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AN EVALUATION OF MORPHOMETRICAL TRENDS IN A POPULATION OF *WOODRINGINA HORNERSTOWNENSIS* OLSSON, 1960 (FORAMINIFERA) REVEALS THE ROLE OF INTRASPECIFIC VARIATIONS FOR PALEOCEANOGRAFICAL STUDIES

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ABSTRACT – The foraminiferal species *Woodringina hornerstownensis* is stratigraphically limited between the stages Danian and Selandian and was adapted to inhabit the mixed layer water column. We present a case study based on morphometry of *W. hornerstownensis* recovered in upper Danian strata (biozone P2) in the Pernambuco-Paraiba Basin at the Poty quarry. The morphometric data, associated with abundance and geochemical indicators, point to (i) an increase in size towards the top of the studied interval, associated with the shallowing-upward trend of the Maria Farinha Formation, and (ii) an increase in size directly related to the increase in abundance. By integrating and incorporating a specific variation of *W. hornerstownensis* into abundance parameters, we conclude that the shell increase appears to be consistent. Our results suggest that the increase in size responds to environmental optimum conditions for the species *W. hornerstownensis*. In a broader context, our work demonstrates the usefulness of morphometric indicators and the significance of intraspecific variation when interpreting macroecological patterns.

Keywords: planktic foraminifera, paleoceanography, intraspecific variation, upper Danian, South Atlantic Ocean.

RESUMO – A espécie *Woodringina hornerstownensis* apresenta uma distribuição estratigráfica entre o Daniano e o Selandiano e habitava a porção da coluna d'água da camada de mistura. Neste trabalho apresentamos um estudo de caso com base na morfometria da *W. hornerstownensis* recuperada em estratos do Daniano superior (biozona P2) na Bacia Pernambuco-Parnaíba, pedreira Poty. Os dados morfométricos associados à abundância, além dos indicadores geoquímicos apontam para (i) o aumento do tamanho e abundância da espécie em direção ao topo do intervalo estudado, associado à progressiva diminuição de profundidade da Formação Maria Farinha, e (ii) o aumento do seu tamanho diretamente relacionado com o aumento da sua abundância relativa. Ao integrar e incorporar uma variação específica de *W. hornerstownensis* com os parâmetros de abundância, concluímos que o aumento da testa parece ser consistente. Nossos resultados sugerem que o aumento do tamanho dos espécimes parece estar associado ao ótimo ecológico para a espécie *W. hornerstownensis*. Em um contexto mais amplo, nosso trabalho demonstra a utilidade dos indicadores morfométricos e a importância dos estudos de variação intraespecífica na interpretação de padrões macroecológicos.

Palavras-chave: foraminíferos planctônicos, paleoceanografia, variação intraespecífica, Daniano superior, Oceano Atlântico Sul.

INTRODUCTION

The deposition of the Danian stage occurred in the aftermath of one of the largest mass extinctions in Earth's geological history, marking the K/Pg boundary (Molina, 2015). At this boundary, the assemblage of planktic foraminifera was largely affected with ~ 85% of species becoming extinct (Molina, 2015). The surviving species successively gave rise to all species of the Cenozoic (Aze *et al.*, 2011). The planktic foraminifera at the earliest Danian was characterized by low diversity, a high single-species dominance, rapid evolutionary turnovers (Koutsoukos, 1996; Arenillas *et al.*, 2000; Huber *et al.*, 2020; Lowery *et al.*, 2021; Krahl *et al.*, 2020), and blooms of smaller generalist or opportunist species related to environmental stress (Punekar *et al.*, 2014).

One of the characteristics of the Danian planktic foraminifera assemblages is its diversification in the number of microperforated species (pore size >1µm) and normal perforated species (pore size < 1µm), as a response to the K/Pg boundary extinction (*e.g.*, Liu & Olsson, 1992; Koutsoukos, 1996, 2014; Olsson *et al.*, 1999). According to the Cenozoic Planktonic Foraminifera ("PF@mikrotax" = Huber *et al.*, 2016), all microperfotared species reported for the early Danian are associated to the families Guembelitriidae and Chiloguembelinidae (Superfamily Guembelitrioidea). Specifically, the family Guembelitriidae, to which the genus *Woodringina* belongs, is characterized by tests triserial, trochospiral, or nearly triserial in initial whorl becoming biserial (Olsson *et al.*, 1999). Species belonging to the genus *Woodringina* (*W. claytonensis* and *W. hornerstownensis*) are limited to the Paleocene (Olsson *et al.*, 1999). Phylogenetically, *Woodringina* species are considered to have descended from *Guembelitria cretacea*, which *W. hornerstownensis* having done so via *W. claytonensis* (Liu & Olsson, 1992; Olsson *et al.*, 1999) (Figure 1). Biogeographic and stable isotopic data suggest an open-ocean, warm shallow-water habitat

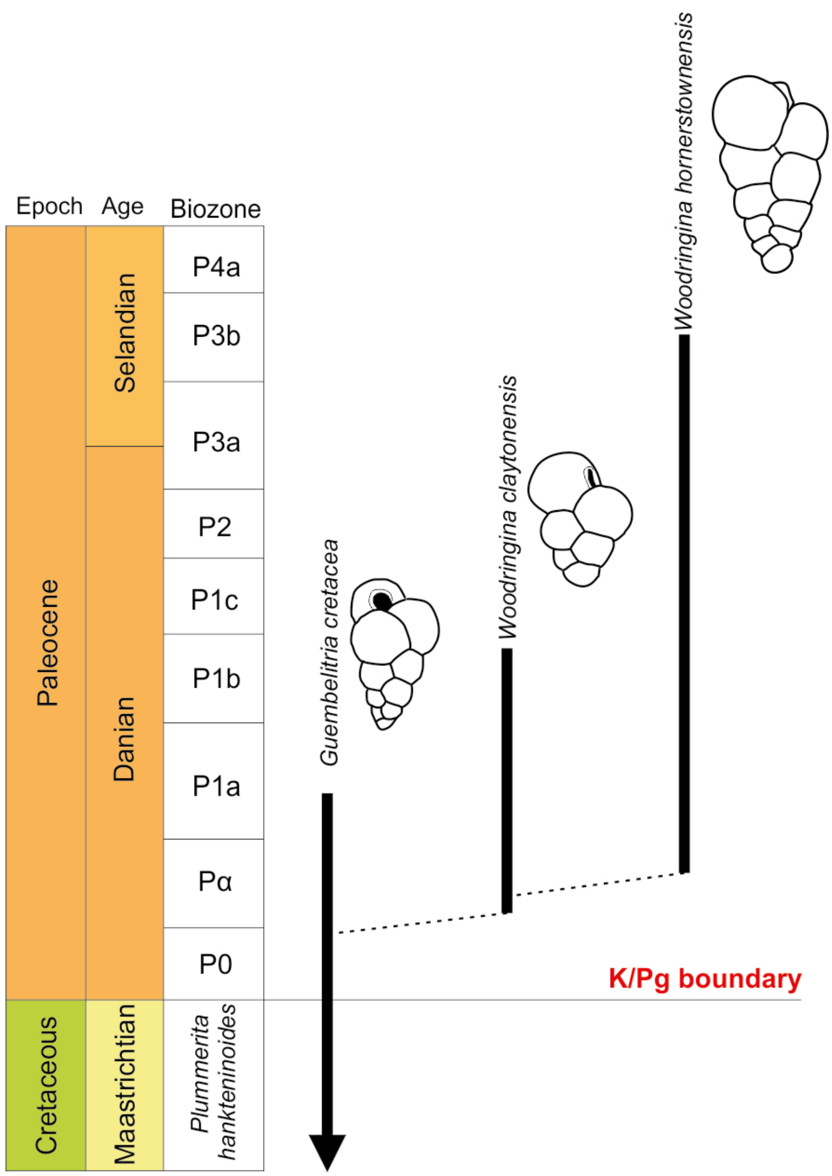

Figure 1. Stratigraphic ranges and phylogenetic relations of the evolution of species *Guembelitria cretacea*, *Woodringina claytonensis* and *W. hornerstownensis*. Biozones following Wade *et al.* (2011). **Abbreviations: P**, Paleocene.

for *W. hornerstownensis*, similar to that of *W. claytonensis* (D'Hondt & Keller, 1991; Liu & Olsson, 1992; D'Hondt & Zachos, 1993).

The planktic foraminifera assemblage is closely related to the study of past ocean conditions and their relationship to climate (Hemleben *et al.*, 1989). Planktic foraminifera may have their distribution influenced by various conditions, resources such as food availability, temperature, salinity, turbidity, sunlight, and predation (Schiebel & Hemleben, 2017). However, planktic foraminifera do not respond to environmental changes only by changes in their relative abundances, but also by changes in size within each species (Schmidt *et al.*, 2004). Paleoenvironmental changes, which directly affect the assemblages of planktic foraminifera, can be caused by different mechanisms, for instance variations in sea level (*e.g.*, Leckie, 1989).

The recovery of a planktic foraminifera assemblage for the time spanning the Danian has been reported in different sections for the South Atlantic: Pernambuco-Paraiba Basin (Poty quarry; Koutsoukos, 1996, 2006; Piovesan *et al.*, 2017; Melo *et al.*, 2023), Campos Basin (Koutsoukos, 2014), DSDP Site 356 (São Paulo Plateau; Krahl *et al.*, 2017) and ODP Site 1262 (Walvis Ridge; Krahl *et al.*, 2023). Specifically for the Paraíba Basin, the transition between the K/Pg boundary was previously studied by Koutsoukos (1996, 2006) for planktic foraminifera (Figure 2). This work recognized the interval between the *Plummerita hatkeninoides* (Maastrichtian) and P2 (Danian) biozones. Apparently, the entire P0 zone and part of the lower Pα Zone are missing, which may have been eroded and/or mixed into the lower Danian beds (Koutsoukos, 2006). The planktic foraminiferal assemblage reported in the first strata at Maria Farinha Fm. (*e.g.*, Koutsoukos, 1996; Melo *et al.*, 2023), belong to the P2 biozone following

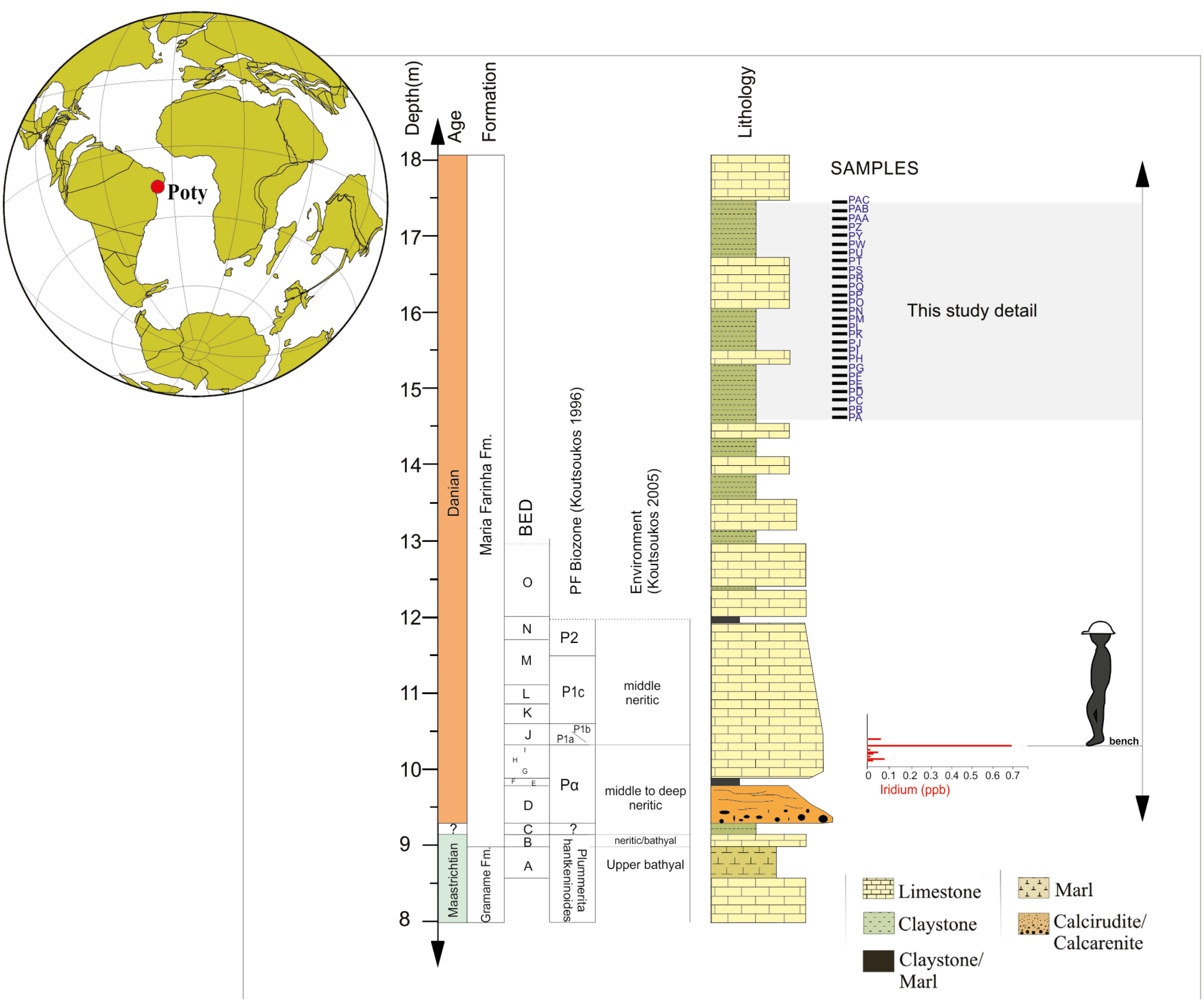

Figure 2. Paleogeographic reconstitution of the 66 Ma. (K/Pg boundary) with the localization of Poty quarry. Stratigraphic column along Maastrichtian (Gramame Formation) and Danian (Maria Farinha Formation). The "BED" layers follow Albertão & Martins Jr. (2002), planktic foraminifera biozone Koutsoukos (1966), and environmental Koutsoukos (2005). The lithological outcrop description and Iridium (**Ir**) abnormality follow Albertão *et al.* (1994). **Nomenclature of the samples: PA**, base; **PAC**, top.

Wade *et al*. (2011). The paleoenvironmental context for Poty quarry shows a Maastrichtian succession deposited in an upper bathyal context transitioning to a middle to deep neritic environment for the early Danian (Koutsoukos, 2006). The uppermost Danian beds exposed in the quarry represent deposition in progressively shallower neritic environments, with stronger influence of storm events. The benthic foraminifera decline sharply in diversity and are characterized by assemblages dominated by anomalinids with vaginulinids (Koutsoukos, 2005).

The Poty quarry section represents a shallow marine paleoenvironment at low latitude (Figure 2), providing an opportunity to report paleoecological setting for planktic foraminifera species recognized in shallow marine conditions. In this perspective, the main objectives of this study are (i) to conduct a morphometric evaluation of the population of planktic foraminifera of the *Woodringina hornerstownensis* species and (ii) to correlate it with paleoenvironmental patterns raised by means of geochemical and geophysical sediment signatures.

GEOLOGICAL SETTING: MARIA FARINHA FORMATION

The Pernambuco-Paraíba Basin sedimentary record comprises deposits aged between the Campanian and upper Danian (Albertão & Martins Jr., 2002; Barbosa *et al*., 2003; Rossetti *et al*., 2012). The Pernambuco-Paraíba Basin has been the subject of several studies, mainly from the point of view of its fossil content (Albertão & Martins Jr., 2002). Poty quarry section was the first description of a reasonably complete sequence along the K/Pg boundary transition at low latitudes in the Southern Hemisphere and throughout South America, including an iridium anomaly (Figure 2) (Albertão *et al*., 1994). The contact between the Gramame (upper Cretaceous) and Maria Farinha (Danian) formations is defined by the positioning of the K/Pg boundary as proposed by Albertão & Martins Jr. (2002). Regarding the K/Pg limit, with emphasis on the outcrop of the Poty quarry, pioneering studies include Beurlen (1967), Tinoco (1967) and Mabesoone *et al*. (1968). Albertão (1993) presents a complete description of this section and record the occurrence of the K/Pg boundary. In this understanding, a succession of works was published as a result of these studies, from which can be cited Albertão *et al*. (1994), Albertão & Martins Jr. (1996, 2002), Marini *et al*. (2000), and Martins *et al*. (2000). Specifically, micropaleontological studies were extensively developed, based on planktic foraminifera (Koutsoukos, 1996, 2005, 2006; Piovesan *et al*., 2017; Melo *et al*., 2023), calcareous nannofossils (Grassi, 2000), ostracods (Fauth *et al*., 2005; Barros *et al*., 2018) and palynology (Sarkis, 2002).

Stratigraphic framework of Maria Farinha Fm.: previous study

The Maria Farinha Fm. has an average thickness of 18 m in the area and is characterized by an alternation of finely stratified limestones of marine origin, marly limestones and calcareous marls, intensely bioturbated (Albertão & Martins Jr., 2002; Barbosa *et al*., 2003; Rossetti *et al*., 2012). In general terms, its sedimentary sequence characterizes the beginning of a regression process (Albertão & Martins Jr., 2002). Progressively from the basal portion to the top of the sequence, a general trend of decrease in carbonate content and progressive increase in marly sediments is recognized, controlled by the sedimentary process of marine regression (Albertão & Martins Jr., 2002; Barbosa *et al*., 2003; Rossetti, *et al*., 2012).

The stratigraphic interval under investigation in this study for the upper portion of the Maria Farinha Fm. is associated with alternating layers of limestone and claystone, with a notable prevalence of the latter towards the top (see Figure 2), according to Shyu's (2022) findings. The studied interval displays a clear trend of high $CaCO_3$ values near the limestone layers. Inversely proportional to the $CaCO_3$ values, the trend of magnetic susceptibility (MS) is recognized, which exhibits an increase along the claystone layers.

MATERIAL AND METHODS

Sampling strategy

The Poty quarry section is situated within the Paraíba Basin (Latitude 07°59'S; Longitude 34°51'W) (Figure 2). The outcropping section of the Poty quarry is composed of the Gramame and Maria Farinha formations (Albertão & Martins Jr., 2002). In this study, the samples under investigation correspond to the upper portion of the Poty quarry, which is stratigraphically positioned above the range studied by Koutsoukos (1995, 2005). Strategically for the elaboration of this work, 27 samples were used from the interval between of ~14.6 m to 17.4 m (Figure 2), referring to the Maria Farinha Fm. (Danian) (samples spaced ~10 cm apart). This stratigraphic interval is composed of cyclic variations of claystone and limestone (Albertão & Martins Jr., 2002). The nomenclature of the samples studied in this work follows between PA (base) and PAC (top).

This stratigraphic interval is composed of cyclic variations of claystone and limestone (Albertão & Martins Jr., 2002). To characterize the depositional context, we used XRF data from Shyu (2022). The main assumption in the use of XRF data used here is to evaluate changes in carbon content from Log(TERR/Ca) oscillations, where TERR= Al, Fe, K, Si and Ti. The elements Al, Fe, K, Si and Ti generally have a terrigenous origin, especially in marine depositional contexts (Mulitza *et al*., 2008; Govin *et al*., 2012). The forehead of marine organisms contributes most of the calcium in the form of calcium carbonate. The logarithmic ratio of the sum of Al, Fe, K, Si, and Ti normalized by Ca, ratio Log(TERR/Ca) is therefore used as a proxy for terrestrial vs terrestrial clastic material, marine biogenic carbonate (*e.g.*, Beil *et al*., 2018; Krahl *et al*., 2020).

Planktic foraminifera morphometric analysis

Samples were prepared following the conventional methodology for the recovery of calcareous microfossils, which consisted of: (a) washing samples over a >63 and 125 µm sieve, after immersion in deionized water for

~48 hours; (b) oven drying the residues for ~24 hours at 40°C; (c) selection of approximately 300 specimens of planktic foraminifera; (d) identifying specimens under a stereomicroscope and with a scanning electron microscope (SEM). Taxonomic identifications at genus and species levels followed Olsson *et al*. (1992, 1999), Liu & Olsson (1992), and Koutsoukos (2014).

The *Woodringina hornerstownensis* specimens were counted in the 63 and 125 μm fractions. For biometric evaluation we used 20 individuals for each sample. The biometric parameters used to delimit the *Woodringina hornerstownensis* species were length (**L**), width (**W**) and height (**H**) of the test (Figure 3A). The 2-D area of *W. hornerstownensis* specimens was obtained from images of oriented tests on a microslide cell (Figure 3B). Biometric measurements were made using a Zeiss SteREO Discovery V20 stereomicroscope equipped with 10X oculars and micrometer, and capable of 225X maximum magnification.

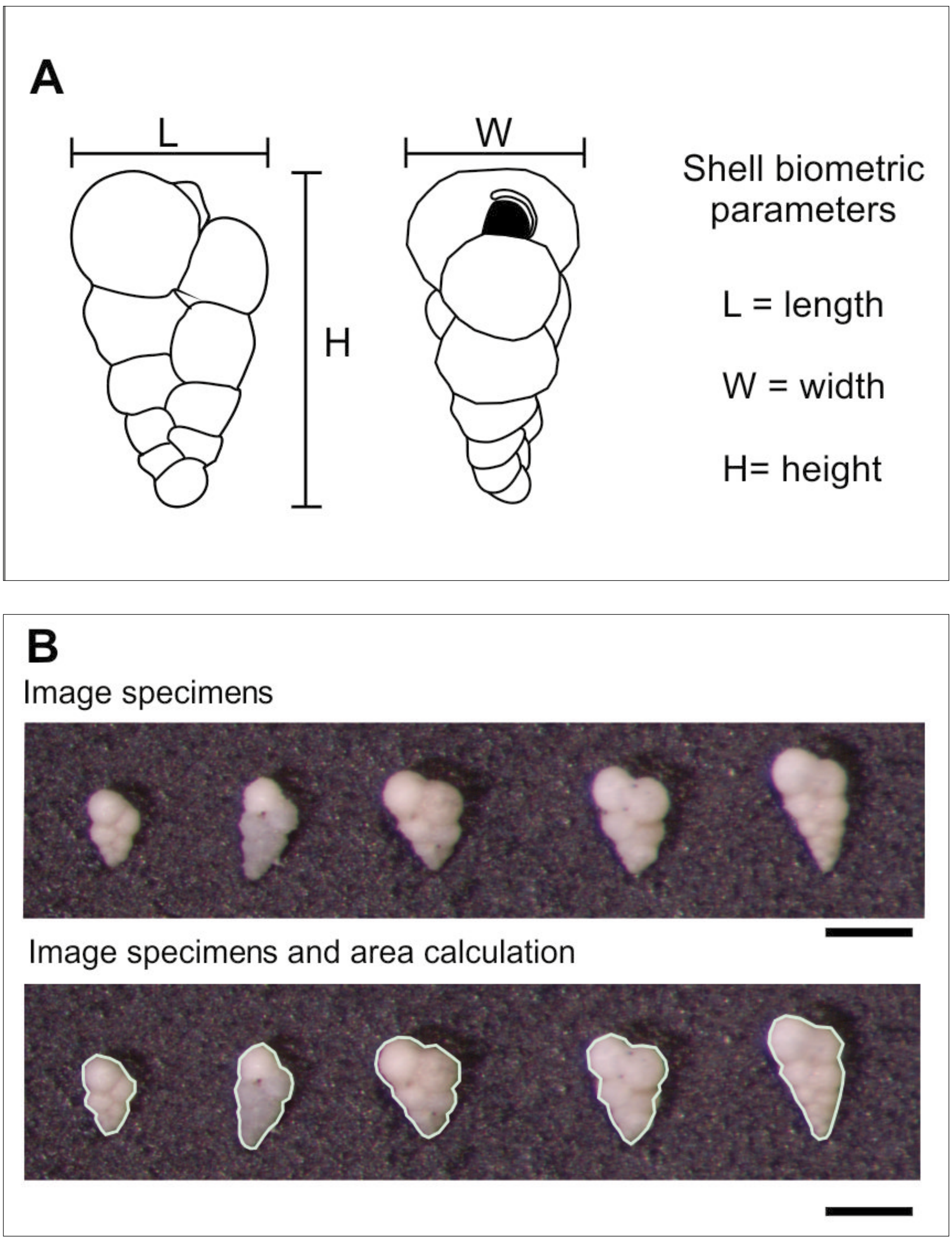

Figure 3. **A**, shell biometric parameters evaluation *Woodringina hornerstownensis*. **B**, image of a microslide cell with oriented specimens for species recognition, automated specimen counting, and silhouette 2-D area calculation. Scale bars = 20 μm.

RESULTS

Planktic foraminifera distribution trend

The preservation of planktic foraminifera recovered in the studied interval is moderate (M) to good (G) (Figure 4A). The proportion between planktic and benthic foraminifera (P/B ratio) was estimated in order to evaluate eustatic variations (van der Zwaan et al., 1990). The proportions of benthic specimens throughout the studied interval exhibit a notable dominance in relation to planktic forms (mean=85.68%; max.=93,5%; min.=78,2%), as well as a slight tendency towards an increase in benthic forms towards the top of the section (Figure 4B), which reinforces that it indicates shallow sea conditions (inner-middle neritic conditions), also suggested by Tinoco (1971), based on foraminifera, and Fauth *et al*. (2005) based on ostracods.

The stratigraphic distribution of planktic foraminifera recovered in the studied interval shows a constancy for the species *Parasubbotina pseudobulloides*, *Praemurica inconstans*, *Eoglobigerina edita*, *Praemurica uncinata, Subbotina triloculinoides* and *Guembelitria cretacea* (Figure 4C). Based on the presence of the species *P. uncinata* the strata deposited for the studied interval suggest that they were deposited in the biozone P2 (*Praemurica uncinata* Lowest-occurrence Zone; Wade, *et al*., 2011) for the Danian, briefly reported by Shyu (2022). The P2 biozone observed for Poty quarry, up to ~ 16.00 m, appears to be coeval with that observed by Koutsoukos (1996, 2005), suggesting an accumulation of at least ~200 kyr (amplitude of P2 biozone) for 4.5 m of sediment (see Figure 1: Biostratigraphic biozones framework).

Woodringina hornestowensis distribution

The structure of *Woodringina hornerstownensis* (Figure 5) population at Poty quarry modified significantly across the studied interval (Figures 4A-6A). The mean relative abundance of *W. hornerstownensis* (> 63 µm) species for the whole interval was 60.88%, with relative abundances ranging between 41% and 75.40%. The distribution trend of this species appears to be higher and with constant values above sample PG (15.20 m) up to the top of the studied range in sample PAC (17.40 m), with an average of 66.71%. In the basal portion of the studied interval, between Sample PA (14.6 m) and Sample PG (15.20 m) the proportions of *W. hornerstownensis* appear to be lower (average= 44.21%).

Woodringina hornerstownensis: biometric inferences and behavior trend

The morphometric characteristics width (W), length (L), height (H), and 2-D area of the population of *Woodringina*

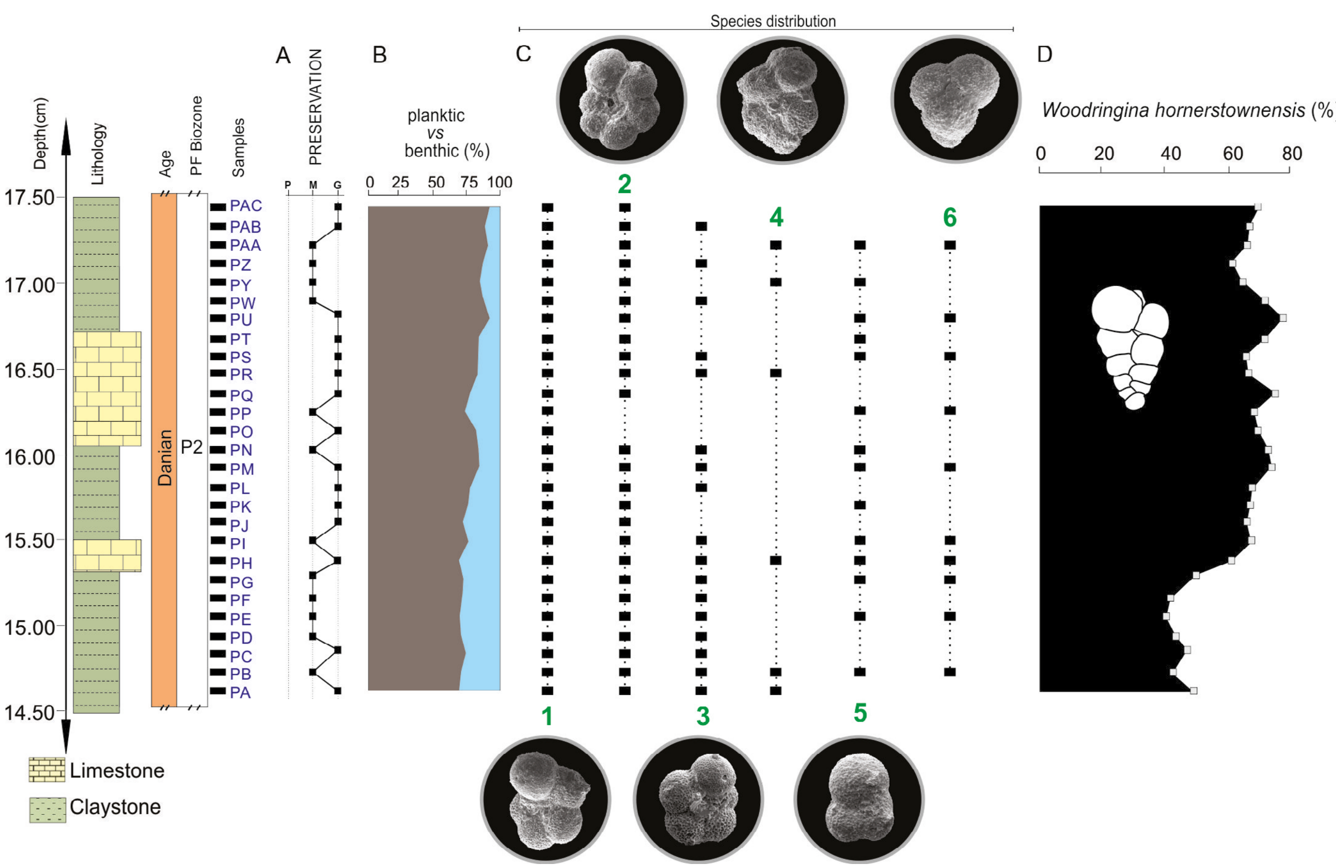

Figure 4. Stratigraphic column, following Albertão & Martins (1996). **A**, preservation relative scale: poor (**P**), moderate (**M**), and good (**G**). **B**, P/B ratio (%). **C**, stratigraphic distribution of planktic foraminifera in interval studied. Species reference: **1**, *Parasubbotina pseudobulloides*; **2**, *Praemurica inconstans*; **3**, *Eoglobigerina edita*; **4**, *Praemurica uncinata*; **5**, *Subbotina triloculinoides*; **6**, *Guembelitria cretacea*. **D**, *Woodringina hornerstownensis* abundance in the fraction >63 µm (%) (Figure 5).

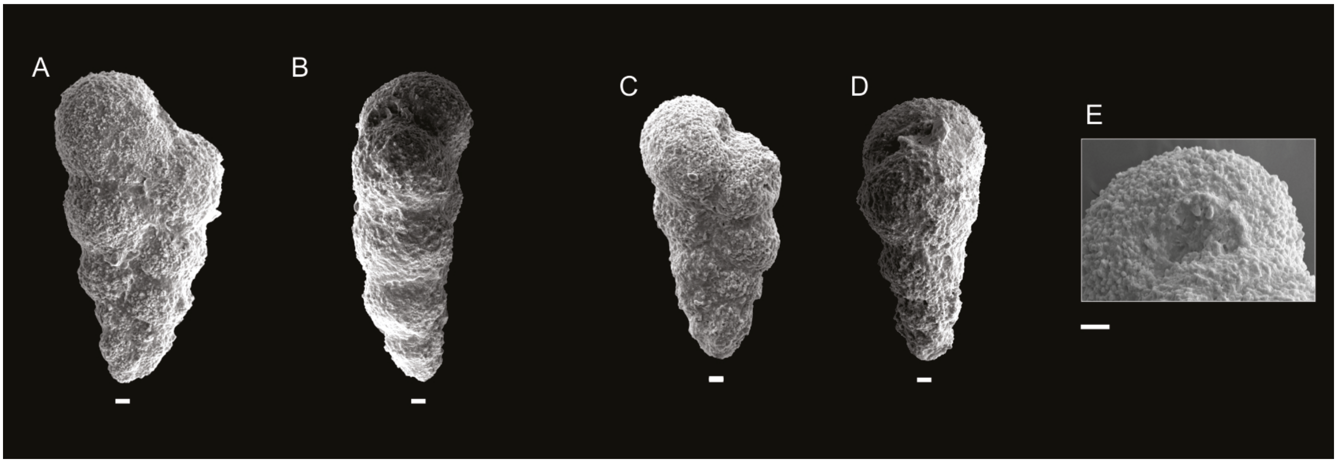

Figure 5. Photomicrographs of the planktic foraminifera. **A**–**B**, *Woodringina hornerstownensis* (Sample PU). **C**–**D**, *Woodringina hornerstownensis* (Sample PA). **E**, detail of aperture area. Scale bars = 10 µm.

hornerstownensis are available in the Supplementary Material (S1) and shown in Figure 6. All variables are expressed in terms of average, maximum and minimum values.

The width (W) shows an average of 66.25 µm (with averages per sample varying between 56 µm and 73.7 µm). The maximum values for the studied interval varied between 61.8 µm and 82 µm and the minimum values between 45.85 µm and 66.90 µm (Figure 6B). Regarding the average behavior of width (W) the values of maximums and minimums seem not to have deviated from the average trend.

The behavior for length (L) in the studied interval has an average of 146 µm, with variations between samples between 134.72 µm and 156.9 µm (Figure 6C). The maximum values varied between 145 µm and 170.21 µm and minimum values between 119.7 µm and 141.9 µm (Figure 6C). The average length displays an increase trend towards the top of the studied interval (Figure 6C).

The height (H) values display mean values of 234.41 µm (maximum = 256.55 µm; minimum = 209.66 µm). The maximum values varied between 234.66 µm and 294 µm, and the minimum between 164.65 µm and 211.55 µm (Figure 6D). In general terms, the trend observed for height is similar to that of other recognized morphometric parameters. We observed a tendency for H to increase towards the top of the studied interval, mainly above sample PG (13.60 m).

The 2-D area of the *Woodringina hornerstownensis* population has an average of 22946.33 µm^2, with mean values per sample between 18955.3 µm^2 and 26000.15 µm^2 (Figure 6E) The maximum area oscillates between 22341 µm^2 and 29533 µm^2, showing a variation in the order of 7192 µm^2 over the average. The minimum values of 2-D area oscillate between 15897 µm^2 and 22457 µm^2, with variation in the order of 6560 µm^2 (over the average). Regarding the observed trend of the 2-D area of the population of *W. hornerstownensis*, lower values can be noted in the lower portion of the studied interval between the PA and PG samples. Above, between the PG and PAC samples (top), higher values of 2D area are recognized (Figure 6E). This observed trend seems to converge with all other parameters, which show an upward trend towards the top of the studied interval (Figure 7).

DISCUSSION

Relative abundances of *Woodringina hornerstownensis* and biometric parameters changes

Studies analyzing the size variation of recent planktic foraminifera suggest that maximum size generally coincides with maximum relative abundance, and occurs at a specific optimum temperature (optimum-size hypothesis; Hecht, 1976; Moller *et al*., 2013; Schmidt *et al*., 2004). Our morphometric data set in the population of *Woodringina hornerstownensis* allowed us to explore its correlations with other parameters. We tested the hypothesis that planktic foraminiferal species have larger sizes under ideal environmental conditions (*e.g.*, Hecht, 1976; Schmidt *et al*., 2004). Here, we use the P/B ratio, relative abundance and influx of terrigenous material (*e.g.*, TERR/Ca and MS) (Figure 7). The integrated analysis of magnetic susceptibility and Log(TERR/Ca) indicates changes in terrigenous input, probably as a consequence of changes in hydrodynamic conditions. These oscillations enhance claystone formation, suggesting greater terrigenous input to the latter and limestones, under a regime of lower terrigenous input. The proportions of *Woodringina hornerstownensis* observed in the studied range represented >40%, of which two distribution patterns are recognized: (i) between samples PA (14.6 m) and PG (15.2m) with an average of 42.5%; (ii) representing >60% of *W. hornerstownensis* from the assembly above the Sample PG sample to the top of the studied interval. Noticeably, the increase in the relative abundance of *W. hornerstownensis* towards the top of the section seems to be associated with an increase in the P/B ratio (*i.e.*, shallowing) and/or also with an increase in terrigenous influx (based on TERR/Ca and MS), recorded by Shyu (2022) (Figure 7). Additionally, the increasing trends in the proportion of benthic

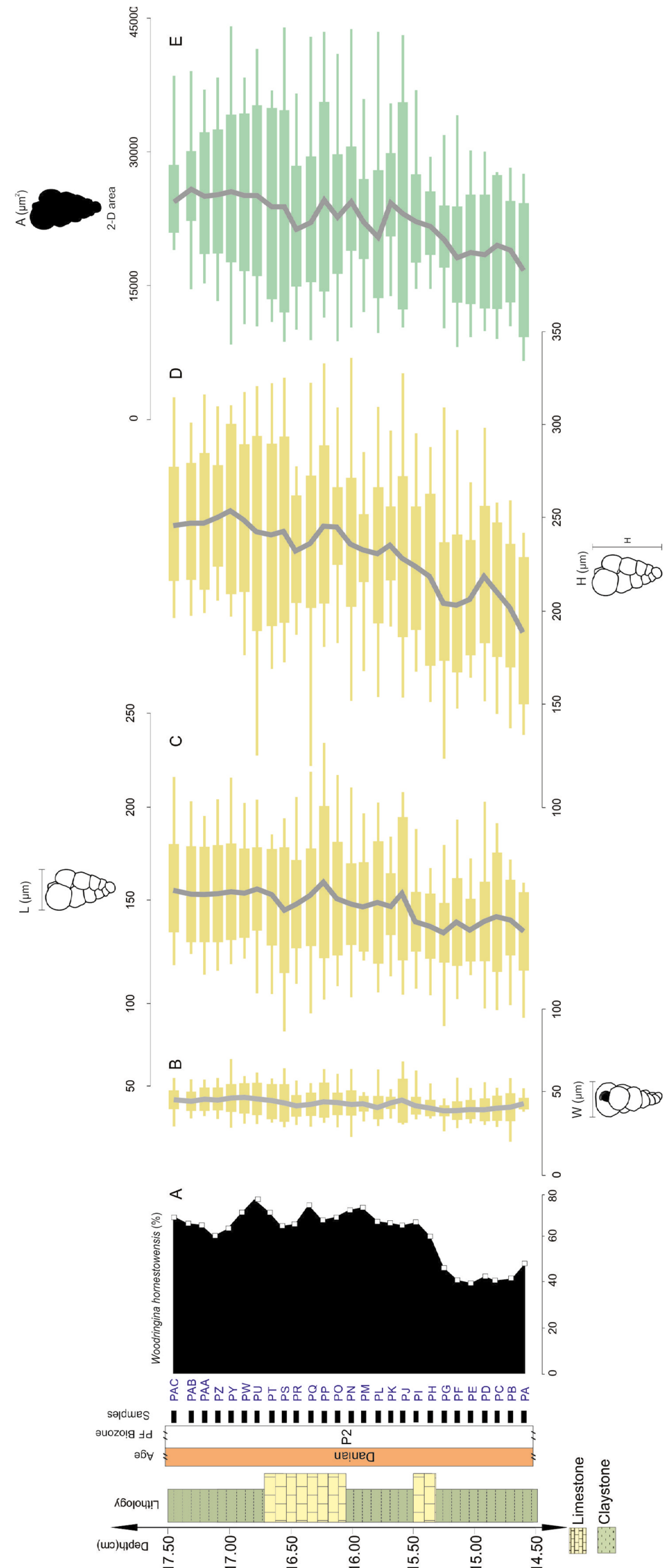

Figure 6. Stratigraphic trend of distribution and morphometric parameters. **A**, *Woodringina hornerstownensis* abundance (%); **B**, width (**W**); **C**, length (**L**); **D**, height (**H**); **E**, 2-D area (**A**).

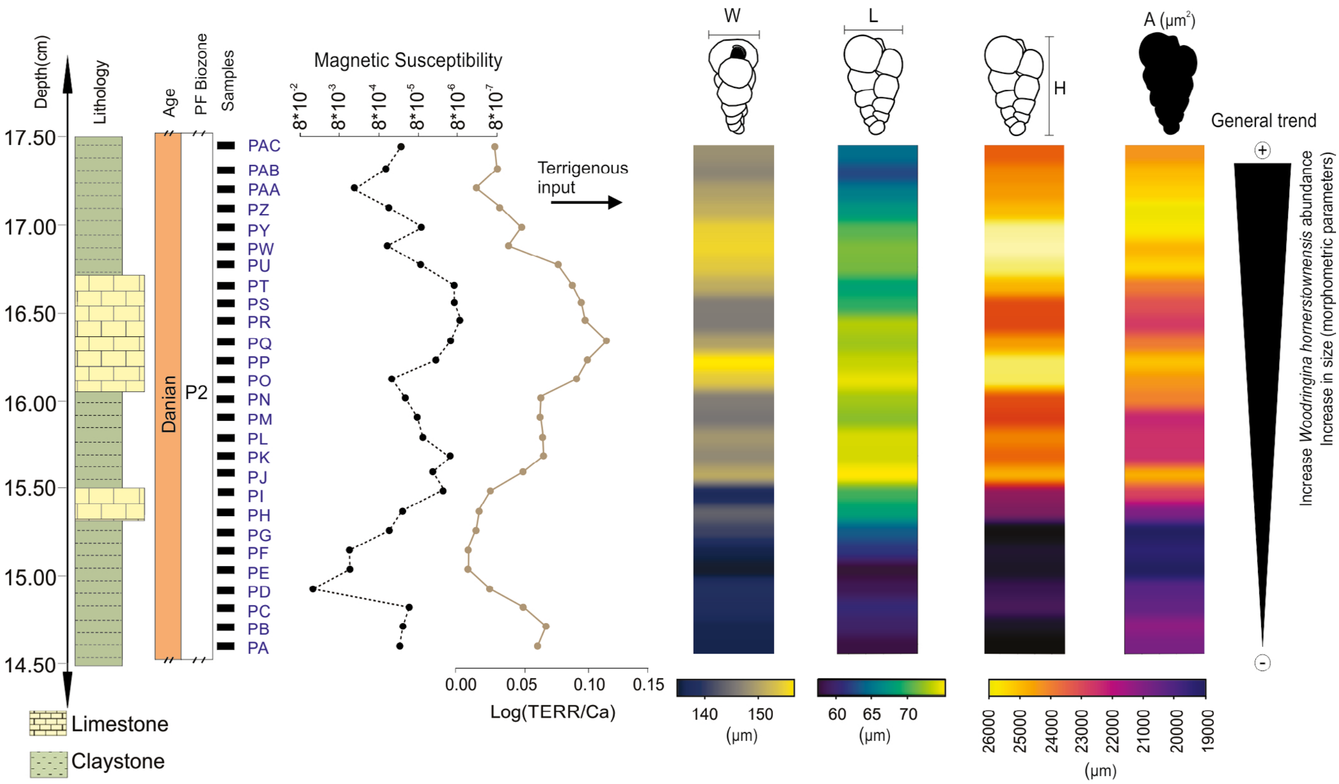

Figure 7. Stratigraphic data, magnetic susceptibility, and Log (**TERR/Ca**) ratio (following Shyu, 2022). Morphometric trend of *Woodringina hornerstownensis* over the interval studied. Gradient of values (**colors**) refers to the average value (Supplementary material S1).

foraminifera in relation to planktic forms towards the top of the studied interval are consistent with the trend observed by Tinoco (1971), suggesting an intensive marine regression towards Maria Farinha Fm. (*e.g.*, Nascimento-Silva *et al.*, 2011; Albertão *et al.*, 2014).

The relationship observed between the morphometric parameters W, L and H seems to be coeval with the increase in abundance of the population of *Woodringina hornerstownensis* (Figure 8). The increase in *W. hornerstownensis* abundance is also recognized in the 2-D area (Figure 8). Specifically, the height ratio (H) and also the 2-D area exhibit the most remarkable tendency to increase toward the top of the studied range. In general, the correlation between the size of *W. hornerstownensis* specimens and their abundance, although weak, appears to be consistent throughout the upper portion of the studied range. Moreover, morphometric patterns appear to increase in size similar to increases in the influx of terrigenous material, usually associated with increased nutrient availability due to continental outflow.

Woodringina hornerstownensis: a link between ecological behavior

Each organism is adapted to a specific "optimal" environmental condition under which it is able to best proliferate (Kennett, 1968; Bé *et al.*, 1973). These optimal environmental conditions can facilitate rapid reproduction and, consequently, fast growth rates and large carapace size (Schmidt *et al.*, 2004, 2006). Foraminifera typically reach maximum size in their preferred body of water and decrease in size away from such areas (Schmidt *et al.*, 2004). For planktic organisms, "optimal" environmental distributions are not only geographic but also depth-related, *i.e.*, a shallow-water species would be under stress in greater water depth (Hecht & Savin, 1972) where its growth rate will decrease. Each species has a set of conditions that leads to optimal growth (Bradshaw, 1961). Under more ideal environmental conditions, planktic foraminifera will grow faster, reach larger sizes and will be more abundant (Schmidt *et al.*, 2004).

For the species *Woodringina hornerstownensis*, a notable tendency towards an increase in abundance and, in general, and, specifically its increase in 2-D area and height (H and 2-D area-) was observed. Stable isotopic data suggest an open-ocean, warm shallow-water habitat for *W. hornerstownensis*, similar to that of *W. claytonensis* (D'Hondt & Keller, 1991; Liu & Olsson, 1992; D'Hondt & Zachos, 1993). *W. hornerstownensis* is considered by Koutsouksos (1996) to be a species adapted to shallow-dwelling specialized trophic. This means that well-oxygenated hydrological and nutritional conditions in the upper portion of the water column promoted better conditions in the superficial portion of niches in the upper water column, where these organisms could adapt in a restricted way (Schmidt *et al.*, 2006). In our case study, the use of relative abundance with the increase in planktic foraminifera appears to be correlated with the downward trend in relative sea level (P/B ratio) and the influx of terrigenous material (TERR/Ca ratio and MS). These results appear to converge with the interpretations of

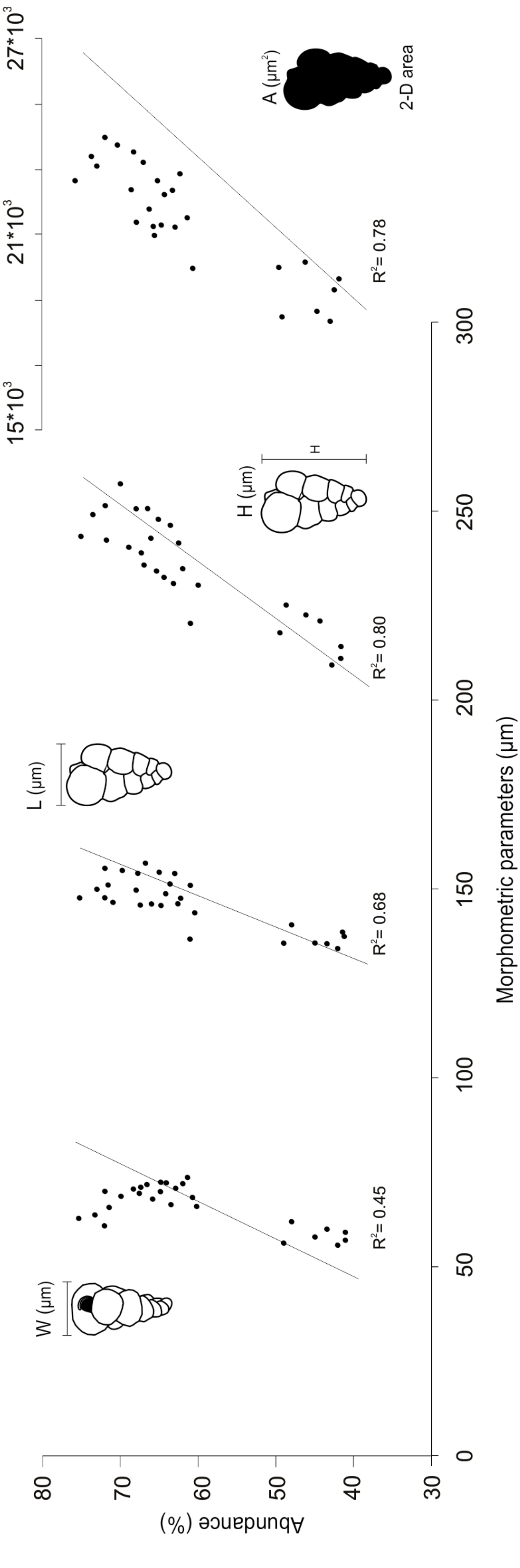

Figure 8. Cross-plot between abundance of planktic foraminifera assemblage and morphometric parameters (**W**, width **L**, length **H**, height and **A**, area-2D).

shallow water habitat observed based on isotope data (*e.g.*, D'Hondt & Keller, 1991; Liu & Olsson, 1992; D'Hondt & Zachos, 1993). This is evidenced by the observed increases in size and abundance, which appear to be associated with a gradual decline in eustatic sea level (P/B ratio). Another pertinent observation from our study is the positive correlation between Log (TERR/Ca), suggesting that this species, in addition to being associated with well-oxygenated conditions (*e.g.*, Koutsoukos, 1996), is also adapted to high nutrient availability conditions. The latter highlights that more studies must be carried out, in the case of evaluating total organic carbon, for a better assessment of nutrient availability. In general terms, the increase in abundance and size confirms the species *Woodringina hornerstownensis* adapted to mixed-layer conditions. Moreover, the increase in its size towards the top of the section suggests it may be associated with optimal ecological conditions for this species.

CONCLUSIONS AND FUTURE PERSPECTIVES

Based on the qualitative quantification of the population of *Woodringina hornerstownensis* recovered in the stratigraphic interval of ~14.6 m and 17.4 m in the Poty quarry (biozone P2) and the integration with morphometric and stratigraphic data, it was possible to collaborate on the understanding of its paleoecological preference conditions. The results of length (L), width (L) and height (H), together with the 2-D Area demonstrated a positive relationship between these variables and the *Woodringina hornerstownensis* relative abundance. This population increase relationship, and its diverse morphometric patterns (size) suggest optimal ecological conditions for this species towards the top of the section. In conjunction with the observed increase in the population of *W. hornerstownensis*, a shallowing trend of the section towards the top of the studied interval (P/B ratio) and increased influx of terrigenous content (Log TERR/Ca and magnetic susceptibility), suggesting adaptive conditions to shallow sea and good oxygenation conditions.

This work is undoubtedly far from objectively closing the ecology of the species *W. hornerstownensis*. The following research steps will be to evaluate isotope analysis obtained from all recovered planktonic taxa and selected benthic taxa (*e.g.*, Krahl *et al.*, 2023) and determine the relative pelagic habitation preferences among planktic foraminiferal species in relation to specimen size (*e.g.*, Birch *et al*., 2016).

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SUPPLEMENTARY MATERIAL

S1. This supplementary material file presents: (1) Sample Code; (2) $CaCO_3$ content (%); Magnetic Susceptibility (MS) and Log (TERR/Ca) ratio (following Shyu, 2022); (3) Planktic vs benthic foraminifera (P/B ratio; %); (4) Preservation index (M = Moderate; G = good); (5) *Woodringina hornerstownensis* abundance (%); (6) Morphometric parameters length (L), width (W), height (H) and 2-D area.

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