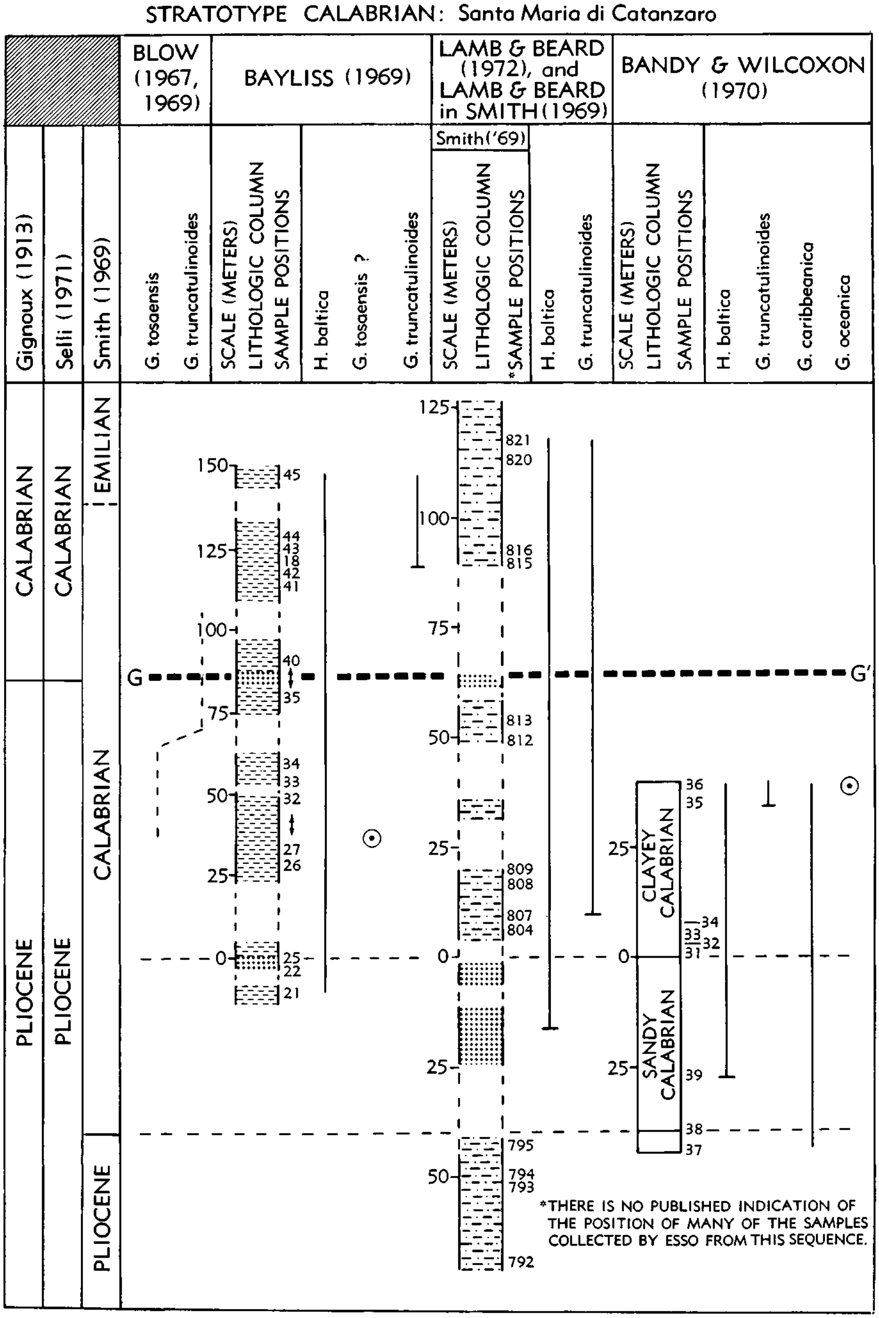

FIG. 2. Basic biostratigraphic data in Santa Maria di Catanzaro section based on published sources (afte data supplied by A. R. Edwards). The position of Bed G-G′ is shown as a dashed line between the 75 an 100 m level in the BAYLISS (1969) column and between 50 and 75 m in the SMITH (1969) colum Taxa with abbreviated generic names are *Gephyrocapsa caribbeanica, Gephyrocapsa oceanica, Globorotali tosaensis, Globorotalia truncatulinoides,* and *Hyalinea baltica* (Berggren & Van Couvering, n).

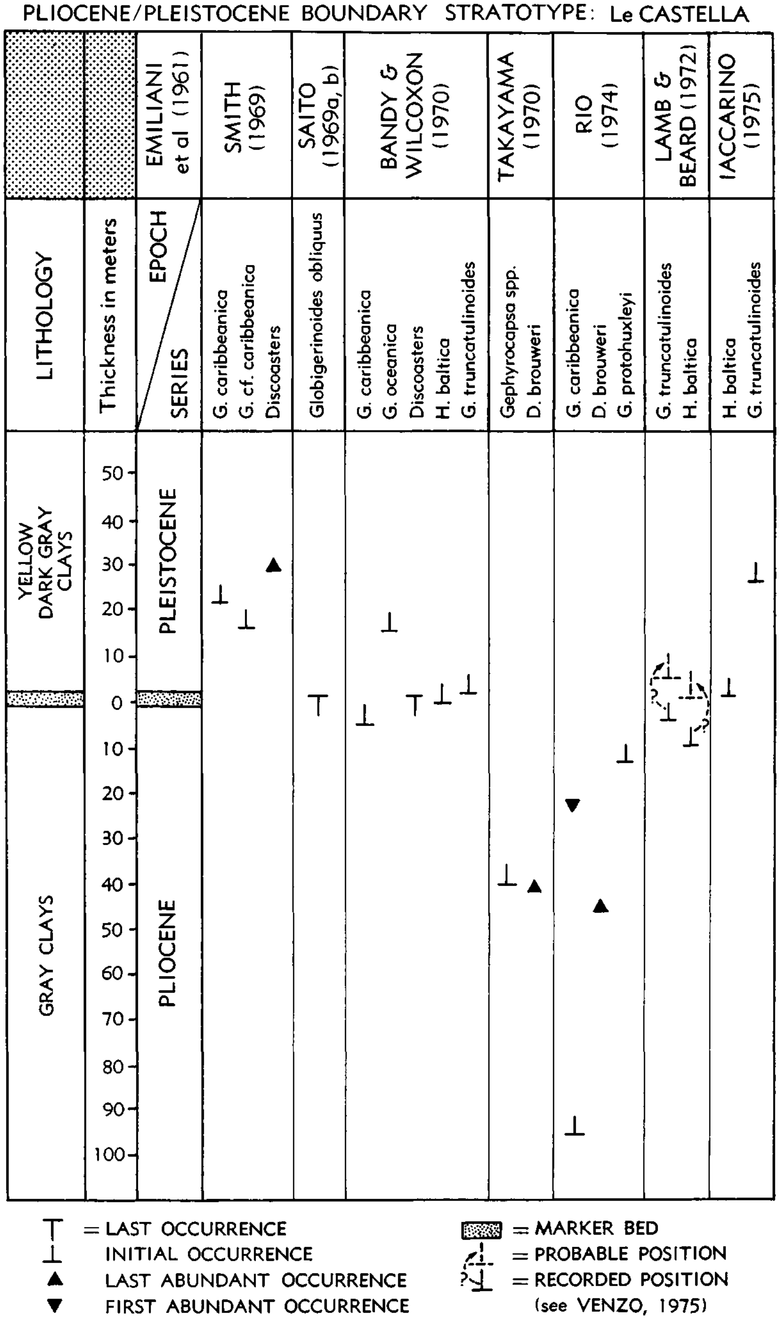

FIG. 3. Basic biostratigraphic data in Le Castella (Italy) section from published sources. Taxa with abbreviated generic names are *Discoaster brouweri, Gephrocapsa protohuxleyi,* and those names cited in the caption of Figure 2 (Berggren & Van Couvering, n).

caribbeanica, and *G. oceanica*)—important in determining the biochronology of the Pliocene-Pleistocene boundary—are already present at the base of the Catanzaro section

(Haq, Berggren, & Van Couvering, 1977) together with *Hyalinea baltica,* at a level more than 75 m below the level designated as the base of the Calabrian by Gignoux (1913).

Banner and Blow (1965) claimed to have recognized the evolution of the planktonic foraminiferal species *Globorotalia truncatulinoides* and *G. tosaensis* in the lower part of the Calabrian at Santa Maria di Catanzaro. Blow (1969) also used this datum to define the base of the planktonic foraminiferal Zone N.22. Abundant *G. tosaensis* or *G. truncatulinoides* do not occur in this sequence, however, and only very scattered, in most places single, specimens have been noted in a few of the samples from Catanzaro (Bayliss, 1969; Bandy & Wilcoxon, 1970; Lamb & Beard, 1972). This fact accounts for the various levels here, as at Le Castella (below), at which the local first occurrence of *G. truncatulinoides* has been reported (see Fig. 2) and thus the initial evolutionary appearance of *Globorotalia truncatulinoides* within the stratotype Calabrian must be viewed as inadequately documented.

LE CASTELLA

For the Le Castella section the relationship between biostratigraphic data of different authors is shown in Figure 3. Important features to note are 1) the extinction of *Globigerinoides obliquus,* which in deep sea cores occurs within the upper part of the Olduvai normal paleomagnetic event; 2) the wide variations in reported first appearance of *Globorotalia truncatulinoides,* due evidently to its extreme rarity in the section as at Catanzaro; 3) marked quantitative diminution in abundance of *Discoaster brouweri,* the last of the discoasters at about 40 to 45 m below the marker bed (we consider this diminution to be a more reliable guide to the extinction of the group than the highest stratigraphic occurrence of specimens because they are so easily reworked); 4) reported first occurrence of *Gephyrocapsa caribbeanica* from levels ranging from 21 m above to 95 m below the marker bed (it should be noted that the occurrence at 95 m is a rare occurrence and that *G. caribbeanica* first becomes common at 25 m below the marker bed); and 5) first appearance of *Gephyrocapsa protohuxleyi* some 10 to 13 m below and *G. oceanica* apparently about 15 m above the marker bed.

In comparison with these generally conflicting reports, an examination of the calcareous nannoplankton at Le Castella (Haq, Berggren, & Van Couvering, 1977) using scanning electron microscopy indicated that *Gephyrocapsa caribbeanica* and *G. oceanica* first appear 30 m and 23 m, respectively, below the marker bed, the latter occurrence coinciding with the initial appearance of *Hyalinea baltica* (Bremer, Briskin, & Berggren, 1977). The variability in stratigraphic records of the calcareous nannoplankton cited in the literature is ascribed in part at least to the use of light microscopy and the consequent difficulty in correctly identifying nannoplankton (especially gephyrocapsid) taxa (Haq, Berggren, & Van Couvering, 1977).

On the basis of these data, it would appear that the Pliocene-Pleistocene boundary is closely linked with the extinction of discoasters and the initial appearance of *Gephyrocapsa caribbeanica, G. oceanica,* as well as the extinction of *Globigerinoides obliquus.* The first appearance of *Globorotalia truncatulinoides* is not an adequate criterion because it cannot be clearly documented in the Calabrian sequence.

AGE AND CORRELATION OF THE PLIOCENE-PLEISTOCENE BOUNDARY

The extinction of discoasters and the evolution of *Globorotalia truncatulinoides* are events that have been securely identified with the long normal paleomagnetic event situated within the Matuyama Reversal Epoch approximately midway between the Gauss and Brunhes normal epochs. The reported chronologic limits for this event range from 1.61-1.79 Ma (Cox, 1969) to 1.71-1.86 Ma (Opdyke, 1972). New radiometric dates centered around 1.58 ± 0.08 Ma attributed to the Gilsa (Watkins, Kristjansson, & McDougall, 1976) and 1.79 ± 0.03 Ma to the type Olduvai (Brock

& Hay, 1976) geomagnetic polarity events have kept alive the issue of whether these two events are, indeed, identical. They are considered identical here, with geochronological limits rounded to 1.6 and 1.8 Ma. As we have seen, the two paleontological phenomena noted above were assumed by a succession of investigators to be recorded in the basal part of the typical Calabrian Stage. This suggested that the base of the Pleistocene could be dated to a time within the Olduvai, probably close to its beginning (Hays & Berggren, 1971; Berggren & Van Couvering, 1974). Attempts to make direct paleomagnetic measurements on the Calabrian of Catanzaro or Le Castella, however, have been fruitless (Lamb & Beard, 1972; Nakagawa, Niitsuma, & Hayasaka, 1969, 1971; Niitsuma, 1970; Watkins, Kester, & Kennett, 1974).

The earlier interpretation of Calabrian micropaleontological correlations has been weakened by recent deep-sea investigations, primarily those of the Deep Sea Drilling Project, which have shown the initial occurrence of *Globorotalia truncatulinoides* near the beginning of the Olduvai event is prior to the extinction of discoasters. This strengthens the impression that the observations of extremely rare *G. truncatulinoides,* above the apparent level of discoaster extinction in the Calabrian, have been erroneously emphasized and do not represent the true datum. Furthermore, recent study (Haq, Berggren, & Van Couvering, 1977) has shown that the initial occurrence of *Gephyrocapsa caribbeanica* just precedes, and that of *Gephyrocapsa oceanica* follows shortly after, the end of the Olduvai Event. Because these relatively reliable nannofossil events either bracket or wholly predate the currently adopted physical definition of the Pleistocene base at Le Castella, the age of the Pliocene-Pleistocene boundary is, on this basis, coincident with or just younger than the end of the Olduvai Event. A reasonable estimate of this age would be very close to 1.6 Ma (see Fig. 4).

Correlations between the Le Castella and Santa Maria di Catanzaro sections, as well as estimates of the age of the marker beds, have been controversial. The "established" point of view has been that the marker beds were stratigraphically equivalent (e.g., Emiliani, Mayeda, & Selli, 1961; Bayliss, 1969; Selli, 1977) and that they have an age of about 1.8 Ma (Hays & Berggren, 1971; Berggren & Van Couvering, 1974). One strongly dissenting opinion (Smith, 1969; Beard, 1969; Lamb, 1969, 1971) has been that the true base of the Calabrian stratotype should be more than 75 m below the G-G′ marker, at the transition between clayey Pliocene beds and the so-called "sandy Calabrian" with *Hyalinea baltica,* and that this contact should define the base of the Pleistocene at an age of about 2.8 Ma. The Le Castella marker bed, at 1.8 Ma, in this view is considered to be near the base of the Emilian Stage. A contrary opinion (Sprovieri *et al.,* 1973; Ruggieri *et al.,* 1976) is that the lower part of the Calabrian Stage—equivalent to the Le Castella section—is missing at Santa Maria di Catanzaro because the "sandy Calabrian" is unconformably transgressive on the Pliocene, and that all of the Catanzaro Calabrian *(s.l.)* is therefore younger than the Le Castella marker bed. Although the existence of an unconformity at Santa Maria di Catanzaro is questioned—Selli (1977) described the contact between clayey and sandy beds as a fault—Bed G-G′ seems to be clearly younger than the marker bed at Le Castella. This is because the entire 75 m of "sandy Calabrian" underlying Bed G-G′ contains *Hyalinea baltica* together with the species of *Gephyrocapsa* noted above, in an association that first appears at Le Castella only a short distance below the Pliocene-Pleistocene boundary marker bed (Haq, Berggren, & Van Couvering, 1977).

If this is so, we are faced with an apparent paradox: if Bed G-G′ at Santa Maria di Catanzaro (which presently denotes the base of the stratotype of the Calabrian Stage) is younger than the marker bed at Le Castella (which presently denotes the Pliocene-Pleistocene boundary), then the section of "sandy Calabrian" below Bed G-G′ is both Pliocene because it is pre-Calabrian, and lower Pleistocene because it is (according to multiple reinforcing micropaleontological criteria) younger than the Le Castella marker bed. If, however, we accept that there is only one definition of the Pliocene-Pleistocene boundary, that of

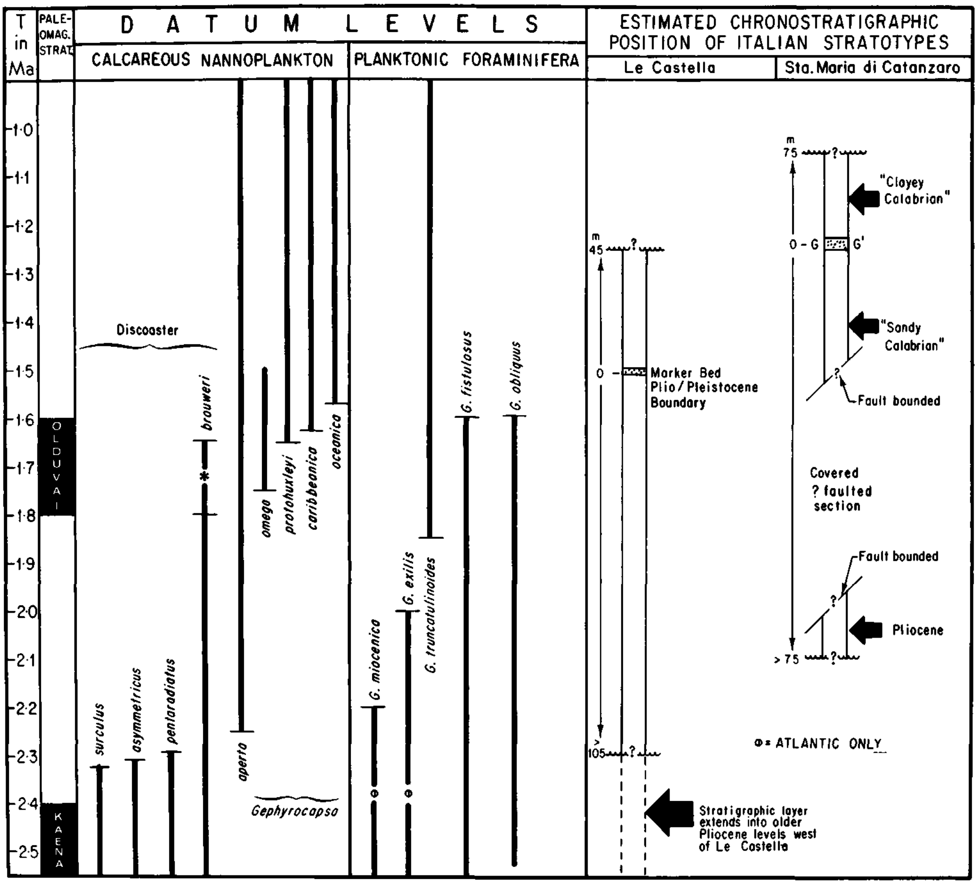

Fig. 4. Pliocene-Pleistocene calcareous plankton biochronology in deep-sea cores and estimated chronostratigraphic position of Calabrian sequences. Extinction of *Discoaster brouweri* occurred at about 1.8 Ma in one of the cores (V12-18) studied. The upper limit of this species, as shown here, may thus be somewhat younger than the actual extinction datum, due to reworking through the interval indicated by asterisk (after Haq, Berggren & Van Couvering, 1977, fig. 5).

Le Castella, this resolves the paradox and simultaneously demonstrates the value of the "golden spike" in picking apart such conundrums.

BIOSTRATIGRAPHY, BIOGEOGRAPHY, AND QUATERNARY CLIMATE CHANGE

Because it is virtually impossible to distinguish between a "pure" biostratigraphy and a "pure" climatology in the geologic record of the late Neogene, the term **climatostratigraphy** is appropriate to describe the study of variations in the stratigraphic record that are due primarily to the effect of global climatic oscillations.

HISTORY OF CONTINENTAL GLACIATION

Recent studies show that the history of the major continental ice caps in the Southern Hemisphere can be extended back at least to the mid-late Miocene (*ca.* 10 Ma) (Shackleton & Kennett, 1975a,b) and of the Northern Hemisphere to about 3 Ma (LAUGHTON *et al.*, 1970, 1972; BERGGREN, 1972; VON HUENE *et al.*, 1971; SCHOLL *et al.*, 1971). In the subantarctic region the evidence indicates that the East Antarctic ice sheet expanded briefly to a volume in excess of present-day size about 6-5 Ma. Subsequent climatic warmings in the Pliocene did not significantly affect the size of the Antarctic ice sheet and this invulnerability to global climatic oscillations has persisted over the past several million years. Minor changes in the isotopic composition of planktonic foraminifers in subantarctic cores at 3 Ma followed by major isotopic changes at 2.6 Ma indicate the onset and growth of a Northern Hemisphere continental ice sheet. In the Northern Hemisphere, the appearance of a major ice cap at high latitudes is indicated by initial ice rafting at about 3 Ma in the northeast Pacific (VON HUENE *et al.*, 1971) and also in the Bering Sea (SCHOLL *et al.*, 1971). In the North Atlantic (Labrador Sea) it consists of ice rafted detritus that appears with polar planktonic microfaunas and microfloras immediately above carbonate oozes with tropical-subtropical microfaunas and microfloras at a level biostratigraphically correlated to the paleomagnetic time-scale at 3 Ma.

The Arctic ice caps have been estimated to have grown to about one-third to one-half of their maximum late Pleistocene volume during the late Pliocene (*ca.* 2.6-2.0 Ma) (SHACKLETON & KENNETT, 1975b).

In the continental sequences of the temperate regions, the evidence clearly indicates unprecedented cooling trends and montane glacial advances, if not the formation of continental lowland ice sheets, beginning approximately 3 Ma ago (SAVAGE & CURTIS, 1970). Also in the southern Andes several montane glacial advances in a conformable sequence of tills and lavas have been dated prior to *ca.* 1.0 Ma by FLECK *et al.* (1972), with the oldest tillite older than 3 Ma (MERCER, 1973). In Europe, the Praetiglian cold-climate stage is marked by the first of numerous subarctic paleofloras seen in late Neogene pollen suites (VAN MONTFRANS, 1971, p. 233; ZAGWIJN, VAN MONTFRANS, & ZANDSTRA, 1971; ZAGWIJN, 1974). It is generally considered by Dutch geologists to be the earliest part of the Pleistocene in North Sea basin sediments where its base is correlated with the *Elphidium oregonense* cold-water microfaunal zone (VAN VOORTHUYSEN, TOERING, & ZAGWIJN, 1972); however, vertebrate fossils, principally primitive *Mammuthus "subplanifrons" (= meridionalis),* indicate that the Praetiglian beds are equivalent in age or slightly older than the middle Villafranchian (e.g., Roccaneyra local fauna *ca.* 2.5 Ma) (AZZAROLI, 1970; V. J. MAGLIO, written commun., 1973) and paleomagnetic analysis agrees in placing the base of this stage "between 2.0 and 3.0, perhaps 2.3 Ma old" (VAN MONTFRANS, 1971, p. 233). The equivalence of the base Villafranchian and the base Calabrian, which was assumed on lithostratigraphic and paleoecological grounds when the two stages/ages were both set equal to the beginning of the Pleistocene (Internatl. Geol. Congress, London, 1948), has since been shown to be erroneous (BERGGREN & VAN COUVERING, 1974). The base of the Calabrian is evidently more than 1 my younger, but in the Netherlands as elsewhere the effects of this mistaken assumption linger.

The continental record, discussed in more detail elsewhere (BERGGREN & VAN COUVERING, 1974), also seems clearly to indicate that the period of progressively more intense montane and high-latitude glacial activity ended in North America with the first major continental glaciation, the Nebraskan. This is tentatively centered at 1.5 Ma, but in Europe (south of England) continental lowland ice-sheets did not form until the Mindel-Elsterian glaciation, dated roughly 0.6 Ma. Several authors (e.g., RICHMOND, 1970; COOKE, 1973) have correlated the Donau-Eburonian cold-climate phase of Europe with the Nebraskan, and REPENNING (1967) reached a similar conclusion based on mammalian correlations before the geophysical information was well developed. We have further concluded that the Kansan glaciation, which is apparently in the Matuyama paleomagnetic age (pre-0.7 Ma), cannot correlate to the post-Matuyama deposits of the Elsterian (VAN MONTFRANS, 1971; ZAGWIJN, VAN MONTFRANS, & ZANDSTRA, 1971), and that the Yarmouthian (post-Kansan) interglacial is characterized by late Irvingtonian mammal faunas comparable in evolutionary grade and geophysical age to those of the Biharian mammal faunas of Europe that lived during the pre-Mindel interglacial. The Biharian-Villafranchian transition in Europe was marked by a cold-climate period, possibly a close-set series of stades and interstades, beginning close to 0.9 Ma, which broadly agrees with estimates of the age of major glacial activity in the North American mountains (cf. COOKE, 1973) and falls within the limits of 1.2 and 0.7 Ma established for the Kansan glaciations. Based on mammalian biochronology the assumed correlation of continental paleoclimatic stages in the Northern Hemisphere is as follows:

Wisconsinan = Weichsel = Würm; began *ca.* 0.073 Ma
Riss-Würm (= Eemian); began *ca.* 0.127 Ma
Riss (includes Alt-Riss); began *ca.* 0.2 Ma
(Sangamonian = Holsteinian interglacial)
Illinoisan = Mindel = Elster; began *ca.* 0.6 Ma
(Yarmouthian = "Cromerian" interglacial) (but not type Cromerian; see BERGGREN & VAN COUVERING, 1974)
Kansan = Günz = Menapian; began *ca.* 0.9 Ma, probably with a second and dominant phase *ca.* 0.8 Ma
(Aftonian = Waalian interglacial)
Nebraskan = (?later part of) Donau = Eburonian; began *ca.* ?1.6 Ma
(Blancan warm-climate phase = Tiglian "interglacial")
Early Blancan cold-climate phase = ?Biber = ?Praetiglian; began *ca.* ?2.5-3 Ma

As we shall see, the marine record contains features that cannot be expressed in such a simple chronology, and that suggest important refinements. To date there has been no general agreement on the correlation of the various glacial episodes on the continents with paleoclimatic cycles reflected in the deep-sea sediments and fossils, and all too often it has been the practice of oceanographers to identify a continental glacial event in marine cores according to some poorly tested paleoclimatological analogy. The difficulty has largely been with the nature of the data. The record on land, with the exception of loess deposits and certain lacustrine sequences beyond the glaciated regions, is essentially discontinuous because of the repeated passage of glaciers and the later erosion of their deposits. The preserved remains of a given "glacial stage" in most places represents but a small fraction of the time during which given climatological conditions prevailed and much of the history of events during that time is unavailable. On the other hand, in the deep-sea record one sees evidence of relatively continuous paleoclimatic changes on a relatively fine scale and for this reason marine paleoclimatological cycles may prove eventually to be the best means of providing a chronology of the late Neogene glacial record.

CALIBRATION OF CLIMATOSTRATIGRAPHY

Temperature variations in the Pleistocene oceans, as reflected in the oxygen isotope ratios in fossil planktonic foraminifers from deep-sea cores, have been examined in detail by EMILIANI (1955, 1961, 1964, 1966a,b) and EMILIANI, MAYEDA, & SELLI (1961). EMILIANI demonstrated isotopic changes, said to represent cyclical climatic variations, with a periodicity of about 100,000 years. These cycles are numbered so that each warm half-cycle is odd and each cold half-cycle is even. OLAUSSON (1965), SHACKLETON (1967), and DANSGAARD and TAUBER (1969) later suggested that because of the isotopic fractionation that occurs between fresh and salt water, oxygen isotope measurements are a measure of the extraction of water from the oceans during periods of glaciation and the recirculation of this water during interglacial periods, rather than a direct reflection of sea-water temperature. The oxygen isotope curve then would be an ice-volume (i.e., sea level) rather than a paleotemperature curve.

SHACKLETON and OPDYKE (1973) further extended the oxygen isotope record by identifying new "stages" 16 to 22 in an equatorial Pacific core, Vema V28-238 (Fig. 5). A direct one-to-one correlation was shown between the carbonate minima (ARRHENIUS, 1952; HAYS *et al.*, 1969) and the oxygen-isotope "stages" for the past 0.9 Ma. The age of each stage boundary was calculated using an extrapolated uniform sedimentation rate between the top of the core and the Brunhes-Matuyama boundary (0.69 Ma) at 12 m in the 16-m core. The isotopic climatic record was then extended down through the Pleistocene and into the late Pliocene in another equatorial Pacific core, V28-239 (Shackleton & Opdyke, 1976; see Fig. 6, this paper). Below stage 22 isotopic fluctuations were shown to have a periodicity of approximately 40,000 years and lower amplitudes down to about 1.4 Ma and even lower-frequency events were recorded in the interval from 1.4 Ma to the Olduvai (*ca.* 1.8 Ma). The isotopic record thus clearly demonstrates that the Brunhes-Matuyama boundary separates two distinct climatic regimes within the Pleistocene, so that the first major northern hemisphere glaciation—the Kansan (= Günz = Menapian), or its second, greater part—occurs in the interval between the Jaramillo and the Brunhes-Matuyama boundary at about 0.8 Ma; prior to this time smaller scale glaciations occurred back into the Pliocene. Broecker and Van Donk (1970) have pointed to the general asymmetrical ("sawtoothed") shape of the major climatic oscillations in which a gradual cooling trend is terminated abruptly by a relatively rapid warming (the rapid warmings were called ^{18}O "terminations"). Similar observations were made earlier by Deuser and Degens (1969) in which ~20,000-year evaporation cycles in the Red Sea were abruptly terminated by rapid (~2,000-year) incursions of normal sea water from the Indian Ocean.

Thus, the combined techniques of paleo-

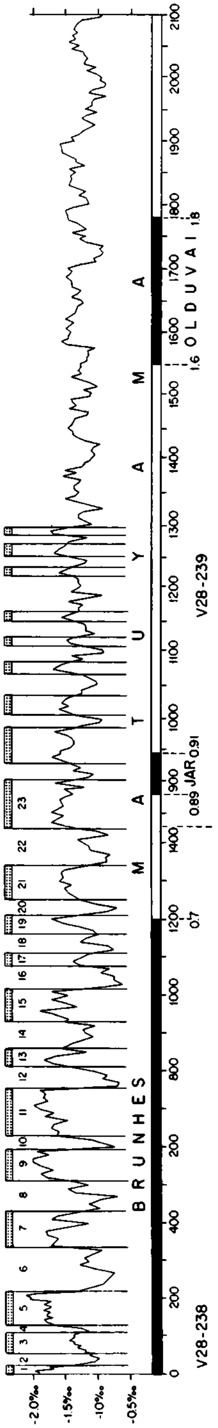

Fig. 5. The oxygen isotope climatostratigraphic record of the last 2 Ma. The oxygen isotope composition of *Globigerinoides sacculifer* in cores V28-238 (01°01'N., 160°29'E.) and V28-239 (3°15'N., 159°11'E.) (overlap of two cores is shown at boundary between "stage" 22 and 23) expressed as deviation from Emiliani B1 Standard. The last 0.7 Ma (Brunhes) contains glacial stages represented by amplitudes in excess of 1 per mil and with periodicities of about 100,000 years. Isotopic minima were approximately the same in the different "core stages." The mid-Matuyama (~1.4-0.7 Ma) interval contains isotopic fluctuations with approximately 40,000 year periodicities. Amplitudes are lower (0.7 per mil) than during the Brunhes (composite figure compiled by N. J. Shackleton; data from Shackleton & Opdyke, 1973, 1976).

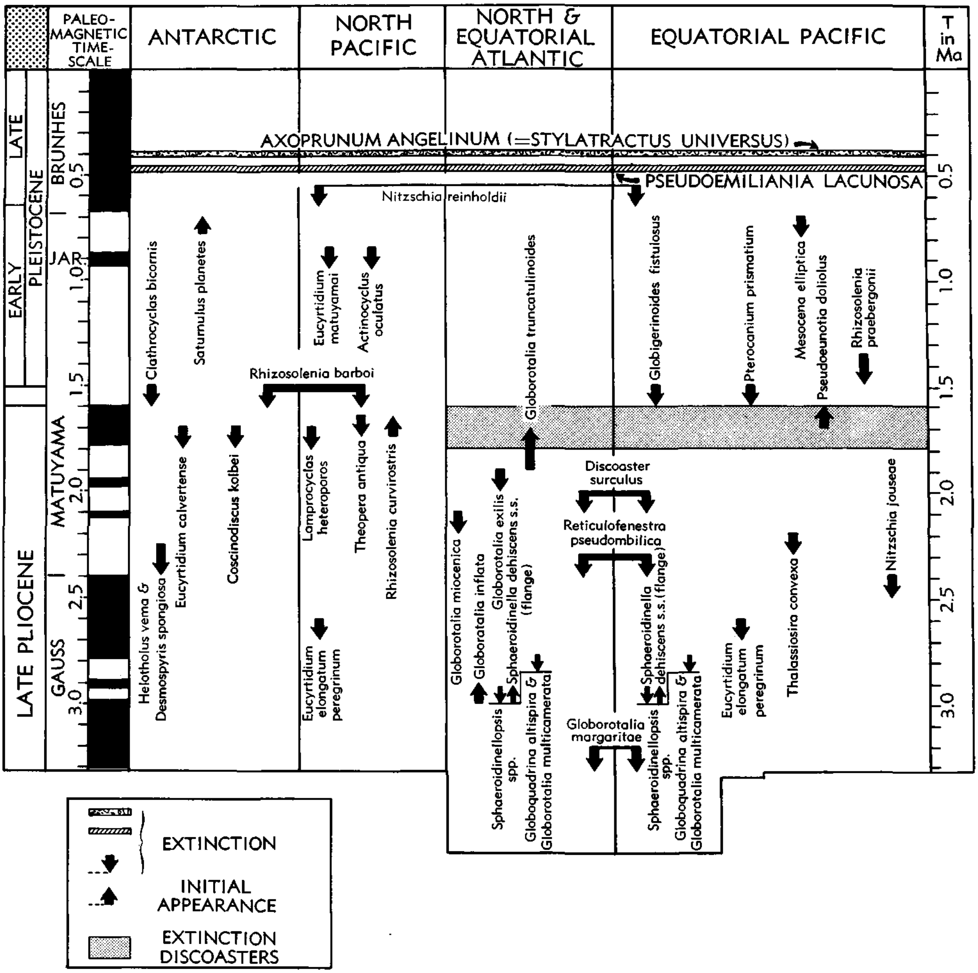

FIG. 6. Marine planktonic biochronologic datum-levels for the last 3 Ma (after Berggren, 1977, fig. 1). [Additional data supplied by L. H. Burckle, J. D. Hays, and N. D. Opdyke.]

magnetism and oxygen isotope analysis have provided the means of erecting an accurate chronology for the last 2 Ma (see Fig. 5). Inasmuch as it depends upon an irreversible phenomenon that occurs essentially synchronously throughout the ocean (limited only by the rate of oceanic mixing) it is unlikely "that any superior stratigraphic subdivision of the Pleistocene will emerge" (SHACKLETON & OPDYKE, 1973, p. 48). Because the underlying variable used is the volume of terrestrially stored ice, this chronologic scheme can serve as a standard method for intra-Pleistocene chronology and, indeed, SHACKLETON and OPDYKE (1973, p. 48) have suggested that the isotopic "stages" that they have established in the Equatorial Pacific be adopted as standard for the latter half of the Pleistocene.

It should be emphasized, however, that the oxygen isotope stratigraphy is *not* a time scale and can only be used to "date" climatic events and associated biostratigraphies to the extent that levels in this stratigraphy can be calibrated—first, by radiometric or biochronological analysis, or second, by association with calibrated magnetostratigraphic boundaries.

Biostratigraphic zonations of Pliocene and Pleistocene marine sediments based upon calcareous and siliceous plankton have been developed over the past decade, primarily as a consequence of the concentrated investigations of deep-sea cores since the inception of the Deep Sea Drilling Project in 1968. By means of interzonal correlation and calibration to oxygen isotope climatic "stage" chronology (Shackleton & Opdyke, 1973, 1976) and the paleomagnetic time scale (Cox, 1969) these zones now provide a biochronologic framework within which global Pliocene-Pleistocene climatostratigraphic investigations may be conducted. Some of the major microplanktonic biochronologic datum levels of the last 3 Ma are shown in Fig. 6.

ATLANTIC OCEAN

Recent analysis of cores from the North Atlantic (Laughton *et al.,* 1970, 1972; Berggren, 1972) has shown that the continental glacial history of the Northern Hemisphere can be extended back three million years. And yet, in comparison with other parts of the world, our information on the stratigraphic record in this region is comparatively incomplete within this interval. This is due, in large part, to the relatively great thickness of ice-rafted terrigenous detritus in late Pliocene-Pleistocene sediments.

The pioneering investigations on the Pleistocene paleoclimatic history of the Atlantic Ocean were made by Ericson and his colleagues at the Lamont-Doherty Geological Observatory (Ericson *et al.,* 1956; Ericson, Ewing, & Wollin, 1963, 1964a,b; Ericson & Wollin, 1956a,b, 1968). As a result of detailed and laborious investigations on numerous deep-sea cores, a letter zonation of the Pleistocene was formulated (Zones Q through Z) based on the presence or absence of *Globorotalia menardii.* Those intervals in which *G. menardii* was absent were interpreted as "cold periods" and correlated with the classic continental glaciations of northern Europe, a procedure that had little justification at the time and in retrospect has been extremely misleading.

More recently, a Quaternary paleoclimatology based on microfossils in the eastern equatorial Atlantic has been described by Ruddiman (1971). In this analysis, large-scale climatic shifts were shown to have occurred at 1.3 Ma and at 0.9 Ma. In the earlier change the mean climatic condition deteriorated and short severe cold pulses punctuated the previously moderate warmth of the late Matuyama. In the latter modification, the duration of cold intervals increased. It was observed that, prior to the Jaramillo (0.9 Ma), no cold pulses exceeded 30,000 years, whereas three post-Jaramillo cold intervals ranged from 50,000 to 150,000 years in duration. The shortest and most recent of these corresponds to the Wisconsin glaciation.

Ruddiman (1971) found that although the absolute input rate of pelagic carbonate to sediments increased during cold intervals, the net carbonate percentage tended to decrease during glacial times due to dilution by greater influxes of terrigenous detrital material. Carbonate percentages were depressed to very low values beginning in the Jaramillo, whereas pre-Jaramillo sections were generally formed from calcareous oozes.

SHIFTS IN PALEOISOTHERMS

Recently McIntyre, Ruddiman, & Jantzen (1972) have demonstrated that in the eastern North Atlantic southward penetration of polar waters occurred at least six times in the past 225,000 years, most severely 165,000 to 135,000 years ago and 30,000 to 15,000 years ago (Fig. 7). At the same time a marked northward incursion of warmer subtropical faunal and floral elements occurred at least six times, the most pronounced being at 175,000 years, 125,000 years, and 8,000 years, respectively. The southern limits of the Pleistocene polar-water incursion was about latitude 42-45° N.

Quantitative paleoclimatologic investigations have recently led to more precise estimates of late Pleistocene climatic conditions in the North Atlantic (Imbrie & Kipp, 1969, 1971; Imbrie, 1972; Kellogg, 1972; McIntyre *et al.,* 1972a; Imbrie, Van Donk, & Kipp, 1973). The polar front that currently extends obliquely from Labrador to the north of Norway 17,000 years ago described

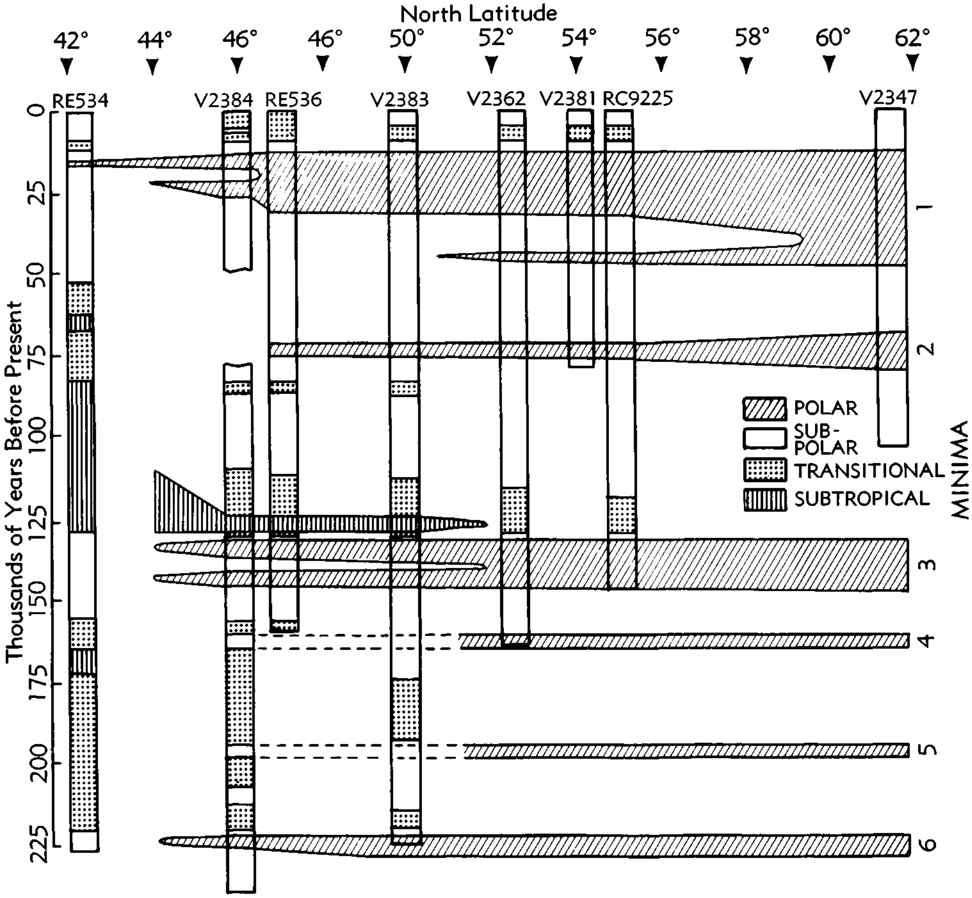

FIG. 7. Polar front and subtropical front migration in the North Atlantic for the last 225,000 years. Paleodistribution of water masses (legend on chart), deduced from faunal and floral data plotted for each core (after McIntyre, Ruddiman, & Jantzen, 1972, fig. 8).

a gentle curve nearly parallel to the latitude from Cape Hatteras to Spain. This represents a northward displacement of 20° latitude in the west to 30° in the east from that time to the present.

The temperature at the termination of the last glaciation (*ca.* 10,000 years ago, referred to by many geologists as the Pleistocene-Holocene boundary) denotes the division of the glacial North Atlantic by the polar front. The difference between today and the 17,000 year B.P. winter-summer temperatures for 50°N. 30°W. is 7.2-12.7°C to 1.2-6.6°C, respectively, an average of 6°C colder than at present. South of the polar front the temperature 17,000 years ago was only about 3°C colder (MCINTYRE, RUDDIMAN, & JANTZEN, 1972).

CHANGES IN SEASONALITY

A quantitative planktonic foraminiferal faunal analysis in the tropical North Atlantic by BRISKIN and BERGGREN (1975) extended the interpretation of climatic fluctuations on this basis back to two million years. Winter changes were estimated to have fluctuated within a range of 4°C and summer temperatures within a range of 2°C. Pleistocene seasonal differences $(T_s\text{-}T_w)$ were estimated to have ranged between 1.5 and 4°C.

From the Olduvai to late Jaramillo the amplitude of winter temperature contrasts (severe to mild) were subdued and temperatures on the average cooler (22.3 to 24.2°C) than during the Brunhes. Beginning in the

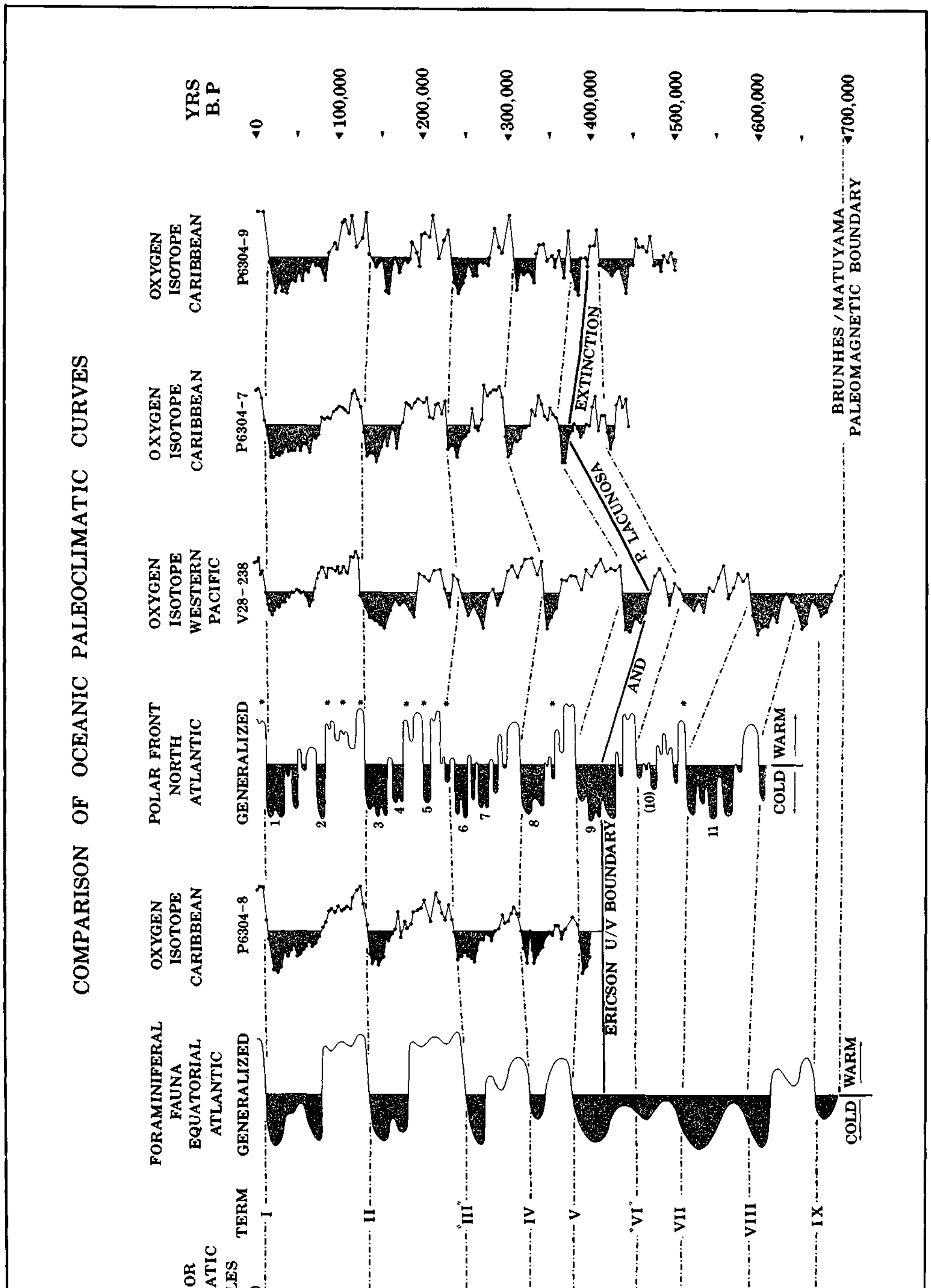

FIG. 8. Climatic cyclic trends in the oceanic deep-sea core record. Equatorial Atlantic faunal curve from RUDDIMAN (1971); Caribbean isotopic curves from EMILIANI (1966a, 1972); North Atlantic curve from

late Jaramillo and continuing into the Brunhes, winter contrasts were greater but the climate was on the average warmer (23° to 23.5°C).

Four roughly symmetrical major climatic cycles with periodicities of 500,000 years were recognized within the Pleistocene (BRISKIN & BERGGREN, 1975). These cycles are more clearly expressed in the winter estimate *(T_w)* than in the summer estimate *(T_s)*. The coldest winters occurred at the following times:

(1) in the lower R Zone (23°C) at 1.5 Ma;
(2) in the lower T Zone (20.1°C) at the base of the Jaramillo, 960,000 years ago;
(3) in the Brunhes (23°C) 610,000 years ago;
(4) in the W and Y zones (23.6°C) 150,000 and 50,000 years ago.

A climatic fluctuation with periodicity averaging 91,000 years becomes conspicuous in the interval from early V time (~0.4 Ma).

A comparison of ^{18}O and the faunal index T_w led the authors to suggest that the winter-cold maxima (1,2) in the early and mid-Matuyama were associated with smaller ice-volume changes than those (3,4) in the late Matuyama and the Brunhes, where ice volumes were of greater magnitude. The timing of the coldest winter periods corresponds with K-Ar-based estimates of age for the major continental glaciations, and it is well documented that the ice volumes of the Illinoisan (= Mindel = Elster) and later ice sheets were greater than those of the preceding glaciations.

In the Matuyama, records of cold episodes in the North Atlantic cores are characterized by the cold, high-latitude, dextrally coiled *Neogloboquadrina pachyderma,* whereas records of Brunhes cold episodes are characterized by temperate-cool *Globorotalia inflata.* This suggests that maximum southward displacement of the Canaries Current occurred during the cold-water intervals in the Matuyama. In the Brunhes a more moderate displacement of the Canaries Current brought temperate rather than arctic waters into the tropical province.

QUATERNARY CLIMATIC HISTORY

RUDDIMAN and McINTYRE (1976) recently summarized the paleoclimatologic evidence in Atlantic deep-sea studies. They showed that water mass migrations in the North Atlantic across more than 20° of latitude (equivalent to oceanic surface water temperature oscillations of at least 12°C) have occurred along a NW-SE axis at least 11 times in the last 0.6 Ma and perhaps as many as 20 times in the past 1.2 Ma. At least seven complete climatic cycles have been recorded in the past 0.6 Ma (see Fig. 8) and can be correlated directly with the oxygen isotope (SHACKLETON & OPDYKE, 1973) and carbonate (HAYS *et al.,* 1969) cycles in the equatorial Pacific and Caribbean and with the palynologic record from the eastern Mediterranean (VAN DER HAMMEN, WIJMSTRA, & ZAGWIJN, 1971).

The interpretation of RUDDIMAN and McINTYRE (1976) indicated the presence of long-term climatic changes with lengths varying from 56,000 to 113,000 years in the faunal and lithic record. Additional short term but severe climatic pulses with 20,000 year periodicities are also seen.

Furthermore, any or all of the polar water advances recorded over the past 0.6 Ma may correspond to expansion and advance of continental ice sheets because a significant amount of ice-rafted detritus is associated with each of these maxima. Thus, continental glaciers probably reattained similar, equivalent sizes despite the brevity of these climatic pulses (support for this view is

FIG. 8. *(Continued from facing page.)*
RUDDIMAN and McINTYRE (1976); Pacific isotopic curve from SHACKLETON and OPDYKE (1973). Major climatic cycles, *A-I*; discrete glacial maxima, 1-11; terminations, *I-IX*; asterisks indicate high sea-levels, all from MESOLELLA *et al.* (1969). The U/V boundary refers to the zone of that denomination and is part of the Pleistocene planktonic foraminiferal zonal system developed by ERICSON *et al.* (1964a,b). This boundary, and the extinction of *Pseudoemiliania lacunosa,* coincides closely with the oxygen isotope stage 11/12 boundary. P6304-8, V28-238, etc. = piston cores (from Ruddiman & McIntyre, 1976, fig. 13).

seen in the fact that similar oxygen isotope values occur in successive cold cycles; SHACKLETON & OPDYKE, 1973; see also FAIRBRIDGE, 1972) and that the vigor of trade winds during glacials varied within similar limits (PARKIN & SHACKLETON, 1973).

Short, intensive oceanic coolings are correlative with high herbaceous concentrations in the pollen record (= open, dry to desertic conditions) and occur within interglacial phases of cycles B, C, D and G. Cycle E in Atlantic and Pacific cores contains a short glacial and a long, well-developed interglacial phase, the latter denoted by an unusually high carbonate maximum, high $^{18}O/^{16}O$ values, and high subtropical coccolith abundances. This warm interglacial phase just postdates the *Pseudoemiliania lacunosa* and *Stylatractus universus (vel Axoprunum angelinum)* extinction datum levels within the glacial portion of climatic cycle F (= climatic "stage" 12 of EMILIANI, 1966a,b, and the U Zone of ERICSON & WOLLIN, 1968). In the Macedonian pollen record cycle E is similar in that this interglacial is the longest and corresponds most likely, in classic continental chronostratigraphy, to the Mindel-Riss Interglacial.

The most recent global retreat (warming) of polar waters in the North Atlantic was time transgressive; between latitudes 45° and 64° N. the local termination of glacial conditions ranges from *ca.* 13,500 years B.P. near Great Britain to about 6,500 years B.P. or younger in the northwest near Greenland. This indicates that climatically controlled cycles cannot serve as a basis for drawing chronostratigraphic boundaries.

From Figure 8 it can be seen that the classic view of an interglacial period as a protracted warm interval with a span of about 30,000 to 50,000 years is inaccurate. On the contrary, numerous warm intervals, on the average 8,000 years long, separated by cooler intervals, some of which approach glacial interstadials, is a more accurate picture of Quaternary climate change. Thus, the Holocene, the base of which, climatically speaking, may be said to extend to about 13,000 years B.P., already exceeds the interglacial average by about 5,000 years (see also similar results presented in KUKLA, MATHEWS, & MITCHELL, 1972).

GULF OF MEXICO CLIMATIC RECORD

Rapidly changing climatic conditions with little evidence of prolonged climatic stability seems to have been the pattern in the Gulf of Mexico with three interglacials and two glacials being recorded over the late Pleistocene-Holocene interval. A subdivision of the standard V-Z zonation (ERICSON & WOLLIN, 1968) based on *Globorotalia menardii* frequency oscillations into 18 climatically controlled zones has provided the biostratigraphic framework for climatic interpretations as well as for comparison with the climatostratigraphic record in the Caribbean and elsewhere. A relatively rapid cooling event was identified at *ca.* 90,000 years (KENNETT & HUDDLESTUN, 1972) and correlated with a similar event recorded in the oxygen isotope record in a Greenland ice core (DANSGAARD *et al.*, 1971, 1972; JOHNSEN *et al.*, 1972) and in a cave stalagmite from a cave in southwestern France (DUPLESSY *et al.*, 1970).

An insight into the nature, extent, and rate of Laurentide deglacial processes was afforded by the investigations of KENNETT and SHACKLETON (1975) on Gulf of Mexico cores. A major isotopic anomaly between 15,000-12,000 years B.P. resulted from major influx of isotopically lighter glacial meltwaters via the Mississippi River drainage system from the Laurentide ice sheet, which was then situated some 2,000 km to the north. By 12,000 years B.P. the Laurentide ice sheet had disintegrated to about a third of its maximum Wisconsin size. At the time of maximum input of glacial meltwaters the Gulf of Mexico was estimated to have undergone a reduction in surface water salinity of about 10 percent (2-3 per mil).

As the authors pointed out, earlier glacial meltwater phases would have influenced salinities in the Gulf of Mexico and will eventually provide us with information on the geographic extent of earlier (pre-Wisconsin) ice sheets because it may be assumed that no significant meltwater would have been discharged into the Gulf of Mexico unless the southern extent of the ice sheet was greater than that of the Wisconsin ice sheet 11,500 years ago, at which time isotope values returned to normal. Inasmuch as each successive glacial readvance across the land obliterated much of the preceding glacial record, the geographic distribution of former ice sheets is difficult to reconstruct from the continental record. Thus, the oceanic record (with its inherently more complete record and accurate chronology) may eventually provide us with the most suitable means for paleogeographic reconstructions of past glacial intervals and, ultimately, a comprehensive climatostratigraphic history of the Quaternary.

ARCTIC REGION

It is 20 years since the EWING-DONN (1956) theory was first promulgated, in which it was suggested that the Arctic Ocean remained ice-free during times of continental glaciation and ice-covered during interglacial times. The oldest erratics recorded in the Arctic Ocean have been dated within the Gauss Normal Epoch at about 3 Ma (CLARK, 1971), representing the first evidence that ice-cap glaciers reached sea level in the vicinity.

Fluctuations in the abundance of planktonic foraminifers (primarily *Neogloboquadrina pachyderma*) also suggest climatic variations within the Arctic Ocean although the interpretation of these results varies somewhat. For instance, CLARK (1971) suggested that a thicker ice pack could have significantly affected the productivity of organisms whose economy is based on photosynthesis. Thus, thicker ice conditions would correlate with those periods in which planktonic foraminifers were absent or rare, whereas thinner ice conditions, similar to the present time, would have allowed a larger standing population of planktonic foraminifers to develop. He concluded that the surface of the Arctic Ocean has been frozen at least since the middle Pliocene and that the most significant change in the Arctic ice cover has been its thickness.

The conclusions of CLARK (1971) are interesting in that they suggest that the ice cover of the Arctic Ocean remained relatively stable while continental glaciers expanded and retracted repeatedly in the Northern Hemisphere. If this is true, the Arctic Ocean has not been a major factor in the growth or melting of continental glaciers. Support for this idea was provided by KU and BROECKER (1967) who observed that sedimentation rates (0.2 cm/1,000 years) in the Arctic Ocean were relatively constant during the past 150,000 years and that the biological productivity rates have not exceeded those of the present-day ice-covered Arctic Ocean in the past 150,000 years and that these are much lower than in the Atlantic Ocean. The implication of these observations, according to KU and BROECKER (1967, p. 102), is that they do not favor theories of glaciation that call upon the influence of an open Arctic Ocean (cf. EWING & DONN, 1956, 1958; DONN & SHAW, 1967).

HUNKINS *et al.* (1971) noted that *Neogloboquadrina pachyderma* shows predominantly left coiling during the Brunhes, whereas a zone of right coiling forms is evident near the Jaramillo Event. This suggests warm conditions at that time, which conflicts with the abundance data that show a markedly lower percentage below the Brunhes-Matuyama boundary. The authors suggested that solution effects may have been more pronounced prior to a million years ago. The presence of manganese nodules and low foraminiferal counts in the Matuyama, at least to 1.5 Ma, suggest that climatic conditions were more uniform and without the wide fluctuations of the Brunhes epoch. Most of their cores show seven cycles in the Brunhes with periodicities of about 100,000 years. They concluded that the ice pack has been similar to that of the present day for the past 80,000 years, but that prior to this time a number of cycles with conditions similar to today fluctuated with colder intervals during which the ice pack was extremely tight and during which there was no open water even in the summer.

A somewhat different interpretation has been presented by HERMAN (1969, 1970, 1974), who concluded that the Arctic has been frozen only since the beginning of the Brunhes and was ice free during the Matuyama and Gauss; however, this interpretation seems unlikely in the light of the recent results of Leg XII (North Atlantic) of the Deep Sea Drilling Project, in which it has been shown that major sea-level berg-calving began 3 Ma ago, indicating the initiation of climatic conditions similar to those of the present interglacial with seasonally (at least) frozen Arctic waters.

Subsequent investigations (Larson, 1973, 1975; Clark *et al.,* 1975) in the Arctic Ocean have revealed that the replacement of an arenaceous benthonic by a calcareous hyaline benthonic foraminiferal assemblage occurs near the Brunhes-Matuyama boundary and may be due to a change in oceanic circulation patterns (increased oxygenation due to greater overturn connected with more intense glaciation and the entry of North Atlantic deep water during interglacial periods) rather than to ice-cover changes. Correlation of the Quaternary Arctic deep-sea core climatostratigraphic record with climatostratigraphic curves developed elsewhere (e.g., Atlantic, Caribbean) is vague and unclear, but the relatively uniform cold polar conditions during that time may be expected to have left a blurred record of climatic change in comparison with the distinct, oscillatory changes that are recorded at mid-latitudes.

The late Neogene geologic and stratigraphic history of Beringia (western Alaska, northeastern Siberia, and shallow parts of the Chukchi and Bering seas) has been summarized by Hopkins (1967a,b, 1972, 1973) and Nelson, Hopkins, & Scholl (1974a,b). In the marine strata, three distinct glacial episodes can be distinguished, Siberian glaciers having extended over 150 km beyond the Chukotka Peninsula shoreline. Related to these are three major interglacial transgressions: in ascending age the Anvilian, Einahnuhtan, and Kotzebuean, followed by a brief double transgression separated by a brief regression, the Pelukian. This last (and youngest) transgression is radiocarbon-dated at more than 38,000 years (Hopkins, 1973). During the Anvilian transgression (which is considered to be of early Pleistocene age, between 1.8-0.7 Ma) circulation was dominantly northward through the Bering Strait, relative sea level somewhat higher and water deeper on the Bering Shelf; molluscan and foraminiferal faunas indicate that water temperatures did not differ significantly from those of the present day (Hopkins *et al.,* 1974).

The Einahnuhtan transgression is thought to represent Termination III of Broecker and Van Donk (1970), dated at about 0.225 Ma. The series of progressively colder interglacial marine transgressions culminated in the Kotzebuean transgression, which represents a positive fluctuation that modulated a generally falling sea level in the 100,000 years that followed the Einahnuhtan and during which time normal northward circulation through the Bering Strait was reversed. Arctic molluscan faunas penetrated southward along the coasts of eastern Siberia and southwestern Alaska during Kotzebuean time, which is correlated with the Holstein interglacial in northwest Europe (Hopkins, 1973). Shackleton and Opdyke (1973) have suggested that the Holsteinian, generally thought to be correlative with a level within oxygen-isotope "stage" 7, may in fact be older (?stage 11 = 400,000 years B.P.). If the correlation of Kotzebuean = Holsteinian is correct, it may necessitate a lowering of the ages of the Einahnuhtan and Kotzebuean transgressions.

Sea level fell to about −135 m in the Bering Sea during the maximum phase of the penultimate glaciation. Following this, the Pelukian shorelines may represent high sea level stands of Termination II (*ca.* 125,000 years B.P.) of Broecker and Van Donk (1970) and one of the two high sea level stands dated at about 106,000 years B.P. and 80,000 years B.P. that modulated the generally falling sea level during the later part of the last interglacial (= Eemian). Another positive modulation brought sea level to at least −20 m about 30,000 years B.P. Sea level fell to about −90 to −100 m during the late Wisconsinan regression but a substantial part of the Bering shelf remained submerged.

According to Hopkins *et al.* (1971), the tundra biome replaced a predominantly beech and spruce forest in southern Alaska similar to present-day forests in southeastern Alaska and British Columbia sometime later than 5.7 Ma and more probably not until the early Pleistocene (Hopkins, 1972). Evidence cited above of the growth and development of Northern Hemisphere continental ice sheets within the late Pleistocene suggests that this major floral replacement may have occurred as early as 3 Ma.

PACIFIC OCEAN

EQUATORIAL PACIFIC CLIMATIC CHANGES

The late Neogene paleoclimatic history of the equatorial Pacific region, based on carbonate maxima in deep sea cores, has been described by Hays *et al.* (1969). Eight distinct carbonate cycles were recorded in the Brunhes (last 0.7 Ma) with periodicities of about 75,000 years in the later part to about 100,000 years in the early part of the Brunhes.

Slightly lower average carbonate content was observed in the interval between the Olduvai and the Brunhes (i.e., the late Matuyama). Average periodicities here were on the order of 100,000 years. The generally lower concentration of calcium carbonate in the late Matuyama was interpreted as suggestive of warmer average climates during that time. A sharp rise in calcium carbonate content in the upper Gauss Normal series may reflect mid-Pliocene cooling at about 3 Ma. Hays and his colleagues observed that no marked change in the carbonate content occurred during the Olduvai Event, although in Antarctic cores there is a lithologic change (see below) in the neighborhood of the Olduvai Event (Hays, 1965, 1967; Opdyke *et al.*, 1966), which may have been due to cooling. The comparison of this record agrees in timing and in paleoclimatic interpretation with the ^{18}O record described by Shackleton and Opdyke (1973, 1976).

Quaternary paleoclimates have been described in the marginal northeastern Pacific by Ingle (1973). In this area the glacial interval of the Pleistocene was characterized by sustained subarctic temperatures at least as far south as latitude 30°N. and probably to 20°N. allowing the biofacies with dextrally coiled *Neogloboquadrina pachyderma* to move up into the Gulf of California where it was subsequently trapped by northward readjustment of isotherms in the Holocene. Such populations are reminiscent of similar conditions in the Gulf of Mexico that led to populations of *Globigerina bulloides* being trapped in the Gulf of Mexico following the retreat of the last glaciers (Phleger, 1961).

SEA OF JAPAN

Four significant surface temperature events were delineated in the Sea of Japan during the Quaternary (Ingle, 1975) beginning with a significant cooling event at about 0.9 Ma, which apparently correlates with other evidence of intense midlatitude glaciation (Kent, Opdyke, & Ewing, 1971; Ingle, 1973; Ruddiman, 1971).

ANTARCTIC-SUBANTARCTIC OCEAN

The investigations of Shackleton and Kennett (1975a,b) have shown that the East Antarctic ice sheet became established, and subsequently reached dimensions in excess of its present-day extent, during the Miocene and has remained relatively stable and immune to fluctuations in global climate since that time.

Major climatic changes related to the expansion and contraction of Northern Hemisphere, and to a lesser extent the Antarctic, ice sheets have been placed within the time-stratigraphic framework of the New Zealand stages, which have, in turn, been correlated with the European stage units (Fig 9).

AUSTRALIA-NEW ZEALAND AREA

Ten climatic cycles within the Matuyama (2.43 to 0.7 Ma) have been delineated in northern Antarctic and subantarctic waters south of Australia and New Zealand, which are based on alternation of cold and warmer water planktonic foraminiferal faunas (Keany & Kennett, 1973). Eight climatic cycles over the last 1.3 Ma, six of which

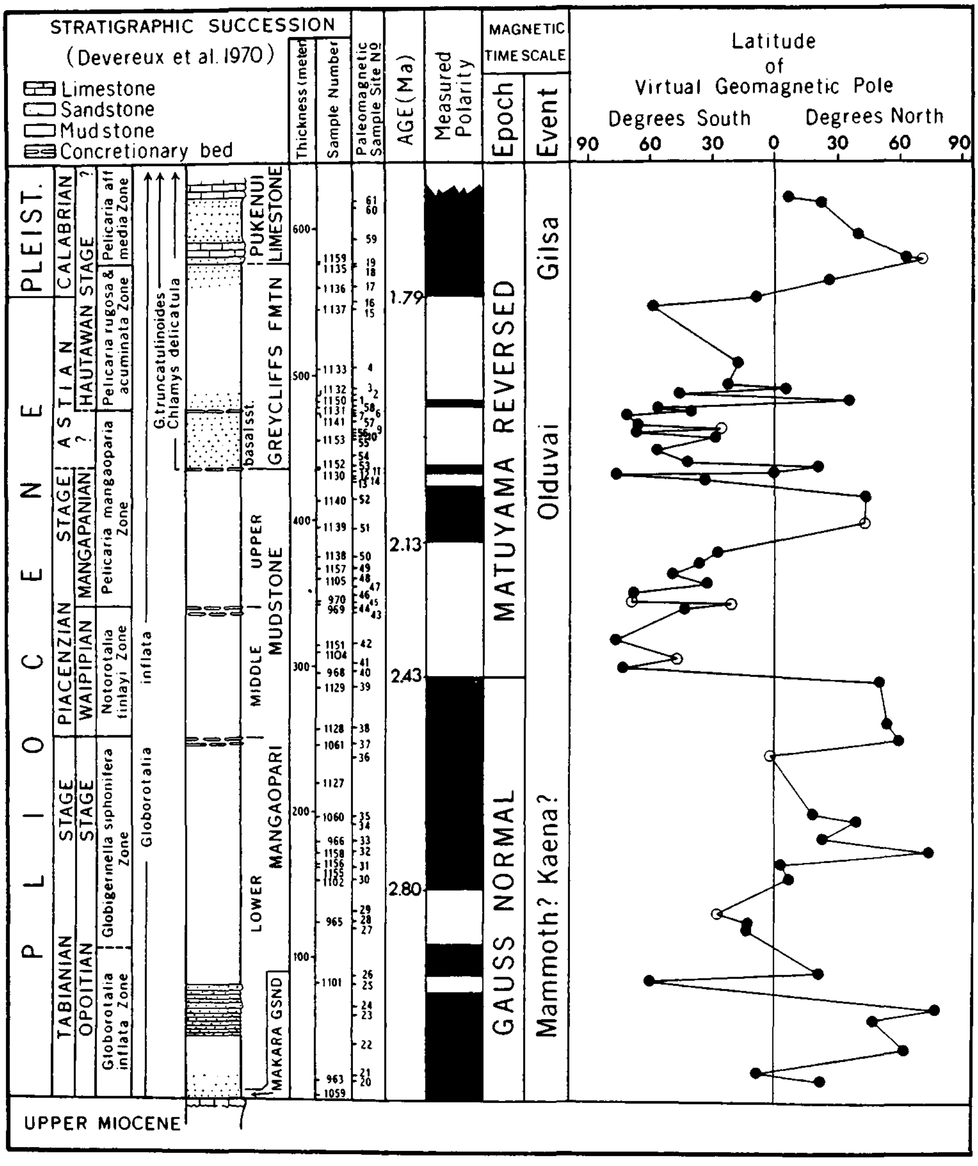

Fig. 9. Paleomagnetic stratigraphy, stratigraphic succession, and paleoclimatic trends at Mangaopari Stream-Makara River, New Zealand. Sample positions, ranges of some key fossils, local stratigraphic units, and possible European correlations are shown. Magnetic polarity in the section (left polarity column) is interpreted from the latitude of the virtual magnetic pole; black denotes normal polarity and clear denotes reversed polarity, which corresponds to the latitude of the virtual geomagnetic pole being higher than 10° N. and 10° S., respectively. The paleoclimatic curves are, from left to right: *a* and *b,* oxygen isotope ratios of planktonic and benthonic foraminiferal tests; *c,* abundance of *Globorotalia pachyderma* as a percentage of all planktonic foraminiferal tests. The position of the Pliocene-Pleistocene boundary and the base of the Calabrian have been modified from that previously determined by Devereux *et al.* (after Kennett, Watkins, & Vella, 1971, fig. 2). [Note that Gilsa and Olduvai are considered separate events by these authors.]

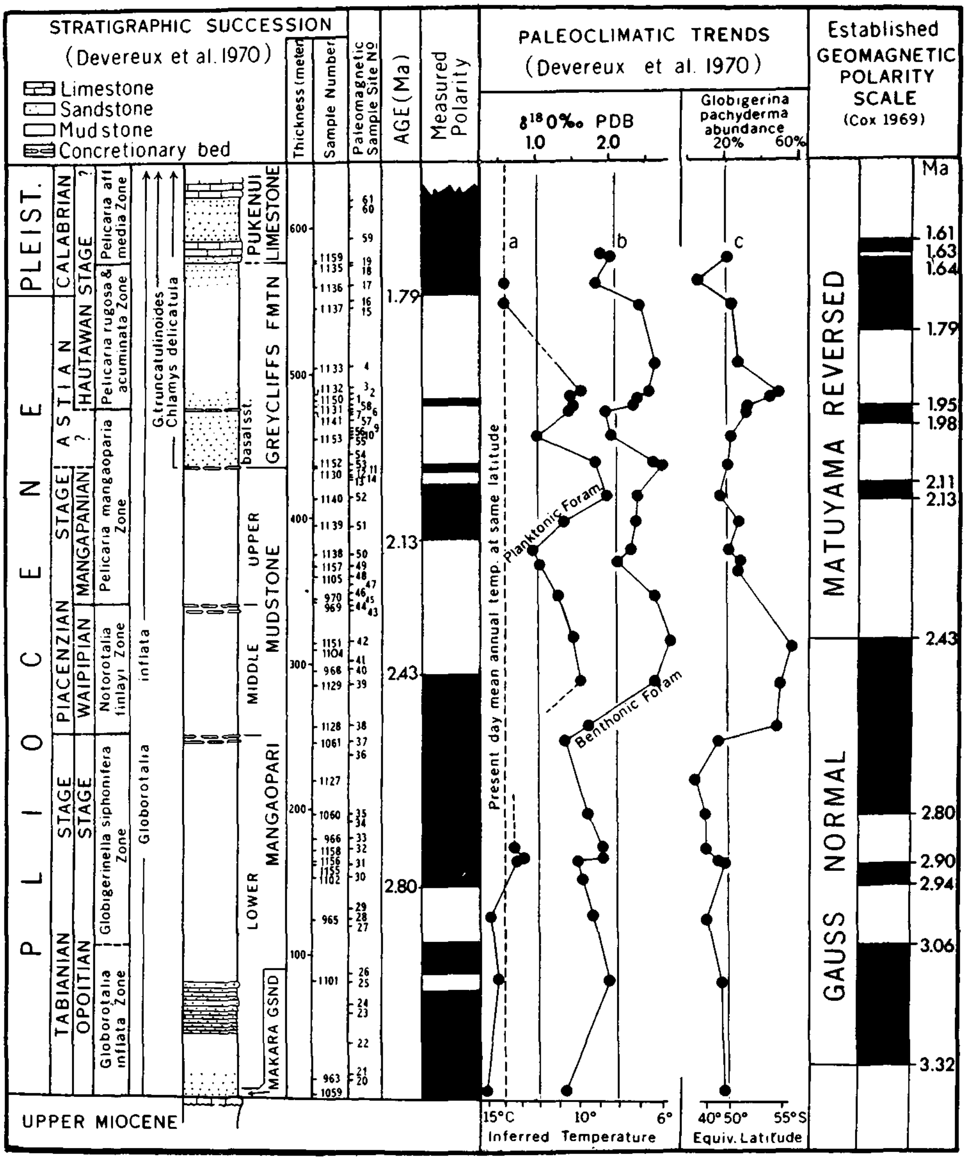

FIG. 9. *(Continued from facing page.)*

occur within the last 0.7 Ma, had been previously recorded in the study of Southern Ocean cores by KENNETT (1970). As we have seen in other oceans, the relative amplitude of the climatic cycles during the Matuyama is somewhat lower than those recorded in the late Pleistocene (the last 0.7 Ma).

In contrast to most investigators who have claimed that the general picture is one of declining climatic conditions during the Pleistocene, but with much colder climates during the Brunhes (last 0.7 Ma) than the late Matuyama (~1.8-0.7 Ma), KEANY and KENNETT (1973) found evidence that subantarctic climatic conditions were more stable and average temperatures lower during the late Matuyama (*ca.* 0.9 Ma) than during the Brunhes, whereas the Brunhes, in general, was a time of erratic, high-intensity climatic cycles with an average warmer temperature range. One of the most convincing arguments for this view is the fact that *Globorotalia inflata,* which appears in the North Atlantic, the Mediterranean, and New Zealand about 3 Ma ago (Berggren, 1972; Cita, 1973; Kennett, Watkins, & Vella, 1971) appears for the first time in the subantarctic region at the base of the Brunhes (0.7 Ma ago). As Keany and Kennett (1973) pointed out, if subantarctic-northern Antarctic conditions were warmer during the Matuyama than later, as suggested by Bandy, Casey, & Wright (1971), *G. inflata* would be expected to occur throughout this interval as it does in New Zealand and equivalent latitudes.

ANTARCTIC MARGINAL SEAS

Fillon (1972) has recorded evidence of widespread submarine erosion in the Ross Sea sometime after late Gauss time ($\lesssim$2.4 Ma), and has suggested that this was due to significant net cooling (see also Watkins & Kennett, 1971, 1972). A major break in sedimentation and a change in ecofacies (Pliocene calcareous benthonic foraminifers below, agglutinated foraminifers of late Brunhes age above) was probably due to a sharp decrease in the amount of debris delivered from the Ross Ice Shelf to the Ross Sea owing to a significant northward advance and thickening of the Ross Ice Shelf, and also to a consequent increase in bottom scour. Keany and Kennett (1973) have attributed increased erosion in the Southern Ocean and Tasman Sea to major cooling with a resulting increase in bottom-water production and velocities in post-Gilbert or post-Gauss time (~3.0 to 2.4 Ma).

Late Neogene paleoglacial history of Antarctica has been recorded in sub-Antarctic deep-sea cores (Margolis & Kennett, 1970, 1971; Kennett & Brunner, 1973) by the presence of ice-rafted grains and variations in planktonic foraminiferal diversity. Ice-rafted grains are locally abundant in the uppermost Miocene and Pliocene and are generally abundant within the Pleistocene, supporting the idea that the Antarctic ice cap grew to present-day proportions during the late Miocene (approximately 10 Ma ago).

RADIOLARIAN EVIDENCE OF CLIMATIC CHANGE

Hays (1965, 1967) has observed that the distribution of radiolarians and various sediments in the Pleistocene in the Antarctic Ocean is strongly influenced by the northern limit of pack ice and the Antarctic Polar Front (Antarctic Convergence). The Pleistocene sediments between the polar front and the pack ice are primarily diatom oozes. At the boundary between radiolarian zones Ø/X there is a lithologic change from clay below to diatom ooze above, which apparently resulted from the initiation of large-scale freezing of sea ice around Antarctica. This led to greater vertical circulation (upwelling) in the Antarctic Ocean and the development of high productivity of the Antarctic surface water that persists to the present day. Thus, alternation of radiolarian and diatom-rich sediments with layers poor in siliceous microfossils north of the limit of modern pack ice as well as the alternation of warm- and cold-water radiolarian species are apparently a reflection of changing limits of the Antarctic pack ice.

Cold-water conditions appear to have prevailed in the late Gilbert, Gauss and early Matuyama (>2.4—<0.7 Ma), with a return toward temperate conditions during most of the Matuyama indicated by the almost continuous presence in Antarctic cores of this age of *Pterocanium trilobum* and *Saturnulus planetes.* A significant temperature reduction occurred at the Brunhes-Matuyama boundary as shown by the local disappearance of warm-water polycystines. Temperate conditions were reintroduced toward the end of the Brunhes (Holocene) as shown by the reappearance of *Saturnulus planetes, Theocanus zancleus,* and other forms. Temperature cycles in the early Gilbert may have been on the order of 15-20°C (average summer), in the 5-15° range during the late Gilbert, Gauss, and Matuyama. On the other hand, four cooling cycles well below 5°C were said to have occurred during the Brunhes (Bandy, Casey, & Wright, 1971).

CALCAREOUS NANNOFLORAL EVIDENCE OF CLIMATIC CHANGE

GEITZENAUER (1969, 1972) has investigated the Pleistocene calcareous nannoplankton biostratigraphy and paleoclimatology of the subantarctic region.

Within the last 400,000 years, interglacial periods within the subantarctic have been characterized by a relatively high frequency of *Cyclococcolithus leptoporus* and *Coccolithus pelagicus.* During glacial intervals these two forms were sharply reduced, the dominant form being the eurythermal *Gephyrocapsa caribbeanica*; however, a maximum peak of *G. caribbeanica* occurred between 0.4 and 0.5 Ma ago and resulted in a nearly monospecific coccolith ooze, which was correlated by KENNETT (1970) with the climatic optimum that occurred during the V interglacial zone of ERICSON and WOLLIN (1968). (In this connection, see also IMBRIE & KIPP, 1971; and BRISKIN & BERGGREN, 1975.) The apparent contradiction between foraminiferal and coccolithophorid data within this specific interval suggests that *G. caribbeanica* exhibits an apparent bimodal distribution pattern, with maxima at glacial stages and at the warmest interglacial. GEITZENAUER (1972) cautioned that a simple coccolithophorid-temperature relationship may be dangerous in Antarctic paleoclimatic interpretations; other factors such as salinity and nutrients may also have been significant determinants in the distribution of Pleistocene coccolith flora.

On the basis of present-day temperature ranges governing the distribution of *Coccolithus pelagicus* and *Cyclococcolithus leptoporus,* the similarity in frequency peaks in both of these species in the late Pleistocene indicates that the optimum conditions for both species were similar and that the climate of the "cool" interglacial stages of the late Pleistocene were very similar to the present time (GEITZENAUER, 1972).

In summary, it may be said that a substantial similarity exists between the currently adopted Quaternary climatic curves from Atlantic, Caribbean, Pacific, and subantarctic ocean-floor sediments.

MEDITERRANEAN

The late Neogene geological histories of the Mediterranean, Red, and Black seas are intimately related. Indeed, the Black and Caspian seas may be viewed as but remnants of a once extensive shallow-water sea of intermediate salinity—the Paratethys—which extended eastward to central Europe and was itself connected with the Mediterranean Sea until about 13 Ma. The Mediterranean and Red seas may have been connected intermittently during the late Neogene as well.

Of particular importance to our understanding of the Quaternary marine climatostratigraphy is the fact that alternating glacial-interglacial climatic oscillations in the Northern Hemisphere caused significant changes in Mediterranean climatic conditions (FAIRBRIDGE, 1972). During early (anaglacial) times, the prevailing westerlies were deflected southward, bringing increased precipitation over the Mediterranean and North Africa. During maximum (pleniglacial) times oceanic cooling led to reduced precipitation and cold, arid climates. Dry, northeasterly winds resulted in the extensive distribution of loess deposits as far south as southwestern France and Portugal, the migration of sand dunes far to the south of the present-day North African Sahara, and increased amounts of eolian biogenic detritus (opal phytoliths and freshwater diatoms) in the equatorial Atlantic west of Africa (PARMENTIER & FOLGER, 1974). Increased precipitation characterized the late (kataglacial) glacial phases and the postglacial warming. During interglacial phases the Mediterranean was characterized by a gradual warming trend and increased precipitation, leading to humid conditions and reforestation even in North Africa, followed by cooling accompanied by widespread desiccation.

DEEP-BASIN CORE RECORD OF CLIMATIC CHANGE

A broad picture of the climatostratigraphic history of the last 4 Ma in the

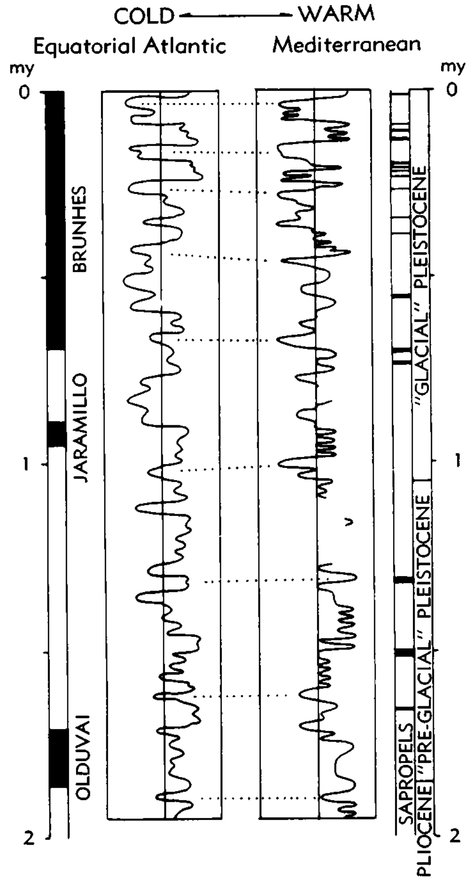

FIG. 10. Generalized climatic curves for the equatorial Atlantic and the Mediterranean. The Mediterranean curve has been constructed by weighing all the data from the various drill cores and piston cores and has been normalized to the geomagnetic time scale. The equatorial Atlantic curve is a "total fauna" assessment of RUDDIMAN (1971). The dotted lines are suggested levels of correlation. The heavy bars on the right column show levels of sapropelitic sedimentation in the Mediterranean, and seem to correspond to periods of marked warming (after Cita *et al.*, 1973, fig. 14).

Mediterranean Sea has emerged over the last few years. Building upon the classic study of the eastern Mediterranean late Pleistocene by PARKER (1958), RYAN (1972) extended the climatostratigraphic record back to about 0.4 Ma by combining various piston cores from different parts of the Mediterranean. This record, in turn, was subsequently extended to about 4 Ma using the data from cores taken by the Deep Sea Drilling Project Leg 13 (CITA, 1973; CIARANFI & CITA, 1973). Generalized paleoclimatic curves based on analysis of planktonic foraminiferal faunas reveal numerous fluctuations during the last 2 Ma (Pleistocene) (Fig. 10). As in open-ocean cores, climatic oscillations in late Pliocene and early Pleistocene were not as great as those beginning about 1 Ma, and RYAN's (1972) curve agrees closely with the ^{18}O curve of SHACKLETON and OPDYKE (1973, 1976).

Sapropel layers in the eastern Mediterranean bottom-sediments are attributed to stagnation caused by inflow of glacial meltwaters from the Black Sea and consequent density-stratification of the Mediterranean water-mass, at a time when glacio-eustatic sea level was recovering from below −40 m, the elevation of the Bosporus sill, and the Black Sea was still a freshwater lake; the sapropels are thus keyed to deglacial phases when landlocked ice was being returned to the sea. The earliest of these sapropels (OLAUSSON, 1961; RYAN, 1972) at *ca.* 2.4 Ma in the Ionian basin (eastern Mediterranean) indicates that glacio-eustatic sea level change occurred significantly earlier than the first major Alpine glaciation, the Günz at about 0.9 Ma, or even before the less well-dated Donau, *ca.* 1.5 Ma. The estimated age of 2.4 Ma for this earliest sapropelic layer is tantalizingly close to the 2.6 Ma estimated by SHACKLETON and KENNETT (1975a,b) for the establishment of the Northern Hemisphere polar ice sheet, an event that may be expected to have had a pronounced effect on sea level, nor is it greatly different than the 3 Ma estimated for the beginning of ice-rafting (BERGGREN, 1972), which is unquestionably related to the same event.

Of particular paleoecologic interest is the discovery by RYAN (1972) that relatively high percentage values of the planktonic foraminifer *Globigerinoides ruber* in association with *Neogloboquadrina dutertrei* (≅ *N. eggeri*) occur in the sapropel layers. BÉ and TOLDERLUND (1971) have shown that *G. ruber* is a euryhaline species with optimum salinity preferences below 34.5 percent and above 36 percent. Thus, the high value of *G. ruber* in the sapropel layers support the idea that the sapropels are a result of stagnant conditions resulting from lowered surface water salinity as a result of freshwater discharge of glacial meltwater from the Black Sea. In the Red Sea, on the contrary, the numerical dominance of *G. ruber* during glacial phases (to the near exclusion of all other taxa) is associated with increased salinity and evaporation rates and lowered surface water temperatures (Berggren & Boersma, 1969; see discussion below). Here we have a dramatic illustration of the response of a single taxon to opposite extremes of the same ecologic variable.

Inasmuch as the sapropel layers appear to reflect glacio-eustatically controlled sea level changes in the world ocean they themselves can serve as the basis of a sea level curve as well as providing an excellent means of calibrating the sea level curve of the eastern Mediterranean (Ryan, 1972). Sapropels are noted at 2.4 Ma, 1.5 Ma (?Donau) and at several levels in the warm part of isotopic stages 11, 9, 7, 5, 3 and 1 (Ryan, 1972). The youngest sapropel occurs in the Holocene at a thermal maximum at about 7,000 years B.P. (Herman, 1972), and similar sapropels have been recorded in the Adriatic Sea and dated at 7,500-9,000 yrs B.P. (Van Straaten, 1972). The sapropels should further provide an excellent means of correlating the marine to the continental stratigraphic record in lakes, terraces, moraines and loesses.

RED SEA

Detailed climatostratigraphic information in the Red Sea is available only for the past 80,000 years (essentially the record of the last glacial and postglacial interval). Prior to this time the stratigraphic record is patchy and the sequence of planktonic foraminiferal faunas in deep sea cores suggest that since the end of evaporite conditions in latest Miocene time (*ca.* 5 Ma) faunal evolution may be viewed in terms of an overall progression from less to more diverse faunas related to a gradual decrease in salinity rather than to decreasing temperature (Fleischer, 1974). There is apparently no evidence of Early Quaternary climatic deteriorations in Red Sea cores.

The combined investigations of the distribution patterns of dinoflagellates, foraminifers, calcareous nannoplankton, pteropods, and radiolaria from a series of cores yield a remarkably uniform interpretation of the climatostratigraphic history of the Red Sea over the past 80,000 years. The basic climatostratigraphic framework was provided by the planktonic foraminifers (Berggren & Boersma, 1969) when it was realized that the fluctuating percentages between two species, *Globigerinoides ruber* and *G. sacculifer,* were primarily controlled by salinity rather than temperature as originally suspected.

According to these studies, a tropical-subtropical climate existed in the Red Sea region from at least 80,000 to about 50,000-60,000 years ago and corresponds approximately to the first of four cycles. During this time surface water temperatures probably varied between 21°-30°C, similar to present-day values in the area. The second evaporative cycle began about 50,000 years ago and lasted until about 25,000 years ago. Climatic cooling and lowering of sea level are suggested by micropaleontologic data and oxygen isotopic measurements (Berggren, 1969; Deuser & Degens, 1969). Cycle III (*ca.* 23,000-13,000 years ago) corresponds to the coolest part of the Late Pleistocene. The general impoverishment of the microfauna leading to a nearly monospecific assemblage of *Globigerinoides ruber,* during this interval, is probably directly related to lowered water temperatures, in addition to the effects of pronouncedly higher relative salinities. Surface water temperatures may have reached values as low as 13°-14°C during this time. Cycle IV (corresponding to the Holocene) witnessed the reestablishment in the Red Sea of a normal marine microfauna from the Indian Ocean and a gradual rise in temperature to present-day values.

BLACK SEA

The marine Quaternary history of the Black Sea is preserved as a series of transgressive littoral-marine deposits separated by wash-out horizons and isolated pockets of subaerial sediments that represent regressions. These deposits crop out in a series of terraces that descend stepwise nearly con-

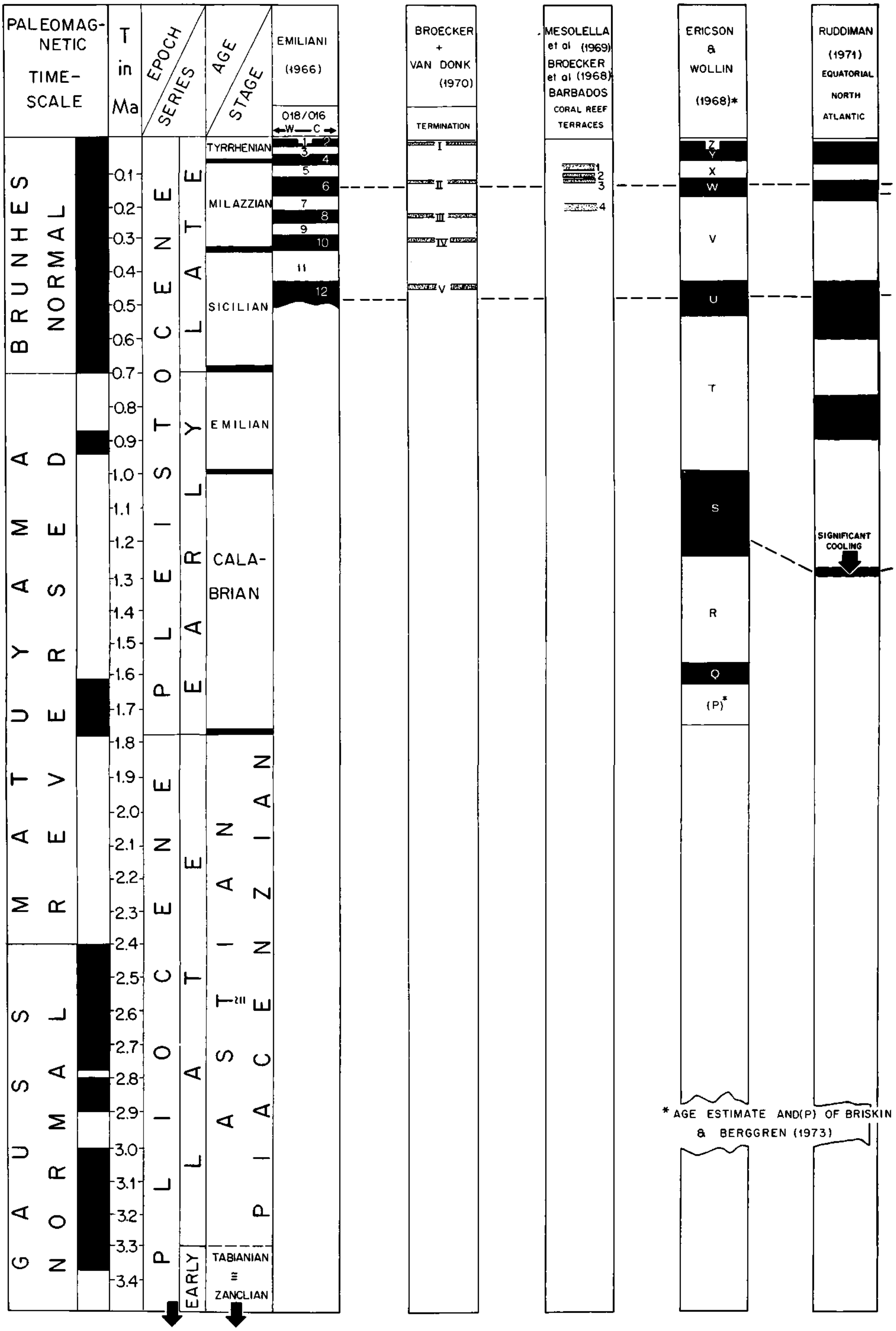

FIG. 11. Correlation of some late Pliocene and Pleistocene marine climatic events. Three major climatic events (right hand column) include: 1) mid-Pliocene (3.0 Ma) initiation of northern hemisphere

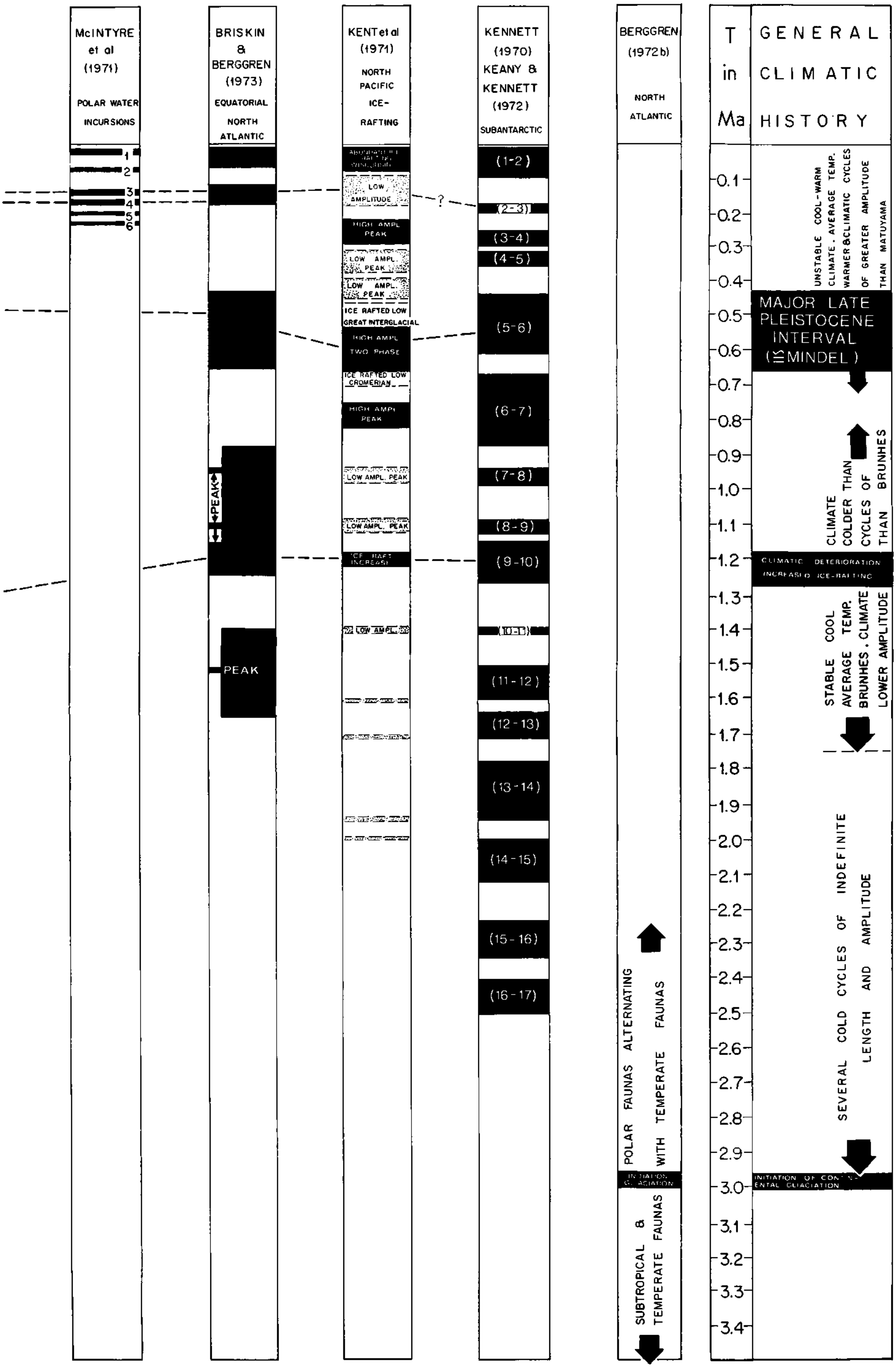

FIG. 11. *(Continued from facing page.)*

glaciation; 2) early Pleistocene (1.2-1.3 Ma) glaciation; 3) major late Pleistocene glaciation (centered on about 0.5 Ma) (after Berggren & Van Couvering, 1974, fig. 13).

tinuously along the entire Western Caucasus coast of the Black Sea (Muratov, Ostrovsky, & Fridenberg, 1974). Repeated ingressions of Mediterranean waters across the Bosporus sill during interglacial high sea-level stands provide the basis for a biostratigraphic subdivision of the littoral-neritic facies of the circum-Black Sea region. To date piston cores from the bottom sediments of the Black Sea have penetrated only into deposits of the last glacial, which have been dated at about 25,000 years B.P., but recent drilling by the *Glomar Challenger* has penetrated an apparently complete Pleistocene succession (Ross *et al.,* 1975).

Regressions of the Black Sea were accompanied by substantial freshening and coincided with the early stages of glaciation. Transgressions of the Black Sea were accompanied by influx of water from the Caspian and Azov seas and immigration of faunas from these areas. At such times, as well as during regressions, there must have been unilateral surficial runoff from the Black Sea into the Mediterranean. As Black Sea transgressions waned, inflow of saline water from the Mediterranean was accompanied by the introduction of euryhaline Mediterranean faunal elements; this phase coincided with the later interglacial (or interstadial) stages.

Although accurate biochronologic control is lacking for the earlier part of the stratigraphic sequence, a generally accepted correlation with the European glacial-interglacial sequence is possible. The "earliest" Pleistocene Chaudian transgressive unit contains an endemic Black Sea fauna with elements of the Bakunian Stage of the Caspian Sea, which suggests approximate correlation with basal Brunhes (the Bakunian is equivalent to the Tiraspol continental sequence within which the Brunhes-Matuyama boundary has been located; see Berggren & Van Couvering, 1974). It should be recalled that the "official" base of the Quaternary in the Soviet Union is drawn at a stratigraphic level approximately coincident with the base of the Brunhes, *ca.* 0.7 Ma.

Subsequent transgressions increased in intensity and attendant thermophilic faunal elements. The three maxima—Ashe, Karangat, and Surozh—contain virtually monotypic faunas (as do the lesser Paleo-Euxinian and Pshada transgressions).

Radiocarbon and thorium-uranium dating suggests that the Ashe transgression (= Odontsovo Interglacial in Eastern Europe) is correlative with the Riss-Würm (= Eemian) Interglacial, and the Karangat (= Mikulino Interglacial) and Surozh (= Mologo-Sheksna Interglacial) transgressions with intra-Würmian or Wisconsinan relatively high stands of sea level. The Chaudian, as an equivalent to Biharian mammal age via correlation to Bakunian Stage, apparently corresponds to pre-Mindel "Cromerian" but also, at least in part, to an interglacial within the Mindel. The Pshada transgression appears to correspond to an interglacial phase within the Riss.

Of particular interest in the history of the Black Sea is the convergence of faunal, floral, and geochemical evidence from isotope data (Deuser, 1972, 1974) that the Black Sea was essentially a freshwater lake between 25,000 to 7,000 years ago, and gradually evolved into its present form over the period of *ca.* 9,000 to 7,000 years ago. The influx of the saline waters from the Mediterranean 7,000 years ago (with minor input beginning *ca.* 9,000 years ago) is marked in the Black Sea by sapropelic sediments and the introduction of euryhaline forms. This event is seen to correspond with the formation of dated sapropelic layers in the Mediterranean that have been interpreted to have formed under stagnant bottom conditions caused by outflow of glacial meltwaters from the Black Sea into the Mediterranean.

SUMMARY AND CONCLUSIONS

1) The Pliocene-Pleistocene boundary is approximately 1.5-1.6 Ma, and is at, or slightly younger than, the top of the Olduvai normal paleomagnetic event. A set of multiple reinforcing biostratigraphic criteria can be used to recognize the approximate position of this boundary in deep-sea sediments. Intra-Pleistocene biochronology is possible by means of various biochronologic datum levels

that have been calibrated to the paleomagnetic time scale, the oxygen isotope record, or both.

2) The integration of paleontology, paleomagnetic stratigraphy, and oxygen isotope analysis in the relatively complete and continuous deep-sea record is providing a chronologic framework within which glacial-interglacial cycles can be accurately delimited. Within this framework it is now becoming possible to make an approximate correlation between the climatic record of the deep sea and the classic glacial-interglacial record in terrestrial sequences.

3) With minor adjustments and calibration to a uniform time scale there is a remarkable degree of correspondence in the climatostratigraphic curves of various authors from various parts of the world in the Northern and Southern hemispheres, which suggests essentially synchronous response over a large part of the earth to major climatic changes. The global correlation of paleoclimatic cycles is shown in Fig. 11.

4) As pointed out in the introductory paragraph to this chapter, the Quaternary is a unique time in earth history, even by the most conservative standard of comparison. In the relatively short time span of the last 1.5 Ma the earth has witnessed such diverse events as:

   a) repeated (perhaps as many as 30 or more) glaciations at high and mid-latitudes in the Northern Hemisphere, which have drastically altered the biogeographic distribution patterns of marine and terrestrial plants and animals alike;

   b) repeated and drastic latitudinal displacement of climatic zones by as much as 20 to 30 degrees;

   c) dramatic changes in oceanographic circulation patterns in the oceans and Mediterranean Sea; dramatic oscillations in circulation between the Mediterranean and Black Sea; repeated isolation of, and increased salinity in, the Red Sea; repeated subaerial exposure of the Bering shelf and subaerial connection between North American and Siberian land areas.

5) Integrated geophysical, geochemical, and paleontologic studies on the deep-sea stratigraphic record are leading to a better understanding of the history of global climate over the past million years. These studies may be expected to lead to a more precise construction of past global climatic conditions at specific "moments" in time (McIntyre *et al.*, 1976), which can, in turn, serve as boundary conditions for modeling general atmospheric circulation patterns in the Pleistocene (Gates, 1976).

   Just as the present has been amply demonstrated to be a reliable guide in reconstructing the past, so the past is seen to be a reliable guide to predicting the future.

6) Having shown uncharacteristic restraint above, we here feel constrained to point out, in passing only, that this same interval has witnessed the passage from East African "stone-pebble culture," through the development of intricate and perfect bifacial implements, to the paleolithic tool industries (which began about 0.5 Ma), through the artistic inspiration of Altamira, Lascaux, and other caves in southwestern France and Spain, to the genius of Leonardo. Although hominid evolution has recently been pushed back into the Pliocene Epoch (*ca.* 3-4 Ma) it seems fair to say that, in general terms, Man is a child of the Quaternary.

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