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# Biometry of *Emiliana huxleyi* and its biostratigraphic significance in the Eastern North Atlantic Ocean and Western Mediterranean Sea in the last 20 000 years

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## Abstract

A detailed biometric study of coccoliths of *Emiliana huxleyi* has been performed on 34 samples from three sediment cores of the North Atlantic Ocean and the Western Mediterranean Sea (SU90-08, M39029-7 and MD95-2043). All three cores contain the last glacial–interglacial transition (marine isotopic stages 1–2), enabling us to study in detail the morphology of this taxon during this period of change. One hundred coccoliths of *E. huxleyi* were randomly chosen in each sample; distal shield length and width measurements were performed on each of the individuals selected. The data show that *E. huxleyi* specimens larger than 4  $\mu\text{m}$  are frequent in glacial samples and that these larger forms decreased sharply in abundance during the deglaciation and Holocene; smaller forms are more abundant in this latter group of samples. The decrease in larger forms seems to be time-transgressive, since it is recorded between 12 and 11 kyr cal. BP in southern locations (Alboran Sea and Gulf of Cadiz) and around 8.4 kyr cal. BP in the central North Atlantic. Scanning electron microscope analyses indicated that the two forms have the same degree of calcification and hence this parameter should not be used in taxonomic classifications. We suggest that the larger coccoliths belong to a cold-water variety of *E. huxleyi*, which can be distinguished from the small-coccolith variety in light-microscope analyses by its distal shield length. The decrease in the abundance of this larger variety during the deglaciation period could be used as a biostratigraphic event in the North Atlantic and Mediterranean areas.

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## 1. Introduction

Together with marine diatoms, dinoflagellates and cyanobacteria, coccolithophores are one of the main groups of phytoplankton and a major

oceanic sediment former. Of the approximately 200 living species of coccolithophores (Winter and Siesser, 1994), the vast majority live in warm waters of low latitudes. However, sea-surface temperature (SST) is not the main controlling factor of all taxa. Some species are also controlled by other parameters (such as nutrients, light and turbulence) and are characteristic of particular water masses. Because of this, the geographic distribution of certain taxa has been used for paleo-

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ecological, paleoceanographical and paleoclimatic reconstructions (e.g. McIntyre, 1967; Weaver and Pujol, 1988; Fincham and Winter, 1989; Flores et al., 1997).

*Emiliana huxleyi* (Lohmann, 1902) Hay and Mohler in Hay et al., 1967 is the most abundant living coccolithophore and has dominated coccolithophorid assemblages for 73 000 years (Thierstein et al., 1977). It forms spherical coccospheres consisting of between 10 and 50 interlocked elliptical coccoliths. The first appearance datum of *E. huxleyi* has been dated at 268 kyr (Thierstein et al., 1977). This species has probably evolved from a member of the *Gephyrocapsa* group. It is a cosmopolitan species (McIntyre and Bé, 1967; Geitznauer et al., 1977; Okada and McIntyre, 1979; Winter, 1985), and is able to live within a broad range of SST and salinity conditions (e.g. McIntyre et al., 1970; Bukry, 1974; Winter et al., 1979; Winter, 1982). It is found in the entire photic zone (Okada and Honjo, 1973), with higher abundances in nutrient-rich subpolar waters (McIntyre and Bé, 1967; Okada and Honjo, 1973; Brand, 1994). It also occurs in high numbers in nutrient-rich waters along the border of subtropical oceanic gyres, in equatorial upwel-

lings, in other upwellings, and in outer shelf areas (Winter, 1985; Verbeek, 1990; Brand, 1994).

This biometric study of *Emiliana huxleyi* aims to verify the existence in the North Atlantic and Mediterranean waters of two different-sized morphotypes, gain insight into their behavior and determine their biostratigraphic significance since the Last Glacial Maximum (LGM).

## 2. Taxonomy of *Emiliana huxleyi*

*Emiliana huxleyi* has usually been considered a monospecific group composed of several morphotypes, each characterizing a different range of environmental conditions. Okada and Honjo (1973) and Honjo (1977) observed three different varieties (subarctic, cold and warm forms) in the Pacific Ocean, while McIntyre and Bé (1967), Geitznauer et al. (1977) and Schneidermann (1977) identified two varieties (cold and warm forms) in the Atlantic Ocean. The differences between these morphotypes are mainly based on the degree of calcification, but also on the number and arrangement of elements and the structure of the central area.

However, other researchers have pointed out

Table 1  
List of classifications of *Emiliana huxleyi* and adopted terminology in them

| Reference                  | Material                         | Area                                    | Age of samples     | Adopted terminology of <i>Emiliana huxleyi</i>   |
|----------------------------|----------------------------------|---|--------------------|--|
| Pujos-Lamy (1977)          | sediment cores                   | Azores (N. Atlantic)                    | NN19–21            | Forme 1 'grande': 2.80–3.60 $\mu\text{m}$<br>Forme 2 'petite': 2.20–2.80 $\mu\text{m}$   |
| Bréhéret (1978)            | sediment cores                   | Azores (N. Atlantic)                    | NN19–21            | var. 1: 1.9–2.7 $\mu\text{m}$<br>var. 2: 2.7–3.4 $\mu\text{m}$<br>var. 3: 4.4–5.8 $\mu\text{m}$  |
| Verbeek (1990)             | sediment cores                   | N. Atlantic                             | NN19–21            | <i>Emiliana huxleyi</i> (< 3.5 $\mu\text{m}$ )<br><i>Emiliana pujoseae</i> (> 3.5 $\mu\text{m}$ )  |
| Young and Westbroek (1991) | culture strains<br>water samples | N. Atlantic<br>N. Atlantic–Indian Ocean | present<br>present | <i>E. huxleyi</i> type A: 2.5–3.5 $\mu\text{m}$<br><i>E. huxleyi</i> type B: 3.8–4.8 $\mu\text{m}$<br><i>E. huxleyi</i> type C<br><i>E. huxleyi</i> var. <i>corona</i>   |
| Flores et al. (1993, 1997) | sediment cores                   | W. Mediterranean                        | MIS 1–5            | <i>E. huxleyi</i> (< 5 $\mu\text{m}$ )<br>large <i>Emiliana</i> (> 5 $\mu\text{m}$ )   |
| Medlin et al. (1996)       | culture strains                  | N. Atlantic                             | present            | <i>E. huxleyi</i> var. <i>huxleyi</i> : (2.0) 2.5–3.5 (4.0) $\mu\text{m}$<br><i>E. huxleyi</i> var. <i>pujoseae</i> : (3.4) 3.8–4.8 (5.0) $\mu\text{m}$<br><i>E. huxleyi</i> var. <i>kleijniae</i> : 2.5–3.5 $\mu\text{m}$ |

Measurements in  $\mu\text{m}$  refer to lengths of distal shields.

the invalidity of these classification schemes in the Pacific waters off California (Winter, 1985), the Agulhas Current in SW Africa (Fincham and Winter, 1989), and in the Gulf of Lions in the Mediterranean Sea (Riaux-Gobin et al., 1995). Other classifications (Table 1), mainly based on coccolith size, have been used in studies of Quaternary sediments from the North Atlantic (Pujos-Lamy, 1977; Br  h  ret, 1978; Verbeek, 1990; Weaver et al., 1999; Colmenero et al., 2000), the Equatorial Pacific (Pujos, 1985) and from the Western and Central Mediterranean (Flores et al., 1993, 1997; Esposito, 1999). Cultured strains and water column samples from the North Atlantic Ocean have also shown the present-day existence of at least three different varieties with similar degrees of calcification (Young and Westbrook, 1991; Van Bleijswijk et al., 1991). The separation of these varieties (termed A, B and C) is based on differences in distal shield and central area element shape, immunological cross-reactivity of coccolith-associated polysaccharids and size. *Emiliania huxleyi* types A and C have been recently identified in water samples

from the Southern Ocean and the Western-Central Pacific Ocean (Findlay and Giraudeau, 2000; Hagino et al., 2000). DNA analyses performed by Medlin et al. (1996) have revealed no genetic differences, but these authors concluded that there were sufficient biochemical and physiological differences between them to support this classification and they formally proposed the names *E. huxleyi* var. *huxleyi*, *E. huxleyi* var. *pujoseae* and *E. huxleyi* var. *kleijniae* for types A, B and C of Young and Westbrook (1991), respectively.

Nevertheless, size variation is the main tool used in classifications based on light-microscope studies. Pujos-Lamy (1977) and Br  h  ret (1978) recognized several forms of *Emiliania huxleyi* using size criteria in samples from eastern North Atlantic cores. A new species, *Emiliania pujoseae*, was proposed by Verbeek (1990) to include all forms larger than 3.5  $\mu\text{m}$ . Flores et al. (1997) distinguished a morphotype larger than 5  $\mu\text{m}$  in two Western Mediterranean cores. These classifications have been successfully used by other researchers in recent years (e.g. Esposito, 1999; Weaver et al., 1999).

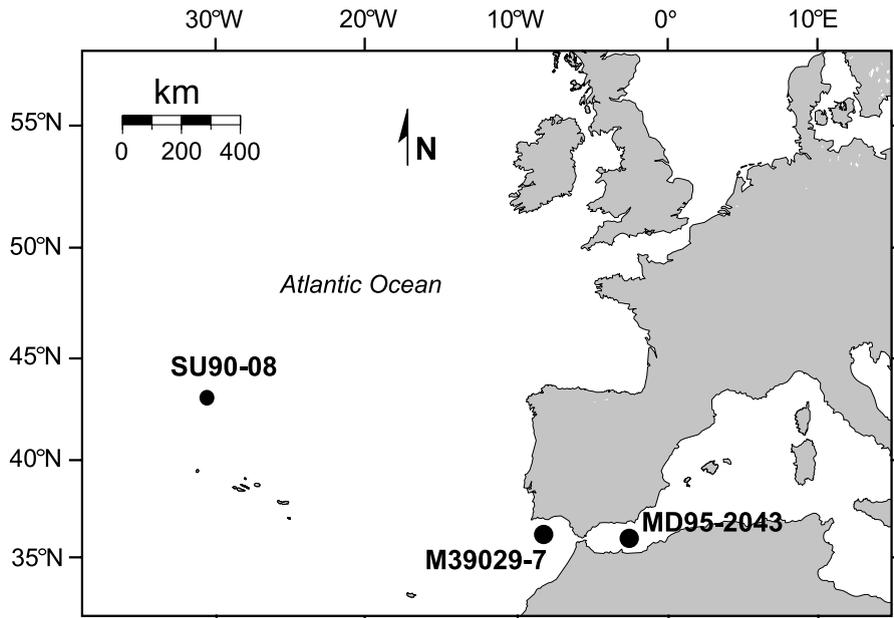


Fig. 1. Location of the three cores considered in this study.

### 3. Core location and oceanographic setting

In the present study, samples from three different cores were analyzed. The three sites form a W to E latitudinal transect from the central North Atlantic to the Western Mediterranean (Fig. 1). Gravity core SU90-08 (43°41'2N, 30°24'5W; 3080 m water-depth; 12.27 m core-length) was recovered during the PALEOCINAT I cruise in 1990 on the western flank of the mid-oceanic ridge (Grousset et al., 1993). The core location is dominated by the north-flowing warm surface waters of the Subtropical North Atlantic Gyre (Bout-Roumazeilles et al., 1999; Calvo et al., 2001). Gravity core M39029-7 (36°2'5N, 8°13'8W; 1917 m water-depth; 5.02 m core-length) was recovered in 1997 by R/V *Meteor* (cruise M-39) in the outer zone of the Gulf of Cadiz (Schott et al., 1999). In this location the water column is dominated by cold North Atlantic Intermediate and Surface Water masses (NAIW and NASW), which flow southwards following the Subtropical North Atlantic Gyre. Mediterranean Outflow Waters (MOW), characterized by higher temperatures and salinities, can be found at about 1000 m water-depth (Schott et al., 1999), flowing as a separated current mixing progressively with NAIW. NASW follows the Iberian margin and passes into the Alboran Sea through the Strait of Gibraltar, where it describes two anticyclonic gyres and forms upwelling cells before going further into the Mediterranean. Piston core MD95-2043 (36°8'6N, 2°37'2W; 1841 m water-depth; total core-length 36 m) is located in the middle path of those anticyclonic gyres and is under their direct influence (Cacho et al., 1999, 2001). This core was obtained by R/V *Marion Dufresne* during IMAGES I cruise in 1995 (Cacho et al., 1999).

Core SU90-08 is mainly composed of foraminifer and nannofossil oozes and muds, interbedded with clays and terrigenous muds (Bout-Roumazeilles et al., 1999). Cores M39029-7 and MD95-2043 are composed of calcareous oozes and clays.

### 4. Materials and methods

Samples used for nannofossil counts were pre-

pared following the methodology of Flores and Sierro (1997). In this technique a weighed amount of dry sediment is diluted in a volume of liquid mixture. A small fraction is extracted with a micropipet and dropped onto a Petri-dish, which has been previously filled with more liquid mixture and has a cover slide in the bottom. The surface over which the sediment is uniformly distributed and the observed surface are controlled, which allows easy comparison of data between samples. A total of 34 samples (13 samples from core M39029-7, 11 from MD95-2043 and 10 from SU90-08), corresponding to the Holocene–deglaciation–LGM interval of the three cores, were selected and analyzed in the biometric study. One hundred specimens of *Emiliania huxleyi* were randomly chosen in each sample, and distal shield lengths and widths were measured (Fig. 2). Measurements were made with a Leica DMRXE polarized light microscope and a Leica DC 250 digital camera, using 1600× magnification. Images of several randomly chosen visual fields of each sample were captured and enlarged using the Leica QWin Pro software, improved to perform automatic biometric studies by the Oceanic Micropaleontology Group of the University of Salamanca. All *E. huxleyi* present in each image were selected and measured with an accuracy of a tenth of a micrometer (1 pixel = 0.066 μm). Scanning electron microscope (SEM) analyses were performed in Zeiss DSM 940 and Hitachi H-3000 microscopes in order to estimate the state of preservation and the degree of calcification of the

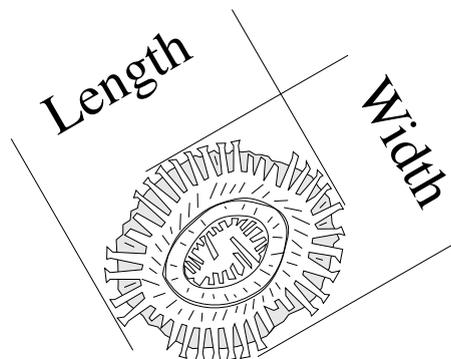


Fig. 2. Morphological scheme of *Emiliania huxleyi* from a distal view based on SEM photographs (Plate I, 15). The parameters measured are shown.

*E. huxleyi* population in cores M39029-7 and MD95-2043.

The degree of preservation of *Emiliania huxleyi* specimens is good to moderate in all cores. Partial dissolution of some elements on the distal shield and central area grill is frequent, especially in the larger forms (Plate I, 13 and 14). These problems have not hampered the measurements. Easily dissolved coccoliths such as *Syracosphaera* spp. and very small placoliths are also common in all the samples studied, confirming the good preservation of the materials.

## 5. Stratigraphy and age model

The stratigraphy and age model of core MD95-2043 have been previously established elsewhere (Cacho et al., 1999). For the last 21 kyr, 17 radiocarbon atomic mass spectroscopy (AMS) ages were obtained and converted into calendar ages using the Calib. 4.1 program (Stuiver and Reimer, 1993), which uses an updated dataset (Stuiver et al., 1998) and contains the 400-yr correction for the ocean surface reservoir effect (Bard et al., 1994). The average sedimentation rate of the last 21 kyr is 50.4 cm/kyr (Fig. 3).

The age model of core SU90-08 was established by Grousset et al. (1993) through correlation to the spectral mapping SPECMAP stack (Martinson et al., 1987). Isotope stages and their limits were also recognized from magnetic susceptibility and color reflectance data (Grousset et al., 1993; Cortijo et al., 1995). The upper part of the core (0–107.6 kyr cal. BP) has an averaged sedimentation rate of 5.3 cm/kyr (Bout-Roumzeilles et al., 1999) (Fig. 3).

The stratigraphy and age model of core M39029-7 (Colmenero-Hidalgo, in preparation) (Table 2) have been established by making a peak to peak correlation of oxygen isotope data (Löwemark, 2001) between this core and nearby core M39008-3, recovered from the upper slope of the Gulf of Cadiz. This latter core contains  $^{14}\text{C}$  AMS dates and its age model has been established by Cacho et al. (2001). Three additional control points (Younger–Dryas (YD), Bølling–Allerød (BA) and Heinrich 1 (H1) events) were identified, added to core M39029-7 age model and dated with the ages proposed by Cacho et al. (2001) for core M39008-3. The Holocene/deglaciation boundary, also dated in core M39008-3, was used as another control point. H1 was identified in core M39029-7 using its ice-rafted debris (IRD)

Table 2  
Age points for core M39029-7 (Gulf of Cadiz)

| Depth in core<br>(cm) | Age source                                  | Dated species                | AMS $^{14}\text{C}$<br>age<br>(yr) | Cal. BP<br>age<br>(yr) |
|-----------------------|---|------------------------------|------------------------------------|------------------------|
| 9                     | corr. with Cacho et al. (2001) <sup>a</sup> | <i>Globigerinoides ruber</i> | 2660                               | 2332                   |
| 31                    | corr. with Cacho et al. (2001) <sup>a</sup> | <i>G. ruber</i>              | 4195                               | 4282                   |
| 60                    | corr. with Cacho et al. (2001) <sup>a</sup> | <i>G. ruber</i>              | 8755                               | 9238                   |
| 71                    | corr. with Cacho et al. (2001) <sup>b</sup> |                              |                                    | 10 000                 |
| 87                    | corr. with Cacho et al. (2001) <sup>a</sup> | <i>G. ruber</i>              | 9860                               | 10 610                 |
| 112                   | corr. with Cacho et al. (2001) <sup>b</sup> |                              |                                    | 12 400                 |
| 117                   | Bard et al. (1994) <sup>c</sup>             |                              | 11 080                             | 12 626                 |
| 123                   | corr. with Cacho et al. (2001) <sup>b</sup> |                              |                                    | 14 525                 |
| 140                   | Bard et al. (1994) <sup>c</sup>             |                              | 13 980                             | 16 143                 |
| 154.5                 | corr. with Cacho et al. (2001) <sup>b</sup> |                              |                                    | 16 500                 |
| 172                   | establ. age for LGM                         |                              |                                    | 18 000                 |
| 178                   | corr. with Cacho et al. (2001) <sup>a</sup> | <i>G. ruber</i>              | 15 800                             | 18 285                 |
| 222                   | corr. with Cacho et al. (2001) <sup>a</sup> | <i>G. ruber</i>              | 18 370                             | 21 243                 |

<sup>a</sup>  $^{14}\text{C}$ -AMS data obtained in core M39008-3 by Cacho et al. (2001).

<sup>b</sup> Calendar ages obtained by direct correlation with M39008-3 isotopic curve and age model from Cacho et al. (2001).

<sup>c</sup> Data taken from Cacho et al. (2001). No correction for reservoir effect.

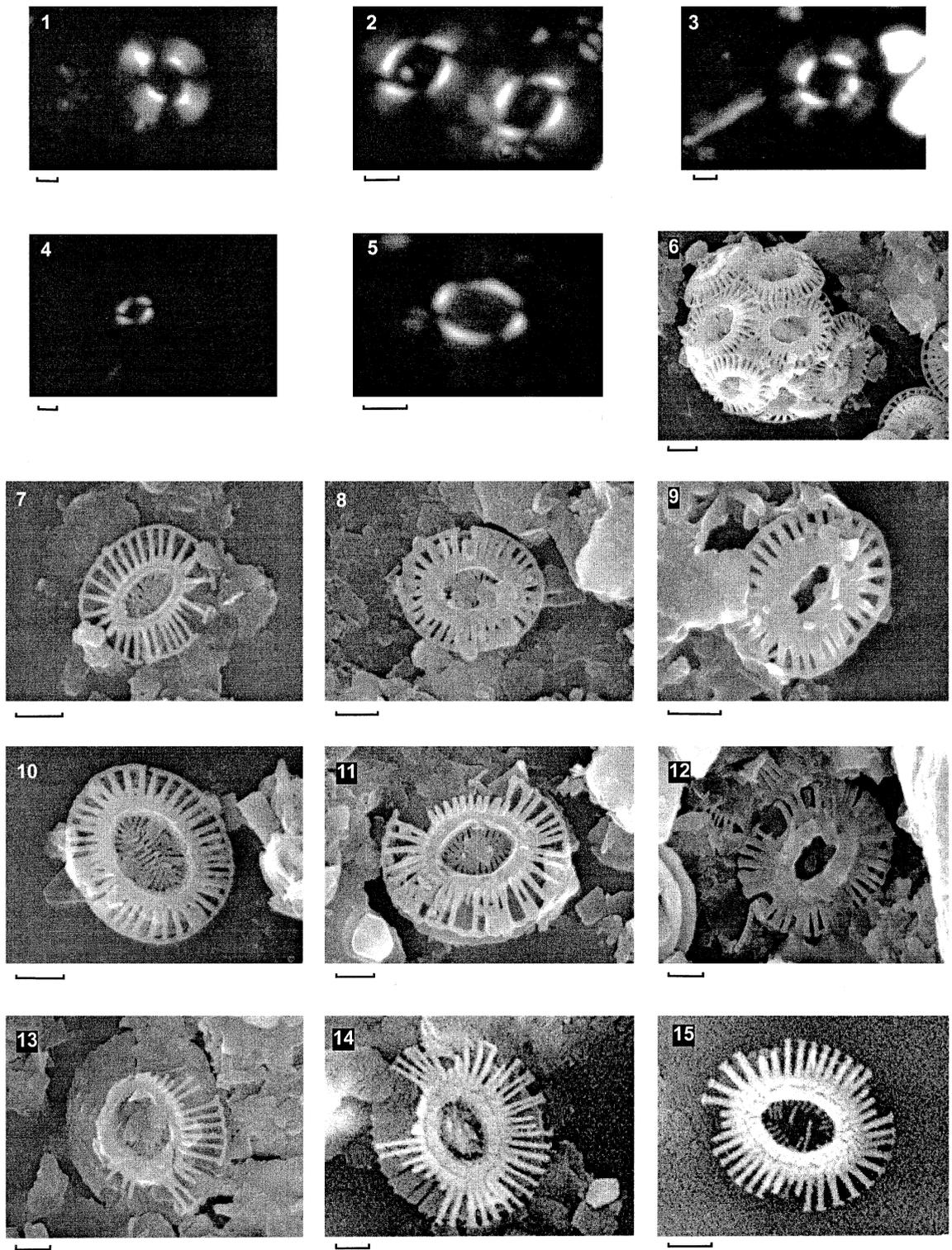


Plate I.

curve (Schönfeld, 1999, unpublished data) and the abundance curves of taxa such as the coccolithophore *Florisphaera profunda* Okada and Honjo, 1973, and the planktonic foraminifer *Neoglobobulimina pachyderma* (Ehrenberg, 1861) (Reguera, 2001). The average sedimentation rate of this upper part of core M39029-7 is 16.3 cm/kyr (Fig. 3).

## 6. Results

Light-microscopy data shows that the lengths of the distal shields of the group of *Emiliania huxleyi* placoliths vary between 1.84 and 5.40  $\mu\text{m}$  in core SU90-08, between 1.92 and 5.42  $\mu\text{m}$  in core M39029-7, and between 1.78 and 6.01  $\mu\text{m}$  in the Alboran Sea core (MD95-2043). A single specimen measuring more than 6  $\mu\text{m}$  (6.13  $\mu\text{m}$ ) was found in core SU90-08. Two very small placoliths (1.56 and 1.60  $\mu\text{m}$ ) have been measured in core M39029-7, though their identification as *E. huxleyi* is doubtful due to their small size. Widths vary between 1.45 and 4.84  $\mu\text{m}$  in core SU90-08, 1.26 and 5.04  $\mu\text{m}$  in core M39029-7 and between 1.50 and 5.75  $\mu\text{m}$  in the Alboran Sea (Fig. 4). In all three cores good correlation is seen between the lengths and widths of the dis-

tal shields ( $r^2 = 0.88$ ). SEM-based morphometric analysis of a Holocene and a glacial sample from core M39029-7 (Fig. 5) also provided a good correlation ( $r^2 > 0.88$ ). It can be observed that in all cases there is a broad inverse relationship between the eccentricity (ratio between the length and width of the placolith) and length of the distal shield (Figs. 4 and 5), showing that the placoliths of *E. huxleyi* tend to be less oval as their size increases, as has been previously noticed (Young and Westbroek, 1991; Riaux-Gobin et al., 1995).

For each sample, frequency graphs of lengths and widths against abundance were also performed (Figs. 6–8). Each graph was plotted next to the isotopic curve of the cores, used as chronostratigraphic scales. A clear tendency of greater unimodality and smaller lengths and widths towards the top of all three cores can be observed. Samples from the lower part of the three cores show a polymodal appearance with several peaks, and in some of them two groups of *Emiliania huxleyi* can be easily differentiated. SEM analyses of core M39029-7 (Fig. 5) confirmed that the length and width distributions of the glacial sample are much more heterogeneous than the Holocene sample. These groups of smaller and larger *E. huxleyi* are characterized by different mean

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Plate I. Coccoliths and coccospheres of *Emiliania huxleyi*. Photographs 1–5 are light-microscopy digital images, performed with a Leica DC 250 digital camera on a Leica DMRXE microscope. SEM micrographs 6–13 have been taken using a Hitachi H-3000 microscope, and SEM micrographs 14 and 15 were obtained by a Zeiss DSM microscope. All SEM micrographs are distal views. Scale bars: 1  $\mu\text{m}$ .

1. *E. huxleyi* (>4  $\mu\text{m}$ ), core SU90-08, 92 cm (18 kyr cal. BP).
2. *E. huxleyi* (>4  $\mu\text{m}$ ), core M39029-7, 223 cm (21.2 kyr cal. BP).
3. *E. huxleyi* (>4  $\mu\text{m}$ ), core MD95-2043, 760 cm (16.6 kyr cal. BP).
4. *E. huxleyi* (<4  $\mu\text{m}$ ), core MD95-2043, 120 cm (4.9 kyr cal. BP).
5. *E. huxleyi* (<4  $\mu\text{m}$ ), core M39029-7, 223 cm (21.2 kyr cal. BP).
6. Coccosphere of *E. huxleyi* (<4  $\mu\text{m}$ ), core MD95-2043, 324 cm (9.4 kyr cal. BP).
7. *E. huxleyi* (<4  $\mu\text{m}$ ), core M39029-7, 118 cm (13 kyr cal. BP).
8. *E. huxleyi* (<4  $\mu\text{m}$ ), core M39029-7, 118 cm (13 kyr cal. BP).
9. *E. huxleyi* (<4  $\mu\text{m}$ ), core MD95-2043, 324 cm (9.4 kyr cal. BP).
10. *E. huxleyi* (<4  $\mu\text{m}$ ), core MD95-2043, 324 cm (9.4 kyr cal. BP).
11. *E. huxleyi* (>4  $\mu\text{m}$ ), core MD95-2043, 1140 cm (32.5 kyr cal. BP).
12. *E. huxleyi* (>4  $\mu\text{m}$ ), core MD95-2043, 1140 cm (32.5 kyr cal. BP).
13. *E. huxleyi* (>4  $\mu\text{m}$ ), core MD95-2043, 1140 cm (32.5 kyr cal. BP).
14. *E. huxleyi* (>4  $\mu\text{m}$ ), core M39029-7, 162.8 cm (17.2 kyr cal. BP).
15. *E. huxleyi* (>4  $\mu\text{m}$ ), core M39029-7, 162.8 cm (17.2 kyr cal. BP).

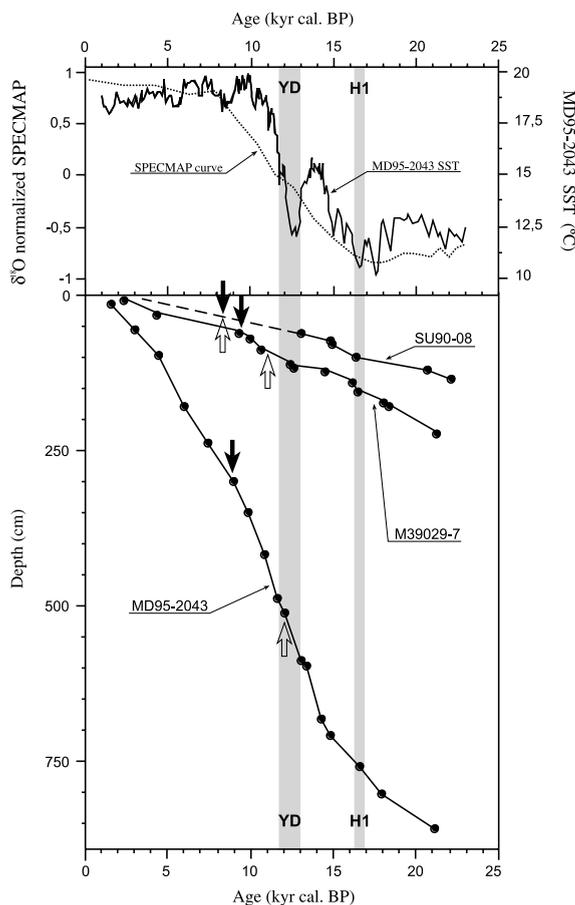


Fig. 3. Age models of cores MD95-2043, M39029-7 and SU90-08. The sedimentation rate in the Alboran Sea is much higher than in the Gulf of Cadiz or in the Central North Atlantic. The SPECMAP stacked curve (dotted line) (Martinson et al., 1987) and the  $U_{37}^k$  SST data (solid line) from core MD95-2043 (Cacho et al., 1999) provide a paleoceanographic reference for this interval. The YD and H1 are the major cooling events for this interval of time. Age model points of the three cores are marked by black dots. Black arrows indicate the moments of maximum degree of unimodality, and white arrows show the depths from where practically only small forms appear in the samples.

dimensions: smaller placoliths range between around 2 and 3.5–4  $\mu\text{m}$  and have a mean length of 3–3.25  $\mu\text{m}$ , while larger placoliths range between 4 and 6  $\mu\text{m}$  and their mean length is around 4.5–5  $\mu\text{m}$ .

This distribution of *Emiliana huxleyi* placoliths in a polymodal scheme is observed in the three cores until the deglaciation. A single population

with unimodal distribution can be clearly distinguished in the Alboran Sea core (MD95-2043) at about 12 kyr cal. BP, while this is recorded at about 11 kyr cal. BP in the Gulf of Cadiz (M39029-7) and at about 8.4 kyr cal. BP in the Central Atlantic (SU90-08). The figures also show that the maximum peak of unimodality (narrower range of mean deviations) is reached at about 9 kyr cal. BP in the Alboran Sea, and at about 9.5 kyr cal. BP in the Gulf of Cadiz. This event appears to occur in the Central North Atlantic after 8.4 kyr cal. BP. Thus, larger *E. huxleyi* populations seem to decrease progressively with time from south to north, and this trend is also shown if comparing the moments of maximum degree of unimodality. It can also be observed that samples showing the highest abundances of larger *E. huxleyi* (i.e. samples with a higher degree of polymodality) are those which are located next to or within H1 or the LGM.

During the Holocene, the mean dimensions of *Emiliana huxleyi* are 3–3.5  $\mu\text{m}$  length and 2–2.5  $\mu\text{m}$  width. SEM analyses of core M39029-7 (Fig. 5) revealed that smaller distal shield lengths (between 2.2 and 4  $\mu\text{m}$ , mean 3.25  $\mu\text{m}$ ) dominate in the Holocene sample, while in the glacial sample larger placoliths are more abundant and the maximum size increases to 5.7  $\mu\text{m}$ . Widths vary between 1.5 and 5.5  $\mu\text{m}$  in the glacial population and between 1.8 and 3.5  $\mu\text{m}$  in the Holocene sample.

Analysis of frequency graphs (Figs. 6–8) from all three cores reveal a consistent frequency minimum around 4  $\mu\text{m}$  in the samples characterized by a polymodal pattern. This size can be considered as a reference to separate the two size populations. The SEM study shows that the glacial population of *Emiliana huxleyi* from core M39029-7 (Fig. 5) can be readily divided in two groups using the 4- $\mu\text{m}$  boundary.

SEM images reveal that the larger forms of *Emiliana huxleyi* (Plate I, 11–15) show a distal shield composed by either radial T- or I-shaped elements, occasionally very thin; the proximal shield is composed of flattened radial elements with slits between some of them. Its central area is usually gridded. The smaller form (Plate I, 6–10) is characterized by its stronger appearance; distal

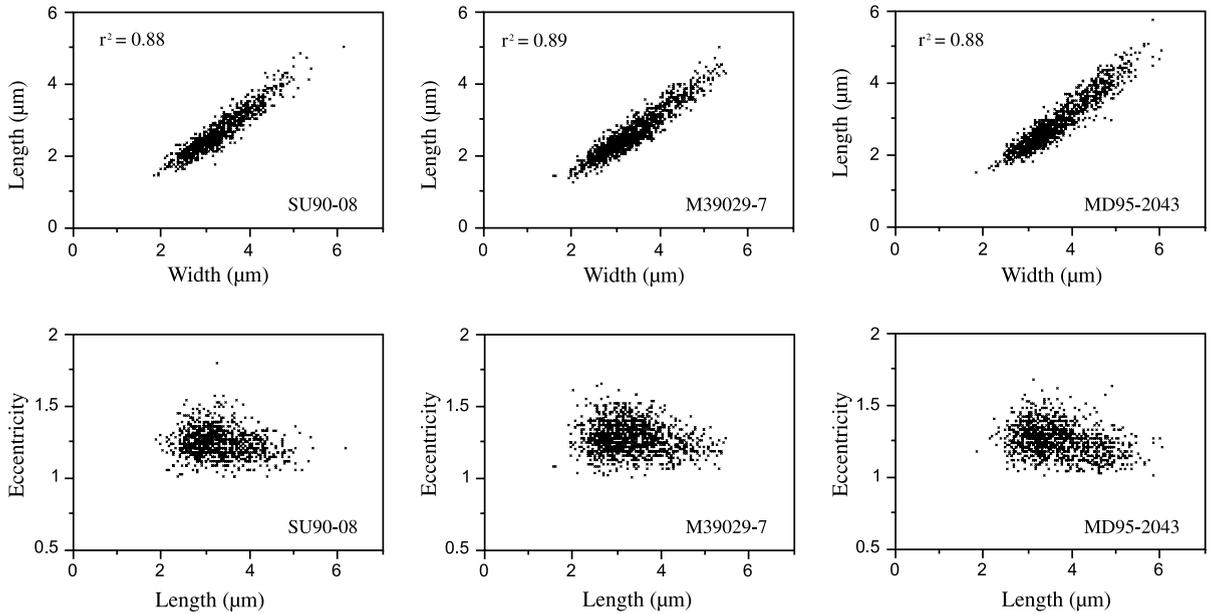


Fig. 4. Plots of the length/width and length/eccentricity ratios of cores SU90-08, M39029-7 and MD95-2043. Relationship between lengths and widths in the three cores is very good ( $r^2 = 0.88$ ). Eccentricity is lower as size increases.

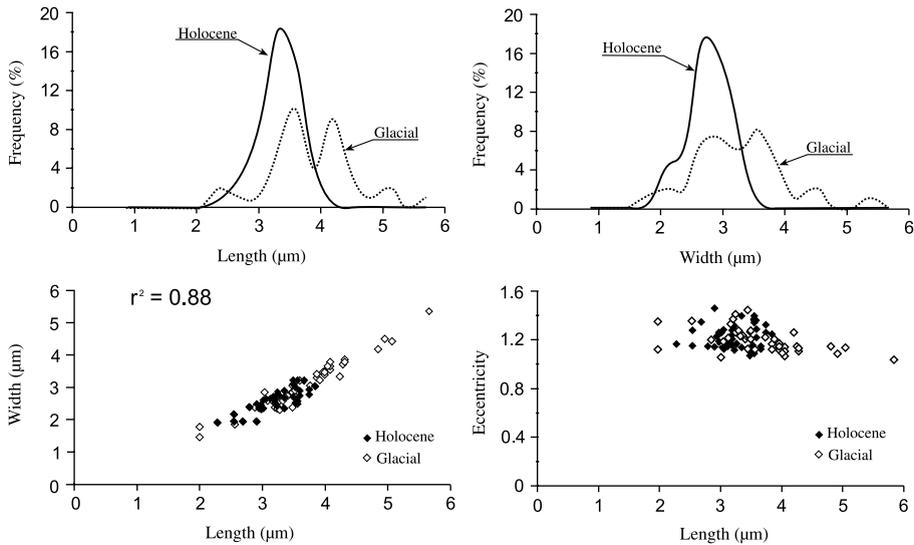


Fig. 5. SEM analyses of two samples from core M39029-7 (53.5 cm/8.1 kyr cal. BP and 162.8 cm/17.2 kyr cal. BP). It can be observed that the distribution of mean distal shield lengths and widths varies greatly between Holocene and glacial sediments. The size of glacial *Emiliania huxleyi* is much more heterogeneous than that of the Holocene population. Eccentricity decreases as size increases.

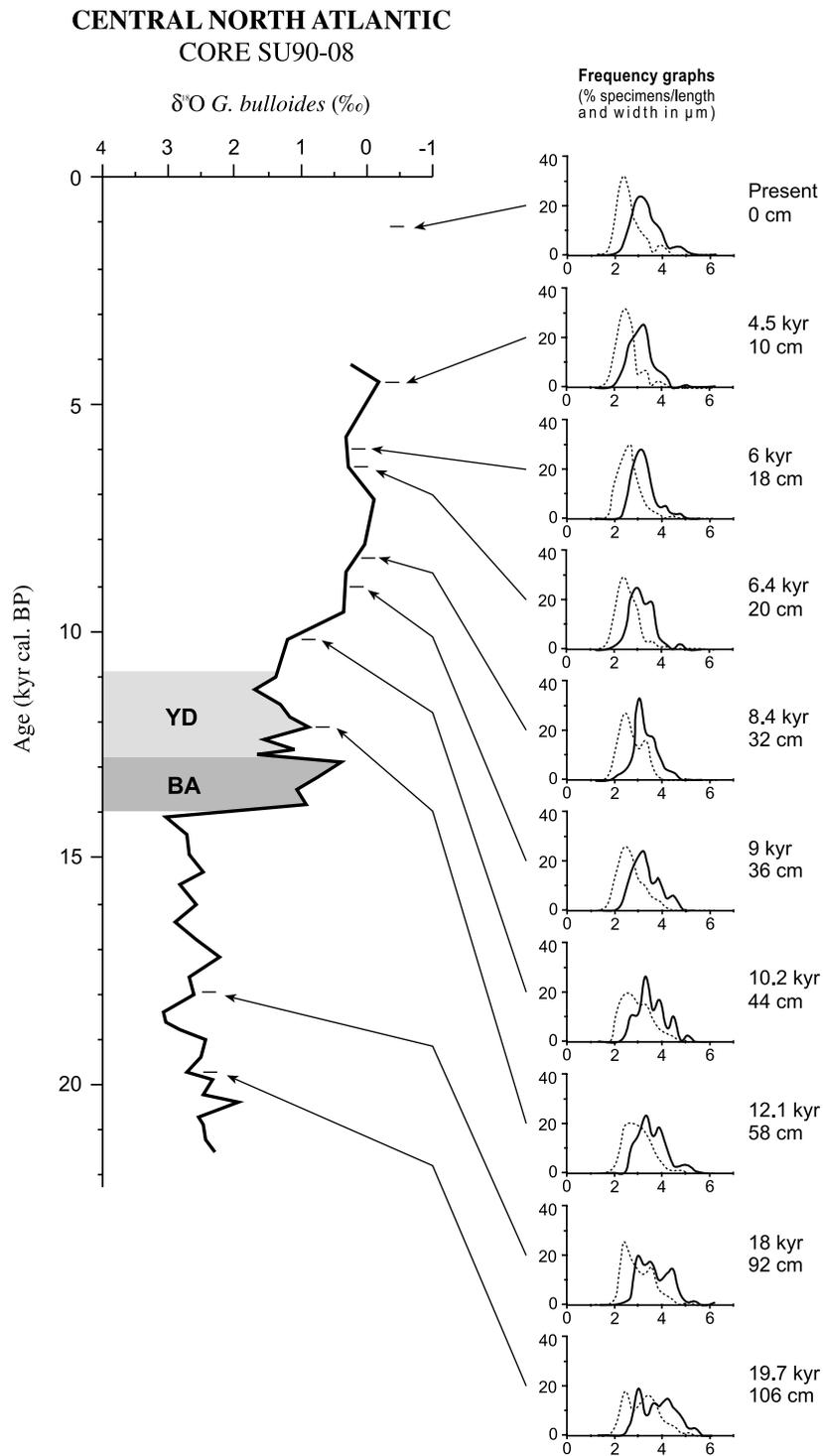


Fig. 6. Results of the biometric study of core SU90-08. Frequency graphs of distal shield length (solid line) and width (dotted line) are plotted against the isotopic curve.

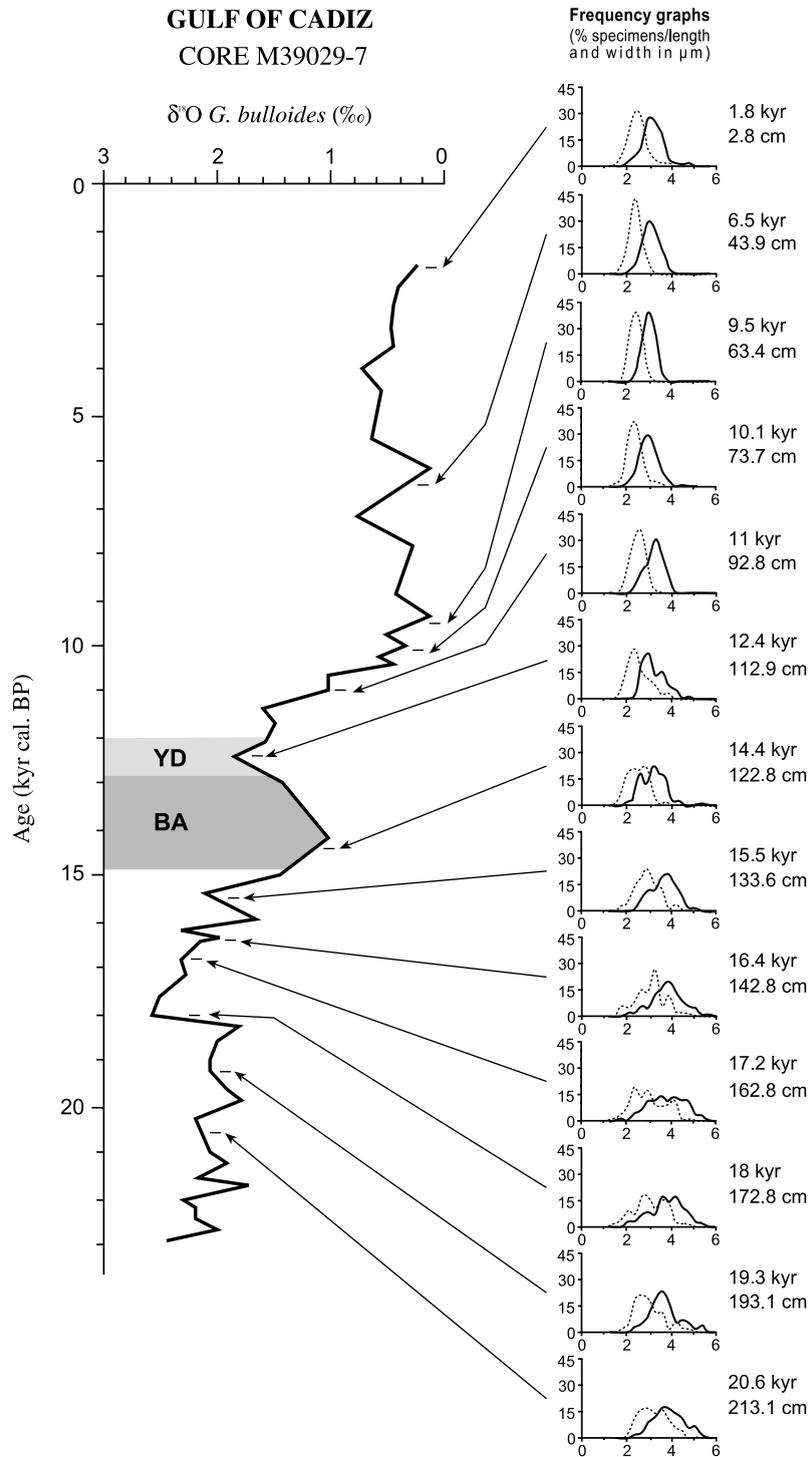
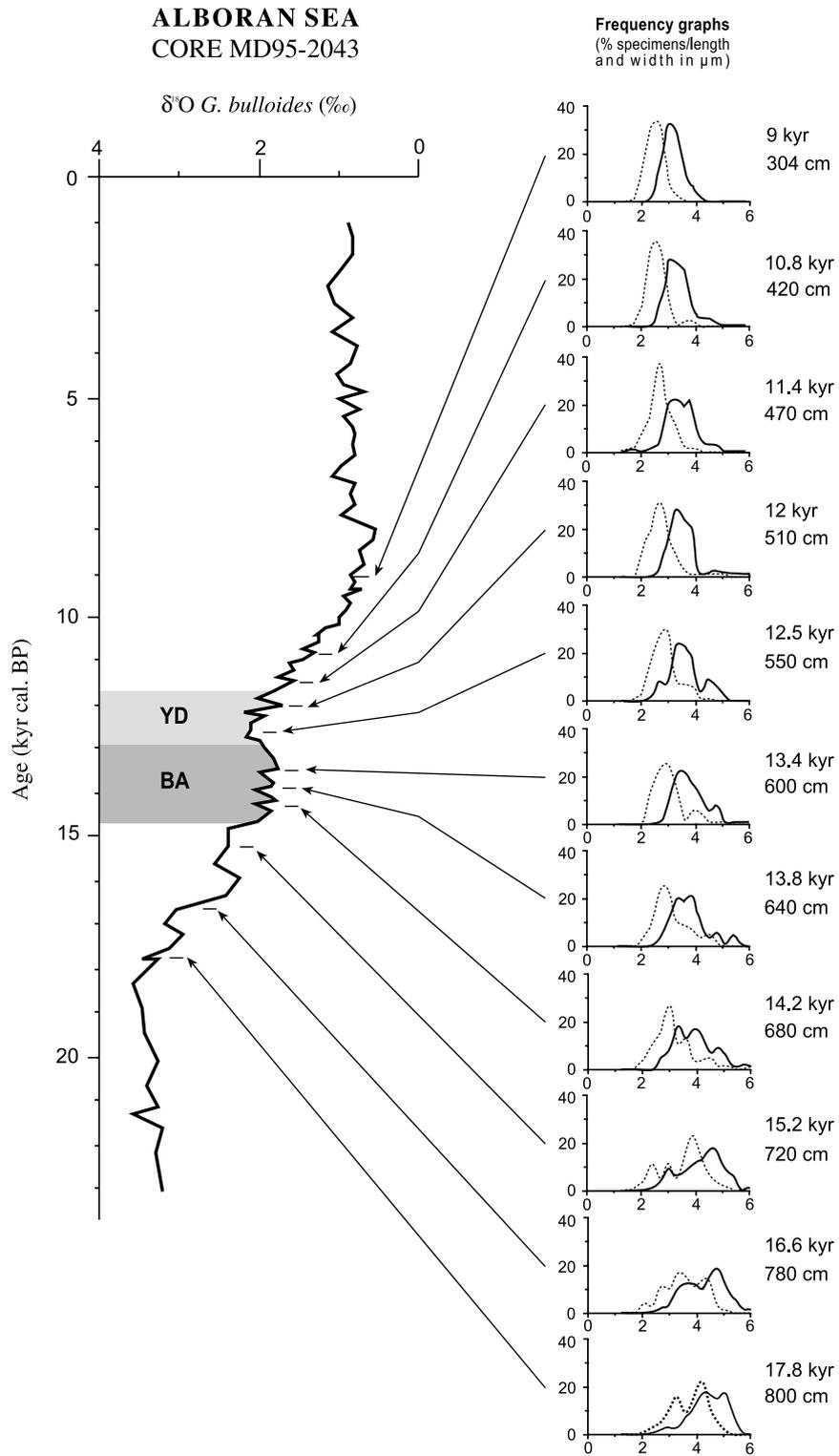


Fig. 7. Biometric study of core M39029-7. Frequency graphs of distal shield length (solid line) and width (dotted line) of specimens from samples are plotted against the isotopic curve.



shield elements are T-shaped, although wider, and the proximal shield and central area are similar to those of larger forms.

## 7. Discussion

### 7.1. Biometric analysis

In this biometric study two different-sized populations of *Emiliana huxleyi* have been distinguished in the glacial samples of cores SU90-08, M39029-7 and MD95-2043. The larger forms decrease abruptly in the southern cores (Alboran Sea and Gulf of Cadiz) during the deglaciation, while their decline is recorded in the early Holocene in the central North Atlantic. Holocene sediments are thus characterized by small-sized *E. huxleyi* placoliths, although larger forms do not disappear (Figs. 6–8). SEM image analysis of samples from cores M39029-7 and MD95-2043 show that the degree of calcification of specimens (i.e. the general weight of calcification) in both Holocene and glacial sediments can be either high or low (Plate I, 7 and 8, 9 and 10, 11 and 12), and that this factor is independent of the size of the placolith. Therefore, differences in this parameter are not associated with a particular morphotype or specific water masses as has been previously suggested (e.g. McIntyre and Bé, 1967; Okada and Honjo, 1973; Honjo, 1977; Geitzner et al., 1977; Schneidermann, 1977). Winter (1985) and Fincham and Winter (1989) reported the co-existence of more- and less-calcified coccoliths of *E. huxleyi* in the same water masses in locations off the Pacific coast of California and in the Agulhas Current (SW Africa). Young and Westbroek (1991) recommended that the terms ‘cold-’ and ‘warm-water form’ should be abandoned since they were based on a confusion of degree of calcification and genotypically controlled morphotype characteristics.

By contrast, our results show that different-sized coccoliths dominate in the samples from

all three cores, depending on their age: well and poorly calcified larger forms are restricted to glacial and deglaciation periods, while well and poorly calcified coccoliths of the smaller morphotype dominate the *Emiliana huxleyi* population during the Holocene. Other investigations based on cores spanning the last climatic cycle (Pujos-Lamy, 1977; Bréhéret, 1978; Pujos, 1985; Verbeek, 1990; Flores et al., 1993, 1997; Esposito, 1999; Weaver et al., 1999) have successfully divided *E. huxleyi* according to its size. Pujos-Lamy (1977), Bréhéret (1978), Verbeek (1990) and Flores et al. (1997) developed alternative classifications to those employing the degree of calcification, which are mainly based on light-microscope observations and placolith size (Table 1). According to all data, the smaller form from this study can be identified as ‘Forme 2 petite’ (Pujos-Lamy, 1977), Types 1, 2a and 2b (Bréhéret, 1978), *E. huxleyi* (Verbeek, 1990) and *E. huxleyi* type A (Young and Westbroek, 1991). The larger forms of the present study are equivalent to *E. huxleyi* ‘Forme 1 grande’ (Pujos-Lamy, 1977); *E. huxleyi* var. 3 (Bréhéret, 1978) or *Emiliana pujoseae* (Verbeek, 1990). *E. huxleyi* type B of Young and Westbroek (1991) also seems to identify the same group of placoliths, although these authors mainly used differences in the elements of the distal shield and the central area to define this larger type and stated that biometric analysis alone is not sufficient to consistently separate between types A and B placoliths. However, light-microscopy is the most widely used tool in laboratories and paleoceanographic investigations, and size is the only parameter that can be measured precisely and used to distinguish morphotypes.

Our results indicate that eccentricity varies as a function of size, and that larger *Emiliana huxleyi* tend to have less oval-shaped forms (Figs. 4 and 5). Young and Westbroek (1991) and Riaux-Gobin et al. (1995) have also noticed this in their samples from present cultures and traps and recent sedimentation.

Our biometric study also shows that in Holo-

Fig. 8. Results of the biometric study of the samples from core MD95-2043. Frequency graphs of distal shield length (solid line) and width (dotted line) are plotted against the isotopic curve of this core.

cene samples of all three cores the number of placoliths whose length is larger than 4  $\mu\text{m}$  is minimum, while deglaciation and glacial samples are characterized by the increase and even domination of the population larger than 4  $\mu\text{m}$  (Figs. 6–8). Verbeek (1990) suggested that *Emiliana huxleyi* and *Emiliana pujoseae* should be separated using the 3.5- $\mu\text{m}$  length limit; Young and Westbroek (1991) agreed that this could be a good criterion for light-microscope analyses if coccoliths grown under exceptional conditions were excluded. Our study shows that this limit might result slightly small to include all small populations of *E. huxleyi*. Hence, we propose that the size limit for separation between larger and smaller populations should be established at 4  $\mu\text{m}$ .

Verbeek (1990) included the larger placoliths in his new species *Emiliana pujoseae* on the basis of their different temporal patterns and ecological behaviors. He justified the marked similarities in morphology between *Emiliana huxleyi* and *E. pujoseae* in terms of a form convergence phenomenon. By contrast, other researchers (Pujos-Lamy, 1977; Br  h  ret, 1978; Young and Westbroek, 1991) accept that *E. huxleyi* is a single species composed of several types or varieties with different ecological requirements. Medlin et al. (1996), despite inconclusiveness of their DNA analyses, defined three varieties based on other evidences of genotypic differentiation. The data from the present biometric study cannot really give new ideas about this matter, although it seems that this latter option (varieties rather than species) is more probable. In this line, we have referred to the smaller and larger morphotypes as *E. huxleyi* (< 4  $\mu\text{m}$ ) and *E. huxleyi* (> 4  $\mu\text{m}$ ), respectively.

## 7.2. Paleocological and biostratigraphic interpretation

The sharp decrease of larger forms towards the Holocene in all the cores studied is interpreted to indicate that *Emiliana huxleyi* (> 4  $\mu\text{m}$ ) is a cold-water form whose number was reduced as a consequence of the progressive warming of North Atlantic waters during the deglaciation. Previous studies (Verbeek, 1990; Flores et al., 1997; Wea-

ver et al., 1999) showed that this variety only has been recorded in high abundances during the last glacial period (marine isotopic stages (MIS) 2, 3 and 4). The sequences of graphs show that in cores MD95-2043 and M39029-7, unimodality and domination of smaller forms was reached at around 12 and 11 kyr cal. BP, respectively (Figs. 3, 7 and 8). In core SU90-08, situated further north, this fact is recorded at about 8.4 kyr cal. BP (Figs. 3 and 6), which is in agreement with evidences showing that the Polar Front did not retreat from this site and reach its current position at higher latitudes until 9–6 kyr cal. BP (Ruddiman and McIntyre, 1981). While core SU90-08 was directly affected by polar waters during the LGM (Calvo et al., 2001), the Gulf of Cadiz and Alboran Sea were influenced by colder NASW as a consequence of this southern expansion of the Polar Front. This southern flow of cold waters was strongly enhanced during short-term cooling events, such as H1. IRD records in the Gulf of Cadiz indicate the arrival of icebergs in the zone (Sch  nfeld, 1999, unpublished data; Cacho et al., 2001). Samples from those intervals show the maximum degree of polymodality and highest number of *E. huxleyi* (> 4  $\mu\text{m}$ ), in agreement with the alkenone-SST data from the Gulf of Cadiz and Alboran Sea (Cacho et al., 1999, 2001), which shows that this period of time recorded the lowest SST of the studied interval. Between 9 and 9.5 kyr cal. BP (early Holocene) the maximum degree of unimodality of smaller forms is seen in the Gulf of Cadiz and Alboran cores (Figs. 3, 7 and 8), just about the same time SST increased sharply and attained the highest values in the zone as a consequence of the withdrawal of the Polar Front to more northerly positions after the YD event (Cacho et al., 2001).

Changes in the size of the *Emiliana huxleyi* population can be used as a stratigraphic level. This horizon has a time-transgressive character, since it occurs between 12 and 11 kyr cal. BP (second phase of deglaciation) in the Gulf of Cadiz and Alboran Sea and about 8.4 kyr cal. BP (early Holocene) in the central North Atlantic, probably as an effect of the process of retreat of the Polar Front to northern positions during the deglaciation. Pujos-Lamy (1977) and Br  h  ret

(1978) indicated the value of this event for biostratigraphic studies in order to establish a higher resolution calcareous nannoplankton stratigraphy than the existing one (based on the Martini (1971) and Gartner (1977) schemes), which is clearly insufficient in high-resolution late Quaternary cores, such as those used in this study.

## 8. Conclusions

This biometric study of *Emiliania huxleyi*, performed on samples from the LGM to the Present from three cores located in the central North Atlantic, Gulf of Cadiz and Alboran Sea shows that *E. huxleyi* can be separated into two types, depending on placolith size. The larger forms (*E. huxleyi* > 4 µm) are mainly present in glacial sediments and almost disappear during the deglaciation and Holocene, while the smaller forms (*E. huxleyi* < 4 µm) are the most abundant type during the Holocene.

This study proposes that the size limit for differentiating between these two types should be drawn at 4 µm. In SEM analyses, the larger and smaller types show no significant differences in degree of calcification and in both groups both well and poorly calcified placoliths are present.

*Emiliania huxleyi* (> 4 µm) is interpreted as a cold-water indicator. Its sharp decrease in abundance during the deglaciation can be seen in all three cores and can be considered as a biostratigraphical level that dates the retreat of the Polar Front and associated cold-water masses to northern positions after the last glacial period, at least in the central and eastern North Atlantic and in central and Western Mediterranean. This event would have occurred in the Gulf of Cadiz and Alboran Sea at about 11–12 kyr cal. BP, and about 8.4 kyr cal. BP in the central North Atlantic Ocean.

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