Short communication

Sutural complexity and body size in Cretaceous ammonoids: Macroevolutionary decoupling of correlated features

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A B S T R A C T

The relationship between sutural complexity (estimated as fractal dimension) and body size is analysed for a sample of 204 genera of Cretaceous ammonoids. Although both characteristics are significantly correlated with each other, their evolutionary dynamics are opposite: i) the duration of genera is not correlated with body size but is correlated with sutural complexity and ii) throughout the Cretaceous there is an increase in the body size of the ammonoids in the sample but no increase in the complexity of their septa is detected. This indicates the difficulty of predicting macroevolutionary patterns for a trait on the basis of its correlation with other features on wide stratigraphic scales.

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1. Introduction

At a very general scale both body size and complexity of living things have increased over geological time (Bonner, 1988; McShea, 1996; Carroll, 2001; McShea and Brandon, 2010; Heim et al., 2015; Smith et al., 2016). However, there are very few works that study the relationship between both aspects within specific groups from a quantitative perspective. Ammonoids constitute an ideal group for this type of studies given that both the complexity of some of their characteristics (such as septa) and body size can be easily quantified.

The primary function of ammonoid septa like that of present-day *Nautilus* is to maintain watertight portions of the shell (chambers) in order to be gradually filled with gas to compensate for weight gain as the animal grows and maintain neutral buoyancy (Jacobs and Chamberlain, 1996; Tajika et al., 2015; Naglik et al., 2016). However, unlike nautiloids, the septa of ammonoids increased in complexity over geological time (Boyajian and Lutz, 1992; Klug and Hoffmann, 2015; Peterman et al., 2021). The functional role of septal folding is still an unresolved question. Although several functional hypotheses have been proposed since the nineteenth century (see Klug and Hoffmann, 2015 for a comprehensive review) new hypotheses continue to be published (e.g., Arkhipkin,

2018). In the case of ammonoids (especially in those Mesozoic), septa fold peripherally becoming more complex as ontogeny progresses in a more accentuated manner at the beginning and more gradual throughout development (Arkell et al., 1957; Landman, 1988).

In fact, it is the ontogenetic increase in septal complexity (manifested by the complexity of the suture line) that allows the characterization of heterochronies in septa. The morphogenesis of the septum suggests that differences in septal complexity between species can be explained by simple heterochronies (Hammer, 1999). Given that the age of ammonoids has to be generally approximated by size, it is very difficult to characterize the specific heterochronic processes (hypomorphosis, hypermorphosis, progenesis, etc.) involved in each case (Klingenberg, 1998). However, since both shell size and suture complexity increase monotonically throughout ontogeny, it is relatively feasible to characterize paedomorphosis or peramorphosis by ontogenetic scaling, i.e., by analyzing whether the ontogeny of descendants has undergone either truncation or extension relative to their ancestors (Klingenberg, 1998). Numerous heterochronies have been described in the suture line of ammonoids at different taxonomic levels and in different geological periods (Landman, 1988; Dommergues, 1990). Although some studies on heterochronies in ammonoids indicate that paedomorphosis is somewhat more common than peramorphosis (Landman and Geyssant, 1993), Landman (1988) indicates that peramorphosis is more common than paedomorphosis in the case of septa. However,

paedomorphosis has also been frequently described in both Mesozoic and Palaeozoic ammonoids (e.g. Landman et al., 1991; Korn et al., 2013). The family Flickiidae is a paradigmatic example of paedomorphosis in the Cretaceous (Wright and Kennedy, 1979), although there are also examples in other families of this period such as *Falloticeras* for the family Brancoceratidae (Kennedy and Cooper, 1977) or *Protacanthoceras* within Acanthoceratidae (Wright and Kennedy, 1980). Furthermore, in the case of sexual dimorphism, microconchs have been considered paedomorphic analogues of macroconchs (Neige et al., 1997). Therefore, within a specific temporal framework, the idea that there must be a relationship between septal complexity and body size in ammonoids not only seems logical but has been empirically obtained for ammonoids from different geological periods (e.g., Olóriz et al., 2002; Pérez-Claros, 2005; Pérez-Claros et al., 2007; Monnet et al., 2011; Peterman and Barton, 2019).

In the specific case of Upper Jurassic ammonoids, there is a significant correlation between sutural complexity (approximated by fractal dimension) and phragmocone size (Olóriz et al., 2002; Pérez-Claros, 2005; Pérez-Claros et al., 2007). In fact, septal surface grows as the ¾ power of body mass, which is the exponent of Kleiber's law, an empirical law in biology, which is well known to be the scaling exponent of basal metabolic rate in animals (Pérez-Claros, 2005). In other words, the surface area of septa grows according to the metabolic rate of the animal. This indicates that septal folding is a mechanism for increasing septal area as a requirement of metabolic and physiological processes (e.g., respiration or body chamber transport). It is important to note that although phragmocone size is one of the factors most related to sutural complexity (e.g. Pérez-Claros, 2005), other aspects such as cross section, degree of involution or ornamentation can also be important (e.g., Pérez-Claros et al., 2007; Aiba and Wani, 2016).

Pérez-Claros and Bengtson (2018) showed that Cretaceous ammonoids with more complex sutures showed larger stratigraphic ranges, evidencing that ecological specialisation implies suture simplification. However, this did not translate into a macroevolutionary trend towards a net increase in complexity throughout the Cretaceous. This was because almost all of the variation in sutural complexity (as quantified by fractal dimension) is due to the emergence and disappearance of genera with simple sutures. Pérez-Claros and Bengtson (2018) also indicated that given the relationship between septal complexity and body size, it is theoretically expected that macroevolutionary dynamics of the former could be reflected in the latter as both phragmocone size and sutural complexity increase during ontogeny. It is important to clarify that the correlation between both characteristics via ontogenetic development does not assume a causal relationship between them. Paradoxically, as will be shown below, the evolutionary dynamics for sutural complexity and phragmocone size are clearly different despite a high correlation between them.

2. Material and methods

The database and method used to estimate sutural complexity are the same as in Pérez-Claros and Bengtson (2018). The sample is composed of 204 genera of planispiral ammonoids distributed throughout the Cretaceous. The peripheral complexity of septa (manifested in sutural complexity) can be characterised by fractal dimension (Df), which may intuitively be conceived as an estimate of the degree to which sutures depart from a straight line (Df = 1) to fill a plane (Df = 2). The fractal dimension was estimated following the methodology of Pérez-Claros et al. (2002). This methodology is designed in order to obtain the Df for scales where the suture behaves as a fractal object (for details and examples of application, see Olóriz et al., 1997, 2002; Pérez-Claros, 2005; Pérez-Claros et al., 2002, 2007).

The whorl height (Wh), whorl perimeter (Wp) and the diameter of the phragmocone at the level of the suture analysed are variables commonly reported in the literature. However, the whorl height or whorl perimeter are more appropriate as a proxy for body size than the shell diameter for this type of study (Newell, 1949; Pérez-Claros et al., 2007). In the present work, whorl perimeter at the level of the suture analysed has been used as a proxy for phragmocone size. This variable has been obtained in most cases directly as the length in mm of the straight line joining the two ends of the external hemisuture projected in a plane (Fig. 1A and B). In other cases Wp has been approximated from Wh and the ratio between Wp and Wp obtained from the cross-section of the phragmocone (Fig. 1C). In any case Wh and Wp are highly correlated (r = 0.978, p = 1.468 10^{-129}).

The data used in this paper are available in the Supplementary data and in Pérez-Claros and Bengtson (2018). We follow the taxonomy and biostratigraphic ranges of the Treatise on Invertebrate Palaeontology (Wright et al., 1996). All other details regarding the sample analysed are in Pérez-Claros and Bengtson (2018).

The present study has adopted the general definition of trend used by McKinney (1990) p. 29: "trend is defined as a persistent (rarely monotonic) change in some state variable (…), resulting in a significant net gain or loss in that variable through time". Consequently, an evolutionary trend is evidenced if and only if there is a significant correlation (positive or negative) between the studied
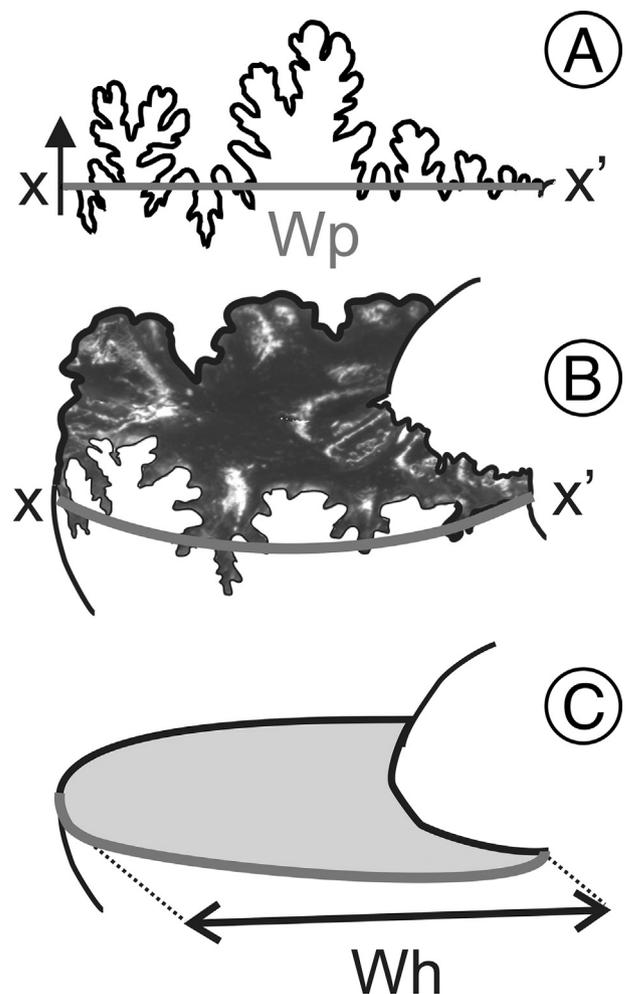

Fig. 1. Estimation of the whorl perimeter (Wp) at the level of the suture analysed. In most cases Wp was obtained by matching the ends (X-X') of the suture (A) with the flank of the phragmocone (B). In the rest of the cases Wp was deduced from Wh from the ratio Wp/Wh of the cross section (C).

variable and the geologic time. There are methodologies to analyse in detail time series by parameter estimation (e.g., Hunt, 2006) that have been applied to various fossil groups (e.g., Hunt, 2007; Monnet et al., 2011; Hunt et al., 2015). However the data analysed here do not meet the requirements for parameter estimation necessary for its application (homogeneity and temporal independence). Consequently, to further examine the relationship between mean phragmocone size in each stratigraphic interval and geologic time, a permutation test has been performed, which does not involve parameter estimation (e.g., Roopnarine, 2001). The empirical distribution of the correlation coefficient (r) was obtained by randomly permuting the log-transformed Wp values between ammonoid genera and recalculating the value of the correlation coefficient between such variable and the geologic time. This procedure has been repeated 10^5 times to obtain the correlation distribution according to the null hypothesis (Ho: r = 0). The existence of a trend in the data can be affirmed if the observed value of r is within the 0.05 rejection region. If the null hypothesis is rejected, it is ruled out that the time series can be explained as random walk or stasis since in both cases r is not statistically different from zero.

3. Results

The distribution of Wp in the analysed sample (Fig. 2A) is strongly skewed to the right, being clearly non-normally distribute (z Kolmogorov-Smirnoff = 2.19, p < 10^{-7}). However the normality of the distribution of its log-transformed values (Fig. 2B) cannot be rejected (z Kolmogorov-Smirnoff = 1.08, p = 0.191). Consequently, the logarithmically transformed Wp values have been used to test correlations.

When the fractal dimension is plotted on the Whorl perimeter (Fig. 3A) despite the large scatter a very significant relationship is obtained (r = 0.419, p = 4.37 10^{-10}). This fact corroborates that those larger phragmocones show statistically more complex sutures.

Given that in the sample analysed those genera with more complex sutures present larger stratigraphic ranges (Pérez-Claros and Bengtson, 2018) the logical prediction would be that those genera with larger phragmocones would also show larger stratigraphic ranges. However, this prediction is not confirmed (Fig. 3B) and a non-significant value was obtained for the correlation between Wp and stratigraphic range (r = −0.075, p = 0.286). This result raises the question of whether there is an inhibitory effect of size on the relationship between stratigraphic range and sutural complexity. The results obtained by Pérez-Claros and Bengtson (2018) showed a highly significant correlation between Df and stratigraphic range (r = 0.416, p = 5.88 10^{-10}). The partial correlation between such variables controlling for Wp provides a slightly higher correlation value (r = 0.495, p = 6.32 10^{-14}). However, the difference between the two values is not significant (z = 0.999, p = 0.161), so the relationship between complexity and stratigraphic range is not affected by phragmocone size.

On the other hand, Pérez-Claros and Bengtson (2018) showed that despite the positive relationship between Df and stratigraphic range for the analysed genera, there was no trend of increasing sutural complexity throughout the Cretaceous. Surprisingly, the phragmocone size of the analysed sample does increase significantly throughout the Cretaceous (Fig. 4A) as the correlation between Wp with the midpoint of the stratigraphic interval for each genus is weak but significant (r = 0.231, p < 0.001). This correlation seems to be largely due to the increase in variance in phragmocone size throughout the Cretaceous, which can be seen more clearly in Fig. 4B where the values are presented without logarithmic transformation.

To analyze in more detail the relationship between mean and variance of Wp during this time interval, the Wp values of the genera in each stratigraphic interval have been averaged (Fig. 5). Although with oscillations, again a general trend of increasing Wp is observed throughout the Cretaceous (r = 0.721, p = 6.82 10^{-6}). The permutation analysis for Log-transformed Wh values produced similar results (r = 0.815, p = 0.043).

4. Discussion

It is difficult to overestimate the importance of body mass for living organisms both because of the intrinsic physical and geometrical properties associated with size (McMahon and Bonner, 1983) and because of its physiological and ecological implications
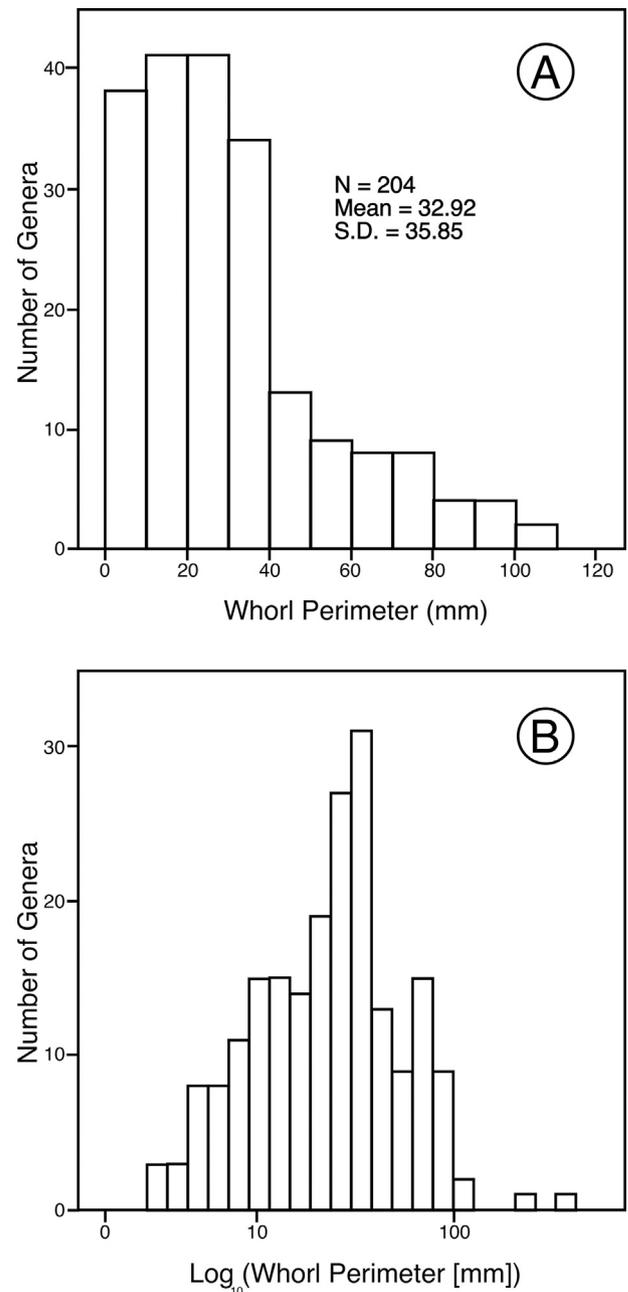

Fig. 2. Histogram of the whorl perimeter values obtained for the sample of Cretaceous ammonoid genera studied: A, linear scale; B, logarithmic scale.
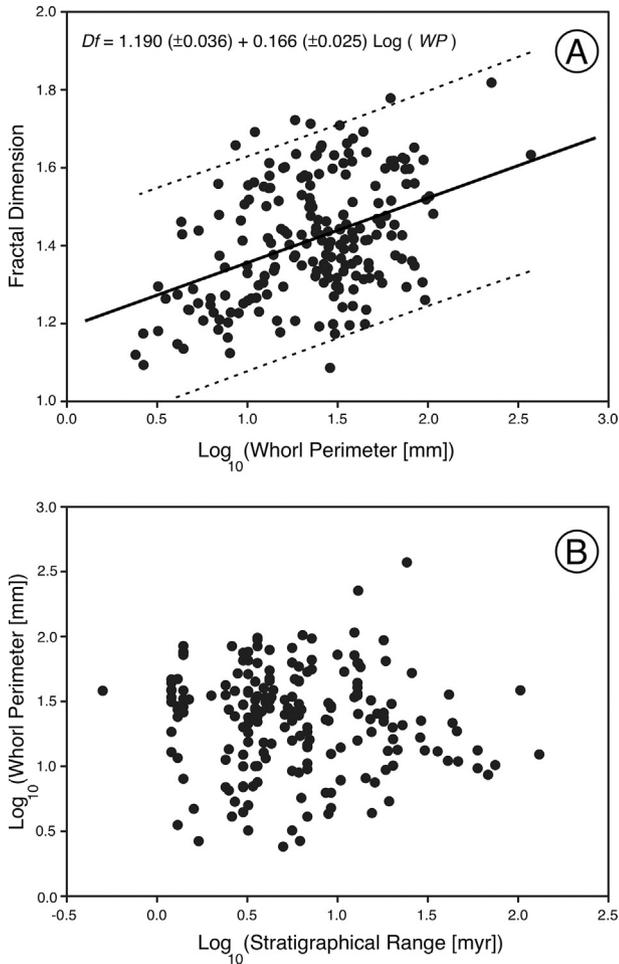
Fig. 3. A: Plot of the fractal dimension on the decimal logarithm of whorl perimeter. Despite the scatter, the relationship is highly significant (p = 4.37 10^{-10}). B: Plot of the latter on the generic duration. In this case the correlation value is statistically indistinguishable from zero (p = 0.161).

(Peters, 1983; Damuth, 2001; Ernest et al., 2003). However, some macroevolutionary implications of body mass such as species duration or extinction risk do not seem to be clearly deduced from neontological observations (Jablonski, 1996).

In the case of the marine fossil record, Payne and Heim (2020) find a higher extinction risk for the larger genera within each class, even controlling for geographic range. However, in the case of ammonoids, the database used by Heim et al. (2015), as well as the sample used in the present work, shows no clear relationship between stratigraphic rank (duration of genera) and the logarithm of biovolume for ammonoids that lived during the Cretaceous (r = 0.040, p = 0.235, N = 888). Regardless of whether the phragmocone size of the sample is representative of that of all Cretaceous ammonoids there is no clear relationship between body size and duration of genera despite the fact that genera with more complex sutures are statistically larger and show larger stratigraphic ranges.

On the other hand, the sample analysed shows a statistical trend towards increasing size over geological time, which is consistent with Cope's law (Jablonski, 1996; Smith et al., 2016). However, the sample analysed was not collected to evaluate this phenomenon but to analyse the relationship between complexity and size. Actually, the database published by Heim et al. (2015) does not show an increase over geological time of the logarithm of the average biovolume of the ammonoid genera in each Cretaceous stage (r = 0.060, p = 0.854, N = 12) although there is an increasing trend for the

ammonoids as a whole over the entire existence of the group from the Devonian to Cretaceous (r = 770, p = 2.54 10^{-10}, N = 47).

The increase in the range of phragmocone sizes (size disparity) during the middle Cretaceous seen in Fig. 4B roughly coincides with an increase in the number of genera analyzed in such time interval. Perhaps both phenomena are related to the high increase in global sea level during this period because biological diversity increases during transgressions. Such a relationship between global sea level and diversity is not only observed in ammonoids (e.g., Kennedy, 1977; House, 1989) but is a common phenomenon for all post-Paleozoic marine fossils (Smith, 2001). Regardless of whether this reflects a biological reality (species-area relationship) or is a sampling artifact (Smith, 2001), such an increase in the middle Cretaceous is not observed for the fractal dimension (Fig. 4 in Pérez-Claros and Bengtson, 2018). This indicates that even in this aspect the temporal dynamics of fractal dimension and phragmocone size are different.

The results obtained here show that in the sample analysed there is no trend towards an increase in sutural complexity over geological time but there is a trend towards an increase in body size. This indicates that complexity and phragmocone size have the opposite macroevolutionary behaviour during the Cretaceous despite being directly correlated.

The reason for this phenomenon lies largely in the large dispersion that can be observed when plotting one variable against
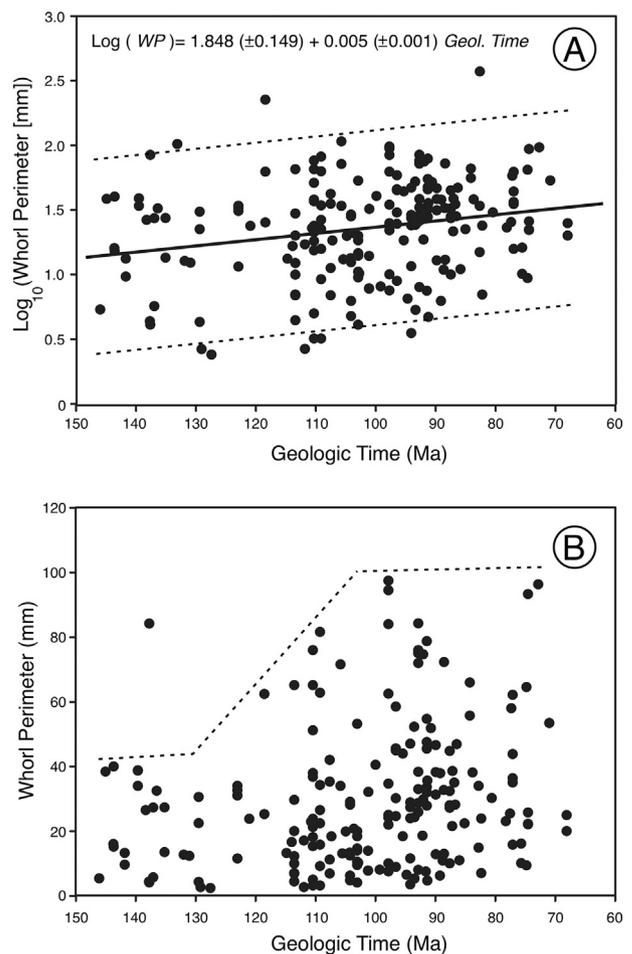

Fig. 4. A: Plot of the whorl perimeter through geological time in logarithmic scale. B: Same as in A but in linear scale. Each genus has been plotted at the midpoint of its stratigraphic interval. The dashed line in B represents approximately the range of sizes. The outlier value corresponding to approximately 140 Ma in B is the genus *Homolsomites*. Four other outliers with Wp larger than 100 mm (*Parapuzosia*, *Ammonitoceras*, *Simbirskites* and *Knemiceras*) are not shown in B.
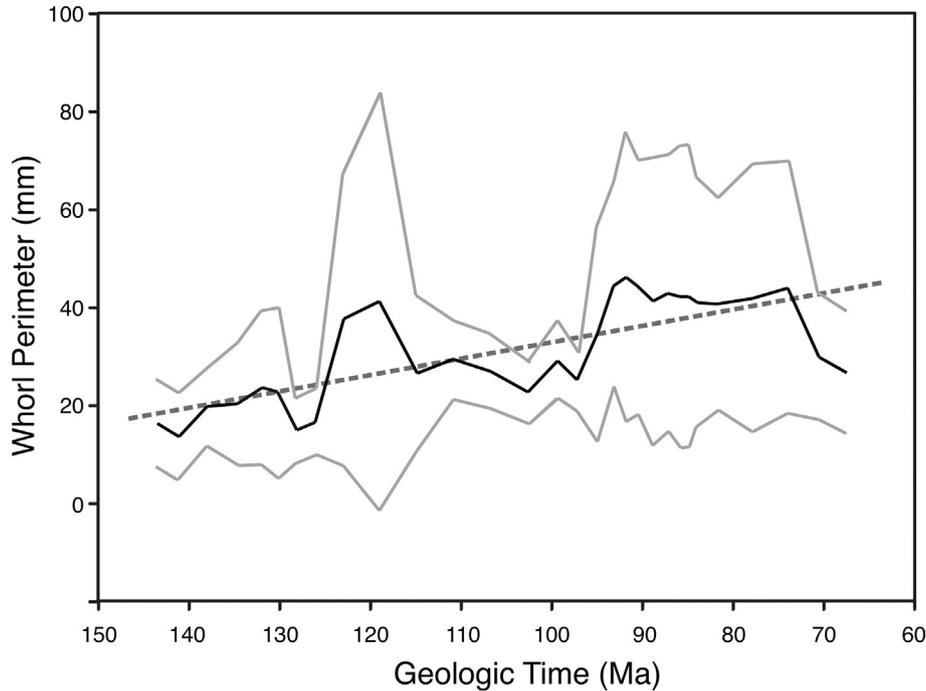
Fig. 5. Plot of the whorl perimeter through geological time averaging all the genera occurring in each stratigraphical unit. The grey lines show the 95% confidence intervals for means. The dashed line is the regression line of Wp on geological time.

another: the variance portion of two correlated variables that are related to a third variable need not be the same. These results indicate the risk of making predictions about the macroevolutionary behaviour of one characteristic from another correlated one. Another element of reflection is that macroevolutionary conclusions based on mean values have to be assessed in the context of the dispersion around them.

5. Conclusions

Although ammonoid septal complexity increases allometrically with body size both throughout ontogeny and among adult individuals at certain specific periods, some macroevolutionary aspects of both features, such as their correlation with generic duration or their trends over geological time, may be different. This indicates the difficulty of predicting macroevolutionary patterns for a trait on the basis of its correlation with other features.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2021.105120.