



Biometric insights on the calcareous nannofossil genus *Aspidolithus* across the Santonian–Campanian boundary: Western Interior (Niobrara, USA) vs. Tethys (Loibichl and Postalm, Austria) sections

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Abstract. The taxonomic subdivision of *Aspidolithus parvus* has long relied on biometric parameters, particularly the ratio between the central area width and the outer rim width (b/a). However, its reliability as a taxonomic criterion remains uncertain. This study applies biometric and statistical analyses to specimens from the Niobrara Formation (Western Interior Seaway, USA) and the Postalm and Loibichl sections (Tethyan Realm, Austria) to reassess the validity of arbitrary taxonomic subdivisions and their biostratigraphic implications. We also examine the distribution of calcareous nannofossil assemblages to explore palaeoenvironmental influences on biometric variation. Mixture analysis of b/a values reveals three statistical groups in the Postalm and Niobrara sections. However, overlapping ranges suggest that b/a is influenced by palaeoenvironmental factors rather than reflecting stable taxonomic boundaries. In contrast, total coccolith length (L), as previously shown in the published data from the Loibichl section, provides a more robust criterion for distinguishing the precursor species *Aspidolithus enormis* from *A. parvus*, with a statistically significant threshold at $\sim 8.5\ \mu\text{m}$. Our biometric analysis refines previous subspecies definitions as follows: *A. parvus constrictus* ($b/a < 1.6$), *A. parvus expansus* ($1.6 \leq b/a < 2.2$), and *A. parvus parvus* ($b/a \geq 2.2$). Statistical results indicate a correlation between the b/a ratio and surface water temperature, supporting the idea that environmental factors play a role in shaping *Aspidolithus* morphology. Nevertheless, similarities with data reported from other Tethyan sections (Austria) suggest that evolutionary trends also contributed to the observed biometric variations. The unexpected stratigraphic pattern at Bottaccione (Italy), where smaller specimens appear later than larger ones, contrasts with trends in Niobrara and Postalm. This suggests that, while palaeoenvironmental factors influence *A. parvus* morphology, its overall evolutionary trajectory may not be strictly controlled by local environmental conditions. These findings emphasise the need for reassessing *A. parvus* taxonomy and standardising biometric criteria to improve biostratigraphic resolution and ensure consistency in Santonian–Campanian stage and age correlations.

1 Introduction

The *Aspidolithus parvus* group, including the subspecies *Aspidolithus parvus constrictus*, *Aspidolithus parvus expansus*, and *Aspidolithus parvus parvus*, plays a significant role in biostratigraphy. The first occurrence (FO) of *A. parvus parvus* provides a secondary marker for the base of the Campanian stage in the Upper Cretaceous and is closely associated with the boundary marker, the C34n/C33r magnetic reversal (Gale et al., 2023). Consequently, the reliable identification of these subspecies is crucial for regional and global correlations. However, the morphological transitions among the subspecies, along with different (sub)species and genus concepts (e.g., Stradner and Steinmetz, 1984; Noël, 1969; Wolfgring et al., 2018), often make their distinction challenging, potentially leading to misinterpretations in biostratigraphic studies. This highlights the need for a robust biometric framework to refine the taxonomy of the group and to better understand their evolutionary trends in time. The use of the generic name *Aspidolithus* (type species *Aspidolithus angustus* Noël) in this study follows the terminology employed in biostratigraphic and morphometric analyses concerning this group (e.g., Wise, 1983; Gardin et al., 2001; Kita et al., 2017; Miniati et al., 2020), particularly those that analysed evolutionary trends across the Santonian–Campanian boundary. Although the usage of the genus *Broinsonia* (*Broinsonia parva* (Stradner) Bukry) is currently adopted in Nannotax3 (Young et al., 2022) and reflects the formal nomenclatural priority, a taxonomic debate persists regarding whether *Aspidolithus* represents a distinct morphogenus or a synonym of *Broinsonia*. This debate hinges in structural criteria, as *Aspidolithus* is defined by the sole presence of central plates, whereas *Broinsonia* typically has a distinct axial cross in the central area (Lauer, 1975; Perch-Nielsen, 1985). In our material, no cross is present, and most of the specimens exhibit central plates with variable perforations, supporting the use of *Aspidolithus* in the morphological sense. Moreover, keeping this nomenclature facilitates direct comparison with previous studies, including Granero et al. (2024), and avoids inconsistencies in morphotype attribution that may arise from unresolved synonymy.

The biometric criteria used to differentiate these subspecies rely on the (b/a) ratio between the width of the central area (b) and the distal margin width (a) and coccolith length (L) (e.g., Forchheimer, 1972; Lauer, 1975; Verbeek, 1977; Perch-Nielsen, 1979; Hattner et al., 1980; Crux, 1982; Wise, 1983; Gardin et al., 2001; Wolfgring et al., 2018). While earlier studies focused on establishing biometric thresholds, particularly for *Aspidolithus enormis* and *A. parvus*, there remains ambiguity in distinguishing subspecies, especially when considering overlapping biometric characteristics. These evolutionary trends, including the transition from *A. enormis* to *A. parvus*, have been studied recently in detail across three Tethyan deep-water sections: the GSSP section at Bottaccione, Italy (Gardin et al., 2001;

Miniati et al., 2020); the auxiliary stratotype at Postalm, Austria (Wolfgring et al., 2018); and Loibichl, Austria (Granero et al., 2024).

In the Bottaccione section, Gardin et al. (2001) identified five morphotypes within the *Aspidolithus* lineage based on the total length and the b/a ratio, regarding specimens with a total coccolith length less than $10\text{ }\mu\text{m}$ as “small” morphotypes, including *A. parvus expansus* ($b/a \geq 2$) and *A. parvus parvus* “small” (b/a 1–2). On the other hand, in the Postalm section, Wolfgring et al. (2018) regarded specimens with a length less than $9\text{ }\mu\text{m}$ as *A. enormis*, including *A. enormis* subs. 1 ($b/a \geq 2$) and *A. enormis* subs. 2 (b/a 1–2), while, in the Loibichl section, Granero et al. (2024) used $8.5\text{ }\mu\text{m}$ to distinguish between *A. enormis* and *A. parvus parvus*. Further details on the morphotype subdivisions are discussed in Appendix A. However, despite these differences in size thresholds, clear separation between *A. enormis* and *A. parvus* remains complex, as the biometric ranges overlap considerably (Granero et al., 2024). This highlights the need for more detailed biometric analysis to better refine these boundaries attributed to species and/or subspecies definitions. Additionally, the differentiation of subspecies within *A. parvus* (*constrictus*, *expansus*, and *parvus*) has historically been arbitrarily based on the b/a ratio (Hattner et al., 1980; Wise, 1983). It is crucial to conduct further statistical analysis to assess how these subspecies can be differentiated and to understand how this parameter evolves in a biostratigraphic context. In our previous work on a restricted interval, in a single Tethyan section (Granero et al., 2024), no statistically significant differences were identified to enable a clear separation of these subspecies based on the b/a ratio. However, we observed that changes in the b/a ratio seem to also be correlated with palaeoenvironmental changes, particularly with shifts in surface water temperatures.

To further investigate this group, we choose a section outside the Tethys, within the Western Interior Seaway. The Smoky Hill Chalk (SHC) Member of northern Kansas, USA, consists of a marly chalk facies and includes the palaeomagnetic reversal marking the base of Chron C33r (Gale et al., 2022). It provides a high-resolution calcareous nannofossil record, including the FO of *A. parvus parvus* and *A. parvus constrictus* (Kita et al., 2017). For this reason, it has been considered a suitable study area for a comparative biometric analysis of the *Aspidolithus* group using recent approaches by Granero et al. (2024).

Given the biostratigraphic and palaeoenvironmental importance of these species, this study aims to compare and integrate the results from the Western Interior reference section of the Santonian–Campanian boundary interval (SCBI) with those obtained from coeval Tethyan sections (Wolfgring et al., 2018; Granero et al., 2024) in the Austrian Alps, aiming for a more comprehensive understanding of the biometric changes and their drivers within this group. In particular, the study seeks to identify the palaeoenvironmental factors driv-

ing these variations, ultimately providing a more complete evolutionary trend in the *A. parvus* lineage.

1.1 Santonian/Campanian biostratigraphy

Several markers have been proposed for the definition of the Santonian/Campanian boundary, with the FO of *A. parvus* standing out as a key biostratigraphic event. This nannofossil species, alongside its subspecies, has been used as a classical nannofossil marker for the base of the Campanian for a long time (e.g., Thierstein, 1976), observed across a wide range of pelagic environments globally. The FO of *A. parvus* has been used to correlate the boundary in the Gubbio section in Italy (Gardin et al., 2001), and its evolution is recognised in sections of the Western Interior Basin, USA (Kita et al., 2017). Additionally, the FO of *A. parvus* has been considered a useful event for defining the base of the Campanian in specific shallow marine environments (Hancock and Gale, 1996). Carbon isotope excursions, particularly the Late Santonian Event (LSE; former Santonian–Campanian Boundary Event, SCBE) of Jarvis et al. (2006), have been employed to refine the global correlation around the boundary (Jarvis et al., 2023). Recent advancements, including high-resolution magnetostratigraphy (Maron and Muttoni, 2021), have led to the establishment of the reversal from Chron 34n to Chron 33r as the primary marker for the base of the Campanian (Gale et al., 2022).

1.2 Geological settings

The SHC of the Niobrara Chalk Formation is located in western Kansas, within the Western Interior Basin, a retroarc foreland basin formed during the Late Jurassic and Cretaceous. This basin developed as a result of the subduction of the Farallon Plate beneath the North American Plate, which triggered regional subsidence. Over time, this subsidence, combined with a global sea level rise, led to repeated marine transgression across the area, depositing thick sequences of carbonate-rich deposits, including chalk, marls, limestones, and shales (Kauffman and Caldwell, 1993).

The SHC consists primarily of rhythmically bedded marly chalk with interbedded limestones and shale layers. This sequence reflects a dynamic marine environment influenced by transgressive and regressive cycles within the Western Interior Seaway. Overlying the Fort Hays Limestone and the Pierre Shale, the SHC marks a transitional lithostratigraphic interval that captures changes in oceanographic conditions and sedimentary processes throughout the Santonian and Campanian.

Previous studies of SHC, notably by Hattin (1982), Cobban (1952, 1969), and later Kita et al. (2017), provided essential stratigraphic, sedimentological, and palaeontological insights into this unit. Hattin (1982) reported lithological logs and descriptions, identifying key fossil assemblages and sedimentary patterns across 12 localities in the Logan, Gove,

and Trego counties to construct a composite section 181.8 m thick for the entire SHC. Kita et al. (2017) conducted a high-resolution biostratigraphy based on calcareous nannofossil of the localities 20, 24, 25, and 21 of Hattin (1982), indicating that *A. parvus parvus* first occurs at 166.3 m (locality 24) and *A. parvus constrictus* first occurs at 193.15 m (locality 21). Subsequently, Gale et al. (2022) showed that magnetostratigraphic data (Paul Montgomery, unpublished data) indicate that the boundary between Chron 34n and Chron 33r lies at 174 m in the profile.

Our studied section interval is 43.9 m thick (from Hattin, 1982; 160.1 to 204.45 m) and records predominantly shaly to limestone chalks from the upper Santonian to the lower Campanian (UC13–UC14b), spanning localities 21, 24, and 25 of the SHC of the Niobrara Chalk (38°42.857' N, 100°55.649' W or SW1/4, Sec. 30, T15S, R32W, Logan County Kansas; Fig. 1), with samples collected at 1 m intervals (Fig. 2). The sequence contains well-preserved material with distinct assemblages of calcareous nannofossils, foraminifera, and other marine microfossils. Generally good preservation enables detailed biometric analysis of *Aspidolithus* taxa, with emphasis on *A. enormis*, *A. parvus expansus*, *A. parvus parvus*, and *A. parvus constrictus*.

2 Materials and methods

2.1 Calcareous nannofossil assemblages

A total of 44 samples from localities 24 (18 samples), 25 (7 samples), and 21 (19 samples) of the Smoky Hill Chalk Member type area were analysed on a Leica DM 2700 polarising light microscope (LM) at 100× magnification using a slightly modified smear slide method (see Wolfgring et al., 2018; Granero et al., 2024). Calcareous nannofossil samples were prepared for field emission scanning electron microscope (FE-SEM) by applying the centrifugation method (Bown and Young, 1998). Afterwards, samples were coated with gold, analysed, and then examined with a Hitachi TM4000Plus II to assess the nannofossil state of preservation. Counting of specimens of calcareous nannoplankton was carried out under the LM until at least 300 specimens per sample (see Bown and Young, 1998). The total counts of the taxa were then converted to percent relative abundances to further quantitative analysis. The species richness (SR), Shannon index (H' ; Shannon and Weaver, 1949), nannoplankton productivity index (NPI; Eshet and Almogi-Labin, 1996), productivity index (PI; Gale et al., 2000), and nannofossil temperature index (NTI; Jain et al., 2022; Granero et al., 2024) were calculated. NTI was calculated following Jain et al. (2022) as $NTI = [(\% \text{ Watznaueria barnesiae}) / (\% \text{ W. barnesiae} + \% \text{ Arkhangelskiella cymbiformis} + \% \text{ L. cayeuxii} + \% \text{ Reinhardtites anthophorus} + \% \text{ Micula staurophora} + \% \text{ Tranolithus orionatus})]$. Higher values (towards 1) indicate the presence of warm-water masses (Granero et al., 2024). Two NPIs were cal-

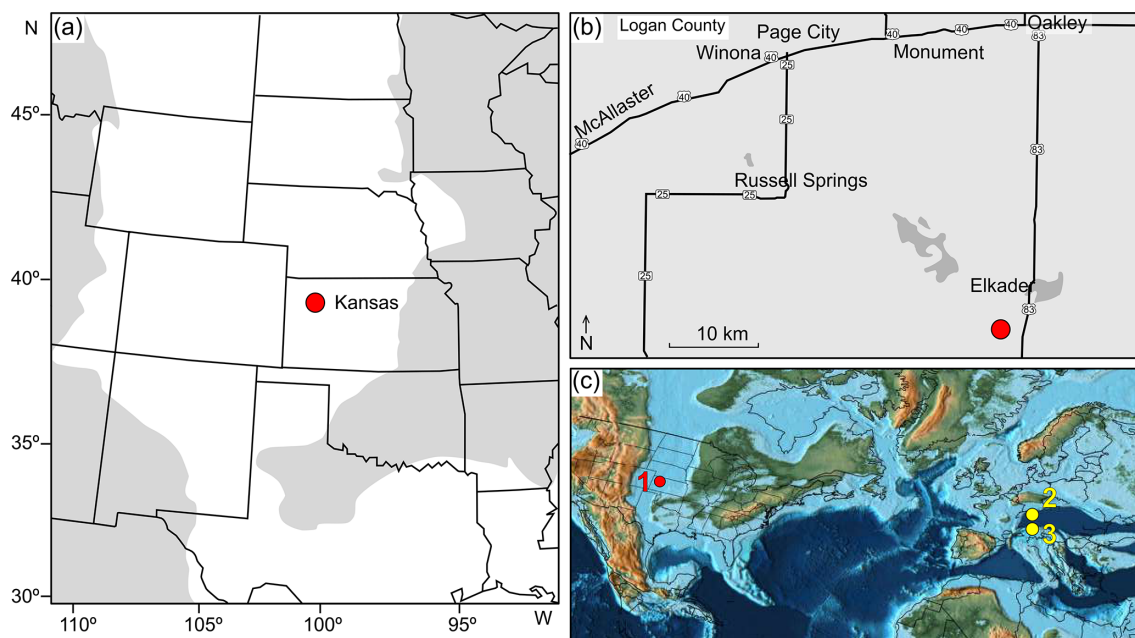


Figure 1. (a) Study section area (red dot) for the Santonian/Campanian boundary. Extent of the Western Interior Seaway (white) and land (grey) modified from Blakey (2015). (b) Location of the auxiliary boundary section 24 in Logan County (red dot). (c) Palaeogeographic reconstruction of the Campanian. (1) Niobrara, Kansas; (2) Loibichl, Austria; (3) Postalm, Austria.

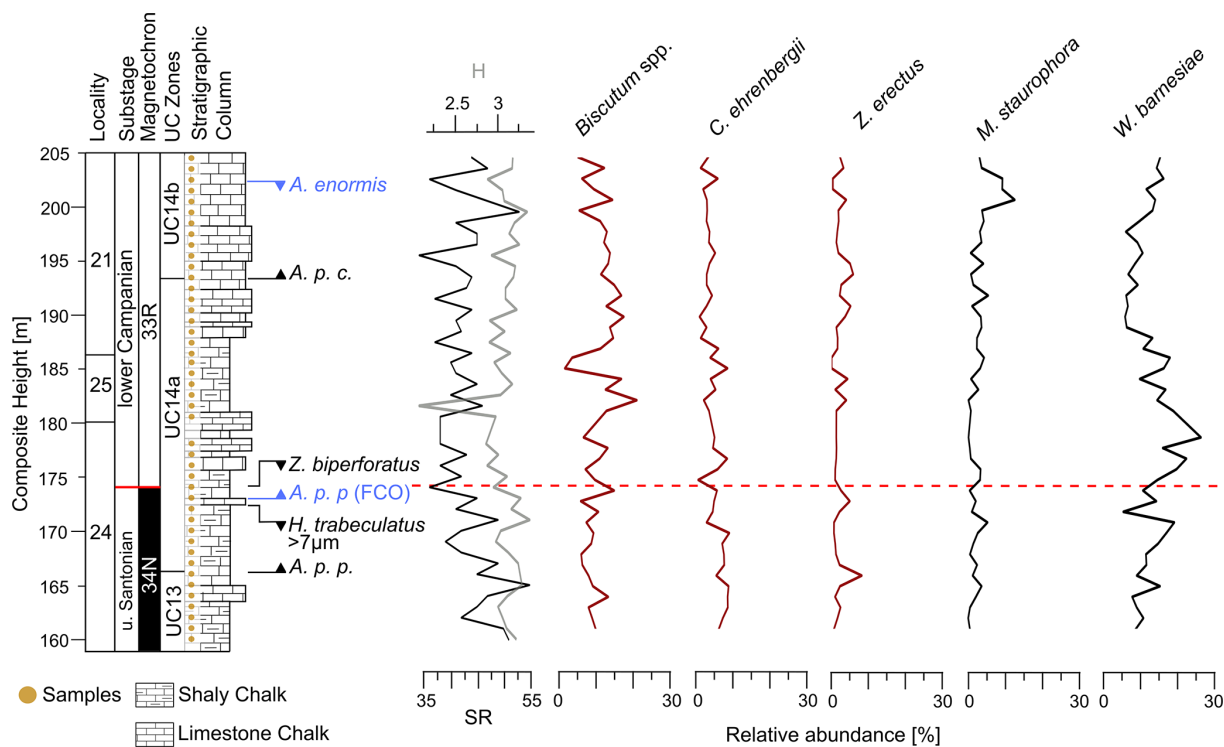


Figure 2. Stratigraphic column of the Niobrara section with the most relevant bioevents marked. Events in black correspond to those identified by Kita et al. (2017), while events in blue are newly reported in this study. On the right, Shannon index (H) values, species richness (SR), and relative abundances of the dissolution-resistant species (black) and dissolution-susceptible species (red) throughout the section are displayed.

culated, (1) following Eshet and Almogi-Labin (1996) with $NPI = [(\% \text{ Biscutum spp.} + \% \text{ Zeugrhabdotus spp.})/(\% \text{ Eiffellithus spp.} + \% \text{ Prediscosphaera spp.} + \% \text{ Lithraphidites spp.} + \% \text{ Microrhabdulus decoratus})]$ and (2) following Gale et al. (2000) with $NPI = (\% \text{ Zeugrhabdotus spp.} + \% \text{ Biscutum spp.})/\% \text{ W. barnesiae}$. Lower values of NPI indicate oligotrophic conditions, while higher values suggest enhanced nanoplankton productivity.

Nannofossil taxonomy largely follows Nannotax3 (Young et al., 2022), with some amendments (Kita et al., 2017; Miniati et al., 2020).

2.2 Carbon isotopes

Stable carbon isotope analyses ($\delta^{13}\text{C}$) were conducted on 44 bulk carbonate samples collected at approximately 1 m intervals (Kita, 2015). Standard methods for stable isotope analysis of carbonates were followed, using phosphoric acid digestion at 25 °C to extract CO_2 . Analyses were performed at the Keck Paleoenvironmental and Environmental Stable Isotope Laboratory (University of Kansas) using a ThermoFinnigan GasBench II coupled to a Finnigan MAT 253 isotope-ratio mass spectrometer. Results are expressed in δ notation relative to the Vienna Pee Dee Belemnite (VPDB) standard. For details on methods, see Kita (2015).

2.3 Statistical treatment

To determine whether changes in temperature and productivity indexes truly influence the distribution of the species identified in the study area, a factor analysis (CABFAC) and a correlation analysis were performed using the relative abundance data of the most dominant and variable species in the section (explaining > 80 % of the abundance of the entire section). In addition, a principal component analysis (PCA) was conducted using only the relative abundances of the taxa included in the NTI and NPI, in order to evaluate whether these taxa show ecological separation consistent with their assigned roles as warm- or cold-water indicators and productivity proxies.

2.4 Biometric measurements

A total of 2421 specimens of the *Aspidolithus* group (*A. enormis* and *A. parvus*) from 44 SHC samples were analysed under a polarised LM to measure various key biometric parameters using JMicrovision software (Roduit, 2019). Images were acquired using a Leica MC170 HD digital camera (resolution: 2592 × 1944 pixels). The pixel-to-micron ratio was calculated using the integrated scale bar provided by the Leica software, which had previously been calibrated. Based on this, the resolution at 1000× magnification was determined to be 1 pixel = 0.05 µm. This value was applied consistently in JMicrovision for all measurements. Although repeated measurements of the same specimens were not per-

formed, the pixel resolution defines the minimum measurable size difference. Therefore, we estimate the measurement error to be ±0.1 µm (equivalent to 2 pixels), which represents a conservative and realistic value under our imaging and measurement conditions. For each specimen, the coccolith length (*L*), coccolith width (*W*), and *b/a* ratio were measured (including *a* and *b* separately). The number and arrangement of perforations were not considered in this study because they were not visible in all specimens due to diagenetic alterations. The mean values and standard deviation of the measurements were calculated. Raw data for every specimen were analysed without differentiating the previously defined subspecies to reassess and review the differences among them. Statistical analysis was performed on the dataset and focused on potential differentiation among previously defined subspecies (Hattner et al., 1980; Wise, 1983; Gardin et al., 2001; Wolfgring et al., 2018). Mixture analysis was conducted using the measurements of *L* and the *b/a* ratio for all specimens and was conducted for *A. enormis* and *A. parvus* individually using PAleontological STatistics (PAST) data analysis software (Hammer et al., 2001). The Akaike information criterion (AIC; Akaike, 1974) was applied as the model selection basis. To statistically differentiate between normally distributed components identified in the mixture analysis, optimal cutting points were determined by solving the equality of weighted normal distributions. Group sizes were calculated as the product of the total number of specimens and the relative proportions. Statistical significance between adjacent components was tested using a two-sample *t* test assuming unequal variances. To improve the understanding of biometric variations and enhance correlation, a mixture analysis was also performed using lower-resolution *Aspidolithus* biometric data from the Postalm section (Austria) by Wolfgring et al. (2018) (unpublished). These data were obtained using a calibrated measuring eyepiece on a non-digital Zeiss Axiolab microscope, 100× oil immersion objective, with an estimated error range of minimum ±0.3 µm due to the blurred appearance of nannofossils.

To analyse whether the changes in the *Aspidolithus* spp. measurements could be correlated with variations in palaeoenvironmental proxies (PI, NTI, and $\delta^{13}\text{C}$ stable isotope ratio values), three analytical approaches were undertaken: (1) a correlation matrix analysis including Pearson correlation coefficients (*r*) and *p* values (*p*); (2) a two-way cluster analysis (R-mode and Q-mode) (Anderberg, 1973; Tan et al., 2006) using the Pearson correlation coefficient (PCC; Pearson, 1895); and (3) a canonical correspondence Analysis (CCA; ter Braak, 1986) using PAST, following the methodology outlined in Granero et al. (2024).

3 Results

3.1 Nannofossil assemblage

The chalks of the SHC contain a rich assemblage of moderately to well-preserved calcareous nannofossils, with a total of 91 taxa identified. The largely unaltered state of the assemblages is reflected by the independent distribution of solution-resistant taxa, such as *Watznaueria barnesiae* (mean 12.7 %) or *Micula staurophora* (mean 2.9 %); more susceptible taxa, such as *Cribrosphaerella ehrenbergii* (mean 4.7 %); or small taxa, such as *Biscutum* spp. (mean 10.4 %) and *Zeugrhabdotus erectus* (2.2 %) (Fig. 2). SEM images further reinforce this moderate to good preservation, showing a well-preserved *C. ehrenbergii* central area with its perforated net and revealing the presence of perforations in the central area of some *A. parvus* (Fig. 3). However, signs of dissolution or etching damage were observed without affecting the taxonomic identification of the counted specimens. Species richness ranges from 34 (195.45 m, sample N21/9.3) to 55 (165.1 m, sample N24/5.3), and the Shannon diversity index of all counted samples ranges from 2.1 (181.6 m, sample N25/1.3) to 3.4 (171.1 m, sample N24/11.3), with an average of 3.1. The values of species richness and *H* values are shown in Fig. 2.

The calcareous nannofossil assemblage is dominated by high relative abundances above 5 % of *Prediscosphaera* spp. (mean 15.2 %), *Watznaueria* spp. (mean 13.6 %), *Tranolithus* spp. (mean 11 %), *Biscutum* spp. (mean 10.4 %), and *Zeugrhabdotus* spp. (mean 5.3 %). Taxa with a relative abundance below 5 % are *Cribrosphaerella* spp. (mean 4.8 %), *Eiffellithus* spp. (mean 4.6 %), *Chiastozygus* spp. (mean 4.4 %), *Aspidolithus* spp. (mean 3.6 %), *Micula* spp. (mean 3.1 %), *Reinhardtites anthophorus* (mean 3 %), *Retecapsa* spp. (mean 2.9 %), *Discorhabdus ignotus* (mean 2.8 %), *Corollithion* spp. (mean 2.35 %), *Microrhabdulus* spp. (mean 2.2 %), *Ahmuellerella* spp. (mean 1.38 %), *Lucianorhabdus* spp. (mean 1.61 %), *Helicolithus* spp. (mean 1.32 %), and *Gartnerago obliquum* (mean 1.04 %). The relative abundances of the dominant taxa are shown in Fig. B1, while the complete relative abundance data for each sample are available at <https://doi.org/10.5281/zenodo.17093271> (Granero Ordóñez, 2025).

The species that exhibit the most significant changes in their relative abundance within the depths of 161.1 to 178.1 m and 180.6 to 204.45 m are *Biscutum ubiqueum* (4.03 % variance), *W. barnesiae* (3.82 % variance), *Prediscosphaera cretacea* (2.66 % variance), *Tranolithus orionatus* (2.50 % variance), and *Prediscosphaera spinosa* (2.08 % variance). These calcareous nannofossils show notable fluctuations, suggesting possible palaeoenvironmental changes within the section.

3.2 Biostratigraphy

According to the Burnett (1998) scheme, the lower part of the section belongs to the latest Santonian Zone UC13, in which the top is defined by the FO of *A. parvus parvus* at 171.1 m (sample N24/11.3) for specimens with a length (*L*) $\geq 10 \mu\text{m}$, at 166.1 m (sample N24/6.3) for specimens with a length (*L*) $> 8.5 \mu\text{m}$, and at 168.1 m (sample N24/8.3) for specimens with a length (*L*) $\geq 9 \mu\text{m}$. *A. parvus parvus* is rare at the beginning of its range, becoming continuous and common from 173.1 m (sample N24/13.3) upwards: we labelled this change (from 0.2 % to 3 %) as the first common occurrence (FCO) in this study. The last occurrence (LO) of *Helicolithus trabeculatus* ($> 7 \mu\text{m}$) was identified at 172.1 m (sample N24/12.3), about 1.7 m below the base of Chron C33r. Additionally, the LO of *Zeugrhabdotus biperforatus* Burnett was recorded at 177.1 m (sample N24/17.3), approximately 3.1 m above the base of Chron C33r. The FO of *Cylindralithus crassus* Caratini was documented by Bergen and Sikora (1999) as occurring below the Santonian/Campanian boundary but was absent in the Niobrara section. The acme of *Retecapsa crenulata* (7.84 %) is recorded at 174.1 m (sample N24/14.3), 0.1 m above the C33r/C34n reversal. In this sample, the lowest relative abundance for *C. ehrenbergii* is observed (0.63 %). *Arkhangelskiella cymbiformis* is present throughout the entire section, being rare or infrequent in the lower part of the section and slightly increasing up-section.

The middle to higher part of the section is referred to as the lower Campanian Subzone UC14a, which is defined as the interval between the consecutive FOs of *A. parvus parvus* and *A. parvus constrictus*. The FO of *A. parvus constrictus*, recognised at 185.6 m (sample N25/5.3) for specimens with a length (*L*) $> 10 \mu\text{m}$, allows the establishment of the base of the UC14b Subzone. The FO of *Bukryaster hayi* (Bukry) Prins and Sissingh in Sissingh marks the upper boundary of Subzone UC14b, and the FO of *Ceratolithoides verbeekii* Perch-Nielsen defines the lower boundary of Subzone UC14d. As these species are not present, it has been interpreted that the section ends within Subzone UC14b. The LO of *A. enormis* with length (*L*) $\leq 8.5 \mu\text{m}$ occurs at 202.45 m (sample N21/15.3). *C. obscurus* and *Lucianorhabdus cayeuxii* were not found in the lower part of the section, having a significant peak in *C. obscurus* (2 %) and *L. cayeuxii* (16.2 %) at 192.45 m (sample N21/6.3) and 189.45 m (sample N21/3.3), respectively. *A. parvus expansus* is recorded in the entire section. Based on these biohorizons, the studied section spans the UC13 and UC14b zones (Fig. 2).

3.3 Palaeoenvironmental indexes

The NTI values show a fluctuating pattern throughout the section, reflecting changes in temperature trends over time (Fig. 4). The base of the section begins with a slight decrease in NTI from 0.41 (160.1 m, sample N24/0.3) to

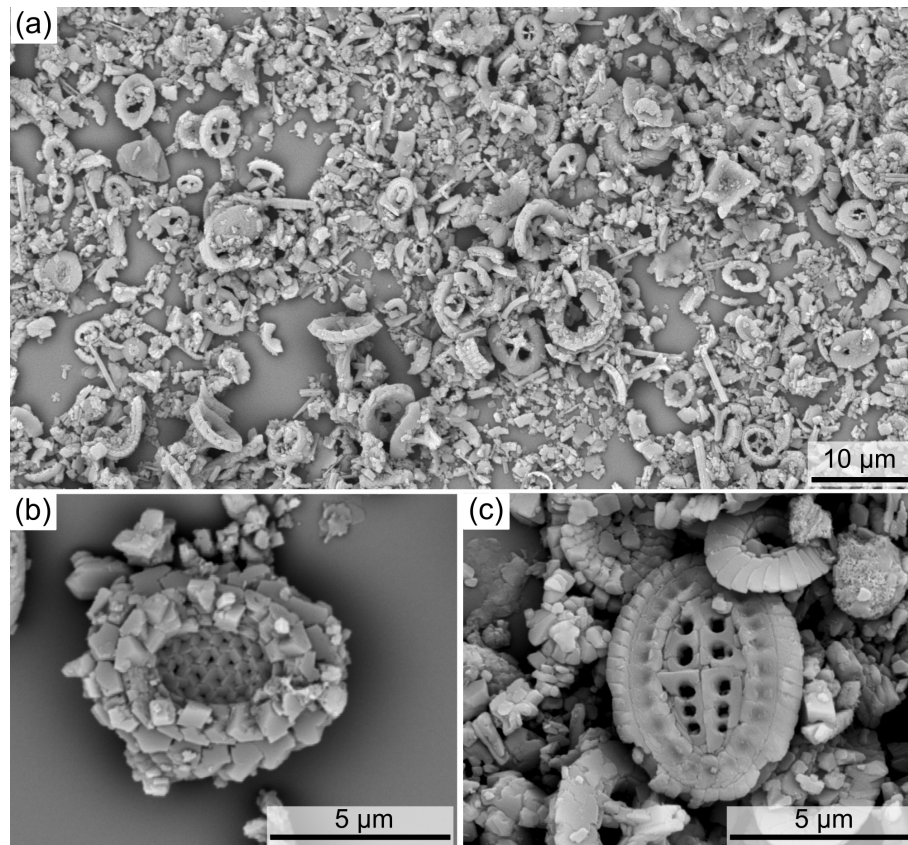


Figure 3. SEM images of calcareous nannofossils. (a) General view of the calcareous nannofossil assemblage. (b) *C. ehrenbergii*, exhibiting good preservation with a well-defined net structure in the central area. (c) *A. enormis*, showing the presence of perforations in the central area.

0.33 (163.1 m, sample N24/3.3), followed by a rise to 0.53 (164.1 m, sample N24/4.3), suggesting a warming event, before decreasing again to 0.36 (166.1 m, sample N24/6.3), reflecting a cooling trend. Subsequently, there is a gradual upward trend in NTI values, peaking at 0.52 (168.1 m, sample N24/8.3), which is followed by a significant drop to 0.27 (170.1 m, sample N24/11.3), marking a notable cooler trend. In the middle of the section, the NTI values exhibit fluctuating patterns. Initially, there is a pronounced general increase that peaks at 0.63 (176.1 m, sample N24/16.3), the highest recorded value in the section, representing the major warming trend of the section. This warming trend is followed by a decline to 0.47 (177.1 m, sample N24/17.3), indicating a slight cooling trend, a brief recovery to 0.63 (178.1 m, sample N24/18.3), and then a sharp drop interspersed with smaller positive and negative peaks. This ends in the lowest NTI value of the section, 0.15 (189.45 m, sample N21/3.3). Towards the top, a general upward trend in NTI is observed, suggesting general warming punctuated by smaller positive and negative peaks, reflecting short-term fluctuations in temperature conditions, which stabilise near 0.46 (204.45 m, sample N21/18.3) at the top of the section. Overall, the NTI data show a dynamic pattern of temperature trends. The same

NTI trends were calculated using the abundances reported by Kita et al. (2017) (Fig. 4).

Similarly to the NTI values, the NPI (Gale et al., 2000) was calculated. Its values exhibit significant fluctuations throughout the section (Fig. 4). The NPI values rise from 1.22 (161.1 m, sample N24/1.3) at the base of the section to 2.18 (163.1 m, sample N24/3.3), indicating an initial increase in the productivity trend. This is followed by a drop to 0.87 (164.1 m, sample N24/4.3), marking a temporary decrease. Subsequently, the values climb to 1.79 (165.1 m, sample N24/5.3), reaching a significant peak. After this, there is a decline, with values fluctuating between 0.92 (166.1 m, sample N24/6.3) and 0.42 (170.1 m, sample N24/10.3), reflecting moderate variability. The NPI then increases again to 2.31 (171.1 m, sample N24/11.3), followed by a sharp drop to 0.45 (175.1 m, sample N24/15.3), after which it rises gradually and oscillates until reaching 2.24 (183.6 m, sample N25/3.3). A steep decline follows, hitting the lowest recorded value of 0.14 (184.6 m, sample N25/4.3). From there, the values rise, reaching the highest peak of the section at 3.56 (187.45 m, sample N21/3.3). Towards the top of the section, the trend continues fluctuating, with a gradual decline. This oscillatory descent includes minimums of around

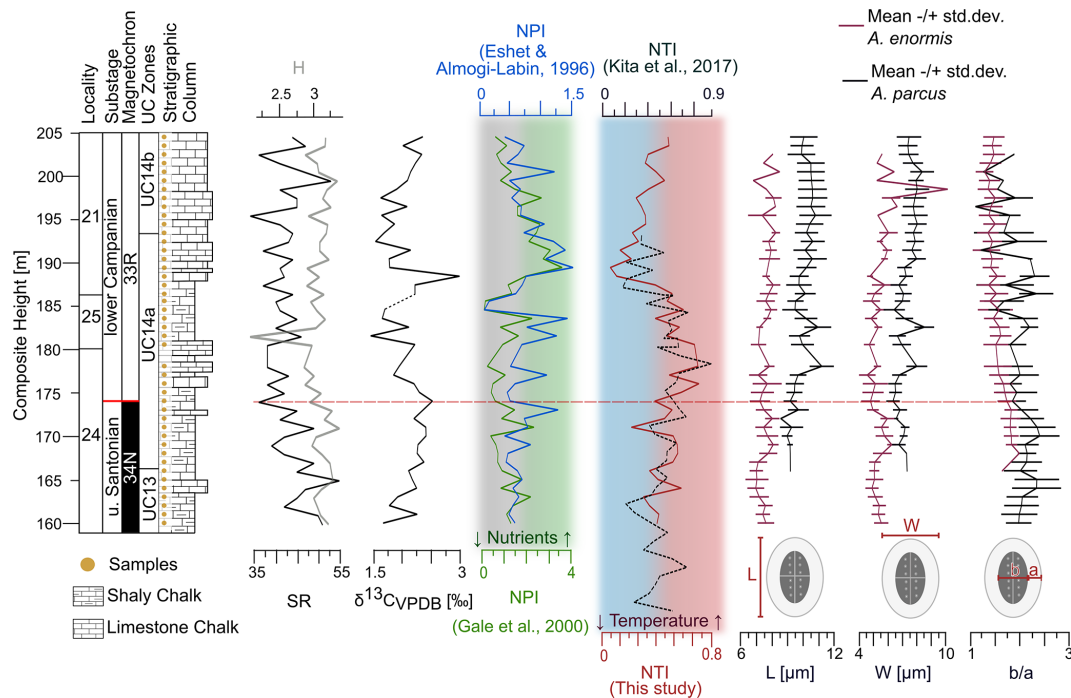


Figure 4. Changes in $\delta^{13}\text{C}$, NTI, NPI, H , and SR values together with variations in the morphometric parameters analysed for *Aspidolithus enormis* and *A. parvus* along the Niobrara section. The graphs of the morphometric parameters show separate curves for *A. enormis* (in red) and *A. parvus* (in black). Abbreviations: NTI, nannofossil temperature index (Jain et al., 2022); NPI, nannoplankton productivity index (Eshet and Almogi-Labin, 1996; Gale et al., 2000); H , Shannon index; SR, species richness; std. dev., standard deviation.

0.68 (202.45 m, sample N21/16.3), marking a progressive decrease in productivity towards the top. These fluctuations in NPI based on Gale et al. (2000) are similar for the values of NPI based on Eshet and Almogi-Labin (1996).

Principal component analysis (PCA) was applied to test whether the taxa selected for palaeoenvironmental indices (temperature and productivity) display contrasting ecological patterns. The loadings for PC1 (eigenvalue 38.06; variance 43.14 %) and PC2 (eigenvalue 15.52; variance 17.59 %) confirm that *W. barnesiae*, used as a warm-water indicator, loads strongly and positively on PC1, whereas taxa associated with cold-water conditions (*A. cymbiformis*, *M. staurophora*, *R. anthophorus*, *T. orionatus*) show lower or even negative correlations with the same component. Likewise, the taxa used to represent high productivity (*Biscutum* spp., *Zeugrhabdotus* spp.) and low productivity (*Prediscosphaera* spp., *Eiffellithus* spp., *M. decoratus*) tend to load in opposite directions along PC2. While some overlap exists, as expected in natural assemblages with complex ecological gradients, the overall distribution of taxa in the loading space supports the conceptual foundation of the NTI and NPI, reinforcing their ecological significance.

Importantly, the selected taxa were not chosen arbitrarily; their palaeoecological affinities have previously been discussed by other authors (e.g., Thierstein, 1981; Roth and Krumbach, 1986; Watkins, 1989; Erba, 1992; Erba et al.,

1992; Mutterlose et al., 2005; Linnert and Mutterlose, 2015). The loadings plots supporting this interpretation are provided in Fig. C1. The CABFAC factor analysis of total calcareous nannofossil relative abundance data indicates that Factor 1, which accounts for 86.75 % of the variance (eigenvalue = 38.17), is strongly correlated with palaeoenvironmental indexes (NPI and NTI). Specifically, Factor 1 shows a significant positive correlation with the NPI ($r = 0.75/0.85$, $p = 3.24 \times 10^{-9}/3.31 \times 10^{-13}$), suggesting that higher productivity conditions correspond to higher values of this factor. Conversely, Factor 1 exhibits a strong negative correlation with NTI ($r = -0.71$, $p = 5.1 \times 10^{-8}$) and a strong positive correlation with NPI, indicating that lower temperatures and high nutrient availability are associated with higher values of this factor (Fig. 5). These results imply that the primary environmental driver influencing the distribution of dominant nannofossil species in the studied area is a combination of surface water nutrient availability and temperature variations, with productivity playing a particularly significant role. No significant correlation has been observed with SR and H . Other factors showed weaker correlations with the analysed indexes, indicating that species distribution was influenced by multiple environmental parameters but primarily driven by the conditions captured by Factor 1.

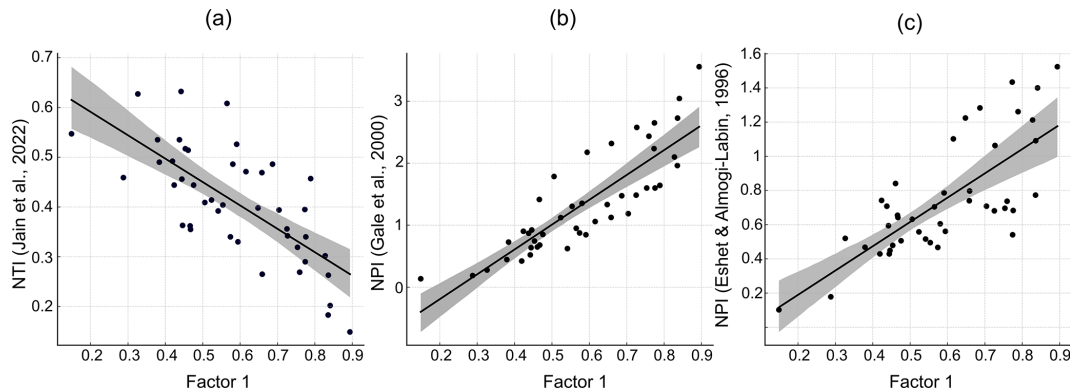


Figure 5. Correlations between palaeoenvironmental variables and Factor 1. **(a)** Negative correlation between NTI and Factor 1, with a regression trendline and confidence interval. **(b)** Positive correlation between NPI (Gale et al., 2000) and Factor 1. **(c)** Positive correlation between NPI (Eshet and Almogi-Labin, 1996) and Factor 1.

3.4 $\delta^{13}\text{C}$ isotope stratigraphy

The $\delta^{13}\text{C}$ isotope record in the Niobrara section shows variability (Fig. 4), with values ranging from 1.46‰ (181.6 m, sample N25/1.3) to 2.98‰ (188.45 m, sample N21/2.3). These values are consistent with the expected worldwide range of upper Santonian–lower Campanian bulk carbonate carbon isotope values in various shelf seas and oceanic basins (+1.5‰ and +2.5‰; Thibault et al., 2016; Dubicka et al., 2017). At the base of the studied section, the $\delta^{13}\text{C}$ values start at 1.67‰ (160.1 m, sample N24/0.3), showing an initial increase that reaches a positive peak of 2.25‰ (161.1 m, sample N24/1.3). This is followed by a drop to a negative peak of 1.77‰ (162.1 m, sample N24/2.3) and an increase reaching another positive peak at 2.24‰ (164.1 m, sample N24/4.3). The next fluctuation shows a drop to a negative peak of 2.11‰ (166.1 m, sample N24/6.3), followed after recovery by a higher positive peak of 2.37‰ (167.1 m, sample N24/7.3). This recovery is followed by a slight decrease to 2.25‰ (168.1 m, sample N24/8.3) before another positive peak at 2.41‰ (170.1 m, sample N24/10.3). The trend then reverses, with a decline to 2.20‰ (172.1 m, sample N24/12.3), before peaking again at 2.51‰ (175.1 m, sample N24/17.3). In the middle part of the section, there is a significant drop in the values, reaching the lowest value recorded at 1.46‰ (181.6 m, sample N25/1.3). This marks a turning point, as the values begin to increase again. The recovery is marked by fluctuations, ending in the highest positive peak of the entire section at 2.98‰ (188.45 m, sample N21/2.3). After this maximum, the values decrease again, settling at 1.77‰ (190.45 m, sample N21/4.3). The upper part of the section displays smaller oscillations, with single positive peaks up to 2.34‰ and negative peaks down to 1.54‰.

3.5 Biometric and statistical analyses

A. enormis, *A. parvus constrictus*, *A. parvus expansus*, and *A. parvus parvus* have been identified (Fig. 6). The dataset for all *Aspidolithus* specimens exhibits the following morphological characteristics: (1) coccolith length ranges from 5.6 μm (165.1 m, sample N24/5.3) to 13.6 μm (178.1 m, sample N24/18.3), with a mean of 9.3 μm and a standard deviation of 1.6. There is an observable general increase in coccolith length towards the top of the section. (2) Rim width spans 3.7 μm (177.1 m, sample N24/17.3) to 11.2 μm (195.45 m, sample N21/9.3), with a mean of 6.8 μm and a standard deviation of 1.3. (3) Central area–rim width ratio (b/a) varies from 0.8 (185.6 m, sample N25/5.3) to 3.5 (171.1 m, sample N24/11.3), with a mean of 1.7 and a standard deviation of 0.5. This ratio shows a decreasing trend along the section. All the measurements are shown in <https://doi.org/10.5281/zenodo.17093271> (Granero Ordóñez, 2025).

The mixture analysis of coccolith length (L) for all the specimens in this study identifies two normally distributed components, with means of 7.166 and 10.014 μm and standard deviations of 0.59 and 1.13 μm , respectively. The proportions for each component are 24.8 % and 75.2 %, with an optimal cutting point calculated at 8.14 μm . A total of 2421 specimens were analysed, resulting in effective group sizes of 601.6 and 1819.4. The separation between the two components is statistically significant ($t = 59.21$, $p < 0.001$). Similarly, the mixture analysis performed on the rim width (W) measurements reveals two distinct normal populations with means of 7.169 and 4.963 μm and standard deviations of 1.045 and 0.4409 μm , respectively. The estimated proportions for each component are 80.2 % and 19.8 %, with an optimal threshold at 5.62 μm (Fig. 7). This boundary allows a clear distinction between the two morphometric groups based on width. The same number of specimens ($n = 2421$) was included in the analysis, resulting in effective

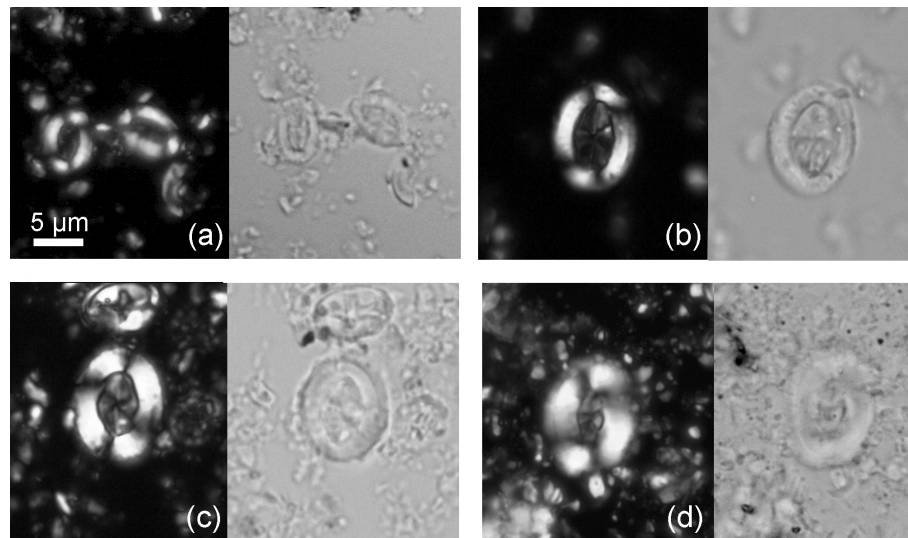


Figure 6. Light photomicrographs of selected *Aspidolithus* specimens at 1000 $\times$ magnification. All images are shown in crossed and parallel nicols and are at the same scale. (a) *A. enormis*, sample N24-2.3. (b) *A. parvus expansus*, sample N25-2.3. (c) *A. parvus parvus*, sample N21-6.3. (d) *A. parvus constrictus*, sample N21-17.3.

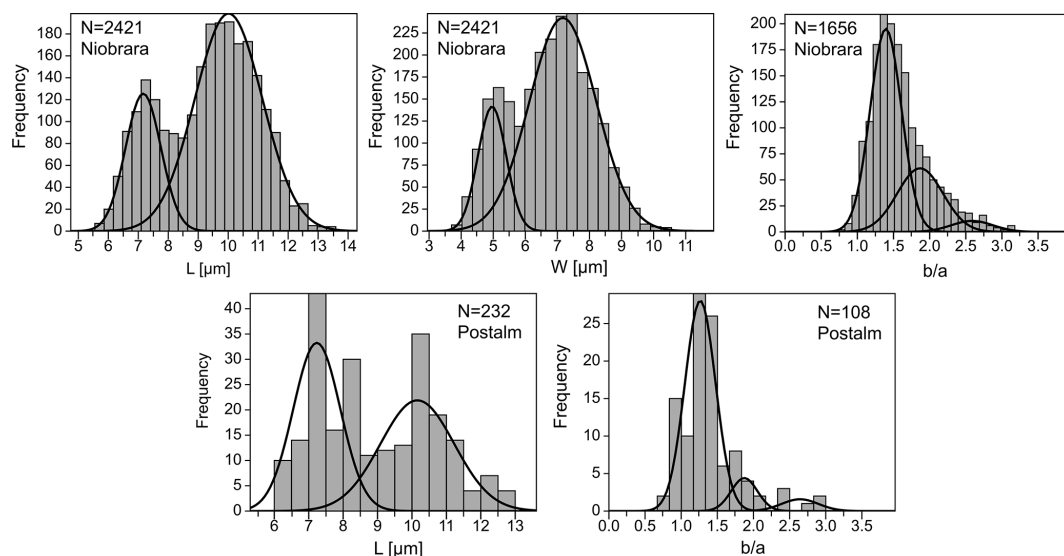


Figure 7. Mixture analysis of morphometric parameters. The top graphs represent the analysis of L , W , and b/a in the Niobrara section, while the bottom graphs show the analysis of L and b/a in the Postalm section. Abbreviations: L , total coccolith length; W , total coccolith width; b/a , ratio between the central area width and the outer rim width.

group sizes of 1942.8 and 478.2. The statistical significance of this separation is supported by a t value of 45.16 and a p value < 0.001 . The L values for *Aspidolithus* spp. specimens follow an inverse general trend to b/a ratio (Fig. 4). The mixture analysis of b/a for all *A. parvus* specimens ($n = 1656$) identifies three morphogroups with proportions of 65.47 %, 29.97 %, and 4.55 % and means of 1.4396, 1.872, and 2.599, respectively. Standard deviations for each component are 0.22, 0.32, and 0.29. The optimal cutting point between the first and second components is calculated at 1.589,

yielding effective group sizes of 1084.3 and 496.3 specimens. The statistical test confirmed a significant separation between these two groups ($t = 34.69$, $p > 0.001$). The second and third components are also significant ($t = 18.75$, $p > 0.001$), separated at 2.255, supporting the presence of three morphometrically distinct populations based on the b/a ratio. The results of the mixture analysis based on the b/a ratio for *A. enormis* exclusively indicate the presence of a single population, with no significant differences observed between *A. enormis* subs. 1 and *A. enormis* subs. 2.

Using unpublished biometric data from *Aspidolithus* specimens measured by Wolfgring et al. (2018: Postalm section), the mixture analysis of L suggests the presence of two distinct groups with nearly equal proportions of 49.29 % and 50.71 % and means of 7.236 and 10.158 μm , respectively. Standard deviations for each component are 0.69 and 1.07 μm , with an optimal cutting point between the two distributions at 8.376 μm , resulting in effective group sizes of 114.4 and 117.6 specimens ($n = 232$). The separation between the two components is statistically robust ($t = 24.65$, $p < 0.001$), supporting the existence of two distinct morphometric groups in this database. On the other hand, the mixture analysis of the b/a data from the Postalm section (Wolfgring et al., 2018) indicates the differentiation of three distinct groups with proportions of 83.18 %, 11.23 %, and 5.59 % and means of 1.263, 1.871, and 2.644, respectively. The corresponding standard deviations are 0.21, 0.18, and 0.25. The optimal cutting point between the first and second components is 1.59, with effective group sizes of 89.8 and 12.1 specimens, respectively. This separation is statistically significant ($t = 9.48$, $p < 0.001$). The second and third components are separated at 2.194, with a sample size of 6 for the third component, and the difference is also significant ($t = 7.47$, $p < 0.001$), indicating the presence of three distinct morphometric groups based on the b/a ratio (Fig. 7).

The mixture analysis of L based on data from Granero et al. (2024: Loibichl section) identified two normally distributed components with proportions of 8.5 % and 91.5 % and mean values of 7.1 and 10.5 μm , respectively ($n = 1021$). The optimal cutting point between the two groups was calculated at 8.337 μm , with effective group sizes of 86.8 and 934.2 individuals ($n = 1021$). The separation between the two components is statistically robust ($t = 31.45$, $p > 0.001$).

The correlation analysis between morphometric parameters, palaeoenvironmental indexes, and relative abundances of *Aspidolithus* spp. has revealed statistically significant relationships. The correlation matrix indicates a total of 14 negative correlations and 11 positive correlations, all with $p < 0.05$ (Table 1). Among these, the most relevant in this study are (1) a strong positive correlation between L and W ($r = 0.95$, $p = 2.08 \times 10^{-18}$), suggesting a consistent proportionality between length and width in *Aspidolithus* spp.; (2) a negative correlation between L and b/a ($r = -0.77$, $p = 1.34 \times 10^{-5}$), indicating that, as the coccolith length increases, the b/a ratio becomes relatively smaller; (3) a negative correlation between NTI and NPI ($r = -0.43/-0.8$, $p = 0.002/5.53 \times 10^{-7}$); (4) a negative correlation between L and SR ($r = -0.36$, $p = 0.02$), which may suggest that larger coccoliths are associated with lower species richness; and (5) a positive correlation between NTI and the b/a ratio ($r = 0.34$, $p = 0.02$), implying that variations in temperature could influence the b/a ratio. The individual values of a and b were tested for inclusion, but no significant correlations were found with the rest of the data. Since these

values are already incorporated into the b/a ratio, they were excluded from the statistical analyses to obtain a clearer result.

To further explore the relationships between samples and environmental or morphometric parameters, a two-way cluster analysis was performed in PAST, combining R-mode and Q-mode hierarchical clustering (Fig. 8a). This approach highlights consistent associations both among variables and among samples. The two productivity indexes (NPI from Gale et al., 2000, and Eshet and Almogi-Labin, 1996) cluster together with near-perfect similarity, confirming their strong correlation. L and W are also tightly grouped, reflecting their common morphological origin. The NTI and the b/a ratio form another cluster, suggesting a potential link between surface water temperature and coccolith proportions. $\delta^{13}\text{C}$ values group separately, possibly reflecting a distinct environmental or diagenetic signal not significantly related to productivity or surface temperature.

Moreover, the CCA results (Fig. 8b) identified complex relationships between morphological and palaeoenvironmental data (S , H , $\delta^{13}\text{C}$, NTI, and NPI) data. These results show that the first axis (Axis 1), explaining 61.6 % of the variance, captures the primary relationship between palaeoenvironmental variables and the size of *Aspidolithus* subspecies. Axis 2, which accounts for 25.57 % of the variance, reveals secondary patterns, particularly highlighting the role of NTI in opposing the distributions of *A. parvus expansus* and *A. parvus constrictus*. The position of *A. parvus expansus* and *A. enormis* (higher b/a) on the positive end of Axis 1 and NTI suggests a stronger association with high NTI values, while *A. parvus constrictus* (lower b/a values), positioned negatively along Axis 1 and closer to the NTI opposite direction, indicates a weaker or potentially inverse relationship with this variable. Additionally, the variable b/a ratio aligns with the NTI positive direction, suggesting that the b/a ratio may be influenced by changes in NTI. On the other hand, variables such as SR and $\delta^{13}\text{C}$ strongly influence *A. enormis* and *A. parvus expansus* (lower L values), as reflected by their proximity to the positive end of Axis 1. In contrast, *A. parvus constrictus* and *A. parvus parvus* (higher L values) are positioned near NPIs (Gale et al., 2000; Eshet and Almogi-Labin, 1996), suggesting their preference for palaeoenvironmental conditions characterised by lower SR and different productivity levels. The clear separation between *A. parvus expansus* and *A. parvus constrictus* along both axes highlights the opposing responses of these subspecies to NTI, reinforcing the idea that this variable may have played a crucial role in driving their ecological differentiation.

4 Discussion

4.1 Nannofossil preservation

Calcareous nannofossils are a major component of pelagic carbonates from the Mesozoic and Cenozoic, but their preser-

Table 1. Correlation matrix between palaeoenvironmental indexes (SR, *H*, NPI 1, NPI 2, NTI, $\delta^{13}\text{C}$), morphometric parameters (*L*, *W*, *b/a*), and relative abundances of *A. parvus constrictus*, *A. parvus expansus*, *A. parvus parvus*, and *A. enormis*, showing the *p* values (upper part) and *r* values (Pearson correlation; lower part) in bold. Abbreviations: SR, species richness; *H*, Shannon index; NPI 1 (Gale et al., 2000) and NPI 2 (Eshet and Almogi-Labin, 1996), nannoplankton productivity index; NTI, nannofossil temperature index (Jain et al., 2022); *L*, total coccolith length; *W*, total coccolith width; *b/a*, ratio between the central area width and the outer rim width.

	SR	H	NPI 1	NPI 2	NTI	$\delta^{13}\text{C}$	<i>L</i>	<i>W</i>	<i>b/a</i>	<i>A. p. c.</i>	<i>A. p. e.</i>	<i>A. p. p.</i>	<i>A. enormis</i>
SR		0.006	0.989	0.363	0.760	0.723	0.017	0.137	0.077	0.325	0.055	0.001	0.324
<i>H</i>	0.41		0.36	0.43	0.238	0.12	0.29	0.992	0.355	0.67	0.47	0.375	0.221
NPI 1	0.00	−0.14		0.002	0.004	0.056	0.181	0.235	0.140	0.750	0.031	0.885	0.727
NPI 2	0.14	0.12	0.70		5.50×10^{-7}	0.01	0.33	0.260	0.066	0.45	0.02	0.397	0.171
NTI	−0.05	−0.18	−0.43	−0.80		0.41	0.29	0.157	0.022	0.11	0.02	0.862	0.104
$\delta^{13}\text{C}$	−0.06	0.24	−0.29	−0.37	0.13		0.13	0.155	0.022	0.140	0.36	0.919	0.063
<i>L</i>	−0.36	−0.16	0.21	0.15	−0.16	−0.23		2×10^{-18}	1.30×10^{-5}	0.04	0.17	1.40×10^{-4}	5.30×10^{-4}
<i>W</i>	−0.23	0.00	0.18	0.17	−0.22	−0.22	0.95		1.70×10^{-5}	0.08	0.66	0.003	4.30×10^{-4}
<i>b/a</i>	0.27	0.14	−0.23	−0.28	0.34	0.35	−0.77	−0.73		0.03	0.03	5.30×10^{-4}	0.003
<i>A. p. c.</i>	−0.15	0.07	−0.05	0.12	−0.25	0.23	0.31	0.27	−0.34		0.05	0.129	0.080
<i>A. p. e.</i>	0.29	0.11	−0.33	−0.36	0.35	0.14	−0.60	−0.56	0.64	−0.30		0.061	0.018
<i>A. p. p.</i>	−0.49	−0.14	−0.02	−0.13	−0.03	−0.02	0.54	0.44	−0.50	0.23	−0.28		0.760
<i>A. enormis</i>	0.15	0.19	−0.05	−0.21	0.25	0.29	−0.50	−0.51	0.44	−0.27	0.36	−0.09	

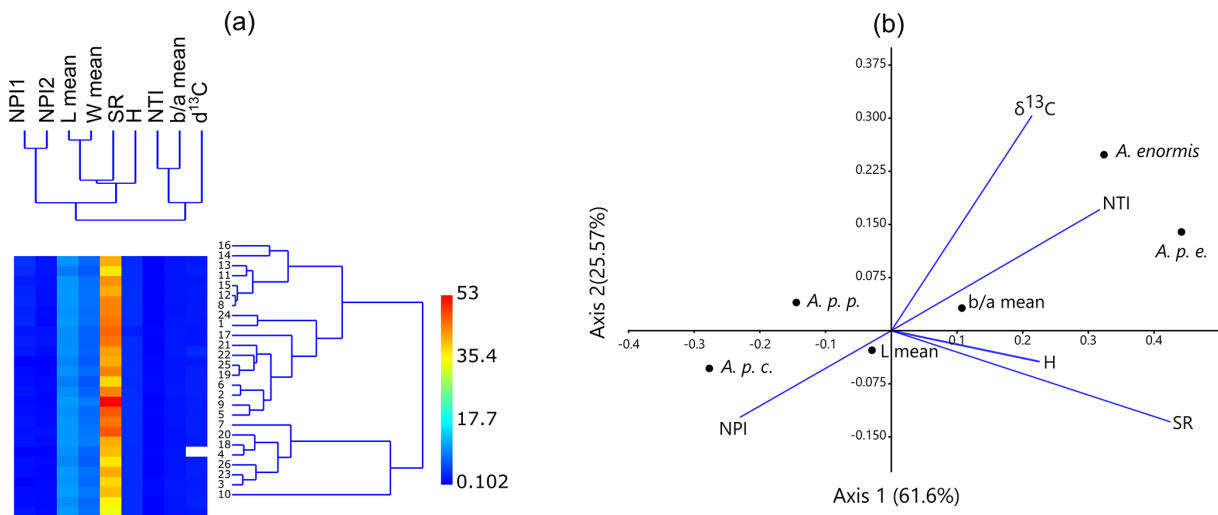


Figure 8. (a) Canonical correspondence analysis results indicating that the first axis explains 61.6 % of the variation. The second axis explains just 25.57 % of the variability. (b) Two-way cluster analysis (R-mode and Q-mode) of morphometric and environmental variables using hierarchical clustering and heatmap. Colours indicate standardised values; dendrograms show similarities among variables (top) and among samples (left). Abbreviations: NTI, nannofossil temperature index (Jain et al., 2022); NPI, nannoplankton productivity index (1: Gale et al., 2000; 2: Eshet and Almogi-Labin, 1996); *H*, Shannon index; SP, species richness; *L*, total coccolith length; *W*, total coccolith width; *b/a*, ratio between the central area width and the outer rim width.

vation can be significantly affected by diagenetic processes, which may alter their abundance and morphology and complicate their use as palaeoenvironmental indicators (e.g., Thierstein and Roth, 1991). Preservation has been assessed using a combination of semiquantitative criteria, including the relative abundance of dissolution-resistant taxa (particularly *W. barnesiae*) and direct SEM observations of the coccoliths (Fig. 3a).

W. barnesiae is considered to be highly resistant to dissolution and is commonly used as a proxy for preservation quality (Thierstein, 1981; Roth and Krumbach, 1986;

Williams and Bralower, 1995; Eeleson and Bralower, 2005). Assemblages with over 40 % *W. barnesiae* are often interpreted as diagenetically altered (Roth and Krumbach, 1986), although some authors suggest a more conservative threshold of 70 % (Williams and Bralower, 1995). In the Niobrara section, the relative abundance of *W. barnesiae* ranges between 5.5 % and 26.5 %, which falls well below these thresholds, suggesting overall moderate to good preservation.

Nevertheless, SEM analysis reveals signs of etching, overgrowth, and fragmentation in some samples, particularly in the chalkier intervals. These features are common in soft,

highly calcareous sediments and reflect typical low-grade diagenetic overprint in chalk facies, where coccolith fragments may partially dissolve and reprecipitate, contributing to crystal overgrowth. Such processes may locally affect coccolith dimensions, especially in taxa with delicate structures, and could potentially bias morphometric data.

To minimise these effects, only well-preserved specimens were selected for measurement, avoiding clearly etched or overgrown individuals. Moreover, no major shifts in preservation state are observed along the studied interval, suggesting that diagenesis is relatively homogeneous through the section. However, we acknowledge that even subtle diagenetic alteration common in chalk may influence coccolith size to some extent.

4.2 Carbon isotope stratigraphy

Carbon isotope stratigraphy has proven to be a powerful tool for correlating and dating Cretaceous sections (Jarvis et al., 2006, 2023; Thibault et al., 2016; Gale et al., 2023). Recent studies have applied this technique to refine our understanding of the Santonian–Campanian boundary, using $\delta^{13}\text{C}$ profiles from various regions (e.g., Seaford Head; Thibault et al., 2016). The present study explores $\delta^{13}\text{C}$ data from the upper Santonian to lower Campanian of the Niobrara section, showing a significant $\delta^{13}\text{C}$ trend characterised by excursions and fluctuations that can be linked to global carbon cycle perturbations and palaeoceanographic events.

The Late Santonian $\delta^{13}\text{C}$ Event (LSE; previously known as the Santonian–Campanian Boundary Event, SCBE), with a double (or even triple) positive excursion in bulk carbonate $\delta^{13}\text{C}$, provides a key correlation level between Boreal and Tethyan sections (Jarvis et al., 2006, 2023; Gale et al., 2023). It enables precise correlation of base Campanian markers, such as the FO of the calcareous nannofossil *A. parvus parvus* and the C34n/C33n magnetochron boundary (the primary marker). In this study, a double positive $\delta^{13}\text{C}$ excursion is observed before the reported C34n/C33r reversal, with an increase of +0.26‰ from 2.11‰ at 166.1 m to 2.37‰ at 170.1 m and a posterior positive excursion of +0.16‰ at 168.1 m to 2.41‰ at 170.1 m. Subsequently, a positive $\delta^{13}\text{C}$ excursion with a positive shift of +0.31‰ is observed at 174.1 m, defining the Santonian–Campanian boundary. However, comparing the data obtained in this study with those from Kita (2015) would indicate that these multiple peaks found just below the Santonian/Campanian boundary correspond to the LSE, specifically the last peak, “c”. In Niobrara, the FO of *A. parvus parvus* and the LO of *H. trabeculatus* > 7 µm are observed within this carbon isotope event (CIE). The Pilula Zone Event is characterised by a negative $\delta^{13}\text{C}$ excursion, reaching 1.8‰ in various sections (Jarvis et al., 2023). In the Niobrara section, a similar decline is observed, with values falling to 1.78‰ at 181.6 m. This constitutes the lowest recorded $\delta^{13}\text{C}$ value in the studied interval, followed by a gradual recovery. The Meeching CIE

is a broad positive excursion recorded in European sections, reaching values up to 2.3‰ (Jarvis et al., 2023). In the Niobrara section, this event appears to be represented by a peak value of 2.98‰ at 188.45 m. The carbon isotope stratigraphy and key calcareous nannofossil bioevents of the Niobrara section are shown in Fig. 9.

4.3 Calcareous nannofossil markers for the Santonian/Campanian boundary interval (SCBI)

Previous studies have shown that the FO of *A. parvus parvus* is diachronous, likely due to its attribution to different morphotypes and/or subspecies (Hancock and Gale, 1996; Gardin et al., 2001). Using nannofossil data from Filewicz (1986), Verosub et al. (1989) identified its FO near the base of Chron C33r in the Forbes Member of the Sacramento Valley, California. Similarly, Bralower et al. (1995) and Erba et al. (1995) documented its FO near the base of Chron C33r, with the latter observing it in the central and western Pacific during Ocean Drilling Program (ODP) Leg 144. Tremolada (2002) also recorded the FO at the Bottaccione section in Gubbio, Italy (GSSP), near the base of Chron C33r, later reviewed by Gardin et al. (2001) and Miniati et al. (2020). In Austria, Wolfgring et al. (2018) reported a similar FO at the Postalm section, as did Dubicka et al. (2017) in the Bocieniec section in Poland and Thibault et al. (2016) in the Seaford Head section in the UK (auxiliary sections). In contrast, Stradner and Steinmetz (1984) documented the FO of *A. parvus parvus* approximately 15 m above the base of Chron C33r in the Angola Basin during Deep Sea Drilling Program (DSDP) Leg 75. They reported *b/a* ratios between 1.0 and 1.25, which represent the lower range of observed values. This suggests that their dataset may not have included specimens with *b/a* ratios between 1.25 and 2.0, potentially overlooking older specimens closer to the base of Chron C33r (Kita et al., 2017).

The present study documents the FO of *A. parvus parvus* at 168.1 m (sample N24/8.3) for specimens with a length (*L*) ≥ 10 µm and at 166.1 m (sample N24/6.3) for specimens with *L* > 8.5 µm and for those with *L* ≥ 9 µm. Kita et al. (2017) recorded the FO at 166.3 m, aligning more closely with the FO of *A. parvus parvus* with *L* > 8.5 µm in this study. When considering specimens with *L* ≥ 10 µm, the FO occurs 5.9 m below the base of Chron C33r and approximately 7.9 m below for those with *L* > 8.5 µm.

As in Kita et al. (2017), other biohorizons (e.g., last occurrences of *H. trabeculatus* > 7 µm and *Z. biperforatus*) were found closer than the FO of *A. parvus parvus* to the magnetostratigraphically defined boundary in the Niobrara Formation. The FO of *A. parvus parvus* and the LO of *H. trabeculatus* > 7 µm mark the base of the KN21 Zone of Bergen and Sikora (1999), while the LO of *Z. biperforatus* is positioned within Zone KN21. Bergen and Sikora (1999) placed this zone in the early Campanian, suggesting that these biohori-

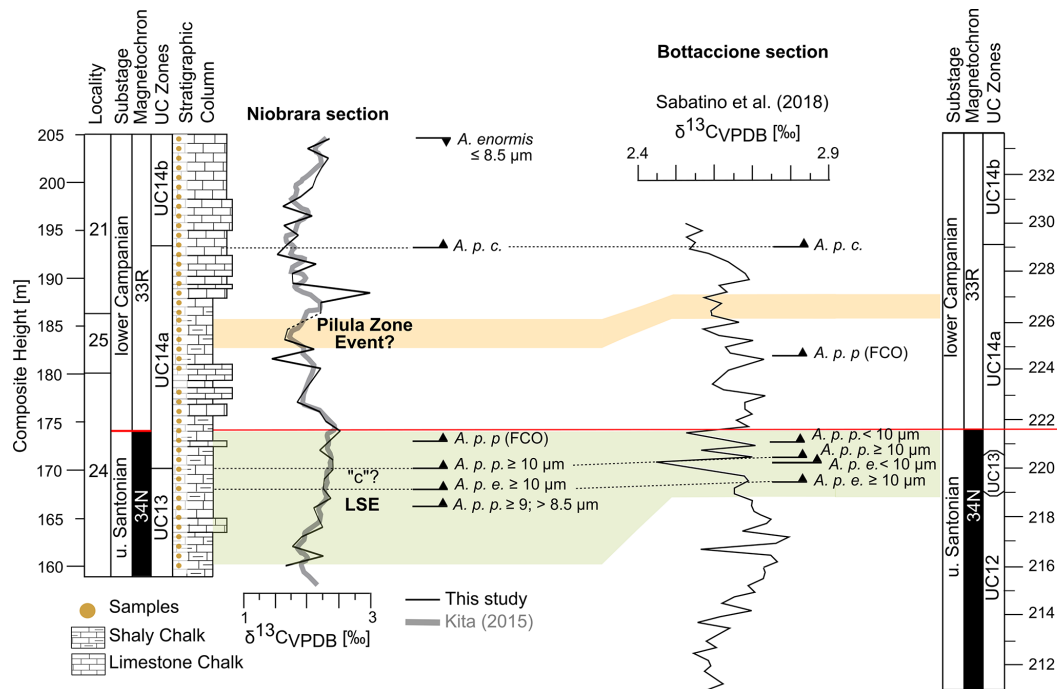


Figure 9. Carbon isotope stratigraphy, *Aspidolithus* bioevents, and carbon isotope values from this study (black curve) and from Kita (2015; grey curve) compared to the $\delta^{13}\text{C}$ curved from the Bottaccione section in Italy (Sabatino et al., 2018) and *Aspidolithus* bioevents (Miniati et al., 2020). Isotope events (LSE, Late Santonian $\delta^{13}\text{C}$ Event; Pilula Zone Event) were defined by Jarvis et al. (2023) and Gale et al. (2023).

zons occurred later in the North Sea compared to the Western Interior Basin (Kita et al., 2017).

Tethyan markers, such as *C. obscurus*, its wide morphotype, curved *L. cayeuxii*, and *C. verbeekii* (e.g., Wolfgring et al., 2018) were absent in the study section. In this study, *C. obscurus* and *L. cayeuxii* are missing in the lower part of the section, first appearing at 178.1 m (sample N24/18.3) and 183.6 m (sample N25/3.3), respectively. Additionally, this study identifies four new regional events for this section: (1) an acme of *R. crenulata* (7.84 %) at 174.1 m (sample N24/14.3); (2) the lowest peak in the relative abundance of *C. ehrenbergii* (0.63 %) at 174.1 m (sample N24/14.3), just 0.1 m above the base of C33r; (3) the FCO of *A. parvus* at 173.1 m (sample N24/13.3), just 0.9 m below the base of C33r; and (4) the LO of *A. enormis* ($L \leq 8 \mu\text{m}$) at 202.45 m (sample N21/15.3).

4.4 Palaeoenvironmental indexes vs. calcareous nannofossil abundances

The correlation analysis of relative abundances of calcareous nannofossil with palaeoenvironmental nannofossil indexes (NTI and NPI) reveals patterns that align with previous studies. Our findings, using the Pearson correlation coefficient (PCC), highlight significant relationships between certain species and temperature or productivity fluctuations, supporting their potential as additional palaeoenvironmental indicators.

The NPI of Gale et al. (2000) is based on the relative abundance of the high-productivity indicator species *Biscutum* spp. (e.g., Roth and Krumbach, 1986; Watkins, 1989; Erba, 1992; Erba et al., 1992; Mutterlose et al., 2005) and *Zeugrhabdotus* spp. (e.g., Roth and Krumbach, 1986; Watkins, 1989; Erba, 1992; Erba et al., 1992; Mutterlose et al., 2005; Linnert et al., 2011a; Linnert and Mutterlose, 2015) and the low-productivity indicator *W. barnesiae* (Watkins and Self-Trail, 2005; Hardas and Mutterlose, 2007). The NPI of Eshet and Almogi-Labin (1996) is based on the relative abundance of the same high-productivity indicator species, *Biscutum* spp. and *Zeugrhabdotus* spp., vs. low-productivity indicators, *Eiffellithus* spp. (Thierstein, 1981; Watkins, 1992; Watkins and Self-Trail, 2005), *Lithraphidites* spp., *Microrhabdulus decoratus*, *Prediscosphaera* spp., and *Stauroolithites* spp. On the other hand, the NTI based on Jain et al. (2022) is calculated from warm-water indicators (*W. barnesiae*; Thierstein, 1981; Perch-Nielsen, 1985; Doeven, 1983; Erba et al., 1992; Watkins et al., 1996) vs. cooler- or cold-water species, such as *A. cymbiformis* (Thierstein, 1981; Watkins, 1992; Lees, 2002), *L. cayeuxii* (Thierstein, 1976), *R. anthophorus* (Thierstein, 1981; Linnert et al., 2011a), and *M. staurophora* (Doeven, 1983; Watkins, 1992; Watkins and Self-Trail, 2005). Therefore, species directly included in both indexes, such as *W. barnesiae*, show inherently strong correlations.

The genus *Biscutum* shows a strong positive correlation with NPI ($r = 0.71$, $p = 0.001$) and a negative correlation with NTI ($r = -0.43$, $p = 0.005$). This aligns with its recognition as a marker of mesotrophic to eutrophic conditions, indicative of high-productivity settings (e.g., Roth and Krumbach, 1986; Watkins, 1989; Erba, 1992; Erba et al., 1992; Mutterlose et al., 2005). The observed negative correlation with NTI suggests that *Biscutum* spp. might also be linked to cooler water conditions. *W. barnesiae* shows a strong negative correlation with NPI ($r = -0.83$, $p = 2.60 \times 10^{-9}$) and a strong positive correlation with NTI ($r = 0.86$, $p = 6.94 \times 10^{-10}$). At first glance, this supports its widely accepted role as an indicator of warm oligotrophic waters, as noted in multiple studies (Thierstein, 1981; Perch-Nielsen, 1985; Doeven, 1983; Erba et al., 1992; Watkins et al., 1996). However, since this species was explicitly included in the NTI as the (only) warm-water indicator and in the NPI as one of the low-productivity indicators, its strong correlation with these indexes is expected rather than an independent confirmation for its palaeoecological significance.

The genus *Corollithion* spp. displays a moderate positive correlation with NPI ($r = 0.32$, $p = 0.04$) and a negative correlation with NTI ($r = -0.44$, $p = 0.03$). *C. obscurus* also exhibits a positive correlation with NPI ($r = 0.61$, $p = 1.01 \times 10^{-5}$) and a negative correlation with NTI ($r = -0.61$, $p = 1.32 \times 10^{-5}$). This suggests that both *Corollithion* spp. and *C. obscurus* may be linked to higher productivity and cooler environments.

4.5 Niobrara vs. Loibichl assemblages

The calcareous nannofossil assemblages from the Niobrara section and the Loibichl section (Austria; Granero et al., 2024) show notable differences in calcareous nannofossil distribution. Niobrara is characterised by higher abundances of *B. ubiquem*, *C. ehrenbergii*, *E. eximius*, and *Pre-discosphaera columnata*, suggesting a mesotrophic environment with fluctuating productivity. In contrast, Loibichl shows a higher abundance of *C. obscurus* and *L. cayeuxii*, indicating a more stable, oligotrophic setting characteristic of the Tethyan realm. Some taxa appear to have regional distributions, with *C. obscurus*, *L. cayeuxii*, and *Zeugrhabdotus embergeri* being more abundant at Loibichl and Postalm, suggesting palaeoceanographic influences on species distribution. A distinct set of taxa is more frequently found in Niobrara, with species such as *Biscutum zulloi*, *Corollithion madagascariensis*, *Corollithion exiguum*, *Helicolithus anceps*, and *Zeugrhabdotus praesigmoides* being present in this section but absent or very rare in Loibichl. On the other hand, *Orastrum campanensis* has only been identified in Loibichl (Table D1). Despite these comparisons, direct correlation between the two sections remains challenging due to the lower sampling resolution at Loibichl, which complicates precise temporal assignments. This limitation hinders a robust stratigraphic alignment with Niobrara, preventing a

detailed assessment of potential synchronicity or diachronicity in species distribution and morphometric trends.

4.6 Biometry vs. palaeoenvironmental indexes

The morphometric analysis of *Aspidolithus* spp. from the Smoky Hill Member of the Niobrara Formation suggests that its morphometric variation is influenced by palaeoenvironmental factors, particularly by surface water temperature. Our results indicate a significant positive correlation between the ratio of the central area width to the outer rim width (b/a) and the nannofossil temperature index (NTI), meaning that higher temperatures are associated with a larger proportion of the central area relative to the outer rim. These findings are consistent with those reported in Granero et al. (2024), who also demonstrated a similar relationship between morphometric variation in *Aspidolithus* and palaeoenvironmental conditions, reinforcing the hypothesis that temperature plays a key role in shaping its morphology. This observation “aligns” with the current understanding of heterococcolith biomineralisation. Studies suggest that coccolith formation typically starts with the nucleation of a proto-coccolith ring around the edge of an organic base plate, followed by the growth of calcite crystals outward and inward to form the final structure (Young et al., 1992, 2004). In some cases, additional nucleation and calcification occur in the central area at a later stage (Young et al., 1999, 2004). Given this sequence, it is plausible that temperature influences the rate or extent of calcification across the entire coccolith, leading to a greater expansion of the central area compared to the outer ring. Alternatively, temperature may have affected the cellular regulation of calcification, resulting in morphological differences in response to environmental conditions.

Additionally, a significant negative correlation was found between the total coccolith length (L) and species richness (SR), indicating that *Aspidolithus* spp. in this section tends to be smaller in samples with higher species richness. This suggests that greater species richness may have led to increased ecological competition, potentially limiting the resources available for *Aspidolithus* spp. calcification and resulting in reduced coccolith size. Another possible explanation is that periods of higher species richness corresponded to environmental conditions that were more favourable for a diverse species assemblage but less optimal for the growth of *Aspidolithus* spp. This pattern could reflect shifts in nutrient availability, where a more diverse community may have partitioned resources more efficiently, leading to smaller individual coccoliths. Alternatively, it may be related to different ecological strategies, where *Aspidolithus* spp. exhibited a trade-off between size and reproductive success in response to changing competition dynamics. Interestingly, no significant correlation was found between the NPI and the coccolith length. This suggests that the coccolith size was not directly controlled by variations in surface water productivity and instead may have been more biologically regulated.

The absence of a clear link between productivity and coccolith length further supports the idea that temperature and ecological interactions were the primary factors influencing the morphology of *Aspidolithus* spp. These findings reinforce the hypothesis that *Aspidolithus* responded dynamically to temperature fluctuations and ecological pressures. The significant correlation between morphometric parameters and NTI, along with the observed relationship between coccolith size and species richness, suggests that *Aspidolithus* species may be useful in refining palaeoenvironmental reconstructions in the Western Interior Seaway during the Late Cretaceous.

The apparent influence of temperature on changes in the b/a ratio raises an important question regarding the FO of *A. parvus constrictus* across different sections. If the FO of this form is diachronous, it would provide further support for the hypothesis that its morphological shift is primarily controlled by palaeoenvironmental parameters (regional influence), rather than reflecting a true evolutionary event. Conversely, if its FO is observed to be synchronous across multiple sections, this would suggest a more biologically intrinsic process, potentially linked to evolutionary changes within the lineage. Resolving this issue requires further high-resolution biostratigraphic and biometric studies to determine whether the FO of *A. parvus constrictus* is a reliable chronostratigraphic marker or an environmentally driven morphological response, and how the morphological changes continue upwards up to the early Maastrichtian, when *Aspidolithus* went extinct. However, the extinction of this genus is not globally synchronous, several studies have reported diachronous LO, and further work is needed to better constrain its stratigraphic range and potential regional differences (Wise, 1983; Burnett, 1998; Linnert et al., 2014; Thibault et al., 2016). The comparison between the Niobrara and Bottaccione sections (Fig. 9) further refines the understanding of morphometric variation in the *A. parvus* group. The FOs of *A. parvus parvus*, *A. parvus expansus*, and *A. parvus constrictus* appear to be synchronous in both sections, suggesting that their development was not driven by local palaeoenvironmental conditions but rather reflects an evolutionary change occurring on a global scale, probably driven by a global cooling trend from the Late Santonian to the lowermost Campanian (Wolfgring et al., 2018). This clearly challenges the previous interpretation that b/a ratio variations were primarily controlled by temperature fluctuations. Instead, the observed synchronicity supports the hypothesis that these morphotypes represent stages within an evolutionary continuum rather than independent responses to environmental shifts. While temperature may still play a role in shaping subtle morphological trends, the strong alignment of FO events across geographically distant sections indicates that evolutionary processes likely drive the emergence of these morphotypes. However, in the western Tethyan Bottaccione section, Miniati et al. (2020) reported that the FO of *Aspidolithus* specimens with coccolith length $< 10\ \mu\text{m}$ (*A. parvus* “small” sensu Gardin et al., 2001, or *A. enormis*) occurs stratigraphically above the FO of

larger specimens ($> 10\ \mu\text{m}$). This pattern is unexpected, as it contradicts the typical evolutionary sequence where smaller forms are assumed to precede the larger ones. This discrepancy might reflect changing sedimentation rates, taphonomic biases, or a more complex evolutionary history than previously considered. Further detailed biostratigraphic work is needed to determine whether this inversion is a true signal of morphological evolution or a consequence of local depositional and preservational factors.

This finding highlights the need for reconsidering the taxonomic subdivision of *A. parvus* and suggests that b/a ratio variations alone may not be sufficient for defining discrete subspecies. However, despite its limitations as a taxonomic criterion, the b/a ratio retains high biostratigraphic value in defining standard nannofossil (sub)zones (Burnett, 1998). Its gradual trends in different sections provide a useful tool for correlation, even if it does not strictly delineate evolutionary boundaries. The progressive decrease in b/a during the early Campanian, observed across multiple sections, suggests that it can still serve as a reliable indicator for relative dating and stratigraphic alignment. Further high-resolution morphometric and biostratigraphic studies across multiple sections are required to clarify the relative contribution of environmental and evolutionary drivers in shaping *Aspidolithus* morphology.

4.7 Taxonomic challenges in the *Aspidolithus* group

The taxonomic subdivision within the *Aspidolithus parvus* group (also referred to as *Broinsonia parva* (Stradner) Bukry, a name currently in use in Nannotax3 as of 8 April 2025) has traditionally relied on morphometric parameters, particularly the ratio between the central area width and the outer ring width (b/a ; Wise, 1983). However, our results from the Niobrara section suggest that this parameter alone does not follow precisely the b/a criteria as defined by Wise (1983) (*A. parvus constrictus* $b/a < 1$, *A. parvus parvus* b/a 1–2, *A. parvus expansus* $b/a > 2$). Our data indicate a general increase in the coccolith length trend and a general decrease in the b/a ratio trend of *A. parvus parvus* specimens, consistent with previous records (Lauer, 1975; Wise, 1983; Gardin et al., 2001; Kita et al., 2017; Miniati et al., 2020; Granero et al., 2024).

Our mixture analysis identified three potential groups within *A. parvus* at Niobrara ($b/a < 1.59$, $1.59 \leq b/a < 2.25$, $b/a \geq 2.25$) and Postalm ($b/a < 1.59$, $1.59 \leq b/a < 2.19$, $b/a \geq 2.19$) sections. The overlap between the groups across sections suggests a consistent pattern that may reflect underlying population-level structure. Although the mixture model mathematically defines clusters based on variance, these groupings may correspond to population-level differentiation rather than discrete taxonomic units. Further interpretation within a framework of quantitative population genetics may help to evaluate whether the observed morphometric distributions reflect intra-specific variation, ecophe-

notypic response, or incipient divergence. This supports the hypothesis that the b/a ratio is influenced by palaeoenvironmental factors rather than representing a stable diagnostic feature of subspecies. If these groups represented truly distinct subspecies, in the sense of the International Code of Zoological Nomenclature (ICZN, 1999), we might expect clearer separation across different sections, which does not appear to be the case.

The differentiation between *A. enormis* and *A. parvus* based on coccolith length (L) in the Niobrara, Loibichl (Granero et al., 2024), and Postalm (Wolfgring et al., 2018) sections yielded results that diverge from those of previous studies. For instance, without further statistical analyses, Wolfgring et al. (2018) rather arbitrarily defined *A. enormis* as $L < 9\mu\text{m}$, and Gardin et al. (2001) and Miniati et al. (2020) used a $10\mu\text{m}$ threshold. In contrast, the mixture analysis of L conducted in this study suggests significantly lower thresholds for separating *A. enormis* from *A. parvus*: (1) $8.1\mu\text{m}$ in the Niobrara section, (2) $8.3\mu\text{m}$ at Loibichl, and (3) $8.4\mu\text{m}$ at Postalm. Considering the highest value obtained ($8.4\mu\text{m}$), and accounting for a possible light microscope measurement error of $\pm 0.1\mu\text{m}$, this study proposes a revised and statistically supported threshold of $8.5\mu\text{m}$ to differentiate *A. enormis* from *A. parvus*. This value is considerably lower than those suggested in earlier works and reflects a more consistent and data-driven approach to species delimitation. Such discrepancies from author to author highlight the lack of consensus in defining taxonomic size limits within this group and may impact stratigraphic correlations. The variability in thresholds could be attributed to palaeoenvironmental factors influencing coccolith morphology or differences in measurement methodologies and statistical data evaluation among studies. Standardising morphometric classification may be key to improving biostratigraphic resolution and comparability between different geological records. Since these thresholds have been applied in different regions (Tethys vs. Western Interior Seaway), it is crucial to assess whether they reflect real biological differences or simply methodological variations. Using mixture analysis on independently (from this study) derived data from the Postalm section (Wolfgring et al., 2018; see Supplement) showed similar results to the Niobrara and Loibichl sections, with a threshold at approximately $8.5\mu\text{m}$. In both Niobrara and Postalm, the statistical test confirms that the differences between the groups are highly significant, meaning that the separation based on L between *A. enormis* and *A. parvus* is not arbitrary. The clusters are real statistical groups, at least within each section individually.

Similar challenges in defining subspecies within the *A. parvus* group have been highlighted in previous studies, where morphometric parameters were used to establish biostratigraphic schemes (e.g., Stradner and Steinmetz, 1984; Almogi-Labin et al., 1991; Gardin et al., 2001; Kita et al., 2017; Dubicka et al., 2017; Wolfgring et al., 2017, 2018; Miniati et al., 2020). However, the reliance on these fea-

tures is complicated by their high variability and possible ecophenotypic plasticity due to changing natural conditions. Moreover, environmental influences, particularly sea surface temperature, appear to play a key role in the morphometric variation in *A. parvus*, as observed in our dataset, where a positive correlation was found between NTI and the b/a ratio. This raises concerns about the stability of taxonomic subdivisions when applied to different stratigraphic sections and palaeoceanographic settings, suggesting that some morphotypes traditionally considered distinct subspecies may instead represent phenotypic variations of a single, environmentally responsive species.

On the other hand, one of the main challenges in biostratigraphic interpretations based on the distribution of *A. parvus* subspecies is the continuity and overlap of their morphometric parameter ranges, particularly the b/a ratio. Because the thresholds between subspecies are defined by consecutive intervals, even small measurement errors can lead to incorrect taxonomic assignments. For instance, the distinction between *A. parvus expansus* ($b/a < 2$) and *A. parvus parvus* (b/a 1–2) becomes critical because *A. parvus expansus* appears stratigraphically lower (Turonian according to Burnett, 1998) than *A. parvus parvus*. This proximity and overlap can cause confusion, particularly if the b/a ratio is not precisely determined, potentially leading to errors in the identification of the base of biozones CC18a or UC14a. Since the FO of *A. parvus parvus* is the primary marker for defining the base of these biozones, distinguishing between these two subspecies with accuracy is crucial to avoid misinterpretations in biostratigraphic correlations. Future taxonomic work should incorporate high-resolution morphometric datasets and statistical approaches to assess whether these forms truly warrant separate taxonomic status or if they should be considered part of a continuous spectrum within *A. parvus*.

However, a limitation in the biostratigraphic application of these morphometric findings is the absence of other sections where a detailed and statistically significant biometric analysis of the *Aspidolithus* group has been conducted. Currently, precise (bioevent) correlation between sections remains unattainable due to the lack of comparable biometric datasets behind subspecies attributions across multiple locations. This gap highlights the necessity of future work aimed at integrating high-resolution biometric data from additional sections to establish a more robust framework for biostratigraphic correlation. Without such comprehensive studies, distinguishing true synchronous biostratigraphic events from local environmental influences remains challenging.

In addition to biometric parameters, we recognise that other morphological parameters may improve the reproducibility and clarity of species and subspecies identifications within the *Aspidolithus* group. One feature we consider potentially valuable is the variation in the structure of the outer rim, particularly the width of the outermost cycle of the distal shield (see Crux, 1982, Fig. 5.3). This element is clearly visible under crossed nicols due to its distinct

birefringence and may provide a complementary criterion to the b/a ratio when differentiating morphotypes. Among the three traditional *A. parvus* subspecies, *A. parvus constrictus* appears to be the most consistently recognisable form, even though transitions between groups remain gradual. Its lower b/a values and frequent association with the early Campanian make it a practical and relatively robust marker across different sections and studies.

Biometric measurements on calcareous nannofossils remain challenging, especially when comparing data from different studies. Discrepancies may arise from differences in measurements tools, calibration settings, magnification, and even the type of microscope used (LM, SEM, or transmission electron microscope (TEM)), as already noted by Stradner and Steinmetz (1984). In earlier works, such as Gardin et al. (2001) and the Postalm data by Wolfgring et al. (2018) used in this study, measurements were performed directly through the microscope without digital images, and different techniques and calibrations were applied. In our case, all measurements of SHC were obtained from calibrated digital images using JMicrovision, with an estimated error of $\pm 0.1 \mu\text{m}$. While these methodological differences are often subtle, they may still influence morphometric parameters such as the b/a ratio, particularly when used for taxonomic purposes. This highlights the need to clearly report measurement protocols and to move towards a standardised approach that enhances reproducibility and interstudy comparability. These methodological aspects are not the only source of variability between datasets. Geological context and preservation also play a role. For example, the indurated limestones at Bottaccione presents different preservation conditions compared to the marly chalks of the Niobrara section, which may affect the visibility of the morphological features. Moreover, differences in sampling resolution, counting procedures, and the overall taxonomic framework applied in earlier and more recent studies (e.g., Gardin et al., 2001; Miniati et al., 2020) likely contributed to the observed discrepancies. While such comparisons remain valuable for recognising broader patterns, caution is needed when interpreting detailed biometric thresholds across studies based on different methodological approaches and settings.

Finally, we also considered the potential role of lithology and preservation in influencing the biometric dataset. The preservation state of the Niobrara samples was evaluated using both LM and SEM observations. Most samples were regarded as moderately to well preserved based on the visibility of key structures, such as the central area and distal shield, and the lack of higher frequencies of diagenesis-resistant taxa. Nonetheless, occasional signs of etching, overgrowth, and fragmentation were noted (see Fig. 3), which are common features in chalk-rich lithologies. While these did not hinder taxonomic identification or measurement in most cases, it is important to acknowledge that chalk facies are prone to microdissolution and recrystallisation processes driven by compaction, which may affect coccolith

size and structure. In contrast, sections such as Bottaccione, composed of indurated limestones, are subject to a different type of diagenetic overprint, where features may be obscured by pervasive calcite recrystallisation. These lithological and taphonomic differences may partly explain observed biometric variability between sections and highlight the need for caution when comparing data across different depositional and diagenetic settings. Future work would benefit from integrating more systematic and possibly quantitative preservation assessments to better constrain the impact of these factors on morphometric parameters.

5 Conclusions

This study highlights the importance of rigorous morphometric analyses in palaeontological taxonomy and bioevent correlation. Our results from the Smoky Hill Member of the Niobrara Formation and two Tethyan sections reveal that the morphometric variability observed in the *Aspidolithus parvus* group is influenced by both evolutionary and palaeoenvironmental factors. While morphometric analysis in Loibichl, Postalm, and Niobrara suggests that the b/a ratio was primarily controlled by temperature fluctuations, the observed synchronicity of FOs across geographically distant sections (WIS vs. Tethys) supports the idea that these morphotypes represent stages within an evolutionary continuum rather than independent environmental responses. However, the discrepancy observed at Bottaccione, where *Aspidolithus* specimens with $L < 10 \mu\text{m}$ (*A. enormis*) appear later than those with $L > 10 \mu\text{m}$ (*A. parvus*), contrary to the trends in Niobrara and Postalm, raises new questions about the controls on morphometric variations.

The statistically consistent threshold of $8.5 \mu\text{m}$ for differentiating *A. enormis* from *A. parvus* across Postalm, Loibichl, and Niobrara sections reinforces its reliability as a biostratigraphic marker for the Santonian–Campanian boundary. Our morphometric data refine former arbitrary subspecies definitions to the following results: *Aspidolithus parvus constrictus* $b/a < 1.6$, *Aspidolithus parvus parvus* $1.6 \leq b/a < 2.2$, *Aspidolithus parvus expansus* $b/a \geq 2.2$.

Future research should employ high-resolution morphometric datasets and advanced statistical tools to explore the potential for taxonomic differentiation. Standardising measurement methodologies across multiple sections and integrating palaeoenvironmental proxies will be crucial for addressing taxonomic challenges and enhancing biostratigraphic resolution in the Upper Cretaceous. This study highlights the dynamic interplay between environmental conditions and morphological expression in calcareous nannofossils, advocating for a more integrative and methodologically consistent approach to palaeontological taxonomy. This pattern could be the result of differences in sedimentation rates, taphonomic biases, or an evolutionary scenario that is more complex than previously assumed. Resolving this issue will

require further high-resolution biostratigraphic and morphometric studies across multiple basins.

Despite these uncertainties, the b/a ratio retains strong biostratigraphic value. Even if it does not delineate stable taxonomic boundaries, its gradual change through time provides a useful tool for correlation and relative dating. Similarly, the coccolith length (L) remains the most reliable morphometric criterion for distinguishing *A. enormis* from *A. parvus*, with a statistically supported threshold at $\sim 8.5\ \mu\text{m}$. Standardising these morphometric classifications across different sections will be key to refining biostratigraphic resolution in the Upper Cretaceous and improving global stage correlations.

Future research should integrate detailed morphometric, biostratigraphic, and palaeoenvironmental proxies to better understand the evolutionary and ecological dynamics of *Aspidolithus* and its role in Cretaceous nannoplankton assemblages.

Appendix A: Systematic palaeontology

Order **Arkhangelskiales** Bown & Hampton in Bown and Young (1997)

Family Arkhangelskiellaceae Bown & Hampton, 1997 in Bown & Young, 1997

Genus *Aspidolithus* Noël, 1969

Type species: *Aspidolithus angustus* Noël, 1969

Description. Elliptical placolith composed of two rims (inner and outer) with axial sutures clearly visible under cross-polarised light. The central area is spanned by a plate composed of tile-like elements arranged symmetrically. The inner cycle typically shows higher birefringence than the outer rim. In distal view, both cycles are visible; in proximal view, usually only the outer cycle is observed.

Remarks. Following Lauer (1975), Perch-Nielsen (1985), Gardin et al. (2001), and Miniati et al. (2020), *Aspidolithus* is differentiated from *Broinsonia* by the presence of solid plates in the central area rather than a distinct cross. The *Aspidolithus parvus* lineage includes several morphotypes that vary in central area–margin ratio (b/a ratio; Wise, 1983). Subspecies such as *A. parvus parvus*, *A. parvus constrictus*, and *A. parvus expansus* have previously been proposed and are formally identified in this study based on the b/a ratio. However, our morphometric analysis reveals a continuous distribution in these parameters, lacking a clear bimodal separation. Therefore, we interpret them as morphological variants within a single, variable species. In contrast, we recognise two distinct species based on total length: *A. parvus*, with a total length $> 8.5\ \mu\text{m}$, and *A. enormis*, distinguished by significantly smaller coccoliths ($< 8.5\ \mu\text{m}$). This separation is supported by biometric measurements in both the Loibichl (Granero et al., 2024) and Niobrara sections.

Aspidolithus enormis (Shumenko, 1968)

1968 *Arkhangelskiella enormis* – Shumenko, p. 33, pl. 1, Figs. 1–3.

1969 *Broinsonia bevieri* – Bukry, p. 21, pl. 1, Figs. 8–12.

1969 *Aspidolithus angustus* – Noël, p. 196, pl. 1, Figs. 1a–c, 2a, b.

Remarks. This taxon corresponds to the smallest specimens observed in our dataset and can be separated statistically from *A. parvus* by total length alone. In both the Loibichl and Niobrara sections, these specimens occur consistently $\leq 8.5\ \mu\text{m}$ threshold, showing a stable biometric expression across different depositional settings. Previous studies have proposed different thresholds to distinguish *A. enormis* from *A. parvus* based on total coccolith length. Shumenko (1968) reported $7\text{--}8\ \mu\text{m}$, Bukry (1969) noted a diameter of up to $7.8\ \mu\text{m}$, Gardin et al. (2001) used a $10\ \mu\text{m}$ threshold, and Linnert et al. (2014) and Wolfgring et al. (2018) applied a $9\ \mu\text{m}$ cutoff. Our results show no significant overlap in the length distribution with *A. parvus*, supporting its interpretation as a distinct species. The size of the central area is variable, although no statistically significant differences have been found in the b/a ratio to justify separation into distinct morphotypes. The absence of a perforate plate may be influenced by preservation, and distinction from *B. furtiva* remains tentative, as discussed by Thierstein (1974). In the studied Niobrara section (this work), *A. enormis* specimens display a total length varying between 5.5 and $8.5\ \mu\text{m}$ with no correlation with the stratigraphic position.

Aspidolithus parvus constrictus (Hattner et al., 1980) Perch-Nielsen, 1984

1980 *Broinsonia parva constricta* – Hattner, Wind and Wise, p. 23, pl. 2, Figs. 1–3, 5–8.

1984 *Aspidolithus parvus constrictus* – Perch-Nielsen, p. 43.

Remarks. Originally defined by Hattner et al. (1980) as having a b/a ratio < 1 and being the youngest subspecies in the *Aspidolithus parvus* lineage. In our study, this morphotype could not be confidently distinguished in the Loibichl section due to the continuity of b/a values and the absence of clear statistical separation. This may be related to the more limited temporal coverage and lower sample resolution in the Loibichl section. However, in the Niobrara and Postalm sections, specimens with $b/a < 1.6$ were considered consistent with *A. parvus constrictus*. The stratigraphic distribution of this morphotype shows consistency, suggesting a potential biostratigraphic relevance despite the biometric overlap. In the Niobrara section, *A. parvus constrictus* has a length varying between 8.7 and $10.8\ \mu\text{m}$.

Aspidolithus parvus expansus (Wise and Watkins in Wise, 1983) Perch-Nielsen, 1984

1983 *Broinsonia parva expansa* – Wise and Watkins in Wise, p. 506, pl. 9, Figs. 1–5; pl. 10, Figs. 5–9; pl. 11, Figs. 1–9.

1984 *Aspidolithus parvus expansus* – Perch-Nielsen, p. 43.

Remarks. Wise and Watkins in Wise (1983) described *A. parvus expansus* as a subspecies of *A. parvus* with a wide central area ($b/a \geq 2$) and two or more perforations per quadrant aligned along the major and minor axes. Although *A. parvus expansus* was identified in Loibichl samples, biometric analysis did not allow statistical separation from other subspecies. In contrast, in the Niobrara and Postalm sections, specimens with $b/a \geq 2.2$ were differentiated and appear consistent with this morphotype. Total coccolith length in Niobrara section ranges from 8.5 to 13 μm , showing a gradual increase up-section. Its potential confusion with *A. enormis*, due to its single differentiation based on a consecutive cut-off value in total coccolith length, limits its biostratigraphic utility.

Aspidolithus parvus parvus (Stradner, 1963) Noël, 1969

1963 *Arkhangelskiella parva* – Stradner, p. 10, pl. 1,

Figs. 3, 3a.

1969 *Aspidolithus parvus* – Noël, p. 196, pl. 1, Figs. 3–4.

Remarks. Characterised by an intermediate central area with b/a values ranging from 1 to 2. It is characterised by a perforate plate divided by axial sutures, with perforations aligned along the ellipse axes. In the latest Santonian, *A. parvus parvus* started to evolve from *A. parvus expansus* with a reduction in the central area width. In our samples, specimens with b/a values between 1.6 and 2.2 and total length $\geq 8.5 \mu\text{m}$ are abundant in both Loibichl and Niobrara. However, biometric analysis shows a continuous distribution, and the morphotype does not form a statistically distinct cluster. Our data show that coccolith length ranges between 8.5 and 13.5 μm , with a general upward increase in the Niobrara section.

Figure 1 consists of two panels, (a) and (b), showing stratigraphic correlation and relative abundance of foraminifera species. Both panels share a common stratigraphic column on the left, which includes localities, substage, magnetostratigraphic zones, and UC zones. The composite height in meters (m) is indicated on the y-axis, ranging from 160 to 205 m. A red dashed line marks the boundary between substage 21 (UC14b) and substage 25 (UC14a).

Panel (a): Shows the lower Campanian stage. The stratigraphic column includes localities 21, 25, and 24. The magnetostratigraphic zones are 33R, 34N, and 34R. The UC zones are UC14b, UC14a, and UC13. The relative abundance profiles are plotted for the following species: *Aspidolitus* spp., *Biscutum* spp., *Ammuellerella* spp., *Chiastozygus* spp., *Corollithion* spp., *C. ehrenbergii*, *D. ignotus*, *Eiffellithus* spp., and *G. obliquum*.

Panel (b): Shows the lower Campanian stage. The stratigraphic column includes localities 21, 25, and 24. The magnetostratigraphic zones are 33R, 34N, and 34R. The UC zones are UC14b, UC14a, and UC13. The relative abundance profiles are plotted for the following species: *Helicolithus* spp., *Lucianorhabdus* spp., *Micronorhabdus* spp., *Micula* spp., *Prediscosphaera* spp., *R. anthophorus*, *Reticapsa* spp., *T. orionatus*, *Watznaueria* spp., and *Zeughrabdotus* spp.

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Appendix C

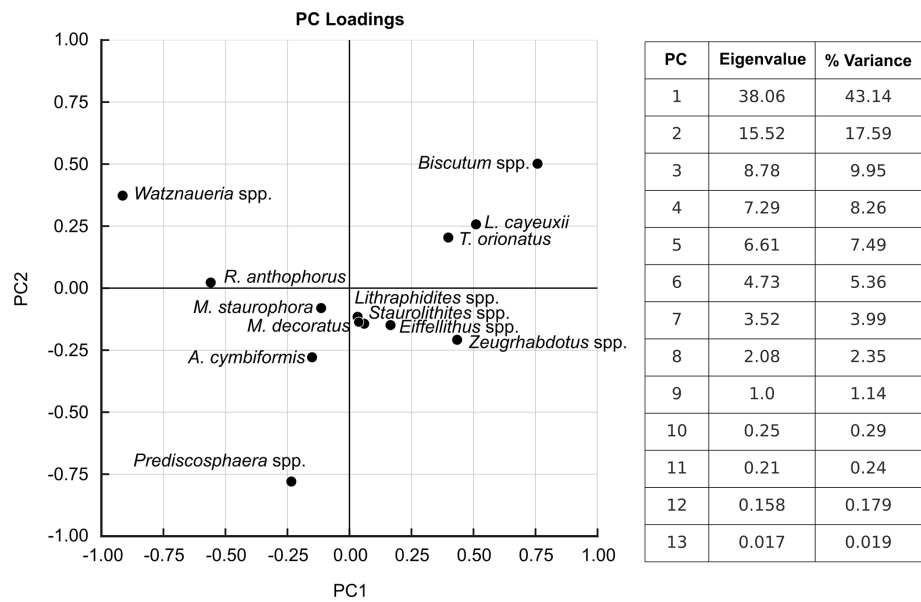


Figure C1. Principal component analysis (PCA) of selected calcareous nannofossil taxa used in the NTI and NPI, based on relative abundances. The scatterplot shows the distribution of taxa along the first two principal components (PC1 and PC2). Eigenvalues and percentage of variance explained by each principal component are shown in the table.

Appendix D

Table D1. List of calcareous nannofossil taxa recognised in this study and in Granero et al. (2024).

Species	References	Loibichl	Niobrara
<i>Acuturris scotus</i>	(Risatti) Wind & Wise in Wise & Wind	X	X
<i>Ahmuellerella octoradiata</i>	(Górka) Reinhardt	X	X
<i>Ahmuellerella regularis</i>	(Górka) Reinhardt & Górka	X	X
<i>Amphizygus brooksii</i>	Bukry	X	X
<i>Arkhangelskiella cymbiformis</i>	Vekshina	X	X
<i>Aspidolithus enormis</i>	Shumenko	X	X
<i>Aspidolithus parvus constrictus</i>	(Hattner et al.) Perch-Nielsen	X	X
<i>Aspidolithus parvus expansus</i>	(Wise and Watkins in Wise) Perch-Nielsen	X	X
<i>Aspidolithus parvus parvus</i>	(Stradner) Noël	X	X
<i>Biscutum coronum</i>	Vekshina	X	X
<i>Biscutum ubiquem</i>	Brace and Watkins	X	X
<i>Biscutum zulloi</i>	Covington		X
<i>Braarudosphaera bigelowii</i>	(Gran and Braarud) Deflandre	X	
<i>Broinsonia signata</i>	(Noël) Noël	X	X
<i>Calculites obscurus</i>	(Deflandre) Prins & Sissingh in Sissingh	X	X
<i>Calculites ovalis</i>	(Stradner) Prins & Sissingh in Sissingh	X	X
<i>Chiastozygus amphipons</i>	(Bramlette and Martini) Gartner		X
<i>Chiastozygus bifarius</i>	Bukry	X	X
<i>Chiastozygus litterarius</i>	(Górka) Manivit	X	X
<i>Chiastozygus synquadriperforatus</i>	Bukry	X	X
<i>Corollithion exiguum</i>	Stradner		X
<i>Corollithion madagascariensis</i>	Perch-Nielsen		X
<i>Corollithion signum</i>	Stradner		X
<i>Cretarhabdus conicus</i>	Bramlette & Martini	X	X
<i>Cribrosphaerella circula</i>	(Risatti) Lees		X
<i>Cribrosphaerella ehrenbergi</i>	(Arkhangelsky) Deflandre in Piveteau	X	X
<i>Cyclagelosphaera margerelii</i>	Noël	X	X
<i>Cylindralithus biarcus</i>	Bukry	X	X
<i>Discorhabdus ignotus</i>	(Górka) Perch-Nielsen	X	X
<i>Eiffellithus casulus</i>	Shamrock in Shamrock & Watkins		X
<i>Eiffellithus collis</i>	Hoffmann		X
<i>Eiffellithus eximius s.s.</i>	(Stover) Perch-Nielsen	X	X
<i>Eiffellithus eximius s. Verbeek</i>	(Stover) Perch-Nielsen	X	X
<i>Eiffellithus nudus</i>	Shamrock in Shamrock & Watkins		X
<i>Eiffellithus perch-nielseniae</i>	Shamrock in Shamrock & Watkins		X
<i>Eiffellithus turreseiffelii</i>	(Deflandre in Deflandre and Fert) Reinhardt	X	X
<i>Eprolithus floralis</i>	(Stradner) Stover	X	
<i>Gartnerago obliquum</i>	(Stradner) Noël	X	X
<i>Grantarhabdus coronadventis</i>	(Reinhardt) Grün in Grün & Allemann		X
<i>Helicolithus anceps</i>	(Górka) Noël		X
<i>Helicolithus compactus</i>	(Bukry) Varol & Girgis		X
<i>Helicolithus trabeculatus</i>	(Górka) Verbeek	X	X
<i>Helicolithus cf. varolii</i>	Blair & Watkins		X
<i>Kamptnerius magnificus</i>	Deflandre <i>Taxonomic rank: species</i>	X	X
<i>Lithastrinus grillii</i>	Stradner	X	X
<i>Lithraphidites carniolensis</i>	Deflandre	X	X
<i>Lucianorhabdus cayeuxii</i>	Deflandre	X	X
<i>Lucianorhabdus maleformis</i>	Reinhardt	X	X
<i>Manivitella pemmatoidea</i>	(Deflandre in Manivit) Thierstein	X	X
<i>Marthasterites furcatus</i>	(Deflandre in Deflandre and Fert) Deflandre	X	X
<i>Marthasterites simplex</i>	(Bukry) Burnett	X	X
<i>Microrhabdulus belgicus</i>	Hay & Towe	X	X

Table D1. Continued.

Species	References	Loibichl	Niobrara
<i>Microrhabdulus decoratus</i>	Deflandre	X	X
<i>Micula concava</i>	(Stradner in Martini and Stradner) Verbeek		X
<i>Micula cubiformis</i>	Forchheimer	X	X
<i>Micula staurophora</i>	(Gardet) Stradner	X	X
<i>Miravetesina bergenii</i>	Lees		X
<i>Octolithus multiplus</i>	(Perch-Nielsen) Romein	X	X
<i>Placozygus fibuliformis</i>	(Reinhardt) Hoffmann	X	X
<i>Placozygus spiralis</i>	(Bramlette and Martini) Hoffmann		X
<i>Prediscosphaera cretacea</i>	(Arkhangelsky) Gartner	X	X
<i>Prediscosphaera columnata</i>	(Stover) Perch-Nielsen		X
<i>Prediscosphaera grandis</i>	Perch-Nielsen,	X	X
<i>Prediscosphaera ponticula</i>	(Bukry) Perch-Nielsen		X
<i>Prediscosphaera spinosa</i>	(Bramlette and Martini) Gartner	X	X
<i>Quadrum gartneri</i>	Prins & Perch-Nielsen in Manivit et al.	X	X
<i>Reinhardtites anthophorus</i>	(Deflandre) Perch-Nielsen	X	X
<i>Retecapsa angustiforata</i>	Black	X	X
<i>Retecapsa crenulata</i>	(Bramlette and Martini) Grün in Grün & Allemann	X	X
<i>Retecapsa ficula</i>	(Stover) Burnett	X	X
<i>Retecapsa surirella</i>	(Deflandre and Fert) Grün in Grün & Allemann	X	X
<i>Rhagodiscus angustus</i>	(Stradner) Reinhardt	X	X
<i>Rhagodiscus reniformis</i>	Perch-Nielsen		X
<i>Rhagodiscus splendens</i>	(Deflandre) Verbeek	X	X
<i>Staurolithites ormae</i>	Rawahi & Dunkley Jones	X	X
<i>Staurolithites stradneri</i>	(Rood et al.) Bown in Bown & Cooper		X
<i>Tegumentum stradneri</i>	Thierstein in Roth & Thierstein	X	X
<i>Tetrapodorhabdus decorus</i>	(Deflandre in Deflandre and Fert) Wind & Wise	X	X
<i>Tranolithus gabalus</i>	Stover	X	
<i>Tranolithus minimus</i>	(Bukry) Perch-Nielsen		X
<i>Tranolithus orionatus</i>	(Reinhardt) Reinhardt	X	X
<i>Watznaueria barnesia</i>	(Black in Black and Barnes) Perch-Nielsen	X	X
<i>Watznaueria biporta</i>	Bukry	X	X
<i>Watznaueria britannica</i>	(Stradner) Reinhardt	X	
<i>Watznaueria fossacincta</i>	(Black) Bown in Bown & Cooper	X	X
<i>Watznaueria ovata</i>	Bukry	X	X
<i>Zeugrhabdotus birescenticus</i>	(Stover) Burnett in Gale et al.	X	X
<i>Zeugrhabdotus biperforatus</i>	(Gartner) Burnett		X
<i>Zeugrhabdotus diplogrammus</i>	(Deflandre in Deflandre and Fert) Burnett in Gale et al.	X	X
<i>Zeugrhabdotus embergeri</i>	(Noël) Perch-Nielsen	X	
<i>Zeugrhabdotus erectus</i>	(Deflandre in Deflandre and Fert) Reinhardt	X	X
<i>Zeugrhabdotus moulladei</i>	Bergen		X
<i>Zeugrhabdotus noeliae</i>	Rood et al.		X
<i>Zeugrhabdotus praesigmoides</i>	Burnett		X

Data availability. All morphometric, taxonomic, and isotopic data supporting the findings of this study are available at <https://doi.org/10.5281/zenodo.17093271> (Granero Ordóñez, 2025).

Sample availability. All the slides containing calcareous nannofossils studied and pictured in this contribution are stored at the University of Vienna, Institute of Geology, under the inventory numbers 320000001 to 320000044.

Supplement. The supplement related to this article is available online at <https://doi.org/10.5194/jm-44-469-2025-supplement>.

Author contributions. PG conceptualised the study, conducted the specimen measurements and counting, performed the statistical analyses, designed the figures, managed software and data processing, and wrote the original draft. MW contributed to the conceptualisation and supervision and provided text contributions and data.

AW assisted with measurements, figure design, and article revision. DW provided samples and carbon isotope data.

Competing interests. The contact author has declared that none of the authors has any competing interests.

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