in solution can be large. Interaction of silica-rich brines with flood runoff may cause relatively sudden supersaturation with respect to amorphous silica, and thereby lead to inorganic precipitation of chert. If there is rapid mixing of runoff with brine, much silica may remain in the diluted waters. If a stratified lake forms, however, biogenic CO_2 may be retained in the hypolimnion and reduce the *p*H of the bottom brines; in this manner the bulk of the dissolved silica can be precipitated. Figure 1 shows that a drop in *p*H from 11.0 to 8.5 can cause precipitation of as much as 3000 ppm SiO_2, which corresponds to a 1.5-mm-thick layer of chert for each meter of depth of brine. Silica layers that were probably formed by this mechanism have been found in the High Magadi beds, of Pleistocene age, and within the Alkali Valley playa deposits (*17*).

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Coccoliths as Paleoclimatic Indicators of Pleistocene Glaciation

Abstract. *Selected species of Coccolithophoridae from recent sediments and mid-Wisconsin glacial sediments of the North Atlantic were examined in an attempt to determine cooling effects. All species showed a definite shift southward during the glacial period. The average shift in this planktonic population was 15 degrees of latitude, with the greatest change in the eastern Atlantic. A paleoisotherm map can be drawn on the basis of the temperature boundaries of coccolithophorids. The species boundaries indicate a possible shift in position of the subtropical gyral to a glacial position roughly parallel to the 33-degree line of latitude.*

The dramatic fluctuations in Pleistocene climate are recorded in sediments in the Atlantic Ocean (*1*), but unfortunately the means of procuring these data are poorly developed. The only direct technique available at the present time is the use of oxygen isotopes (*2*). This report deals with a new approach —plotting the migration of biogeographic boundaries for temperature-restricted species of Coccolithophoridae due to Pleistocene glaciation.

Among all the microorganisms that leave fossil records in oceanic sediments, the Coccolithophoridae probably have the greatest potential as paleoclimatic indicators. In addition to their wide geographic distribution and stable mineral skeleton (calcite), these marine algae inhabit the upper euphotic zone (*3–5*) and consequently are under direct climatic control. In living species it is possible to correlate biogeographic boundaries with surface water isotherms (*4*), and this is the basis of my report.

The method of attack, being biogeographic, requires the widest possible geographical distribution of core material. This is not easily obtained, for, although the North Atlantic has been the site of intensive sampling, there remain large gaps in the core distribution. A limiting factor is that large areas of the North Atlantic basin are below the carbonate compensation level, with a consequent lack of coccolith flora. Thus the 23 cores sampled (Table 1) are restricted to three linear belts. Two cover the shelf, slope, and rise of both North America and Europe-Africa; the third, the Mid-Atlantic Ridge.

Choice of the particular species to be examined requires that two separate cri-

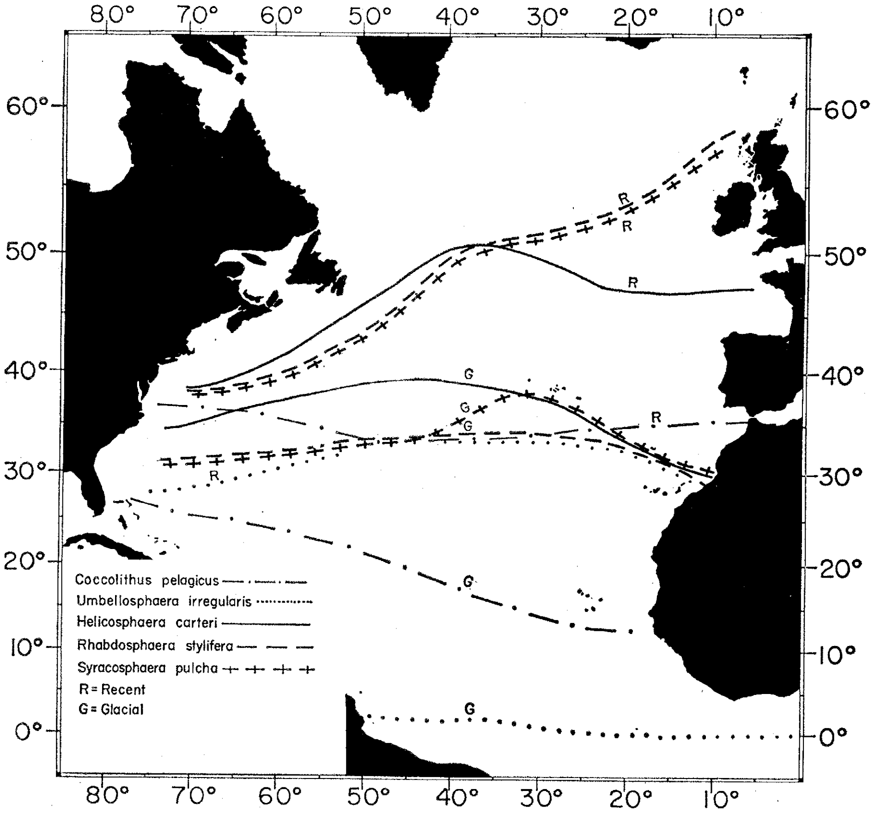

Fig. 1. Species population boundaries for Recent and mid-Wisconsin time.

teria be met. They must have relatively limited temperature ranges and a good paleontologic record. This is made difficult by the differential preservation of coccolith structural types. Some of the best temperature indicators are found among the delicate caneoliths where fossil recording is minimal.

Eight species, *Coccolithus pelagicus, Cyclococcolithus leptoporus, Helicosphaera carteri, Rhabdosphaera stylifera, Syracosphaera pulchra, Umbellosphaera irregularis, Umbellosphaera tenuis,* and *Umbilicosphaera mirabilis,* were selected on the basis of preservation and temperature range and their present distribution in the North Atlantic, compared with that of the mid-Wisconsin (last glacial period). Counts and identification of species were done with the electron microscope.

Synchronous samples from a finite time in the Wisconsin glaciation can be obtained by C^{14} dates or, where these are inadequate, by use of sedimentation rates established by radioactive dating. The rates for each core, expressed in centimeters per 1000 years, can be multiplied by a unit time in years (24 = 24,000 years of the glacial period) that would represent the mid-Wisconsin. This gives a depth in centimeters for each core from which synchronous samples are taken. While this technique is regularly used in geological oceanography, it is open to criticism since one must often assume that the sedimentation rate established for the upper portion of the glacial section in each core remains constant for the entire section. It is necessary to bear the limitations in mind since there is as yet no other means of obtaining the samples needed. The midglacial position of these samples was verified by planktonic foraminiferal stratigraphy.

The data (Table 2) from eight species, when plotted on distributional maps (Figs. 1 and 2), indicate a marked change in biogeographic distribution between recent and glacial sediments. The ranges of each species are delineated in Figs. 1 and 2 by two lines marking the boundaries of the recent and glacial populations. These lines are drawn on the extreme northern or southern appearances for warm and cold species, respectively.

Coccolithus pelagicus, the only species limited to cold water presently recognized in the North Atlantic (*4*), is restricted to subarctic and transitional waters. Its maximum southern limit coincides with the 14°C isotherm. At present this species extends to 35°N

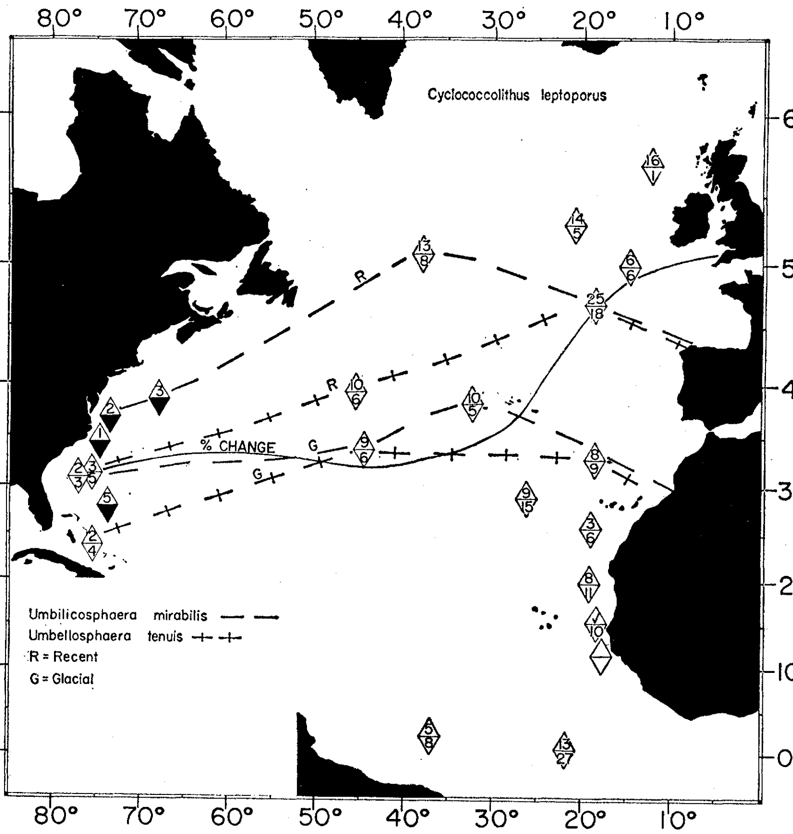

Fig. 2. Species population boundaries for Recent and mid-Wisconsin time and percent values for *Cyclococcolithus leptoporus* in diamonds with the upper recent and the lower glacial values.

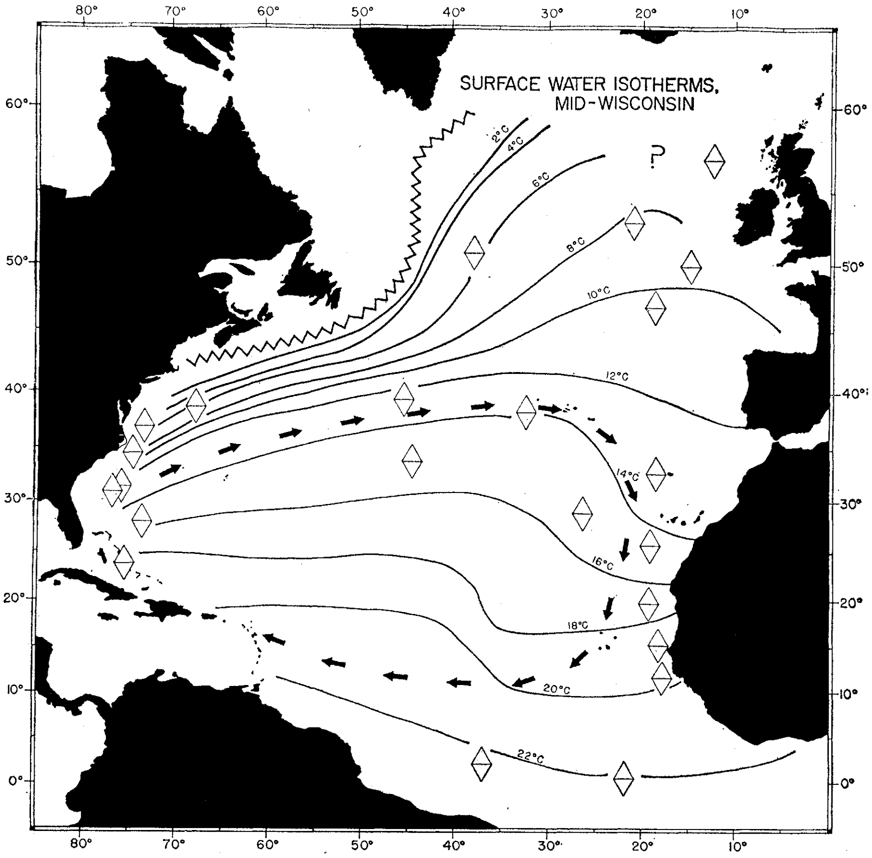

Fig. 3. Paleoisotherm map of the mid-Wisconsin North Atlantic erected with the use of coccolithophorid temperature data. The dark arrows indicate presumed position of the subtropical gyral based on coccolith boundaries of subtropical forms. The jagged line represents pack ice [after Flint].

latitude in the cold Labrador water found between the Gulf Stream and the coast of North America. In the mid-Wisconsin it ranged as far south as 13°N latitude along the African coast (Fig. 1). The average latitude shift between recent and glacial is approximately 15° latitude and even greater between living material and glacial (*4*).

At the opposite extreme in temperature tolerance is *Umbellosphaera irregularis* (Fig. 1), a tropical species. The minimum shift between recent and glacial boundaries for this form is approximately 20° latitude. The accuracy to which such shifts can be determined reflects the spacing of core samples. Between the glacial presence (core Nos. V16-200 and A180-72) and absence (core No. A180-56) there is a gap of 10° latitude (see Table 1).

The temperature ranges of *Helicosphaera carteri, Rhabdosphaera stylifera*, and *Syracosphaera pulchra* are not as limited as those of the two preceding species (Fig. 1). They are presently found in subtropical to transitional waters. All show a much more limited distribution during mid-Wisconsin time. *Helicosphaera carteri* has an average distributional difference of 10° latitude while *Rhabdosphaera stylifera* and *Syracosphaera pulchra* both have an approximate shift of 17° latitude. Note that in these three species the recent maximum distributional lines follow the northern border of the subtropical gyral (Gulf Stream) across the Atlantic Ocean. This agrees with plankton data from the North Atlantic, where the boundary between subtropical and subarctic species approximates the northern border of the Gulf Stream (*4*).

Umbellosphaera tenuis and *Umbilicosphaera mirabilis*, while having a satisfactory preservation record, do not show as distinctive a difference in their recent and glacial distributions as the preceding species.

Umbellosphaera tenuis is found at higher latitudes and is limited today by the 16°C isotherm; it is typical of subtropical waters. Its glacial to recent shift is from 10° to 15° latitude (Fig. 2). It is not as abundant in glacial as in recent sediments. This may be due to the fragility of its macrococcoliths.

The coccoliths of *Umbilicosphaera mirabilis*, like *Coccolithus huxleyi*, have temperature-dependent structural variations (*4, 6*). While these changes are gradational in *C. huxleyi, U. mirabilis* appears to have separate cold- and warm-water forms. The distribution of *U. mirabilis* is today bounded by the 18°C isotherm; this may be too high a value since the colder-stage coccoliths are present at higher latitudes in sediment samples from this study than was observed with either living or surface sediment material in the survey of modern forms. It is possible that the colder stage of *U. mirabilis* has a distribution similar to that of *R. stylifera* and *S. pulchra*. Nevertheless, the species shows a definite shift between recent and glacial sediments which averages 15° latitude (Fig. 2). Further evidence indicative of a cooling of the Atlantic in glacial times is the preponderance of cold-form coccoliths in glacial-age sediments from the mid-North Atlantic, a situation reversed in recent surface sediments.

Cyclococcolithus leptoporus (Fig. 2) is among the most eurythermal of the Coccolithophoridae. Today it ranges from the equator to Arctic waters. There is no apparent difference in maximum range between recent and glacial, although this is probably due to the lack of core material further north than the line Sp 10-1 through R 10-2 (see Table 1). There is a marked change in percentage distribution between recent and glacial populations, with the higher percentage (which today occurs in this species in transitional waters) indicative of the optimum range. Thus the line representing percentage change may be a rough indicator of the subtropical boundary in the Wisconsin. This type of subtle biogeographic change will require further work before definite conclusions can be drawn.

Table 1. Core locations in the North Atlantic and the depth of the glacial sample in each core.

Core No.	Location		Depth of glacial sample (cm)
	Latitude	Longitude	
A153-146	33°43′N	44°45′W	80
A156-4	34°49′N	74°41′W	844
A156-5	37°07′N	73°37′W	95
A164-59	38°42′N	67°52′W	245
A167-13	31°39′N	75°21′W	300
A167-14	31°28′N	76°28′W	300
A179-13	23°56′N	75°45′W	97
A179-17	28°00′N	73°47′W	280
A180-9	39°27′N	45°57′W	115
A180-16	38°21′N	32°29′W	140
A180-32	29°07′N	26°15′W	59
A180-48	15°19′N	18°06′W	488
A180-56	12°15′N	17°46′W	207
A180-72	00°36′N	21°47′W	120
R5-36	46°55′N	18°35′W	162
R5-54	25°52′N	19°03′W	35
R5-57	19°40′N	19°06′W	270
R10-2	56°59′N	12°28′W	100
SP8-4	32°50′N	18°32′W	65
SP9-3	53°53′N	21°06′W	220
SP9-4	50°02′N	14°46′W	200
SP10-1	51°23′N	38°04′W	150
V16-200	01°58′N	37°04′W	120

A number of other species showed some degree of biogeographic change by a shift in maximum boundaries; however, they are not plotted because of relative rarity in the core material. In the case of the ubiquitous eurythermal species (*Coccolithus huxleyi* and *Gephyrocapsa oceanica*), their distribution is similar to that of *Cyclococcolithus leptoporus*.

One interesting change, presently not usable for paleoclimatic work but important in systematics, is the reversal in dominance of *Coccolithus huxleyi* and *Gephyrocapsa oceanica* from glacial to recent (Table 2).

In today's ocean *Coccolithus huxleyi* usually constitutes over 50 percent of the flora, but in the mid-Wisconsin it shared and in some latitudes was dominated by *Gephyrocapsa oceanica*. I consider that *Coccolithus huxleyi* is a relatively recent form, none being found before the Pleistocene, and that it evolved from the *Gephyrocapsa oceanica* complex during the late Pleistocene. Similarities in form and ecology, combined with the finding of intermediate forms in Pleistocene core samples that I am now investigating, support this theory.

A comparison of the latitudinal change in flora from northern cold waters to southern warm waters in recent and glacial sediments indicates the dominance of cooler water forms in lower latitudes during the mid-Wisconsin. *Umbilicosphaera mirabilis* and *Syracosphaera pulchra* constitute a much larger percentage of the flora in glacial times in this area, while *Cyclococcolithus fragilis* and *Umbellosphaera irregularis*, subtropical to tropical forms, are nearly absent during glacial time from the North Atlantic.

The biogeographic boundaries of Coccolithophoridae species in today's seas can be correlated with surface water isotherms (*4*). If we assume that the present temperature ranges of the species held for the last glacial period, then the paleogeographic boundaries of species can also be assigned temperature values. If all these boundaries are

Table 2. Species composition of recent and glacial samples for each core (expressed as percentages). Since only eight species are reported from the total flora, the percentage values do not equal 100. Abbreviations: R, recent; G, glacial; x represents values that are less than 1 but greater than 0.5 percent.

Core No.	*Coccolithus pelagicus*		*Cyclococcolithus leptoporus*		*Helicosphaera carteri*		*Rhabdosphaera stylifera*		*Syracosphaera pulchra*		*Umbellosphaera irregularis*		*Umbellosphaera tenuis*		*Umbilicosphaera mirabilis*	
	R	G	R	G	R	G	R	G	R	G	R	G	R	G	R	G
A153-146	x	5	9	6	1	2	1	x	1	0.5	x		1	1	4	3
A156-4		x	1	x		x	1									
A156-5	x	x	2	x												
A164-59	x	x	3	x	6		x		2				2		4	
A167-13		1	3	5			1	1		1						x
A167-14		x	2	3	2	4	1	1					x			1
A179-13			2	4	2	3	2	6	2	4	2			2		7
A179-17		x	5	x	1	x	1		3		3		4		6	x
A180-9	18	7	10	6	2	1	x		1				x		3	
A180-16	x	1	10	5	1	2	x		1	2.5			2	1	3	1
A180-32		1	9	15	2	3	2	1	1	x			2	1	4	8
A180-48		3	x	10	4	1			1						1	2
A180-56								2		2						6
A180-72			13	27	2	2	1	1	1	1	2	1	x		7	11
R5-36	x	6	25	18	1		x		1				1		x	
R5-54		1	3	6	2	4	2	2	3	1	4		4	1	9	5
R5-57	x	1	8	11	3	1	1	1	9	1					2	1
R10-2	4	2	16	1			2		4							
SP8-4		0.5	8	9	1	0.5	1	x	1	1	x		2	2	3	1
SP9-3	1	1	14	5					2							
SP9-4	1	5	6	6			x		x							
SP10-1	30	3	13	8	4		x		6						2	
V16-200			5	8	2.5	3	2	x	x	2	4	1	3	1	14	22

plotted on a map and each boundary is given the present value of the maximum temperature (isotherm), it should be possible to draw a paleoisotherm map for the glacial period. Having laid out the temperature lines for the species and interpolating between overlapping ranges, I found it possible to draw a tentative paleoisotherm map (Fig. 3). Although insufficient core coverage makes any fine adjustment of these lines impossible (a gap remains in the northwest portion of the Atlantic), two lines, the 14° and the 22°C isotherms, are established on the basis of a number of overlapping species. The addition of more core material and the mapping of other species boundaries should result in a paleoisotherm map that will be an accurate representation of the average temperature of surface water of the glacial North Atlantic.

In seven species the amount of latitudinal shift between glacial and recent is greatest along the eastern side of the Atlantic. In the three species with subtropical to transitional ranges it is a factor of 2 to 3. This distributional difference is presumably the result of the main current system in existence today and in the Wisconsin. At present the distribution of *R. stylifera, H. carteri, U. tenuis,* and *S. pulchra* is encompassed by the northern boundary of the subtropical gyral (Gulf Stream). This boundary rises from approximately 40°N latitude off North America to over 55°N latitude off Europe. This is also true for other subtropical coccolith species not included in this report. In the mid-Wisconsin the line of species presence is relatively horizontal, running roughly parallel to the 30° latitude line with a slight southern turn along the eastern edge of the Atlantic (Fig. 3).

Admittedly the core density is somewhat low; nevertheless, the core coverage is sufficient to allow no more than a 5° fluctuation in latitude without a major change in azimuth of this line since it is bracketed by cores. If one compares data (Figs. 1 and 2), it is possible to say that the northern border of the subtropical gyral during mid-Wisconsin time flowed along or near the 33° latitude line.

From this first report, based on information gained from modern species of Coccolithophoridae, it appears that coccoliths can be used for paleoecologic studies and that the application of these studies to the problem in this report has led to the following conclusions about the effect of cooling on the North Atlantic during the Wisconsin glaciation: (i) That the maximum cooling in the mid-Wisconsin resulted in a southward shift of planktonic populations of approximately 15° latitude, with the greatest shift occurring in the eastern Atlantic; (ii) that it may be possible to erect paleoisotherm maps of surface water with the use of population boundaries of Coccolithophoridae species of known temperature range as isotherms, particularly if greater core coverage can be combined with data on additional species; and (iii) that the northern boundary of the subtropical gyral, from a present position of approximately 40° latitude off North America to over 55° latitude off Europe, was displaced to a position extending from approximately 30°N latitude off North America to approximately 38° off Europe.

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