



Palaeoenvironmental vs. evolutionary control on size variation of coccoliths across the Lower-Middle Jurassic

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ARTICLE INFO

Article history:

Received 20 June 2016

Received in revised form 18 October 2016

Accepted 20 October 2016

Available online 24 October 2016

Keywords:

Calcareous nannofossils

Biometry

Toarcian-Aalenian

Western Tethys

Lotharingius

ABSTRACT

Size is an easily quantifiable trait probing the respective influence of evolution and palaeoenvironment on organisms through time. After the stressed period that spanned across western Tethys epicontinental seas during the early Toarcian, the following rebuilding of a restored water column ecosystem is coeval with the size increase of the *Lotharingius* genus coccoliths, one of the main pelagic producers at that time. In order to quantitatively assess the coccolith size evolution during a time span of ~10 myr, measurements of seven morphospecies of *Lotharingius* across the Toarcian and early Aalenian were performed. This study was carried out on a total of 5500 specimens from samples retrieved from two distinctive palaeoenvironmental settings in the western Mediterranean Tethys: three sections from the Lusitanian Basin in Portugal and one section from the Causses Basin in southern France. For each specimen, coccolith length, width and central area length and width were measured using specific measurement software. Statistical and data analysis tools were used in order to evaluate significant resemblances and/or differences between different size groups and samples. Two main clusters are acknowledged from this study. Small-sized *Lotharingius* is <4 µm and large-sized *Lotharingius* is >4 µm. In addition to common evolutionary processes, changes in palaeoenvironmental conditions were taken into account to explain such a size distribution. Although background evolution pushed the *Lotharingius* genus toward larger sizes, palaeoenvironmental conditions seemed to play an important role in the Toarcian-early Aalenian morphological evolution of this taxon. The production of larger coccoliths profited from stable environmental conditions, whereas smaller morphotypes dominated during periods marked by stress. The transition from small to large *Lotharingius* was synchronous in the two investigated western Tethys basins at the Bifrons-Gradata (or Variabilis) ammonite zone boundary (middle Toarcian), thus representing an important event for the Lower Jurassic calcareous nannofossil biostratigraphy.

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1. Introduction

The respective importance of biotic versus abiotic factors in shaping the evolution of life on Earth is still a fertile debate topic (van Valen, 1973; Stenseth and Maynard Smith, 1984). Organism size is a paramount parameter involved in biological processes, which can be constrained with confidence using the fossil record. Morphometric studies of marine microfossils have been applied in the past in order to understand evolution or ecological and phenotypic responses of organisms to palaeoenvironmental changes. Although biometric studies of Jurassic coccoliths and nannoliths have already been carried out (Mattioli and Pittet, 2002; Mattioli et al., 2004; Bornemann et al., 2003; Giraud et al., 2006; Suan et al., 2008a; Suchéras-Marx et al., 2010; Tiraboschi and Erba, 2010; Fraguas and Erba, 2010; Fraguas and Young, 2011; López-Otálvaro et al., 2012), none of them addressed the

morphological evolution of the *Lotharingius* genus, the most abundant coccolithophore taxon across Lower-Middle Jurassic sediments. Though a significant size increase in *Lotharingius* coccoliths across this time period has already been qualitatively acknowledged in the Lusitanian Basin (Portugal; Ferreira et al., 2015), no biometric evaluation has been made so far. Here, we compare the size evolution of *Lotharingius* coccoliths throughout the Toarcian-early Aalenian of two distinct basins of the western Tethys, the Lusitanian Basin (Portugal) and the Causses basin (southern France). These two regions were selected since they contain continuous and biostratigraphically well-constrained successions. Moreover, high-resolution isotopic data from $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ from brachiopods in Portugal and bulk rock and belemnites in France are available, allowing the comparison with abiotic and biotic parameters such as water temperature, and oceanic primary productivity.

The Toarcian was a period of major palaeoceanographic and palaeoenvironmental changes across the western Tethys. Warm surface and bottom water temperatures during the early Toarcian (~183 Ma) coincided with the Toarcian Oceanic Anoxic Event (T-OAE), which was

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marked by widespread organic matter-rich deposits and by a prominent negative carbon isotope excursion recorded in oceanic and continental carbon reservoirs (Jenkyns, 1988; Duarte, 1998; Jenkyns et al., 2001; Bailey et al., 2003; Hesselbo et al., 2000, 2007; McArthur et al., 2008; Suan et al., 2008a). In the middle Toarcian, global sea level and seawater temperature started a long-term descent that lingered until the Aalenian stage (Hallam, 1981; Duarte et al., 2007; Gómez et al., 2008; Dera et al., 2009, 2011a; Pittet et al., 2014).

This work addresses the coccolith size evolution of the *Lotharingius* taxon, the most abundant group of coccolithophores during a time span of ~10 myr. All the species of the genus were included in the biometric evaluation, since working on entire assemblages is a taxon-free approach and therefore avoids the bias of subjective grouping (Schmidt et al., 2006). The *Lotharingius* genus belongs to the family Watznaueriaceae and is the oldest known imbricating placolith coccolithophore, representing a major component of Lower Jurassic calcareous nannofossil assemblages (Bown, 1987; Mattioli and Erba, 1999). This taxon is likely the phylogenetic ancestor of the genus *Watznaueria* (Cobianchi et al., 1992; Mattioli, 1996), a cosmopolitan coccolithophore that dominated the global phytoplanktonic community for >100 myr until the K/Pg extinction event. The first occurrence of *Lotharingius* spp. happened during the late Pliensbachian (Bown, 1987; Mattioli, 1996), and two of its species, *L. hauffii* and *L. sigillatus*, are important biostratigraphic markers defining the calcareous nannofossil zone NJ5 (Bown and Cooper, 1998) and subzone NJT5b (Mattioli and Erba, 1999). Different species of *Lotharingius* genus dominated Toarcian assemblages until the lowermost Middle Jurassic when a gradual increase in the abundance of *Watznaueria* spp. is recorded in the western Tethys (Ferreira et al., 2015).

The purpose of this study is to test whether changes in the size of the *Lotharingius* genus through the Toarcian–early Aalenian reflect either an evolutionary trend, interspecific size variations and abundance shifts between the distinct species, or a phenotypic response to long-term environmental changes. In order to test these hypotheses, long-term changes in the size of all species of the genus have been studied in the Lusitanian and Causses basins and compared to previously published paleoenvironmental proxies. Statistical parameters and robust analysis tools such as Principal Components and Mixture Analysis were used, and inference tests such as ANOVA were performed in order to disclose trends and appraise the significance of the results obtained.

2. Geological settings

In the Early Jurassic, the western Tethys Ocean mainly consisted of a shallow sea comprised between the African and the European landmasses (Fig. 1). It was in this sector that during an aborted rift phase in the Late Triassic, the Lusitanian Basin started to open (Pinheiro et al., 1996). The Lusitanian Basin was a relatively narrow, elongated and shallow (<200 m in depth according to Bjerrum et al., 2001) epicontinental seaway connecting the western Tethys to the NW European basins. Roughly N–S orientated, this basin was bounded in the east by the Iberian Meseta and in the west by the Berlengas-Farilhões igneous and metamorphic horst. In this narrow seaway, the mixing between higher NW European and lower latitude Mediterranean waters has been described by various authors and supported by the mixing of ammonite fauna and calcareous nannofossils during the Early Jurassic (Mouterde and Ruget, 1975; Dommergues and Mouterde, 1980; Dommergues and Meister, 1991; Mattioli et al., 2008; Reggiani et al., 2010; Dera et al., 2011a). Similar mixing of marine organisms has also been acknowledged for ostracods (Arias and Whatley, 2005), bivalves (Damborenea, 2002) and brachiopods (Vörös, 2002). The Lusitanian Basin was located at a palaeolatitude between 25 and 30°N (Dercourt et al., 2000), which corresponds in modern oceans to the transition between the subtropical and temperate climatic belts.

The three sections studied in Portugal represent 286 m of a complete and continuous succession of marine hemipelagic marlstone and

limestone couplets deposited on a homoclinal, low-angle ramp with a NW dipping (Duarte, 2004). The Rabaçal section is located in the proximal part of the basin, Cabo Mondego in the distal part, and the Brenha section is in an intermediate position. In all the three sections macrofossils such as ammonites, brachiopods, belemnites, bivalves and some fossilized wood fragments are commonly found. Though the Rabaçal section spans from the uppermost Pliensbachian to the uppermost upper Toarcian, only the first 42 m comprising the Polymorphum, Levisoni (lower Toarcian) and the lowermost Bifrons (middle Toarcian) ammonite zones were sampled for nannofossil study. Though black shales or their equivalents are recorded throughout Europe, there is no sedimentological evidence for anoxia in the Rabaçal section studied here. In fact, sediments recording the negative carbon isotope excursion, which is the equivalent to the T-OAE, are calcilutites and calcisiltites devoid of organic matter. Their formation is probably related to storm events held in a proximal setting, responsible for the water column re-oxygenation (Duarte, 1997; Pittet et al., 2014; Ferreira et al., 2015). The 157 m of the Brenha section correspond to the uppermost part of the lower Toarcian up to the lower Aalenian. The 87 m of the Cabo Mondego section include the Speciosum, Meneghinii, Aalensis (upper Toarcian) and the Opalinum (lower Aalenian) ammonite zones. The three sections are correlated by means of ammonite and nannofossil biostratigraphies, and by means of lithostratigraphy.

The Truc-de-Baldac section is located 5 km southeast of the city of Mende, situated in the Causses Basin in southern France (Fig. 1). During the early Toarcian this basin was a small, partly enclosed, intracratonic basin in the western Tethys epicontinental sea, and was positioned at a palaeolatitude comprised between 25 and 30°N. Bounded by Hercynian crystalline rocks (Trümpy, 1983), its morphology was largely controlled by the late Hercynian structural evolution. Subsidence was more pronounced in the central part of the basin and the Lower Jurassic succession thickness varies from its margins to its depocentre (Morard, 2004). In this region an abrupt facies transition occurred in the lowermost Toarcian with the onset of deposition of organic matter-rich shales belonging to the Schistes Cartons Formation. On top of this formation stands the Fontaneilles Formation, a monotonous marl succession of the middle and upper Toarcian. The gradual transition to Aalenian sediments is characterized by sandy limestones bearing abundant bioturbation (Harazim et al., 2013).

3. Materials and methods

Fifty-five samples from two West-Tethyan basins were used in *Lotharingius* coccoliths biometry. Thirty-four samples were collected from three sections in the Coimbra to Figueira da Foz region (5 from Rabaçal, 13 from Brenha, 16 from Cabo Mondego) and 21 from Truc-de-Baldac. Furthermore, 65 samples from Truc-de-Baldac were scanned for nannofossil absolute abundance and diversity determination. Smear slides following the random settling technique by Beaufort (1991) and Geisen et al. (1999) ensured a homogeneous dispersion of coccoliths on the slide. The morpho-taxonomy of the genus *Lotharingius* used in this work follows that of Mattioli (1996) and Mattioli and Erba (1999), which is based upon, but slightly diverges from Bown (1987), and focuses on seven morphospecies identified throughout the lower Toarcian to lower Aalenian: *L. barozii*, *L. crucicentralis*, *L. frodoi*, *L. hauffii*, *L. sigillatus*, *L. umbriensis* and *L. velatus*. Excellent to poorly preserved coccoliths were recorded in the analysed samples. Partial etching of distal shield and central area elements were frequent both in small and large specimens. Well-preserved specimens or those slightly to moderately etched or overgrown were used for biometry, whereas damaged or poorly preserved coccoliths were measured only if their landmarks could be unequivocally determined. For each of the 55 samples, the image from the first 100 coccoliths randomly observed was captured with a Leica EC3 digital camera coupled with an optical polarized light microscope with ×1000 magnification. On the system used, 1 µm correspond to 17.5 pixels, thus the accuracy of size measurements yields

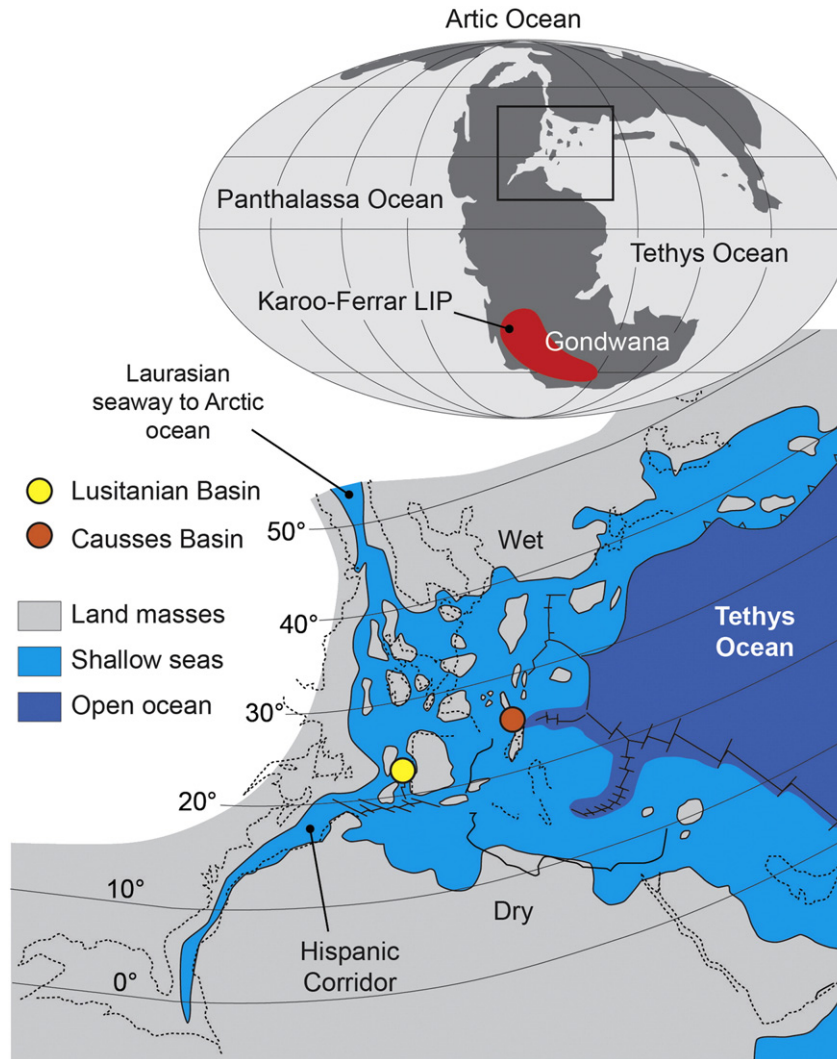


Fig. 1. Location of the Lusitanian and Causses basins during the Early Jurassic in western Tethys epicontinental sea (modified after Bassoulet et al., 1993) and Karoo-Ferrar Large Igneous Province.

0.057 μm per pixel at a microscope magnification of 1000 \times . For each coccolith, length (L) and width (W), and central area length (CAL) and width (CAW) were measured (Fig. 2) using the public domain image analysis software ImageJ[®].

Statistical analysis was performed using the PAST 3.01 software package. Measurements of the coccolith length were used to calculate simple statistical parameters, such as mean, standard deviation, median, 25th and 75th percentile and total range of values. For each sample, the percentiles of the frequency of the length measurements were plotted using the box and whiskers chart. The geometric mean, the coccolith ellipticity (L/W), central area ellipticity (CAL/CAW), and the proportion occupied by the central area relative to the area of the coccolith were also determined. Since the goal of a correlation analysis is to test whether two measurement variables covary, and to measure the strength of any relationship between these variables, the coefficient of correlation (r) and the coefficient of determination (r^2) between the coccolith parameters were calculated. If r measures the strength and the direction of a linear relationship between two variables, r^2 denotes the strength of the linear association between those same variables, or the proportion (%) of the variance of one variable that is predictable from the other variable.

The relative abundance between six different species of *Lotharingius* was compared against the coccolith length percentiles in order to assess if changes in the pool size are related to shifts in the relative abundance

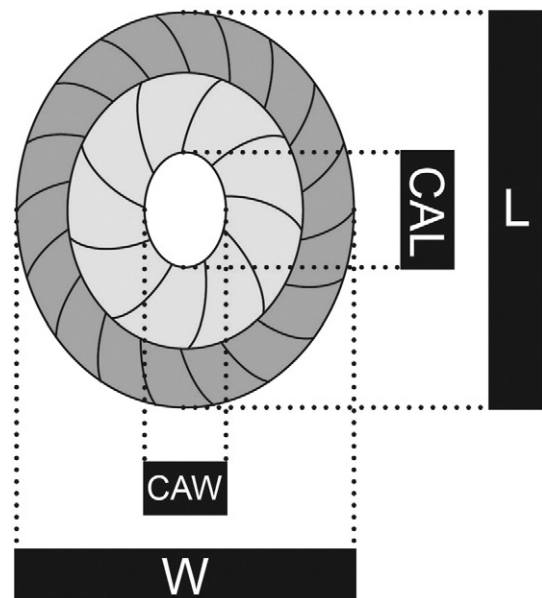


Fig. 2. Different coccolith parameters measured in distal view: length (L), width (W), central area length (CAL) and central area width (CAW).

of the different *Lotharingius* taxa, are due to a size increase in all of the species, or result from a combination of these two processes. The species *L. umbriensis* was left out, as its relative abundance is extremely low.

The L variable of the whole dataset was tested for normal distribution using the Shapiro-Wilk test. Though merely 26 out of the 55 samples show normal distribution, L mean values were compared using a parametric test since non-parametric ones often have less statistical power than parametric tests (Hammer and Harper, 2006). Parametric univariate analysis of variance (ANOVA) was performed on *Lotharingius* L values in order to test if our samples correspond to populations with equal means using a significance level of 0.05 (null hypothesis). ANOVA tests for significant differences between independent variables by comparing the average variance of each sample against the variance of all samples combined. As the variables means drift apart, the overall variance increases. If significant differences are proved, then Tukey's honestly significant difference (HSD) test allows the identification of the variables that most contribute to those differences. Though ANOVA assumes for each sample normal distributions and equality of variances, these assumptions are less critical if the samples are of the same size (Hammer and Harper, 2006), which is the case in this work. For PCA, a bin of 0.5 μm was used and the frequency of the L axis size in each sample was calculated. The number of classes/bins used in PCA follows the Sturges' formula $K = (\log_2 n) + 1$. Being K the number of bins and n the number of observations (5500), hence 13 bins of 0.5 μm each were created. Loadings for the totality of the samples and the stratigraphic evolution of PC1 scores for each of the studied basins were calculated. Mixture Analysis is a maximum-likelihood method which was used in this work to identify the existence of two or more distinct groups within the totality of L measurements and estimate their descriptive parameters. The minimum values of Akaike Information Criterion (AIC) helped identifying the groups obtained by Mixture Analysis with the lowest overfitting (Hammer et al., 2001). Also for mixture analysis the number of bins follows the Sturges' formula.

4. Results

In the lower Toarcian, *Lotharingius* relative abundances in the Lusitanian Basin are quite high ranging from 40% of the total coccolith assemblage prior to the tempestite interval, to 80% and more after that (Fig. 3). Across the middle Toarcian up to the lower Aalenian its abundances vary around 60% of the total assemblage. In the Causses Basin during the upper Pliensbachian, the *Lotharingius* abundance varies between 30 and 60%. Across the lower and middle Toarcian though, its abundance stays fairly constant, varying around 40%. In the upper Toarcian and lowermost Aalenian the abundance of *Lotharingius* slightly increases to values around 50% (Fig. 4).

All the seven species of *Lotharingius* were considered together for biometric purposes, and statistical parameters such as mean, median, percentiles, minimum and maximum L values were calculated and displayed on a box plot chart (Figs. 3 and 4). Throughout the Toarcian and lower Aalenian a general increasing trend in the coccolith size is observed in the sections of both basins, although a slight decrease in the taxon size is observed across the Toarcian/Aalenian boundary. In the two studied sections, there is both a replacement of *Lotharingius* coccoliths $<4 \mu\text{m}$ by specimens $>4 \mu\text{m}$ and a species-specific change in the upper part of the middle Toarcian (Ferreira et al., 2015).

Complementary to the standard statistics, the geometric mean was calculated and displayed in a box plot chart in order to assess if a trend from all the measured variables could be recorded. As a result, the geometric mean closely follows the coccolith length stratigraphic trend throughout both successions (Lusitanian Basin $r^2 = 0.81$, $p = 0$ and for the Causses Basin $r^2 = 0.83$, $p = 0$), putting into evidence the importance of the major axis size as a proxy for the total dimension of the coccolith. Moreover, since r^2 reach the highest values between the coccolith length (L) and width (W) (Fig. 5), L is thus herein used to describe the coccolith size. In fact, when the determination coefficient

between the different variables is calculated, we observe that L is strongly correlated with W ($r^2 = 0.80$) and to a lesser extent with CAL ($r^2 = 0.59$), with zero probability ($p = 0$) of these two variables not being correlated. It is also possible to assess that both the coccoliths ellipticity and their central areas ellipticity is not strongly correlated ($r^2 = 0.23$, $p = 0$), neither it is with any of the other variables. Conversely, the proportion of the central area is correlated with the coccolith CAL and CAW ($r^2 = 0.53$, $p = 0$ and $r^2 = 0.54$, $p = 0$ accordingly).

As for the evolution of the coccoliths ellipticity, their mean value varies in both basins between 1.2 and 1.3, and a very weak correlation between the stratigraphic evolution of coccoliths ellipticity and their size (length) is obtained ($r^2 = 0.07$, $p < 0.0001$). Though in the long-term a gradual decrease in relative abundance of small subcircular *L. hauffii* coeval with an up-section increase in larger species such as *L. velatus* during the middle Toarcian is observed, the *Lotharingius* pool ellipticity does not change significantly. The drop in *L. hauffii* abundances can also explain the up-sequence apparent trend in both sections of more elliptical central areas within the genus. Yet, the correlation between these two variables is very weak ($r^2 = 0.03$, $p < 0.0001$). Regarding the proportion of the coccolith central area to the total coccolith area, we observe that their mean values vary in almost all of the studied samples between 10 and 20% and that there is neither any noticeable link between this parameter with the composition of the *Lotharingius* assemblages, neither with the stratigraphic evolution of their size ($r^2 = 0.04$; $p < 0.0001$).

For the total of 5500 measurements of coccoliths length, PCA loadings show that for Factor 1, which represents 74% of the total variance, there is a boundary at 4 μm within the *Lotharingius* pool (Fig. 6). Although when PCA is computed separately for each section, loadings set a threshold of 4.5 μm in Portugal and 4.0 μm in France between small and large morphotypes. The difference in 0.5 μm obtained for the Portuguese samples can be explained due to the dimension of the bins initially selected, as we can observe that the loadings in the Lusitanian Basin at the transition between 4 and 4.5 μm are quite feeble (Fig. 6). Moreover, the stratigraphic evolution of PC1 scores in both basins show this same transition between small and large specimens during the middle Toarcian (Figs. 3 and 4). The same bimodal frequency and split around 4 μm for the variable L is also validated when applying Mixture Analysis to the whole dataset. This best fit method renders two distinct populations at 4 μm boundary, where the first one representing ~27% of the specimens has a mean value of $3.6 \pm 0.4 \mu\text{m}$ and the second one including ~73% of the specimens has a mean value of $4.7 \pm 0.8 \mu\text{m}$ (Fig. 7). This size division in the assemblages clearly represents small and large *Lotharingius* populations prior to and after the middle Toarcian.

In order to assess the degree of equality of means for each pair of samples, ANOVA and Tukey's HSD test was calculated for each basin. In both basins two sets of samples share the same population mean: below and above the middle Toarcian (Fig. 8). Moreover, in the Lusitanian Basin one can also observe that the lower Aalenian sample CAB 57 share the same mean with the lower Toarcian ones. This can also be acknowledged from looking at the box plot chart and the PCA scores (Fig. 3), where a decrease in the *Lotharingius* pool size is observed across the Toarcian/Aalenian boundary in the Lusitanian Basin. After running ANOVA on the whole dataset, quantitative data rendered no significant difference between the means of the coccoliths ellipticity and central area ellipticity, whereas for the proportion of the central area significant differences between most of the samples pairs were evidenced, as also shown by the means and standard deviation values (Figs. 3 and 4).

5. Discussion

5.1. *Lotharingius* biometry and assemblage shifts

The coccolithophore community underwent drastic and important changes during the middle Toarcian, as shown by qualitative

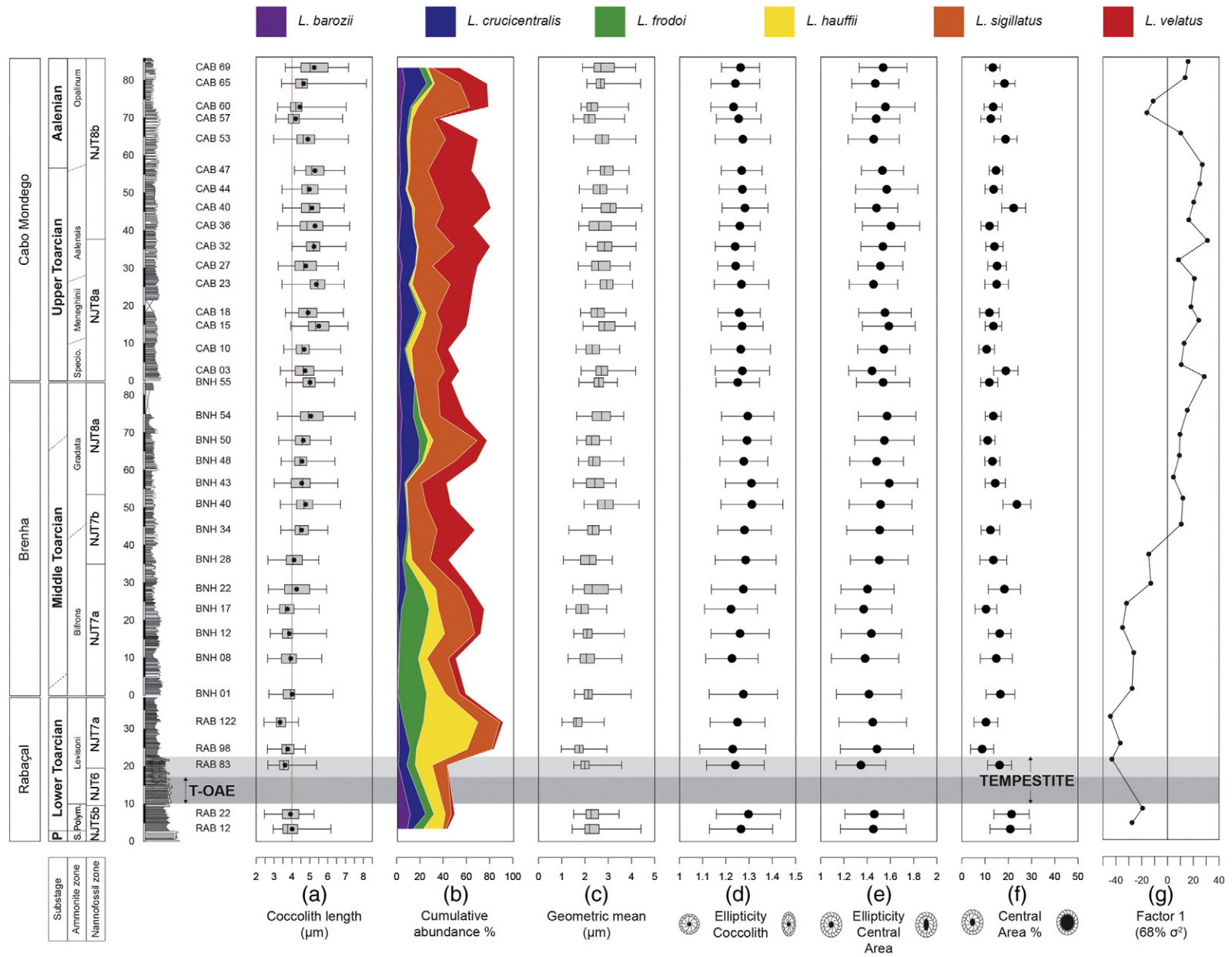


Fig. 3. Lusitanian Basin. (a) mean (black dots), median (vertical lines), 25th and 75th percentile (boxes), and total range of values; (b) cumulative percentage of the different species of *Lotharingius* compared to the total coccoliths abundance; (c) median (vertical lines), 25th and 75th percentile (boxes), and total range of values; (d, e and f) mean and standard deviation values of coccoliths ellipticity, central area ellipticity, central area proportion; (g) stratigraphic evolution of Factor 1 PCA scores. Although no black shales were recorded in the studied section but a tempestite-rich interval, grey shaded area indicates the T-OAE-equivalent interval. Note that ammonites were not recorded in the Brenha section, but a very tight correlation is possible using nannofossil zones and lithostratigraphy with the Rabaçal section (Ferreira et al., 2015), where ammonite zonation is available for the middle Toarcian. Nannofossil zones are according Mattioli and Erba (1999) because the assemblage shows a S-Tethyan affinity.

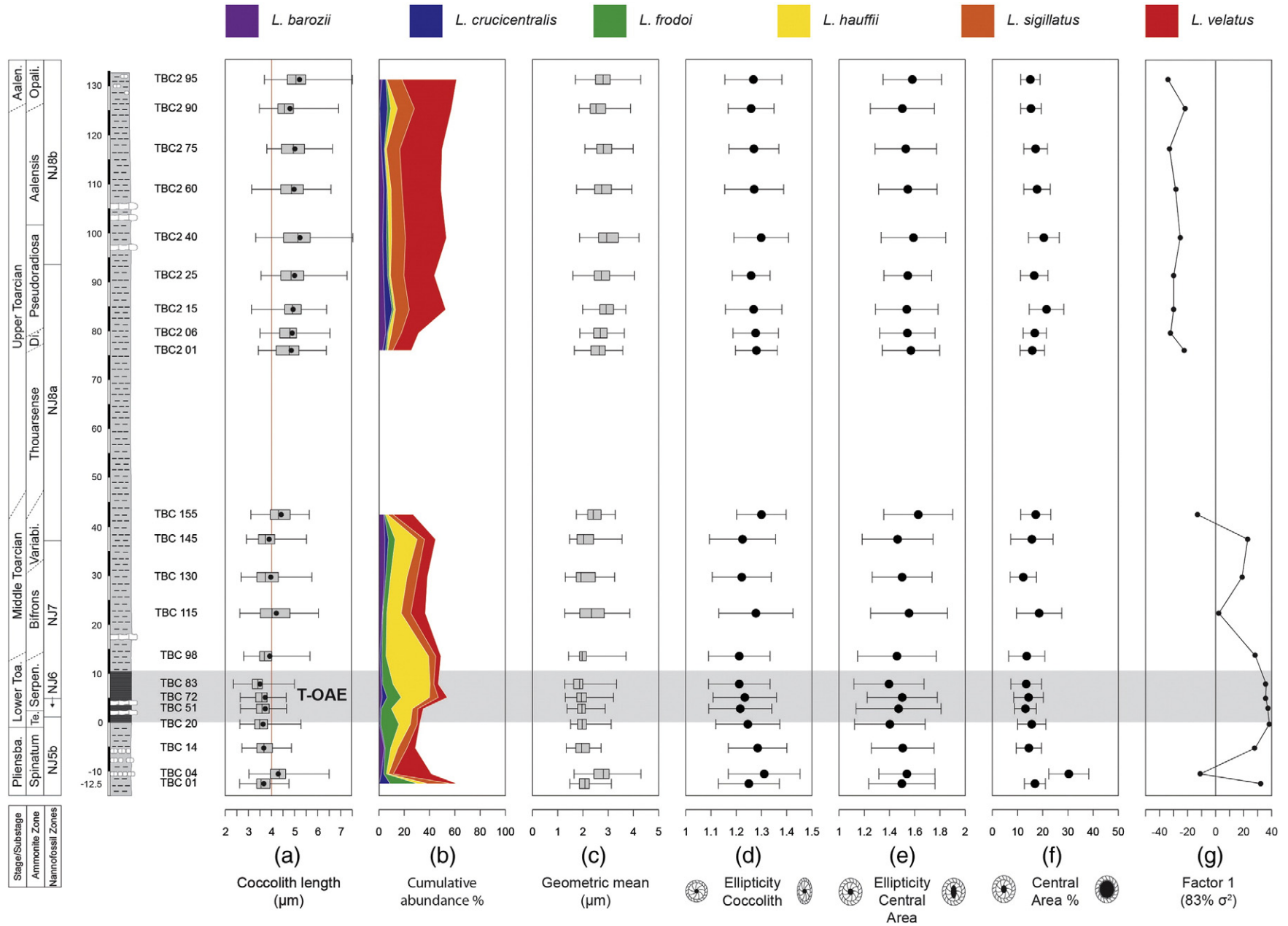


Fig. 4. Causses Basin. (a) mean (black dots), median (vertical lines), 25th and 75th percentile (boxes), and total range of values; (b) cumulative percentage of the different species of *Lotharingius* compared to the total coccoliths abundance; (c) median (vertical lines), 25th and 75th percentile (boxes), and total range of values; (d, e and f) mean and standard deviation values of coccoliths ellipticity, central area ellipticity, central area proportion; (g) stratigraphic evolution of Factor 1 PCA scores. Please note that, although PCA scores are reversed in terms of absolute values with respect to Fig. 3, the general trend is very similar and the shift in the PCA scores occurs in the Causses Basin at the same time as in the Lusitanian Basin. Nannofossil zone are according Bown and Cooper (1998) because the assemblage shows a NW-Tethyan affinity.

r^2	r	L	W	CAL	CAW	E	CAE	CAP
L			0.895	0.767	0.691	0.264	0.175	0.193
W	0.800			0.642	0.682	-0.186	-0.041	0.084
CAL	0.589	0.412			0.869	0.306	0.276	0.730
CAW	0.477	0.465	0.755			0.056	-0.210	0.735
E	0.070	0.035	0.094	0.003			0.483	0.257
CAE	0.037	0.007	0.533	0.540	0.066			0.005
CAP	0.031	0.002	0.076	0.044	0.233	0.000		

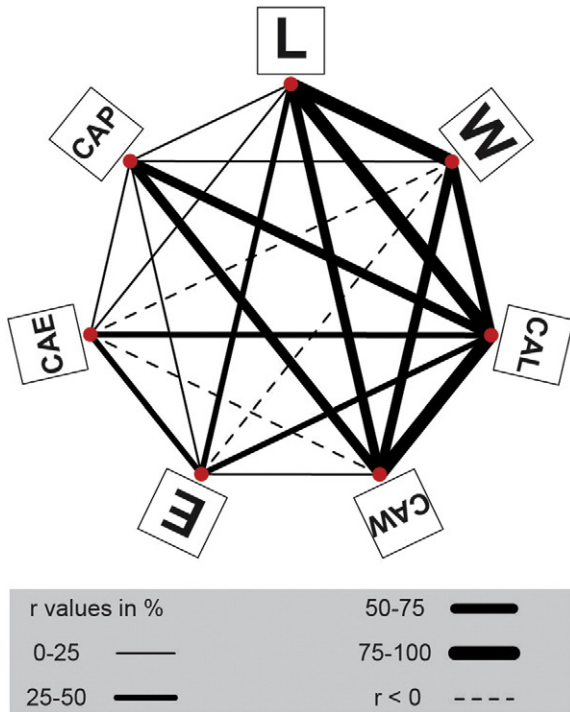


Fig. 5. Graphic displaying the correlation coefficient (r) between the different coccoliths parameters: length (L), width (W), central area length (CAL), central area width (CAW), coccolith ellipticity (E), central area ellipticity (CAE) and central area proportion (CAP). Also determination coefficient (r^2) is shown amidst the coccoliths measurements and calculated parameters.

observations made by Mattioli and Erba (1999) and Aguado et al. (2008). In this work, a well-defined size partition in the *Lotharingius* pool is clearly identifiable in the whole dataset analysed whether we use Mixture Analysis, PCA, ANOVA and Tukey's HSD test, or the box plot charts from both studied basins. The mean size values of *Lotharingius* coccoliths length are clearly split in both basins into two populations: smaller than $4 \mu\text{m}$ before the middle Toarcian (nannofossil zone NJT7a and Bifrons/Gradata ammonite zone of Lusitanian Basin; nannofossil zone NJ7 and Bifrons/Variabilis ammonite zone of Causses Basin), and larger than $4 \mu\text{m}$ after that. The small-sized *Lotharingius* ($<4 \mu\text{m}$ on average) dominated during the upper Pliensbachian-lower Toarcian interval being replaced by large-sized *Lotharingius* from the middle Toarcian. This prominent shift in size matches a change in the

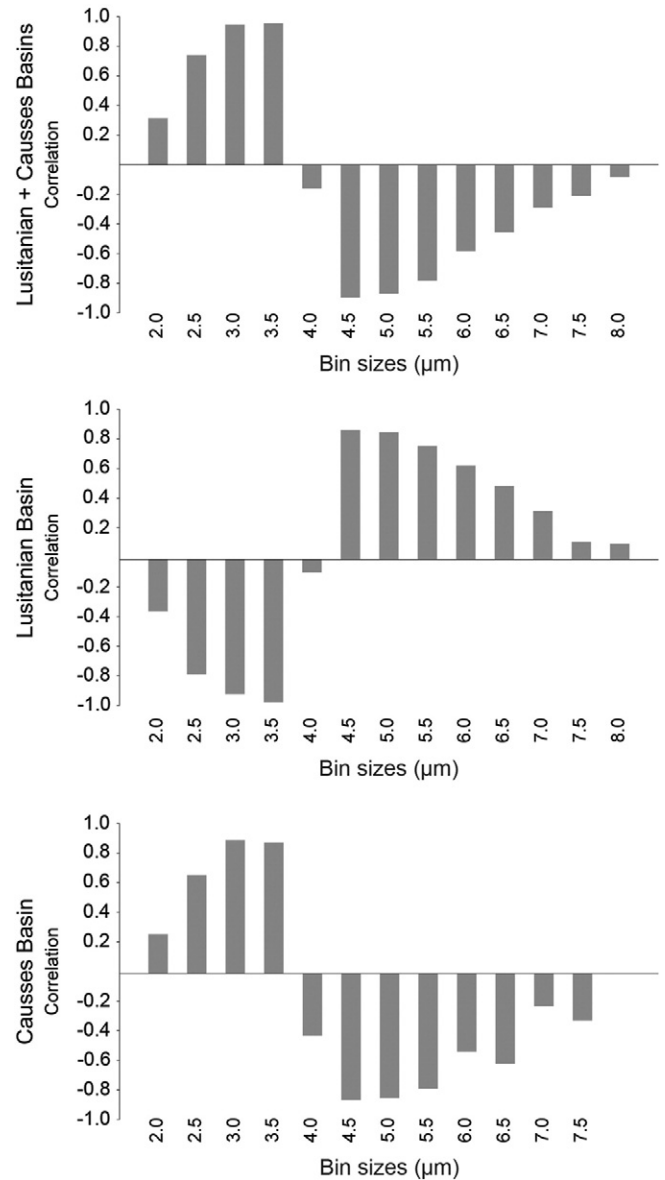


Fig. 6. PCA correlation loadings for coccoliths length in each of the studies basins and for the total *Lotharingius* coccoliths pool.

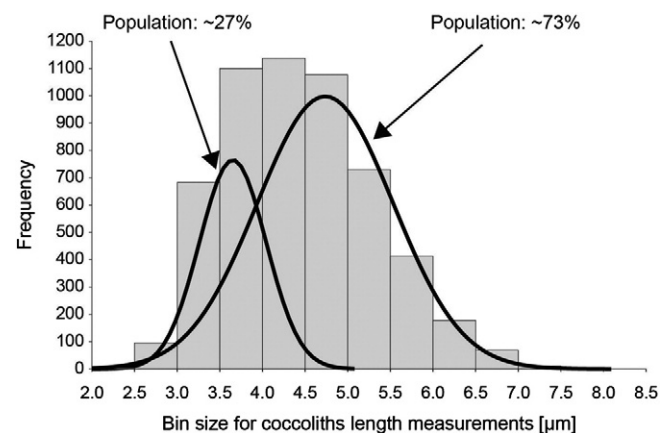


Fig. 7. Best fitted populations after running Mixture Analysis on the total measurements of coccoliths lengths from both studied basins.

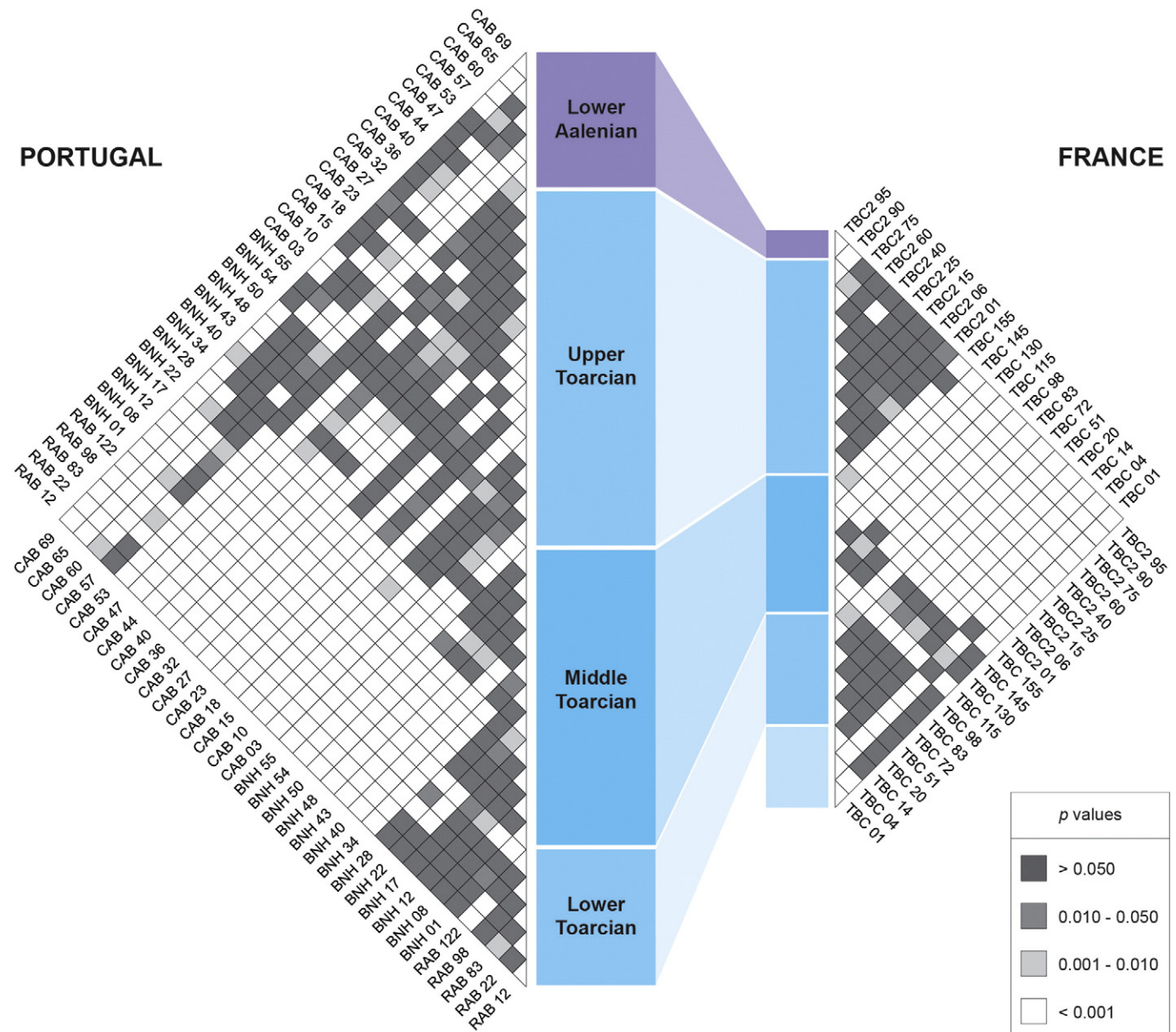


Fig. 8. Tukey's HSD test results between all pairs of samples from the Lusitanian (on the left hand side) and Causses basins (on the right hand side), showing the probability p of each pair of samples belonging to the same population. Dark grey colours indicate the correlation probability between each pair of samples.

assemblage composition: small morphospecies like *L. hauffii* and *L. frodoi* dominated the upper Pliensbachian-lower Toarcian assemblages and the large morphospecies of *Lotharingius* (such as *L. velatus*) although already present in the uppermost Pliensbachian-base of Toarcian, become abundant from the middle Toarcian (Ferreira et al., 2015).

Our statistical data show that the shift from $<4 \mu\text{m}$ to $>4 \mu\text{m}$ in the mean coccoliths length does not correspond uniquely to a change in the assemblages composition but also to a general increase in size of all the morphospecies. A strict stratigraphic replacement among the different species of *Lotharingius* is expected to yield high determination coefficients (r^2) between the different species abundances as they would negatively covariate. However, r^2 values in the Lusitanian Basin between the relative abundance of the most important *Lotharingius* species are relatively low. The highest r^2 values were obtained between the percentage of *L. hauffii* and *L. frodoi* ($r^2 = 0.262$, $p = 0.0019$), *L. velatus* and *L. frodoi* ($r^2 = 0.321$ with negative r , $p = 0.0005$), and *L. velatus* and *L. hauffii* ($r^2 = 0.344$ with negative r , $p = 0.0003$). In the

Causses Basin similar correlation coefficients are observed. Actually, a relatively weaker r^2 values obtained between the small species *L. hauffii* and *L. frodoi* ($r^2 = 0.146$, $p = 0.0871$), is probably related to the North-Tethyan affinity of *L. frodoi* (Mattioli et al., 2008). Also, a relatively stronger r^2 between the large *L. velatus* and the small *L. hauffii* ($r^2 = 0.454$ with negative r , $p = 0.0008$), and between *L. velatus* and *L. frodoi* ($r^2 = 0.384$ with negative r , $p = 0.0027$) is observed in the Causses Basin with respect to the Lusitanian Basin, probably because *L. velatus* was more abundant in North-Tethyan settings (Mattioli et al., 2008). Statistics show that each of the variables/species is undeniably independent or weakly correlated, and hence a strict interspecific swap within the *Lotharingius* community during the middle Toarcian is not sufficient to explain the observed size change.

Changes in coccoliths ellipticity and central area proportion are also perceived to occur in the middle Toarcian (Figs. 3 and 4) although, according to ANOVA results, they are not significant. Our results are thus partially different from Fraguas and Young (2011) who reported a stratigraphic increase in the *Lotharingius* coccoliths ellipticity, and in the

proportion of their central area across the Pliensbachian-Toarcian boundary in northern Spain. Underlying different taxonomic concepts are the probable reason for this discrepancy as some pictures showing the measured specimens in [Fraguas and Young \(2011; their figures 3 and 4\)](#), belong to the more elliptical genus *Bussonius*.

In synthesis, despite minor differences between the two studied sites, it seems like the stratigraphic replacement of small *Lotharingius* (*L. hauffii* and *L. frodoi*) by larger morphospecies (*L. velatus* and *L. crucicentralis*) is not an effective cause for the size shift observed in the middle Toarcian, even though to some extent it certainly contributes to it. The most likely mechanism to explain the size shift in this taxon is a sensible increase in size of all its morphospecies. It is however unclear whether such a change is environmentally- or evolutionary-driven. We therefore discuss separately the potential impact of environmental changes that occurred during the Toarcian and the hypothesis of possible evolutionary mechanisms.

5.2. Environmental changes

5.2.1. Direct CO₂ control on *Lotharingius* size

Changes in climate and ocean chemistry are among the most probable causes for inducing global environmental stress, since they directly affect the particularly climate-sensitive carbon cycle. The negative $\delta^{13}\text{C}$ excursion recorded in lower Toarcian sediments (see [Fig. 9](#)) is linked with massive injection into the ocean-atmosphere reservoir of isotopically light carbon either related to volcanic degassing or to methane release from continental margins ([Hesselbo et al., 2000, 2007; Jenkyns et al., 2001; Suan et al., 2008a, 2008b; Ruebsam et al., 2014](#)). Although still controversial, the most consensual cause for the early Toarcian ocean anoxia and carbon isotope perturbations has been associated with the eruption and emplacement of the basaltic Karoo-Ferrar large igneous province (LIP). Radiogenic ages from ^{40}Ar – ^{39}Ar and U–Pb geochronometers place the onset of the Karoo-Ferrar LIP magmatism at the Pliensbachian-Toarcian boundary, at ~183 Ma ([Suan et al., 2008b; Svensen et al., 2012; Sell et al., 2014; Burgess et al., 2015](#)). The duration of this event, however, is still poorly constrained. [Jourdan et al. \(2008\)](#) inferred the Karoo-Ferrar LIP emplacement as not one, but rather several brief magmatic events spanned across ~9 myr until the late Toarcian at ~176 Ma. According to [Burgess et al. \(2015\)](#) a short-lived episode occurred for ~350 kyrs, making it the most credible trigger of the early Toarcian environmental change.

The major biocalcification crisis inferred for the T-OAE has been linked to pulses of massive carbon input and concomitant higher $p\text{CO}_2$ and change in ocean chemistry ([Tremolada et al., 2005; Suan et al., 2010; Trecalli et al., 2012](#)). Actually, changes in dissolved CO₂ affect modern coccolithophore cultures. However, species-specific and even genotypic-specific responses to CO₂ variation are reported (e.g. [Riebesell et al., 2000; Langer et al., 2009; Rokitta and Rost, 2012; Meier et al., 2014; Meyer and Riebesell, 2015; Bolton et al., 2016; Oviedo et al., in press; Rickaby et al., 2016](#)), that render very difficult to infer the influence of CO₂ levels in the size of fossil coccolithophores.

Data from both the Lusitanian and Causses basins show that the small-sized *Lotharingius* occurred during the upper Pliensbachian, long before any reference to the Karoo-Ferrar LIP emplacement/eruption, and persists long after the anoxic event is over. In fact, the small-sized *Lotharingius* continue to dominate the coccolithophore assemblages in the upcoming ~2 myr throughout the Bifrons ammonite zone (middle Toarcian). Although the impact of high CO₂ levels on marine biota cannot be excluded, our biometric results show no alteration on *Lotharingius* coccoliths calcification that can be directly induced by ocean chemistry alteration. Actually, hampered carbonate biomineralization has also been deduced for the T-OAE after drastic abundances ([Erba, 2004](#)) and size reductions ([Mattioli et al., 2009; Suan et al., 2008a, 2010](#)) in *Schizosphaerella*, the main Lower Jurassic carbonate producer, were observed. In this latter work, however, small size is also observed before the T-OAE, during the negative carbon isotope

excursion occurring at the Pliensbachian-Toarcian boundary. It is thus more realistic that the most important effect of CO₂ increase in the coccolith size was indirect, as already suggested by [Mattioli et al. \(2009\)](#). Actually, increase in CO₂ levels may have rather affected pelagic producers by inducing climate changes and increasing the environmental stress.

5.2.2. Environmental changes induced by CO₂

According to several authors, early Toarcian oceans and ecosystems experienced widespread stress. Besides important temperature and sea level fluctuations, sea-bottom anoxia also occurred, which in turn generated substantial accumulation of organic matter in most epicontinental seas (e.g., [Hallam, 1981; Jenkyns, 1988; Duarte, 1998; Jenkyns et al., 2001; Bailey et al., 2003; Duarte et al., 2007; Hesselbo et al., 2007; Gómez et al., 2008; McArthur et al., 2008; Suan et al., 2008b; Dera et al., 2009, 2011a; Pittet et al., 2014](#)). This was also a period of recurrent accelerated continental weathering and flooding of emerged lands which are deemed to have increased oceanic nutrient supply and turbidity (e.g., [Mattioli et al., 2008; Suan et al., 2008a; Bodin et al., 2010; Montero-Serrano et al., 2015](#)). Thus the two positive $\delta^{13}\text{C}$ excursions, separated by an abrupt negative shift (T-OAE time equivalent), recorded in both basins during most of the early Toarcian ([Fig. 9](#)) likely represent a flourishing water column ecosystem since positive $\delta^{13}\text{C}$ values are interpreted as reflecting oceanic primary productivity (e.g., [Jenkyns and Clayton, 1986; Kump and Arthur, 1999; Bartolini et al., 1999; Jenkyns et al., 2002; Sandoval et al., 2008; Brigaud et al., 2009; Gómez et al., 2009; Price, 2010; Porter et al., 2014](#)).

Oscillations in nutrification levels over the early Toarcian recorded in different Tethyan basins corroborate the interpretation of environmental instability. Environmental stress is well expressed in the sedimentary record of both studied basins. In the section of the Lusitanian Basin, water vertical mixing induced by frequent storms contributed to bottom waters re-oxygenation and prevented the development of true black shales in lower Toarcian sediments ([Duarte, 1997; Pittet et al., 2014; Ferreira et al., 2015](#)). On the other hand, black shales in the Causses Basin testify an expanded water stratification and bottom water anoxia ([Harazim et al., 2013](#)). The *Lotharingius* genus in general and *L. hauffii* in specific reached their highest absolute and relative abundances (sometimes >80% of the total coccolith assemblage in the Lusitanian Basin) during the early Toarcian. Such stressed environmental period seemed to gather the optimum conditions for *L. hauffii* and *L. frodoi*, species adapted to relatively high trophic levels ([Pittet and Mattioli, 2002; Mattioli and Pittet, 2004; Giraud, 2009](#)), to thrive. It is thus plausible that, under unstable or hostile lower Toarcian conditions, small-sized *Lotharingius* coccoliths resulted from an accelerated growth rate in the population.

Early Toarcian environmental instability is followed by a steady and long lasting global decrease in seawater temperature (e.g., [Dera et al., 2009, 2011b; Jenkyns et al., 2002](#)) likely as a direct consequence of accelerated atmospheric CO₂ drawdown by increased organic matter burial during the early Toarcian ([Krencker et al., 2014](#)). The enduring negative $\delta^{13}\text{C}$ drift recorded from the end of the early Toarcian suggests a steady long-term decline in oceans fertility, which is mirrored in both basins by increasing diversity in calcareous nannoplankton ([Fig. 9](#)). Attenuation of continental weathering and nutrient runoff during this global cooling period likely supported the gradual decline in primary productivity and an overall progressive environmental stasis. During this period, all *Lotharingius* morphospecies progressively began to increase their coccolith size as all taxa contribute to the pool size increase ([Figs. 3, 4 and 10](#)). Moreover, the ongoing plunge in seawater temperature recorded from the middle Toarcian was probably an additional stimulus for *Lotharingius* coccolithophores to enlarge their cell and intracellular calcification, as acknowledged by [Sorrosa et al. \(2005\)](#) on cultured *Emiliania huxleyi* and *Gephyrocapsa oceanica* when exposed to lowered temperatures. Actually, size increase of Mesozoic nannoliths and coccoliths has already been linked to sea surface temperature

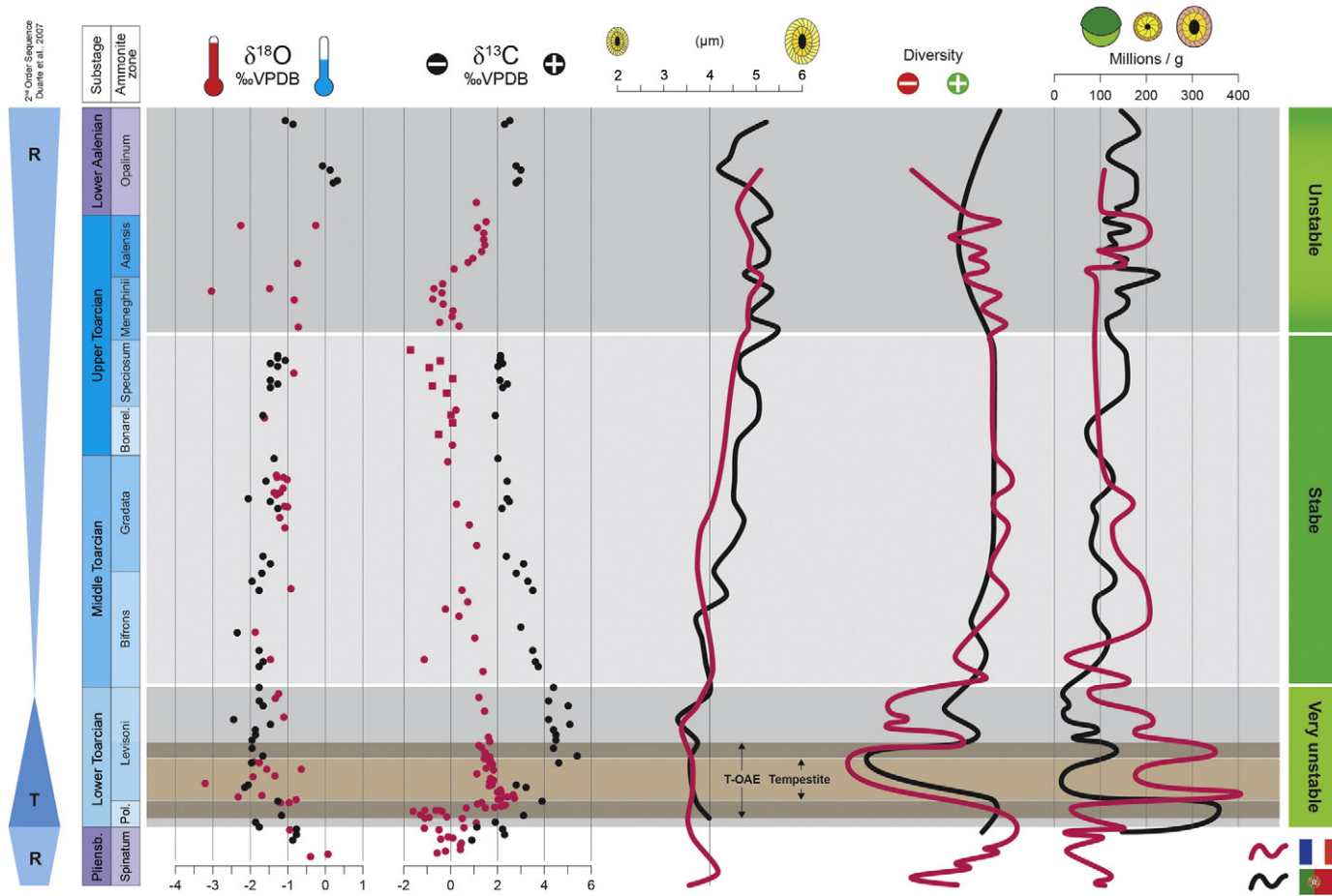


Fig. 9. Composite table of the stratigraphic evolution of $\delta^{18}\text{O}_{\text{brachiopods}}$ and $\delta^{13}\text{C}_{\text{brachiopods}}$ from the Lusitanian Basin, $\delta^{18}\text{O}_{\text{belemnites}}$ and $\delta^{13}\text{C}_{\text{bulk}}$ from the Causses Basin, mean value of *Lotharingius* coccoliths length, calcareous nannofossil diversity and absolute abundance. Data related to the Lusitanian Basin are from Ferreira et al. (2015) whereas $\delta^{18}\text{O}_{\text{belemnites}}$ and $\delta^{13}\text{C}_{\text{bulk}}$ data from the Causses Basin are from Harazim et al. (2013). Square symbols in $\delta^{13}\text{C}_{\text{bulk}}$ excursion refer to the Fontaneilles section, in the Causses Basin.

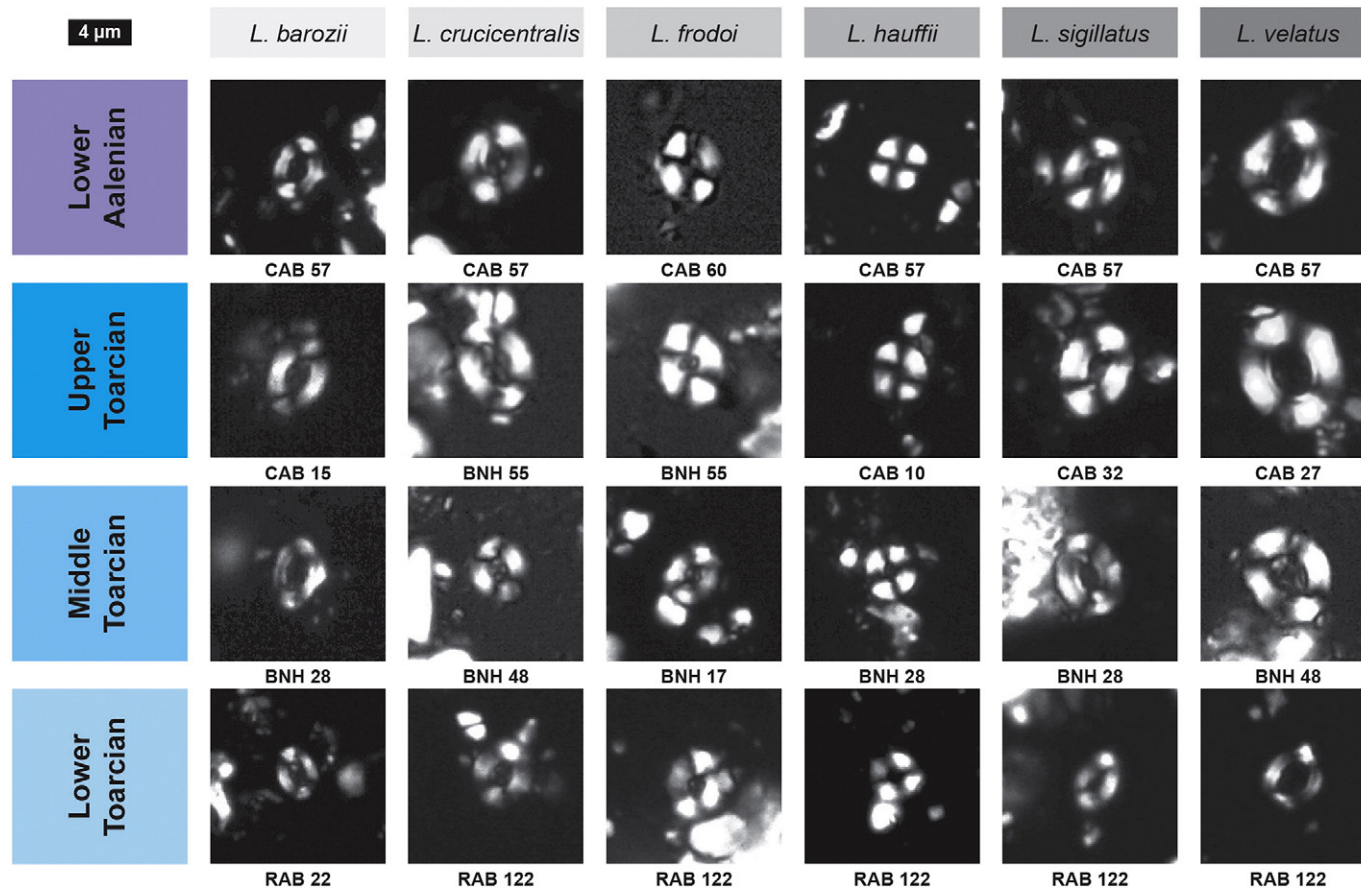


Fig. 10. Selected pictures showing the size evolution of the six most abundant *Lotharingius* species across the Toarcian and early Aalenian in the Lusitanian Basin sections: Rabaçal (RAB), Brenha (BNH) and Cabo Mondego (CAB).

drop. That is the case for *Schizosphaerella* during the late Pliensbachian (Suan et al., 2008a, 2010), *Crepidolithus crassus* and *C. crucifer* across the Pliensbachian (Fraguas and Erba, 2010) and for *Nannoconus* during the Valanginian (Barbarin et al., 2012).

Although one cannot exclude an internal underlying mechanism linked to the changes in *Lotharingius* morphological traits observed during the middle Toarcian (such as allometry related to physical or physiological properties of an organism), an external cause reflecting changes in interaction with abiotic and biotic environment such as predator–prey relationships or population density (McKinney, 1990) have also to be considered.

5.2.3. Evolutionary push

During the middle-late Toarcian environmental quiescence, the large majority of the *Lotharingius* population progressively increased its size from less, to $>4\ \mu\text{m}$ (see Figs. 9 and 10). Such close relationship between the *Lotharingius* size evolution and environmental change is in accordance with the stationary model proposed by Stenseth and Maynard Smith (1984), which suggests that evolution is largely driven by abiotic changes such as temperature, water column stratification and/or primary productivity. The stationary model also corroborates the correlation observed between size evolution of Cenozoic foraminifera and palaeoceanographic perturbations (Wei and Kennett, 1983; Schmidt et al., 2004a, 2004b). It is thus fairly plausible that the absence of environmental stress would naturally promote the background genetic expression of *Lotharingius* and the increase of its coccolith size. Such a size increase seems to follow the Cope's rule, as already proposed for different marine microorganisms (Schmidt et al., 2006; López-Otálvaro et al., 2012) and the “left wall” model (Stanley, 1973), i.e., evolution often starts near some “limiting boundary”, and then diffuses away from an originally small-sized ancestor. Moreover, ecological stability would uphold a faster coccolith growth rate and the occurrence of larger coccoliths as stressed by Schmidt et al. (2006), besides enhancing the population interspecific variability.

Size change can also be attributed to either adaptation or to speciation. Whereas speciation is the formation of a new species, adaptation is conventionally regarded as an evolutionary process involving genetic change by which natural selection picks out organisms in a given population to fit pre-established environmental “templates” (Laland et al., 2004). Whichever the process we ponder, neither adaptation nor speciation is fully observed in either of the basins studied here. In fact, neither the occurrence of new species of the genus *Lotharingius* are recorded in the middle Toarcian, as they all first occur during the late Pliensbachian or basal Toarcian, nor selective environmental adaptation can be considered, as all the seven *Lotharingius* species coexisted and likely shared the same habitat. Actually, the *Lotharingius* group is interpreted as shallow-dwellers, inhabiting the upper photic zone (Mattioli and Pittet, 2004; Tremolada et al., 2005; Mattioli et al., 2008; Reggiani et al., 2010). Therefore, the causes behind the *Lotharingius* size change is different from that inferred for the fossil record of other species such as *Reticulofenestra* (Young, 1990) and *Calcidiscus* (Knappertsbusch, 2000), whose size changes likely occurred through selection of closely related species/sub-species (Schmidt et al., 2006).

6. Conclusions

Since it is probably impossible to categorize biotic and abiotic phenomena as independent factors, it is a complex task finding a single and straightforward cause for the biometric changes observed in *Lotharingius* coccoliths across the Toarcian. Nonetheless, after the analysis of 5500 specimens, some significant conclusions can be drawn. Dataset analysis and statistics clearly show two different populations in *Lotharingius* at $4\ \mu\text{m}$ boundary. Although no statistically significant differences are observed in the *Lotharingius* coccoliths shape, the two different-sized groups (smaller and larger than $4\ \mu\text{m}$) undoubtedly define a consistent stratigraphic boundary in the middle Toarcian at the

transition between the Bifrons and Gradata (or Variabilis) ammonite zones. This size change is partly related to a species-specific replacement within the *Lotharingius*, with small-sized morphospecies (mainly *L. hauffii* and *L. frodoi*, but also small *L. sigillatus* and *L. crucicentralis*) being abundant in the early Toarcian and large-sized morphospecies (mainly *L. velatus*, but also large *L. sigillatus* and *L. crucicentralis*) in the middle-late Toarcian. However, our data also show a contribution of size increase, recorded for all the *Lotharingius* morphospecies across the middle Toarcian.

Despite the long-term evolution of the *Lotharingius* genus was likely genetically driven leading to larger sizes, thus following the Cope's rule and the “left wall” model, our data suggest that drastic environmental changes can also affect its morphological evolution. An important relationship between stable/unstable environmental conditions (likely related to seawater temperature fluctuations, water trophic character and expansion/contraction of the photic zone and nutricline) and *Lotharingius* morphological evolution can be made. Under the environmentally unstable conditions that took place during the early Toarcian, likely fast reproduction rates occurred, and small coccoliths were produced. Small *Lotharingius* morphospecies, likely better adapted to fluctuating environmental conditions (in terms of nutrient supply, sea-surface temperatures, etc.) displayed their highest relative abundance across this period. During the middle-late Toarcian, ecological stability likely supported either a faster or a longer coccolith growth and the occurrence of larger coccoliths is observed. Moreover, also short-time scales (100 thousands of years) size changes in *Lotharingius* coccoliths are recorded, like during the lower Aalenian, probably related to the onset of environmental instability. Actually, such conditions have already been interpreted as reinvigorate productivity (Aguado et al., 2008) and hence the *Lotharingius* size across the Torcian/Aalenian should be further investigated in future studies.

Table 1

Average values of coccolith length (L; μm), width (W; μm), coccolith ellipticity (E; L/W) and central area proportion (CAP; %) split by substages, for each analysed species. It is in the upper Toarcian that all the species reach their largest sizes and the most reduced CAP.

		Upper Pliensbachian	Lower Toarcian	Middle Toarcian	Upper Toarcian	Lower Aalenian
<i>Lotharingius barozii</i>	L	4,09	3,85	4,07	4,5	4,37
	W	3,13	2,96	3,14	3,56	3,5
	E	1,3	1,31	1,31	1,27	1,26
	CAP	27,06	25,59	24,16	21,09	20,56
<i>Lotharingius crucicentralis</i>	L	4,25	4,69	4,62	5,08	4,7
	W	3,27	3,63	3,62	4,12	3,81
	E	1,31	1,3	1,29	1,24	1,24
	CAP	17,62	16,91	15,6	13,7	15,51
<i>Lotharingius frodoi</i>	L	3,49	3,55	3,75	4,19	3,98
	W	2,79	2,87	3,02	3,38	3,25
	E	1,25	1,24	1,25	1,24	1,23
	CAP	13,08	11,44	10,85	9,29	11,2
<i>Lotharingius hauffii</i>	L	3,47	3,42	3,63	4,12	3,89
	W	3,1	2,98	3,15	3,54	3,41
	E	1,12	1,15	1,16	1,17	1,15
	CAP	11,38	9,96	9,57	9,4	9,59
<i>Lotharingius sigillatus</i>	L	4,34	4,39	4,78	5,14	5,05
	W	3,24	3,24	3,55	3,94	3,85
	E	1,35	1,36	1,35	1,31	1,32
	CAP	19,38	18,76	14,61	13,77	14,51
<i>Lotharingius velatus</i>	L	4,99	5,2	5,27	5,52	5,47
	W	3,63	3,89	4,04	4,37	4,33
	E	1,38	1,35	1,31	1,27	1,27
	CAP	32,07	30,61	23,16	20,24	20,33

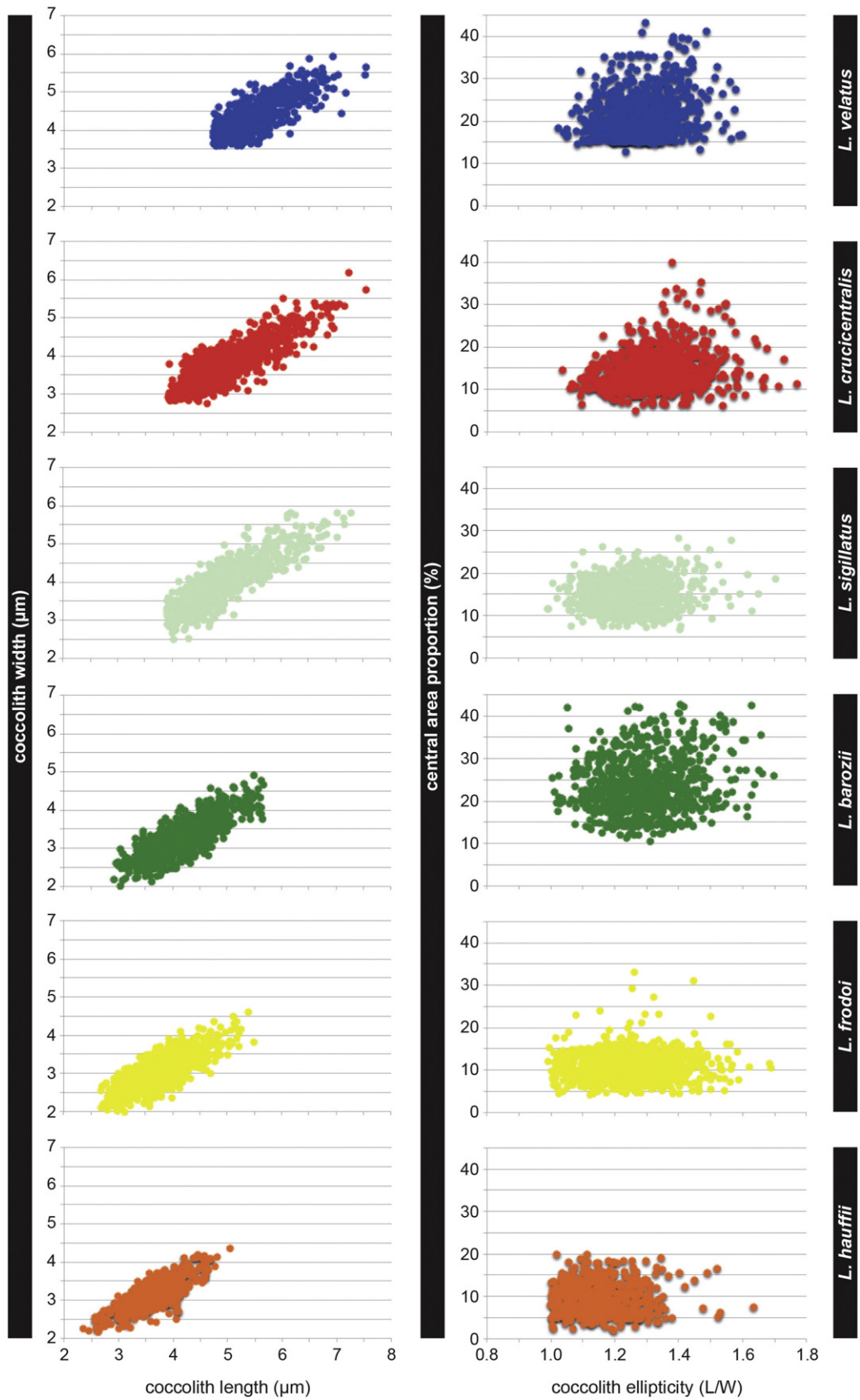


Fig. 11. Scatter plots showing for each analysed species, coccolith length (L) versus width (W) on the left side, and coccolith ellipticity (E) versus central area proportion (CAP; %) of the measured specimens from Portugal and France. *L. umbriensis* data are not shown because only few specimens could be measured.

6.1. Taxonomic appendix

The original diagnosis of the *Lotharingius* by Noël (1973) described a typical watznaueriacean rim coccolith with a slightly raised distal inner cycle and a central area spanned by a cross supported by lateral bars, giving the type species to *L. barozii*. It was only in 1979 that Goy proposed a corrected and precise description of the genus reaffirming its relationship within the Watznaueriaceae but also stating its independence as a discrete genus (Goy et al., 1979; Bown, 1987). The absence of significant changes across the Toarcian in *Lotharingius* coccoliths parameters such as ellipticity or central area proportion and ellipticity, seems to indicate a somewhat morphologic constrain at the genus level, and eventually in each of its seven different morphospecies. Actually, the coccolith size is the main morphological feature that varies throughout this time period, hence facilitating the taxonomic identification of each of the different species under optical polarized light microscope. In this work the criteria to identify the seven species of *Lotharingius* are described as follow:

- *L. barozii*: Noël (1973) emend. Goy in Goy et al. (1979) described this taxon as a *Lotharingius* with massive buttresses in the axis of the ellipse and asymmetrical radial bars. Here this species is distinguished by its broadly elliptical contour (Table 1) with a narrow rim and a wide and elliptical central area spanned by an axial cross. The inner and outer cycles have approximately the same thickness (Mattioli, 1996). With the exception for the lower Toarcian where the minimum size and greater central area proportion of *L. barozii* are observed, this species size increased from the Pliensbachian to the upper Toarcian (Table 1; Fig. 11).
- *L. crucecentralis*: (Medd, 1971) Grün and Zweili (1980) described this taxon as a species of *Ellipsagelosphaera* with a complex series of elements found in the central pore area. These are arranged as an oblique cross, which may be infilled with minor calcite elements, and a small rosette of plates in its centre. Here this species is identified as a small to intermediate *Lotharingius* coccolith, although generally large (average values in Table 1) and elliptical, with a wide and elliptical central area bearing an axial prominent cross and a system of radially arranged granulations. Similarly to *L. barozii*, *L. crucecentralis* shows bigger sizes in the upper Toarcian (Table 1).
- *L. frodoi*: Mattioli (1996) described this taxon as been small, with a narrowly elliptical central area, bearing two buttresses aligned with the minor axis of the ellipse. Here this species is identified by its small size (on average 3.5 µm during the earlier part of its range, and up to 4.2 µm in the upper Toarcian; Table 1), with an elliptic contour and a small central area (average CAP comprised between 13% in the Pliensbachian up to 9.3% in the upper Toarcian; Table 1) characterized by the presence of two buttresses or bars, aligned with the minor axis of the ellipse.
- *L. hauffii*: Grün and Zweili in Grün et al. (1974) emend. Goy in Goy et al. (1979) described this taxon as a *Lotharingius* of broad elliptical to subcircular shape with bars in the axes of the ellipse and reduced central area. Here this species is identified by its small size ($\leq 4 \mu\text{m}$) and subcircular to elliptical contour (average ellipticity always smaller than 1.17), with a reduced subcircular to elliptical and often empty central area that can sometimes be occupied by a knob or spine. As the other *Lotharingius* species, this taxon reached its largest sizes during the upper Toarcian (Table 1).
- *L. sigillatus*: (Stradner, 1961) Prins in Grün et al. (1974) emend. Goy (1981) described this taxon as a species of *Lotharingius* with a broad marginal rim, and a central area occupied by weakly developed buttresses in the axes of the ellipse and a system of radial bars. Here this species is identified by its elliptical shape (Fig. 11; Table 1) and elongate central area with buttresses or a long bar aligned with the major axis of the ellipse and a system of granular and radially disposed elements. The calcification degree of this taxon reached its maximum during the upper Toarcian, where the biggest size (average L of 5.14 µm) and reduced CAP (13.77%) are observed.
- *L. umbriensis*: Mattioli (1996) described this taxon as subcircular, with a very narrow central area with a cross aligned with the axes of the coccolith. Here this species is identified by its small coccolith size (3.5–5 µm) with a subcircular outline and a very small central area spanned by a small cross. Also this species outer cycle is thicker than the inner one. Due to its scarcity, no average values of size parameters were calculate for this taxon.
- *L. velatus*: Bown and Cooper (1989) described this taxon as a coccolith with a wide central area, closed by a granular plate. Here this species is identified by its generally large (on average $>5 \mu\text{m}$, except for the Pliensbachian specimens) size and elliptical shape coccolith with a very wide central area filled with a granular plate. This species rim can be quite thin in the upper Pliensbachian and lower Toarcian (average CAP $> 30\%$) bearing a thin outer cycle, which progressively becomes thicker across the mid-late Toarcian (average CAP $\sim 20\%$).

Acknowledgments

We thank Gilles Escarguel for fruitful discussion on statistics, the Editor Thierry Corregge, Nicolas Thibault and an anonymous reviewer for their comments, which improved the quality of the manuscript. This work received funding from the Portuguese FCT (SFRH/BD/77762/2011) to JF, and the project PAULF (2012–2014), INSU Syster (2011–2012) and Interrvie (2014) to EM. Slides used for calcareous nannofossil study are curated at the Collections de Géologie de Lyon de l'Université de Lyon 1 (collection numbers FSL 766289 to FSL 766629).

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