

# Paleoenvironmental controls on the morphology and abundance of the coccolith *Watznaueria britannica* (Late Jurassic, southern Germany)

Fabienne Giraud\*, Bernard Pittet, Emanuela Mattioli, Vanessa Audouin

UMR CNRS 5125 PEPS, Université Lyon 1, Bâtiment Géode, 2 rue Raphaël Dubois, F-69622 Villeurbanne cedex, France

Received 29 November 2005; received in revised form 21 April 2006; accepted 27 April 2006

## Abstract

The coccolithophore species *Watznaueria britannica* is dominant in Middle-Upper Jurassic calcareous nannofossil assemblages and presents morphological variation, including different coccolith size, shape and length of the central area and of the bridge. Six morphotypes can be recognized in the polarizing light microscope. The aim of this work is to better understand the morphological variability of *W. britannica* and determine if this variability is controlled by paleoecological factors. In order to investigate the potential paleoecological controls on *W. britannica* morphology and abundance, we carried out a biometric study on a restricted temporal interval: the Late Oxfordian, in the Swabian Alb (southern Germany), characterized by increasing carbonate production linked to climatic changes. The Balingen–Tieringen section, where previous works on sedimentology, nannofossil assemblage composition, and  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  analyses were performed, was selected for this study. The variations in morphology and abundances of *W. britannica* were studied on 40 samples of the Balingen–Tieringen section, presenting variable lithologies and calcium carbonate contents. For each level, seven biometric parameters (coccolith length, width and ellipticity, central area length, width and ellipticity and central area proportion with respect to the coccolith) were measured or calculated on digitally captured images of the first 100 *W. britannica* coccoliths observed in the light microscope. The relationships between the different biometric variables were described using bivariate and Principal Component Analyses. Biometric parameters and Principal Component factors extracted from nannofossil assemblages as well as other paleoenvironmental proxies, were investigated using regression, and their stratigraphic trends were compared. Principal component analysis of the six biometric variables (3938 measurements) on *W. britannica* coccoliths shows a reduced morphological variability compared to a significant size gradient. An allometric trend recognized on the total placolith and on the central area within the *W. britannica* assemblages suggests that the different morphotypes may represent intra-specific variability rather than different species. The general trend through Late Oxfordian shows an increase in size of *W. britannica* coccoliths, mainly driven by an increase in the contribution of the large morphotypes. Increasing placolith size is associated with drier and warmer climatic conditions during the latest Oxfordian.

© 2006 Elsevier B.V. All rights reserved.

**Keywords:** calcareous nannofossils; biometry; paleoecology; Late Jurassic

## 1. Introduction

The Family Watznaueriaceae (coccolithophorids) represents one of the most important planktonic carbonate producers in Middle-Upper Jurassic sediments (Giraud et al., 1998). The dominance of this family over other

\* Corresponding author. Tel.: +33 4 72 44 62 45; fax: +33 4 72 44 83 82.

E-mail address: [Fabienne.Giraud@univ-lyon1.fr](mailto:Fabienne.Giraud@univ-lyon1.fr) (F. Giraud).

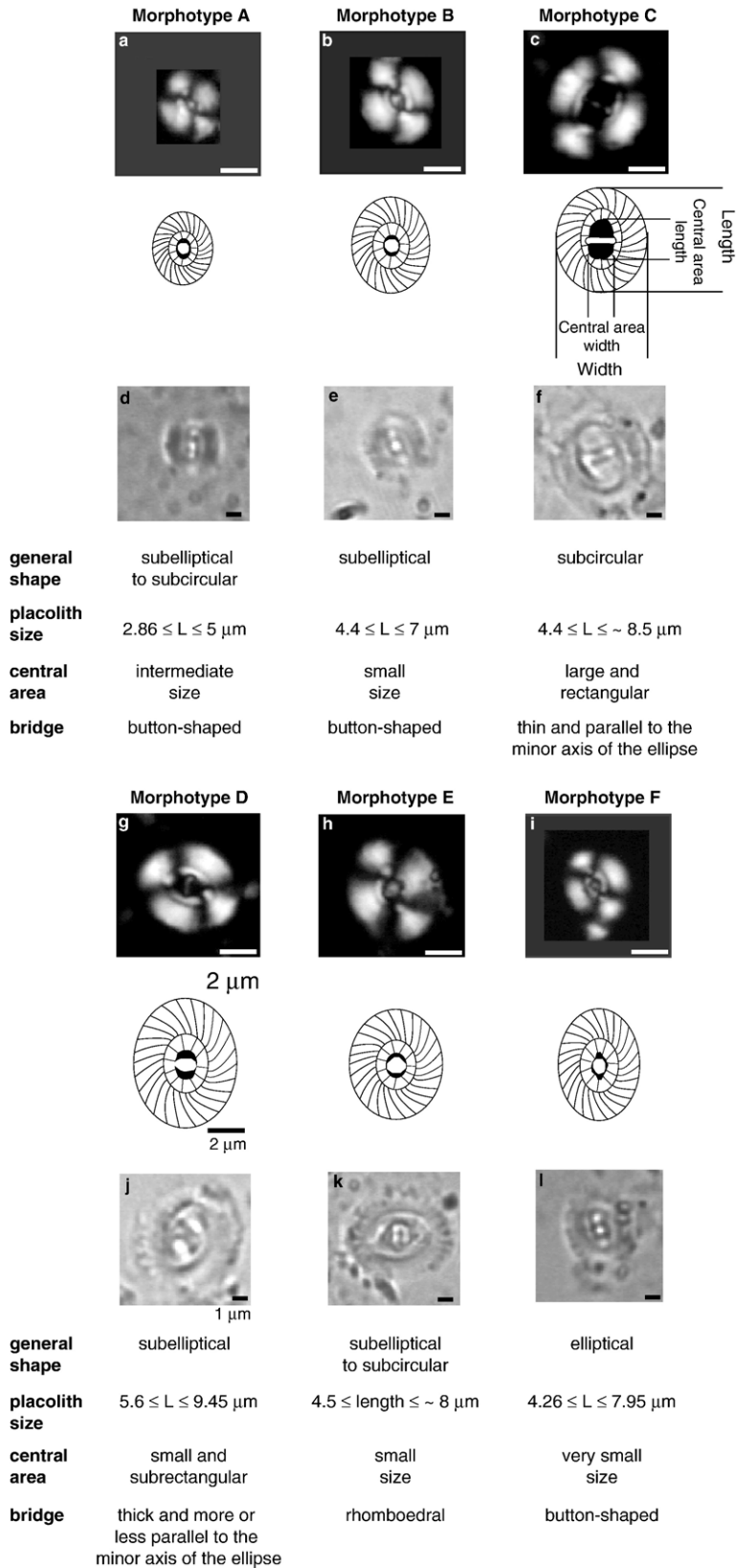


Table 1  
Statistics of the measured biometric parameters for all the *Watznaueria britannica* and for each morphotype

		Coccolith length ( $\mu\text{m}$ )	Coccolith width ( $\mu\text{m}$ )	Coccolith ellipticity	Central area length ( $\mu\text{m}$ )	Central area width ( $\mu\text{m}$ )	Central area ellipticity	Central area proportion
<i>W. britannica</i>	Mean	5.3	4.358	1.221	1.218	0.959	1.318	23.49
	min.	2.865	2.326	1	0.401	0.324	0.597	6.61
	max.	9.45	8.746	1.833	2.529	2.425	3.172	44.533
	std. dev.	1.032	0.85	0.113	0.263	0.262	0.29	5.305
	std. error	0.016	0.014	0.002	0.004	0.004	0.005	0.085
	<i>N</i>	3938	3938	3938	3938	3938	3938	3938
Morphotype A	Mean	4.252	3.578	1.195	1.124	0.825	1.394	26.533
	min.	2.865	2.326	1	0.504	0.324	0.644	12.269
	max.	5.005	4.704	1.655	1.949	1.419	3.171	44.516
	std. dev.	0.386	0.402	0.213	0.167	0.103	0.279	4.956
	std. error	0.01	0.011	0.006	0.004	0.003	0.007	0.132
	<i>N</i>	1409	1409	1409	1409	1409	1409	1409
Morphotype B	Mean	5.483	4.474	1.233	1.214	0.943	1.327	22.257
	min.	4.405	3.148	1.001	0.401	0.352	0.612	6.604
	max.	7.019	6.242	1.744	2.13	1.726	2.801	38.275
	std. dev.	0.455	0.486	0.112	0.226	0.209	0.293	4.375
	std. error	0.011	0.012	0.003	0.006	0.005	0.007	0.109
	<i>N</i>	1599	1599	1599	1599	1599	1599	1599
Morphotype C	Mean	5.297	4.567	1.165	1.813	1.503	1.25	34.304
	min.	4.425	3.907	1.047	1.347	1.035	0.966	26.29
	max.	6.422	5.387	1.312	2.367	1.944	1.856	43.417
	std. dev.	0.576	0.538	0.1	0.32	0.319	0.331	5.194
	std. error	0.192	0.179	0.033	0.107	0.106	0.11	1.731
	<i>N</i>	9	9	9	9	9	9	9
Morphotype D	Mean	7.024	5.654	1.252	1.422	1.228	1.193	20.306
	min.	5.643	3.723	1.002	0.615	0.551	0.597	8.395
	max.	9.45	8.746	1.833	2.529	2.425	2.249	32.31
	std. dev.	0.573	0.652	0.12	0.283	0.286	0.255	4.037
	std. error	0.026	0.029	0.005	0.013	0.013	0.011	0.181
	<i>N</i>	495	495	495	495	495	495	495
Morphotype E	Mean	6.062	5.049	1.207	1.407	1.239	1.16	23.376
	min.	4.531	3.471	1.01	0.704	0.478	0.644	11.136
	max.	7.968	6.823	1.678	2.148	1.853	2.328	37.939
	std. dev.	0.541	0.53	0.108	0.261	0.241	0.23	4.754
	std. error	0.029	0.029	0.006	0.014	0.013	0.013	0.259
	<i>N</i>	337	337	337	337	337	337	337
Morphotype F	Mean	6.111	4.71	1.307	0.878	0.713	1.277	14.469
	min.	4.26	2.543	1.084	0.459	0.324	0.764	8.206
	max.	7.955	6.255	1.675	1.376	1.244	2.204	26.483
	std. dev.	0.796	0.705	0.12	0.203	0.188	0.306	3.339
	std. error	0.087	0.077	0.013	0.022	0.021	0.033	0.364
	<i>N</i>	84	84	84	84	84	84	84

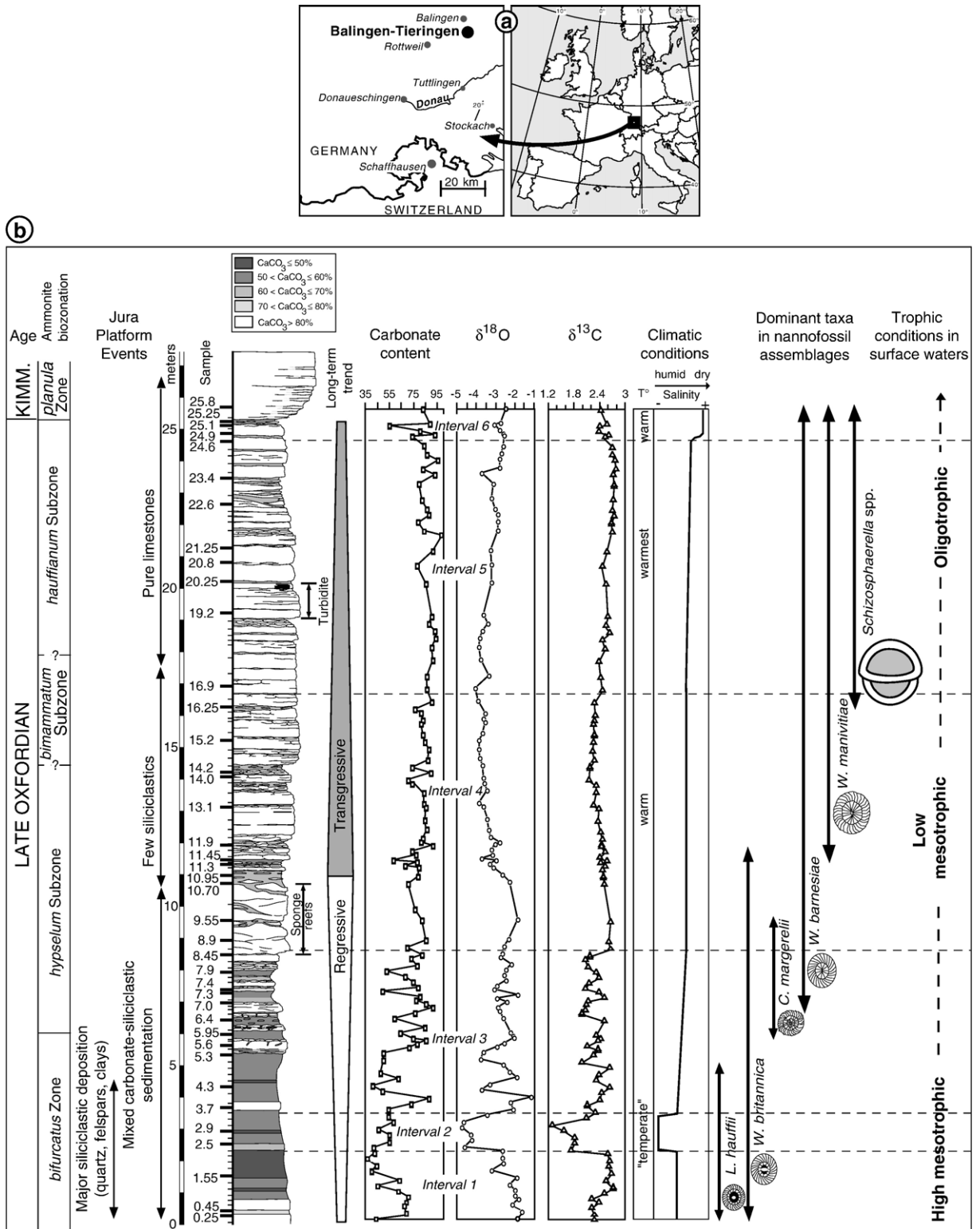
Abbreviations: min.: minimum; max.: maximum; std. dev.: standard deviation; std. error: standard error; *N*: number of measurements.

coccoliths began after a period of significant evolutive radiation of the nannoplankton at the Aalenian/Bajocian boundary (Middle Jurassic; Mattioli and Erba, 1999). After this period, characterized by the appearance of numerous species of the genus *Watznaueria* (Mattioli and Erba, 1999), the nannofossil species richness dramatically decreased while the abundance remained high. Assem-

blages were then dominated worldwide by the genus *Watznaueria* until the Tithonian (Bown et al., 1988; Bown and Cooper, 1998).

The dominance of *Watznaueria* has been compared to the dominance of some taxa of the family Noelaerhabdaceae in the Quaternary and in living nannoplankton, such as *Gephyrocapsa* and *Emiliania huxleyi*, respectively

Fig. 1. Light microscope images (crossed polars (above) and parallel polars (below)) of the six *Watznaueria britannica* morphotypes and description of the placolith shape and length, central area size and shape, and form of the bridge. Measured biometric parameters are shown. The range size of Morphotype C is deduced from complementary measurements realized on samples from Aulfingen section (Late Oxfordian, southern Germany).



(Street and Bown, 2000; Lees et al., 2004). Three causes are generally proposed to explain such a dominance in the Quaternary: preservation, evolution and ecological adaptation (Bollmann et al., 1998). The *Watznaueria* group, which is formed by robust placoliths, is considered as being more resistant to dissolution than other coeval nannofossils (Roth and Bowdler, 1981). As the dominance of *Watznaueria* is recognized in poorly preserved assemblages of oceanic sites (Roth, 1983; Bralower et al., 1989) as well as in well-preserved assemblages recovered from open-ocean environments (distal shelves, Medd, 1979; pelagic environments, Bown, 1992; Noël et al., 1994), this dominance is not always a consequence of selective diagenesis. A preliminary study on the morphology of *Watznaueria* coccoliths in Hauterivian clay–marl alternations reveals that the size and shape distribution of coccoliths strongly reflects variable ontogenetic development and appears to correlate with the sediment geochemical data (Geisen et al., 1998).

Among the *Watznaueria* group, *Watznaueria britannica* is a long-ranging species (uppermost Aalenian; Mattioli and Erba, 1999–Cenomanian; Lees, 1998) and is generally dominant in nannofossil assemblages during the Bajocian–Tithonian interval (Bown et al., 1988). *Watznaueria britannica* presents variations in size and shape of the coccolith, of the central area, and differences in bridge morphology that spans the central area. Six morphotypes can be recognized in the polarizing light microscope (Giraud et al., 1998). The main goals of this work are (1) to better understand the morphological variability of *Watznaueria britannica*, and (2) to determine if this variability is controlled by paleoecological processes. In order to investigate the potential paleoecological control on *W. britannica* morphology and abundance, we carried out a study on material from southern Germany through a restricted temporal interval, the Late Oxfordian, characterized by increasing carbonate production linked to climatic changes (Pittet et al., 2000). The variations in morphology and abundances of *W. britannica* are analysed and compared to sediment geochemical data.

## 2. Materials and methods

### 2.1. Definition of the morphotypes

We assign to the species *Watznaueria britannica* the specimens that present in their central area a bridge,

which is parallel to the minor axis of the ellipse and disjunct with respect to the inner cycle of the coccolith rim. We present in the Appendix taxonomic remarks about *Watznaueria britannica* and other species of *Watznaueria* very close in morphology to *W. britannica*.

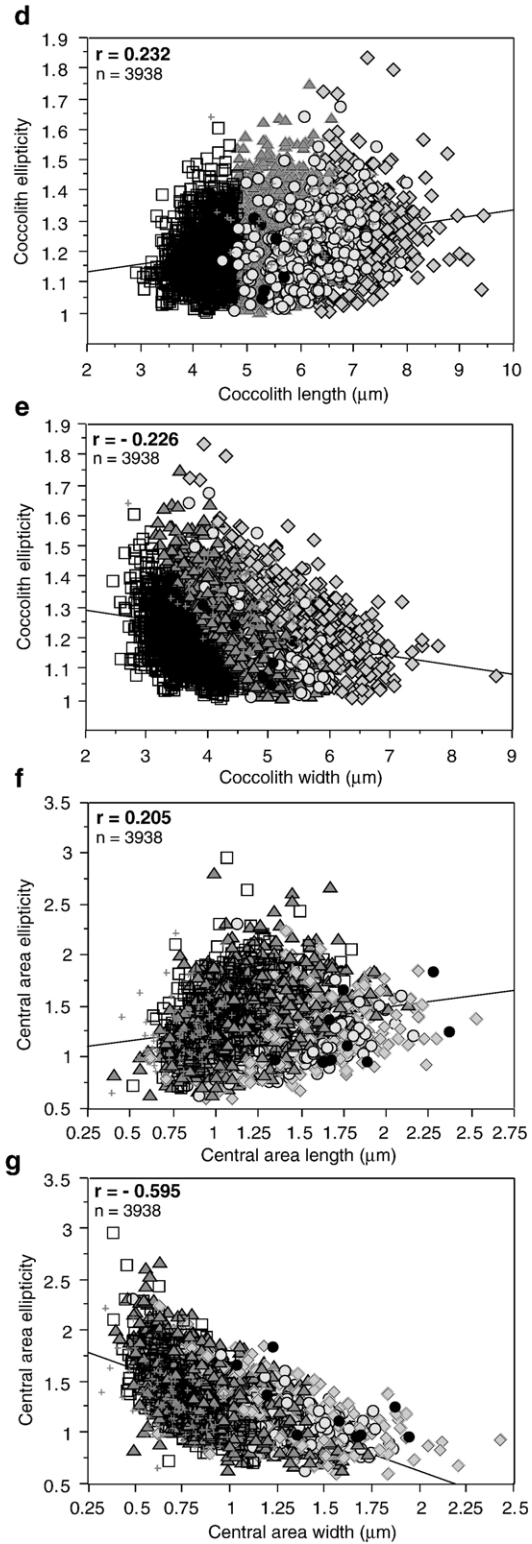
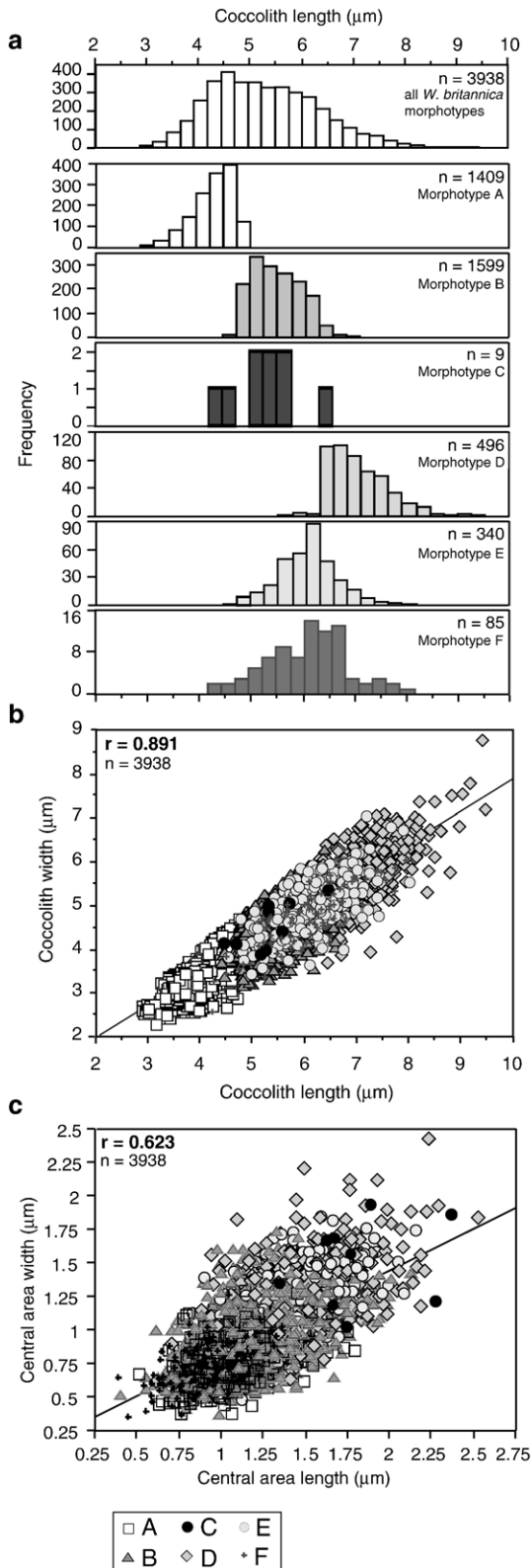
*Watznaueria britannica* presents six morphotypes that can be recognized in the polarizing light microscope (Fig. 1). These morphotypes differ in their overall size, shape and the size of the central area, and shape and thickness of the bridge (Fig. 1 and Table 1). As the bridge is disjunct, it appears optically discontinuous under crossed-nicols (Fig. 1a, b, c, g, h, i). Some forms present a very discontinuous bridge (button-shaped) under crossed-nicols (Fig. 1a, b) but under parallel-nicols, we can see that this button occupies all the central area along the minor axis of the ellipse (Fig. 1d, e).

Walsworth-Bell (2000) observed, in the nannofossil assemblages of the Oxford Clay (Middle Callovian–Early Oxfordian), a dominance of *W. britannica* that presents widely variable size and central area morphology. He recognized a continuous spectrum of variability in size that he has interpreted as intra-species variation. However, these conclusions were based on qualitative data.

### 2.2. Geological setting and previous works

The Balingen–Tieringen section is located in the western Swabian Alb (southern Germany; Fig. 2a), which paleogeographically corresponds to an epicontinental basin with a depth of less than 200 m, lying between the Jura and the Bohemian shallow platforms (Meyer and Schmidt-Kaler, 1989). Ammonites allow us to date the Balingen–Tieringen section as the Late Oxfordian (*bifurcatus* and *bimammatum* Zones) and Early Kimmeridgian (*planula* Zone; Schweigert, 1995a,b). The base of the succession, from 0 to 5.3 m, is constituted of marly sediments of the *bifurcatus* Zone (Fig. 2b). Above, from 5.3 to 11.1 m, the sediment become more calcareous and limestone beds are bioturbated, and enriched in glauconite, cephalopods, suggesting a decrease in the sediment accumulation rate (Pittet and Strasser, 1998; Fig. 2b). This part of the succession is capped by a condensed interval, from 11.1 to 12 m (Fig. 2b). Above this interval, from 12 to 25.3 m, the succession is dominated by calcareous sediments (Fig. 2b). The top of the succession comprises micritic limestones bearing few sponges of the *planula* Zone (Fig. 2b).

Fig. 2. (a) Location of the Balingen–Tieringen section; (b) Variation of different paleoenvironmental proxies in the Late Oxfordian–Early Kimmeridgian Balingen–Tieringen succession. Jura platform events, carbonate content, dominant nannofossil assemblages and interpreted trophic conditions in the surface-waters are from Pittet and Mattioli (2002);  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values and stratigraphic intervals from Bartolini et al. (2003). Ammonite biostratigraphy after Schweigert (1995a,b). Positions of samples selected for biometric measurement are shown.



Carbon and oxygen isotopes measured on the carbonate fraction (bulk rock; Fig. 2b) strongly fluctuate in the Balingen–Tieringen section. Based on these fluctuations, successive stratigraphic intervals (Intervals 1 to 6 in Fig. 2b) were defined by Bartolini et al. (2003). From Intervals 1 to 3, both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values strongly fluctuate (from 1.2 to 2.8‰) and negative shifts of both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  characterize Interval 2 (Bartolini et al., 2003; Fig. 2b). Smooth fluctuations of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  are observed in Intervals 4 to 6 (Bartolini et al., 2003; Fig. 2b).

Geochemical data combined with sedimentological data, nanofossil abundances and assemblage characteristics, allowed the reconstruction of paleoenvironmental and paleoclimatic conditions prevailing during the Late Oxfordian–Early Kimmeridgian in southern Germany (Bartolini et al., 2003; Fig. 2b). In particular, the carbonate mud deposited in the deep shelf (Balingen–Tieringen section) was essentially of allochthonous origin, and increasing carbonate content during the Late Oxfordian (Fig. 2b) was related to an intensified carbonate mud export from the Jura shallow platform to the Swabian Alb deep shelf. This resulted in dilution of the autochthonous (macrofossils, microfossils, sponges, sponge-reef derived intraclasts) and para-autochthonous elements (nanofossils) by a carbonate mud of allochthonous origin. Consequently, a decrease in the intensity of export of platform carbonate mud resulted in a decrease in the accumulation rate in the deep-shelf, and the formation of condensed intervals, characterized by intense bioturbation, glauconite formation, the accumulation of abundant cephalopods, and marl deposition. Moreover, Pittet and Mattioli (2002) show that calcareous nanofossils were only abundant in the marls and in condensed intervals; in limestones the pelagic carbonate fraction was strongly diluted by the carbonate mud exported from the platform environments. As carbonates are essentially derived from platform environments,  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  fluctuations measured on bulk carbonates in the deep shelf indirectly reflect paleoenvironmental conditions on the platform, rather than paleoceanographical conditions in the relatively deep Swabian Alb realm (<200 m; Meyer and Schmidt-Kaler, 1989). These shallow-platform carbonates are mainly inorganically and/or microbially produced (Pittet, 1996; Pittet and Mattioli, 2002). As only one aragonitic needle was detected in the 700 thin sections of the Jura platform sediments observed by Pittet (1996), the carbonate material was probably originally made of high-Mg calcite. The long-term fluctuations in carbon and oxygen isotopes

throughout the Late Oxfordian–Early Kimmeridgian have thus been interpreted as being dominantly the result of salinity and temperature changes that affected platform environments where carbonates precipitated (Bartolini et al., 2003). A decrease in salinity due to freshwater input would imply lighter values of both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ . Consequently, salinity changes due to variable input of freshwater in marine environments can explain the positive correlation between  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  observed in successive stratigraphic intervals (Bartolini et al., 2003). Temperature strongly affects the isotopic composition of the oxygen, but only weakly the  $\delta^{13}\text{C}$  (Grossman and Ku, 1986; Salomons and Mook, 1986; Turi, 1986). Therefore, an increase in temperature will result in a decrease in  $\delta^{18}\text{O}$  and a slight increase in  $\delta^{13}\text{C}$  (Grossman and Ku, 1986). Such changes in temperature probably explain the shift towards lighter  $\delta^{18}\text{O}$  and slightly heavier  $\delta^{13}\text{C}$  passing from one stratigraphic interval to the other (Bartolini et al., 2003). The general trend translates a change from a humid climate in the earliest Late Oxfordian to a drier climate with increasing temperature in the latest Oxfordian–earliest Kimmeridgian (Bartolini et al., 2003). This climatic interpretation is supported by palynofacies (Pittet and Gorin, 1997) and reef paleoecology (Dupraz, 1999) analysis from the Jura mountains.

### 2.3. Samples and biometry

We selected 40 samples from the Balingen–Tieringen section, presenting variable lithologies and calcium carbonate contents. Smear slides, previously prepared for nanofossil quantification (Pittet and Mattioli, 2002), were observed under a polarising light microscope at a constant magnification of 1250 $\times$ . Across each slide, the first 100 specimens of *Watznaueria britannica*, encountered along random traverses, were collected as digitally captured images using a Sony CCD-video camera mounted on a Leitz Laborlux optical polarising light microscope connected to a PC-type pentium with GIPSVISION software. Biometric measurements were performed with the software ScionImage. At a microscope magnification of 1250 $\times$ , the pixel scale is 12.7 pixels/ $\mu\text{m}$  (1 pixel = 0.0787  $\mu\text{m}$ ). The coccoliths were measured for overall size, and length and width of the central area (Fig. 1). Repeated measurements on the same coccolith allowed us to determine that the accuracy of measurements is  $\pm 1$  pixel (0.0787  $\mu\text{m}$ ). We also calculated three ratios allowing a better definition of the shape of the placoliths: the

Fig. 3. (a) Frequency distribution of length measured in *W. britannica* for each morphotype; (b) Bivariate plot of coccolith length–width; (c) Bivariate plot of central area length–width; (d) Bivariate plot of coccolith length–ellipticity; (e) Bivariate plot of coccolith width–ellipticity; (f) Bivariate plot of central area length–ellipticity; (g) Bivariate plot of central area width–ellipticity. Probabilities  $P < 0.0001$ .

ellipticity of the coccolith (length/width) and of the central area (central area length/central area width), and the proportional size of the central area relative to the coccolith length ((central area length/total length of the coccolith) × 100). The relative abundance counts of the different species within the nannofossil assemblages are those of Pittet and Mattioli (2002) where a variable number of 125–350 specimens was counted in each sample.

Following the method of Renaud et al. (2002), for each sample, the mean coccolith length as well as the 75 percentile (value corresponding to the 75% of the distribution) and 25 percentile (25% of the distribution) were calculated in order to provide morphological indicators independent of the morphological definition, and characteristic of the entire *W. britannica* assemblage. Intra-morphotype morphological variability was first studied using simple linear regression between the different parameters. Then, a principal component analysis (PCA) was used to better describe the relationship between the different biometric variables within the total *Watznaueria britannica* assemblage. The PCA was computed with the software STATVIEW. Variation through time of different biometric parameters measured within the total *W. britannica* assemblage, and of the relative abundances of each morphotype, were also considered and compared.

#### 2.4. Nannofossil assemblages: nutrient index

Along the lithological profile of the Balingen–Tieringen section, analysis of the variations in nannofossil assemblages highlights a succession of six dominant species in relation to gradual increase in carbonate content (Fig. 2b; Pittet and Mattioli, 2002). This succession was interpreted as a trophic preference continuum from high mesotrophic conditions (dominance of small forms, first *Lotharingius hauffii*, then *Watznaueria britannica*) to oligotrophic conditions (dominance of larger forms, such as *Schizosphaerella* spp. and *W. manivitiae*, Fig. 2b). Such a continuum was also evidenced in a contemporaneous section of the same area (Olivier et al., 2004). We carried out a principal component analysis on these relative abundances in order to see if the successive highest relative abundances of these species, interpreted as reflecting different trophic conditions, can be discriminating factors.

In order to investigate the potential paleoecological control on *W. britannica* dynamics, the variables related to morphology and relative abundances were compared to paleoenvironmental factors (trophic conditions in marine surface-waters, deduced from nannofossil assemblages, calcium carbonate content, and stable isotopic data). The relationships between biometric measurements, and Prin-

cipal Component (PC) factors extracted from nannofossil assemblages as well as other paleoenvironmental proxies, were investigated using regression. Finally, their stratigraphic trends were compared.

### 3. Results

#### 3.1. Biometry

The frequency distribution of coccolith length for all the *W. britannica* morphotypes (3938 measurements on 40 samples) shows an unimodal distribution with a mean length of 4.7 μm (Fig. 3a). Morphotypes A and B are the most abundant, whereas Morphotypes D and E are less frequent, and Morphotypes C and F rare (Fig. 3a). The frequency distribution histograms (Fig. 3a), and bivariate plots between the different biometric parameters for all the morphotypes (Fig. 3b–g) show the existence of overlap in size distribution of different morphotypes.

*W. britannica* coccolith size: a strong correlation exists between coccolith length and width considering all the morphotypes ( $r=0.891$ ; Fig. 3b); this correlation is lower if each morphotype is considered separately (Table 2). The length and the width of the central area are also correlated, but display a moderate correlation coefficient of  $r=0.623$  when considering all the morphotypes (Fig. 3c) and of 0.448 to 0.583 if each morphotype is analysed separately (Table 2). This indicates that coccolith length is sufficient to characterize the overall coccolith size, but central area length is insufficient to describe central area size, possibly due to a larger error bar in size measurement or greater variability of length and width of the central area.

*W. britannica* coccolith shape: considering all the morphotypes, ellipticity of the placolith does not show any strong correlation with length (Fig. 3d) or width (Fig. 3e). However, for each morphotype, a negative correlation exists between placolith width and ellipticity (Fig. 3e and Table 2). For the smallest forms (Morphotype A), different shapes, from nearly circular to elliptical forms, were found for similar widths (Fig. 3e), whereas for the largest morphotypes, in particular Morphotype D, the specimens became more circular with increasing width (Fig. 3e and Table 2). The ellipticity of the central area is not correlated with the central area length (Fig. 3f). However, this parameter decreases with increasing central area width (Fig. 3g). For the central area, there is a common pattern to all the *W. britannica* morphotypes (Table 2): when the width of the central area increases, central area becomes more circular. So, central area ellipticity is more related to variations in width than in length.

As it is not possible, due to the overlaps between morphotypes, to discriminate between them based on biometric



Table 2  
Linear regression between different biometric parameters for five of the six morphotypes

Morphotype A				
N=1409	Placolith length	Placolith width	Central area length	Central area width
Placolith width	$r=0.675, p<0.0001$			
Placolith ellipticity	$r=0.190, p<0.0001$	$r=-0.590, p<0.0001$		
Central area width			$r=0.519, p<0.0001$	
Central area ellipticity			$r=0.399, p<0.0001$	$r=-0.546, p<0.0001$
Morphotype B				
N=1599	Placolith length	Placolith width	Central area length	Central area width
Placolith width	$r=0.6, p<0.0001$			
Placolith ellipticity	$r=0.192, p<0.0001$	$r=-0.664, p<0.0001$		
Central area width			$r=0.449, p<0.0001$	
Central area ellipticity			$r=0.371, p<0.0001$	$r=-0.625, p<0.0001$
Morphotype D				
N=496	Placolith length	Placolith width	Central area length	Central area width
Placolith width	$r=0.614, p<0.0001$			
Placolith ellipticity	$r=0.108, p=0.0166$	$r=-0.708, p<0.0001$		
Central area width			$r=0.543, p<0.0001$	
Central area ellipticity			$r=0.313, p<0.0001$	$r=-0.594, p<0.0001$
Morphotype E				
N=340	Placolith length	Placolith width	Central area length	Central area width
Placolith width	$r=0.620, p<0.0001$			
Placolith ellipticity	$r=0.263, p=0.0166$	$r=-0.588, p<0.0001$		
Central area width			$r=0.557, p<0.0001$	
Central area ellipticity			$r=0.360, p<0.0001$	$r=-0.542, p<0.0001$
Morphotype F				
N=85	Placolith length	Placolith width	Central area length	Central area width
Placolith width	$r=0.809, p<0.0001$			
Placolith ellipticity	$r=0.051, p=0.6489$	$r=-0.535, p<0.0001$		
Central area width			$r=0.583, p<0.0001$	
Central area ellipticity			$r=0.273, p=0.0117$	$r=-0.582, p<0.0001$

Abbreviations:  $r$ : coefficient of correlation;  $p$ : probability;  $N$ : number of measurements.

measurements, size and shape of the *W. britannica* morphotypes were analysed all together using a multivariate statistical analysis. A principal component analysis of the biometric variables (coccolith length and width, central area length and width, central opening proportion and ellipticity of the placolith and of the central area) retained three factors with different loading scores for each variable (Fig. 4 and Table 3). The variables describing the overall size (length and width) contribute heavily to the first factor, with also a contribution of the central area width (Fig. 4). This first factor then well describes the overall size of the placolith. The variables describing the central area (central area length) and its opening (central area proportion) strongly contribute to the second factor. The shape of the placolith (ellipticity) loaded heavily on the third factor.

The general pattern of the coccolith length shows an increase in mean size of *W. britannica* during the Late Oxfordian (Fig. 5). When examining in detail the variation through time of the different biometric parameters and of the relative abundance of each morphotype, different steps are recognized roughly corresponding to the stratigraphic intervals defined by Bartolini et al. (2003).

In Interval 1 (Fig. 5), the assemblage of *W. britannica* is dominated by small specimens with a trend towards larger sizes at the top. Morphotypes A and B are the most abundant in this interval and an increase in the relative abundance of Morphotype B is observed. A trend towards more open specimens at the top of this interval, is observed and placoliths are subcircular. The

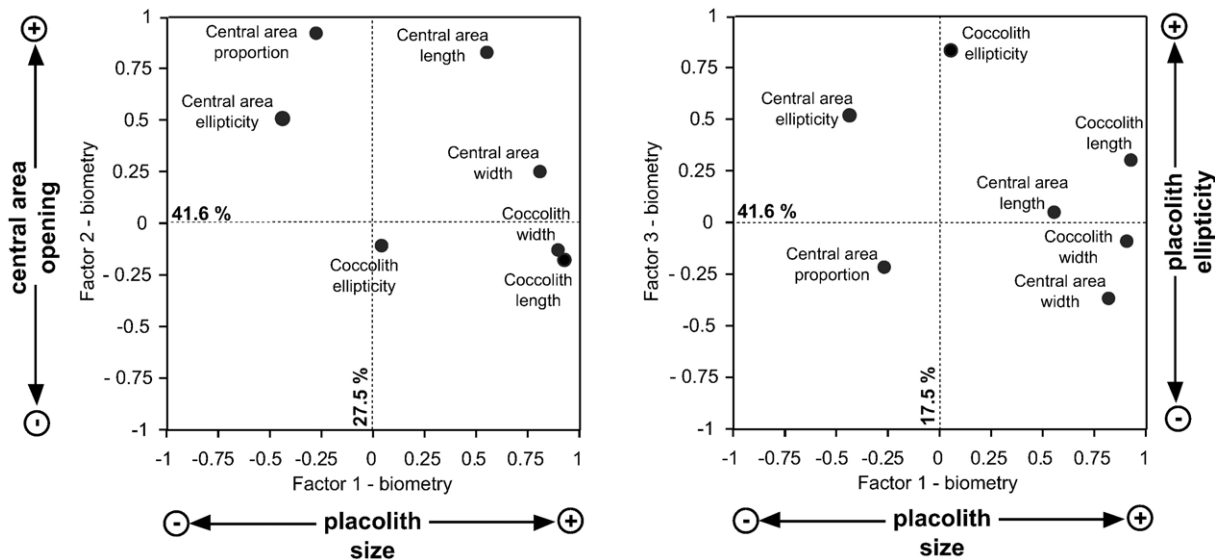


Fig. 4. Results of principal component analysis of biometric parameters of *W. britannica*. Bold numbers correspond to the variance contribution of the estimated factors.

relative abundance of *Watznaueria britannica* compared to all nannofossils slightly decreases during this interval (Pittet and Mattioli, 2002; Fig. 5).

In Interval 2 (Fig. 5), the overall mean size of *W. britannica* placoliths is relatively constant with respect to the top of Interval 1, whereas the proportion of the central area strongly increases. The ellipticity is relatively constant with respect to the Interval 1. All these trends are explained by the highest abundance of Morphotype E, which is subelliptical to subcircular and presents with Morphotype A, also well represented in this interval, the more opened central area (Fig. 1). The morphotype E is abundant only in this interval. The relative abundance of *Watznaueria britannica* compared to all nannofossils is at its highest here (Pittet and Mattioli, 2002; Fig. 5).

In Interval 3 (Fig. 5), placoliths are small, and became subelliptical towards the top. The central area is slightly reduced with respect to the Interval 2. Morphotype A is

dominant within the *W. britannica* population. The percentage of *W. britannica* in the nannofossil assemblages is always high (Pittet and Mattioli, 2002; Fig. 5).

In Interval 4 (Fig. 5), major changes are recorded. An increase in the overall mean size of *W. britannica* placoliths is recorded; placoliths are characterized by a reduced central area, and are more elliptical. These trends are partly explained by an increase in the relative proportion of Morphotypes B and D, with the largest size corresponding to a maximum percentage of Morphotype D between 15 and 17 m. Significant increase in size of both the largest specimens (75 percentile) and the smallest (25 percentile) placoliths of *W. britannica* is also observed. The relative abundance of *W. britannica* compared to other nannofossils starts to decrease in this interval (Pittet and Mattioli, 2002; Fig. 5).

In Interval 5 (Fig. 5), the trend is reversed, with a shift towards decreasing placolith mean size accompanied by a

Table 3

Additional statistical information on the varimax rotated principal component analyses (PCA) for both the biometric analysis and the nannofossil assemblage

	Factor 1 biometry	Factor 2 biometry	Factor 3 biometry	Factor 1 assemblage	Factor 2 assemblage	Factor 3 assemblage
<i>N</i>	3938	3938	3938	97	97	97
Nb of variables	7	7	7	6	6	6
Nb of factors estimated	3	3	3	3	3	3
Nb of factors extracted	3	3	3	2	2	2
Eigen values	2.912	1.923	1.224	3.161	1.463	0.559
% variance	41.6	27.5	17.5	52.7	24.4	9.3

Abbreviations: *N*: number of data; Nb: number.

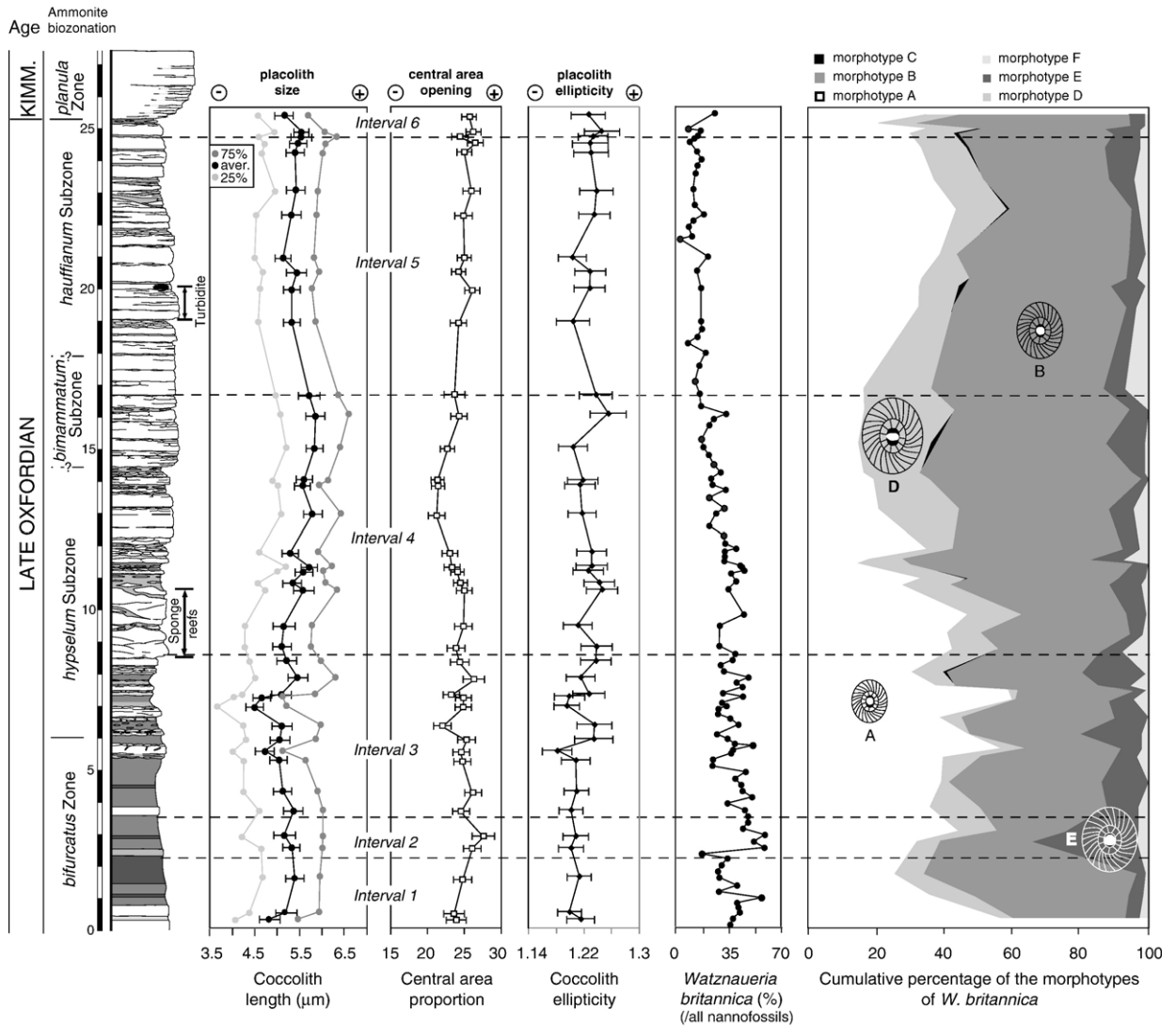


Fig. 5. Stratigraphic changes in placolith size, central area opening and coccolith ellipticity. They are here compared to the relative abundance of *W. britannica* with respect to the entire nannofossil assemblage, and to the percentage of each morphotype within the *W. britannica* assemblage. Error bars: 95% standard error.

significant decrease in size of the largest and the smallest specimens. Placoliths are characterized by a larger central area opening, are more circular at the beginning of the interval with respect to the Interval 4, but became more elliptical at the top. These trends reflect an increase in the relative abundance of Morphotype A. Low percentages of *W. britannica* are recorded in this interval (Pittet and Mattioli, 2002; Fig. 5).

In Interval 6 (Fig. 5), both the placolith mean size and the central area opening slightly increase. More elliptical forms are observed. These trends correspond to an increase in the relative abundance of Morphotype B. The relative abundance of *W. britannica* compared to other nannofossils stays low (Pittet and Mattioli, 2002; Fig. 5).

### 3.2. Nannofossil assemblage: nutrient index

The principal component analysis using the relative abundances of the six most abundant species of nannofossils retained two factors (Fig. 6). *Schizosphaerella* spp. and *W. manivittae* show a high positive contribution to the first factor, whereas *W. britannica* and *Lotharingius hauffii* are in opposition (Fig. 6). *Cyclagelosphaera margerelii* and *W. barnesiae* show high positive loadings on the second factor (Fig. 6). The opposite position of the two nannofossil groups *Schizosphaerella* spp.–*W. manivittae* and *W. britannica*–*L. hauffii* on the first principal component can be interpreted in terms of different trophic preferences. Pittet and Mattioli (2002) and Olivier et al.

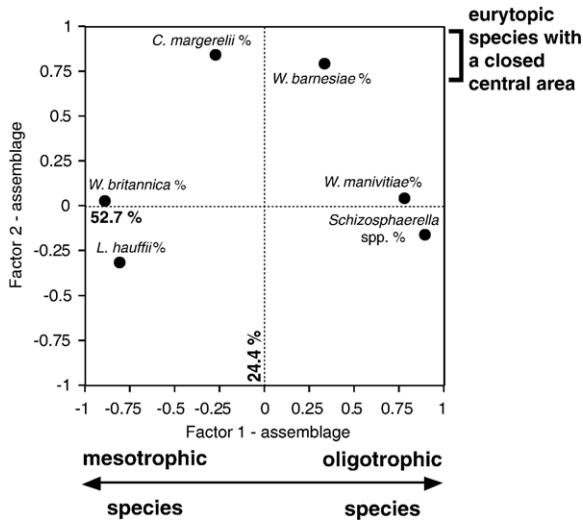


Fig. 6. Results of the principal component analysis applied to the relative abundance of the six dominant taxa in the nannofossil assemblage. Bold numbers correspond to the variance contribution of the 3 estimated factors.

(2004) demonstrated that high abundances of large forms, such as *Schizosphaerella* spp. and *W. manivittiae*, characterized limestone lithologies and represented oligotrophic conditions in surface-waters, whereas smaller forms, such as *W. britannica* and *L. hauffii* were abundant and dominant in marls and represent high mesotrophic conditions (Fig. 2b). So, the first factor extracted from this Principal Component Analysis (PCA) can be interpreted in terms of trophic condition. The positive and negative loadings correspond to oligotrophic and high mesotrophic conditions, respectively. The second factor is more difficult to interpret. Pittet and Mattioli (2002) showed that the behaviour of *W. bamesiae* and *C. margerelii* with respect to trophic levels is not very clear and can be explained by an intermediate position along the trophic preference continuum. These two species are also considered as eurytopic taxa (*W. bamesiae*, Mutterlose, 1991; Street and Bown, 2000; Lees et al., 2004; *C. margerelii*, Bown, 2005; Giraud et al., 2005). Bown (2005) also suggests that they could be adapted to unstable and/or neritic environments. Both these two eurytopic species, are characterised by a closed central area and are represented by the PC factor 2 (positive loadings).

The stratigraphic evolution of the PC factor 1 extracted from the nannofossil assemblage composition is binary (Fig. 7). From the base of the section up to 12 m, mesotrophic species characterize the nannofossil assemblages (Fig. 7). From 12 m to the top of the section, oligotrophic species characterize the nannofossil assemblages. This change exactly coincides with the lithologic change from alternating marl and limestone sediments to more calcareous sediments (Fig. 7). The stratigraphic variation of PC

factor 2 extracted from nannofossil assemblage composition is more complex, with different intervals that do not correspond to the stratigraphic intervals defined by Bartolini et al. (2003) (Fig. 7). Eurytopic species, characterized by a closed central area, are well represented within the stratigraphic Intervals 3 and 4, as well as in few samples of Interval 5 (Fig. 7).

### 3.3. Relationships between biometric factors and paleoenvironmental proxies

Fig. 8 only presents significant correlations between the different variables considered. Fig. 8a shows the bivariate

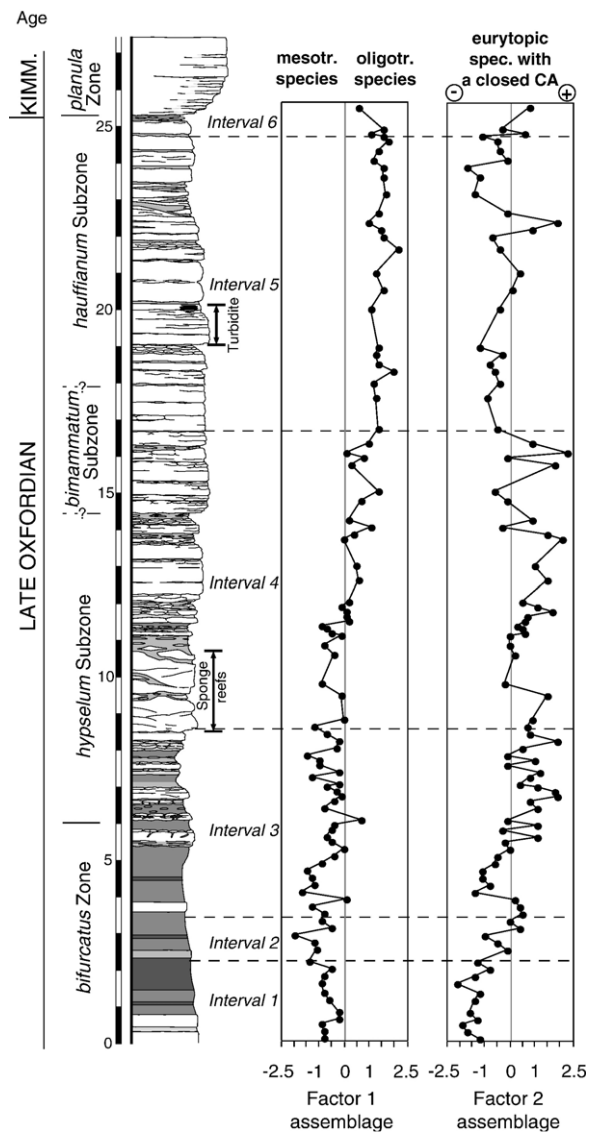


Fig. 7. Stratigraphic patterns of the 2 principal component factors extracted from nannofossil assemblages.

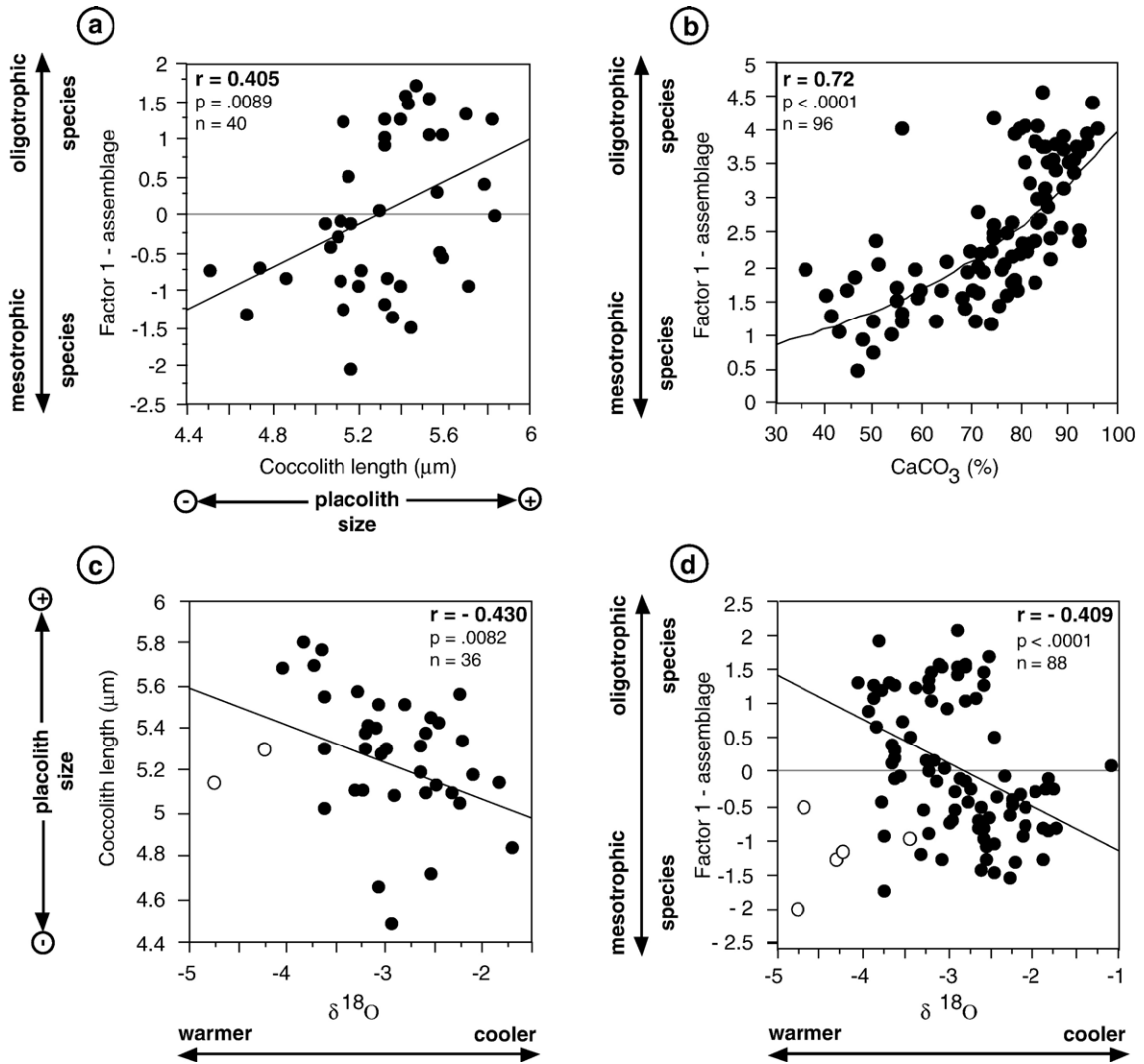


Fig. 8. Bivariate plots showing relationships between (a) coccolith size and PC Factor 1 extracted from nannofossil assemblage; (b) PC factor 1 extracted from nannofossil assemblage and calcium carbonate content (as the relation between the two variables is exponential, we have transformed into positive values the negative values of the Factor 1-assemblage axis); (c) coccolith size and oxygen isotope data, and (d) PC factor 1 extracted from nannofossil assemblage and oxygen isotope data. White dots represent samples not considered in the regression; they correspond to samples of Interval 2, where δ<sup>18</sup>O values record salinity changes rather than temperature changes (Bartolini et al., 2003).

plot between coccolith length and PC Factor 1 extracted from nannofossil assemblage composition. With respect to Fig. 7, only 40 samples corresponding to the samples selected for biometric studies are considered in this plot. The observed positive correlation between these two variables suggests that increasing placolith size may partly be associated with oligotrophic conditions (positive values on Factor 1-assemblage). Fig. 8b presents the bivariate plot between PC Factor 1 extracted from nannofossil assemblage composition and calcium carbonate content. Ninety-six samples, corresponding to the samples studied by Pittet and Mattioli (2002), are considered in this figure. A good

positive correlation is found between these two variables and confirms the observations of Pittet and Mattioli (2002), namely that oligotrophic conditions in the deep shelf surface-waters were linked to a dominant carbonate sedimentation. Fig. 8c shows the correlation between coccolith length, and the δ<sup>18</sup>O composition of the carbonates; with respect to Fig. 8a, only 38 samples corresponding to the samples selected for geochemistry are considered and two of them are not taking into account for the regression (cf. Fig. 8 legend). The negative correlation observed shows that the size of the placoliths and temperature are linked, and increasing size of the coccoliths is associated with

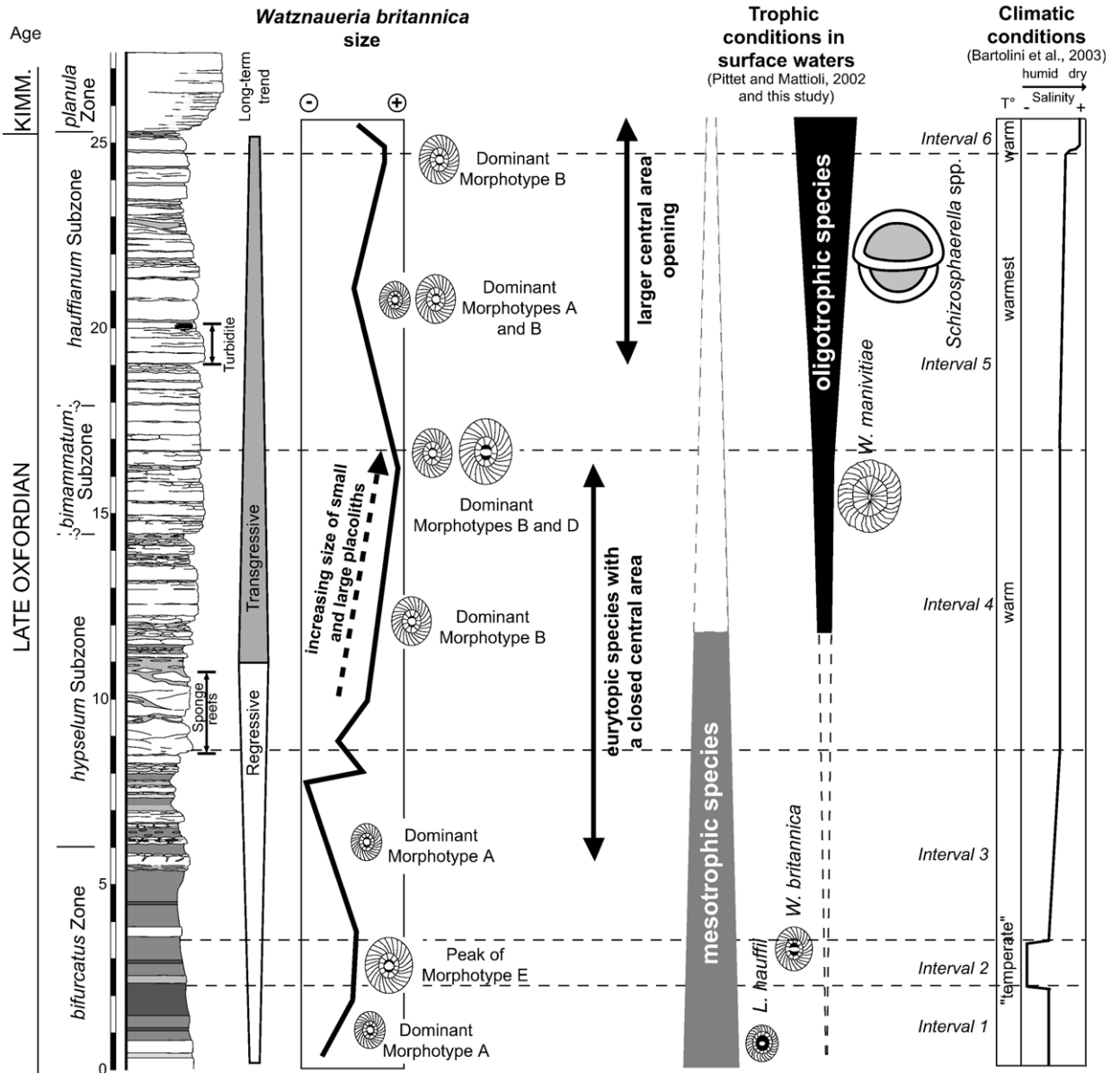


Fig. 9. Synthesis representing the main trends in size variation of *W. britannica* relative to variations in paleoenvironmental conditions for the Late Oxfordian–Early Kimmeridgian in the Balingen–Tieringen section. Interpretations of the climatic conditions are from Bartolini et al. (2003).

increasing temperature. Fig. 8d displays the bivariate plot between PC Factor 1 extracted from nannofossil assemblage composition, and the  $\delta^{18}\text{O}$  composition of the carbonates; with respect to Fig. 8b, only 93 samples corresponding to the samples selected for geochemistry are considered and five of them are not taking into account for the regression (cf. Fig. 8 legend). A negative correlation is found between these two variables, suggesting that more oligotrophic conditions correspond to warmer climatic conditions.

#### 4. Discussion

Coccolith size probably results from interaction between the mechanisms of coccolith biosynthesis, morphotype/species replacement in assemblages, and environmental control. The size of nannofossils may also be an important factor controlling preservation. Preservation may also be a function of the calcium carbonate content of the samples (Stoll and Schrag, 2001). Pittet and Mattioli (2002) evaluated the

preservation of nanofossils of the Balingen–Tieringen section in different ways. They studied the relationship between nanofossil assemblage composition and  $\text{CaCO}_3$ , and also the relationships between the different-sized nanofossils and the carbonate content. *Watznaueria britannica*, which is considered to represent one of the most delicate taxa with *Lotharingius hauffii* in the Balingen–Tieringen section, presents its highest percentage in carbonate-rich sediments (50–70%  $\text{CaCO}_3$ ). A decrease in the relative abundance of this species in the most carbonate-rich samples ( $\text{CaCO}_3 \geq 90\%$ ) could be partially the result of diagenetic control. Pittet and Mattioli (2002) also tested the relationship between the three size-ranges (<6  $\mu\text{m}$ , 6–8  $\mu\text{m}$ , and >8  $\mu\text{m}$ ) recognized for *W. britannica* and the carbonate content. They showed that the smallest and the largest specimens of *W. britannica* decrease in relative abundance over 70%  $\text{CaCO}_3$ , whereas specimens with intermediate size are most common in samples over 55%  $\text{CaCO}_3$  and less abundant in marls. The control on the percentages of *W. britannica* specimens of different size is therefore not diagenetic but more likely paleoenvironmental.

#### 4.1. Coccolith growth patterns

Young and Bown (1991) recognized within *Watznaueria fossacineta* coccoliths a wide range in morphology and size including protococcolith morphologies, that they interpreted as an ontogenetic growth sequence. They also suggest that *W. lucasii* and *W. reinhardtii* could represent early growth stages of *W. britannica*. Contrary to the assessment of Young and Bown (1991), Walsworth-Bell (2000) suggests that specimens possessing a bar which bifurcates at both ends (a description which corresponds to *W. reinhardtii*) could represent a late stage of *W. britannica* growth. Walsworth-Bell (2000) recognized in the Oxford Clay Formation (Middle Callovian–Early Oxfordian), what he considered to be protococcoliths *W. britannica*, characterized by a large central area spanned by an incomplete bar. These different authors interpret the morphological variability and size observed within the *Watznaueria* genus as variable ontogenetic development. As reported in the taxonomic Appendix, *W. lucasii* and *W. reinhardtii* are here considered as different species with respect to *W. britannica*. In a way similar to the modern coccolithophore *Coccolithus pelagicus*, the bridge spanning the central area of *W. britannica* is a structure formed from crystal units separate from the rim (Young et al., 1999). In the very early growth stage (small forms) of *C. pelagicus*, a very thin bar is present, spanning a wide open central area and becomes a thick bar spanning a narrower central area in the later growth stage (large forms; Young and Henriksen, 2003). In

*W. britannica*, a thin bridge spanning a large central area is characteristic of the large Morphotype C, whereas a thicker bridge spanning a central area of small size is characteristic of the large Morphotype D (Fig. 1). The smallest Morphotypes A do not present a thin bridge spanning a large central area but a central area of intermediate size with a bridge with intermediate thickness between Morphotypes C and D (Fig. 1). According to these remarks, the different morphotypes of *W. britannica* distinguished here cannot be considered as different ontogenetic stages. They could conversely represent members of a morphological continuum as suggested for the *W. barnesiaefossacineta* group by Lees et al. (2004) and Bormemann et al. (in press).

As first demonstrated for *Pseudoemiliana lacunosa* or *Emiliana huxleyi* (Young, 1989), the form of coccoliths varies with changing size, and size has a higher variability than shape (ellipticity; Young, 1989). Larger placoliths are less elliptical. The allometric trend recognized for *W. britannica* coccoliths is analogous to those described for modern placoliths. The placoliths of *W. britannica* tend to be more circular as their width increases (Fig. 3e and Table 2) because the growth of placoliths is more effective for the minor axis.

The shape of the bridge is a qualitative parameter useful to distinguish between the different morphotypes of *W. britannica*. However, it is not yet possible to quantify its morphological variability. The allometric trend recognized within the morphotypes of *W. britannica* on the total placolith and on the central area suggests that they can represent intra-specific variability rather than different species. However, as the shape of the bridge is very different for the six morphotypes, and our study limited to one section and one stratigraphic interval, it is suggested here for further studies to take into consideration the different morphotypes of *W. britannica* in order to know if they represent intra-specific variants or are different species.

A morphological trend through time is also present for *W. britannica*. De Kaenel (1990) and E. Mattioli (personal observation) recognized that *W. britannica* coccoliths show an evolution from small forms with a small central area (uppermost Aalenian–Lower Bajocian) to larger forms with a larger bridge more similar to *W. reinhardtii* (Upper Bajocian). These observations argue against the assessment of Young and Bown (1991) that *W. reinhardtii* could represent early growth stages of *W. britannica*.

#### 4.2. Morphological variation through time and relationships with paleoenvironmental parameters

What promotes an increase in size of a coccolith within the *W. britannica* population? The stratigraphic increase in mean placolith size is mainly driven by

relative abundance changes of the different-sized morphotypes with an increase in the contribution of large coccoliths (Morphotype D; Figs 5 and 9).

Very recent studies have shown that among extant coccolithophorids, morphological variability (mainly size) of a species which was currently interpreted as intraspecific variations in fact represent genotypically discrete species but with strong ecological differences (Geisen et al., 2002; Saez et al., 2003; Quinn et al., 2004). Amongst the different parameters which can affect the size of the coccoliths, fertility of the surface-waters and temperature are important (e.g. McIntyre et al., 1970; Winter et al., 1994), but variations in size observed can be opposite from one species to another one. During the Late Oxfordian, the Swabian Alb deep shelf records major paleoenvironmental changes and, in particular, changes in trophic conditions of the surface-waters, deduced from the analysis of nannofossil assemblage composition by Pittet and Mattioli (2002), Olivier et al. (2004) and by the present study (Figs 7 and 9), as well as changes in temperature, as suggested by Bartolini et al. (2003) (Figs. 2b and 9).

Studies from laboratory experiments on growth rate (number of coccoliths produced) and calcification of *Emiliania huxleyi* and *Gephyrocapsa oceanica*, two coccolithophorid species dominating in modern oceans, showed that successive different trophic conditions stimulate these two processes. The growth rate of the cell was increased under nutrient-sufficient supply and then the calcification was stimulated by an increase in cell volume when the nutrient supply was reduced by algal growth (Shiraiwa, 2003). For other species, observed in natural environments, calcification can be stimulated when nutrient supply is high. *Calcidiscus leptoporus* (sensu lato) consists of three subtaxa or species (e.g. Quinn et al., 2004), previously described as large, intermediate and small specimens (Bollmann, 1997). The large form of *C. leptoporus* (sensu lato) occurs primarily in higher productivity, mesotrophic waters (Renaud et al., 2002). In the Balingen–Tieringen section, there is a positive correlation between an increase in larger forms and a decrease in abundance of *W. britannica* coccoliths (Fig. 5). The high abundance of *W. britannica* placoliths is indicative of mesotrophic conditions (Figs 2b and 9), whereas the increasing size of *W. britannica* placoliths corresponds to more oligotrophic conditions in the surface-waters (Figs 8a and 9). Oligotrophic conditions are positively correlated to the carbonate content (Figs 8b and 9). Geisen et al. (1998) firstly recognized, in Hauterivian sediments a morphological difference between the placoliths of *Watznaueria* between pale, carbonate-rich beds showing a dominance of large coccoliths (greater length) with large outer shields (considered as mature coccoliths sensu Young and Bown,

1991), compared with non-mature (small) coccoliths in dark and argillaceous beds, but they did not interpret these differences. These different observations suggest that, for *W. britannica*, algal growth (represented by the number of placoliths produced) seems to increase when nutrient supply is high, whereas calcification seems to be stimulated (large and well-calcified placoliths) when nutrient supply is lower and when carbonate supply is dominant over siliciclastic (and nutrient) supply.

In the Balingen–Tieringen section, when the surface-waters became more oligotrophic, temperature increased (Fig. 9). Temperature is also a dominant parameter affecting the size of placoliths. For instance, the living large species *Coccolithus pelagicus* is restricted to high latitudes, and *Emiliania huxleyi* tends to be more heavily calcified in cold waters (Burns, 1977; Jordan, 1988; Okada, 1989; Young and Westbroek, 1991). More recently, Colmenero-Hidalgo et al. (2002) recognized an increase in abundance of large *E. huxleyi* during the cold Heinrich (HE) and Dansgaard–Oeschger (DO) events. A nice example of the relationship between the sea-surface temperature and morphological variability is illustrated with *Gephyrocapsa* (Bollmann, 1997; Bollmann et al., 2002): small group with low bridge angle (*Gephyrocapsa* cold: GC) only occurs below a mean sea surface temperature of 14 °C, while larger morphotypes with high bridge angle (*Gephyrocapsa* equatorial: GE) are more abundant in high sea-surface temperature (Bollmann et al., 2002). However, the fertility of the surface-water often co-varies with temperature in modern oceanic environments, and it becomes very difficult to distinguish the influence of these two parameters on coccolith size. Henderiks and Renaud (2004) have shown in Atlantic during the Last Glacial Maximum that the overall increase in size of *C. leptoporus* (sensu lato) mainly due to dominant production of large coccoliths, was an expression of enhanced productivity in cooler glacial surface-waters. Beaufort and Heussner (2001) have also shown in sediment trap samples from North Atlantic that the abundance pattern of the two large and small forms of *C. leptoporus* (sensu lato) could be related to seasonal variations of the thermo-nutricline. For the fossil species, Mattioli et al. (2004) have suggested that an increase in coccolith size of the placolith genera *Biscutum* and *Similiscutum* can be related to high surface-water temperatures and/or to high nutrient concentrations. Bornemann et al. (2003) observed that during the mid to Late Tithonian, a higher abundance of strongly-calcified nannoliths, associated with large-sized *Watznaueria* such as *W. manivittiae*, was linked to oligotrophic surface-waters but cooler temperatures in a period of low pCO<sub>2</sub> conditions. In the Lower Berriasian, a size reduction of *Watznaueria* was associated with higher abundances of



coccolith taxa indicative of higher fertility of the surface-waters (Bornemann et al., 2003). In the Balingen–Tieringen section, the increase in temperature starts in stratigraphic Interval 4 and warmer conditions prevailed until the top of the section. In the fourth interval, more oligotrophic conditions prevailed, with respect to the base of the section (Fig. 9). In the fifth and sixth intervals, drier conditions (lower nutrient levels with respect to Interval 4) prevailed (Fig. 9). An increase in the relative abundance of large morphotypes is observed in Intervals 4 to 6, but in the fourth interval only, an increase in size of the largest specimens occurred parallel with a slight increase in size of the smallest coccoliths (Figs. 5 and 9). These latter results suggest that temperature and fertility of the surface-waters control *W. britannica* placolith size.

Central area opening size can also be taken into consideration, because it could be ecologically controlled. Backman (1980), Wise (1983), and Backman and Hermelin (1986) have shown that some reticulofenestrifid species with central area openings, exhibit smaller relative opening size under cooler conditions. High-latitude Neogene reticulofenestrifid assemblages are often dominated by coccoliths with closed central areas, whereas low-latitude assemblages are dominated by coccoliths with open central areas (Young, 1990). McIntyre et al. (1970), Gartner (1972), and Bukry (1973) have observed, for *Gephyrocapsa* species, an increase in the size of central area opening with increasing temperature, but a trend towards larger opening sizes may also be related to oligotrophic conditions (Hagino et al., 2000 for *Gephyrocapsa oceanica*). Beaufort and Heussner (2001) have observed the opposite trend for *Emiliania huxleyi*, with dominance of heavy calcified morphotype (closed central area) in summer (high light intensity) and calm conditions, and dominance of less calcified morphotype (open central area) during bloom periods in winter (low light intensity). The fourth interval of the Balingen–Tieringen section presents the largest specimens of *W. britannica* with a reduced central opening (Figs 5 and 9). At the same time, the eurytopic species, *W. barnesiae* and *C. margerelii*, both characterized by closed central areas, are well represented in the nannofossil assemblages (Figs 7 and 9). The fifth and sixth intervals show an increase in the size of central area opening. So it seems that warm temperatures, associated with low oligotrophic conditions, are optimal for the calcification of *W. britannica* (more calcified, i.e., larger specimens with reduced central area), whereas when surface-waters become increasingly oligotrophic (lower nutrient concentration), the specimens of *W. britannica* are less calcified (more elliptical with a greater relative central area opening). The peak in abundance of Morphotype E, characterized by a large central opening, observed at the

base of the section (Figs 5 and 9), occurs when the most humid conditions are recorded (Figs 7 and 9). This observation seems to be in contradiction to the previous statement. However, a “strong” (2–4‰; Bartolini et al., 2003) decrease in salinity recorded in the Interval 2 may explain the increase in abundance of Morphotype E, which was possibly favored by low salinity (Fig. 9). Salinity effects on coccolith morphology have been demonstrated for *E. huxleyi*. Coccoliths of coastal isolates grown in media of 17‰ salinity exhibit reduced length of the proximal and distal shield elements with no reduction in the central area diameter, compared to coccoliths of oceanic isolates (Green et al., 1998).

The increasing calcification of *W. britannica* occurs at the base of a transgressive system tract (Pittet and Mattioli, 2002; Fig. 9). The general transgressive trend created an extension of the area of carbonate production on the platform and thus intensified the export of carbonates towards deeper environments. During this period, climate, sea level and sedimentation changes are recorded in different areas. A decrease in  $\delta^{13}\text{C}$  values measured in bulk carbonate rock is recorded, starting in the upper Middle Oxfordian (Tethyan sections, Bartolini et al., 1999; Poland, Wierzbowski, 2002; Germany, Gröcke et al., 2003). This change has been related to changes in sea level associated with an episode of carbonate platform growth and increasing carbonate sedimentation rate, as a consequence of more oligotrophic conditions (Bartolini et al., 1999; Wierzbowski, 2002). The carbonate platform growth could not only be linked to more oligotrophic conditions but also to a warming of surface-waters as demonstrated on the Jura platform, starting in the Late Oxfordian and recorded until the Kimmeridgian (Gröcke et al., 2003; Lécuyer et al., 2003). These latter authors estimated up to a 5 °C thermal increase of the surface-waters in the western Tethys. Oligotrophic conditions in surface waters are also linked to drier climatic conditions, as demonstrated for southern Germany (Pittet and Mattioli, 2002; Bartolini et al., 2003; this study). The distribution of reefal facies observed between 10°S and 32°N during the Late Oxfordian–Early Kimmeridgian further imply aridity in the Tethyan Mediterranean area (Cecca et al., 2005), in agreement with the observations in southern Germany.

## 5. Conclusions

The six morphotypes of *Watznaueria britannica* recognized in the light microscope present overlaps in their distributions, based on the different biometric parameters measured, and show a reduced morphological variability compared to a significant size gradient.

An allometric trend is recognized for the total placolith and the central area within the total *W. britannica* assemblage, suggesting that the different morphotypes may represent intra-specific variability rather than different species. However, as the shape of the bridge, a qualitative parameter, is very different for the six morphotypes of *W. britannica*, and as our study is limited to one section and one stratigraphic interval, we suggest further studies to address the different morphotypes of *W. britannica*, in order to find out if these represent intra-specific variants or are different species.

During the Late Oxfordian, the overall size of *W. britannica* coccoliths increases, mainly driven by an increase in the contribution of large morphotypes.

The variations in size and abundance of *W. britannica* observed for the Late Oxfordian in the Balingen–Tieringen section (southern Germany) are related to paleoenvironmental factors. Increasing sizes are associated with a lowering of the trophic level in the surface-waters and warm climatic conditions. In detail, low oligotrophic conditions in the surface-waters, associated with warm temperatures, seem to be optimal for the calcification of *W. britannica* (producing more calcified specimens), and when these conditions became increasingly oligotrophic but always warm, the specimens of *W. britannica* became less calcified (more elliptical, with a relative wider central area opening). Salinity seems to have had no influence on the placolith size, but low salinity conditions could have been responsible for the increase in abundance of one morphotype of *W. britannica* (E).

## Acknowledgements

We are extremely grateful to S. Renaud for many useful suggestions. The manuscript was considerably improved following the comments of Dr Jackie Lees and an anonymous reviewer. This research was financed by ECLIPSE II — CNRS, 2004–2005.

## Appendix A. Taxonomy

This appendix includes taxonomic discussions about *Watznaueria britannica*. Following the guidelines of Bown et al. (1988), *Ellipsagelosphaera* Noël, 1965 is considered to be a synonym of *Watznaueria* Reinhardt, 1964 and the former is not used.

*Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964.

1963 *Coccolithus britannicus* Stradner, p. 10, pl. 1, Figs. 7–7a.

1964 *Watznaueria britannica* (Stradner, 1963) Reinhardt, p. 753, pl. 2, Figs. 3–5a–b.

1965 *Coccolithus britannicus* Stradner, 1963; Black, p. 132, Fig. 6.

1965 *Ellipsagelosphaera lucasii* Noël, pl. 11, Fig. 5.

1966 *Coccolithus britannicus* Stradner, 1963; Marsch, p. 378, pl. 2, Figs. 1–4.

1966 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Reinhardt, 1966, p. 17, Figs. 4a–b; pl. 4, Fig. 7.

1968 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, text p. 71.

1971 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Rood et al., p. 269, pl. 5, Fig. 5.

1973 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Noël, pl. 14, Fig. 6.

1973 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Roth, p. 723, pl. 26, Fig. 2.

1974 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Barnard and Hay, pl. 2, Fig. 7; pl. 5, Fig. 6.

1975 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Grün and Allemann, p. 159–160, pl. 1, Fig. 12; pl. 2, Figs. 1, 3.

*non* 1975 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Grün and Allemann, p. 59–160, pl. 1, Fig. 12; pl. 2, Figs. 2, 4.

1976 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Keupp, p. 363, Figs. 2, 5.

1976 *Ellipsagelosphaera communis* (Reinhardt, 1964) Perch-Nielsen, 1968; Moshkovitz and Erlich, pl. 3, Figs. 2, 3, 6, 7, 10, 11, 12; pl. 4, Figs. 2, 5, 6, 9, 10.

1976 *Ellipsagelosphaera* sp. cf. *E. britannica*; Moshkovitz and Erlich, pl. 4, Figs. 16–19.

1976 *Watznaueria communis* Reinhardt, 1964; Thierstein, pl. 2, Figs. 12, 13.

1977 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Keupp, p. 36, pl. 8, Figs. 1, 2, 3, 4, 6.

*non* 1977 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Keupp, p. 36, pl. 8, Fig. 5.

1977 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Wise and Wind, p. 485, pl. 86, Fig. 4; p. 489, pl. 88, Fig. 8.

1978 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Hamilton, p. 39, pl. 1, Figs. 1, 4.

*non* 1978 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Roth, p. 755, pl. 1, Fig. 9.

1979 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Hamilton, p. 17, pl. 12, Figs. 1, 2.

*non* 1979 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Medd, pl. 8 Figs. 1, 2.

1980 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Grün and Zweili, p. 311, pl. 1, Fig. 12; p. 313, pl. 2, Figs. 1–3.

1982 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Hamilton, p. 37, pl. 3.3, Figs. 13, 14.

1982 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1982; Taylor, p. 63, pl. 4.2, Fig. 12.

1983 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Hemgreen et al., p. 123, pl. 6, Figs. 1, 3, 12.

1985 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Perch-Nielsen, p. 373, Figs. 40.8, 40.9; p. 336, Figs. 5.26–5.28.

1986 *Watznaueria communis* Reinhardt, 1964; Aita and Okada, p. 125, pl. 8, Fig. 6.

*non Watznaueria britannica* (Stradner, 1963) Reinhardt 1964; Aita and Okada, p. 125, pl. 8, Fig. 7.

1987 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Erba and Quadrio, p. 89, pl. 2, Figs. 4, 6, 9, 12, 13.

1988 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Bown et al., p. 111, pl. 1, Fig. 22.

*non* 1989 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Crux, p. 183, pl. 8.1, Fig. 10; p. 201, pl. 8,10, Fig. 12.

1990 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Baldanza et al., p. 235, pl. 2, Fig. 6.

1990 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Erba, p. 255, pl. 3, Figs. 1, 2. 1990 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; de Kaenel, pl. 25, Figs. 10, 12, 13.

*non Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; de Kaenel, pl. 25, Fig. 11.

*non* 1991 *Ellipsagelosphaera britannica* (Stradner, 1963) Perch-Nielsen, 1968; Fiorentino, p. 121 pl. 1, Fig. 9; p. 133, pl. 3, Fig. 4.

1992 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Cobianchi, p. 101, Fig. 22e.

1992 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Cobianchi et al., p. 22, Fig. 1.

1992 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Reale et al., p. 65, pl. 3, Figs. 17–20.

1995 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Mattioli, p. 184, pl. 16, Figs. 1–6.

1997 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Gardin in Cariou and Hantzpergue, p. 328, pl. 41, Figs. 12, 13.

1998 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Bown, p. 68, pl. 4.8, Figs. 3–6; p. 82, pl. 4.15, Figs. 25–26; p. 180, pl. 6.7, Fig. 23.

2003 *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; Kessels et al., p. 748, Figs. 4.7, 4.8.

2003 *Watznaueria communis* Reinhardt, 1964; Kessels et al., p. 748, Figs. 4.9, 4.10.

*Diagnosis*: “Elliptical coccoliths consisting of two closely appressed plates; the oval central opening is transversely spanned by a short sturdy bridge” (Stradner, 1963, p. 10).

*Description*: Following the remarks of Reale et al. (1992, taxonomic notes: Appendix) we assign to the species *Watznaueria britannica* the specimens that present in their central area a bridge, which is parallel to the minor axis of the ellipse and is bright and optically discontinuous (Fig. 1) with respect to the inner cycle of the coccolith rim under crossed-nicols. *Watznaueria britannica* varies considerably in placolith size, opening of the central area, and shape of the bridge. We can subdivide it into six morphotypes, A (Fig. 1a, d), B (Fig. 1b, e), C (Fig. 1c, f), D (Fig. 1g, j), E (Fig. 1h, k), and F (Fig. 1i, l).

*Remarks*: Specimens with a bridge inclined with respect to the minor axis of the ellipse are assigned to *Watznaueria frequens* (Noël, 1965) Bukry, 1975, as it is clearly seen on the holotype photograph (Noël, 1965). *Watznaueria communis* Reinhardt, 1964, is retained for the forms which have a small central hole spanned by a bridge, optically continuous with the inner cycle of the coccolith under crossed nicols (e. g. Cobianchi, 1992 p. 101, Fig. 22f). We consider as *Watznaueria lucasii* (Noël) Bown et al., 1988, the specimens which have a diameter of central opening equal or exceeding 50% of the total diameter of the coccolith, as illustrated by Noël (1965). We consider as *Watznaueria reinhardtii* Rood, Hay and Barnard 1971 the specimens with a narrow rim, a large central opening, and a bridge which bifurcates laterally, as described by Rood et al. (1971).

## References

- Bartolini, A., Baumgartner, P.O., Guex, J., 1999. Middle and Late Jurassic radiolarian palaeoecology versus carbon-isotope stratigraphy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 145, 43–60.
- Bartolini, A., Pittet, B., Mattioli, E., Hunziker, J.C., 2003. Regional control on stable isotope signature in deep-shelf sediments: an example of the Late Jurassic of southern Germany (Oxfordian–Kimmeridgian). *Sediment. Geol.* 160, 107–130.
- Backman, J., 1980. Miocene–Pliocene nannofossils and sedimentation rates in the Hatton–Rockall Basin, NE Atlantic Ocean. *Stockh. Contrib. Geol.* 36, 1–91.
- Backman, J., Hermelin, J.O.R., 1986. Morphometry of the Eocene nannofossil *Reticulofenestra umbilicus* lineage and its biochronological consequences. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 57, 103–116.
- Beaufort, L., Heussner, S., 2001. Seasonal dynamics of calcareous nannoplankton on a West European continental margin: The Bay of Biscay. *Mar. Micropaleontol.* 43, 27–55.
- Bollmann, J., 1997. Morphology and biogeography of *Gephyrocapsa* coccoliths in Holocene sediments. *Mar. Micropaleontol.* 29, 319–350.

- Bollmann, J., Baumann, K.-H., Thierstein, H.R., 1998. Global dominance of *Gephyrocapsa* coccoliths in the late Pleistocene: selective dissolution, evolution, or global environmental change? *Paleoceanography* 13, 517–529.
- Bollmann, J., Henderiks, J., Brabec, B., 2002. Global calibration of *Gephyrocapsa* coccolith abundances in Holocene sediments for paleotemperature assessment. *Paleoceanography* 17, 1–9.
- Bornemann, A., Aschwer, U., Mutterlose, J., 2003. The impact of calcareous nannofossils on the pelagic carbonate accumulation across the Jurassic–Cretaceous boundary. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 199, 187–228.
- Bornemann, A., Mutterlose, J., in press. Size analyses of the coccolith species *Biscutum constans* and *Watznaueria barnesiae* from the Late Albian ‘Niveau Breistroffer’ (SE France): taxonomic and palaeoecological implications. *Geobios.* 39 (5).
- Bown, P.R., 1992. New calcareous nannofossil taxa from the Jurassic/Cretaceous boundary interval of Sites 765 and 261, Argo Abyssal Plain. In: Gradstein, F.M., Ludden, J.N., et al. (Eds.), *Proc. ODP Sci. Results*, vol. 123. U.S. Govt. Printing Office, Washington, pp. 369–379.
- Bown, P.R., 2005. Selective calcareous nannoplankton survivorship at the Cretaceous–Tertiary boundary. *Geology* 33, 653–656.
- Bown, P.R., Cooper, M.K.E., 1998. Jurassic. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*. British Micropaleontological Society Series. Kluwer Academic Press, Dordrecht, pp. 34–85.
- Bown, P.R., Cooper, M.K.E., Lord, A.R., 1988. A calcareous nannofossil biozonation scheme for the early to mid Mesozoic. *Newsl. Stratigr.* 20, 91–114.
- Bralower, T.J., Monechi, S., Thierstein, H.R., 1989. Calcareous nannofossil zonation of the Jurassic–Cretaceous boundary interval and correlation with the geomagnetic polarity timescale. *Mar. Micropaleontol.* 14, 153–235.
- Bukry, D., 1973. Low-latitude coccolith biostratigraphic zonation. In: Edgar, N.T., Saunders, J.B., et al. (Eds.), *Initial Rep. DSDP*, vol. 15. U.S. Govt. Printing Office, Washington, pp. 685–703.
- Burns, D.A., 1977. Phenotypes and dissolution morphotypes of the genus *Gephyrocapsa* Kamptner and *Emiliania huxleyi* (Lohmann). *N. Z. J. Geol. Geophys.* 20, 143–155.
- Cecca, F., Martin Garin, B., Marchand, D., Lathuilière, B., Bartolini, A., 2005. Paleoclimatic control of biogeographic and sedimentary events in Tethyan and peri-Tethyan areas during the Oxfordian (Late Jurassic). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 222, 10–32.
- Cobianchi, M.A., 1992. Sinemurian–Early Bajocian calcareous nannofossil biostratigraphy of the Lombardy Basin, southern calcareous Alps; northern Italy. *Atti Ticin. Sci. Terra* 35, 61–106.
- Colmenero-Hidalgo, E., Flores, J.-A., Sierro, F.J., 2002. Biometry of *Emiliania huxleyi* and its biostratigraphic significance in the Eastern North Atlantic Ocean and Western Mediterranean Sea in the last 20 000 years. *Mar. Micropaleontol.* 46, 247–263.
- de Kaenel, E., 1990. Etudes biostratigraphiques fondées sur les nannofossiles calcaires. Unpublished PhD Thesis, Université de Neuchâtel, 239 pp.
- Dupraz, C., 1999. Paléontologie, paléocéologie et évolution des faciès récifaux de l’Oxfordien Moyen-Supérieur (Jura suisse et français). *GeoFocus* 2, 1–200.
- Gartner, S., 1972. Late Pleistocene calcareous nannofossils in the Caribbean and their interoceanic correlation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 12, 169–191.
- Geisen, M., Mutterlose, J., Young, J.R., 1998. Coccolith biometrics: a high resolution case study in the Hauterivian (early Cretaceous) and planned work in the CODENET Project. *INA 7 Newsletter Spec. Issue, La Parguera (Puerto Rico), Abstract book.*
- Geisen, M., Billard, C., Broerse, A., Cros, L., Probert, I., Young, J.R., 2002. Life-cycle associations involving pairs of holococcolithophorid species: intraspecific variation or cryptic speciation? *Eur. J. Phycol.* 37, 531–550.
- Giraud, F., Mattioli, E., Pittet, B., Atrops, F., Courtinat, B., 1998. Comparison of the *Watznaueria* genus signal recorded in Tethyan and Boreal areas during the Middle and Upper Jurassic. *INA 7 Newsletter Spec. Issue, La Parguera (Puerto Rico), Abstract book.*
- Giraud, F., Courtinat, B., Garcia, J.P., Baudin, F., Guillocheau, F., Dromart, G., Atrops, F., Colleté, C., 2005. Palynofacies and calcareous nannofossils in the Upper Kimmeridgian, southeastern Paris Basin (France). *Bull. Soc. Géol. Fr.* 176, 457–466.
- Green, J.C., Heimdal, B.R., Paasche, E., Moate, R., 1998. Changes in calcification and the dimensions of coccoliths of *Emiliania huxleyi* (Haptophyta) grown at reduced salinities. *Phycologia* 37, 121–131.
- Gröcke, D.R., Price, G.D., Ruffell, A.H., Mutterlose, J., Baraboshkin, E., 2003. Isotopic evidence for Late Jurassic–Early Cretaceous climate change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 202, 97–118.
- Grossman, E.L., Ku, T.-L., 1986. Oxygen and carbon isotope fractionation in biogenic aragonite: temperature effects. *Chem. Geol.* 59, 59–74.
- Hagino, K., Okada, H., Matsuoka, H., 2000. Spatial dynamics of coccolithophore assemblages in the Equatorial Western-Central Pacific Ocean. *Mar. Micropaleontol.* 39, 53–72.
- Henderiks, J., Renaud, S., 2004. Coccolith size increase of *Calcidiscus leptoporus* offshore Morocco during the Last Glacial Maximum: an expression of enhanced glacial productivity? *J. Nannoplankton Res.* 26, 1–12.
- Jordan, R.W., 1988. Coccolithophore communities in the North East Atlantic. Unpublished Thesis, University of Surrey, 350 p.
- Lécuyer, C., Picard, S., Garcia, J.-P., Sheppard, S.M.F., Grandjean, P., Dromart, G., 2003. Thermal evolution of Tethyan surface waters during the Middle-Late Jurassic: evidence from  $\delta^{18}\text{O}$  values of marine fish teeth. *Paleoceanography* 18, 1076, doi:10.1029/2002PA000863.
- Lees, J.A., 1998. Upper Cretaceous. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*. British Micropaleontological Society Series. Kluwer Academic Press, Dordrecht, pp. 132–199.
- Lees, J.A., Bown, P.R., Young, J.R., Riding, J.B., 2004. Evidence for annual records of phytoplankton productivity in the Kimmeridge Clay Formation coccolith stone bands (Upper Jurassic Dorset, UK). *Mar. Micropaleontol.* 52, 29–49.
- Mattioli, E., Erba, E., 1999. Synthesis of calcareous nannofossil events in tethyan Lower and Middle Jurassic successions. *Riv. Ital. Paleontol. Stratigr.* 105, 343–376.
- Mattioli, E., Pittet, B., Young, J.R., Bown, P.R., 2004. Biometric analysis of Pliensbachian–Toarcian (Lower Jurassic) coccoliths of the family Biscutaceae: intra- and interspecific variability versus palaeoenvironmental influence. *Mar. Micropaleontol.* 52, 5–27.
- McIntyre, A., Allan, W.H., Roche, M.B., 1970. Modern Pacific Coccolithophoridae: a paleontological thermometer. *Trans. N.Y. Acad. Sci.* 32, 720–731.
- Medd, A.W., 1979. The Upper Jurassic coccoliths from Haddenham and Gamlingay boreholes (Cambridgeshire England). *Eclog. Geol. Helv.* 72, 19–109.
- Meyer, R.K.F., Schmidt-Kaler, H., 1989. Paläogeographischer Atlas des süddeutschen Oberjura (Malm). *Geol. Jahrb. A* 115, 3–77.
- Mutterlose, J., 1991. Das Verteilungs- und Migrationsmuster des kalkigen Nannoplanktons in der borealen Unterkreide (Valangin-Apt). *Paläontogr.* B 221, 27–152.
- Noël, D., 1965. Sur les coccolithes du Jurassique européen et d’Afrique du Nord. Essai de classification des coccolithes. *Ed. Centre Nat. Rech. Sci. Paris*, 1–209.

- Noël, D., Busson, G., Cornée, A., Mangin, A.M., 1994. Contribution fondamentale des coccolithophoridées à la constitution des calcaires fins pélagiques du Jurassique moyen et supérieur. *Geobios* 17, 701–721.
- Okada, H., 1989. Morphometric and floral variations of nannoplankton in relation to their living environment. *INA Newsl.* 11, 87–88.
- Olivier, N., Pittet, B., Mattioli, E., 2004. Palaeoenvironmental control on sponge-microbialite reefs and contemporaneous deep-shelf marl–limestone deposition (Late Oxfordian, southern Germany). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 212, 233–263.
- Pittet, B., 1996. Contrôles climatiques, eustatiques et tectoniques sur des systèmes mixtes carbonates-siliciclastiques de plate-forme : exemples de l'Oxfordien (Jura suisse, Normandie, Espagne). Unpublished PhD Thesis, Université de Fribourg, Switzerland, 258 pp.
- Pittet, B., Gorin, G.E., 1997. Distribution of sedimentary organic matter in a carbonate-siliciclastic platform environment: Oxfordian of the Swiss Jura mountains. *Sedimentology* 44, 915–937.
- Pittet, B., Strasser, A., 1998. Depositional sequences in deep-shelf environments formed through carbonate mud import from the shallow platform (Late Oxfordian, German Swabian Alb and eastern Swiss Jura). *Eclog. Geol. Helv.* 91, 149–169.
- Pittet, B., Mattioli, E., 2002. The carbonate signal and calcareous nannofossil distribution (Balingen–Tieringen section Late Oxfordian, south Germany). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 179, 73–98.
- Pittet, B., Strasser, A., Mattioli, E., 2000. Depositional sequences in deep-shelf environments: a response to sea-level changes and shallow-platform carbonate productivity (Oxfordian Germany and Spain). *J. Sediment. Res.* 70, 392–407.
- Quinn, P.S., Saez, A.G., Baumann, K.-H., Steel, B.A., Sprengel, C., Medlin, L.K., 2004. Coccolithophorid biodiversity: evidence from the cosmopolitan species *Calcidiscus leptoporus*. In: Thierstein, H.R., Young, J.R. (Eds.), *Coccolithophores: from molecular processes to global impact*. Springer-Verlag, Berlin Heidelberg, 565 pp.
- Reale, V., Baldanza, A., Monechi, S., Mattioli, E., 1992. Calcareous nannofossil biostratigraphic events from the Early–Middle Jurassic sequences of the Umbria–Marche area (Central Italy). *Mem. Sci. Geol. Padova* 43, 41–75.
- Renaud, S., Ziveri, P., Broerse, A.T.C., 2002. Geographical and seasonal differences in morphology and dynamics of the coccolithophore *Calcidiscus leptoporus*. *Mar. Micropaleontol.* 46, 363–385.
- Rood, A.P., Hay, W.W., Barnard, T., 1971. Electron microscope studies of Oxford Clay coccoliths. *Eclog. Geol. Helv.* 64, 245–272.
- Roth, P.H., 1983. Jurassic and Lower Cretaceous calcareous nannofossils in the western North Atlantic (Site 534): biostratigraphy, preservation, and some observations on biogeography and paleoceanography. In: Sheridan, R.E., Gradstein, F.M., et al. (Eds.), *Initial Rep. DSDP*, vol. 76. U.S. Govt. Printing Office, Washington, pp. 587–621.
- Roth, P.H., Bowdler, J., 1981. Middle Cretaceous nannoplankton biogeography and oceanography of the Atlantic Ocean. In: Warme, J.E., Douglas, R.G., Winterer, E.L. (Eds.), *The Deep Sea Drilling Project: a Decade of Progress*. Soc. Econ. Paleontol. Mineral., Sp. Publ., vol. 32, pp. 517–546.
- Saez, A.G., Probert, I., Quinn, P., Young, J.R., Geisen, M., Medlin, L.K., 2003. Pseudocryptic speciation in coccolithophores. *Proc. Natl. Acad. Sci. U. S. A.* 100, 7163–7168.
- Salomons, W., Mook, W.G., 1986. Isotope geochemistry of carbonates in the weathering zone. In: Fritz, P., Fontes, J.C. (Eds.), *Handbook of Environmental Isotope Geochemistry*, 2. The Terrestrial Environment, B. Elsevier Science, Amsterdam, pp. 239–269.
- Schweigert, G., 1995a. *Amoebopeltoceras* n.g., eine neue Ammonitengattung aus dem Oberjura (Ober-Oxfordium bis Unter-Kimmeridgium) von Südwestdeutschland und Spanien. *Stuttg. Beitr. Naturk., B* 227, 1–12.
- Schweigert, G., 1995b. Zum Auftreten der ammonitenarten *Amoeboceras bauhini* (Oppel) und *Amoeboceras schulginae* Mesetznikov im Oberjura der Schwäbischen Alb. *Ges. Naturk. Württ. Jahrgangsch.* 151, 171–184.
- Shiraiwa, Y., 2003. Physiological regulation of carbon fixation in the photosynthesis and calcification of coccolithophorids. *Comp. Biochem. Physiol., Part B Biochem. Mol. Biol.* 136, 775–783.
- Stoll, H.M., Schrag, D.P., 2001. Sr/Ca variations in Cretaceous carbonates: relation to productivity and sea level changes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 168, 311–336.
- Stradner, H., 1963. New contributions to Mesozoic stratigraphy by means of nannofossils. *Proceedings of the Sixth World Petroleum Congress Section 1 Paper 4*, pp. 167–183.
- Street, C., Bown, P.R., 2000. Paleobiogeography of Early Cretaceous (Berriasian–Barremian) calcareous nannoplankton. *Mar. Micropaleontol.* 39, 265–291.
- Turi, B., 1986. Stable isotopes of travertines. In: Fritz, P., Fontes, J.C. (Eds.), *Handbook of Environmental Isotope Geochemistry*, 2. The Terrestrial Environment, B. Elsevier Science, Amsterdam, pp. 207–238.
- Walsworth-Bell, E.B., 2000. Jurassic calcareous nannofossils and environmental cycles. Unpublished PhD Thesis, University College London, London, 137 pp.
- Wierzbowski, H., 2002. Detailed oxygen and carbon isotope stratigraphy of the Oxfordian in Central Poland. *Int. J. Earth Sci.* 91, 304–314.
- Winter, A., Jordan, R.W., Roth, P.H., 1994. Biogeography of living coccolithophores in ocean waters. In: Winter, A., Siesser, W. (Eds.), *Coccolithophores*. Cambridge University Press, Cambridge, pp. 161–177.
- Wise, S.W., 1983. Mesozoic and Cenozoic calcareous nannofossils recovered by DSDP Leg 71 in the Falkland Plateau region, Southwest Atlantic Ocean. In: Ludwig, W.J., Krasheninnikov, V., et al. (Eds.), *Initial Rep. DSDP*, vol. 71. U.S. Govt. Printing Office, Washington, pp. 481–550.
- Young, J.R., 1989. Observations on heterococcolith rim structure and its relationship to developmental processes. In: Crux, J.A., van Heck, S.E. (Eds.), *Nannofossils and their applications*. Ellis Horwood, Chichester, pp. 1–20.
- Young, J.R., 1990. Size variation of Neogene Reticulofenestra coccoliths from Indian Ocean DSDP cores. *J. Micropaleontol.* 9, 71–86.
- Young, J.R., Bown, P.R., 1991. An ontogenetic sequence of coccoliths from the Late Jurassic Kimmeridge Clay of England. *Palaeontology* 34, 843–850.
- Young, J.R., Westbroek, P., 1991. Genotypic variation in the coccolithophorid species *Emiliania huxleyi*. *Mar. Micropaleontol.* 18, 5–23.
- Young, J.R., Henriksen, K., 2003. Biomineralization within vesicles: the calcite of coccoliths. In: Deve, P., de Yoreo, J.J., Weiner, S. (Eds.), *Biomineralization. Reviews in Mineralogy and Geochemistry*, vol. 56, pp. 189–215.
- Young, J.R., Davis, S.A., Bown, P.R., Mann, S., 1999. Coccolith ultrastructure and biomineralization. *J. Struct. Biol.* 126, 195–215.