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Globorotalia crassaformis morphotype variations in Atlantic and Caribbean deep-sea cores

ABSTRACT

Temperature-dependent and temperature-independent changes in shell structure are exhibited through time by mature morphotypes of the eurythermal planktonic foraminifer *Globorotalia crassaformis* (Galloway and Wissler) found in undisturbed Quaternary sediments from the Atlantic and the Caribbean. Parallel morphological variations are observed in the cores from three ecologically distinct regions, but the degree of variation is largest in the North Atlantic core, reflecting a greater glacial/interglacial temperature range at the more northern latitude. Direction of coiling in the species is not related to temperature.

INTRODUCTION

Stratigraphic continuity with a time resolution of a few thousands of years or less is essential for accurate, detailed analysis of foraminiferal evolution on the basis of fossil remains. Uninterrupted accumulations of rich foraminiferal oozes are found occasionally on the deep-sea floor and provide excellent records for observing variations in natural parameters through time. Changes in morphology, abundance and specimen sizes of many planktonic foraminiferal monospecific populations are qualitatively correlative with major changes in oxygen isotopic temperatures during the Quaternary (Emiliani, 1969, 1971a) and thus yield potentially significant data on the variation of paleoclimatic conditions, particularly temperature, of the ancient water bodies.

One of the areas best known for stratigraphic continuity across a long time span is the central Caribbean, where pelagic ooze has been accumulating undisturbed for half a million years or more (Emiliani, 1966). Two piston cores from this basin, P6304-8 and P6304-9, have been described by Emiliani (1966) in terms of isotopic paleotemperatures and by Lidz (1966) in terms of micropaleontology. The stratigraphically longer core, P6304-9, was used, together with two others, core 234 from the equatorial Atlantic and core 280 from the North Atlantic, for analysis of temperature-dependent and temperature-independent variations among selected species of planktonic foraminifera (Emiliani, 1969) during the past 425,000 years (see table 1 for core data). These variations were compared with the oxygen isotope ratios published previously (Emiliani, 1955, 1956, 1958, 1966). A very close relationship between isotopic paleotemperatures and temperature-dependent foraminiferal parameters was found, the conditioning factor appearing to be the yearly temperature minimum of the sea water. Other ecological conditions, such as the amount of food available and the chemistry and light penetration of the water, appear to be lesser influences on the mode of morphological development (Bé, 1960).

As observed by Emiliani (1969) in the above cores, individual planktonic species have reacted differently to both genetic and environmental changes during the 425,000-year interval. The genetically most stable species appears to be *Globigerinoides conglobata*, the most unstable one *Globorotalia menardii*. Irreversible evolutionary changes in morphology are recognized (core P6304-9: variations in the test size and thickness of *G. menardii* and in the degree of thickness and granularity of its keel), as well as reversible evolutionary changes (all three cores: differences in the specimen size and in the height of the spire of *Globigerina eggeri*).

TABLE 1

Location and other pertinent data for cores P6304-9, 234 and 280. The lengths shown for cores 234 and 280 refer to the undisturbed Quaternary sections (from Emiliani, 1969, table 1). Glacial (G) and interglacial (I) stages and their ages are derived from the generalized temperature curve of Emiliani (1966).

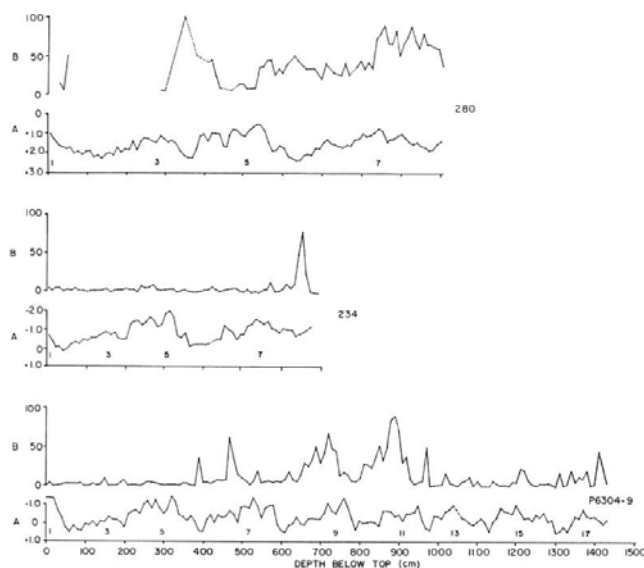
Core no.	Latitude	Longitude	Depth of water (m.)	Length of core (cm.)	Oldest stage	Earliest age B.P.
P6304-9	14°57'N	68°55'W	4126	1429.0	17 (I)	425,000
234	5°45'N	21°43'W	3577	673.5	8 (G)	175,000
280	34°57'N	44°16'W	4256	1002.5	8 (G)	175,000

Environmentally induced morphological variations appear mainly to be of a reversible nature (core 280: changes in the wall color, size and shape of *Globigerinoides rubra* and in the specimen size of the *G. triloba*-*G. sacculifera* group). Differences in surface polish (wall texture) and test size of *Pulleniatina obliquiloculata* in core P6304-9 are also influenced by the living conditions. Population abundance is a temperature-dependent parameter common to all of these species.

PREVIOUS WORK ON *GLOBOROTALIA CRASSAFORMIS*

Among the species not included in the analysis by Emiliani is *Globorotalia crassaformis*, a relatively large planktonic foraminifer common in the cores. This species was described and illustrated by Galloway and Wissler (1927) from the Pleistocene Lomita Marl of California. Previously, d'Orbigny (1826) had listed a form he named *Globigerina punctulata* (*nomen nudum*) from the beach sands of Rimini, Italy, and Deshayes (1832) had described the species, attributing the authorship to d'Orbigny but changing the name inadvertently to *Globigerina punctulata*. *Globorotalia crassaformis*, *Globigerina punctulata* and *G. punctulata* have often been considered synonymous in the past. The taxonomic problem was clarified in 1960, when Banner and Blow designated as lectotype for *Globigerina punctulata* Deshayes (and also for *G. punctulata* d'Orbigny) one of d'Orbigny's original specimens. According to Banner and Blow, "*Globigerina punctulata* Deshayes 1832 appears to be consubgeneric with *Globorotalia* (*Turborotalia*) *centralis* Cushman and Bermúdez and, therefore, should be referred to as *Globorotalia* (*Turborotalia*) *punctulata* (Deshayes)." The specimens examined in the present study are morphologically different from d'Orbigny's specimen, as described and illustrated by Banner and Blow (1960, pp. 15-17, pl. 5, fig. 7), and are assigned to the species *Globorotalia crassaformis* (Galloway and Wissler).

Three distinct morphotypes are recognised on the basis of criteria established by Blow (1969): *Globorotalia* (*Turborotalia*) *crassaformis crassaformis* (Galloway and Wissler), *G. (T.) crassaformis oceanica* Cushman and Bermúdez, and *G. (T.) crassaformis ronda* Blow. All have been studied in detail by the present author in



TEXT-FIGURE 1

Cores P6304-9, 234 and 280; curves A, $\delta^{18}\text{O}$ (‰), with respect to the Chicago standard PDB-1, of the pelagic foraminiferal species *Globigerinoides sacculifera*; curves B, percentage of right-coiled specimens of *Globorotalia crassaformis*. Odd numbers identify interglacial stages, even numbers glacial stages. Core numbers to the right.

cores 280 (North Atlantic), 234 (equatorial Atlantic), and P6304-9 (Caribbean), and are found to occur throughout these cores with intermittent absences, apparently the result of unfavorable environmental conditions. Coiling direction is not influenced by temperature and appears to be neither consistent nor interregionally correlative among the cores discussed (text-figure 1). Morphological changes occur rapidly at the subspecific level, the most variable character being the sharpness of the periphery. Forms with a subacute to rounded periphery and lobate shoulders are the most common. In some of the larger, mature specimens of *G. crassaformis crassaformis* there is a trace of an apparently imperforate rim on the later chambers (Cifelli and Smith, 1970). The shape of the chambers also differs, some specimens possessing the typical angular peripheral outline, others having a nearly circular peripheral outline. As noted by Blow (1969) and observed by the writer, the wall structure ranges from finely spinose and relatively thin to a finely pustulate system, the elements of which appear to fuse in *G. crassaformis ronda* into a thickened granular or sub-spinose outer layer over some of the earlier chambers. All of these characters, together with the depth of the intercameral sutures, the degree of ventral vaulting, and the shape, size and depth of the umbilicus, constitute the major criteria for division of the species into its several subspecies.

TABLE 2

Present-day yearly temperature and salinity minima and maxima of the surface water at the locations of cores P6304-9, 234 and 280 (from Emiliani, 1969, table 3).

Core no.	Temperature (°C.)		Salinity (‰)	
	Min.	Max.	Min.	Max.
P6304-9	26.1	27.8	35.5	35.8
234	24.4	29.4	35.0	35.5
280	15.6	28.3	36.5	36.6

It is the writer's opinion that *G. crassaformis ronda* may represent only an early ontogenetic stage throughout the *crassaformis* lineage. As an individual subspecies, it may exemplify the premature developmental stage through which the larger, more advanced specimens of *G. crassaformis crassaformis* and *G. crassaformis oceanica* have already passed. This is suggested by its prevalent concurrence with, and consistently smaller size than, the two latter subspecies in the cores examined. Blow's nomenclature is adhered to, however, because *G. crassaformis ronda* appears to be at least a well-defined ecological morphotype, predominant at the lower isotopic temperatures.

Globorotalia crassaformis is one of several living planktonic foraminiferal species reported by Jones (1966, 1967, 1968) and noted by Bé (1959) as biologic indicators of discrete water masses in the dynamic oceanographic system. In Jones's samples from the Caribbean (location of core P6304-9) and equatorial Atlantic (location of core 234) the species is always present but is generally not very abundant. The maximum share of the total foraminiferal population is 16% for November-December in the southeastern Caribbean and 15% for April-May below the Equatorial Atlantic Undercurrent. Distributions observed by Jones in extant populations show the greatest concentrations of the species in the western Caribbean at depths from 50 to 100 m., where temperature ranges from 26° to 23°C. (Fuglister, 1960), and in the equatorial Atlantic at depths of 150 to 200 m. with temperatures between 13° and 15°C. Investigations of areal distributions in the western North Atlantic by Bé (1959, location of core 280) indicate greatest absolute abundance (25-50 specimens/1000 m³ of water filtered) of the foraminifer in the Gulf Stream system (0-300 m., 25°-12°C.) and greatest relative abundance (more than 2%) south of the Gulf Stream system in the Sargasso Sea (0-300 m., 24°-18°C.). Results from oxygen isotope analysis of Pleistocene specimens from the central Caribbean core P6304-8 (Lidz *et al.*, 1968) indicate that this species thrives best in a mean warm water temperature of

14.6°C. at an estimated 265 m. in depth. These figures, probably reflecting the isotopic ratios at which the greatest mass of shell material was deposited (Berger, 1969; Emiliani, 1971b), coincide with those of most of the present-day occurrences mentioned. Jones (1967) has found that the greatest regional values for standing crops of *G. crassaformis* in the Equatorial Atlantic Undercurrent concur roughly with the measured oxygen minima in the area, displaying a possible correlation with dissolved oxygen variation. According to Emiliani (1971b), however, the ultimate factor controlling the observed depth stratification of many planktonic foraminifera may be the pattern of light penetration through the sea water. This is thought to regulate the vertical distribution of the primary producers that are used specifically by the foraminifera as food sources.

The optimum environmental temperature for *G. crassaformis* determines the apparent gradational morphogenetic development of the interrelated subspecies *G. crassaformis crassaformis* and *G. crassaformis conomiozea* (Blow, 1970). According to Blow, the gene complex of the basic *crassaformis* morphotype carries the latent ability to produce a tropical, fully carinate form when local water temperatures rise above the *crassaformis* optimum. Through foraminiferal zones N18 to N23, alternations of *crassaformis* and *conomiozea* indicate oscillations of temperature. This heterochronous transition from one morphotype to the other was observed by Kennett (1966), who found keeled *conomiozea* grading into non-keeled *crassaformis* at the Kapitean (uppermost Miocene)-Opoitian (lower Pliocene) boundary in New Zealand. On the basis of this transition and isotopic analysis, Kennett interpreted a decrease in temperature across the boundary (cf. Margolis and Kennett, 1970). However, Jenkins (1967) interpreted the temperature as increasing at that time in New Zealand on the basis of a shift in coiling direction in *Globigerina pachyderma*. The reason for this discrepancy is not known.

Bé (1960) has observed that population abundance of *G. crassaformis*, as is true of all zooplankton, seems to be regulated by seasonal cycles in the chemistry of the water. Major causes of population variation are changes in temperature, salinity, degree of light penetration, and plant nutrient content. Data from his North Atlantic investigations show that the species is present throughout the year, with greatest numbers occurring generally during the summer and fall months. At this period the temperature is high, although salinity and the concentrations of nutrients and phytoplankton are low. This suggests greater dependence of the species on temperature than on other environmental parameters.

In cores 280, 234 and P6304-9, *G. crassaformis* populations exhibit both temperature-dependent and temperature-independent variations in morphology, abundance and test size. The writer, following the method of Emiliani (1969), studied the 24 largest tests separated at 10-cm. intervals from the sediment fraction greater than 0.5 mm. Frequency observations refer to the separated assemblages, not to those in the original whole sample, and are not necessarily reflected in the number of specimens photographed (plates 1-7). Isotopic paleotemperature curves of the cores accompany the plates. Coiling ratios (text-figure 1) were obtained from counts, where possible, of 100 individuals.

CORE 280

Core 280 (length of the upper, undisturbed Quaternary section, 1002.5 cm.; see Emiliani, 1958) was recovered from the North Atlantic. It is composed of sedimentary stages thicker than those of the two tropical cores (text-figure 1), resulting from a higher rate of deposition in the northern latitudes (average sedimentation rate of 5.7 cm./1000 years versus 3.5-3.8 cm./1000 years in the Caribbean and equatorial Atlantic; cf. Emiliani, 1955, 1958, 1966). Stages 1 through 8 encompass 1000 cm. of sediment in this core, whereas comparable stages occupy only 700 cm. in cores 234 and P6304-9. Apparently because of the low seasonal temperature minimum in the North Atlantic (table 2) and the presumed low glacial minima of the Pleistocene, *Globorotalia crassaformis* is generally less abundant in the deposits of this region than in those of warmer areas. The direction of coiling changes from 50-90% of right-coiled tests in the bottom 170 cm. of the core to 50% or higher of left-coiled specimens throughout the upper 832.5 cm. (text-figure 1). A single shift to 100% dextral occurs at 347.0 cm. from the top.

According to the generalized temperature curve for the past 425,000 years (Emiliani, 1966, text-fig. 6), the oldest stage in core 280 is glacial stage 8, dating from about 175,000 years ago. Abundant, large, compact (*i.e.*, with closely appressed chambers), subquadrate, *crassaformis-oceanica* morphotypes occur at the bottom of the core (280: 1002.5 cm.), just before the temperature minimum for this stage. Most of these individuals have high ventral vaults (conical angles), with four complete chambers enclosing a deep, open umbilicus. The periphery is subacute to acute, and in some cases the final chamber is flared. At the temperature minimum of glacial stage 8 (core 280: 972.5 cm.), all three subspecies of the *crassaformis* group occur, and there is a general reduction in test size and number of the group. The small, rounded *ronda* form becomes

more abundant with decreasing temperature. Large, mature, four-chambered, distinctly angulate tests appear at the temperature maximum of interglacial stage 7 (core 280: 842.5 cm.) and are found for the next 50 cm. upward in the core. The presence of a slight imperforate rim is suggested on the later chambers of some specimens. One individual shows four and a half to five chambers in the final whorl. Several are compressed laterally and are less conical than either their predecessors or the highly vaulted forms coexisting with them. These "flattened" tests possess more widely flared chambers and are not so compact as the conical ones. Approaching glacial stage 6, a decrease in population and test size occurs. Rounding of the periphery is gradual, until the diminutive, quasicircular *ronda* form becomes dominant at the temperature minimum, approximately 110,000 years B.P. (core 280: 632.5 cm.) These tightly coiled, rather nondescript tests prevail throughout stage 6, with a temporary absence of mature morphotypes at 612.5 cm. (*i.e.*, abundance in the original sample is insufficient to allow separation of any large specimens). Interglacial stage 5 is marked by abundant distinct *crassaformis-oceanica* tests, mature and moderate in size. Larger specimens occur near the temperature maximum for the core, dating from about 96,500 years ago (core 280: 552.5 cm.). These are compressed, widely flared and angulate, with obvious rims on later chambers; one individual has four and a half to five chambers. No large specimens were found at 448.5 cm. A sudden reduction in test size and abundance characterizes glacial stage 4 (core 280: 378.5 cm.), with additional temporary absences at 387.0 cm. and 368.0 cm. Medium-sized specimens of the three subspecies, a few compressed and flared, coexist during stage 3 (core 280: 287.0 cm.), but the majority fail to attain very large size, in accordance with the moderate temperature of this stage. Several individuals with four and a half to five chambers occur. Temperatures during glacial stage 2 were apparently particularly low (see Emiliani, 1958, text-fig. 1), as large tests are extremely scarce or absent throughout this interval. Only a few diminutive specimens of the three morphotypes occur intermittently (core 280: 167.0 cm.). Holocene interglacial stage 1 is marked by a rapid increase in size of *crassaformis-oceanica* tests and in angularity, number, and maturity of specimens, with more four and a half- to five-chambered tests present here than anywhere else in the core (core 280: 37.0 cm.). Large, highly evolved, acute-edged *crassaformis-oceanica* morphotypes coexist with a few smaller, less angulate forms near the top of the piston core. Size decreases slightly, abundance tapers to rare at the very top, and the uppermost 4.5 cm. of pilot core 280A contains only a single specimen (pilot core 280A: 4.5 cm.).

The *Globorotalia crassaformis* complex in North Atlantic core 280 demonstrates apparent reversible temperature-dependent and temperature-independent variations in foraminiferal parameters. There seems to be a direct relationship between temperature and population abundance, and between test size and the acquisition of an imperforate rim on final chambers. Peak concentrations are found at isotopic temperature highs, and temporary absences of large specimens are observed commonly at the lows. Characteristic angulate, compressed tests of the *crassaformis* and *oceanica* morphotypes are dominant during interglacial stages in the core, with the largest, partially carinate specimens occurring at the temperature maxima of interglacial stages 1, 5 and 7. The smaller, more circular *ronda* morphotype prevails during glacial stages 2, 4 and 6. Environmentally induced changes in the subspecies appear to be stronger in core 280 than in the two other cores, probably as an effect of more extreme ecological variations. Other faunal characteristics do not seem to be influenced so directly by changes in temperature, but, because they are interrelated parameters, they respond accordingly to the temperature-dependent changes in shell morphology. Among these are degree of ventral conical vault, sharpness of periphery and angularity of outline, openness and depth of the umbilicus, and number of chambers in the final whorl. There is no correlation between coiling direction and paleotemperatures. Although all of the large tests with four and a half to five chambers belong to the *crassaformis-oceanica* morphotypes, and most are found during interglacial stages, some are also smaller in size and occur at lower isotopic temperatures. An anomaly is observed at the very top of the core in interglacial stage 1, the Holocene, where many larger tests are expected, but only extremely scarce specimens of moderate size are found. There does not seem to be any ready explanation for this phenomenon.

CORE 234

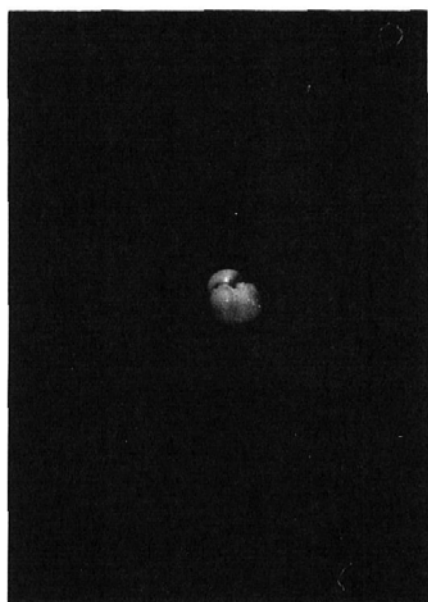
Variations in morphology of the *Globorotalia crassaformis* complex are clearly less extreme in equatorial Atlantic core 234 (length of the undisturbed Quaternary section, 673.5 cm.; Emiliani, 1955) than in core 280. Not only is the modern yearly temperature minimum much higher (table 2), but the inferred glacial/interglacial temperature range of the surface water in the area was probably narrower. Immediately evident in core 234 is the apparent stability of population abundance and direction of coiling (text-figure 1) throughout the core. No temporary absences of the species occur. Specimens are predominantly (87–100%) sinistrally coiled, except for a single major shift to 79% dextral at 653.5 cm. Typical *crassaformis-oceanica* morphotypes of moderate size, partially carinate and possessing four and five chambers in the final whorl, a deep, open umbilicus set in the center of a relatively high ventral vault, a subacute to acute periphery angulate in outline, and deeply incised sutures, are common from the bottom of the core to the top. In no case are these morphotypes fully replaced by the less prevalent, cooler-water *ronda* form.

As in core 280, the oldest stage in core 234 is glacial stage 8 (175,000 years B.P.). Specimens are numerous, uniformly moderate in size, and consist mostly of mature tests of the *ronda* type (core 234: 673.5 cm.) before the temperature minimum. A temporary decline in population occurs at the minimum. Proceeding upward into interglacial stage 7, one observes a diminishing of test size with accompanying increase in angulate forms (core 234: 583.5 cm.) prior to reaching the interglacial maximum. This maximum is dominated by large *crassaformis-oceanica* tests, 40 to 50 per cent of which possess an acute periphery and a complete fifth chamber, distinctly rimmed (core 234: 543.5 cm.). The minor temperature minimum at 512.5–482.5 cm. is reflected by another decrease in abundance and test size, with

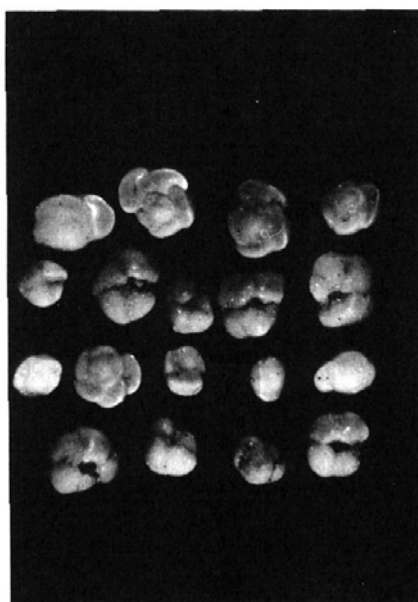
PLATE 1

Globorotalia crassaformis (Galloway and Wissler)

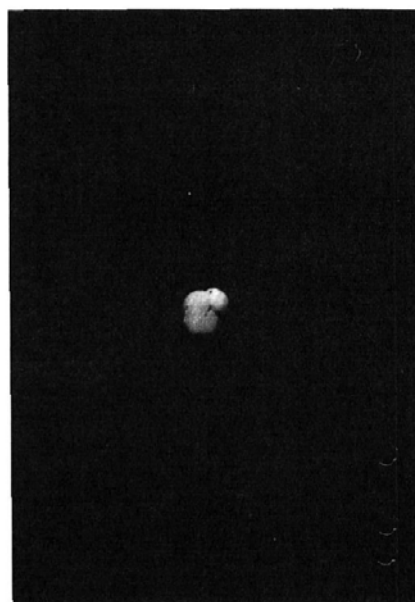
×13. Photographs correspond with the points indicated on the isotopic paleotemperature curve of core 280 (from Emiliani, 1958, text-fig. 2).



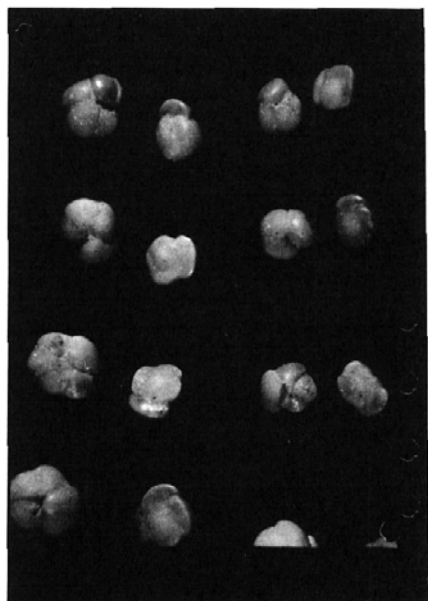
A. 280A: 4.5



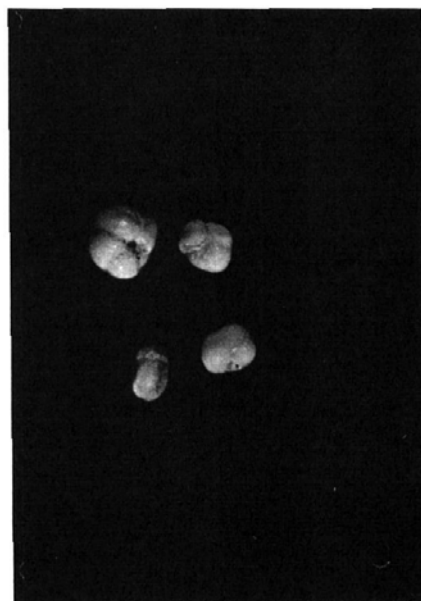
B. 280: 37.0



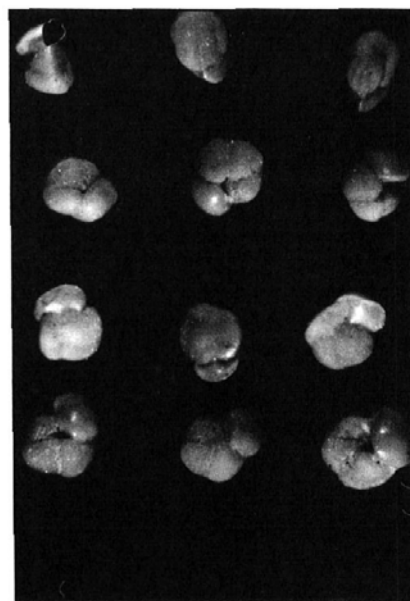
C. 280: 167.0



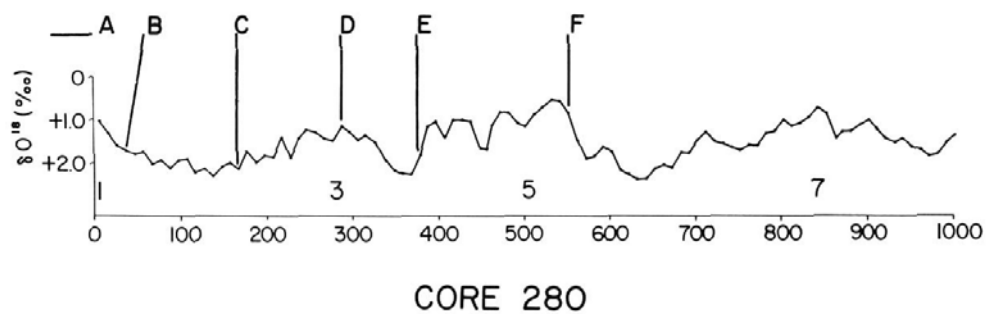
D. 280: 287.0



E. 280: 378.5



F. 280: 552.5



four-chambered, round specimens again constituting the major portion of the populations (core 234: 482.5 cm.). The following minor maximum further demonstrates the influence of even slight temperature changes on foraminiferal structure, as larger, more angulate individuals with rimmed tests and four and a half to five chambers in the outer whorl are once more dominant (core 234: 462.5 cm.). Glacial stage 6 consists mostly of smaller specimens (core 234: 432.5 cm.), roughly circular in peripheral outline, although a few larger angulate forms are also present. Tests increase gradually in size and complexity, until an apparent climax in development of the species is attained during interglacial stage 5 (core 234: 322.5 cm.). As previously noted, the temperature maximum for this stage dates from about 96,500 years ago. Fifty per cent of the specimens are highly evolved, partially carinate, mature individuals with five complete chambers in the final whorl and rather sinuous, deeply incised, ventral interchamberal sutures. The umbilici are open and deep, set in the middle of moderately high ventral vaults. The peripheries range from subacute to acute, and chambers are flared, creating angulate outlines for the tests. Above this level in the core, the average temperature drops slowly for the next 270 cm., until the minimum for the core is attained (core 234: 43.5 cm.) during glacial stage 2, approximately 20,000 years B.P. During this period of progressive cooling, specimens change gradually from the advanced *crassaformis-oceanica* morphotypes to the diminutive, simpler *ronda* type present in glacial stage 4 (core 234: 194.5 cm.), then back to the larger, more complex, and rimmed *crassaformis-oceanica* tests prevalent in stage 3 (core 234: 153.5 cm.). Test size decreases slightly at the temperature minimum (core 234: 43.5 cm.), although the *crassaformis-oceanica* morphotypes remain dominant. Species population, as a whole, seems unaffected by the change in temperature, yet abundance at the subspecific level appears to be responsive. Typical *crassaformis-oceanica* tests once more increase in both number

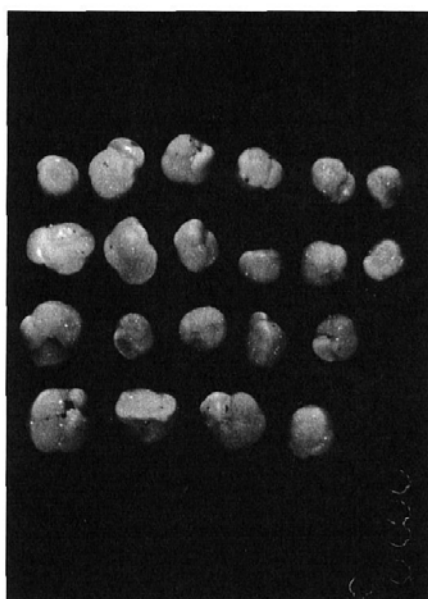
and size, concomitant with a rise in temperature at the beginning of interglacial stage 1, the Holocene. Maximum development occurs in the youngest sample from pilot core 234A, which is only a few thousand years old. Specimens from this sample are large, with the four to four and a half chambers, angulate, subacute peripheries, and distinct rims typical of the *crassaformis-oceanica* subspecies (pilot core 234A: 4.5 cm.).

Probably because core 234 is from the equatorial Atlantic and, therefore, represents a warmer, less variable environment than core 280, reversible temperature-dependent and temperature-independent variations in foraminiferal parameters, and amplitude in the observed variations, are present to a much lesser degree than in the northern core. In most cases, specimens in the original core samples are sufficiently plentiful to allow separation of the 24 largest individuals necessary for analysis, thereby giving the impression that population abundance of the taxon seems unaffected by temperature variations. Abundance of the individual subspecies seems, however, to be temperature-induced, with the *crassaformis-oceanica* morphotypes flourishing in warmer waters and being nearly replaced by the *ronda* type in cooler environments. Other temperature-dependent characters, namely, size of the test, acuteness and angularity of the periphery, and acquisition of an imperforate rim on the final chambers, attain peak development during temperature maxima. Within intervals of minimum temperatures, the opposite situation prevails; specimens are smallest and, in most cases, have a subacute to fully rounded periphery with lobate shoulders. Interrelated parameters, apparently varying more as a consequence of the major temperature-dependent foraminiferal changes than as a direct response to temperature, are variations in umbilical shape, size and depth, depth of incised sutures, number of chambers, degree of ventral conical vault, and degree of flatness or inflation of the dorsal sides of the chambers. Coiling direction is not influenced by temperature. These results are consistent with those observed in core 280.

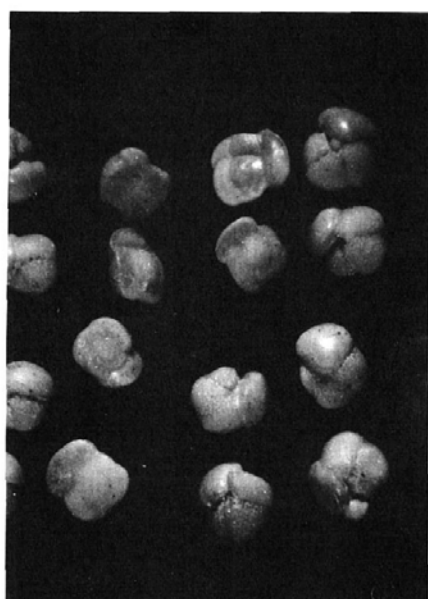
PLATE 2

Globorotalia crassaformis (Galloway and Wissler)

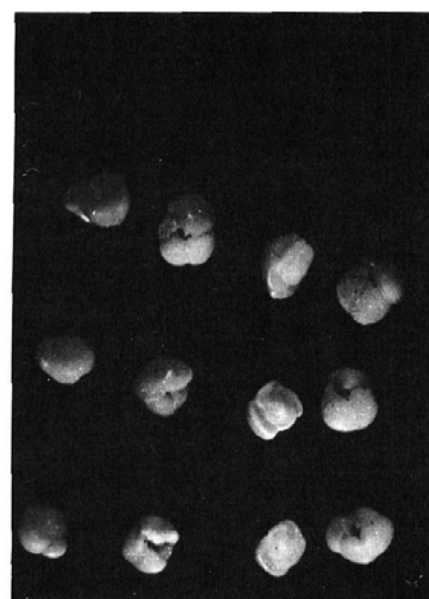
×13. Photographs correspond with the points indicated on appropriate sections of the isotopic paleotemperature curves of cores 280 and 234 (from Emiliani, 1958, text-fig. 2).



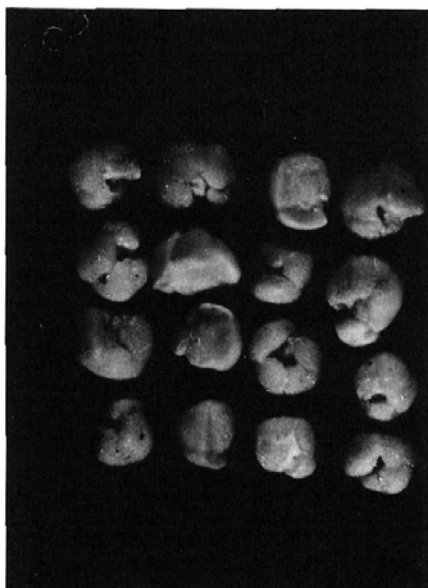
A. 280:632.5



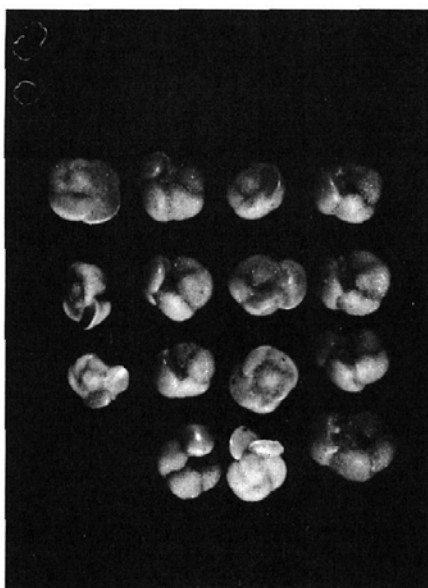
B. 280:842.5



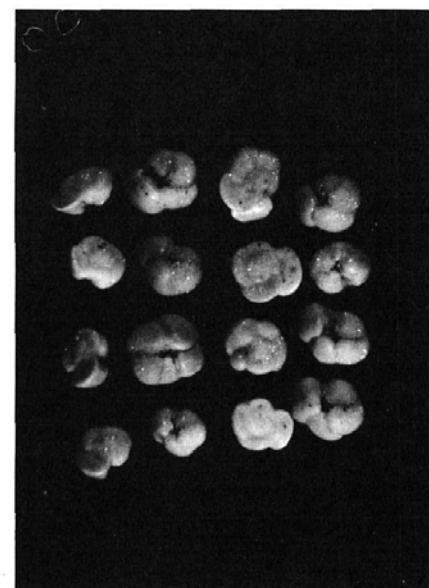
C. 280:972.5



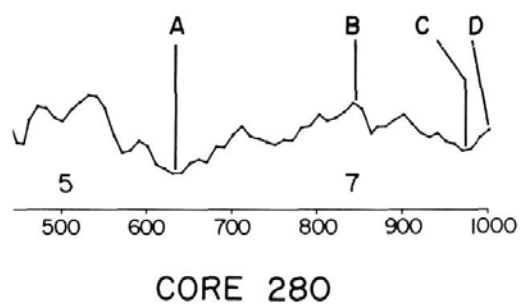
D. 280:1002.5



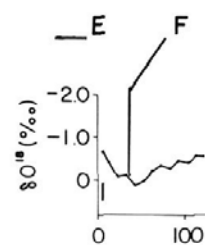
E. 234A:4.5



F. 234:43.5



CORE 280



CORE 234

CORE P6304-9

Central Caribbean piston core P6304-9 (length 1429 cm., Emiliani, 1966) represents the longest stratigraphic section of the Quaternary examined in the present study. Its oldest stage is interglacial stage 17, dating from 425,000 years ago. The highest isotopic temperature for the core, as for the two other cores, occurred during interglacial stage 5, about 96,500 years ago.

Globorotalia crassaformis from core P6304-9 exhibits morphological variations still less intense than those in core 234 and much less intense than those in North Atlantic core 280. Direction of coiling is more than 80% sinistral throughout the core, except for two major shifts to 70% and 90% dextral in interglacial stages 9 and 11, respectively (text-figure 1). A moderately large test size is generally maintained in the core, with *crassaformis-oceanica* morphotypes dominating most samples. More laterally compressed individuals and more specimens with four and a half to five chambers (and a few with six) occur in this core than in the others. Temperature and population abundance appear to be directly related, as the greatest numbers of mature tests occur at temperature highs. The *G. crassaformis* assemblages from this core reveal, however, innumerable minor oscillations in morphology within the larger trends of evolutionary development. These oscillations seem to be independent of temperature, as is the case also for coiling directions (see Emiliani, 1966, text-fig. 5; this paper, text-figure 1). A possible explanation may be that the presumed glacial minima are even higher than in core 234 and well above the minimum of the present temperature range of the species, thereby allowing it to develop minor temperature-independent subspecific structural variations within the same sample without deviating radically from the norm.

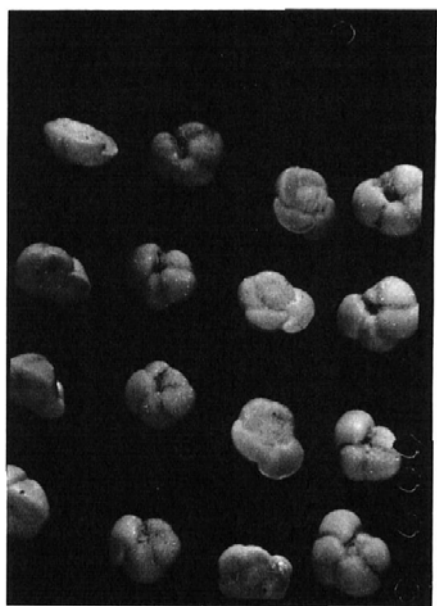
The bottom of the core, which is a cool episode within interglacial stage 17, or possibly the end of glacial

stage 18, is characterized by moderately large specimens typical of the compact *ronda* morphotype (P6304-9: 1420 cm.), which grade with increasing temperature into abundant, angulate *crassaformis-oceanica* forms having subacute to acute peripheries at the temperature maximum of stage 17 (core P6304-9: 1370 cm.). Some of the specimens develop final flared chambers, an occasional one being translucent and thin in appearance (characters not readily distinguishable in the photographs), whereas the walls of earlier chambers of the same tests remain opaque and seem to be thicker. Little difference in size is noted in specimens from glacial stage 16, although the dominant morphotype has become the *ronda* form (core P6304-9: 1300 cm.). These tests are not translucent, and their numbers are reduced. A transition to distinctly larger flared tests, with strongly acute edges, commonly rimmed final chambers, and deep, wide umbilical areas, occurs during interglacial stage 15 (core P6304-9: 1230 cm.). A few chambers appear translucent at the temperature highs of this stage. A sharp drop in temperature leads into the next glacial period and is reflected by a correspondingly rapid decrease in size, peripheral acuteness, and number of specimens (core P6304-9: 1140 cm.). Tests are predominantly subquadrate and darker in color, and appear to have a thickened wall. Large tests are lacking during the temperature low at 1130 cm. Interglacial stage 13 contains abundant moderately large specimens of all three morphotypes with a variety of umbilical characters. Coiling is tight except for the last chamber. Tests typical of the flared, rimmed *crassaformis* morphotypes are dominant toward the end of the stage (core P6304-9: 1010 cm.). None appears to be translucent. Mature specimens of classical *crassaformis-oceanica* forms are abundant at the very end of stage 13 (about 280,000 years ago) and are the largest in the core (P6304-9: 990 cm.). The tests are highly evolved, with four, five

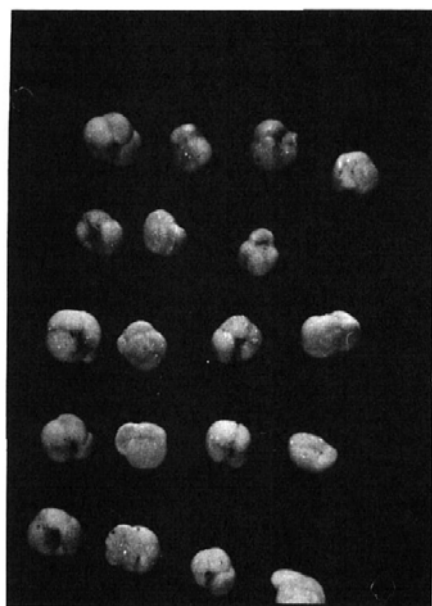
PLATE 3

Globorotalia crassaformis (Galloway and Wissler)

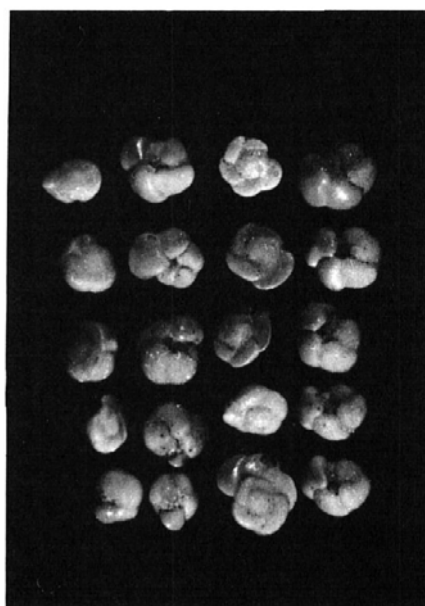
×13. Photographs correspond with the points indicated on the isotopic paleotemperature curve of core 234 (from Emiliani, 1958, text-fig. 2).



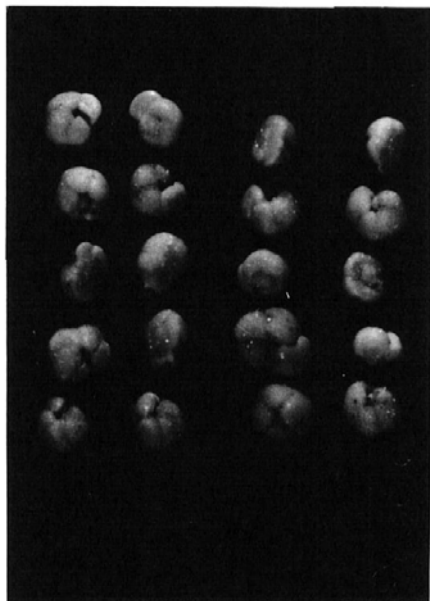
A. 234:153.5



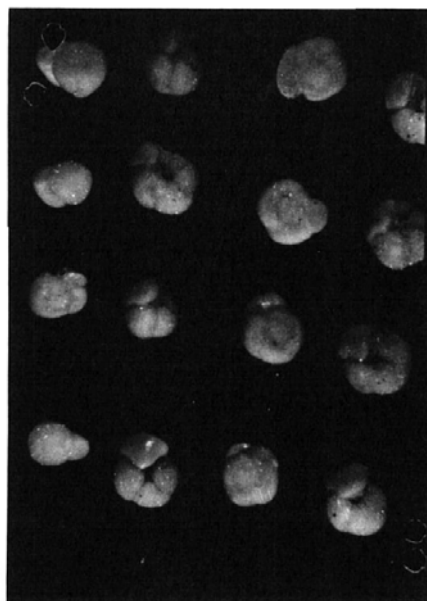
B. 234:194.5



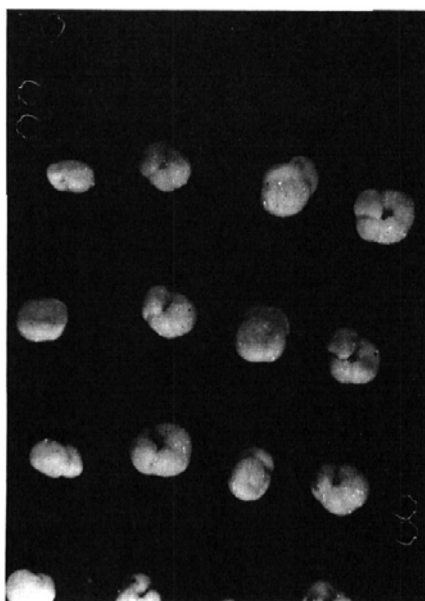
C. 234:322.5



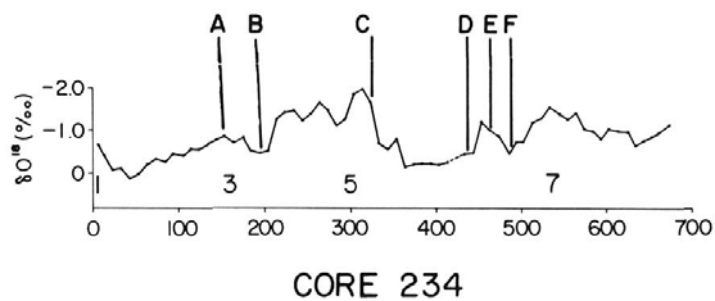
D. 234:432.5



E. 234:462.5



F. 234:482.5



and six flared chambers in the outer whorl, subacute peripheries, and distinct imperforate rims. Ten centimeters above, at the temperature minimum of glacial stage 12, there are no large specimens.

A considerable rise in temperature occurs at the beginning of interglacial stage 11, and the assemblage is dominated by abundant medium-sized tests, highly flared and multichambered (core P6304-9: 950 cm.). These typical, well-developed *crassaformis-oceanica* forms, occasionally rimmed, are gradually replaced by smaller *ronda* forms at a minor interglacial minimum, where abundance also diminishes (core P6304-9: 890 cm.). Throughout glacial stage 10, these *ronda* forms are plentiful (core P6304-9: 800 cm.) with a brief decrease in number at 820 cm., which is not the low for the stage. A sharp rise in temperature leads into the next interglacial period (stage 9). Mixed morphotypes, compact and moderate in size, are abundant (core P6304-9: 750 cm.). An occasional final chamber is lobate and flared. On approaching glacial stage 8, small, nearly spherical *ronda* forms with closed umbilici (core P6304-9: 650 cm.) again compose most of the specimens, evolving near the temperature minimum into mixed morphotypes with lobate peripheral shoulders and some angularity (core P6304-9: 600 cm.).

Several morphological trends are noted from the bottom to the top of interglacial stage 7. The variety of characters seen in the lobate tests with relatively open umbilici, found in glacial stage 8, progresses through similar four- and five-chambered forms at the temperature maximum of interglacial stage 7 (core P6304-9: 530 cm.) and grades into more tightly coiled specimens with narrow umbilici at an intermediate temperature. This trend culminates in compact, mostly *ronda* morphotypes of moderate size at the temperature minimum of glacial stage 6 (core P6304-9: 400 cm.).

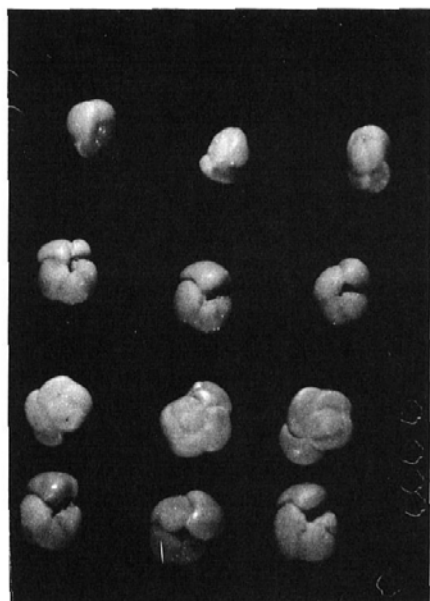
Specimen color changes from dark beige to nearly white. Imperforate rims on final chambers are absent and apparently last seen in interglacial stage 7. During these evolutionary developments, entire tests commonly become translucent, the umbilicus changes from open to closed, lobate shoulders become less distinct and more uniformly round, sutures become less depressed, granularity of the test wall increases, and test shape evolves from dorsally flat and ventrally conical to almost globose. Size remains relatively unaffected by changes in temperature through these intervals. The number of chambers in the final whorl decreases from occasionally more than four in glacial stage 8 to only four in glacial stage 6. All these changes contribute to make the populations of glacial stage 6 (core P6304-9: 400 cm.) quite different in structure from those in glacial stage 8 (core P6304-9: 600 cm.), although the assemblages occurred at the same low isotopic temperatures.

An immediate change is noted in specimens 20 cm. above the temperature minimum of glacial stage 6. Moderate in size, mostly compact and subquadrate, four-chambered *crassaformis-oceanica* tests with subacute to round periphery, nearly concave dorsal sides of the chambers, deep and open umbilicus, depressed sutures, and a high conical angle close glacial stage 6 (core P6304-9: 380 cm.) and prevail during interglacial stage 5 (core P6304-9: 320 cm.). Above 260 cm., the wall again becomes translucent, a feature that is maintained from this point to the top of the core. The *crassaformis-oceanica* morphotypes are abundant at the beginning of glacial stage 4, but the specimens are flared, with relatively closed umbilici. Many are compressed laterally, and all appear compressed at the temperature minimum of the stage (core P6304-9: 200 cm.). Specimens in stage 3 remain "flattened" but are considerably larger and widely flared, with a more open umbilical area (core P6304-9: 140 cm.). Final

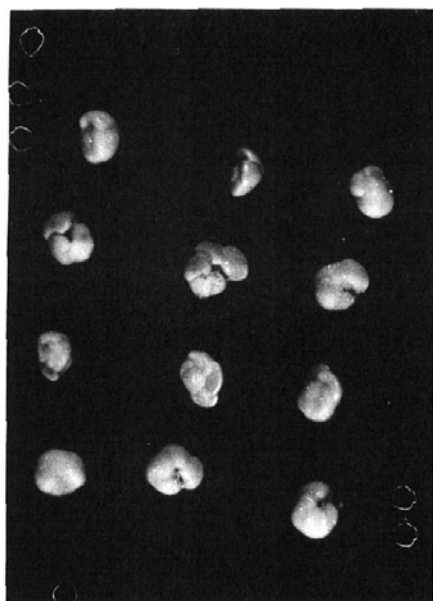
PLATE 4

Globorotalia crassaformis (Galloway and Wissler)

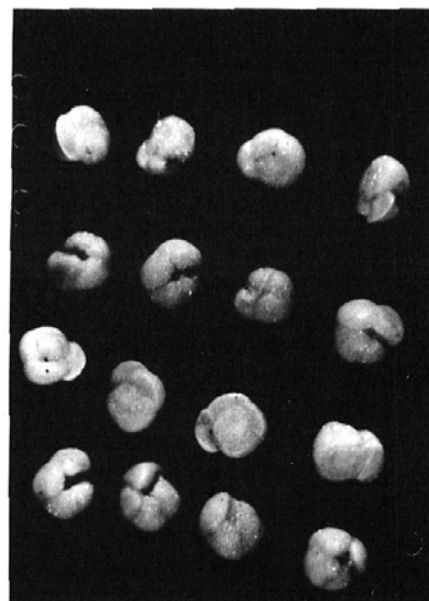
×13. Photographs correspond with the points indicated on appropriate sections of the isotopic paleotemperature curves of cores 234 and P6304-9 (from Emiliani, 1958, text-fig. 2, and Emiliani, 1966, text-fig. 4, respectively).



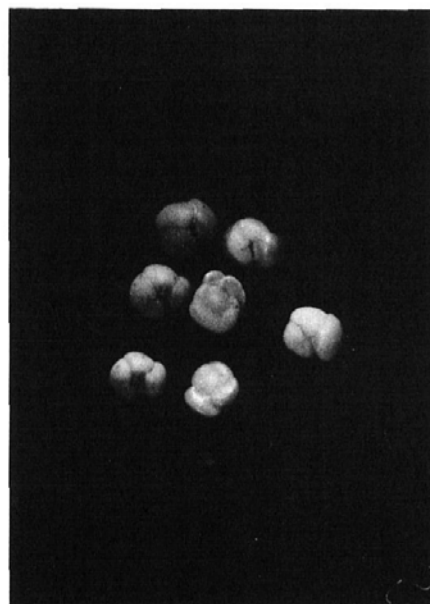
A. 234:543.5



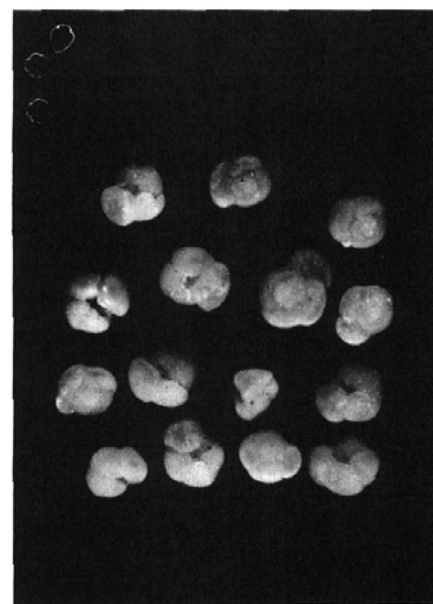
B. 234:583.5



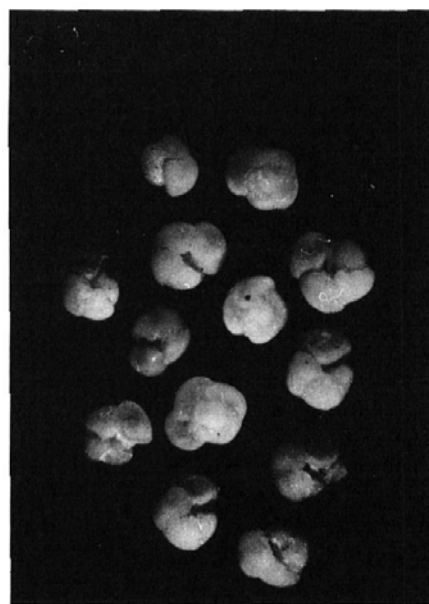
C. 234:673.5



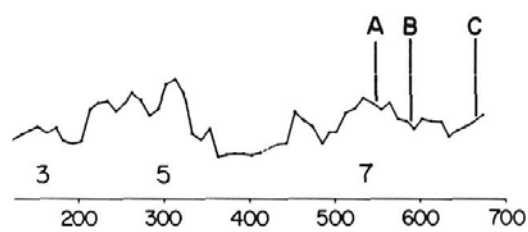
D. P6304-9:0



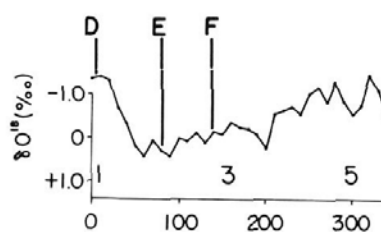
E. P6304-9:80



F. P6304-9:140



CORE 234



CORE P6304-9

chambers are enlarged, and tests are clearly angular in peripheral outline, with an occasional acute edge. Characteristics prevalent during stage 3 generally persist through the last glacial age (core P6304-9: 80 cm.) up to the beginning of interglacial stage 1, the Holocene, although there is a progressive decrease in size. Specimens at the top of the core are mixed morphotypes, smaller and reduced in number as in core 280. Tests are compact, less flared, with subacute to round periphery, high ventral vault, and mostly closed umbilicus (core P6304-9: 0 cm.). Only some appear to be translucent.

Reversible temperature-induced variations in the morphology of *Globorotalia crassaformis* assemblages are generally observed in core P6304-9, as in the two other cores. However, an obvious difference in the degree of change exists among the three cores. On the one hand, North Atlantic core 280 includes presumably the lowest glacial temperature minima, which appear to be outside, or almost outside, the present temperature range of the species, thus providing the harsh marine environment responsible for the rather extreme changes observed in the diversification of foraminiferal structure. On the other hand, the temperature minima postulated for equatorial Atlantic core 234 are well within the lower boundary of the present temperature range of the species, resulting in subspecific variations which are distinct, but to a much lesser extent. Finally, central Caribbean core P6304-9 shows what are probably the highest glacial temperature minima, to which *G. crassaformis* populations have responded with morphological changes, not only indicating the least degree of temperature change, but also demonstrating a great variety of minor modifications within the more significant trends.

The most clearly temperature-dependent parameters exhibited by the species are test size, population abundance, and presence or absence of an imperforate rim. As observed in cores 280 and 234, the largest, most

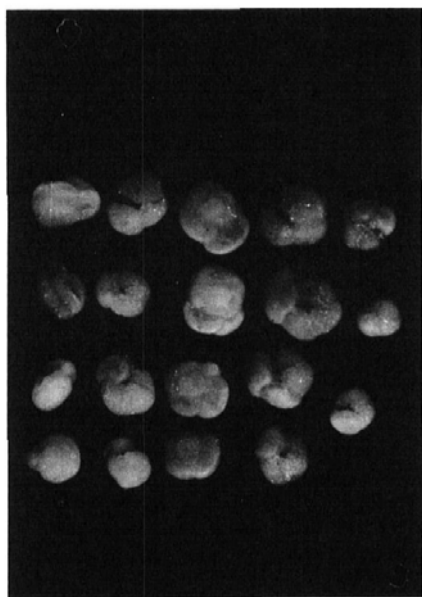
mature, and most highly evolved tests occur during the intervals of highest temperature. Since the glacial temperature minima in core P6304-9 fall well within the present temperature range of *G. crassaformis*, there is little deviation at the temperature minima from the moderately large specimen size which generally prevails throughout the core. Abundance is also relatively stable, although with an occasional reduction in number at the glacial temperature minima. In two cases large specimens are absent. Mature *crassaformis* morphotypes tend to become partially carinate during the interglacial temperature maxima from the bottom of the core upward to approximately 450 cm. from the top. Similarly, the *crassaformis-oceanica* forms tend to develop one or more whiter, thinner-walled and more translucent final chambers during the interglacial maxima at the bottom of the core. This tendency increases to include entire and more numerous specimens in the three uppermost stages. The absence of rims on tests in the uppermost 450 cm. of the core indicates a temperature-independent evolutionary trend.

The remaining foraminiferal parameters discussed previously in this study (conical angle or ventral convexity, umbilical area, depth of sutures, lateral compression, angularity and peripheral acuteness or roundness, flare of the chambers, tightness of coiling and coiling direction) seem also to be temperature-independent in core P6304-9. Diversification tendencies in most of these characters are interrelated. Small, compact *ronda* specimens tend, in most cases, to have tighter coiling and a rounded outline, ventrally convex chambers, clearly visible but non-depressed sutures, and a narrow, partially closed umbilicus. The reverse is usually true for the larger *crassaformis-oceanica* tests, which are more advanced in evolutionary development, may or may not be laterally compressed, and commonly, but not exclusively, possess acute, angulate peripheries. Specimens of the three subspecies from all three cores

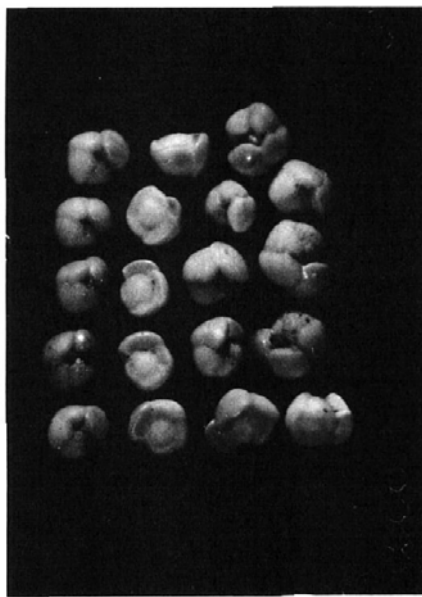
PLATE 5

Globorotalia crassaformis (Galloway and Wissler)

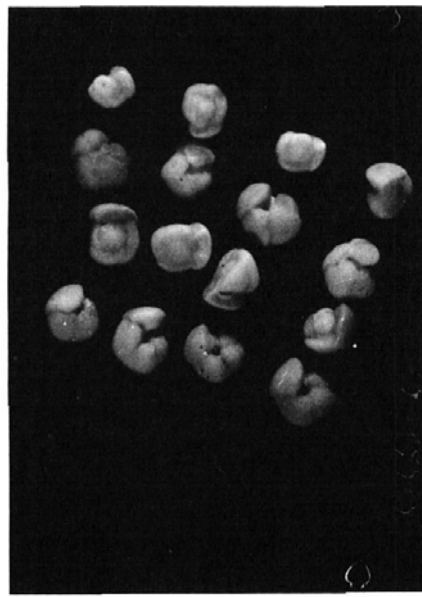
×13. Photographs correspond with the points indicated on the isotopic paleotemperature curve of core P6304-9 (from Emiliani, 1966, text-fig. 4).



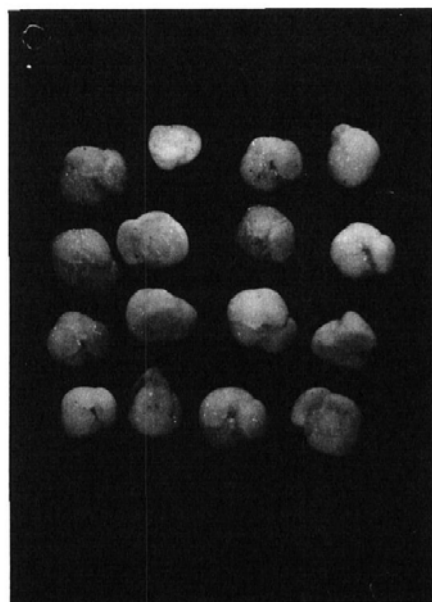
A. P6304-9:200



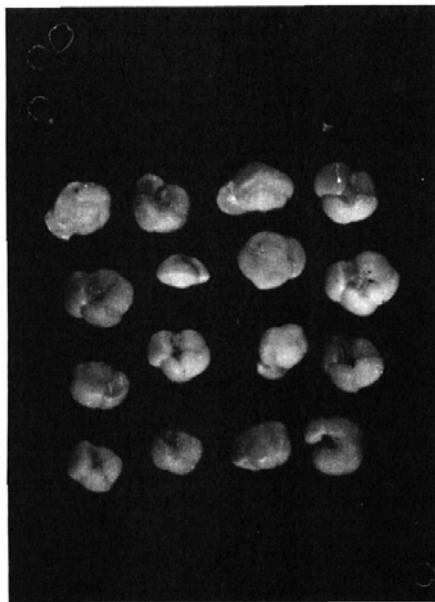
B. P6304-9:320



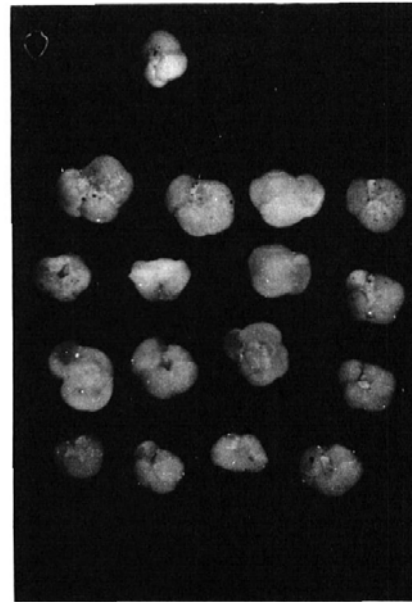
C. P6304-9:380



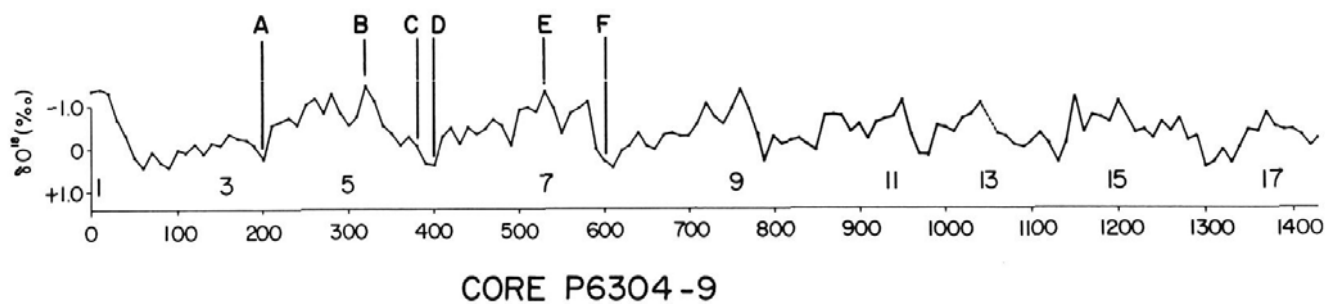
D. P6304-9:400



E. P6304-9:530



F. P6304-9:600



demonstrate the varying interrelationship of these parameters.

CONCLUSIONS

The pelagic foraminifer *Globorotalia crassaformis* (Galloway and Wissler) is present throughout undisturbed Quaternary sedimentary sections, ranging in age from the present to 425,000 years ago, from North Atlantic, equatorial Atlantic and Caribbean deep-sea cores. Mature morphotypes of the subspecies *G. crassaformis crassaformis* and *G. crassaformis oceanica* are predominant during high paleotemperature (interglacial) stages, while those of the subspecies *G. crassaformis ronda* predominate in colder (glacial) stages. The glacial temperature minima apparently are the conditioning factor responsible for environmentally induced variations in shell morphology. Population abundance, test size, and development of thin-walled, translucent chambers and partially carinate tests are characters directly related to temperature. The largest, most complex specimens occur during the temperature maxima in the equatorial Atlantic core, whereas the smallest, simplest individuals are found during the glacial temperature minima in the North Atlantic core. Largely temperature-independent morphological parameters, which are interrelated with those obviously influenced by temperature, include conical angle (ventral convexity) of the test, size, shape and depth of the umbilical area, depth of sutures, tightness of coiling, peripheral angularity and acuteness, flare of the chambers, and degree of lateral compression. Coiling direction in the species does not correlate with temperature oscillations, as is the case of most lower latitude planktonic foraminiferal taxa. This is contrary to the pattern of *Globorotalia truncatulinoides* and *Globigerina pachyderma* in the higher latitudes (Ericson, Wollin and Wollin, 1955; Ericson, 1959). Preferred sinistral coiling is indicated for *Globorotalia crassaformis* assemblages in Quaternary sediments from the Atlantic and Caribbean, regardless of latitude. No attempt was made in this study to

analyze coiling direction in this species in relation to paleoecological parameters other than temperature. As expected, all temperature-induced effects in *G. crassaformis* are strongest in the North Atlantic core and weakest in the Caribbean core, owing to the differences in amplitude between glacial and interglacial temperatures in the respective regions. These observations agree with those made by Emiliani (1969) in similar studies of other species of pelagic foraminifera from the same cores. It is obvious from the above that accurate information on at least some aspects of the oceanic paleo-environment and its evolution can be obtained by detailed morphological analysis of monospecific samples of planktonic foraminifera.

ACKNOWLEDGMENTS

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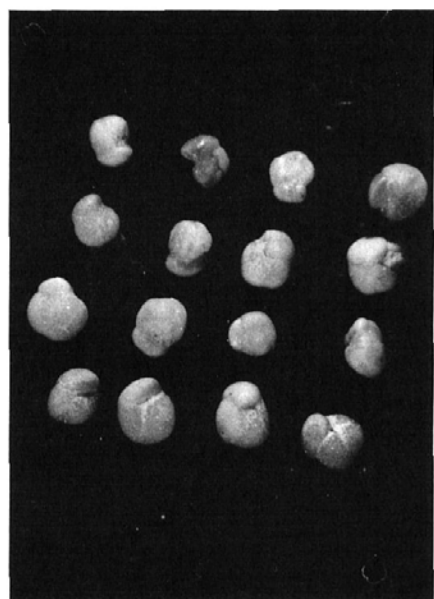
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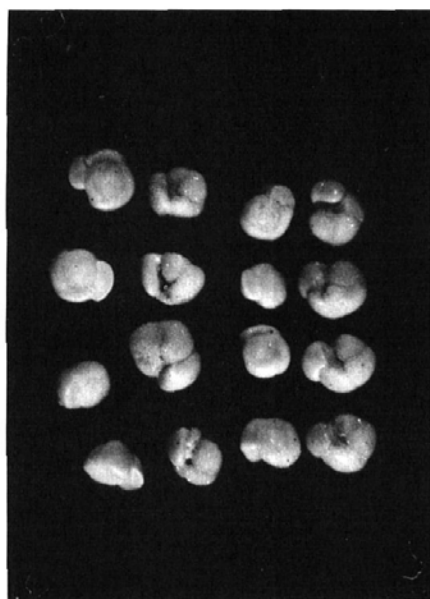
PLATE 6

Globorotalia crassaformis (Galloway and Wissler)

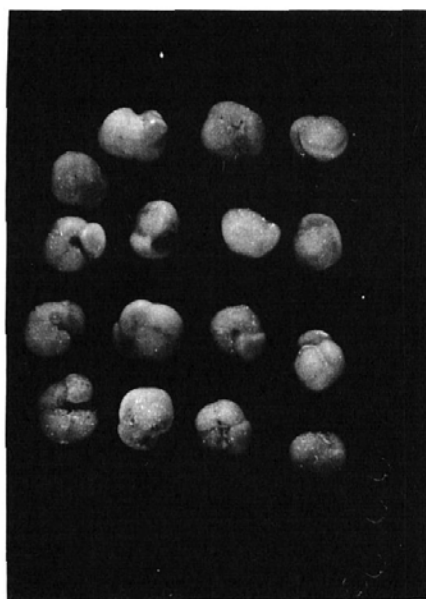
×13. Photographs correspond with the points indicated on the isotopic paleotemperature curve of core P6304-9 (from Emiliani, 1966, text-fig. 4).



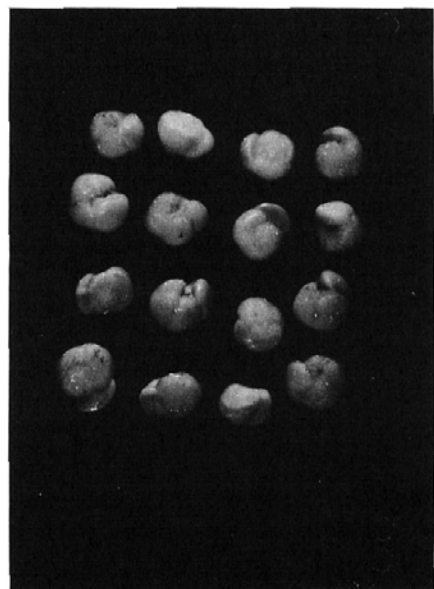
A. P6304-9:650



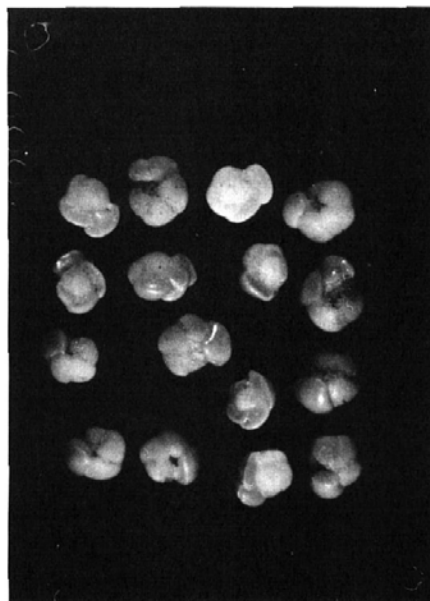
B. P6304-9:750



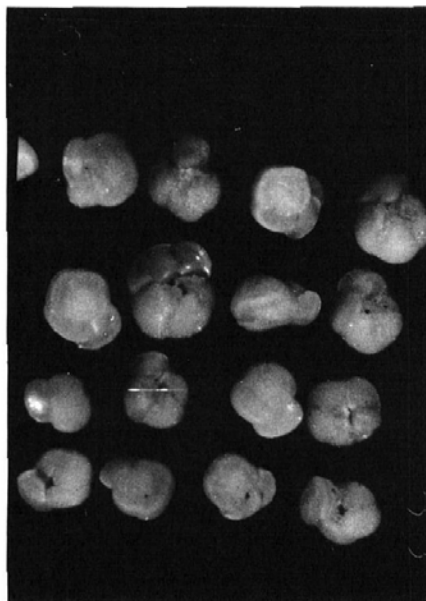
C. P6304-9:800



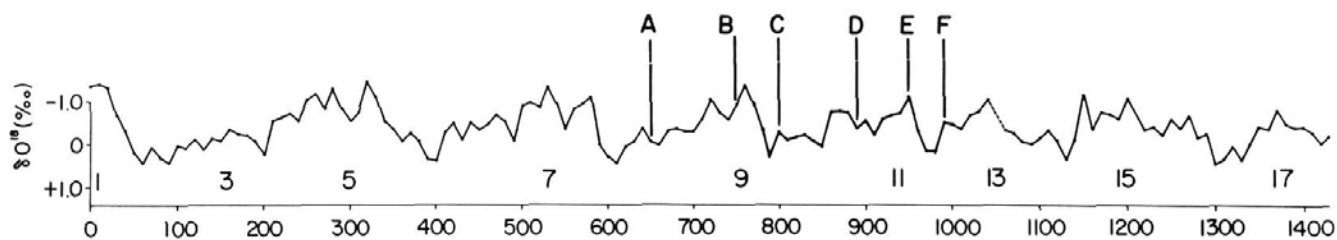
D. P6304-9:890



E. P6304-9:950



F. P6304-9:990



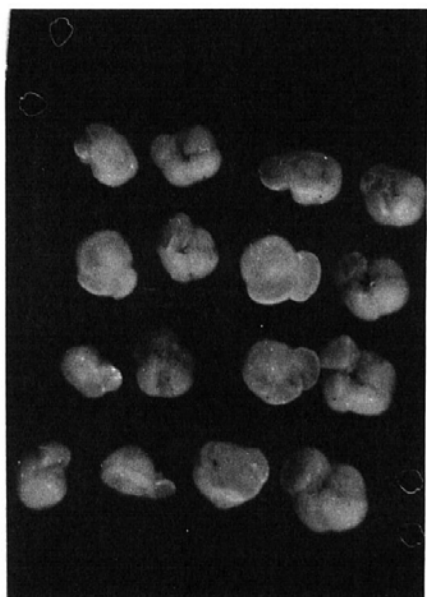
CORE P6304-9

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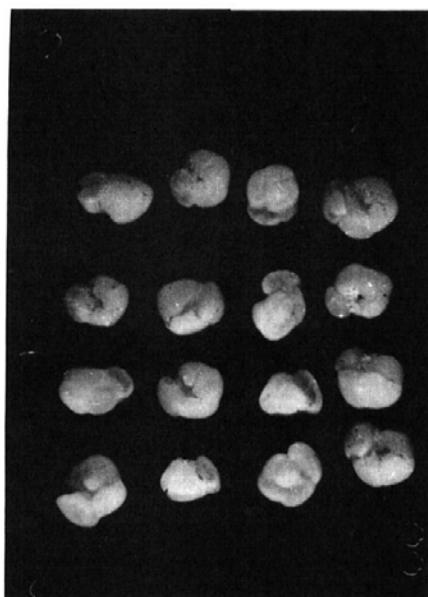
PLATE 7

Globorotalia crassaformis (Galloway and Wissler)

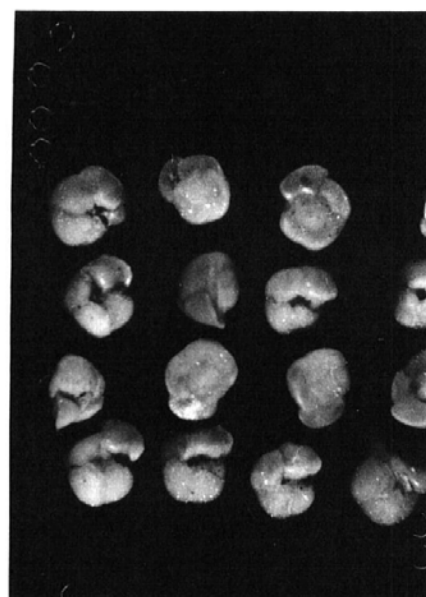
×13. Photographs correspond with the points indicated on the isotopic paleotemperature curve of core P6304–9 (from Emiliani, 1966, text-fig. 4).



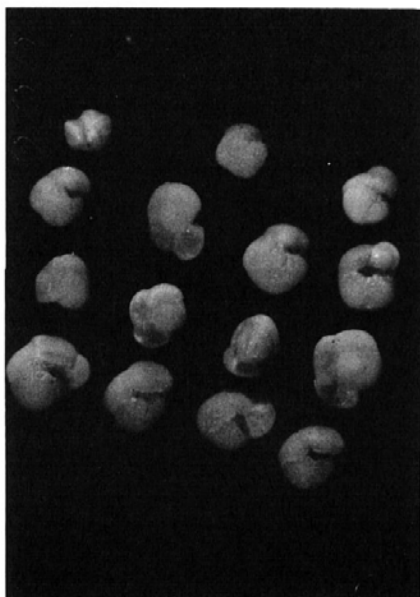
A. P6304-9:1010



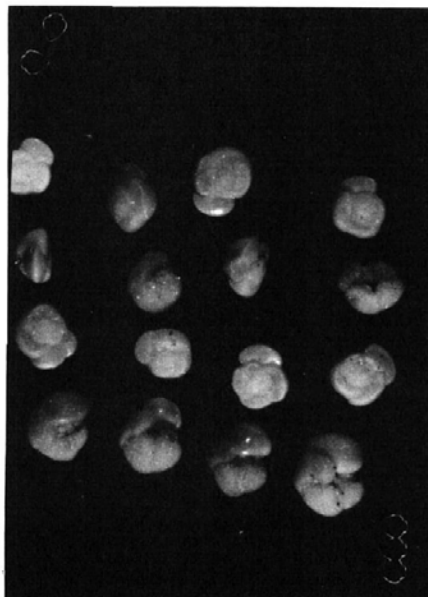
B. P6304-9:1140



C. P6304-9:1230



D. P6304-9:1300



E. P6304-9:1370



F. P6304-9:1420

