

A morphometric methodology to assess planktonic foraminiferal response to environmental perturbations: the case study of Oceanic Anoxic Event 2, Late Cretaceous

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ABSTRACT - Dwarfism of planktonic foraminiferal specimens is recognised across several intervals subject to globally extended environmental disturbances such as the Cretaceous/Palaeogene boundary and the latest Cenomanian-earliest Turonian Oceanic Anoxic Event 2 (OAE 2) in the Late Cretaceous. However, the occurrence of dwarfed specimens is generally based on the observation of a decrease in the size of specimens at the stereomicroscope without acquiring morphometric data. This approach prevents from assessing the inter-sample morphometric variation of species, reconstructing species-specific trends, and comparing data from different localities to extrapolate global from local signals.

We present herein a first step toward the development of a morphometry-based methodology to assess planktonic foraminiferal response to past environmental perturbations. To perform this study, we selected OAE 2 as a target event and we focused on two species, *Rotalipora cushmani* (Morrow, 1934) and *Whiteinella brittonensis* (Loeblich & Tappan, 1961), commonly occurring in the assemblages and likely having different palaeoecological preferences. Specimens analysed are from Eastbourne (England), Clot Chevalier (SE France), and Tarfaya (core S57, Morocco). For both species, we measured selected shell parameters (i.e., the number of chambers in the last whorl, the maximum diameter and the height of the test).

Our study suggests that the maximum diameter across the first chamber of the inner whorl visible in spiral view is the simplest and most objective methodology to estimate shell size variation in trochospiral planktonic foraminifera, and that this morphometric parameter is likely the most sensitive to the Cenomanian-Turonian environmental disturbances, and thus its variability through time appears worth investigating across other key-stratigraphic intervals. Moreover, this study indicates that the acquisition of morphometric data is required to accurately reconstruct planktonic foraminiferal response to environmental perturbations, because specimen dimensions show high inter-sample variability and based on the data collected in this study they do not experience the predicted size reduction.

RIASSUNTO - [Un metodo morfometrico per stabilire la risposta dei foraminiferi planctonici alle perturbazioni ambientali: il caso di studio dell'Evento Anossico Oceanico 2, Cretacico Superiore] - Il nanismo nei foraminiferi planctonici è stato riconosciuto in molti intervalli stratigrafici caratterizzati da importanti perturbazioni ambientali a scala globale come l'estinzione di massa al limite Cretacico/Paleogene e l'Evento Anossico Oceanico 2 (OAE 2) nel Cenomaniano superiore-Turoniano inferiore (Cretacico Superiore). Negli studi precedenti, tuttavia, la presenza di esemplari nani è stata identificata solo sulla base di osservazioni allo stereomicroscopio senza ricorrere all'acquisizione di dati morfometrici. Questo approccio impedisce di quantificare le variazioni morfometriche delle singole specie in campioni diversi in una successione stratigrafica ed il confronto delle variazioni morfometriche acquisite in località diverse per estrapolare eventuali variazioni sincrone a scala regionale e/o globale.

In questo studio viene presentata una metodologia basata sull'analisi morfometrica per valutare la risposta dei foraminiferi planctonici alle perturbazioni ambientali nel passato geologico. A questo scopo è stato selezionato come caso di studio l'OAE 2, poiché non sono mai state acquisite analisi morfometriche sui foraminiferi planctonici in questo intervallo. Le analisi sono state svolte su due specie, *Rotalipora cushmani* (Morrow, 1934) e *Whiteinella brittonensis* (Loeblich & Tappan, 1961), selezionate poiché sono relativamente comuni nelle associazioni ed erano probabilmente adattate ad habitat diversi. I campioni studiati provengono da tre località chiave con un record stratigrafico continuo a cavallo dell'evento anossico: Eastbourne (Inghilterra), Clot Chevalier (SE della Francia) e Tarfaya (carota S57, Marocco). Per entrambe le specie sono state contate e misurate alcune caratteristiche del guscio (ovvero il numero di camere nell'ultimo giro, il diametro massimo del guscio e l'altezza della trocospira), che in base alle informazioni derivanti dalla biologia dei foraminiferi planctonici viventi potrebbero essere state soggette a variazioni in condizioni ambientali di stress.

I risultati di questo studio suggeriscono che: 1) la misura del diametro massimo che attraversa la prima camera in vista spirale è il metodo più semplice ed oggettivo per stimare le variazioni di dimensione dei foraminiferi planctonici con avvolgimento trocospirale, 2) le sue variazioni sono probabilmente legate alla variazione dei parametri ambientali, 3) la ricostruzione della sua variabilità a cavallo di altri intervalli stratigrafici chiave potrebbe essere molto utile per ricostruire la risposta dei foraminiferi planctonici alle perturbazioni ambientali. Inoltre, sulla base dei dati raccolti in questo studio, non si riscontra alcuna riduzione nella dimensione delle specie di foraminiferi planctonici associabile alle perturbazioni legate all'OAE 2.

INTRODUCTION

The taxonomic composition of fossil planktonic foraminiferal assemblages is routinely used to trace

past environmental conditions (e.g., water depth, sea-surface temperature and nutrient concentration). These reconstructions have traditionally been based on the relative abundance of r-strategist vs. K-strategist taxa

according to the theory of MacArthur & Wilson (1967) and its subsequent application to planktonic foraminifera (e.g., Caron & Homewood, 1983; Hart, 1999; Premoli Silva & Sliter, 1999; Petrizzo, 2002), on biofacies comparison in continental margin and deep-water settings (Sliter, 1972; Leckie, 1987), and have been more recently supported by stable-isotope ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) palaeoceanographic and palaeoclimate studies (e.g., Douglas & Savin, 1978; Boersma & Shackleton, 1981; Norris & Wilson, 1998; Wilson et al., 2002; Abramovich et al., 2003; Bornemann et al., 2008; Petrizzo et al., 2008; Ando et al., 2010; Falzoni et al., 2013, 2014, 2016a; MacLeod et al., 2013). In addition, test dimensions are also regarded to be ecologically controlled, because each living/fossil species reaches the largest shell size under its optimum ecologic conditions (e.g., Hecht, 1976; de Villiers, 2004; Schmidt et al., 2006; Moller et al., 2013; Weinkauff et al., 2016). Conversely, specimen dimensions are expected to decrease dramatically under adverse environmental conditions that may inhibit the normal ontogenetic growth and favor early sexual maturity (Lipps, 1979; MacLeod et al., 2000; Keller & Abramovich, 2009).

The Cretaceous Period represents an ideal case-study to test planktonic foraminiferal morphometric variation during environmental disturbances, as it is characterised by a super-greenhouse climate culminating in the mid-Cretaceous and interrupted by short-lived environmental perturbations that abruptly altered the ecologic equilibrium in marine ecosystems (i.e., Oceanic Anoxic Events, OAEs: Schlanger & Jenkyns, 1976; Scholle & Arthur, 1980; Schlanger et al., 1987). Moreover, the Cretaceous ends with one of the five major mass extinctions documented in the Phanerozoic (Raup & Sepkoski, 1982). Accordingly, dwarfism of planktonic foraminiferal specimens has been commonly reported from several mid-low latitude sections across the latest Cenomanian-earliest Turonian OAE 2 (e.g., Atlantic Ocean: Gebhardt, 1997; Jati et al., 2010; Tethyan Ocean: Coccioni & Luciani, 2004, 2005; Scopelliti et al., 2004, 2008; Grosheny et al., 2013; Coccioni et al., 2016; Western Interior Seaway: Ifrim et al., 2011; Elderbak et al., 2014; Dionne et al., 2016; Anglo-Paris Basin: Keller et al., 2001; Vocontian Basin: Takashima et al., 2009) and across the Cretaceous/Palaeogene boundary (e.g., MacLeod et al., 2000; Abramovich & Keller, 2003; “Lilliput Effect” in Keller & Abramovich, 2009). Moreover, planktonic foraminifera underwent an abrupt turnover that led to the extinction of the 69% of species (Leckie et al., 2002) across the Aptian/Albian boundary (Early Cretaceous) and was associated with a sharp decrease in average test size of the newly evolved taxa (Leckie et al., 2002; Huber & Leckie, 2011; Petrizzo et al., 2012, 2013). However, the occurrence of dwarfed specimens has been always described based from the observation of a decrease in the size of specimens within the population without providing measurements with few exceptions (e.g., MacLeod et al., 2000; Coccioni et al., 2016). However, by statistically analysing morphometric data and testing their significance, we can provide the required precision and accuracy to compare data from different sections and extrapolate global from local signals. In fact, although morphometric analyses have been commonly applied to reconstruct shell-size variations of planktonic foraminiferal species across selected stratigraphic intervals of the Cenozoic

(Schmidt et al., 2004a, b, c, 2006; Yamasaki et al., 2008; Wade & Olsson, 2009; Weinkauff et al., 2013, 2014, 2016; Wade et al., 2016), no data are currently available across the severe and unique environmental perturbations that are peculiar of the Mesozoic (i.e., the OAEs) and never recur later in Earth’s history (e.g., Jenkyns, 2010). On the other hand, the automated methodologies used to reconstruct planktonic foraminiferal shell size variation during the Cenozoic (e.g., Schmidt et al., 2004a, b, c, 2006) are extremely useful to infer size changes of the whole assemblage but cannot be used to isolate species-specific responses to changing environmental conditions. Moreover, this methodology is affected, albeit for less than 2.2%, by the random orientation of the specimens measured (Schmidt et al., 2004a, b).

In this study, we aimed to: 1) develop a robust and easily replicable methodology to reconstruct species-specific morphometric variations in planktonic foraminifera, through manually measuring/counting selected shell biometric parameters that based on their known biology might have been subject to variations under changing environmental conditions (number of chambers, maximum diameter, height of the trochospire); 2) testing their mutual relationships; and 3) reconstruct planktonic foraminiferal morphometric variation across the selected case-study interval (OAE 2) and determine the most sensitive shell parameter(s) to the OAE 2-related environmental disturbances. Therefore, our new approach for the study of planktonic foraminifera includes the development of a new methodology to collect and process biometric data, and its application to species and stratigraphic intervals that have never been investigated in previous morphometric studies.

CASE STUDY: THE LATEST CENOMANIAN- EARLIEST TURONIAN OAE (LATE CRETACEOUS)

The latest Cenomanian-earliest Turonian Oceanic Anoxic Event 2 (e.g., Jenkyns et al., 2017) represents the last truly global oceanic anoxic event and approximately coincides with the maximum global warmth of the Late Cretaceous (Wilson et al., 2002; Forster et al., 2007; Friedrich et al., 2012; O’Brien et al., 2017). The lithological expression of OAE 2 is the nearly worldwide deposition of organic-rich shales and marls in hemipelagic and pelagic settings (e.g., Schlanger & Jenkyns, 1976; Scholle & Arthur, 1980; Schlanger et al., 1987), whereas its geochemical signature is represented by a synchronous positive excursion in the $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{org}}$, that is worldwide identifiable in marine and terrestrial sequences and results from the burial of large amounts of organic matter (e.g., Jenkyns, 2010; Jenkyns et al., 2017). Causes for OAE 2 are still the subject of debate, however several studies postulate that a huge submarine volcanic activity (emplacement of the Caribbean Large Igneous Province) pumped greenhouse gases and biolimiting metals in marine ecosystems and fertilized the oceans; this enhanced productivity probably led to increased organic matter preservation at the sea floor as documented by the burial of organic-rich sediments in most basins (e.g., Larson, 1991; Kuypers et al., 2002; Leckie et al., 2002;

Erba, 2004; Pancost et al., 2004; Kuroda et al., 2007; Turgeon & Creaser, 2008; Barclay et al., 2010). Ocean temperature, sea-surface stratification, nutrient availability and carbonate ion saturation were also presumably subject to significant variations during OAE 2 (Jenkyns, 2010 and references therein) and certainly influenced the geographic distribution and abundance of marine species and the dimensions of specimens according to their palaeoecological preferences.

Accordingly, planktonic foraminiferal assemblages underwent a significant diversification across the Cenomanian-Turonian boundary interval with the extinction of the single-keeled genus *Rotalipora* Brotzen, 1942, whose last representative *Rotalipora cushmani* (Morrow, 1934) disappeared shortly after the onset of OAE 2 (e.g., Premoli Silva & Sliter, 1999; Leckie et al., 2002; Falzoni et al., 2018), and the evolution and diversification of the two double-keeled genera (*Dicarinella* Porthault in Donze et al., 1970 and *Marginotruncana* Hofker, 1956) that dominated the assemblages until the Santonian (e.g., Premoli Silva & Sliter, 1995, 1999; Petrizzo, 2000, 2002; Falzoni et al., 2013, 2016a; Petrizzo et al., 2017). Planktonic foraminifera are often absent or very rare in the organic-rich layers deposited during OAE 2, while the assemblages are poorly diversified and indicative of increased sea-surface productivity (Leckie, 1985, 1987; Leary et al., 1989; Leckie et al., 1998, 2002; Luciani & Cobianchi, 1999; Nederbragt & Fiorentino, 1999; Paul et al., 1999; Premoli Silva et al., 1999; Keller et al., 2001, 2008; Coccioni & Luciani, 2004, 2005; Keller & Pardo, 2004; Scopelliti et al., 2004, 2008; Caron et al., 2006; Coccioni et al., 2006; Grosheny et al., 2006, 2013; Falzoni et al., 2016b; Kopaevich & Vishnevskaya, 2016; Reolid et al., 2016 among many others). Likewise, variations in the environmental conditions may have influenced the average dimensions of species, as observed in Cenozoic and living specimens (Bé et al., 1973; Hecht, 1976; Schmidt et al., 2004a, c, 2006; Al-Sabouni et al., 2007; Weinkauff et al., 2013, 2016). Accordingly, a number of studies have highlighted the occurrence of dwarfed specimens during OAE 2 in several regions of the Tethyan Realm (Eastbourne, England: Keller et al., 2001; Italian sections: Coccioni & Luciani, 2004, 2005; Scopelliti et al., 2004, 2008; SE France: Takashima et al., 2009; Tunisia and Algeria: Grosheny et al., 2013), of the central Atlantic Ocean (Nigeria: Gebhardt, 1997; Morocco: Jati et al., 2010; Mexico: Ifrim et al., 2011), and of the Western Interior Seaway (USA: Elderbak et al., 2014; Canada: Dionne et al., 2016), suggesting the development of unfavorable environmental conditions that inhibited the normal ontogenetic growth of specimens.

MATERIALS AND METHODS

The sections examined

Specimens measured during this study were selected from three stratigraphically complete C-T boundary interval sequences from different palaeoceanographic settings, as follows: 1) Eastbourne (England: Tsikos et al., 2004; Falzoni et al., 2018), 2) Clot Chevalier (SE France: Falzoni et al., 2016b, 2018; Gale et al., in press), and 3) Tarfaya (core S57, Morocco: Tsikos et al., 2004;

Falzoni et al., 2018). These sections were carefully selected among the most complete records known for the OAE 2 interval (Falzoni et al., 2018) satisfying three essential requirements: 1) samples yield quite common specimens of the target planktonic foraminiferal species (i.e., *R. cushmani* and *W. brittonensis*, see details in the next paragraph); 2) samples can be processed to obtain washed residues with isolated planktonic foraminifera; 3) specimens show a sufficiently good preservation to be suitable for morphometric analysis. Moreover, despite being geographically close, sedimentation in these sections occurred in different basins and at different latitudes and was therefore subject to diverse palaeoceanographic and palaeoclimatic conditions as indicated by the distinct lithology of the sections.

The stratigraphic succession cropping out at Eastbourne, Gun Gardens (England) represents the most expanded, complete and well-studied Cenomanian-Turonian transition of the English Chalk and the European reference section for the C/T boundary (Gale et al., 1993, 2000, 2005; Paul et al., 1999; Keller et al., 2001; Tsikos et al., 2004; Falzoni et al., 2018 among many others). Most importantly, contrary to other coeval sections where calcareous microfossils are absent in the black shale layers deposited during OAE 2 (e.g., in the Italian sections: Luciani & Cobianchi, 1999; Coccioni & Luciani, 2004, 2005; Scopelliti et al., 2004, 2008), samples from Eastbourne contain relatively rich planktonic foraminiferal assemblages throughout the section, thus providing the unique opportunity to reconstruct phenotypic variations across OAE 2 without major gaps. The section consists of a 27-m thick succession of chalks and marls belonging to the Lower Chalk (Grey Chalk and Plenus Marls Members) and White Chalk (Ballard Cliff and Holywell Members) formations (Gale et al., 2005), which were deposited in the Anglo-Paris Basin at a palaeolatitude of about 35°N (Hay et al., 1999; Philip et al., 2000) (Fig. 1). The litho-, bio-, and chemostratigraphic framework of this section, as well as detailed palaeoenvironmental interpretations, are discussed in Gale et al. (1993, 2000, 2005), Robaszynski et al. (1998), Paul et al. (1999), Keller et al. (2001), Hart et al. (2002), Tsikos et al. (2004), Voigt et al. (2004, 2006), Jarvis et al. (2006), Pearce et al. (2009), Linnert et al. (2011), Zheng et al. (2013, 2016), Du Vivier et al. (2015) and Falzoni et al. (2018). The planktonic foraminiferal zonation applied in this study follows Paul et al. (1999), Tsikos et al. (2004) and Falzoni et al. (2018), who identified the extinction of *R. cushmani*, marking the top of the *R. cushmani* Total Range Zone, in the middle of the Plenus Marls bed 4 (11.4 m above the base of the section), and assigned the overlying stratigraphic interval to the *Whiteinella archaeocretacea* Interval Zone. The lowest occurrence (LO) of *Helvetoglobotruncana helvetica* (Bolli, 1945), identifying the base of the *H. helvetica* Zone and of the Turonian Stage is not identified by Paul et al. (1999), Tsikos et al. (2004) and Falzoni et al. (2018), although it is recognised by Keller et al. (2001) and Hart et al. (2002) in the lower White Chalk Fm. Reasons for such discrepancies likely rely on the different *H. helvetica* species concept adopted by authors (see discussion in Huber & Petrizzo, 2014 and Falzoni et al., 2018).

The Clot Chevalier section (SE France) consists of a 35 m-thick succession of limestones and marls deposited in

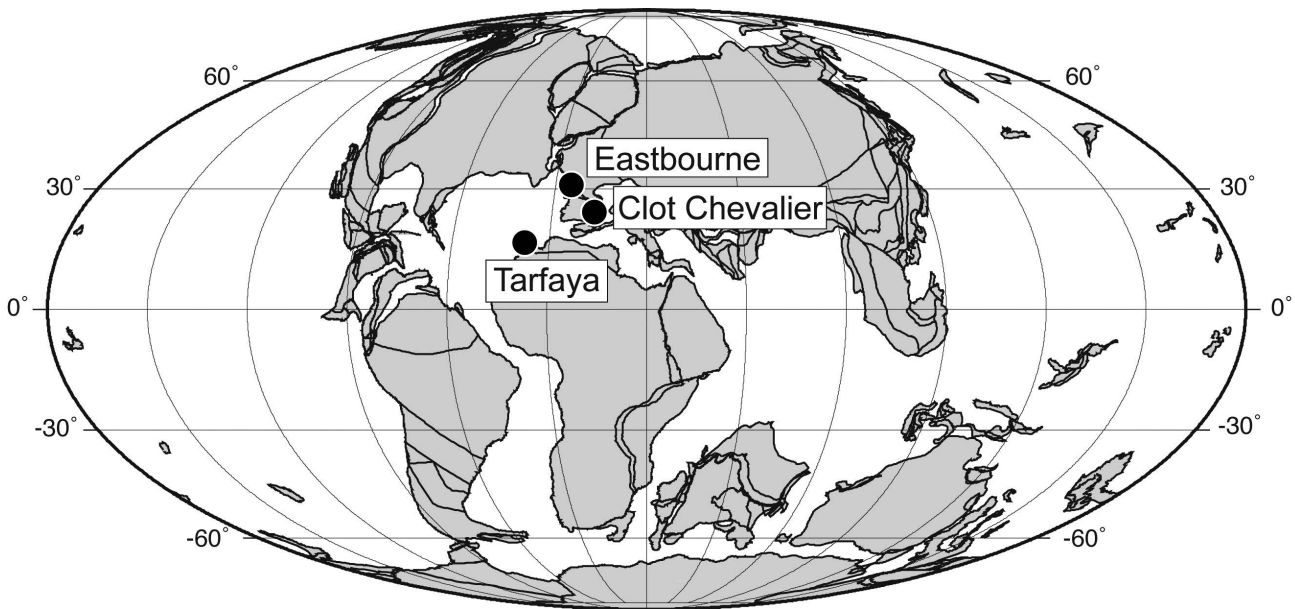


Fig. 1 - Palaeogeographic reconstruction for the late Cenomanian (95 Ma), with location of the sections examined in this study (after Hay et al., 1999).

the Vocontian Trough at a palaeolatitude of $\sim 30^{\circ}\text{N}$ (Hay et al., 1999; Philip et al., 2000) during the latest Cenomanian to earliest Turonian (Fig. 1). The section includes a ~ 28 m-thick succession of organic-rich marls belonging to the Thomel Level representing the local lithological expression of OAE 2 (Falzoni et al., 2016b; Gale et al., in press). Planktonic foraminifera are generally abundant and the assemblages are diverse, except within the lithological unit Th3 of the Thomel Level, where specimens are rare to very rare. The extinction of *R. cushmani* is recorded at 4.8 m above the base of the section, in an earlier stratigraphic interval compared to other coeval sections of the Vocontian Basin. Such earlier extinction is interpreted to be related to the presence of a condensed stratigraphic interval resulting from a very low sedimentation rate or by brief episodes of interruption of sedimentation that reduced the likelihood of preservation of the last representatives of this species (Falzoni et al., 2016b).

Core S57 was drilled by Shell during exploration in the late 1970s to early 1980s at Tarfaya (SW Morocco) (Tsikos et al., 2004; Falzoni et al., 2018). Sediments consist of brown finely laminated to massive limestones with high TOC content (up to 30%wt) that are late Cenomanian-early Turonian in age. Sediments accumulated in the Central Atlantic Ocean at $\sim 15^{\circ}\text{N}$ (Hay et al., 1999; Kuhnt et al., 2001) (Fig. 1). The planktonic foraminiferal zones follow Tsikos et al. (2004) and Falzoni et al. (2018), who assigned the lower part of the core (up to 50.96 m) to the *R. cushmani* Zone and the overlying interval to the *W. archaeocretacea* Zone.

For the purposes of this study, rock samples were processed to obtain washed residues with isolated planktonic foraminifera. To minimise any bias related to the sample size, we processed approximately the same amount of material in each section. Rock samples from core S57 (Tarfaya) and from the Plenius Marls Member (Eastbourne) were processed with a 10% solution of hydrogen peroxide (H_2O_2). Because of the

compact lithology, rock samples from Clot Chevalier, the Grey Chalk Member and the White Chalk Formation (Eastbourne) were treated with a solution of acetic acid (80%) and water (20%) (see Lirer, 2000 and Falzoni et al., 2016b for a detailed description of the procedure). The sampling resolution adopted during this study is 40 cm at Eastbourne, 30 cm to 1.2 m at Clot Chevalier, and 20 to 50 cm at Tarfaya.

Species and number of specimens measured

To perform this study, we selected two species that are usually abundant within the OAE 2 interval and regarded to have different palaeoecological preferences (e.g., Leckie, 1987; Hart, 1999; Huber et al., 1999): *Rotalipora cushmani* (Morrow, 1934) and *Whiteinella brittonensis* (Loeblich & Tappan, 1961). Specifically, based on the known palaeobiogeographic distribution of these fossil species and on the morphologic analogy with modern taxa, the single-keeled *R. cushmani* is considered a deep-dweller likely adapted to oligotrophic regimes, whereas whiteinellids, including *W. brittonensis*, are generally interpreted to be surface-dwellers likely prone to exploit a more mesotrophic to eutrophic resource spectrum (Caron & Homewood, 1983; Hart, 1999; Huber et al., 1999; Premoli Silva & Sliter, 1999). Stable-isotope and quantitative data on Turonian-Santonian assemblages from Exmouth Plateau (eastern Indian Ocean; Falzoni et al., 2016a) and Tanzania (western Indian Ocean; Petrizzo et al., 2017) confirm that whiteinellids inhabited sea-surface waters and were particularly adapted to warm climate conditions, while their tolerance to high nutrient concentrations could not be verified in these studies. Moreover, *W. brittonensis* survives OAE 2, whereas *R. cushmani* becomes extinct slightly after the onset of the event and might have experienced pre-extinction dwarfing in analogy with several Cenozoic species (Wade & Olsson, 2009), and in agreement with data from the Bottaccione section, where *R. cushmani* went through a 10% decrease

in the average shell size below the Bonarelli Level (Coccioni et al., 2016).

For this study, we have performed morphometric analysis on ten specimens per species in each sample. We are aware that ten specimens may be insufficient to fully quantify morphometric variations through time, but this number was selected based on the average abundance of *R. cushmani* and *W. brittonensis* in the sections examined and in order to measure the same number of specimens in each sample (when possible). We selected this approach, which has been already applied by Wade & Olsson (2009), instead of increasing the number of specimens measured in the samples where the target species are more abundant, because the aim of this study is to reconstruct the long-term variation of the morphometric parameters measured across the OAE 2 interval, rather than increase as much as possible their accuracy in the few scattered samples where these species are more abundant.

If less than ten specimens were found in a sample, the analyses here presented are based on all specimens of *R. cushmani* and *W. brittonensis* occurring in the sample. If more than ten specimens occurred in the samples, they were randomly selected in the > 250 μm size fraction, where adult specimens belonging to both species are usually common. Random selection was performed by measuring the first ten well-preserved specimens of *R. cushmani* and *W. brittonensis* encountered during the observation of each washed residue under the stereomicroscope. Specimens were judged as being well-preserved when they did not show broken chambers and their overall preservation was good enough to ensure the acquisition of reliable morphometric data. We looked for additional specimens in the size fraction comprised between 250 and 125 μm in case we could not identify the required number of specimens in the larger size fraction. In fact, the absence of *R. cushmani* and *W. brittonensis* in the > 250 μm size fraction suggests that the largest specimens have to be found in the smaller size fractions. Because one of the aims of this study is to trace variations in the diameter of the largest-sized specimens in each sample and not to establish the within-sample average and variability of the whole assemblage, this procedure does not introduce any biases. Also, because we processed rock samples of approximately the same size in each section, the washed residues obtained were also approximately of equal size and large enough to encounter rare species. This procedure minimises possible biases related to the sample size (i.e., the quantity of washed residue observed). In fact, examination of too small samples may reduce the likelihood of encountering rare large-sized specimens in the > 250 μm size fraction. Consequently, the biometric parameters represent the average values of the largest specimens (adults) in each sample and are not representative of the average values yielded by the entire population of *R. cushmani* and *W. brittonensis* that instead should be estimated based on specimens from all size fractions. We selected this approach because 1) we aimed to exclude smaller-sized juvenile forms in order to avoid any bias related to the ontogenetic stage of the specimens measured; 2) the random selection of foraminifera in an unsieved washed residue yielding specimens of different size mixed together would have caused an underestimation of the measurements, being smaller-sized tests (< 250

μm) much more abundant in the samples; and 3) the minimum shell size of a species is regarded to be usually constant, whereas the largest shell size is more subject to ecologically-controlled variations (Schmidt et al., 2006).

Acquisition of morphometric data

Specimens selected in each sample were picked, placed in a 32-cell slide, numbered from 0 to 20 (1 to 10 *R. cushmani* and 11 to 20 *W. brittonensis*), oriented in spiral and lateral view, as shown in Fig. 2, fixed in the preferred orientation with a water-soluble glue and photographed using a Leica MZ12.5 stereomicroscope equipped with a digital camera Leica DFC295. We choose to photograph specimens at the stereomicroscope, as the preparation of the specimens and the acquisition of digital images at the Scanning Electron Microscope (SEM) is more time-consuming. Digital photographs were acquired using the software Leica Application Suite V3.3.0. Measurements were obtained manually on each specimen using the open source software ImageJ 1.44p. All measurements were performed by a single researcher (M.V.) to reduce the systematic error.

We measured four morphometric parameters for each selected specimen of *R. cushmani* and *W. brittonensis* as follows (Fig. 2): 1) the number of chambers in the last whorl; 2) the height of the trochospire (H); 3) the maximum diameter crossing the first chamber of the inner whorl visible on the spiral side (D_{max_1}); and 4) the absolute maximum diameter (D_{max_2}). These parameters have been selected because they might have been subject to variations under changing environmental conditions. In fact, if the shell size likely reflects the proximity of each species to its preferred ecological parameters as mentioned above (Hecht, 1976; de Villiers, 2004; Schmidt et al., 2006; Moller et al., 2013; Weinkauff et al., 2016), an increase/decrease in the number of chambers in the last whorl might reflect an acceleration/deceleration in the rate of formation of new chambers, which is again presumably ecologically driven (e.g., Weinkauff et al., 2013). Moreover, we measured H, because we observed the occurrence of several high-spined *R. cushmani* specimens in the late Cenomanian and we aimed to check if these specimens consistently have a different shell size compared to the lower-spined population by investigating the relationship (if any) between shell size and H.

The count of the number of chambers is complicated by the presence of half chambers resulting from the overlap of the first chamber of the ultimate whorl with the second and the last one (Fig. 2a-b). However, the identification of the half chamber is very arbitrary, because its degree of overlap with the other chambers varies among specimens.

The approach followed here to estimate the number of outer chambers is as follows: we counted the number of whole chambers in the last whorl, and we added an additional chamber in case the length of the arc delimiting the external periphery of the half chamber represents more than $\frac{1}{4}$ of the semicircle in which it is circumscribed, which means in case the angle comprised between the lines joining the center of the circle and the points where the first chamber overlaps with the second and the last one is greater than 45° (Fig. 2a-b). This choice is supported by the observation that the first chamber of the last whorl is usually considered complete (i.e., not half) in specimens

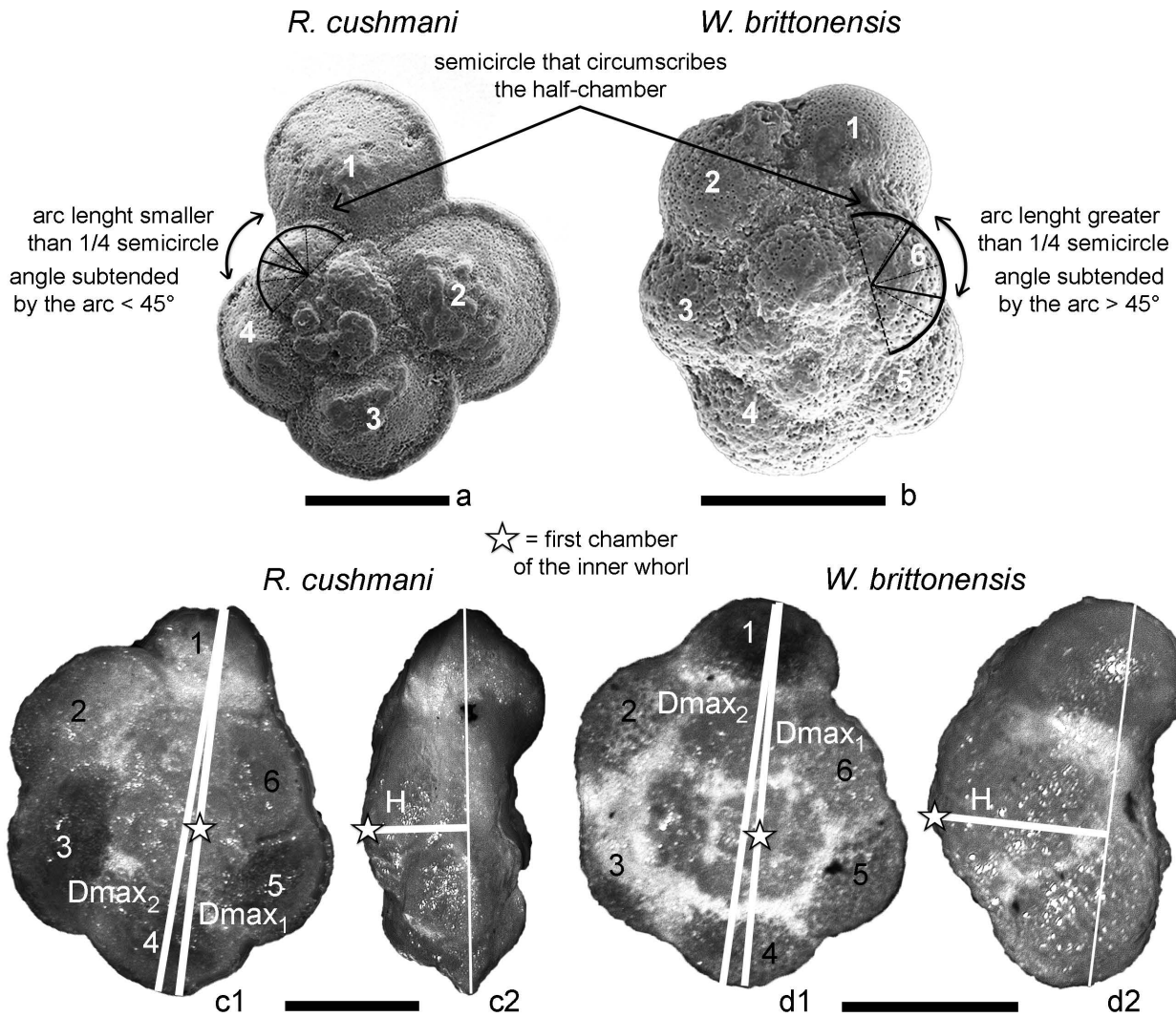


Fig. 2 - Methodology applied to count the number of chambers in the last whorl and to measure the maximum diameter of the shell and the height of the trochospire: a) spiral view of a specimen of *R. cushmani* with four outer chambers; b) spiral view of a specimen of *W. brittonensis* with six outer chambers as counted in this study; c1-2) spiral and lateral view of *R. cushmani*; d1-2) spiral and lateral view of *W. brittonensis*. Dmax₁ = maximum diameter crossing the first chamber of the inner whorl in spiral view, Dmax₂ = absolute maximum diameter, H = height of the trochospire, and number of chambers in the last whorl as measured in this study. Scale bar is 200 µm.

of *R. cushmani* and *W. brittonensis*, when the length of the arc delimiting its external periphery is approximately equal to or greater than 1/2 of the semicircle in which the chamber is circumscribed, thus when the angle comprised between the lines joining the center of the circle and the points where the first chamber overlaps with the second and the last one is equal to or greater than 90° (see specimens in Fig. 2c-d). Therefore, the methodology here applied takes into account the presence of the half chamber that is counted as a whole chamber, in case the arc length corresponds to more than the 1/2 of the external periphery that would have a chamber completely belonging to the last whorl. By contrast, the half chamber is not counted in case the arc length corresponds to less than the 1/2 of the external periphery of a chamber completely belonging to the last whorl. This simplification may slightly reduce the accuracy in the estimation of the number of outer chambers but increases its precision.

Dmax₁ and Dmax₂ are measured on the spiral side of each specimen (Fig. 2c-d): Dmax₁ corresponds to the maximum diameter of the shell starting from the mid point of the peripheral outline of the last chamber and crossing the first chamber visible on the spiral side. Dmax₂ corresponds to the diameter/axis of the circle/ellipse that circumscribes the shell and starts from the mid point of the peripheral outline of the last chamber. The latter parameter was measured exclusively in specimens from the Plenus Marls Formation at Eastbourne and throughout the section at Clot Chevalier, as we aimed to compare the two methods to measure the maximum diameter and establish the most objective approach. Finally, to estimate the value of H, we positioned the specimen in lateral view as shown in Fig. 2c2-d2 and traced a line joining the point in the middle of the last chamber and of the opposite chamber (*W. brittonensis*) or a line joining the keel on the last chamber and of the opposite chamber (*R. cushmani*):

H corresponds to the length of the segment perpendicular to this line that starts from the first chamber observable on the spiral side.

Results of morphometric analyses have been plotted against stratigraphy and the population of values obtained for the two maximum diameters and for the height of the trochospire is represented through box plots obtained using the open source software PAST 3.04 (Hammer et al., 2001). For each examined sample, this graphic representation of data allows a quick visualization of: 1) the median values (central bar); 2) the dimension interval in which the 50% of the population measured falls (Inter Quartile Range or IQR, i.e., the length of the box); 3) the data points that fall within 1.5 times the IQR that determine the length of the whiskers; and 4) the possible presence of outlier values falling outside 1.5 times the IQR (dots) (Figs 3-5). The D_{max_1} , D_{max_2} and H of the holotypes and paratypes of *R. cushmani* and *W. brittonensis* have been superimposed on the box plots, in order to check whether the distribution of values we obtained in the three sections falls within the range shown by the type material (Figs 3-5). The raw data and the standard deviation obtained for the parameters measured are given in the Supplementary Online Material (see Supplementary Figs 1-3 and Supplementary Tables 1-3).

Results of morphometric analyses have been statistically processed using regression analysis to investigate the relation existing between the parameters measured (i.e., D_{max_1} vs. D_{max_2} ; D_{max_1} vs. H, and D_{max_1} vs. number of outer chambers). Finally, the distribution of values obtained for D_{max_1} is also graphically represented through histograms that have been calculated for each species and each section for different time intervals (i.e., separating the results) as follows: 1) pre-OAE 2; 2) during OAE 2; and 3) post-OAE 2.

RESULTS

Eastbourne (England)

ROTALIPORA CUSHMANI - All samples contain specimens with five chambers in the last whorl (Fig. 3). Specimens with four and six outer chambers are also common throughout the section, whereas only one single specimen having seven chambers was observed (at 1.6 m) (Fig. 3). The value of H is comprised between 92 μm (at 4.4 m above the base of the section) and 267 μm (at 6.4 m), although H falls in the 100-200 μm size interval in most specimens. Minimum, median and maximum values of H fluctuate with inter-sample offset (i.e., the offset between consecutive samples) of about 20 to more than 50 μm and tend to increase slightly at the onset of OAE 2. D_{max_1} ranges from 303 (at 4.4 m) to 700 μm (at 10 m), but the D_{max_1} of most specimens is comprised between 400 and 600 μm . Minimum, maximum and median values fluctuate from one sample to another with inter-sample offsets that can be higher than 100 μm . D_{max_2} ranges from 361 (at 10.4 m) to 705 μm (at 10 m) and most specimens have a D_{max_2} larger than 400 μm . The trend shown by D_{max_2} perfectly mirrors that shown by D_{max_1} (Fig. 3).

The values of H, D_{max_1} and D_{max_2} obtained for *R. cushmani* are generally included within the range of values yielded by the holotype and paratype, with the exception

of its H within OAE 2 that is on average 40 μm higher than the holotype and ~ 100 μm higher than the paratype.

WHITEINELLA BRITTONENSIS - Most samples contain specimens with five or six chambers in the last whorl (Fig. 3). Specimens with seven outer chambers are found in nine samples only, mostly in the interval corresponding to the final phase of OAE 2 or after the event. H is comprised between 81 (at 11.8 m) and 282 μm (at 16.1 m), with the maximum value reached within OAE 2. Values of H fluctuate, although they generally fall within 100 and 200 μm . D_{max_1} ranges from 250 (at 10.4 m) to 604 μm (at 16.1 m), although most specimens fall in the 300-500 μm size interval and average values are usually smaller compared to *R. cushmani*. Minimum, maximum and median values fluctuate from one sample to another with inter-sample offsets that occasionally are higher than 100 μm . Minimum values (< 300 μm) are reached in bed 3 and 4 of the Plenus Marls, whereas maximum values are reached at 16.1 m in the lower part of the Holywell Member, both falling within the OAE 2 interval. Average D_{max_1} increases by about 50 μm throughout the stratigraphic interval studied. Average D_{max_2} ranges from 270 (at 11.8 m) and 500 μm (at 9.6 m), most values are comprised between 320 and 420 μm and its trend perfectly mirrors that exhibited by D_{max_1} (Fig. 3).

The values of H, D_{max_1} and D_{max_2} obtained for *W. brittonensis* are generally included within the range of values of the holotype and the paratypes, with the exception of the minimum values of H that fall 20 μm below the range of values exhibited by the paratypes throughout the section.

Clot Chevalier (SE France)

ROTALIPORA CUSHMANI - Most specimens show five to six chambers in the last whorl, whereas morphotypes with four and seven outer chambers are occasionally found in the assemblage (Fig. 4). H is comprised between 122 (at 0.9 m) and 273 μm (at 2.7 m).

D_{max_1} ranges from 371 (at 1.8 m) to 735 μm (at 0.9 m) and median values show inter-sample offsets up to 50 μm . The D_{max_1} (443 μm) of the only specimen found at 4.8 m (i.e., where *R. cushmani* last occurs) is ~ 50 μm higher than the minimum D_{max_1} values yielded by this species at Clot Chevalier and measured below the OAE 2 interval. Maximum D_{max_1} values are reached slightly below the onset of OAE 2. D_{max_2} ranges from 402 (at 1.8 m) and 766 μm (at 0.9 m), and median, maximum and minimum values parallel those shown by D_{max_1} .

Values of D_{max_1} and D_{max_2} obtained for specimens of *R. cushmani* are comprised between those exhibited by its holotype and paratype, whereas H is slightly higher within the OAE 2 interval, as observed at Eastbourne.

WHITEINELLA BRITTONENSIS - Most samples contain specimens with five and six chambers in the last whorl (Fig. 4). Specimens with seven outer chambers are found in five samples in the upper part of the section (after OAE 2). H is comprised between 75 (at 18.6 m) and 240 μm (at 26.7 m), most values are included within 100 and 200 μm and an overall trend toward an increase of H (of about 50 μm) is noticeable throughout the section. D_{max_1} ranges from 246 (at 3.6 m) to 566 μm (at 28.8 m),

CLOT CHEVALIER

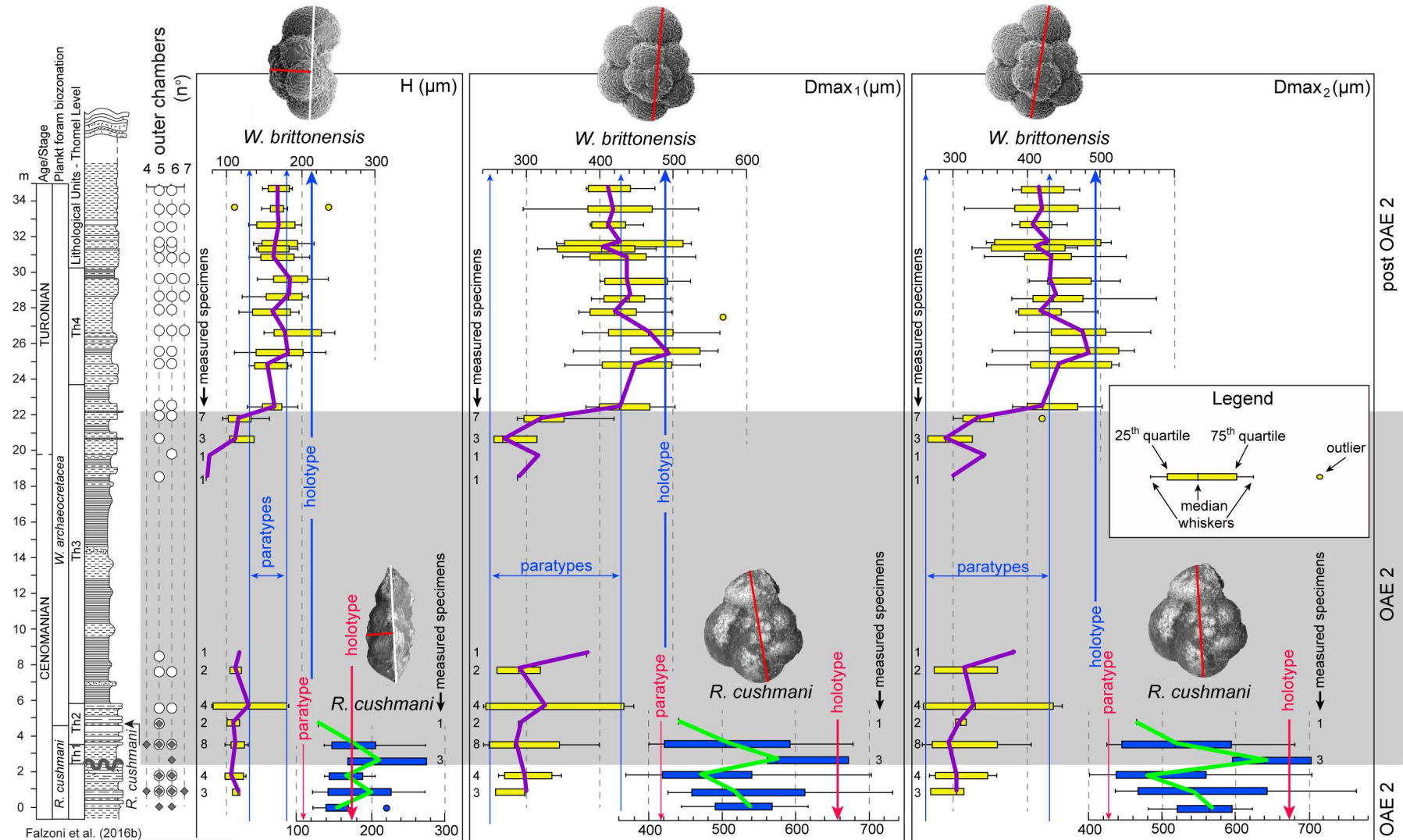


Fig. 4 - Box plots for H, Dmax₁, and Dmax₂ of *R. cushmani* and *W. brittonensis* prior to, during and after OAE 2 at Clot Chevalier. The duration of OAE 2 is according to Falzoni et al. (2016b) and Gale et al. (in press) and it is based on the shape of the carbon isotope profile (i.e., from the first rise of the $\delta^{13}\text{C}$ to the last positive peak that precedes the $\delta^{13}\text{C}$ return to pre-excursion values following its definition by Jarvis et al., 2011 and Jenkyns et al., 2017). The number of specimens having the indicated number of outer chambers is reported for each sample in Supplementary Tab. 2. The number of specimens of *R. cushmani* and *W. brittonensis* analysed during this study is indicated when it is lower than ten. The gap in the measures of H, Dmax₁ and Dmax₂ of *W. brittonensis* within the lithological unit Th3 is due to its absence in this stratigraphic interval. For further details, see caption of Fig. 3.

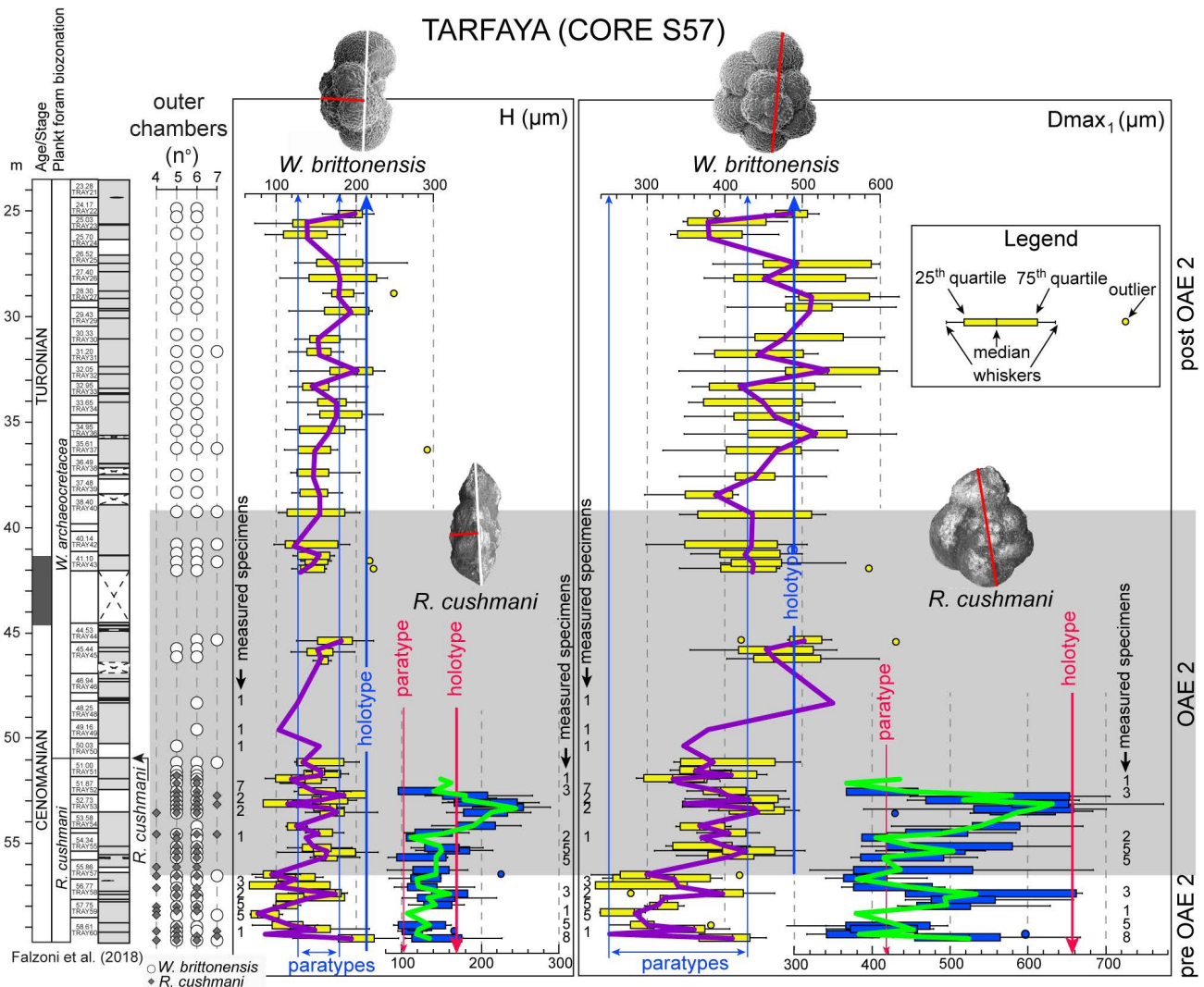


Fig. 5 - Box plots for H, Dmax₁ and Dmax₂ of *R. cushmani* and *W. brittonensis* prior to, during and after OAE 2 at Tarfaya (core S57). The duration of OAE 2 is according to Jarvis et al. (2011) and Jenkyns et al. (2017) and based on the shape of the carbon isotope profile (i.e., from the first rise of the $\delta^{13}C$ to the last positive peak that precedes the $\delta^{13}C$ return to pre-excursion values). The number of specimens having the indicated number of outer chambers is reported for each sample in Supplementary Tab. 3. The number of specimens of *R. cushmani* and *W. brittonensis* analysed during this study is indicated when it is lower than ten. For further details, see caption of Fig. 3.

whereas Dmax₂ is comprised between 258 (at 3.6 m) and 592 µm (at 28.8 m). Maximum and minimum values of Dmax₁ and of Dmax₂ are found in the same samples and trends are identical. Moreover, both diameters show a clear increasing trend that mirrors that exhibited by H with minimum values reached before OAE 2 and maximum values culminating immediately after OAE 2.

Values of Dmax₁ and Dmax₂ obtained for specimens of *R. cushmani* are comprised between those exhibited by its holotype and paratypes, whereas minimum values of H measured throughout the section are lower, as observed at Eastbourne.

Core S57, Tarfaya (Morocco)

ROTALIPORA CUSHMANI - Most samples contain specimens with five to six outer chambers, whereas morphotypes with four and especially with seven chambers in the last whorl are more rarely found in the assemblage (Fig. 5). However, specimens with seven outer

chambers occur more frequently and in a higher number of samples at Tarfaya compared to Eastbourne and Clot Chevalier. H is comprised between 80 (at 56.08 m) and 289 µm (at 53.12 m); in general, values fluctuate and increase up to 300 µm within OAE 2 and later decrease prior to the extinction level of *R. cushmani*. Dmax₁ ranges from 294 (at 58.91 m) to 770 µm (at 52.92 m). Values fluctuate from one sample to another and median, maximum and minimum values show inter-sample offsets up to 200 µm. As for H and as observed at Eastbourne, the highest values of Dmax₁ can be found toward the top of the stratigraphic distribution of *R. cushmani* and are followed by a minimum slightly below its extinction level and a slight increase at its highest occurrence.

Values of H are higher compared to the type material in the OAE 2 interval, as observed at Eastbourne and Clot Chevalier. Moreover, minimum Dmax₁ values measured for several specimens before OAE 2 are lower than those exhibited by the paratype.

WHITEINELLA BRITTONENSIS - Most samples contain specimens with five and six chambers in the last whorl; specimens with seven outer chambers are found occasionally throughout the section (Fig. 5). H is comprised between 65 (57.07 m) and 293 μm (at 36.26 m), although most specimens fall in the 100-200 μm interval. The values of H do not exhibit any noticeable increasing or decreasing trend. D_{max_1} ranges from 228 (at 56.5 m) to 624 μm (at 28.89 m) but median values, although fluctuate from one sample to another (inter-sample offset up to 100 μm), show an overall increase of about 200 μm from prior to after OAE 2.

The minimum values of H measured for *W. brittonensis* are generally lower than those exhibited by the type material, as observed at Eastbourne and Clot Chevalier, whereas the D_{max_1} of several specimens after OAE 2 is up to 100 μm larger than the holotype.

DISCUSSION

General observations

The comparison of the results obtained from Eastbourne, Clot Chevalier and Tarfaya permits the following general observations. These observations are based on the average values measured on the large-sized specimens (adults) in this study, and they do not reflect the intra-sample and inter-sample variability yielded by the entire population of *R. cushmani* and *W. brittonensis*.

1. The trends shown by the median values of D_{max_1} and D_{max_2} of *R. cushmani* and *W. brittonensis* perfectly overlap at Eastbourne (Plenus Marls interval) and Clot Chevalier. In order to better understand the relationship between D_{max_1} and D_{max_2} in both species, we performed a graphic correlation between these two parameters and calculated the regression line (Fig. 6a). Results demonstrate that: 1) values of D_{max_1} and D_{max_2} are strongly correlated, as confirmed by the very high correlation coefficients (Eastbourne: $r^2 = 0.96$ for *R. cushmani* and $r^2 = 0.94$ for *W. brittonensis*; Clot Chevalier: $r^2 = 0.96$ for *R. cushmani* and $r^2 = 0.98$ for *W. brittonensis*); and 2) values of D_{max_1} are usually slightly smaller than or equal to the D_{max_2} in both species. Overall, these observations suggest that the two methods adopted to measure the maximum diameter provide the same results, so that trends of shell size variations from one sample to another are preserved, although measured values of single specimens might differ of several microns. Although variations in the maximum diameters appear independent of the methodology, D_{max_1} represents in our opinion the simplest and most objective methodology to estimate the shell-size of trochospiral planktonic foraminifera, as the first chamber of the spire that is observable in the inner whorl represents a clearly identifiable "tie-point" constraining the measure.

2. The trends of median values of H in *R. cushmani* apparently mirror those exhibited by the maximum diameter(s), although the inter-sample offset is much lower. By contrast, trends exhibited by the maximum diameter(s) and by H do not correspond in *W. brittonensis*. A graphic correlation between D_{max_1} and H is performed

here to better constrain the relation between these parameters (Fig. 6b). The correlation coefficients obtained for both species are very low at Eastbourne ($r^2 = 0.19$ for *R. cushmani* and $r^2 = 0.22$ for *W. brittonensis*), Clot Chevalier ($r^2 = 0.29$ for *R. cushmani* and $r^2 = 0.62$ for *W. brittonensis*) and Tarfaya ($r^2 = 0.45$ for *R. cushmani* and $r^2 = 0.41$ for *W. brittonensis*) (Fig. 6b). These observations imply that large-sized specimens do not necessarily have a higher trochospire compared to conspecific smaller-sized specimens and confirm the taxonomic validity of the height of the trochospire as a distinctive feature for the classification of planktonic foraminifera at the species level (e.g., Robaszynski et al., 1979).

3. For completeness, we tested the relationship between the number of chambers in the last whorl and D_{max_1} in specimens of *R. cushmani* and *W. brittonensis*. The correlation coefficient of the regression line is always < 0.2 for both species at all localities (Fig. 6c), indicating that an increase in the rate of formation of new chambers does not correspond to an increase in the size of the specimens.

4. We compared the range of values here obtained for D_{max_1} , D_{max_2} and H, with those exhibited by the holotypes and the paratypes of *R. cushmani* and *W. brittonensis* here re-measured following the same methodology. We observe that the values of D_{max_1} , D_{max_2} and H of the specimens measured during this study are generally lower compared to the holotypes of both species but are typically between the values of the holotype and the paratype (*R. cushmani*), or more perfectly fit with the range of values shown by the paratypes (*W. brittonensis*) (Figs 3-5). The most important exception is represented by the H of *R. cushmani* within the OAE 2 interval, which is on average 50 μm higher than the holotype at all localities (Figs 3-5).

These observations suggest that the size of the holotype, which is surely controlled by the local ecological conditions at the time of its growth, does not necessarily represent a good estimate of the average size of its species, probably because the holotype is usually selected among the best preserved large-sized specimens clearly showing the diagnostic taxonomic features that permit identification. Therefore, considering the shell size of the holotype as a reference for the average shell size of its species might be strongly misleading. Conversely, the specimens of *R. cushmani* and *W. brittonensis* measured in this study more closely mirror the size variability yielded by the paratypes.

5. In the interval where *W. brittonensis* and *R. cushmani* co-occur, the values of D_{max_1} and D_{max_2} are on average lower in the former compared to the latter species. This observation is consistent with the presumed palaeoecological preferences of both species, being Late Cretaceous oligotrophic planktonic foraminifera usually larger-sized compared to mesotrophic and eutrophic forms (Caron & Homewood, 1983; Hart, 1999; Premoli Silva & Sliter, 1999). This assumption is based on the observation that smaller-sized unkeeled morphotypes are generally more cosmopolitan, can be found in hemipelagic and pelagic depositional settings from low to high latitudes

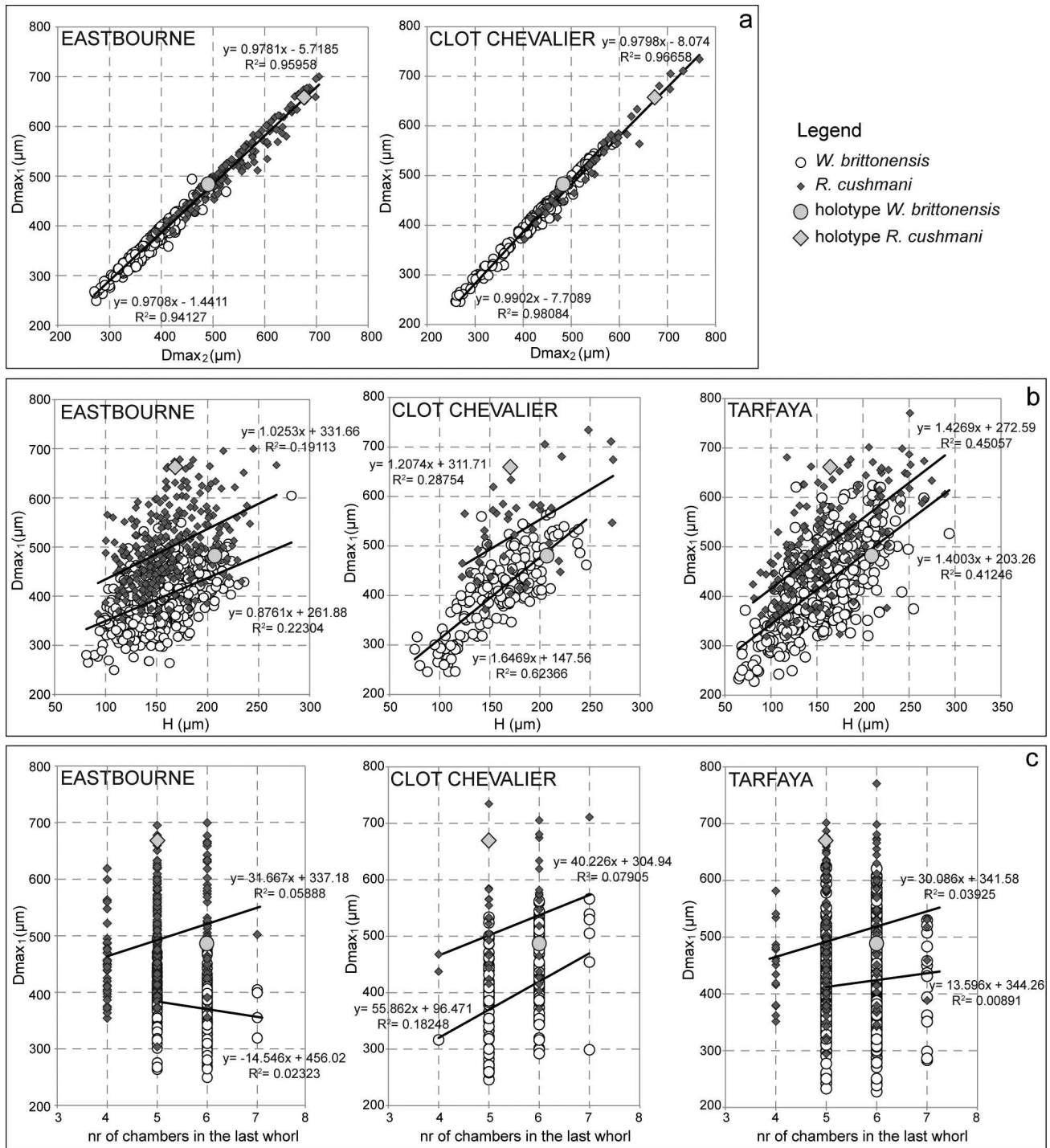


Fig. 6 - Distribution of values and correlation between the morphometric parameters measured in this study at Eastbourne, Clot Chevalier and Tarfaya. a) D_{max_1} vs. D_{max_2} ; b) D_{max_1} vs. H; c) D_{max_1} vs. number of chambers in the last whorl. The position of the holotypes of *R. cushmani* and *W. brittonensis* is superimposed on the values obtained during this study to allow comparison.

and in upwelling areas, whereas large-sized keeled species have more restricted palaeoecological preferences, are less widely distributed and are more commonly found in tropical and subtropical open ocean settings with a well-developed thermocline (Caron & Homewood, 1983; Leckie, 1987; Corfield et al., 1990; Norris & Wilson, 1998; Hart, 1999; Huber et al., 1999; Premoli Silva & Sliter, 1999; Petrizzo et al., 2008). However, the median D_{max_1} and D_{max_2} values of *W. brittonensis* increase throughout the stratigraphic interval analysed and the

largest specimens occurring in the earliest Turonian may reach the same dimensions exhibited by *R. cushmani* during the late Cenomanian. This observation might suggest a variation in the palaeoecological preferences of *W. brittonensis* in the early Turonian, but confirmation of this hypothesis requires further studies.

6. The intra-sample offsets exhibited by H, D_{max_1} and D_{max_2} are usually higher in *R. cushmani* (H generally comprised between 50 and 150 μm ; D_{max_1} and D_{max_2}

generally comprised between 100 and 350 μm) compared to *W. brittonensis* (H generally comprised between 50 and 100 μm ; Dmax₁ and Dmax₂ generally comprised between 50 and 250 μm), possibly indicating that specimens of the former larger-sized species possess a higher variability in the maximum shell size and height of the trochospire. The inter-sample variability in the median values of Dmax₁ and Dmax₂ is also quite high in both species (up to ~100 μm in *R. cushmani* and up to ~50 μm in *W. brittonensis*). Although this result might partly depend on a rather small sample size, we believe that long-term increasing/decreasing trends observed in the median values of Dmax₁ and Dmax₂ (e.g., increase in the shell size of *R. cushmani* in the OAE 2 interval and of *W. brittonensis* within or after OAE 2) mirror increasing/decreasing trends of the maximum diameter of the whole population. This conclusion is supported by the histograms representing the distribution of frequency of the Dmax₁ of both species and in all localities that were subdivided in three intervals 1) pre-OAE 2; 2) within OAE 2; and 3) post-OAE 2 (Figs 7-8). In this case, the distribution of Dmax₁ values shown by *R. cushmani* and *W. brittonensis* is based on a large number of specimens (up to 314 per interval) is generally unimodal and converge to a normal (Gaussian) distribution. Overall, histograms indicate an increase in the relative abundance of specimens with larger shell size

in both species at all localities across the stratigraphic interval studied, suggesting that these trends might reflect true variations of the population. Specifically, the frequency of *R. cushmani* specimens larger than 500 μm increases at all localities, while the frequency of smaller-sized specimens (< 450 μm) decreases at Eastbourne and Tarfaya (Fig. 7). This variation in the shell-size distribution is less clear at Clot Chevalier, possibly because of the lower number of specimens analysed. An increase in the frequency of *W. brittonensis* specimens with larger Dmax₁ is clearly visible at Clot Chevalier and Tarfaya and less apparent, but still observable at Eastbourne (Fig. 8). Histograms illustrate a general shift of the Dmax₁ values of *W. brittonensis* from < 400-450 μm prior to OAE 2 up to 650 μm after OAE 2 at all localities. However, the data collected during this study suggest that such increase in shell size is asynchronous and occurs during OAE 2 at Tarfaya and Eastbourne and after OAE 2 at Clot Chevalier, although the absence of *W. brittonensis* at this latter locality during most of the OAE 2 interval might account for such discrepancy.

7. At Eastbourne and Tarfaya, trends of median Dmax₁ and Dmax₂ values shown by *R. cushmani* and by *W. brittonensis* fluctuate in phase in some intervals but are out of phase in others (Figs 3 and 5), suggesting

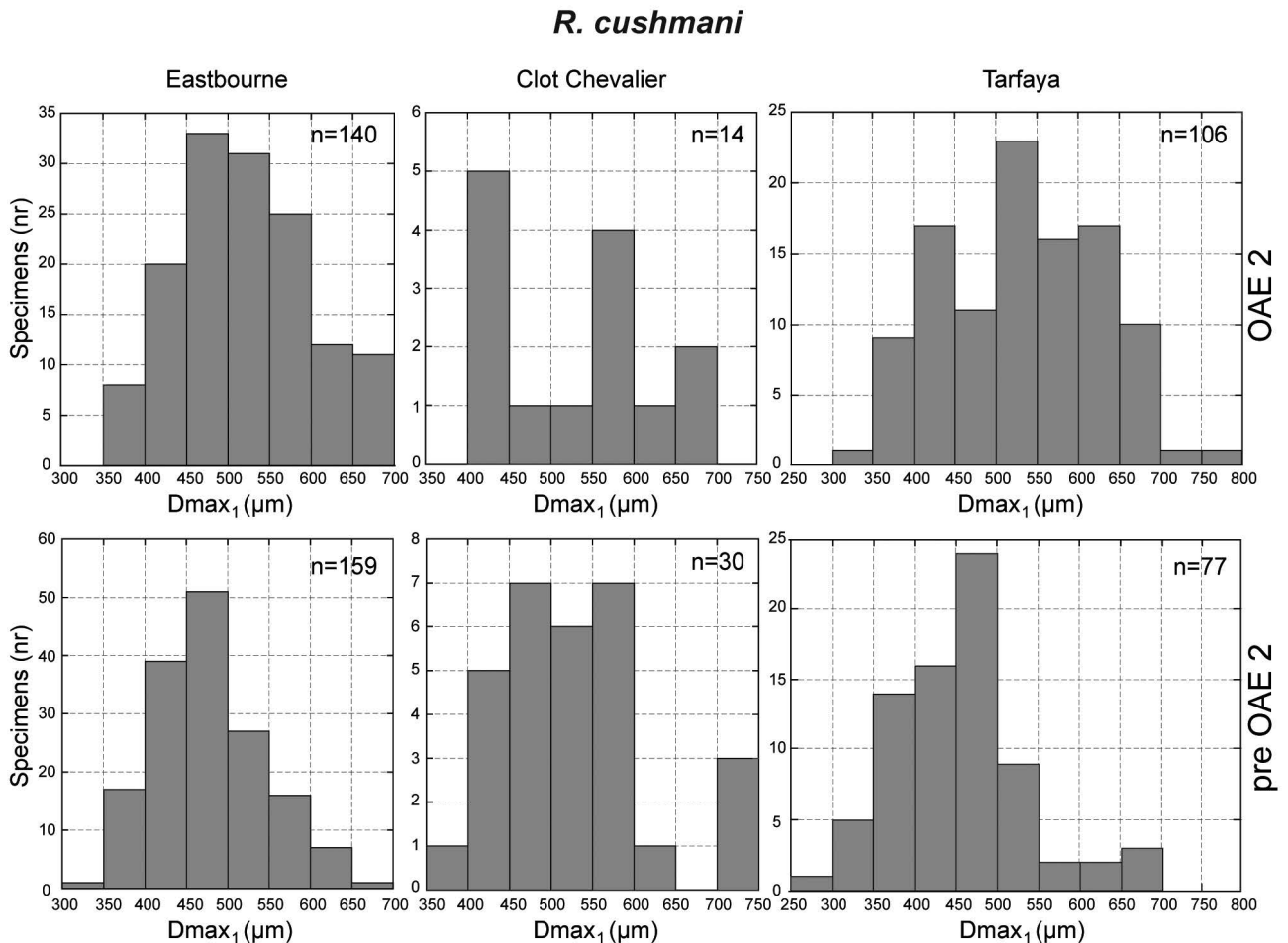


Fig. 7 - Histogram plots showing the variation in the distribution of the Dmax₁ of *R. cushmani* prior to and during OAE 2 at Eastbourne, Clot Chevalier and Tarfaya. The number of specimens measured for each interval (n) is indicated in the upper right corner of each plot.

W. brittonensis

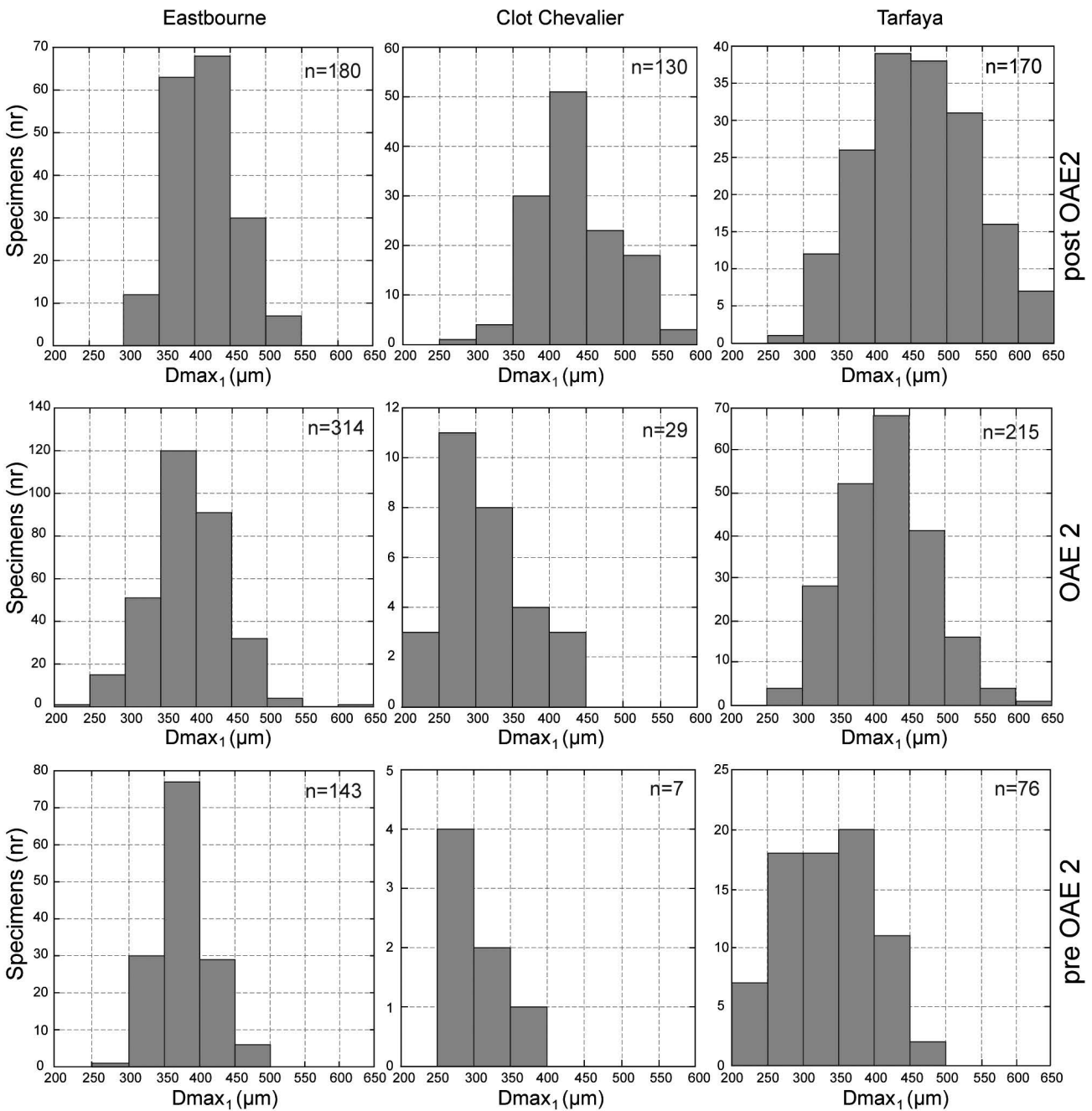


Fig. 8 - Histogram plots showing the variation in the distribution of the Dmax₁ of *W. brittonensis* prior to, during and after OAE 2 at Eastbourne, Clot Chevalier and Tarfaya. The number of specimens measured for each interval (n) is indicated in the upper right corner of each plot.

that synchronous paired shell-size variations might be related to some environmental parameters to which both species are sensitive. However, unpaired intervals indicate the existence of a species-specific response to changing environmental conditions. Trends of median Dmax₁ and Dmax₂ values exhibited by *R. cushmani* and by *W. brittonensis* are unpaired at Clot Chevalier (Fig. 4), but this observation might be biased by the lower number of samples analysed in which these species co-occur (only 6 at Clot Chevalier vs. more than 25 at Eastbourne and Tarfaya).

8. Most specimens of *R. cushmani* and *W. brittonensis* show the same range of values of H at all localities. However, some discrepancies can be found for the range of values of Dmax₁ and Dmax₂ exhibited by both species. The highest (up to 780 µm) and lowest (< 300 µm) Dmax₁ values of *R. cushmani* are measured at Tarfaya, where this species shows the largest intra-sample offset. *Whiteinella brittonensis* reaches the maximum shell size (i.e., the largest Dmax₁) at Tarfaya (> 600 µm), whereas minimum Dmax₁ and Dmax₂ values are lower than 300 µm at all localities but are measured in different stratigraphic

intervals. This observation suggests that environmental parameters (e.g., higher sea-surface temperatures) at Tarfaya might have favored the growth of larger-sized specimens. However, because smaller-sized specimens do occur at the same locality, we postulate that favorable environmental conditions for the growth of large-sized specimens were not persistent but might have been subject to some variations. Regarding *W. brittonensis*, we observe a tendency toward an increase in the average dimension of the population from the mid- (Eastbourne) to the low latitudes (Tarfaya), but further studies are required to better establish if this tendency depends on the sea-surface temperature or it is controlled by other factors. However, we cannot totally exclude that the competition with other species might have partly controlled the size of specimens in the localities examined, but reconstructing the inter-specific relationship in fossil assemblages is complicated, because of the incompleteness of the record. Moreover, we did not observe any difference or variation in the composition of the assemblages at Tarfaya, compared to Clot Chevalier and Eastbourne that may suggest competition as the driver of the growth of larger-sized specimens in the former locality.

Variations in the morphometric parameters counted or measured across OAE 2

At all localities, the number of outer chambers in *R. cushmani* varies from four to seven and specimens do not show any trend toward a decrease/increase in the number of chambers across the stratigraphic interval analysed, suggesting that the rate of formation of new chambers did not significantly change prior to and during OAE 2, nor immediately before the extinction of *R. cushmani*. By contrast, *W. brittonensis* shows a clear trend toward an increase in the number of chambers in the last whorl from five or six below OAE 2 to six or seven above OAE 2 at Eastbourne and Clot Chevalier. However, specimens with seven chambers are found in an earlier stratigraphic interval before the onset of OAE 2 at Tarfaya. Because the occurrence of specimens with six to seven outer chambers is not synchronous across localities, we hypothesize that the trend toward the increase in the number of chambers in the last whorl is neither evolutionary nor related to OAE 2 but might have been controlled by local environmental conditions.

The values of H of *R. cushmani* and *W. brittonensis* fluctuate, but both species show a slight overall increase in the median values throughout the stratigraphic interval analysed, roughly paralleling the more remarkable increase in the median values of Dmax₁ and Dmax₂. Specifically, median values of Dmax₁ and Dmax₂ of *R. cushmani* increase within the OAE 2 interval and reach maximum values followed by a significant drop slightly below its extinction level at all three localities. This phase is followed by a minor increase in the sample where we identified its highest occurrence at Eastbourne and Tarfaya. This latter trend is not visible at Clot Chevalier possibly because the extinction of *R. cushmani* falls in an earlier stratigraphic interval and the last representatives of this species, having a larger maximum diameter, were not preserved in this section. Large-sized specimens of *R. cushmani* occurring at the top of its stratigraphic distribution were already identified during a lower

resolution study of *R. cushmani* shell size variations at Eastbourne (Hart et al., 2002). On the other hand, these results are in contrast with previous observations of a slight reduction in the shell size of *R. cushmani* in the Bottaccione section that, however, were observed in a slightly older stratigraphic interval below the Bonarelli Level (Coccioni et al., 2016).

In contrast to previous observations from other localities including Eastbourne (Keller et al., 2001), our results do not support the occurrence of dwarfed planktonic foraminiferal specimens within the OAE 2 interval for the species and localities examined.

Remarks

The results of this study allow us to propose a primer for performing morphometric analyses aimed to assess planktonic foraminiferal morphometric variability across key stratigraphic intervals subject to environmental disturbances.

1. The record of the sections examined should be as complete as possible. Also, we observed that the sampling resolution required for this kind of studies should be at least one sample/40 cm to one sample/50 cm as adopted for Eastbourne and for some intervals of core S57 and should be calibrated based on the sedimentation rate of the sequence examined. This conclusion relies on the observation of a very high inter-sample variability in the median values of H, Dmax₁ and Dmax₂ obtained in all the sections examined. In fact, a lower sampling resolution might decrease the likelihood to detect significant variations in the median shell size of the population and strongly bias results.

2. Species with different palaeoecological preferences should be selected in order to analyse shell morphometric variations in different morphogroups, as phylogenetically unrelated species might respond differently to the same environmental change. This point is supported by the observation that the median values of the maximum diameter of *R. cushmani* and *W. brittonensis* fluctuate in phase in some stratigraphic intervals, but are unpaired in others, suggesting the existence of a species-specific response to certain ecologic conditions. This observation is particularly important, because all planktonic foraminiferal species, independently from their palaeoecological preferences, were supposed to experience a size reduction across OAE 2 (e.g., Keller et al., 2001; Coccioni et al., 2016).

3. To obtain replicable morphometric results, the specimens measured must be always oriented in the same preferred view. The measurement of H requires particular attention and precision, because very small variations in the tilt of oriented specimens might result in different values of H of the order of few μm . Because H ranges between 100 and 300 μm and the long-term increasing/decreasing trends of H in the species studied are comprised between 40 and 150 μm , possible small variations in the values of H due to the inclination of specimens are negligible. However, the reproducibility of this trait needs to be assessed, in case variations in the height of the trochospire have to be quantified more precisely.

CONCLUSIONS

This study represents a first step toward the development of a robust, simple and objective morphometric methodology to assess planktonic foraminiferal response to severe environmental perturbations during Earth history. Specifically, we examined two species having different palaeoecological preferences and reconstructed the variation of selected morphometric parameters across the globally widespread and well-studied OAE 2 interval.

The results of this study indicate that the measure of the maximum diameter across the first chamber of the inner whorl (D_{max_1}) represents the simplest and most objective methodology to estimate shell size variations of trochospiral planktonic foraminifera, being this chamber a simply identifiable tie point that constrains the measure. Anyhow, the results of this study suggest that measures of the absolute maximum diameter (D_{max_2}) would provide the same results, even if the values measured for each single specimen might differ of several tens of microns.

Concerning the variations of the biometric parameters counted and/or measured for *R. cushmani* and *W. brittonensis*, we observed 1) no significant changes in the total number of outer chambers before, during or after OAE 2 in both species, suggesting that the biochemical mechanisms that control the rate of formation of new chambers were not particularly sensitive to the environmental perturbations that occurred during OAE 2; 2) inter-sample fluctuations in the values of D_{max_1} and D_{max_2} of both species throughout the stratigraphic interval examined; and 3) no evidence supporting the occurrence of dwarfed planktonic foraminifera, in contrast with predicted trends based on simple observations of average shell size of the population at the stereomicroscope.

SUPPLEMENTARY ONLINE MATERIAL

All the Supplementary data of this work are available on the BSPI website at <http://paleoitalia.org/archives/bollettino-spi/>

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TAXONOMIC APPENDIX

The suprageneric classification scheme follows Loeblich & Tappan (1987).

Class FORAMINIFERA d'Orbigny, 1826
 Order GLOBIGERININA Delage & Hérouard, 1896
 Superfamily ROTALIPOROIDEA Sigal, 1958
 Family ROTALIPORIDAE Sigal, 1958
 Subfamily ROTALIPORINAE Sigal, 1958

Genus *Rotalipora* Brotzen, 1942
 Type species *Rotalipora turonica* Brotzen, 1942

Rotalipora cushmani (Morrow, 1934)
 (Fig. 9a-d)

1934 *Globorotalia cushmani* MORROW, p. 199, Pl. 31, fig. 2 (Upper Cretaceous, Greenhorn Formation, Hartland Shale Member, Kansas, USA).

1942 *Rotalipora turonica* BROTZEN, p. 33-34, Pl. 10-11, fig. 4 (Cretaceous, lower Turonian, Pomerania, Germany).

Remarks - Specimens falling in the range of variability of *R. cushmani* show a very strong variation in several morphologic characters including: 1) the number of outer chambers; 2) the height of the trochospire; 3) the thickness of the keel; 4) the degree of chambers inflation on both the umbilical and spiral sides; 5) the morphology of spiral chambers (i.e. petaloid to semicircular); and 6) the degree of development of the calcite thickenings on the umbilical and spiral sides. Luderer & Kuhnt (1997) also noted such strong variation and distinguished five morphotypes having different abundances in the samples from core S75 drilled in the Tarfaya basin.

We include in *R. cushmani* specimens that possess all the following diagnostic features: 1) sutural supplementary apertures on the umbilical side; 2) umbilical depressed and radial sutures; 3) triangular calcitic thickenings on the chambers of the umbilical side; 4) spiral raised sutures; 5) a well-developed keel throughout the last whorl; and 6) strongly to weakly developed spiral ridges.

Distinguishing features - It differs from *Rotalipora montsalvensis* (Mornod, 1950) by having raised instead of depressed spiral sutures, a well-developed keel throughout the last whorl, more ornamented chambers on both the umbilical and spiral sides and umbilical triangular calcitic thickenings on the chambers of the last whorl. It can be distinguished from *Rotalipora praemontsalvensis* Ion, 1976 by possessing a keeled periphery throughout the last whorl, less inflated chambers and a much more developed ornamentation on both the umbilical and spiral sides. It differs from *Rotalipora planoconvexa* (Longoria, 1973) by being keeled throughout the last whorl and by having straight radial sutures on the umbilical side.

Type level - Upper Cretaceous, Colorado Group, Greenhorn Formation, Hartland Shale Member, which is late Cenomanian in age.

Dimensions and features of the holotype and the paratype - Holotype: $D_{max_1} = 658 \mu\text{m}$; $D_{max_2} = 676 \mu\text{m}$; $H = 167 \mu\text{m}$; number of outer chambers = six. Paratype:

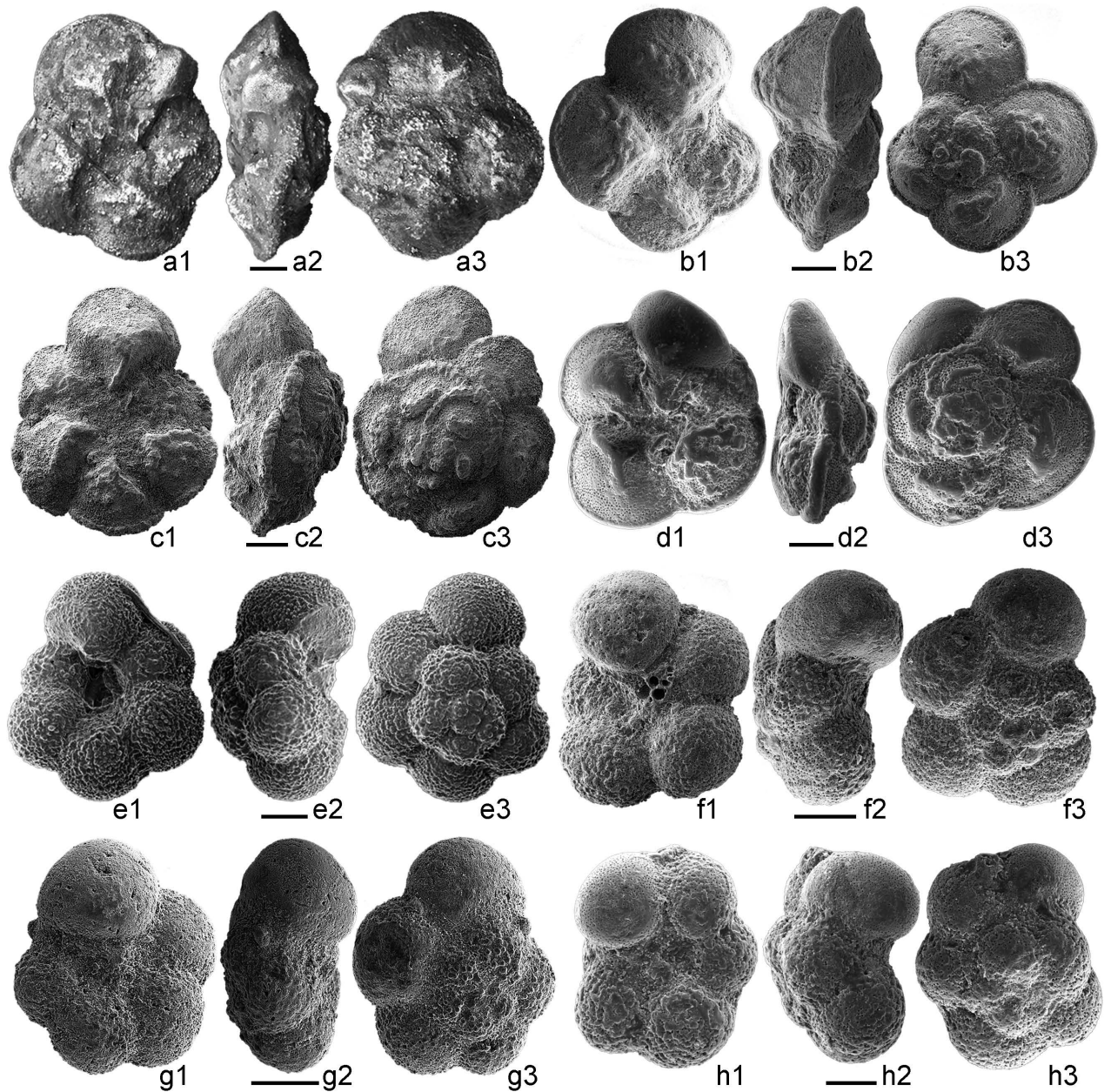


Fig. 9 - Holotypes of *R. cushmani* and *W. brittonensis* and additional specimens identified during this study. a) *Rotalipora cushmani* (Morrow, 1934), holotype, Greenhorn Formation, Hartland Shale Member, Kansas. Repository: Smithsonian Institution's National Museum of Natural History, Washington, DC; Catalog number: USNM-75377. Images available at http://www.mikrotax.org/pforams/index.php?dir=pf_mesozoic (Huber et al., 2016); b) *Rotalipora cushmani* (Micro-Unimi no. 2053), sample GC-600, Eastbourne, *R. cushmani* Zone; c) *Rotalipora cushmani* (Micro-Unimi no. 2054), sample SLT 360, Clot Chevalier, *R. cushmani* Zone; d) *Rotalipora cushmani* (Micro-Unimi no. 2055), sample S57/T52, 80-86 cm, Tarfaya, *R. cushmani* Zone; e) *Whiteinella brittonensis* (Loeblich & Tappan, 1961), holotype, Cenomanian, Eagle Ford Group, Britton Clay, Texas. Repository: Smithsonian Institution's National Museum of Natural History, Washington, DC; Catalog number: USNM-371438. Images available at http://www.mikrotax.org/pforams/index.php?dir=pf_mesozoic (Huber et al., 2016); f) *Whiteinella brittonensis* (Micro-Unimi no. 2056), sample GC-520, Eastbourne, *R. cushmani* Zone; g) *Whiteinella brittonensis* (Micro-Unimi no. 2057), sample SLT 180, Clot Chevalier, *R. cushmani* Zone; h) *Whiteinella brittonensis* (Micro-Unimi no. 2058), sample S57/T56, 4-10 cm, Tarfaya, *R. cushmani* Zone. For each specimen all the three views are provided: 1 = umbilical view; 2 = lateral view; 3 = spiral view. Scale bar = 100 μ m.

D_{max_1} = 420 μ m; D_{max_2} = 426 μ m; H = 104 μ m; number of outer chambers = five.

Type locality - Hodgeman County, Kansas, USA.

Family HEDBERGELLIDAE Loeblich & Tappan, 1961
Subfamily HEDBERGELLINAE Loeblich & Tappan, 1961

Genus *Whiteinella* Pessagno, 1967
Type species *Whiteinella archaeocretacea* Pessagno, 1967

Whiteinella brittonensis (Loeblich & Tappan, 1961)
(Fig. 9e-h)

1961 *Hedbergella brittonensis* LOEBLICH & TAPPAN, p. 274, Pl. 4, fig. 1 (Upper Cretaceous, Cenomanian, Eagle Ford Group, Britton Clay, Texas, USA).

1979 *Whiteinella brittonensis* (Loeblich & Tappan) - ROBASZYNSKI ET AL., p. 177, Pl. 37, figs 1-2 (Dallas County, Texas, USA); p. 179, Pl. 38, fig. 1 (Loffre-Lewarde, N France).

Remarks - Specimens having five to seven chambers in the last whorl are here retained to fall in the range of variability of *W. brittonensis* according to its original description. Loeblich & Tappan (1961) illustrated the holotype and seven paratypes characterised by different morphologic features (i.e., the number of chambers in the last whorl, the height of the trochospire). In our opinion, only four paratypes illustrated belong to *W. brittonensis*, while the other three specimens more closely resemble *Whiteinella paradubia* (Sigal, 1952), because of their higher trochospire. We have re-measured the maximum diameters and height of the trochospire of the holotype and of these four paratypes according to the methodology explained above and obtained for the holotype different values compared to those mentioned in the original description (i.e., “[g]reatest diameter of the holotype 0.37 mm, thickness 0.33 mm”; Loeblich & Tappan, 1961, p. 274). Measurements here presented for the paratypes have to be considered approximate, because they are obtained on the original drawings (Loeblich & Tappan, 1961) and not on SEM images because the latter are not available.

Distinguishing features - It differs from *Whiteinella aprica* (Loeblich & Tappan, 1961) by possessing a higher

trochospire and a less lobate outline and from *Whiteinella paradubia* (Sigal, 1952) by having a lower trochospire. It differs from *Whiteinella baltica* Douglas & Rankin, 1969 by showing a higher trochospire and more chambers (more than four) in the last whorl. It can be distinguished from *Whiteinella archaeocretacea* by having a much smaller umbilical area and a higher trochospire resulting from the absence of a depressed inner whorl and of a nearly flat chamber surface on the spiral side.

Type level - Upper Cretaceous, Cenomanian, Eagle Ford Group, Britton Clay.

Type locality - Dallas County, Texas, USA.

Dimensions and features of the holotype and of the paratypes - Holotype: $D_{max_1} = 489 \mu\text{m}$; $D_{max_2} = 493 \mu\text{m}$; $H = 208 \mu\text{m}$; number of outer chambers = six. Paratype illustrated in Loeblich & Tappan (1961, pl. 4, fig. 2a-c): $D_{max_1} = 360 \mu\text{m}$; $D_{max_2} = 373 \mu\text{m}$; $H = 133 \mu\text{m}$; number of outer chambers = six. Paratype illustrated in Loeblich & Tappan (1961, pl. 4, fig. 5): $D_{max_1} = 250 \mu\text{m}$; $D_{max_2} = 260 \mu\text{m}$; $H = \text{NA}$; number of outer chambers = six. Paratype illustrated in Loeblich & Tappan (1961, pl. 4, fig. 7): $D_{max_1} = 413 \mu\text{m}$; $D_{max_2} = 413 \mu\text{m}$; $H = \text{NA}$; number of outer chambers = five. Paratype illustrated in Loeblich & Tappan (1961, pl. 4, fig. 8a-c): $D_{max_1} = 426 \mu\text{m}$; $D_{max_2} = 440 \mu\text{m}$; $H = 180 \mu\text{m}$; number of outer chambers = five.