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PALEOGENE CALCAREOUS NANNOFLORA

PART IV: PALEOGENE NANNOPLANKTON BIOSTRATIGRAPHY AND EVOLUTIONARY RATES IN CENOZOIC CALCAREOUS NANNOPLANKTON

By

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Paleogene Calcareous Nannoflora

Part IV. Paleogene nannoplankton biostratigraphy and evolutionary rates in Cenozoic calcareous nannoplankton

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Abstract. — Paleogene nannoplankton biostratigraphy is discussed with reference to European stages and correlations are attempted. Previously suggested correlations of Lower Paleocene nannoplankton and planktonic foraminiferal zones are modified on the basis of new data. Variation in the total frequency of the Cenozoic nannoplankton and the evolutionary rates for coccoliths and discoasters are presented. It is shown that nannoplankton diversified rapidly during the late Paleocene and early Eocene, but underwent a gradual reduction in frequency during the remainder of the Eocene and sharply declined during Oligocene and early Miocene with a slight second diversification in middle and late Miocene. A comparison of total frequency with paleotemperatures shows nannoplankton to have greater diversity during the warmer intervals and lower diversity during the cooler ones.

ACKNOWLEDGEMENTS

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INTRODUCTION

In the preceding three parts of the present work (HAQ, 1971 a—c) Paleogene calcareous nannoplankton of various localities of the Middle East and Europe were recorded and their biostratigraphy discussed. In the first part of this paper the results are summarized and correlations are attempted on the basis of the nannoplankton biostratigraphy. In the second part the preliminary results of calculated rates of evolution in the Cenozoic nannofossils are presented.

The Cenozoic calcareous nannoplankton biostratigraphic zones have recently been established and considerably refined through the work of a number of authors. MARTINI (1970) has summarized the Paleogene nannoplankton zones for the tropical and temperate regions. He lists 25 nannoplankton zones in the Lower Tertiary covering a period of about 42 million years. The average length of each zone is 1.7 my and would seem to represent a high stratigraphic resolution. However, the tempo of evolution in the calcareous nannoplankton varied considerably during the Lower Tertiary (see discussion on p. 147), which produces a concentration of zones in some parts of the stratigraphic column leaving other portions poorly resolved. The Oligocene Epoch in particular has a relatively low degree of biostratigraphic resolution (an average of one zone every 3 my) due to the low rates of origination and extinction during this epoch.

PALEOCENE

HAY and MOHLER (1967) recognized seven nannoplankton zones in the Paleocene and presented a correlation of various Paleocene and Lower Eocene sections in Europe. Since that time a number of other Paleocene sections in the Middle East and Europe have been studied and the zonal scheme of these authors has been used extensively. A suggested correlation of various Paleocene sections around the world is presented in fig. 1.

Of the various Paleocene Stages used in Europe only the nannoflora of the Danian and Thanetian has been studied so far. The type sections of Danian at Stevns Klint and Faxe, southwest of Copenhagen, have been equated with the *Globoconusa daubjergensis* foraminiferal Zone (BERGGREN, 1962). According to

BERGGREN (*op. cit.*, fig. 2) the section exposed at Stevns Klint extends from the basal Danian to the Middle Danian and the Faxe section spans only the Middle Danian. The lower boundary of the Upper Danian is now recognized as coinciding with the first evolutionary appearance of *Globorotalia compressa* (BERGGREN, 1971 a, p. 703) which has not been recorded from the section at Faxe. The section at Stevns Klint has been equated with the *Markalius astroporus* and *Cruciplacolithus tenuis* Zones and the section at Faxe with the *C. tenuis* Zone (HAY and MOHLER, 1967 and PERCH-NIELSEN, 1969 b). (*C. tenuis* Zone in this area is now = *Chiasmolithus danicus* Zone.) ,

The intricacies and problems involving the Montian Stage of Belgium have been discussed in some detail by BERGGREN (1971 a, pp. 703—705). It is clear that "the Montian Stage represents a gradually regressive sea (after initial transgression) with gradual transition from a neritic environment, to a littoral, a lagoonal and finally a continental (lacustrine) one" (*op. cit.*, p. 704). The occurrence of calcareous nannoplankton in the upper part of Montian can therefore be ruled out. The marine Tuffeau de Ciply (Lower Montian) which contains an abundant reworked Maestrichtian fauna is considered as time-stratigraphically equivalent to the Lower and/or Middle Danian of Denmark by BERGGREN (*op. cit.*, p. 705). According to him the Upper Montian (the coarse-grained detrital chalk of Calcaire de Mons) may, in part, be younger than the known Danian of Denmark (*op. cit.*, p. 705).

As has been the case with the other stages of the Tertiary the type Landenian of Belgium and type Thanetian of England have been subjects of eager controversy amongst micropaleontologists for many years (see BERGGREN, *op. cit.*, pp. 708—711). Recently, however, it has been shown by FEUGUEUR (1955, 1962) that within the Paris Basin the Landenian Stage is equivalent to the Thanetian (see also discussion in BERGGREN, 1971 a, p. 711). The Thanetian Stage has been equated with P3 to P5 (*Globorotalia pusilla—G. angulata*, *G. pseudomenardii* and *G. velascoensis*) Zones by BERGGREN (1969 a). HAY and MOHLER (1967) place the Thanet Sands of England within the *Heliolithus riedeli* Zone of the Upper Paleocene.

By far the most complete Paleocene section studied to date for its nannofloral content is the Couches de Pont Labau from Pont Labau in southern France (HAY and MOHLER, 1967). These authors established six well differentiated calcareous nannoplankton zones based on the first appearance of easily distinguishable species. The *Heliolithus riedeli* Zone of the lower Upper Paleocene was not recognized and was attributed by them to a possible sampling gap.

MARTINI (1970) has recently revised this zonal scheme and has added two zones to the Lower Paleocene, namely the *Chiasmolithus danicus* and *Ellipsolithus macellus* Zones based on the first appearance of these species. (The former zone replaces most of the *Cruciplacolithus tenuis* Zone.) *E. macellus* is however very rare or absent in the higher latitudes, *e. g.* in Denmark (PERCH-NIELSEN, personal

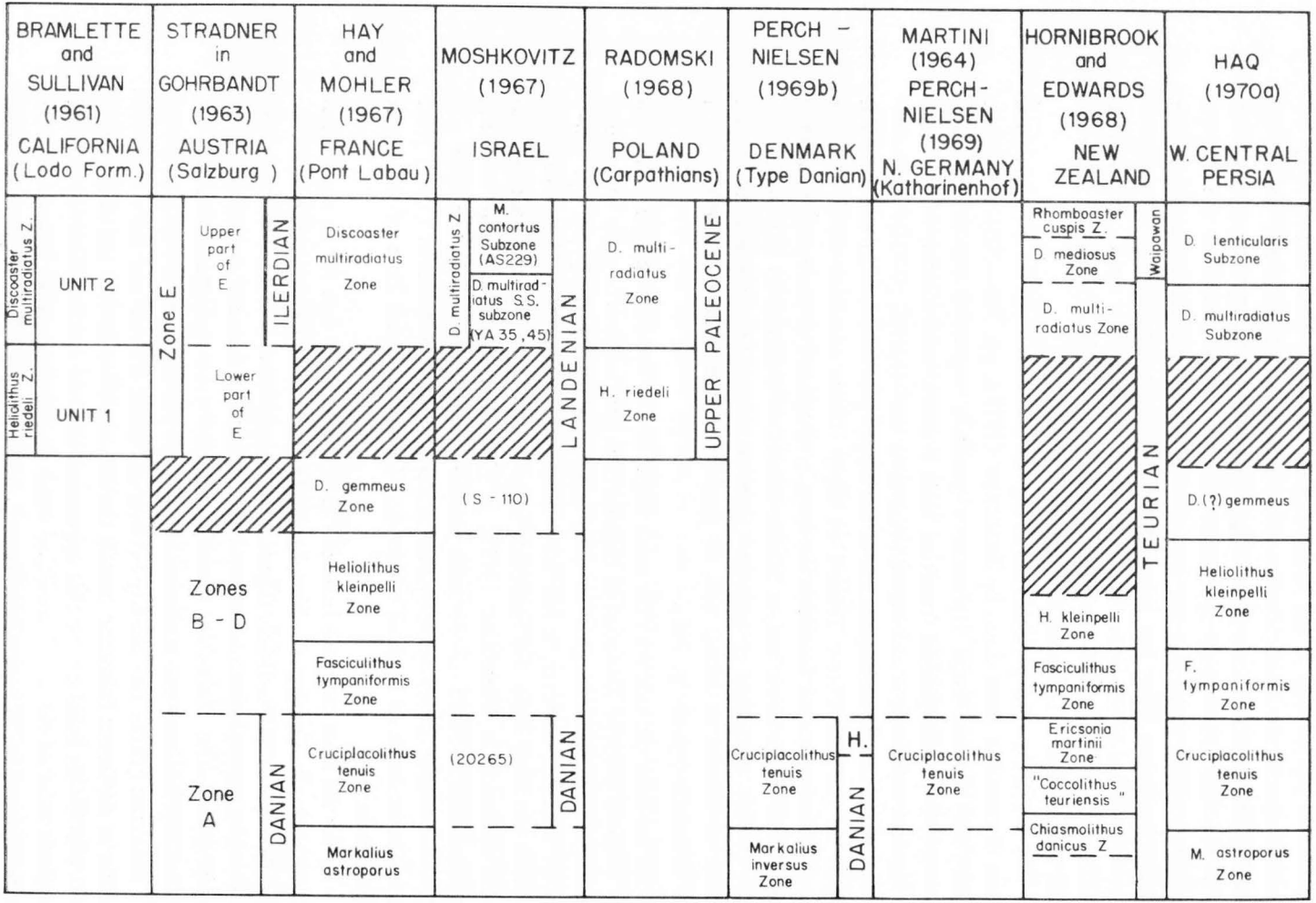

Fig. 1. Suggested correlation of various Paleocene strata. (For: (1970 a) in the extreme right column, read: (1971 a).)

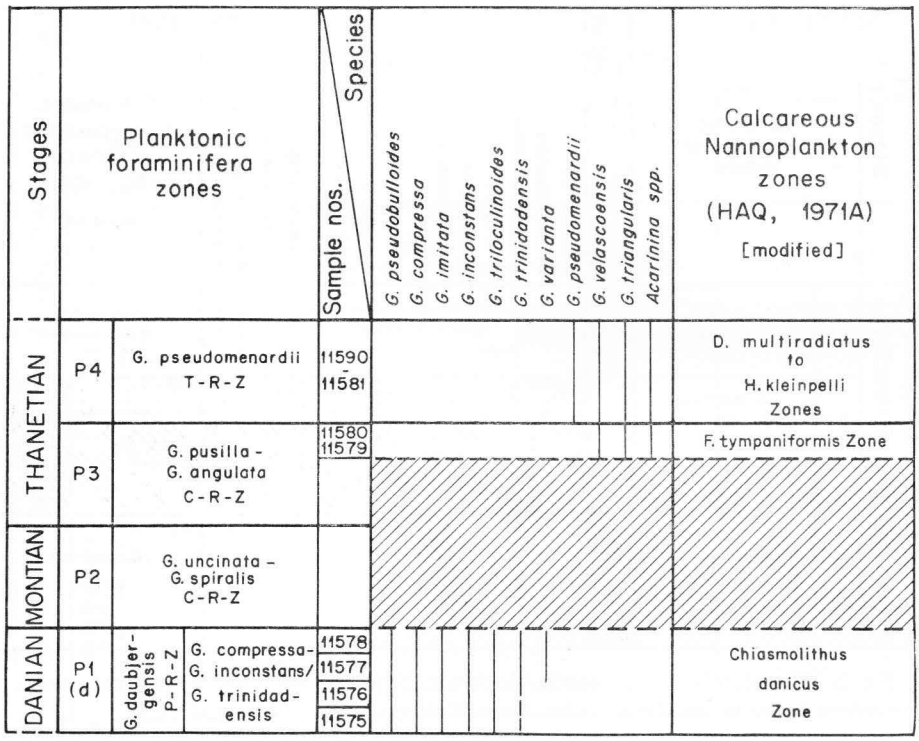

Fig. 2. The distribution of planktonic foraminifera and the foraminiferal and nannoplankton zones in the Tang-e-Bijar section of west central Persia.

communication) and the applicability of this zone on a wider basis remains to be determined.

In the Upper Paleocene of the outer Polish Carpathians RADOMSKI (1967) recognized three biostratigraphic zones, namely a *Heliolithus kleinpelli* Zone associated with a *Globorotalia pseudomenardii* and *G. marginodentata* foraminiferal assemblage; a *Fasciculithus involutus* Zone characterized by the absence of *Heliolithus kleinpelli* and *Discoaster multiradiatus*; and an uppermost *Discoaster multiradiatus* Zone. In the western Polish Carpathians RADOMSKI (1968) was able to recognize the *Heliolithus riedeli* and *Discoaster multiradiatus* Zones. The *H. riedeli* Zone is associated with a *Globorotalia pseudomenardii* and *G. mckannai* assemblage, and the *Discoaster multiradiatus* Zone, which is recognized by the first abundant appearance of this species, is associated with a *Globorotalia rex*, *G. aequa* and *G. marginodentata* assemblage. On the basis of these determinations RADOMSKI (*op. cit.*, p. 596) ascribed this zone to the Paleocene-Eocene transition sediments in this region.

In the Middle East the *Discoaster multiradiatus* Zone has been recognized in

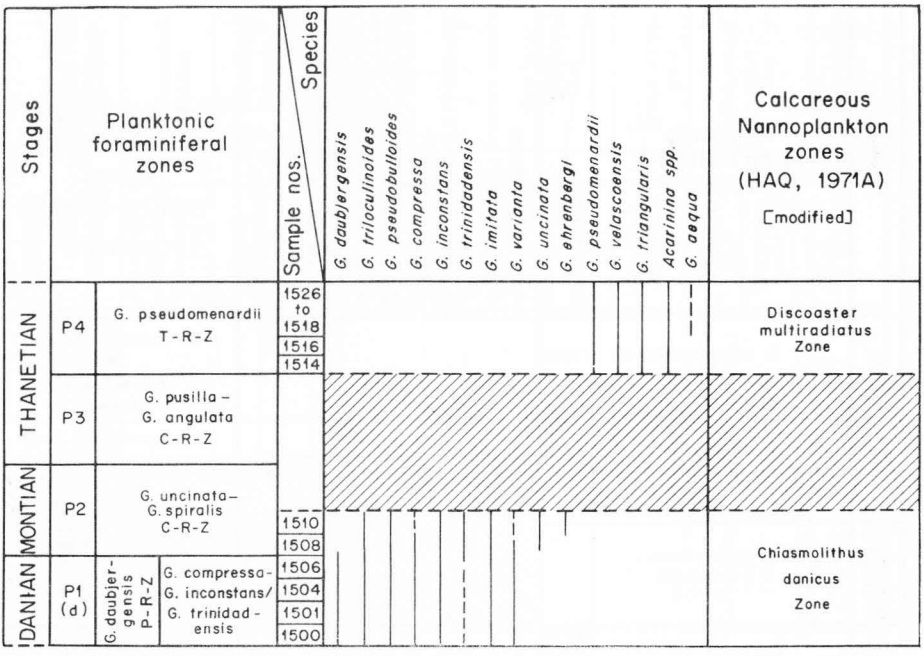

Fig. 3. The distribution of planktonic foraminifera and the foraminiferal and nannoplankton zones in the Garau Valley, Kabir Kuh section of west central Persia.

the Landenian of Israel by MOSHKOVITZ (1967). He subdivides this zone further into the *D. multiradiatus s.s.* and *Marthasterites contortus* Subzones. In the Paleocene of Egypt KERDANY (1970) has recently recognized four nannoplankton zones. He equates the *Cruciplacolithus tenuis* with the *Globorotalia trinidadensis*, *G. unicinata* and the lower part of the *G. angulata* Zones and the *Heliolithus kleinpelli* Zone with the upper part of the *Globorotalia angulata* and the *G. pseudomenardii* Zones. The lower boundary of his *Discoaster multiradiatus* Zone coincides with the lower boundary of the *Globorotalia velascoensis* Zone and the *Marthasterites contortus* Zone spans the boundary between the *Globorotalia velascoensis* and *G. subbotinae* Zones.

In west central Persia at least the lower part of the *Discoaster multiradiatus* Zone is equivalent to a part of the *Globorotalia pseudomenardii* Zone (see HAQ, 1971 a, and this paper figs. 2, 3, and 4). The *Globorotalia velascoensis* Zone (its lower boundary is defined by the last occurrence of *G. pseudomenardii*) could not be established in this area. In one of the Persian sections (see HAQ, 1971 a, table 2) five nannoplankton zones were established (the presence of the *Markalius astroporus* Zone in samples JTP 11575 and 11576 of the Tang-e-Bijar section is now ruled out after subsequent study). The *Cruciplacolithus tenuis* Zone (now considered as the *Chiasmolithus danicus* Zone) (see fig. 2)

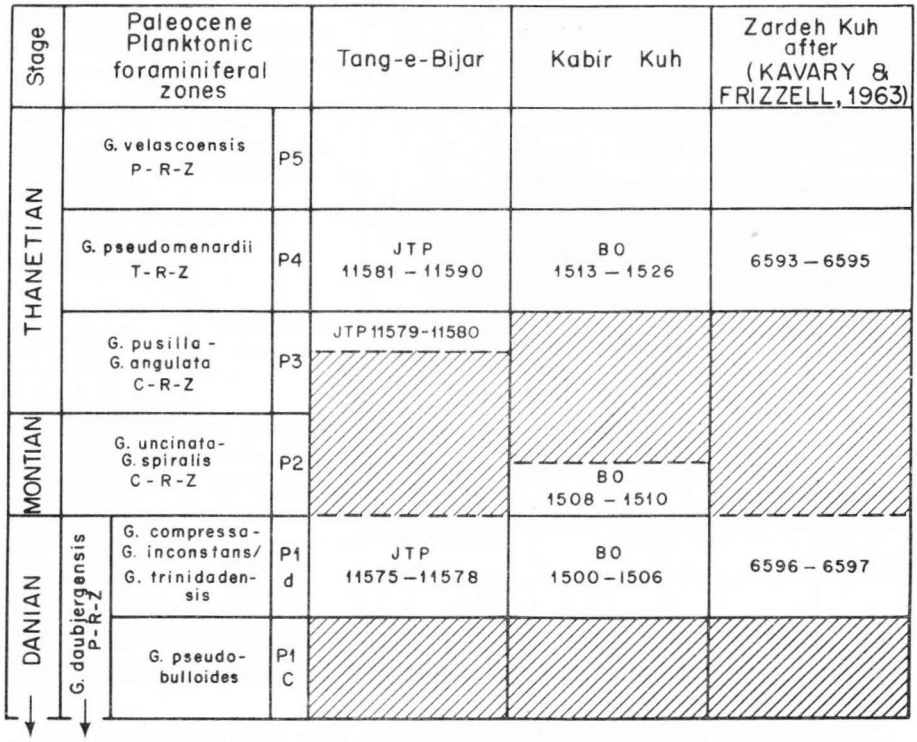

Fig. 4. Suggested correlation of the Paleocene of Tang-e-Bijar, Kabir Kuh and Zardeh Kuh sections of west central Persia.

corresponds to the *Globorotalia compressa—G. inconstans / G. trinidadensis*, or P1(d) Subzone of the Upper Danian (for definitions of foraminiferal zones see BERGGREN, 1969 a). The *Fasciculithus tympaniformis* Zone corresponds to the upper part of the *Globorotalia pusilla—G. angulata*, or P3 Zone and the *Heliolithus kleinpelli, Discoaster* (?) *gemmeus* and *D. multiradiatus* Zones to the *Globorotalia pseudomenardii*, or P4 Zone. In the Garau Valley section only two nannoplankton zones were established (see fig. 3). The *Chiasmolithus danicus* Zone in this section extends into the *Globorotalia uncinata—G. spiralis* or P2 Zone. The missing zones between *Chiasmolithus danicus* and *Discoaster multiradiatus* are represented by a sampling gap. A correlation of these sections with the Zardeh Kuh section (see KAVARY and FRIZZELL, 1963, and this paper fig. 4) reveals that in west central Persia the Upper Maestrichtian is overlain unconformably by the Upper Danian and Lower and Middle Danian are not developed in this area. Similarly at least a part of the P2 and P3 Zones are missing. There is no evidence of a lithologic break in the Tang-e-Bijar and Zardeh Kuh sections and this gap can more likely be attributed to the non-

Foraminiferal zones	Samples	Calcareous Nannoplankton zones
Globorotalia velascoensis (P5) Zone	133	Discoaster multiradiatus Zone
G. pseudomenardii (P4) Zone	134	
	135	
	136	H. riedeli Zone
G. pusilla–G. angulata (P3) Zone	137	F. tympaniformis Zone
	138	Chiasmolithus danicus Zone
	139	
	140	
G. uncinata–G. spiralis (P2) Zone	142	
G. pseudobulloides–Globoconusa daubjergensis (P1c) Subzone	141	Cruciplacolithus tenuis Zone

Fig. 5. Suggested correlation of planktonic foraminiferal and calcareous nannoplankton zones in the Paleocene of Jebel-um-Rejam section, Jordan.

deposition of sediments of this age, unless the strata representing a depositional period of 3 my have been squeezed into a layer thin enough to be excluded from a 3 m sampling interval.

A preliminary study of the Paleocene section from Jebel-um-Rejam, Jordan, yielded a well preserved nannoflora and five biostratigraphic zones were recognized. The relationship of the foraminiferal and calcareous nannoplankton zones is presented in fig. 5. A well developed *Heliolithus riedeli* Zone was recognized in this section. As in west central Persia the lower part of the *Discoaster multiradiatus* Zone coincides with the upper part of the *Globorotalia pseudomenardii* Zone.

Similarly, in the Paleocene of Tunisia five nannoplankton zones have been recognized and the comparison of these zones with the foraminiferal zones indicates that the *Cruciplacolithus tenuis* Zone probably extends at least partly into the *Globorotalia compressa—G. inconstans / G. trinidadensis,* or P1d Subzone. The *Chiasmolithus danicus* Zone which starts within the lower part of the P1d Subzone extends well into the *Globorotalia uncinata—G. spiralis*, or P2 foraminiferal Zone. The *Ellipsolithus macellus* Zone could not be recognized in this section, probably due to lack of samples from this relatively short interval. The *Fasciculithus tympaniformis* Zone, which begins within the upper part of the *G. pusilla—G. angulata*, or P3 Zone, extends to within the lower part of the *G. pseudomenardii*, or P4 Zone. The *Heliolithus kleinpelli* and *Discoaster* (?) *gemmeus* Zones form the upper part of this section and have been correlated with a part of the P4 foraminiferal Zone.

In the Danian of Cherkessk and the Essentuki section of the Caucasus, U.S.S.R.,

Foraminiferal Zones		Calcareous Nannoplankton Zones	Cherkessk by Kuban River	Essentuki by Podkoomsk River	Anapa by Black Sea	Formations
G. pusilla–G. angulata (P3)		Ellipsolithus macellus			142 (3042)	GORYACHI KLIUTCH
				101 (3007)		ELBURGAN
		Chiasmolithus danicus	104 (2995)	99 (2992) 98 (2991)		
G. uncinata–G. spiralis (P2)			105 (2996) 106 (2997)	97 (3006)		
G. daubjergensis (P1)	G. compressa–inconstans / trinid. (P1d)		110 (3009)	96 (3005)		
	pseudobulloides (P1c)	Cruciplacolithus tenuis				
	triloculinoides (P1b)					
	eobulloides (P1a)	Markalius astroporus	109A (3001)			

Fig. 6. The Lower Paleocene foraminiferal and nannoplankton zones in the Elburgan and Goryachi-Kliutch Formations of Caucasus, U.S.S.R. and suggested correlation.

the *Markalius astroporus*, *Chiasmolithus danicus* and *Ellipsolithus macellus* Zones have been recognized in the Elburgan Formation (see fig. 6). The samples from the Goryachi-Kliutch Formation, which overlies the Elburgan Formation, did not yield a well preserved nannoflora. The *Markalius astroporus* Zone of Cherkessk could not be correlated with a foraminiferal zone due to lack of well preserved microfauna. The *Cruciplacolithus tenuis* Zone is missing and is attributed to a sampling gap. The *Chiasmolithus danicus* Zone extends from the P1d Subzone into the P3 Zone and the *Ellipsolithus macellus* Zone, which could only be recognized in the uppermost part of the Elburgan Formation at Essentuki section, falls within the P3 Zone.

On the Black Sea coast of the Soviet Union near Anapa a single sample from the lower part of the Goryachi-Kliutch Formation contained a well preserved nannoflora and microfauna belonging to the *Ellipsolithus macellus* and *Globorotalia pusilla—G. angulata* or P3 Zones.

From the above data it would seem that the correlations of Paleocene calcareous nannoplankton and foraminiferal zones as presented by BERGGREN (1971 b) need revision. The *Chiasmolithus danicus* seems to be a zone of greater extent, extending from at least the P1d of the Upper Danian, covering the P2 Zone and extending into the lower part of the P3 Zone. The *Ellipsolithus macellus* is a Zone of relatively short range and falls within the P3 Zone. The *Fasciculithus*

tympaniformis Zone extends from the upper part of the P3 Zone into the lower part of the P4 Zone. The *Heliolithus kleinpelli*, *Discoaster (?)gemmeus* and *Heliolithus riedeli* Zones are all correlative with a part of the P4 Zone and the *Discoaster multiradiatus* Zone starts in the uppermost part of the P4 Zone and extends into the P5 Zone but does cover this zone completely. The *Marthasterites contortus* Zone corresponds to the upper part of the P5 Zone, and straddles the Paleocene-Eocene boundary.

EOCENE

The Eocene is clearly the best studied epoch for both calcareous nannoplankton and planktonic foraminifera. The ranges of the nannofossil species of this age are particularly well documented and a comprehensive nannoplankton biostratigraphy has been established through the work of BRÖNNIMANN and STRADNER (1960), BRAMLETTE and SULLIVAN (1961), HAY (1964) and HAY *et al.* (1967). MARTINI (1970) has presented a standard zonation scheme incorporating the data presented in all former studies. He recognizes 11 zones in the Eocene, an average of one zone every 1.5 my — a relatively high stratigraphic resolution. Correlation of the various Eocene nannoplankton zonal schemes has been given by HAY *et al.* (1967), and HAY and MOHLER (1967, text-figs. 4, 5) have presented a correlation of various Lower Eocene strata in Europe, North America and the Caribbean. In the present work a suggested correlation between the Eocene strata on a more or less worldwide basis is presented in figure 7 using MARTINI's standard zonal scheme.

The relationships of the Lower Eocene stages of Europe have been discussed by BERGGREN (1971 a, pp. 711—715). According to recent investigations (*op. cit.*, p. 712) the lagoonal-lacustrine beds of Sparnacian age in the Paris Basin are now considered as equivalent to the lagoonal-marine beds of the lower Ypresian (Argiles de Flandre) of Flanders. The marine sands and clays of the upper Ypresian have been shown to contain a microfauna similar to the Cuisian of the Paris Basin. HAY and MOHLER (1967) correlate the Ypern Clay with the *Marthasterites tribrachiatus* and *Discoaster lodoensis* Zones. The nannoflora of the Cuisian of Donzacq, investigated by DEFLANDRE and FERT (1964) and HAY and TOWE (1962), is typical of the *Discoaster lodoensis* Zone.

The Lutetian Stage of the Paris Basin is generally considered to encompass the Middle Eocene. BOUCHÉ (1962) studied the calcareous nannoflora of the Lutetian of the Paris Basin and the assemblages recorded by him place it within the lower zone of the Middle Eocene, namely that of *Discoaster sublodoensis*. The Biarritzian Stage is considered to correspond to the upper part of the Lutetian due to the presence of the *Porticulasphaera mexicana* and *Truncorotaloides rohri* planktonic foraminiferal Zones in the stratotype (SZÖTS, 1964, *fide*

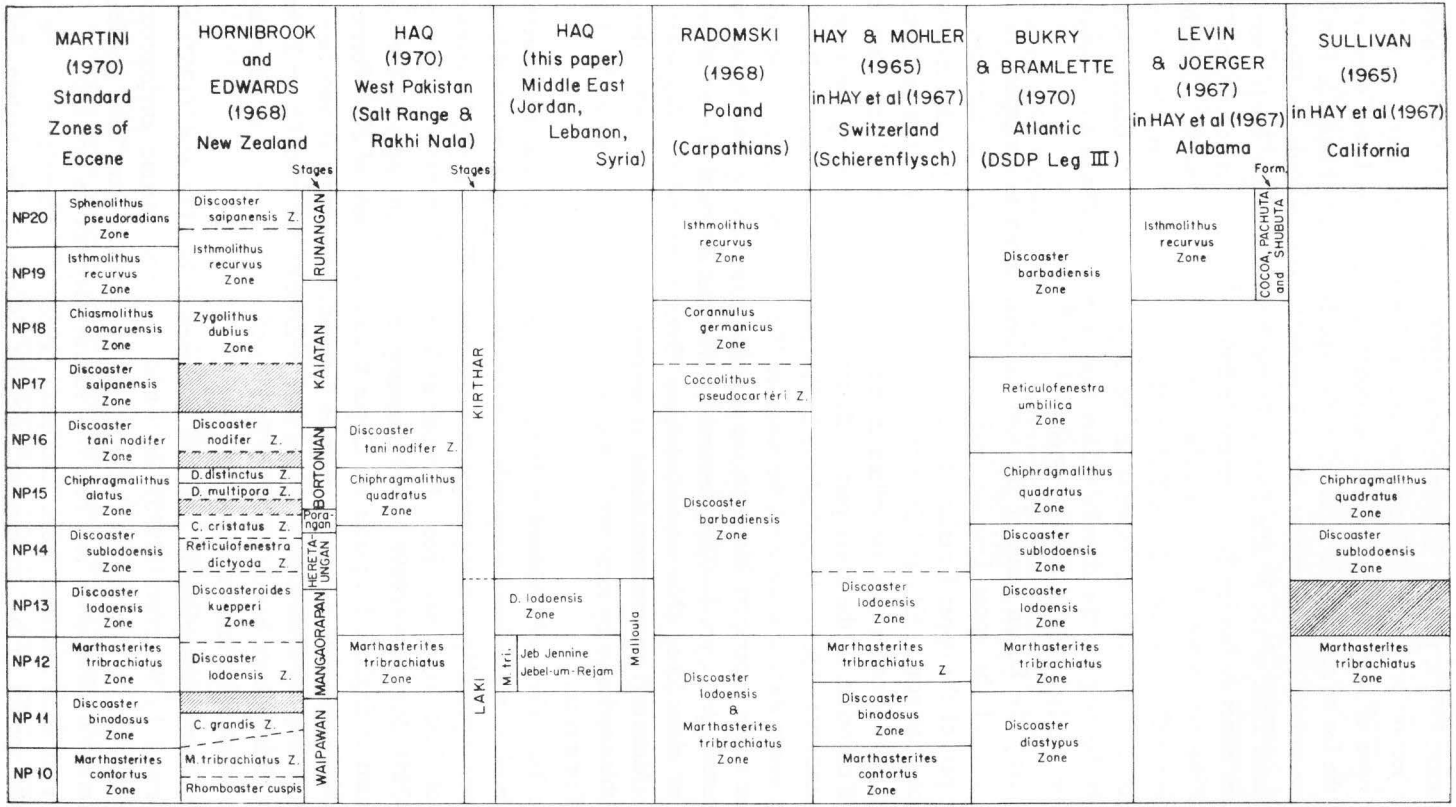

Fig. 7. Suggested correlation of various Eocene strata. (For (1970) in the third column from left, read: (1971 a).)

BERGGREN, 1971 a, p. 719). BILGÜTAY *et al.* (1969) have recorded the nannoflora of the section at Biarritz. Throughout the section the nannofloral assemblages show signs of heavy reworking from sediments as old as the Lower Cretaceous. From the list of nannofossils recorded in the type Biarritzian (Falaise de Handia) by these authors it would appear that it is probably no older than the *Discoaster saipanensis* Zone of the Middle Eocene. In the Bartonian of the Biarritz section (Marnes bleues de l'ancien Établissement de Bains) these authors (*op. cit.*, p. 174) record the occurrence of *Chiasmolithus oamaruensis*, which would place these beds in the *C. oamaruensis* Zone. Earlier, MARTINI (1961) has recorded the rare occurrence of *Isthmolithus recurvus* in the upper Bartonian of Biarritz, which extends the range of the Biarritz section from a possible *Discoaster saipanensis* Zone to the *Isthmolithus recurvus* Zone.

Similarly, the Ledian Stage of Belgium has been shown to correspond to the lower part of the upper Lutetian, and the Sables de Wemmel represent the upper part of the upper Lutetian of the Paris Basin according to the investigations of POMEROL (1961) and BLONDEAU *et al.* (1965). ACHUTHAN and STRADNER (1969) record a rich nannoflora in the Sables de Wemmel and place the type Wemmelian in the lower part of Bartonian, mainly following the view of KAASSCHIETER (1961) who united the Ledian and Bartonian Stages of Belgium into a single stage and included the sands of Wemmel and the clays and sands of Asse in the upper part. However, the assemblage recorded by ACHUTHAN and STRADNER (*op. cit.*, pp. 4—9) in the sands of Wemmel is typical of the *Chiphragmalithus alatus* Zone (*Nannotetrina fulgens* (STRADNER) and *Chiphragmalithus alatus* (MARTINI) are now considered as synonyms). MARTINI (1969) substantiates this conclusion by recording both *C. alatus* and *Rhabdosphaera gladius* from the Wemmelian.

The Bartonian and Priabonian Stages of the Upper Eocene are generally considered as approximately equivalent in the time-stratigraphic sense, although the latter is probably in part younger than the former. The stratigraphic connotations of these stages have been discussed at length by BERGGREN (1971 a, pp. 720—725). MARTINI (1969) lists the nannoplankton assemblages of the type Bartonian of England. He places the Upper Bracklesham beds of New Forest in the *Chiphragmalithus alatus* of the upper Lutetian. The Upper Barton beds of Barton correspond to the *Discoaster tani nodifer* Zone of the lower Upper Eocene and the Brockenhurst bed of Whitecliff Bay, Isle of Wight, contains an assemblage of the *Isthmolithus recurvus* Zone.

The Eocene nannoplankton zonations as presented by HAY *et al.* (1967) and summarized by MARTINI (1970) are useful for most marine environments. However, some of the species that are used as zonal markers have restricted environmental distribution and thus this scheme may not be applicable in its entirety in some restricted areas. RADOMSKI (1968), for example, made use of different species in his attempt to zone the Eocene of the western Polish

Carpathians (except for the *Marthasterites tribrachiatus* and *Isthmolithus recurvus* Zones) due to the rarity or lack of the diagnostic species. STRADNER (1969), on the other hand, was able to present a six-fold zonation of the nearby Eocene Flysch of Austria using the zonation scheme outlined by HAY *et al.* (1967).

In the Middle East the *Marthasterites tribrachiatus* and *Discoaster lodoensis* Zones have been recognized by the present author in Syria, Lebanon and Jordan. In the chalk from Malloula, near Damascus, Syria a rich and well preserved flora of the *Marthasterites tribrachiatus* and *Discoaster lodoensis* Zones could be recognized. The Jebel Jennine section, Lebanon yielded an equally rich and well preserved assemblage of the *Marthasterites tribrachiatus* Zone. An exceptionally well preserved assemblage of the same zone was also recorded from the Jebel-um-Rejam section of Jordan which corresponds to the *Globorotalia rex* foraminiferal Zone. (For correlation between foraminiferal and nannoplankton zones and the radiometric time-scale see BERGGREN, 1971 b).

OLIGOCENE

The Oligocene is an epoch of relatively slow origination and extinction rates for calcareous nannoplankton (see discussion on pp. 147—149). After reaching a peak in diversity in the early Eocene, the nannoplankton gradually declined in diversity during the remainder of the Eocene Epoch. After the late Eocene this downward trend becomes more sharply defined so that in the Oligocene the flora is poor in numbers and morphologically relatively monotonous. For these reasons the biostratigraphic resolution for this epoch remains low, as compared to the earlier intervals of the Paleogene.

The Oligocene nannoplankton zonations were first established by BRAMLETTE and WILCOXON (1967) and HAY *et al.* (1967). They have since been refined and redefined by a number of authors and MARTINI (1970) has given a summary, taking into account most of the available data.

A suggested correlation of the Oligocene strata of various parts of the world is presented in figure 8.

The Tongrian Stage of Belgium has been variously assigned to the Upper Eocene and Lower Oligocene by different workers (see discussion in BERGGREN, 1971 a, pp. 728—735). MARTINI and MOORKENS (1969) studied the marine sands of Grimmertingen, considered by them as the stratotype of the lower Tongrian, and recorded a fairly rich calcareous nannofloral assemblage of the *Ericsonia subdisticha* Zone. The Tongrian is generally considered as equivalent to the Latdorfian (= Lattorfian) of northern Germany, and the former term has generally been ignored in favor of the latter. MARTINI and RITZKOWSKI (1968) suggested that keeping the original contention of BEYRICH (1856) in view, the Latdorfian should by considered as equivalent to the Lower Oligocene.

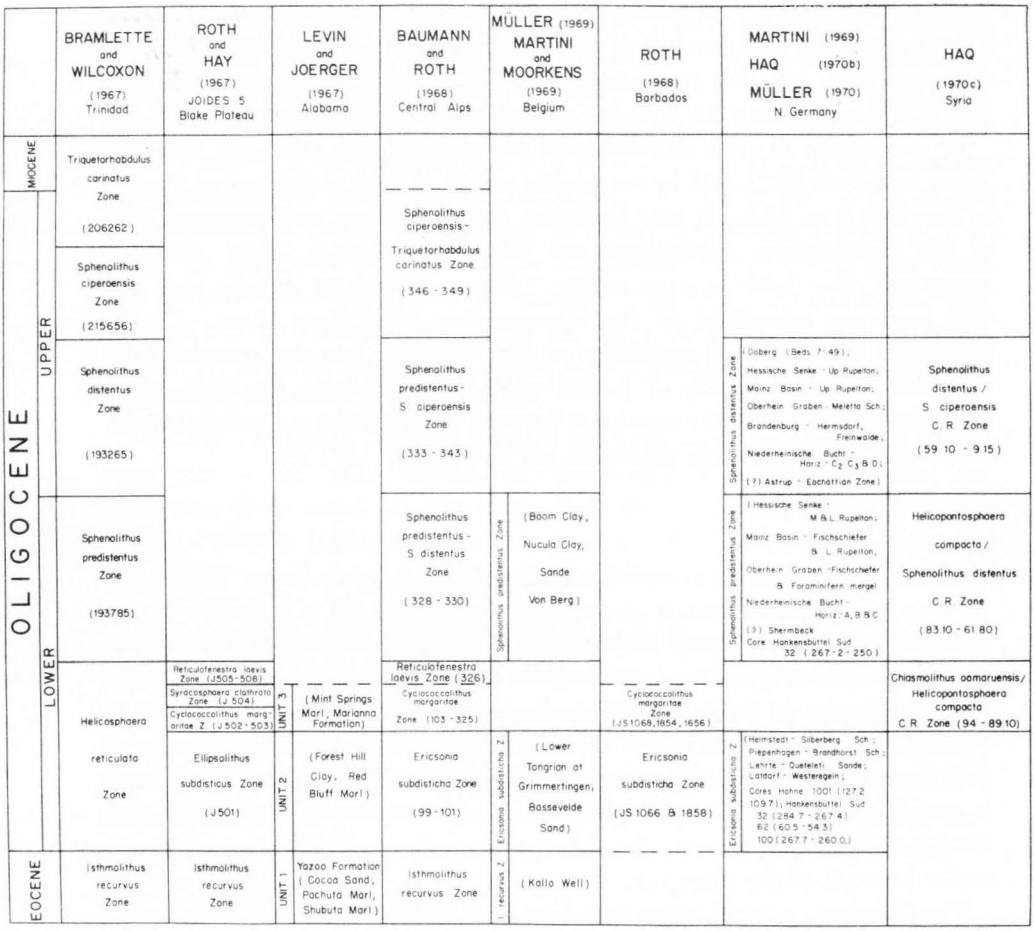

Fig. 8. Suggested correlation of the various Oligocene strata. (For (1970 b) in second column from right and (1970 c) extreme right read: (1971 b) and (1971 c) respectively.)

They consider the Silberberg-Schichten of Helmstedt as a stratum representing the type Latdorfian and place it within the *Ericsonia subdisticha* Zone. The flora of Helmstedt has been subsequently studied in greater detail by ROTH (1970) and the present author (HAQ, 1971 b), and MARTINI and RITZKOWSKI's conclusion have been substantiated

The lagoonal-brackish Sande von Berg are considered as time stratigraphically equivalent to the upper Tongrian by BATJES (1958). MÜLLER (1970), who has investigated the Middle Oligocene nannoflora of northern Germany and Belgium, places the Sande von Berg (together with the overlying *Nucula* and Boom Clays — the latter: stratotype of Rupelian) in the *Sphenolithus predistentus* Zone. She has also shown the occurrence of the *S. distentus* Zone in the Middle Oligocene

of northern Germany. These conclusions have been further substantiated by ROTH (1970) and the present author (HAQ, 1971 b).

The Kasseler Meeressand at Gelben Berg, which is the type locality of the Chattian, does not contain calcareous nannoplankton due to leaching of calcium carbonate. The section at Doberg near Bünde which represents a more complete marine section is considered equivalent to the Chattian in its lower part (beds 7—16) by HUBACH (1922, 1957). The present author studied the nannoflara of this section (see HAQ, 1971 b) and although the nannofossils are rare and generally poorly preserved, enriched suspensions were prepared and a fair number of species were recorded (see *op. cit.*, table II). Diagnostic species such as the sphenoliths are absent in these assemblages. On the basis of the overall impression of the flora I placed the Doberg section within the *Sphenolithus distentus* Zone. A radiometric age of 30.2 ($\pm$1.5) my was determined for these beds by ODIN *et al.* (1970) by the potassium-argon method. A comparison of this figure with the radiometric time-scale and foraminiferal/nannoplankton zone chart of BERGGREN (1971 b) places it near the *Sphenolithus predistentus—S. distentus* Zone boundary. On the basis of his study of the planktonic foraminifera BERGGREN (1971 a, p. 736) correlates the Chattian with the P20/P21 (N1) foraminiferal Zones of BLOW (1969), which is close to the age assigned to this stage by the present author.

At another Chattian section at Höllkopf near Glimmerode the Kasseler Meeressand is not leached and ROTH (1970) was able to record a fairly rich nannoflora. He places this section within his *Reticulofenestra laevis* and *Sphenolithus predistentus / S. distentus* Zones. This suggests that the Chattian is slightly older than the age assigned to it by other workers (see discussion above).

In the Pacific along the 140° longitude the JOIDES Deep Sea Drilling Project recovered a number of more or less continuous sections through the Oligocene. The calcareous nannoplankton of these sections were studied by HAQ and LIPPS (1971, in press). Assemblages contain abundant sphenoliths and a fair number of discoaters, but other important forms, such as helicopontosphaerids, are rare or absent. The Oligocene zonation of BRAMLETTE and WILCOXON (1967) could be used effectively for the middle and upper part, but for the lower part the authors proposed a new Zone (*Discoaster tani ornatus*) which corresponds roughly to the *Helicopontosphaera reticulata* Zone of BRAMLETTE and WILCOXON and P18 and P19 foraminiferal Zones of BLOW (1969).

The correlation of the Oligocene foraminiferal and nannoplankton zones has been suggested by BRAMLETTE and WILCOXON (1967), BAUMANN and ROTH (1969) and HAQ (1971 c), and the relationship of these zones to a radiometric time-scale has been suggested by BERGGREN (1971 b).

EVOLUTIONARY RATES IN CENOZOIC CALCAREOUS NANNOPLANKTON

Concepts of evolutionary rates

According to SIMPSON (1953, p. 3) an evolutionary rate may be defined as "a measure of change in organisms relative to elapsed time or another independent variable related to time". The ideal expression of evolutionary rate in a lineage is "the amount of genetic change in continuous (ancestral and descendant) populations relative to absolute time" (SIMPSON, *op. cit.*, p. 4). When dealing with fossil groups we have to completely rule out the consideration of evolutionary trends from the genetic standpoint for obvious reasons. The changes that can be usefully measured are either morphological or taxonomic. Although taxonomic data indirectly represent morphological data, SIMPSON (*op. cit.*, p. 5) stresses the distinction between morphological and taxonomic rates of evolution. Morphological rates are usually expressed as rates of changes in the phenotypes within a single phylogenetic lineage or within multiple lineages of a larger group (phylogenetic rates). The rates of change in numbers (frequencies) of species or other taxonomic categories with time are known as taxonomic frequency rates. Although time-frequency curves do not directly depict rates of evolution, from them we can calculate the rates of change of total frequency which can serve as an indirect indication of the total evolutionary processes at work. Similarly, from the total first appearances and last occurrences rates of origination (diversification) and rates of extinction can be calculated (SIMPSON, *op. cit.*, p. 8).

When dealing with fossil groups one of the obvious flaws of taxonomic data is the paleontologic rather than biologic concept of species and higher taxa. Different taxonomic inclinations of the students of a discipline add greatly to the problem. In the case of fossil calcareous nannoplankton a number of factors make this problem exceedingly complicated: 1) Fossil coccoliths are usually preserved as single discs and rarely as coccospheres (discoasters and related forms occur only as individual asteroliths). The occurrence of two or more morphotypes of coccoliths on a single cell as seen in some of the modern coccolithophores introduces another factor of uncertainty in the taxonomy. For example, GAARDER (1970) has shown the presence of two different coccoliths, formerly designated as *Scyphosphaera apsteini* LOHMANN and *Pontosphaera japonica* (TAKAYAMA) on the same coccosphere. However, the fossil species in which coccospheres have been found have not shown any signs of polymorphism and this phenomenon

may be an exception rather than the rule. 2) Motile and non-motile stages in the life cycle of species and the possession of entirely different types of coccoliths during these stages (PARKE and ADAMS, 1960) add to the weakness of taxonomic data. However, the very fragile nature of the coccoliths of the motile stage make their preservation unlikely (*e.g.* the motile stage of *Coccolithus pelagicus* (WALLICH)—*Crystallolithus hyalinus* (GAARDER and MARKALI) — has never been observed as a fossil, although the modern *C. pelagicus* first appears in the fossil record in the Miocene.) 3) A third major factor in the weakness of quantitative data is introduced by the widely different concepts of species and other taxonomic categories held by various students in this field. Anyone wading through the literature on calcareous nannoplankton, as for that matter any group of fossil or living organisms, can observe that different authors base the erection of new taxa on dissimilar criteria. It is obvious that in the case of this group of microfossils we are dealing with "form genera" and "form species", at best. However, as SIMPSON points out (1953, p. 30), the taxonomic concept of an "experienced student is a more reliable indication of total differences between organisms (better, between populations of organisms) than any collective measure yet derived for differences in objective characters". The problem of dissimilar taxonomic inclinations can thus be alleviated to a large extent when the whole field can be reviewed and an attempt is made to ensure consistency of concepts. 4) Another factor that can bias the quantitative data on calcareous nannofossils is the stratigraphic bias, the relatively greater attention given to the floras of certain ages. Until recently more nannoplankton studies concerned the Eocene than other Lower Tertiary epochs, Paleocene and Oligocene floras being virtually ignored. This kind of partiality can obviously introduce a false sense of floral diversity for the more popular parts of the geologic column. In recent years however, several workers have paid special attention to the floras of less well studied epochs of the Lower and Upper Tertiary. The work on the deep sea sediments cored by the JOIDES Deep Sea Drilling Project during the past three years, which usually contain well preserved microfloras, has been another balancing factor towards this goal. It would be safe to say at this stage that, although new taxa will evidently be added to the list of Cenozoic nannofossils, no substantial additions will be made to the assemblages already recorded from strata of various ages. The more or less continuous sections recovered by the Deep Sea Drilling Project, representing relatively large slices of time, have also helped in the establishment of a refined and practical nannoplankton biostratigraphy and in the delineation of the vertical ranges of various species of Cenozoic nannoplankton — an important factor for any reliable quantitative work. Nevertheless, quantitative data and results presented here are to be considered preliminary at best, and by no means conclusive. It is hoped that this will present a broad, general picture and serve as a guideline for a more comprehensive study in the future.

UNITS	DURATION in M. Y.
PLEISTOCENE	2
PLIOCENE	3.5
LATE MIOCENE	5
MIDDLE MIOCENE	3.5
EARLY MIOCENE	8.5
LATE OLIGOCENE (Chattian)	9.5
EARLY OLIGOCENE (Lattorfian & Rupelian)	6
LATE EOCENE	7.5
MIDDLE EOCENE	4
EARLY EOCENE	4.5
LATE PALEOCENE (P4 & P5 Zones Only)	5.5

Fig. 9. Time-intervals and their durations in my, as used in this paper.

Cenozoic time scale

The Cenozoic time scale used herein is that proposed by BERGGREN (1969 b, fig. 2) and modified by him recently (BERGGREN, in press). This absolute time scale is based on the relationships of the chronostratigraphic units, planktonic foraminiferal zones and radiometric dates of important boundaries and datum levels (for a complete discussion see BERGGREN, 1969 b).

The duration of the various time-intervals from late Paleocene to Pleistocene as used in the time-frequency curves in the present paper is presented in fig. 9. In the present concept the early Paleocene is considered to comprise the Danian or the P1 foraminiferal Zone (BERGGREN, 1969 b) with a duration of 2 million years. The middle Paleocene encompasses the P2 and P3 foraminiferal Zones

and a length of 4 my and the late Paleocene corresponds to P4 and P5 foraminiferal Zones and a duration of 5.5 my.

The duration of the early, middle and late Eocene is shown in fig. 9. The Oligocene is divided only into 2 chronostratigraphic subdivisions — the early Oligocene consisting of the type Lattorfian and Rupelian (6 my) and the late Oligocene corresponds to the type Chattian with a duration of 9.5 my.

Rates of evolution in Cenozoic nannoplankton

For the purpose of the present study the literature on Cenozoic nannofossils was carefully reviewed to ensure an element of internal consistency in the taxonomic concepts (see discussion on p. 145). References to original descriptions of holotypes were made in most cases and taxonomic synonymies were considered. The resultant data, calculated separately for coccoliths (this concept includes all placoliths, discoliths, lopodoliths, rhabdoliths, cycloliths and zygoliths), discoasters and total calcareous nannoflora of the Cenozoic, is presented in the following pages. The 'species' is considered as the basic unit and the only taxonomic category used for quantitative work. The few subspecies taxa that exist in the nannoplankton literature have been counted as species.

The estimates presented here (see fig. 15) of total frequency of calcareous nannoplankton in the Cenozoic are substantially lower than would be derived by simple tabulation of all the species described in the literature without the above mentioned considerations. Although the present estimates of total frequencies are somewhat conservative, they are probably closer to actual numbers than would be attained by simple acceptance at face value of all described taxa. The methods of calculating rates of origination, extinction and change in total have been outlined by SIMPSON (1953, pp. 49—54). As it is customary, the origination and extinction are considered as occurring in the middle of each time period (*i.e.* middle of: early, middle and late Paleocene; early, middle and late Eocene... etc.) and averaged for the duration of that period. The change in total is considered as occurring between the periods (*i.e.*, between: early and middle Paleocene; middle and late Paleocene... etc.) and averaged for half of each preceding and following time period (sese SIMPSON, *op. cit.*, p. 53).

Frequency of calcareous nannofossils in Cenozoic

At the end of the Mesozoic the massive extinctions of marine biota (BRAMLETTE, 1965) depleted the world oceans of calcareous plankton. Of the more than 150 species of calcareous nannoplankton recorded from Late Maestrichtian sediments by various authors, seemingly only four "hardy" forms survived into the Danian. The number of taxa increased gradually through the Danian (see fig. 15, column 1), rising to more than 20 species by its close. In the mid-Paleocene, after an initial period of taxonomic stability, the number of taxa

increased sharply and by late Paleocene time they had multiplied to over 60 species. This sharp upward trend in the diversity continues into the early Eocene at which time nannofossils show their highest peak in Cenozoic diversity, over 110 species being recorded. After a period of relative stability in the middle Eocene, a marked decline in diversity followed, the number of taxa being reduced to less than 70 species in the late Eocene. The following epochs show a progressive decline in species diversity up to the close of early Miocene, the trend being slightly more distinct during the Oligocene. By early Miocene the number of species was restricted to a little over 30. The mid-Miocene once again shows a slight increase in the diversity of nannoflora; over 50 species have been recorded from the sediments of this age. Late Miocene and Pliocene once again show a downward trend with about 40 species recorded from the late Miocene and 35 from the Pliocene. At the advent of Pleistocene time another distinct reduction in the diversity of calcareous nannoplankton resulted in less than 20 remaining species.

Coccolith evolutionary rates

The quantitative data as tabulated for coccoliths is presented below:

Time Units	Total coccolith taxa	First appearances	Last occurrences
Pleistocene	11	5	4
Pliocene	10	2	4
Late Miocene	9	3	1
Middle Miocene	11	3	5
Early Miocene	10	3	2
Late Oligocene	18	7	10
Early Oligocene	34	18	23
Late Eocene	37	24	21
Middle Eocene	39	20	27
Early Eocene	43	28	22
Late Paleocene	27	17	9
Middle Paleocene	13	5	3
Early Paleocene	11	10	2

The time-frequency curves for coccoliths follow similar trends as those for total calcareous nannoplankton (see fig. 10). A sharp increase in the number of taxa from mid-Paleocene to early Eocene, where they reach their peak in diversity, followed by a gradual decrease to early Oligocene and then a marked reduction during the rest of Oligocene and early Miocene. For the rest of Miocene to Pleistocene this downward trend levels off and the number of coccolith taxa remains more or less the same. During the middle Eocene, early

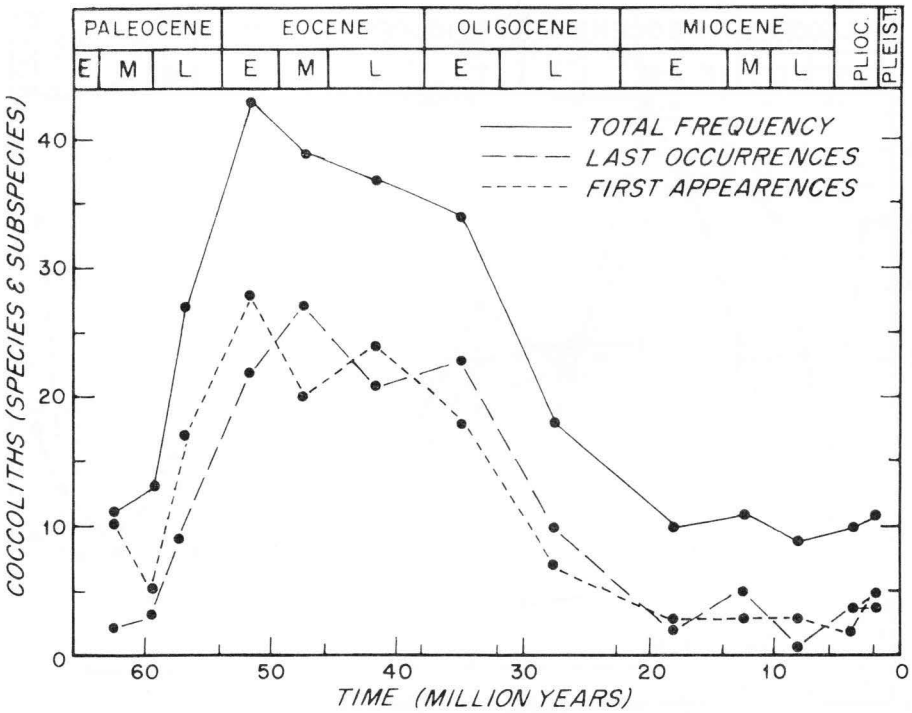

Fig. 10. Time-frequency data for Cenozoic coccoliths.

and late Oligocene, middle Miocene and Pliocene the number of taxa becoming extinct exceeds the number of taxa originating. However, the general trend of both first appearance and last occurrence curves remains the same as that of the total-frequency curve, which in effect is a product of the interrelation of the slopes of these two.

Fig. 11 shows the rates of origination, extinction and the total change for coccoliths as calculated from the above data. It is clear that during the middle Eocene, Oligocene, middle Miocene and at the end of Pliocene, the rate of extinction of coccolith species exceeded the rate of origination. The rate of change in total shows negative values for over 34 million years from the early-middle Eocene to late Oligocene-early Miocene, which signifies a trend towards lower diversities. The changes from negative to positive values, *e.g.*, in middle-late Paleocene, early-middle Miocene and late Miocene-Pliocene reflect trends towards higher diversities, even though extinction rates may be higher than the rates of origination (*e.g.* in middle Miocene).

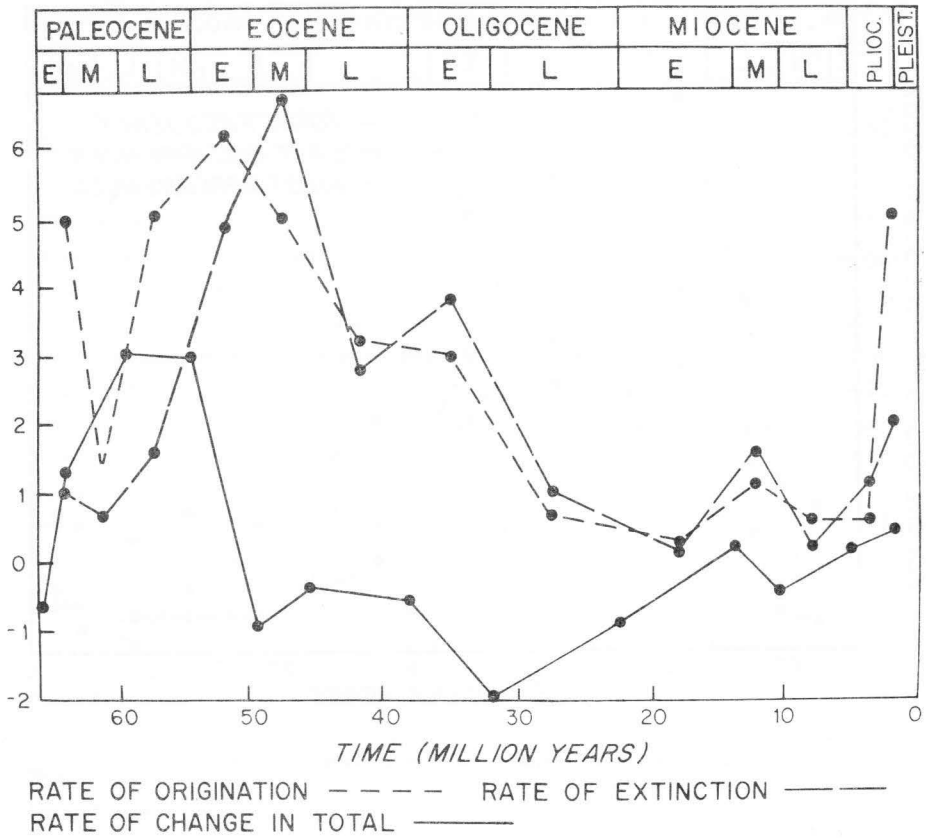

Fig. 11. Rates of evolution for Cenozoic coccoliths. (Vertical scale represents species/my in case of rates of origination and extinction and a ratio in case of rate of change in total.)

Discoaster evolutionary rates

Fig. 12 lists the time-frequency data and taxonomic frequency rates for discoasters, shown graphically in figs. 13 and 14. Discoaster frequencies follow the same general pattern as those of the coccoliths. After the first appearance of this group in the late Paleocene their numbers increase to a peak value of 27 species in the early Eocene. This interval represents the highest diversity for discoasters, both in number of taxa and in their morphological variations. After the middle Eocene their total frequency drops sharply and the trend continues into the early Oligocene. However, unlike the coccolith frequencies, after the early Oligocene discoasters showed no further reduction in number of species, but increased gradually until the mid-Miocene when a second increase in diversity resulted in a jump in the number of species from an early Miocene low

UNITS	DURATION (in my.)	TOTAL DISCOASTERS	FIRST APPEARANCE		LAST OCCURENCE		RATES/ MILLION YEARS		
				%		%	ORIGINATION	EXTINCTION	CHANGE IN TOTAL
PLEISTOCENE	2.0	0							
PLIOCENE	3.5	10	1	10	10	100	0.3	3.0	-0.2
LATE MIOCENE	5.0	11	3	27	2	19	0.6	0.4	-2.1
MIDDLE MIOCENE	3.5	20	10	50	12	60	3.0	3.4	+1.3
EARLY MIOCENE	8.5	12	6	50	2	17	0.7	0.2	+0.1
LATE OLIGOCENE	9.5	11	5	45	5	45	0.5	0.5	+0.1
EARLY OLIGOCENE	6.0	10	3	30	4	40	0.5	0.7	-0.7
LATE EOCENE	7.5	15	3	20	8	53	0.4	1.0	-2.0
MIDDLE EOCENE	4.0	26	12	46	14	54	3.0	3.5	-0.2
EARLY EOCENE	4.5	27	15	55	13	48	3.3	2.9	+2.8
LATE PALEOCENE	5.5	13	13	100	1	8	2.4	0.2	+2.3

Fig. 12. Quantitative data and evolutionary rates for discoasters.

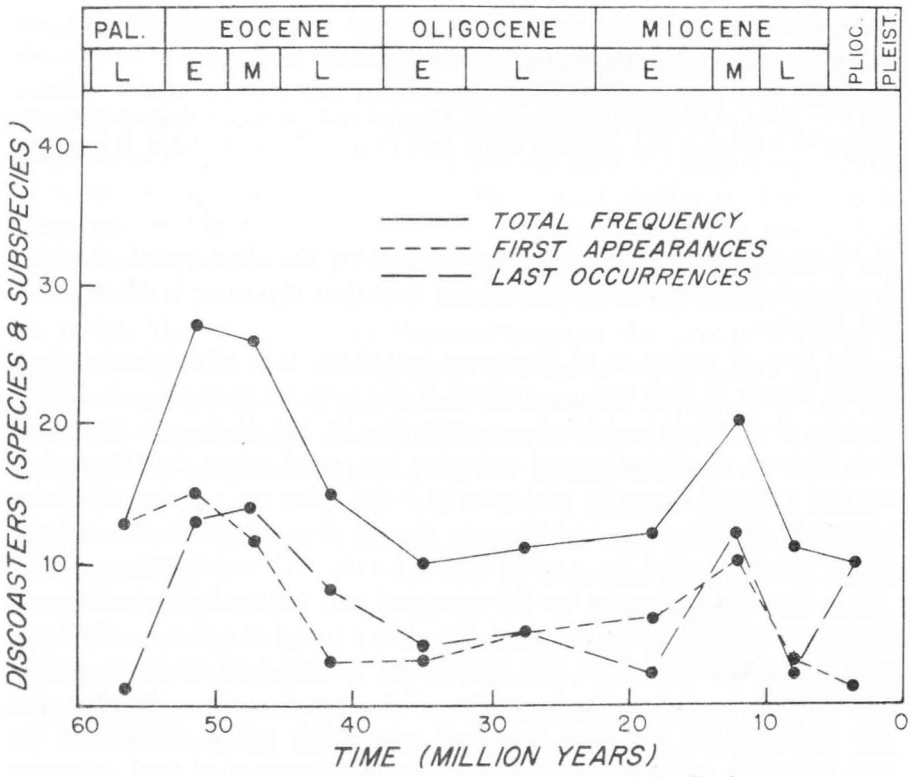

Fig. 13. Time-frequency data for discoasters.

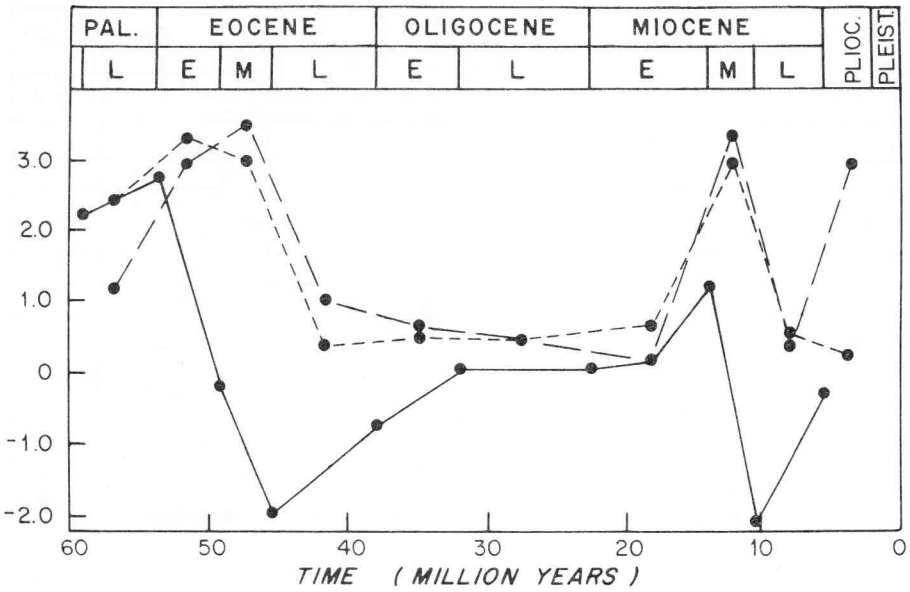

Fig. 14. Rates of evolution for discoasters. (Vertical scale represents species/my in case of rates of origination and extinction and a ratio in case of rate of change in total.)

of 12 up to 20 in the middle Miocene. Following this short period of higher diversity their total frequency dwindles to about half that value in late Miocene and Pliocene.

The rates of extinction of discoasters exceed the rates of origination from middle Eocene to early Oligocene, which is also reflected in the negative values for rates of change in total for these periods (see fig. 14). During the late Oligocene the rates of origination and extinction have equal values, *i.e.*, 0.5 species/my, and a rate of change in total value of -0.7, reflecting a period of relative taxonomic stability. The rates increase sharply after early Miocene and the rate of change in total has a value of $+1$ for the early-middle Miocene.

It is clear that during the late Paleocene and early Eocene both coccoliths and discoasters evolved rapidly; this was followed by a period of reduced evolutionary rates for the remainder of the early Tertiary. For the coccoliths the tempo remains slow throughout the late Tertiary with a slight revival in the middle Miocene. The discoasters, on the other hand, add substantially to the diversity of the total calcareous nannofossils (as reflected in the frequency of total calcareous nannoplankton, fig. 15, col. 1) by their second radiation during the mid-Miocene.

It is interesting to note that in the periods that are followed by a marked change in the nature of nannofloral assemblages, the extinction rates first exceed the rates of origination after a period of relatively higher diversity or a relative taxonomic stability, *e.g.*, in the middle Eocene, early Oligocene, middle Miocene and the Pliocene.

Paleotemperatures and taxonomic frequency of calcareous nannofossils

In fig. 15 the total frequency of Cenozoic calcareous nannoplankton and the total frequency and evolutionary rates data for discoasters has been plotted against the oxygen (δO^{18}) isotope paleotemperature curve from middle Eocene to Pleistocene constructed by DEVEREUX (1967). This curve, as plotted here, has been redrawn by BERGGREN (1969 b) against an absolute time scale on the basis of correlation of the New Zealand stages with European stages and planktonic foraminiferal zones.

It can be seen from fig. 15 that the taxonomic-frequency curves of the total calcareous nannoflora and the discoasters show at least a rough relationship to the paleotemperature curve. Periods with higher temperatures show greater diversity and periods with lower temperatures are followed by a decrease in the number of taxa. The climatic deterioration in late Eocene and early Oligocene followed a similar reduction in taxonomic frequencies and the relatively stable temperatures of late Oligocene and early Miocene show a corresponding stability of taxonomic frequencies, especially in the case of discoasters. The drop in temperature within the early Miocene that is closely followed by a rise of about 7°C at about the early-middle Miocene boundary, shows a corresponding low in the diversity in the early Miocene and an increase in the number of taxa in the middle Miocene. In the late Pliocene-Pleistocene the extreme lowering of temperature shows a corresponding sharp reduction in the taxonomic frequency of calcareous nannoplankton and a total extinction of discoasters. It can also be noticed that pronounced changes in the climate may trigger a corresponding change in the taxonomic frequency, but the optimal result of the change is noticable only after the temperatures have become relatively stabilized again.

A similar relationship between climates and the total frequency of Globigerinidae (see fig. 15, col. 5) has been noted by BERGGREN (1969 b) from middle Eocene to Pleistocene. However, after the low in early Oligocene, the Globigerinidae increase gradually in number and reach a peak of diversity in the late Miocene. From a comparison of the time-frequency curves of the globigerinids and calcareous nannoplankton with the paleotemperature curve, it seems that the factors that effected the evolutionary rates of planktonic foraminifera had similar effects on the nannoflora but that the latter was even more strongly temperature controlled than the former. This may be partly due to the fact that

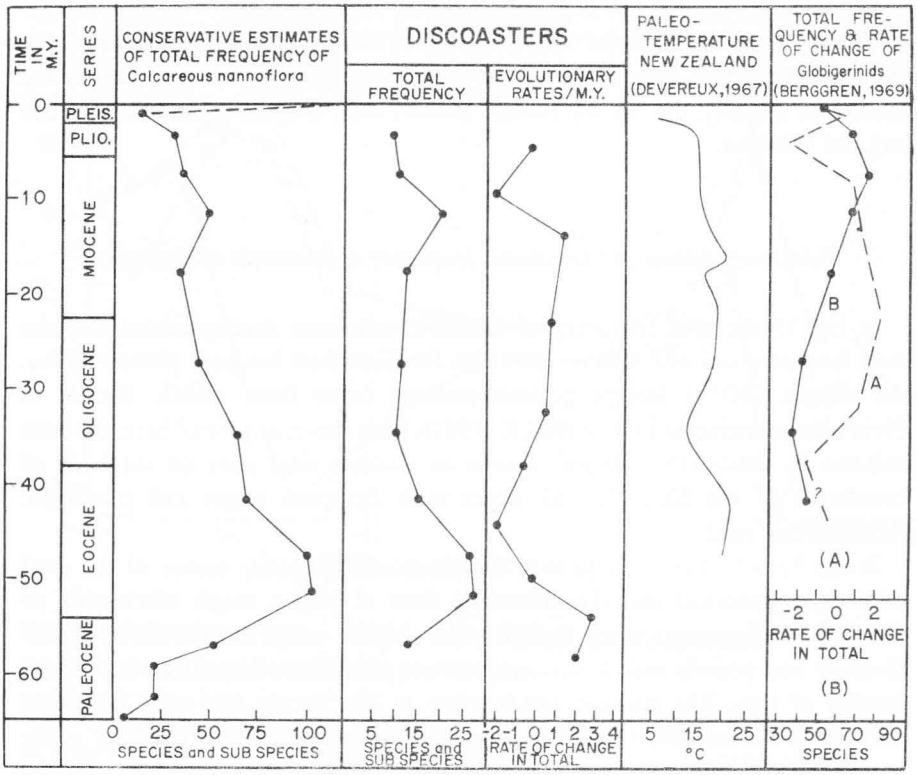

Fig. 15. Total taxonomic frequency of Cenozoic calcareous nannoplankton and total frequency and evolutionary rates of discoasters compared with paleotemperature curve of DEVEREUX (1967) and quantitative data on globigerinids of BERGGREN (1969).

the calcareous nannoplankton are mainly confined to the photic zone of the sea where temperature changes are more pronounced.

Recently, LIPPS (1970) has presented a different hypothesis in his consideration of the evolution of marine plankton in terms of paleoclimate. According to him (*op. cit.*, pp. 1, 14—18) in the times of higher temperatures in the higher latitude seas the vertical and horizontal thermal barriers between habitats are eliminated and there is a tendency towards extinctions and decreased diversity in the marine biota, and periods of cooler climate have an opposite effect on the thermal gradients and an increase in the diversity of biota occurs. These conclusions are contrary to those drawn earlier by BERGGREN (1969 b) for the Cenozoic planktonic foraminifera and to those drawn here for calcareous nannoplankton. However, until more objective data on the diversities of faunas and floras on the regional basis in the higher latitudes becomes available the validity of these opposing conclusions cannot be effectively tested.

It should be mentioned here that although the taxonomic frequencies of plankton groups show some relationship to the climatic fluctuations, the reasons for the highs and lows in the diversities ought not to be sought in the paleotemperatures alone. In their recent work TAPPAN and LOEBLICH (1971) have pointed out that the worldwide changes of phytoplankton diversities with time are to be sought not only amongst the environmental factors but also amongst biochemical, morphological, and physiological ones. Exponential increases in the phytoplankton taxa occur from the exploitation of the various potentialities of the environmental, morphological or physiological innovations (*op. cit.*, pp. 278—280). However, it would seem that the climatic changes over long periods of geologic time would play a relatively important role in influencing the evolutionary rates of photosynthetic organisms such as calcareous nannoplankton.

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