

Paleoecology of mid-Cretaceous planktonic foraminifera: A comparison of open ocean and Epicontinental Sea assemblages

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ABSTRACT: Although our knowledge of living planktonic foraminifera is limited, useful paleoecologic information can be obtained from ancient assemblages. During the mid-Cretaceous, as today, the simple, inflated morphotypes inhabited the near-surface waters while the flatter, keeled forms probably occupied deeper habitats. Three faunal groups are proposed, an Epicontinental Sea Fauna (ESF) characterized by species of *Gubkinella*, *Guembelitria* and *Heterohelix*, an open marine Shallow Water Fauna (SWF) composed primarily of species of *Hedbergella* and *Globigerinelloides*, among others, and finally an open marine Deep Water Fauna (DWF) represented by species of *Planomalina*, *Rotalipora* and *Praeglobotruncana* (keeled taxa). Open ocean assemblages of DSDP Sites 545 and 547 are numerically dominated by species of the SWF in the >63- μm size fraction while the ESF comprises about 5% of the assemblages, and the biostratigraphically important DWF generally comprises less than 2%. These assemblages demonstrate remarkable stratigraphic consistency. In contrast to open ocean assemblages, epicontinental sea assemblages of the Vocontian Basin are characterized by loss of the DWF with decreasing water depth and an increase in the proportion of the ESF. The ESF:SWF ratio also becomes increasingly variable with decreasing water depth. Upwelling also has pronounced effects on the composition of planktonic assemblages as suggested by an increase in the proportion of the ESF, interpreted to include opportunistic species.

INTRODUCTION

Planktonic foraminifera have proved to be vital in high resolution biostratigraphy of mid-Cretaceous and younger marine sequences. They also have been useful for ancient paleoceanographic reconstructions, but their value in studies of paleoecology is more limited. Because so little is known about the ecology of living planktonic foraminifera in terms of reproductive rates, ecological stress, predation, and the ultimate destruction and sorting of their empty tests, paleoecologic interpretations of extinct species and assemblages must be addressed with care. However, when considered within a geologic framework, our basic understanding of planktonic foraminiferal biology and ecology can be applied to paleoecologic/paleoenvironmental problems. The time-averaged nature of geologic samples may actually help us to better understand the long-term composition of modern populations by hedging the problems of patchiness and seasonal variation.

Modern planktonic foraminifera are generally restricted to open marine environments of normal oceanic salinity and clear water. They live predominantly in the euphotic zone, although species-specific ecological and physiological requirements have resulted in a crude depth stratification with the spinose, symbiont-bearing species restricted to the sunlit, near-surface waters while the nonspinose, symbiont-barren species tend to occupy deeper waters (Bé 1982; Hemleben and Spindler 1983). Depth stratification of planktonic foraminifera may partially be a function of water density, especially in the low latitudes where temperature and salinity variation of the uppermost water column may promote vertical niche partitioning and higher diversities. Diversity of planktonic foraminiferal assemblages in low latitude open ocean environments is probably also strongly influenced by nutrient availability and surface water fertility (e.g. Lipps 1979).

Planktonic foraminifera are rare in the nearshore environments of continental shelves but increase in abundance with increasing depth (e.g. Phleger and Parker 1951; Bandy 1956; Murray 1976; Rottman 1978). In a study of marginal seas, Murray (1976) documented an increase of the planktonic foraminifera to benthic foraminifera (P/B) ratio in bottom sediments, a progressive increase in the size of planktonic tests and an increase in planktonic diversity toward the open sea. Similar trends are observed in fossil assemblages.

In this paper, data are presented to further characterize the compositional make-up of mid-Cretaceous planktonic foraminiferal assemblages from low to mid-latitude open ocean and epicontinental sea environments, to document the extent to which assemblage composition is affected by decreasing water depth and distance from shore and changing fertility in surface waters. Methodology is an important aspect of this study. The use of the 63- or 75- μm size fraction for making counts is emphasized, as the finer sieves retain a more representative and ecologically significant foraminiferal assemblage. Berger (1971) clearly demonstrated that species composition and their proportions are sensitive to the sieve size used. In the Santa Barbara Basin, Berger found that a 125- μm screen retains about 19% of the individuals caught on a 63- μm screen, while a 250- μm screen retains only 0.4%! This example dramatizes the fact that considerable ecologic information is potentially lost when the coarser sieves are used. The underlying purpose of this paper is to emphasize the usefulness of the compositional make-up of planktonic foraminiferal assemblages as a paleoecologic indicator and valuable paleoceanographic tool.

Paleoecologic applications

Paleobiogeographic distribution patterns of Cretaceous planktonic foraminifera are useful for paleoceanographic reconstructions and may reflect broad temperature gradients

of the Cretaceous oceans and epicontinental seas (e.g. Berquist 1969; Douglas 1972). Paleobiogeographic distributions are also useful in reconstructing global sea level fluctuations (e.g. Hart and Bailey 1979; Wiedmann et al. 1982). Other paleoceanographic applications include interpretation of ancient upwelling systems based on foraminiferal compositions, associated faunal and floral assemblages, and facies patterns (Butt 1982; Einsele and Wiedmann 1982, 1983; Kemper and Zimmerle 1983; Leckie 1984).

Depth distributions of Cretaceous planktonic foraminifera are thought to have been similar to modern analogs with the globular (i.e. globigerine) morphotypes inhabiting the near-surface waters and the flattened, keeled biconvex, and keeled planoconvex (i.e. globorotaliid-like) forms representing increasing depth habitats (Hart and Bailey 1979; Hart 1980; Caron and Homewood 1982). This general trend has been supported by paleobiogeographic distributions (Eicher 1969a, 1969b; Sliter 1972; Hart and Bailey 1979) and oxygen isotope data (Douglas and Savin 1978). However, it should be noted here that many globorotaliid-like forms of the Early Tertiary, in contrast to the mid-Cretaceous forms, specifically *Acarinina* and perhaps *Morozovella*, were probably spinose or bore spinelike structures covering the test or concentrated along the periphery (McGowran 1968). These latter forms may have been near-surface dwellers, in contrast to globigerine forms like *Subbotina*, which may have included deeper-dwelling species (e.g. Boersma et al. 1979).

Only rare individuals of the deep-dwelling mid-Cretaceous species would be expected in shallow epicontinental seas, because the depth would be insufficient to support their full life cycles (Hart and Bailey 1979). Perhaps, too, the simple, globigerine morphotypes had broader environmental tolerances (i.e. eurytopic) than the more complex, and presumably more specialized globorotaliid-like forms (i.e. stenotopic). Eicher (1969b) and Eicher and Worstell (1970) have shown that the globigerine and globular morphotypes (*Hedbergella*, *Heterohelix*) were the first planktonics to appear during transgression and the last to disappear during regression of shallow epicontinental seas. These data concur with observed species distributions in modern shelf environments. Murray (1976) has shown that only rare individuals of *Globigerina* and *Globigerinoides* (simple, inflated morphotypes) penetrate into the middle shelf environment while predominantly juvenile forms are found in the inner shelf; the bulk of the planktonic tests which accumulate on the shelf have been transported in by currents. Vertical mixing and turbulence in the shelf environment reduce the settling velocities of the empty foraminiferal tests so that lateral transport and differential settling rates can yield highly variable species compositions in the residue assemblages (Murray 1976). This observation also applies to ancient sediment assemblages and will be discussed further in a later section.

Life spans, hence reproductive rates, of living planktonic species are not well documented. However, the limited published data suggest that the spinose, globigerine morphotypes which inhabit the near-surface waters and bear symbiotic algae may have shorter life cycles than the non-spinose, globorotaliid morphotypes (Berger 1970b; Bé 1977; Bé and Hutson 1977; Anderson et al. 1979; Bé et al. 1981; Caron et al.

1982; Hemleben et al. 1985). Caron and Homewood (1982) have suggested that deeper-dwelling morphotypes represent advanced and/or specialized taxa with longer life cycles and lower reproductive rates than the simple, surface-dwelling species. Clearly, differential rates of test production should be reflected in the sediments, particularly those sequences containing well-preserved assemblages deposited above the foraminiferal lysocline. It is reasonable to assume that the juvenile forms of non-spinose or keeled species have just as great a chance of being eaten or perishing due to ecologic stress as the rapidly reproducing globigerine forms. Therefore it is suggested that the difference in rates of production between the globigerine and globorotaliid-like morphotypes in the living populations is translated into the ratio of their shells in sediment assemblages. This premise is strongly supported by examining sediment assemblages, either modern or ancient, which have been processed with a fine sieve (e.g. 63 μm). The simpler, globigerine morphotypes greatly dominate the foraminiferal fraction. The fine size fractions hold valuable (paleo)ecologic information, which has mostly been overlooked in foraminiferal studies.

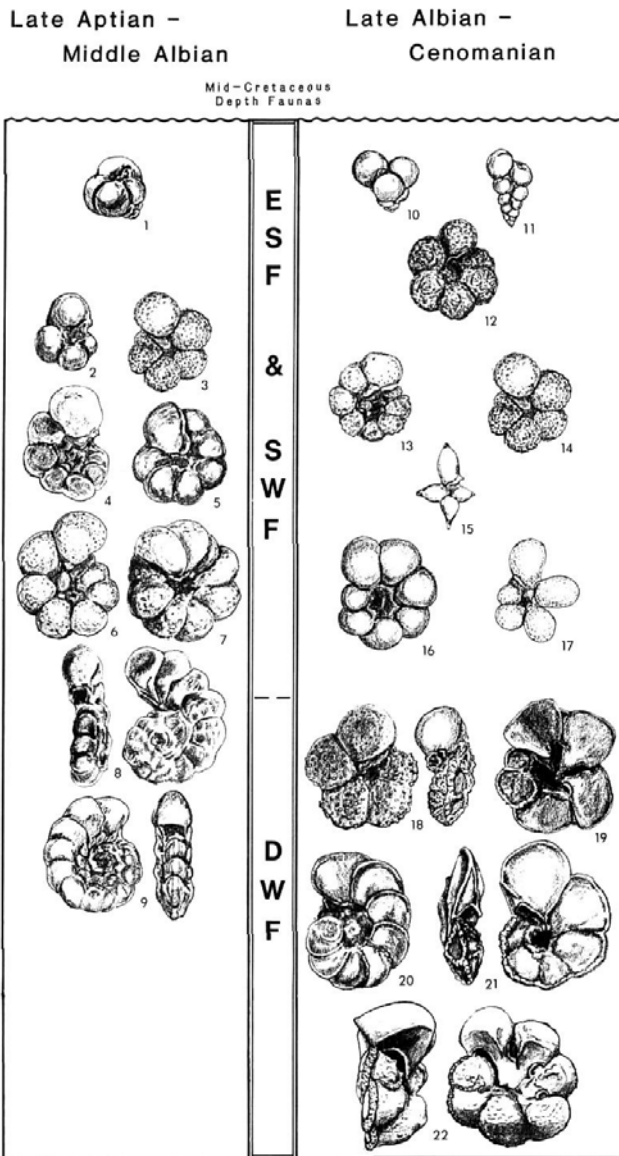
MID-CRETACEOUS DEPTH FAUNAS

Three faunal groups are proposed for low-latitude, mid-Cretaceous planktonic foraminiferal assemblages. They are based on recurrent faunal associations consistent with observed paleobiogeographic distribution patterns (e.g. Tappan 1940, 1943; Loeblich and Tappan 1950; Eicher 1969b; Eicher and Worstell 1970; Sliter 1972; Hart and Bailey 1979; Leckie, unpublished data). Proposed depth ranges refer to adult stages. The 100-m boundary for the deepest-dwelling forms was selected by analogy with present depth distributions of living species of *Globorotalia* (after Bé 1977).

Epicontinental Sea Fauna (<100 m)

This fauna is characterized by species of *Heterohelix*, a biserial form, *Guembelitra*, a triserial form, and *Gubkinkella*, a stout trochospiral form (text-fig. 1). These genera are particularly diagnostic of planktonic foraminiferal assemblages from shallow marine sections of Cretaceous epicontinental seas, for example the Western Interior Seaway of North America (Tappan 1940, 1943; Loeblich and Tappan 1950; Eicher 1969a, 1969b). They occur in greatly reduced abundances in open ocean pelagic sections. It is suggested that they inhabited the near-surface waters (e.g. Hart and Bailey 1979; Hart 1980) and may have had wider ecologic tolerances (i.e. eurytopic) than other mid-Cretaceous genera. These taxa were the principal opportunistic planktonic foraminifers of the mid-Cretaceous. High proportions of generally small specimens of *Hedbergella* spp. and *Globigerinelloides* spp. are associated with the Epicontinental Sea Fauna of relatively shallow epeiric or marginal seas (Eicher 1969b; Eicher and Worstell 1970; Sliter 1972; Leckie, unpublished data).

Tentatively included in the Epicontinental Sea Fauna are these ornamented *Hedbergella* species: *H. washitaensis* (Carsey) and *H. libyca* Barr. These species are particularly characteristic of warm, shallow-water environments, such as marginal seas or carbonate platforms (e.g. Barr 1972; Saint-Marc 1973; Longoria and Gamper 1977). *Hedbergella libyca* was



TEXT-FIGURE 1
Hypothetical vertical distribution of representative mid-Cretaceous planktonic foraminifera. Elements of both the Epicontinental Sea Fauna (ESF) and open marine Shallow Water Fauna (SWF) probably inhabited the upper 100 m of the oceans whereas elements of the open marine Deep Water Fauna (DWF; keeled taxa) are believed to have inhabited greater depths. Note morphologic diversification and implied exploitation of deeper habitats in late Albian-Cenomanian time compared with late Aptian-middle Albian time. 1, *Gubkinella graysonensis*; 2, *Globigerinoides blowi* s.l.; 3, *Hedbergella delrioensis*; 4, *Globigerinelloides ferreolensis*; 5, *Hedbergella trochoidea*; 6, *Ticinella primula*; 7, *Ticinella roberti* s.l.; 8, *Globigerinelloides algerianus*; 9, *Planomalina cheniourensis*; 10, *Guembelitra cenomana*; 11, *Heterohelix moremani*; 12, *Hedbergella libyca*; 13, *Globigerinelloides ultramicrus*; 14, *Hedbergella delrioensis*; 15, *Schackoina cenomana*; 16, *Globigerinelloides bentonensis*; 17, *Clavihedbergella simplex*; 18, *Praeglobotruncana delrioensis*; 19, *Rotalipora cushmani*; 20, *Planomalina buxtorfi*; 21, *Rotalipora appenninica*; 22, *Rotalipora reicheli*. (Conceptually similar to a model proposed by Hart and Bailey 1979.)

widely distributed during latest Albian and earliest Cenomanian time including open ocean environments (Caron 1978;

McNulty and Barr 1979; Leckie 1984), although its greatest relative abundances occur in marginal seas (Leckie, in prep.).

Shallow Water Fauna (<100 m)

The major components of this fauna are *Hedbergella* spp. and *Globigerinelloides* spp. These species are the dominant planktonic foraminiferal elements in open marine pelagic sections. Associated mid-Cretaceous genera include *Clavihedbergella*, *Schackoina*, and *Ticinella* (text-fig. 1).

Species of *Clavihedbergella* have been interpreted by some workers to represent deep-water taxa based on gross morphological characters (Douglas and Savin 1978; Hart 1980). Modern clavate species such as *Globigerinella adamsi* (Banner and Blow) and *Hastigerinella digitata* (Rhumbler) inhabit mesopelagic and bathypelagic environments (Bé 1977). However, these species are characterized by planispiral, biumbilicate tests with gaping apertural areas. The mid-Cretaceous clavihedbergellids, for example *C. simplex* (Morrow), *C. subcretacea* (Tappan), *C. pentagonalis* (Reichel) and *C. moremani* (Cushman), lack these morphocharacters and simply represent modifications of the basic hedbergellid morphology. These taxa may have lived at greater depths than *Hedbergella delrioensis* (Carsey) or *H. planispira* (Tappan), based on their clavate chambers and by analogy with the living species mentioned, but close paleobiogeographic association with *Hedbergella* spp. in Cretaceous epicontinental seas suggests that *Clavihedbergella* spp. were not deep-water forms (data from Eicher and Worstell 1970).

Species of *Schackoina* have been interpreted to represent questionable shallow-water forms by Hart (1980) and deep-water forms by Douglas and Savin (1978). The lack of a clear association of *Schackoina* with species of the Deep Water Fauna suggests that this genus inhabited shallower waters. The persistent occurrence of *Schackoina* spp. with *Hedbergella* spp. in the Cenomanian-Turonian Western Interior Seaway supports a shallow-water depth habitat for this genus (data from Eicher and Worstell 1970).

Also indicative of fairly shallow depths are the ticinellids. This group of planktonic foraminifera, which gave rise to the keeled rotaliiporids, may have lived at greater depths than most species of *Hedbergella* or *Globigerinelloides* as suggested by the flattened tests and thicker walls, particularly taxa such as *Ticinella roberti* (Gandolfi) s.l. and *Biticinella breggiensis* (Gandolfi).

Deep Water Fauna (>100 m)

The keeled genera (*Rotalipora*, *Planomalina* and *Praeglobotruncana*) are believed to have been the deepest-dwelling mid-Cretaceous planktonic foraminifera based on paleobiogeographic distributions, oxygen-isotope data, distributions relative to eustatic changes, and by analogy with the depth habitats of the living keeled globorotaliids (text-fig. 1). These taxa are believed to have been the most sensitive environmentally (i.e. stenotopic) of the mid-Cretaceous planktonic foraminifera.

COMPOSITION OF OCEANIC ASSEMBLAGES: DSDP SITES 545 AND 547

During mid-Cretaceous time, DSDP Sites 545 and 547 were situated in an open ocean environment along the northwest African continental margin (text-fig. 2). The sites were situated in middle bathyal depths (1500–2500 m) beneath the Mazagan Plateau, above the foraminiferal lysocline. Hemipelagic sediments, bearing diverse and well-preserved assemblages of planktonic foraminifera, accumulated on the rather unstable slope. The upper Albian to upper Cenomanian section of Site 547 contains abundant conglomeratic intervals, but faunal reworking is not an obvious problem, as clasts were primarily derived penecontemporaneously from a local source. Age-equivalent strata of Site 545 contain far fewer conglomeratic intervals, and faunal recycling is minimal. However, several of the upper Aptian to middle Albian assemblages of Site 545 may include mixed elements as suggested by the extended ranges of several late Aptian species, probably derived from the Mazagan Escarpment (Leckie 1984).

Site 545

The proportion of planktonic to benthic foraminifera gradually decreases from Core 56 through the lower part of Core 47 (upper Aptian to lowermost Albian). From the upper part of Core 47 through the lowermost part of Core 40 (lower to middle Albian) benthics dominate the foraminiferal assemblages (text-fig. 3). Planktonic foraminiferal diversity (number of species per sample) averages about 11 species through the upper Aptian to lower Albian interval but then drops to an average of less than 9 species per sample in the middle Albian (Cores 44 through 41). This latter interval contains thin, laminated black shales, and also contains the greatest proportion of siliceous skeletons relative to foraminiferal tests, the lowest planktonic to benthic foraminiferal ratios, and a significant increase in fish debris (Leckie 1984). Planktonics again dominate the late Albian to middle Cenomanian foraminiferal assemblages (Cores 40 through 28) with a return to typical slope percentages (>80%; e.g. Pflieger and Parker 1951). Average planktonic diversity is more than 17 species per sample for this interval (excluding the conglomeratic beds).

The upper Aptian-lower Albian assemblages (Cores 56 to 45) are dominated by components of the Shallow Water Fauna (text-fig. 3), mainly *Hedbergella delrioensis*, *H. planispira*, *H. trocoidea*, *Globigerinelloides aptiense* Longoria, and *G. blowi* (Bolli) s.l. while species of *Ticinella* become significant in the upper part. Elements of the Epicontinental Sea Fauna, represented by *Gubkinella graysonensis* (Tappan), comprise an average of 4.5% of the assemblages. Elements of the Deep Water Fauna, represented only by very rare specimens of *Planomalina cheniourensis* (Sigal) (the earliest keeled planktonic), do not constitute a statistical proportion of these assemblages.

In the middle Albian assemblages (Core 44 through the lower part of Core 40) *Gubkinella graysonensis*, an element of the Epicontinental Sea Fauna, increases to an average of 28% of the assemblages at the expense of elements of the open marine Shallow Water Fauna. This is reflected by a marked

decline of *Globigerinelloides* spp. and restricted occurrence of *Ticinella* spp. to the lower part of the interval. *Clavibergella simplex* occurs throughout. Keeled species, elements of the Deep Water Fauna, are absent.

A minor hiatus in the lower part of Core 40 separates middle Albian from upper Albian strata. Above this break in Core 40 the first evolutionary radiation of late Albian keeled planktonics occurs. Although elements of the Deep Water Fauna (*Planomalina* spp., *Praeglobotruncana* spp., and *Rotalipora* spp.) are diagnostic and conspicuous components of the upper Albian to middle Cenomanian strata (Cores 40 through 28), these taxa only constitute an average of less than 1% of the assemblages. Elements of the Shallow Water Fauna dominate the planktonic foraminiferal fraction making up about 92% of the assemblages. Important components include *Hedbergella delrioensis*, *H. planispira*, *Globigerinelloides bentonensis* (Morrow) and *G. ultramicrus* (Subbotina), while *Ticinella* spp. are persistent through the upper Albian and *Schackoina* spp. are diagnostic elements of the assemblages from the uppermost Albian to middle Cenomanian. Elements of the Epicontinental Sea Fauna, *Heterohelix moremani* (Cushman), *Guembelitra cenomana* (Keller), and *Gubkinella graysonensis*, constitute an average of 8% of the upper Albian-middle Cenomanian assemblages.

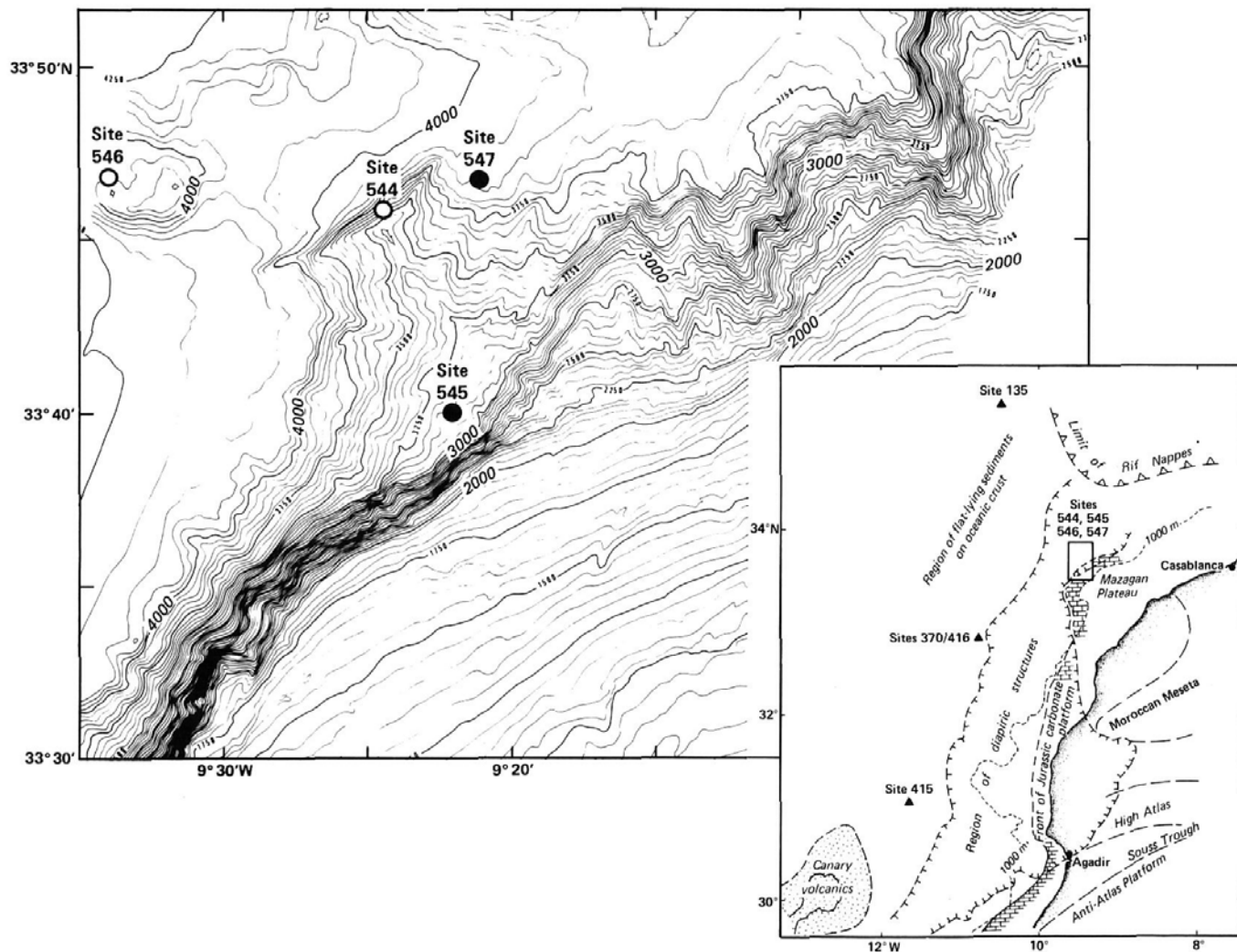
Site 547

The diversity of planktonic foraminifera fluctuates between 12 and 21 with an average of 16 species per sample through the upper Albian to upper Cenomanian section (text-fig. 4). Planktonics dominate the foraminiferal fraction, constituting an average of 90% of the assemblages. Faunal composition is nearly identical to the upper Albian-Cenomanian section of Site 545, with the components of the Shallow Water Fauna representing about 95% of the assemblages and the Deep Water Fauna less than 1%. The proportion of Epicontinental Sea Fauna averages about 4% of the assemblages.

Summary of faunal trends at Sites 545 and 547

An important aspect of the mid-Cretaceous, open ocean planktonic assemblages is their remarkable stratigraphic consistency in overall compositional structure, particularly in the proportions of the three faunal associations recognized here (text-figs. 3 and 4). A major environmental perturbation in the middle Albian at Site 545 is related to upwelling and will be discussed in a later section.

The assemblages of Sites 545 and 547 are dominated by taxa of the open marine Shallow Water Fauna, mainly *Hedbergella* spp., but including *Globigerinelloides* spp. and in the upper Albian, species of *Ticinella*. With the exception of *Planomalina cheniourensis* in the uppermost Aptian, keeled species were nonexistent prior to the upper Albian. The upper Albian-Cenomanian interval corresponds with the first real radiation of the biostratigraphically important keeled morphotypes of the Deep Water Fauna. Species of the keeled genera *Planomalina*, *Praeglobotruncana* and *Rotalipora* are diagnostic elements of the late Albian-Cenomanian assemblages but are greatly diluted by the high proportion of simple, inflated morphotypes. The Deep Water Fauna (all keeled



TEXT-FIGURE 2
Map showing regional setting of Mazagan Plateau and location of sites drilled during Leg 79.

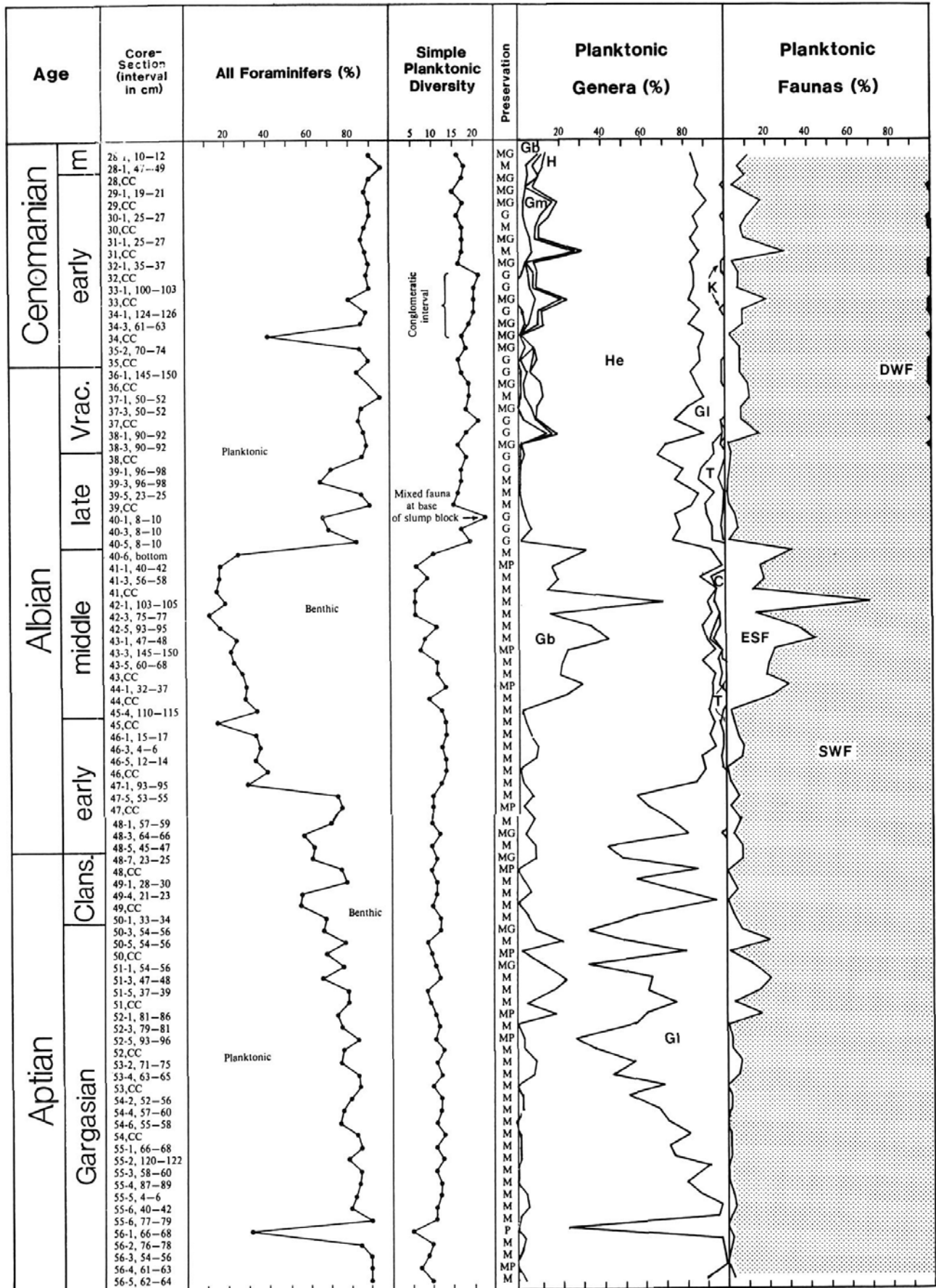
species combined) is only represented by a trace to a maximum of 3% in these assemblages.

The Epicontinental Sea Fauna is composed of *Gubkinella graysonensis* in the late Aptian to middle Albian assemblages but is joined by *Heterohelix moremani* and *Guembelitra cenomana* in the late Albian to Cenomanian assemblages. In the upper Albian-Cenomanian interval of Sites 545 and 547, the Epicontinental Sea Fauna consists of a trace to 28% of the assemblages with an average of about 5%. The upper Aptian to lower Albian interval of Site 545 has similar proportions of Epicontinental Sea Fauna.

Comparison of DSDP Sites 545 and 547 with sites in an Epicontinental Sea: Vocontian Basin

Vast epicontinental seas covered much of Europe during the Cretaceous. One such epeiric sea was centered in the Vocontian Basin of southern France. Eicher et al. (1978) examined latest Albian and Cenomanian benthic foraminifera from three localities representing a transect from inner or middle neritic depths to probable upper bathyal depths: Caussols (shallowest), Les Lattes-Les Mujouls, and Bruis (deepest, near the basin center) (text-fig. 5). The depth gradient is substantiated by planktonic/benthic (P/B) forami-

TEXT-FIGURE 3
Characteristics of foraminiferal assemblages at Site 545. Relative abundances of planktonic and benthic foraminifera based on counts of at least 300 specimens. Simple planktonic diversity includes mixed elements. Foraminiferal preservation: G = good; MG = moderately good; M = moderate; MP = moderately poor; P = poor. Planktonic genera: Gb = *Gubkinella*; Gm = *Guembelitra*; H = *Heterohelix*; He = *Hedbergella*; Gl = *Globigerinelloides*; T = *Ticinella*; C = *Clavibergella*; K = keeled forms (*Planomalina*, *Rotalipora*, and *Praeglobotruncana*). Planktonic faunal groups: ESF = Epicontinental Sea Fauna; SWF = Shallow Water Fauna; DWF = Deep Water Fauna.



niferal ratios, benthic diversity and composition, proportion of radiolarians, and sedimentologic criteria (Eicher et al. 1978). Results of their study suggest that the environments remained relatively unchanged at each locality throughout the study interval.

Washed samples of the Eicher et al. (1978) study were analyzed here for planktonic foraminiferal composition. Splits of the 28 samples through the lower and middle Cenomanian interval were counted for proportions of the three proposed faunal groups. One sample from the Bruis section is too poorly preserved to yield accurate counts. Although a 75- μ m screen was utilized by Eicher et al. to process the Vocontian Basin samples instead of the 63- μ m screen used to process the samples of Sites 545 and 547, useful comparative results were attained between the open-ocean DSDP sites and epicontinental sea localities (text-fig. 6).

Two significant trends in the planktonic foraminiferal compositions are observed with decreasing paleodepth (text-fig. 6). First, the proportions of the Epicontinental Sea Fauna (ESF) increase relative to the Shallow Water Fauna (SWF) from Bruis towards Caussols (i.e. with decreasing depth and distance from the shoreline) (text-fig. 8) while components of the Deep Water Fauna become increasingly rare. The observed distribution patterns are consistent with the hypothesis of bathymetric and/or environmental exclusion of deeper-dwelling species with decreasing depth and distance from the shoreline. Second, the variability in the ratio of Epicontinental Sea Fauna to Shallow Water Fauna increases with decreasing depth. The ESF:SWF ratios of the three Vocontian Basin sections are compared with Sites 545 and 547 in text-figure 7. The ESF:SWF ratio progressively increases with decreasing depth. The increased variability in foraminiferal compositions observed in the shallower sections may reflect environmental variability (e.g. temperature, salinity, nutrients, water clarity), shelf currents, and/or the lateral transport and differential settling rates of empty tests. One sample from the Caussols section (shallowest) is associated with a shell hash and shows an enrichment in open marine Shallow and Deep Water Faunas, perhaps a result of shoreward transport.

The ratio of Epicontinental Sea Fauna to Shallow Water Fauna may be a useful gauge of relative paleodepth and/or proximity to shoreline in epicontinental seas. The proportions of the proposed planktonic faunal groups (e.g. ESF:SWF ratio) in conjunction with P/B ratios may also prove to be useful tools in understanding circulation patterns or current intensities of epeiric or marginal seas and perhaps in determining proximity of marginal seas to the open ocean (e.g. Murray 1976). More detailed studies may also prove that the shallowest dwelling, epipelagic species are useful paleoecologic indicators of productivity or oxygen levels and surface-water parameters, such as salinity and temperature which are of particular significance in epicontinental seas where fluctuating oceanographic variables may have been amplified (e.g. Eicher and Diner 1985; Leckie 1985).

Upwelling off the Mazagan Plateau

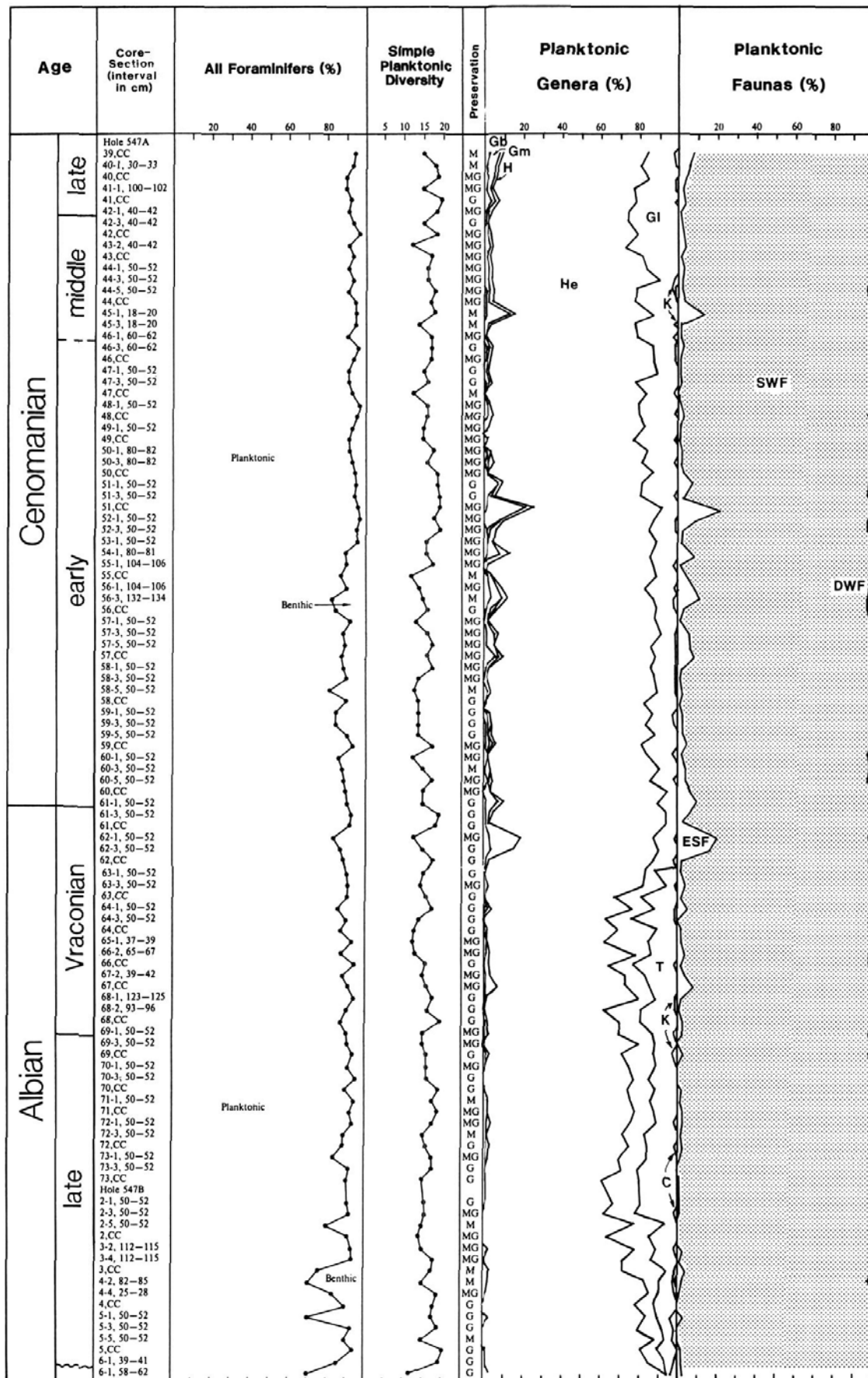
Site 545 was apparently in an area of significant upwelling and associated fertile surface waters off central Morocco dur-

ing latest Aptian through middle Albian time. Siliceous skeletons of radiolarians and sponge spicules dominate the biota from the upper part of Core 50 through the lower part of Core 41 (Leckie 1984). Other supporting evidence for upwelling is the sharp increase in benthic foraminifera relative to planktonic forms, the drop in planktonic foraminiferal diversity, an increase in fish debris, and an increase in benthic organisms including ostracods and echinoderms. The upwelling probably occurred over the outer Mazagan Plateau and upper Mazagan Escarpment, adjacent to Site 545.

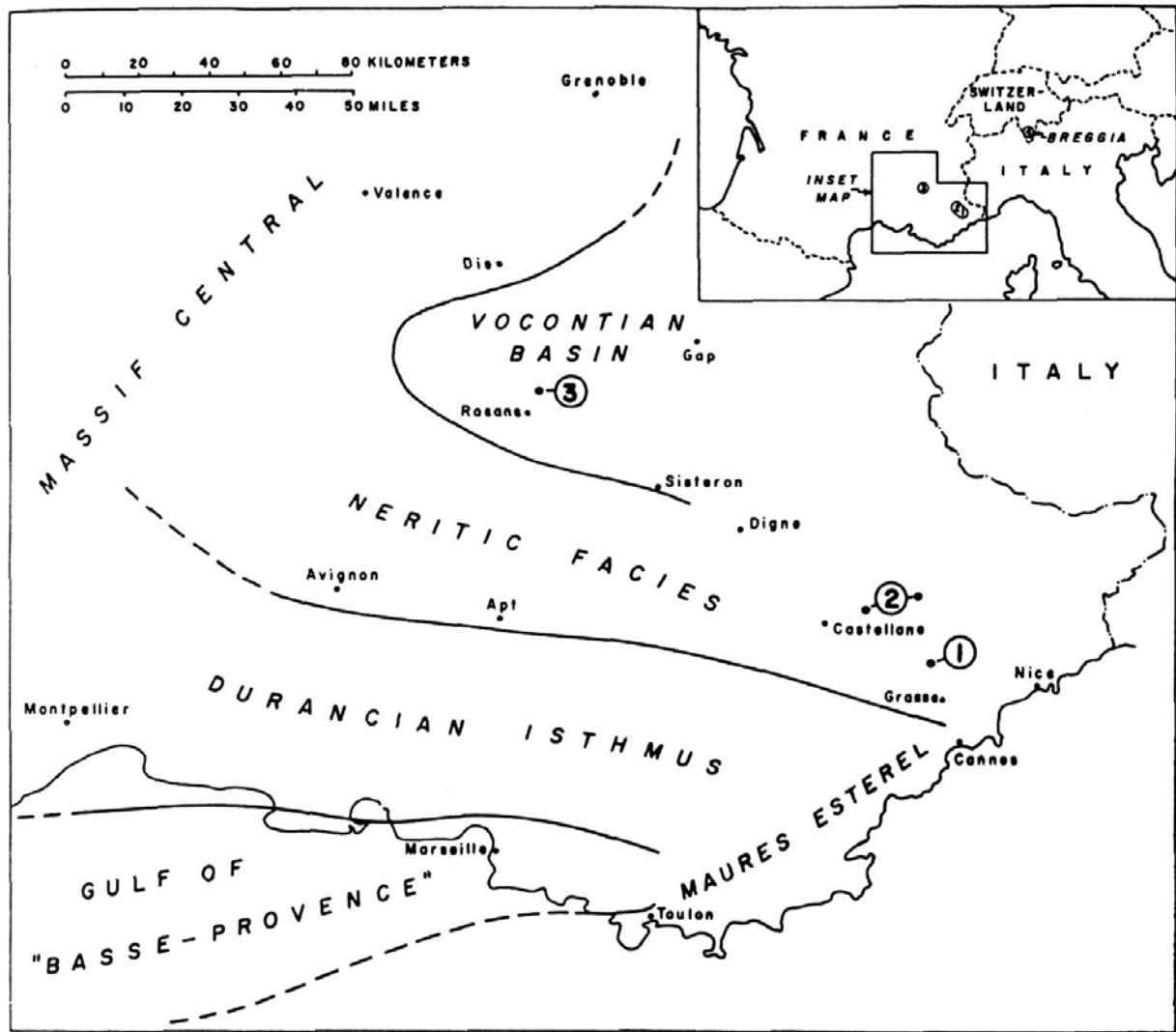
Foraminiferal assemblages were notably affected by the upwelling regime. Foraminifera in general have their lowest proportion relative to other biota in the interval from Core 47 through the lower part of Core 41. The planktonic to benthic ratio steadily decreases from Cores 55 through 48. Then in Core 47 there is a sharp drop in the proportion of planktonics to benthics (text-fig. 3). In fertile regions along the present northwest African margin, Diester-Haass (1978) noted that the proportion of planktonic to benthic foraminifera was less than that observed in other bathyal environments. This is partly a function of selective dissolution of the planktonic foraminifera, either as they fell through the water column or reacted with CO₂-rich interstitial bottom waters related to increased benthic activity and/or increased accumulation of organic matter (Berger 1970c). The CCD and lysocline commonly rise under ocean margin regions where fertility is high (Berger 1970a, 1970c; Diester-Haass 1978). Benthic foraminiferal assemblages clearly indicate that Site 545 was well above the foraminiferal CCD in the early and middle Albian (Cores 48 through 41). However, the increase in accumulation rates of benthic organisms, including benthic foraminifera, ostracods, echinoderms and sponge spicules through this interval, probably reflects increased benthic activity (respiration) and hence increased CO₂ production.

Selective dissolution may be partially responsible for the drop in planktonic diversity, particularly in Cores 44 through 41 where the average diversity drops to less than nine species (text-fig. 3). In this interval *Gubkinella graysonensis* (Epicontinental Sea Fauna) increases markedly. In Cores 42 and 41 all species of *Ticinella* (*T. roberti* s.l., *T. primula* Luterbacher, and *T. praeticinensis* Sigal) drop out of the fauna. However, the exclusion of *Ticinella* probably resulted from environmental factors other than dissolution.

If we assume that *Ticinella* spp. were the deepest-dwelling taxa of the Shallow Water Fauna during middle Albian time (text-fig. 1), perhaps their exclusion was the result of an expanded oxygen minimum zone during the most intense period of upwelling. An intensified oxygen minimum zone off central Morocco during the latest Aptian and early Albian may also have been responsible for the loss of *Planomalina cheniourensis*, the earliest keeled planktonic foraminifer (Deep Water Fauna), and a gradual disappearance of several other planktonic taxa favoring the simpler, and presumably shallower-dwelling morphotypes. The vertical expansion of an oxygen minimum zone may have peaked during the middle Albian (Cores 545-43 to 41) when all species of *Ticinella* virtually disappeared from the planktonic foraminiferal populations. Oxygen-poor water may also have impinged on the



TEXT-FIGURE 4
 Characteristics of foraminiferal assemblages at Site 547. Explanation as for text-figure 3.



TEXT-FIGURE 5
Section localities in the Vocontian Basin of southern France. 1, Caussols; 2, Les Lattes-Les Mujouls; 3, Bruis. From Eicher et al. (1978).

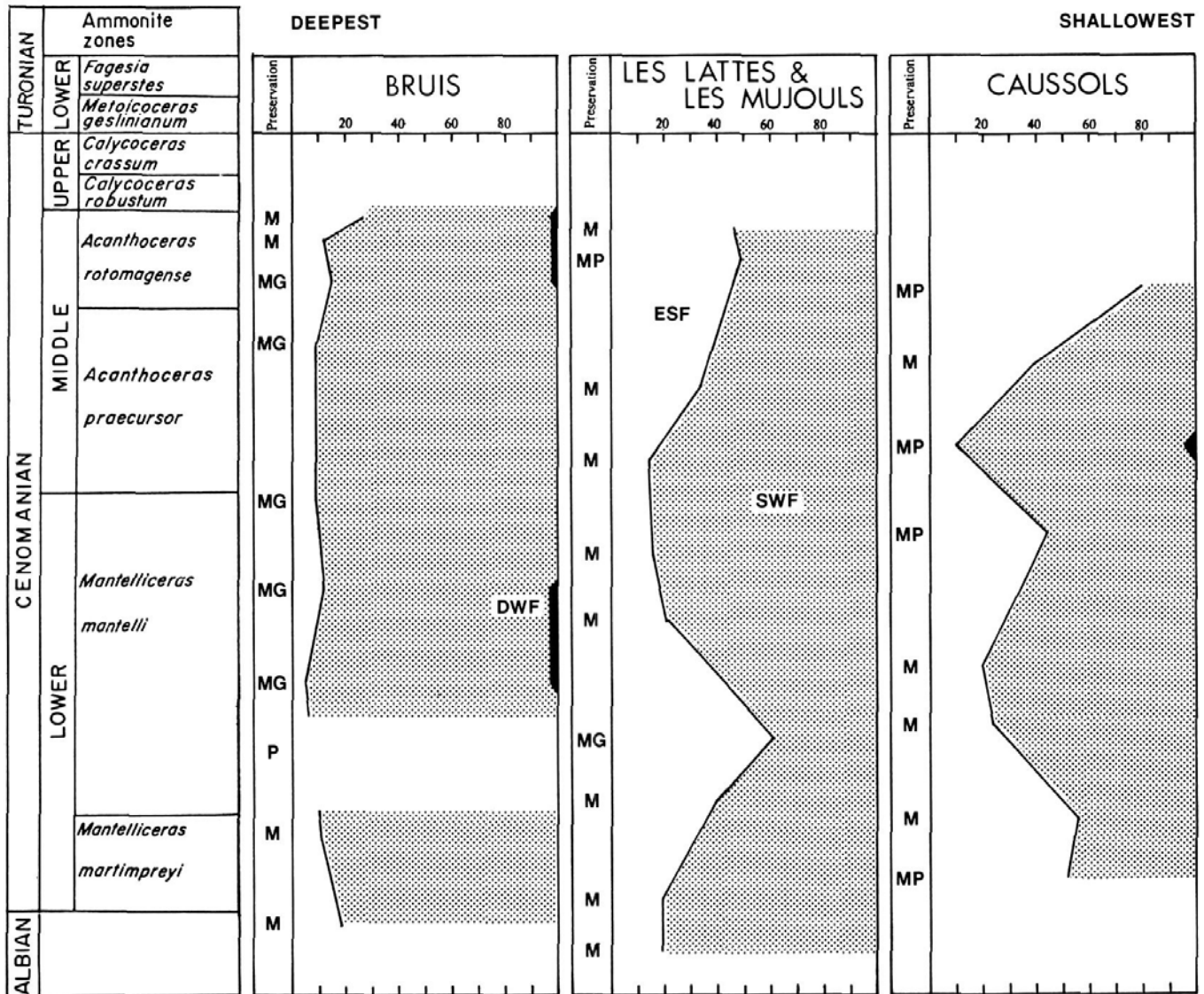
sea floor in the vicinity of Site 545 as recorded by the deposition of thin, organic carbon-rich black shales.

Perhaps the trophic structure associated with the upwelling regime was also partially responsible for the observed loss of species, including *Ticinella*. Increased nutrient supply may have favored those species that utilized resources fastest and had rapid reproductive rates (i.e. opportunistic species) (see Lipps 1979). Sediment trap data from the Panama Basin shows seasonal variation in the flux of planktonic foraminifera; smaller globigerine, predominantly spinose species dominate the foraminiferal fraction during the summer months in association with a phytoplankton bloom (Thunell et al. 1983). During middle Albian time off Morocco, the simple, globigerine morphotypes such as *Hedbergella* spp. and *Gubkinella graysonensis* increased in abundance at the expense of species of *Globigerinelloides* and *Ticinella*, perhaps in a similar scenario of enhanced fertility and productivity. Increased vertical mixing of the upper water column may also have contributed to a breakdown of the stable den-

sity stratification, particularly the thermocline, which may be necessary for the life cycles of the deeper-dwelling forms. Whatever the ultimate cause for the observed compositional changes in these planktonic assemblages, it appears to be related to upwelling off central Morocco during latest Aptian to middle Albian time. Changes in resource distribution and abundance are likely linked to the changes in proportions of the Epicontinental Sea and Shallow Water Faunas while an expanded oxygen minimum zone is likely responsible for the loss of the Deep Water Fauna.

SUMMARY

1. Methodologies utilized in studies of planktonic foraminiferal paleocology must be different from those used for standard biostratigraphic applications. Fine mesh sieves (e.g. 63 μm) retain juveniles and small species and thus better reflect the composition of the living community, although geologic samples are obviously time-averaged. In well-pre-



TEXT-FIGURE 6

Proportions of proposed planktonic foraminiferal faunal groups as recorded in sections representing a paleodepth transect across the Vocontian Basin. ESF = Epicontinental Sea Fauna; SWF = Shallow Water Fauna; DWF = Deep Water Fauna. Foraminiferal preservation: MG = moderately good; M = moderate; MP = moderately poor; P = poor. Note general similarity between the Bruis section and the upper Albian-Cenomanian of DSDP Sites 545 and 547.

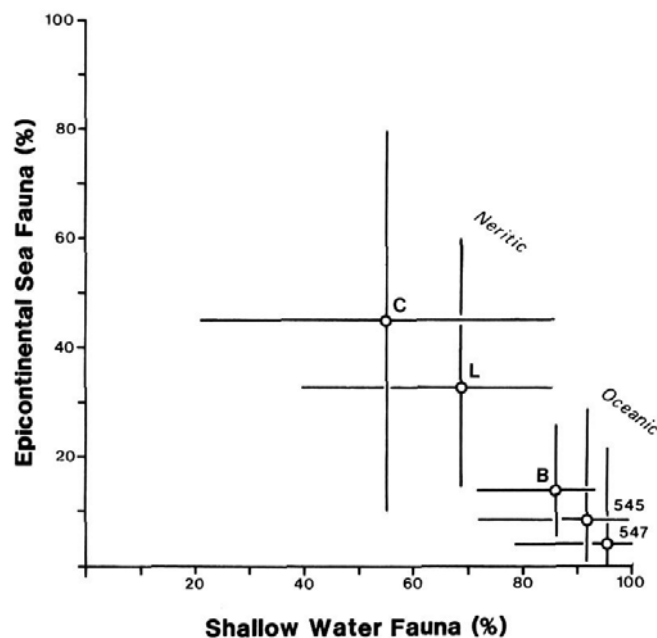
served open ocean assemblages deposited above the foraminiferal lysocline (e.g. Sites 545 and 547) the simple, inflated morphotypes greatly dominate the residue assemblages (text-figs. 3, 4). These forms presumably inhabited shallower environments, and had shorter life cycles and perhaps much greater reproductive rates than the deeper-dwelling keeled morphotypes.

2. Mid-Cretaceous open ocean sediment assemblages show remarkable consistency in gross compositional structure through long intervals of the geologic record (text-fig. 4).

3. Keeled morphotypes are generally not found in shelf environments due to bathymetric/environmental exclusion. Elements of the Epicontinental Sea Fauna (*Guembelitra*, *Heterohelix* and *Gubkinella*) increase relative to elements of

the open marine Shallow Water Fauna (mainly *Hedbergella* and *Globigerinelloides*) with decreasing water depth and distance from the shoreline (text-fig. 8). Perhaps too, the Epicontinental Sea taxa were better adapted (eurytopic) to the variable shelf environment than were the specialized Deep Water taxa.

4. Compositional variability of planktonic assemblages increases in shallower water environments due to environmental variability, differential settling velocities and lateral transport of empty tests, and other post-mortem processes including current sorting, bioturbation and dissolution (text-figs. 6, 7). Detailed sedimentologic and biotic analyses may permit differentiation of physical oceanographic effects from biologic and/or chemical effects on assemblage composition.



TEXT-FIGURE 7

Proportions of Epicontinental Sea Fauna versus open marine Shallow Water Fauna for Vocontian Basin localities and DSDP Sites 545 and 547. The five sections represent a transect from neritic to oceanic paleoenvironments during latest Albian to early late Cenomanian time. C = Caussols (shallowest of Vocontian Basin sites); L = Les Lattes-Les Mujouls; B = Bruis (deepest of the Vocontian Basin sites). Open circles represent average values; bars represent the range.

5. In areas of upwelling, greater environmental variability (instability) and greater stress favor the opportunistic species (text-figs. 3, 8). The increased proportions of Epicontinental Sea elements associated with upwelling off northwest Africa during middle Albian time further supports the hypothesis that these taxa were eurytopic.

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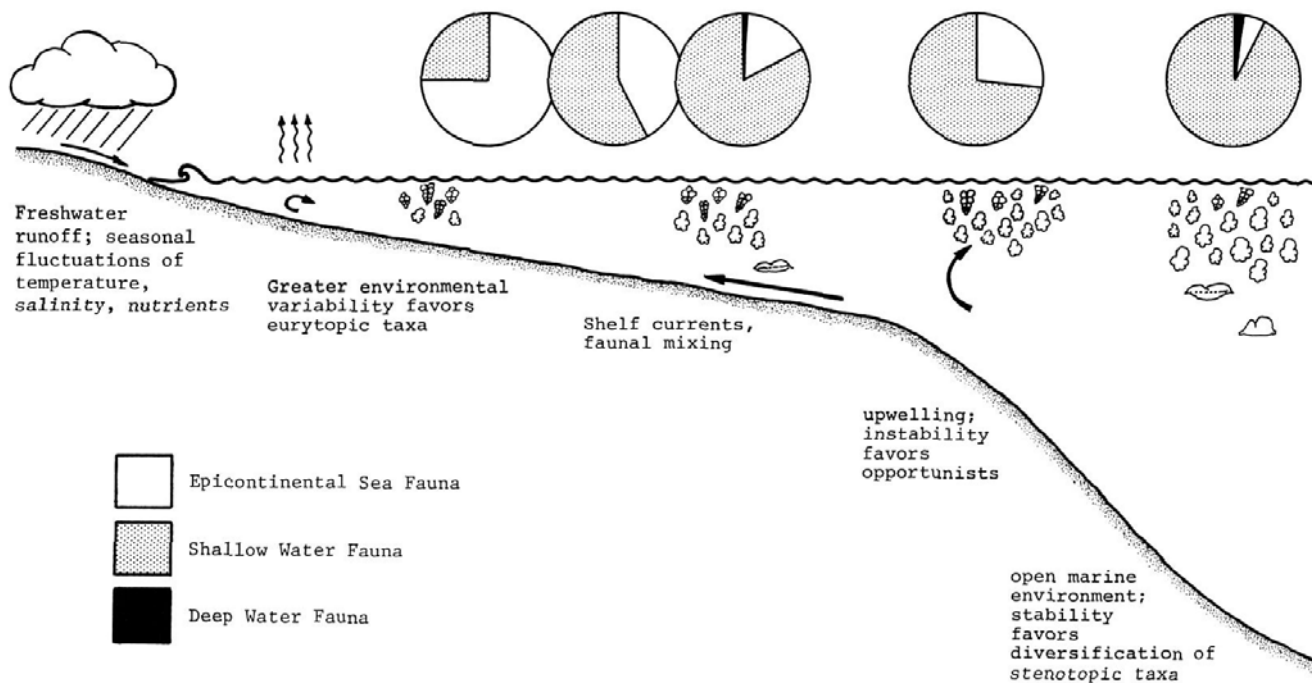
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		MARGINAL SEAS / EPICONTINENTAL SEAS		OPEN OCEAN	
				EUTROPHIC	± OLIGOTROPHIC
DIVERSITY	LATE ALBIAN - CENOMANIAN	1 - 5	5 - 15		15 - 18
	LATE ALBIAN - MIDDLE ALBIAN			6 - 10	10 - 15



TEXT-FIGURE 8

Schematic representation of some compositional variability observed in mid-Cretaceous planktonic foraminiferal assemblages from low-latitude environments. Note that these proportions are based on counts of the greater than 63- or 75- μ m size fractions. Coarser size fraction analysis might yield different results. Generalized diversity values are based on author's data. Open boxes represent environments not sampled in this study.

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