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RESEARCH PAPER

Generic diversity and septal complexity in Cretaceous ammonoids. Effects of oceanic anoxic events on the ammonoid evolutionary dynamic

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Abstract

This paper analyzes the relationship between the number of genera of Cretaceous planiespiral ammonoids and their sutural complexity estimated by their fractal dimension. It is confirmed that the dynamics of generic diversity is associated with the appearance/disappearance of simple suture genera, which are not ascribed to a particular family. The maximum oscillations of generic diversity occur in the Aptian and Albian which are associated with large variations in the number of genera with simple sutures. From the Middle Campanian there is a continued loss of diversity until the end of the Maastrichtian linked to a net reduction of single suture genera. The direct relationship between the number of genera and the range of septal complexity in each substage indicates that different degrees of septal complexity are different ecomorphological strategies of adaptation to different niches. This result confirms that the specialist forms are those with simple sutures while the genera with complex septa are either generalist forms or are adapted to environments that do not undergo major fluctuations over geological time. The ammonoid generic diversity recorded dynamics is different from that of other marine invertebrates, reflecting paleobiological and/or taphonomic differences. The symmetrical distribution of septal complexity values points to the relative fidelity of the fossil record of Cretaceous ammonoids. The effect of seven oceanic anoxic events of the Cretaceous on the number of genera and septal complexity is analyzed, obtaining no statistically distinguishable effects of the oscillations of these variables with respect to those occurring in other intervals where such events are not recorded.

Keywords Ammonoids · Cretaceous · Diversity · Septum complexity · OAE · Oceanic anoxic events

Resumen

En este trabajo se analiza la relación entre el número de géneros de ammonoideos planiespirales del Cretácico y su complejidad sutural estimada mediante su dimensión fractal. Se confirma que la dinámica de la diversidad genérica está asociada a la aparición/desaparición de géneros de suturas simples que no están adscritos a una familia concreta. Las máximas oscilaciones de la diversidad genérica se dan en el Aptiense y el Albiense, las cuales están asociadas a grandes variaciones en el número de géneros con suturas simples. A partir del Campaniense medio se produce una pérdida continuada de diversidad hasta el final del Maastrichtiense ligada a una reducción neta de los géneros con suturas simples. La relación directa entre el número de géneros y el rango de complejidad septal en cada subestadio indica que los diferentes grados de complejidad septal son diferentes estrategias ecomorfológicas de adaptación a diferentes nichos. Este resultado confirma que las formas especialistas son aquellas con suturas simples mientras que los géneros con septos complejos son formas generalistas o que están adaptadas a ambientes que no sufren grandes fluctuaciones a lo largo del tiempo geológico. La diversidad genérica de ammonoideos registrada en la dinámica es diferente de la de otros invertebrados marinos, lo que refleja diferencias paleobiológicas y/o tafonómicas. La distribución simétrica de los valores de complejidad septal apunta a la relativa fidelidad del

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registro fósil de ammonoideos en el Cretácico. Se analiza el efecto de siete eventos anóxicos oceánicos del Cretácico sobre el número de géneros y la complejidad septal, no obteniéndose efectos estadísticamente distinguibles de las oscilaciones de estas variables respecto a las ocurridas en otros intervalos donde no se registran tales eventos.

Palabras claves Ammonoideos · Cretácico · Diversidad · Complejidad septal · OAE · Eventos Anóxicos Oceánicos

1 Introduction

Ammonoids are among the most important fossil groups of both Paleozoic and Mesozoic faunas. In the particular case of the Cretaceous, they are the most biostratigraphically useful macrofossils thanks to high rates of evolution, the cosmopolitan character of many of their genera and their relative independence of facies types (Kennedy & Cobban, 1976; Lehmann, 2015). Because of this, they are also one of the best studied fossil groups, allowing for detailed paleobiological studies.

These characteristics, which are ideal for biostratigraphic correlation and partly linked to the presence of planktic larval stages and nektonic mode of life, mean that some aspects of their biology are practically unknown. In particular, those derived from the knowledge of soft parts, given that when they die, they decompose after spending some time in the water column until their definitive burial (Wani et al., 2005). Such a period of postmortem drifting is perhaps not long enough to invalidate paleogeographic studies (Yacobucci, 2018), but it is long enough to preclude the preservation of evidence of such parts. A notable exception to this general rule is the material described in Klug et al. (2012).

However, there are certain soft parts whose morphology is (indirectly) preserved with some frequency: the shape of the final part of the mantle, since the septum surface is a "template" of them (Herdenson et al., 2002). In general, the septum surface is not studied directly, but its intersection with the inner face of the shell wall that is observable in internal casts, which is called the suture line.

The complexity of the septa, estimated by the fractal dimension of the suture line, has varied considerably from the beginning of the group in the Devonian to its extinction at the end of the Cretaceous (Boyajian & Lutz, 1992). Starting from simple sutures, the group increased both the mean value and the range of complexity values until leveling off at the beginning of the Jurassic, remaining approximately constant until the end of the Maastrichtian. These results corroborated by Pérez-Claros and Bengtson (2018) for the Cretaceous case, also indicate that throughout geological time, ammonoids of simple and complex sutures coexist. A fact also highlighted by Pérez-Claros and Bengtson (2018) is that ammonoid genera of simple sutures present significantly shorter stratigraphic ranges than those of complex sutures, indicating that these would be forms adapted to more ephemeral environmental conditions than those to which complex suture forms are adapted. This implies that the evolutionary dynamics of complexity depend mainly on the emergence/extinction of simple suture forms.

Oceanic anoxic events (OAE) that occurred in the Cretaceous are among the major environmental perturbations that a priori would be good candidates for producing both changes in diversity and an ecomorphological response that could be manifested in the change in frequency of genera with different degrees of septal complexity. Some previous studies have revealed certain morphological changes associated with certain anoxic events (e.g., Lehmann et al., 2016; Rogov et al., 2019) and others have analyzed changes in diversity associated with any such events (e.g., Monnet & Butcher, 2007; Yacobucci, 2017). However, there are no papers that simultaneously address changes in diversity and septal complexity throughout the Cretaceous and how they have been affected by OAEs.

Consequently, the objectives of the present work are to analyze the relationship between septal complexity and ammonoid diversity during the Cretaceous and how oceanic anoxic events during this period have affected both issues, which may improve our understanding of the long-term paleoecological and evolutionary responses of this group of organisms to environmental changes.

2 Material and methods

The studied sample of ammonoid genera is the same as in Pérez-Claros and Bengtson (2018) and Pérez-Claros (2022), which consists of 204 genera of Cretaceous planiespiral ammonoids of which an average of three external sutures per genus have been analyzed. The taxonomic classification and stratigraphic ranges of the analyzed genera follow the Treatise on Invertebrate Paleontology (Wright et al., 1996), though the stratigraphic range of certain genera present before the Cretaceous has been obtained from Arkell et al. (1957). Although there are alternatives to the Treatise for the classification and temporal distribution of genera for some Cretaceous stages (e.g. Klein, 2005), in this paper, as in other studies dealing with diversity over entire epochs (e.g. Yacobucci, 2005), I have opted to use the synthesis of Wright et al. (1996) as an attempt to confer some homogeneity of taxonomic criteria, which is obviously associated with the stratigraphic distribution of genera.

The complexity of sutures has been quantified by fractal dimension (Df). The fractal dimension of suture lines can be considered a measure of the degree of peripheral folding of the septa, which is a real number between the Euclidean dimension of a line (Df = 1) and that of a plane (Df = 2). The value of Df will be higher for those suture lines that are more folded and therefore move away from a straight line in order to tend to occupy a plane. The fractal character of any natural object does not extend to infinitely small scales but has a lower limit (cut-off) below which the object behaves as a Euclidean object. The methodology used follows the method of Pérez-Claros et al., (2002), which only analyzes the Df for the range of scales where sutures have fractal behavior and has been applied to the study of Upper Jurassic (e.g., Olóriz et al., 1997, 2002; Pérez-Claros, 2005; Pérez-Claros et al., 2002, 2007) and Cretaceous (e.g., Pérez-Claros & Bengtson, 2018 and Pérez-Claros, 2022) ammonoids.

In the case of some of the sutures analyzed corresponding to some Lower Cretaceous genera, although they show the same distribution and relative sizes of lobes and saddles as adult sutures, they have not fully developed adult characteristics since no repeated subdivision of main lobes and saddles is developed. Such genera have been retained in the analyses because the first four Cretaceous stages are comparatively poorly represented. Although the methodology presented by Pérez-Claros et al. (2002) would overcome this problem since sutures are analyzed only for larger scales, a potential effect of ontogenetic variation cannot be ruled out in the results. Since both phragmocone size and suture complexity increase monotonically throughout ontogeny (Pérez-Claros et al., 2007; Pérez-Claros, 2022), one approach to make the fractal dimension value independent of ontogeny is to relativize its value to the size of the fragmocone. Consequently, the residual of the regression of Df on Log of the whorl perimeter at the level of the analyzed suture (ResDf) is also analyzed here, which can be considered a value of suture complexity independent of fragmocone size and consequently ontogenetic stage. As far as can be assessed, ontogenetic status is random with respect to stratigraphic range. All the data corresponding to Df and whorl perimeter are in Perez-Claros & Bengtson (2018) and Perez-Claros (2022), respectively.

Numerical ages corresponding to each stratigraphic interval follow the International Chronostratigraphic Chart v 2023/09 (Cohen et al., 2013). According to Baraboshkin (1999) the Upper Volgian has been considered to approximately correspond to the Lower Berriasian and the Ryazanian to the Upper Berriasian. Equal durations of substages have been adopted to subdivide stages.

The total generic diversity of Cretaceous ammonoids in each substage (NGtot) has been obtained from the ages reported in Wright et al. (1996) counting all occurring genera/subgenera in each chronostratigraphic interval. In an attempt to minimize the effect of shell shape on the results, heteromorph ammonoids have not been included. Since the analyzed sample of sutures only includes planiespiral ammonoids, in some analyses the analyzed diversity (NGplan) has been obtained excluding genera of the superfamily Turrilitoidea since they are mostly heteromorphs (Note that in Wright et al. [1996] the superfamily names end in -aceae). The genera of the superfamily Ancyloceratoidea have not been counted either, except for those belonging to the families Ancyloceratidae and Hemihoplitidae, which have planiespiral forms whose sutures have been analyzed. In any case, as shown below, both diversity estimations are strongly correlated.

In addition to generic diversity, the mean, standard deviation, maximum and minimum Df values of all genera in each of the 30 substages considered were calculated for each time interval.

Since the correlations between variables can be influenced by serial correlation (McKinney & Oyen, 1989), such correlations have been calculated both for the observed values for the variables as well as for the first differences (value in one interval minus that of the previous interval), which is equivalent to considering a serial correlation value of 0 and 1, respectively. In the case of discrepancy in the significance values between the two correlations, the value corresponding to the generalized differences obtained according to McKinney and Oyen (1989) was assigned, discarding the value for the first difference. If there is no statistical difference between the correlation between the values and their first differences, those corresponding to the former are reported.

The temporal occurrence and duration of the seven anoxic oceanic events analyzed are presented in Table 1. The effect of the OAEs analyzed on generic diversity and mean fractal dimension values has been assessed by the difference of the analyzed variable with respect to the substage following the one in which the event occurs for those cases where the event occurs at the end of a subinterval (Weissert Event, OAE 1d, OAE 2 and OAE 3), given that its effect is expected to be seen in the substage following the one in which it occurs. In the case of covering a complete or almost complete subinterval (OAE 1a and OAE 1b), the effect is assessed both in the interval itself and in the following substage.

On the other hand, an OAE is considered to severely affect the variable (diversity or septal complexity) if there is a positive increase greater than the 75% percentile of all increases recorded in the Cretaceous (or less than 25% in the case of a negative increase).

All analyses were performed using free software for scientific data analysis PAST v. 3.24 (Hammer et al., 2001).

Table 1 Ocurrences and durations of the analyzed oceanic anoxic events

OAE	Ocurrence	Duration	Substage	References
Weissert Event	~133.2	~1.3	Late Valanginian	Cavalheiro et al., 2021
OAE1a	~120	~1.0 to 1.3	Early Aptian	Li et al., 2008
OAE1b	~111	~4.0	Early Albian	Leckie et al., 2002
OAE1c	~102	~0.56	Late Albian	Navarro-Ramirez et al., 2015; Liu et al., 2022
OAE1d	~100.7	~0.23 to 0.24	Late Albian	Yao et al., 2018
OAE2	~94.2	~0.6	Late Cenomanian	Jones et al., 2023
OAE3	~87	~1.0	Late Coniacian	Joo & Sageman, 2014

3 Results

The generic diversity values and the various statistics associated with the fractal dimension for each chronostratigraphic substage are presented in Table 2.

The mean percentage of genera whose sutures have been analyzed in each chronostratigraphic interval is 44% ranging from 19% for the Late Berriasian to 64% for the Middle Turonian. The correlation of the first difference between the number of extant genera and the number of those for which Df values are available is 0.816 ($p=7.0\ 10^{-8}$), indicating that those intervals with higher generic diversity have been sampled more deeply and consequently, large biases due to differential sampling are not expected.

The correlations between the most relevant variables concerning both the statistics associated with Df and generic diversity are shown in Table 3.

Figure 1 presents the mean, maximum and minimum values in the 30 chronostratigraphic intervals into which the Cretaceous has been divided. As indicated in Pérez-Claros and Bengtson (2018) these three statistics fluctuate throughout the Cretaceous without a clear trend. In fact, the correlation of all analyzed statistics associated with Df with geologic time (midpoint of the chronostratigraphic interval) is not significant ($p>0.1$ in all cases). A fact that is visually apparent in Fig. 1, also indicated in Pérez-Claros and Bengtson (2018), is that the mean Df in each interval correlates to a greater extent with the minimum value than with the maximum value (Table 3). In fact, the correlation between the generalized differences of the mean and the maximum value of Df in each substage does not turn out to be significant ($r=0.341$, $p=0.070$).

Another noteworthy fact is the low turnover rate among the genera showing the maximum value of complexity in each chronostratigraphic interval as opposed to the high turnover rate in the genera showing the minimum values. Of the 29 transitions between the 30 time intervals analyzed, 24 times the same genus shows the maximum interval value. With a few exceptions, the maximum complexity values are occupied exclusively by members of the superfamilies Lytoceratoidea and Tetragonitoidea. In total the genera showing the maximum values belong to 6 different families. In contrast, only 7 times out of 29 occasions the same genus shows the minimum complexity consecutively (Table 4, Fig. 1), such positions being occupied by representatives of 14 different families. In other words, the turnover of simple suture genera is not associated with a particular family and is therefore relatively independent of phylogeny.

On the other hand, the dispersion of Df values (estimated by its standard deviation, Sd.Df) informs us about the spectrum of genera with different sutures coexisting in a given period. This statistic is significantly inversely correlated with both mean and minimum Df values (Table 3). This means that when the range of Df values increases it does so by extending the minimum values downward.

It is interesting to analyze whether the correlation between such dispersion and the mean of Df is independent of its correlation with the minimum values. This can also be formulated as whether the contraction of the range of Df values in each interval is due to the minimum value of Df increasing, independently of the behavior of the mean. To answer this question, the partial correlations between the mean, the minimum and the dispersion of Df values in each interval have been analyzed.

The correlation of the generalized differences between the mean and the dispersion of Df controlling for its minimum value is significant ($r=-0.473$, $p=0.010$), as is the correlation between the minimum and the dispersion controlling for the mean ($r=-0.461$, $p=0.011$), which implies that both statistics correlate independently with the dispersion of Df.

As can be seen in Table 3, the statistics associated with the residuals of Df controlling for fragmocone size maintain the same relationships with each other as those that have not been relativized to whorl perimeter, which is evidence that size does not appreciably affect the relationships between the suture statistics.

Figure 2 shows the total generic diversity of Cretaceous ammonoids and that for the planiespiral ammonoid families studied. In both cases there is no significant trend of increasing or decreasing number of genera throughout the

Table 2 Data analyzed in this study. Numerical age for substages in Ma. NGtot: total number of standing genera/subgenera in each substage. NGpla: total number of standing planispiral genera/subgenera in each substage. Df Mean, Df median, Df Sd., Df Min., Df Max., Df Nobs: mean, median, standard deviation, minimum value, maximum value and sample size for the fractal dimension in each substage, respectively. % Sampled: ratio between Df Nobs and NGplan. ResDf Mean, ResDf median, ResDf Sd., ResDf Min., ResDf Max.: mean, median, standard deviation, minimum value and maximum value of residuals for the regression of fractal dimension on the whorl perimeter in each substage, respectively

Substage	Abrev	Numerical Age	NGtot	NGplan	Df Mean	Df Median	Df Sd	Df Min	Df Max	Df Nobs	% Sampled	ResDf Mean	ResDf Median	ResDf Sd	ResDf Min	ResDf2 Max
Early Berriasian	EBe	(145–142.4)	44	42	1.477	1.472	0.152	1.177	1.674	10	23.8	0.1031	0.1418	0.1612	− 0.2090	0.3121
Late Berriasian	LBe	(142.4–139.8)	45	42	1.534	1.528	0.098	1.429	1.674	8	19.0	0.1717	0.1658	0.0780	0.0477	0.3121
Early Valanginian	EVa	(139.8–136.2)	58	53	1.468	1.471	0.130	1.207	1.674	14	26.4	0.0835	0.1294	0.1395	− 0.1668	0.3121
Late Valanginian	LVa	(136.2–132.6)	55	50	1.494	1.512	0.147	1.207	1.709	14	28.0	0.1169	0.1418	0.1250	− 0.1083	0.3121
Early Hauterivian	EHa	(132.6–129.185)	45	44	1.508	1.518	0.137	1.207	1.709	13	29.5	0.1178	0.1517	0.1269	− 0.1083	0.3121
Late Hauterivian	LHa	(129.185–125.77)	43	40	1.507	1.513	0.127	1.173	1.674	12	30.0	0.1238	0.1560	0.1426	− 0.2636	0.3121
Early Barremian	EBa	(125.77–123.585)	71	59	1.450	1.509	0.191	1.119	1.674	13	22.0	0.0877	0.1603	0.1743	− 0.2636	0.3121
Late Barremian	LBa	(123.585–121.4)	75	62	1.454	1.507	0.170	1.119	1.674	12	19.4	0.0795	0.1560	0.1610	− 0.2636	0.2357
Early Aptian	EAp	(121.4–118.6)	54	49	1.495	1.506	0.152	1.296	1.818	15	30.6	0.0759	0.1288	0.1365	− 0.1418	0.2371
Middle Aptian	MAp	(118.6–115.8)	31	30	1.550	1.551	0.135	1.321	1.818	11	36.7	0.1328	0.1603	0.1078	− 0.0976	0.2371
Late Aptian	LAp	(115.8–113)	84	82	1.492	1.518	0.160	1.093	1.818	29	35.4	0.0991	0.1517	0.1301	− 0.1682	0.3220
Early Albian	EAl	(113–108.8)	92	82	1.468	1.480	0.147	1.093	1.722	38	46.3	0.0593	0.0586	0.1363	− 0.2547	0.3220
Middle Albian	MAl	(108.8–104.7)	85	72	1.446	1.459	0.143	1.181	1.722	36	50.0	0.0398	0.0207	0.1397	− 0.1534	0.3220
Late Albian	LAl	(104.7–100.5)	115	93	1.427	1.424	0.159	1.147	1.722	40	43.0	0.0319	− 0.0055	0.1468	− 0.1764	0.3287
Early Cenomanian	ECe	(100.5–98.3)	82	68	1.467	1.507	0.161	1.163	1.713	38	55.9	0.0545	0.0442	0.1470	− 0.2298	0.3287
Middle Cenomanian	MCe	(98.3–96.1)	59	51	1.468	1.476	0.161	1.207	1.713	27	52.9	0.0603	0.0444	0.1587	− 0.1933	0.3287
Late Cenomanian	LCe	(96.1–93.9)	77	69	1.448	1.446	0.157	1.227	1.713	33	47.8	0.0395	0.0083	0.1446	− 0.1665	0.3287
Early Turonian	ETu	(93.9–92.5)	72	65	1.423	1.416	0.174	1.086	1.713	36	55.4	− 0.0074	− 0.0176	0.1710	− 0.3462	0.3287

Table 2 (continued)

Substage	Abrev	Numerical Age	NGtot	NGplan	Df Mean	Df Median	Df Sd	Df Min	Df Max	Df Nobs	% Sampled	ResDf Mean	ResDf Median	ResDf Sd	ResDf Min	ResDf2 Max
Middle Turonian	MTu	(92.5–91.2)	47	39	1.464	1.468	0.167	1.198	1.713	25	64.1	0.0366	0.0156	0.1640	− 0.2367	0.3287
Late Turonian	LTu	(91.2–89.8)	60	48	1.466	1.462	0.152	1.235	1.713	28	58.3	0.0349	0.0120	0.1551	− 0.2303	0.3287
Early Coniacian	ECo	(89.8–88.1)	71	55	1.477	1.442	0.144	1.198	1.713	25	45.5	0.0550	0.0083	0.1468	− 0.2662	0.3287
Late Coniacian	LCo	(88.1–86.3)	70	55	1.469	1.439	0.146	1.198	1.713	26	47.3	0.0432	0.0069	0.1532	− 0.2662	0.3287
Early Santonian	ESa	(86.3–85.4)	60	47	1.511	1.553	0.138	1.247	1.713	24	51.1	0.0903	0.1432	0.1461	− 0.1760	0.3287
Middle Santonian	MSa	(85.4–84.5)	56	42	1.531	1.558	0.124	1.304	1.713	24	57.1	0.1083	0.1630	0.1384	− 0.1760	0.3287
Late Santonian	LSa	(84.5–83.6)	63	50	1.519	1.555	0.131	1.210	1.713	29	58.0	0.0969	0.1272	0.1332	− 0.1760	0.3287
Early Campanian	ECa	(83.6–79.8)	95	69	1.548	1.580	0.130	1.210	1.778	34	49.3	0.1215	0.1630	0.1352	− 0.2117	0.3287
Middle Campanian	MCa	(79.8–75.9)	74	50	1.582	1.599	0.108	1.306	1.778	27	54.0	0.1571	0.1880	0.1134	− 0.2117	0.3287
Late Campanian	LCa	(75.9–72.1)	70	48	1.562	1.598	0.128	1.260	1.778	29	60.4	0.1320	0.1800	0.1447	− 0.2594	0.3287
Early Maastrichtian	EMa	(72.1–69.1)	37	30	1.532	1.555	0.122	1.260	1.692	19	63.3	0.1176	0.1615	0.1570	− 0.2594	0.3287
Late Maastrichtian	LMa	(69.1–66)	33	26	1.535	1.555	0.106	1.306	1.692	16	61.5	0.1270	0.1609	0.1352	− 0.2117	0.3287

Table 3 Correlations between some of the variables shown in Table 2. Correlation values are below the main diagonal and their corresponding significance levels are above the main diagonal. Values with statistical significance below 0.05 are in bold type. Abbreviations as in Table 2

	NGplan	NGtot	Mean Df	Sd.Df	Df Min	Df2 Max	ResDf Mean	ResDf Sd	ResDf Min	ResDf Max
NGplan		**$p < 10^{-14}$**	**0.001**	**0.006**	**$p < 10^{-4}$**	0.390	**0.004**	0.402	0.414	0.380
NGtot	**0.945**		**0.025**	**0.036**	**0.002**	0.390	**0.012**	0.341	0.183	0.177
Df Mean	**-0.561**	**-0.408**		**$p < 10^{-6}$**	**0.304**	0.070	**$p < 10^{-6}$**	**$p < 10^{-3}$**	0.110	0.831
Df2 Sd	**0.493**	**0.384**	**-0.797**		**$p < 10^{-6}$**	0.794	**$p < 10^{-4}$**	**$p < 10^{-4}$**	**0.019**	0.472
Df2 Min	**-0.653**	**-0.548**	**0.691**	**-0.755**		0.457	**$p < 10^{-3}$**	**$p < 10^{-4}$**	**0.000**	0.517
Df2Max	0.163	0.194	*0.341*	-0.050	0.141		0.479	0.087	0.484	0.130
ResDf Mean	**-0.515**	**-0.452**	**0.869**	**-0.723**	**0.609**	0.134		**$p < 10^{-4}$**	**0.007**	0.379
ResDf Sd	0.159	0.180	**-0.604**	**0.712**	**-0.652**	-0.318	**-0.665**		**$p < 10^{-6}$**	0.372
ResDf Min	-0.155	-0.250	0.298	**-0.426**	**0.613**	0.133	**0.480**	**-0.808**		0.214
ResDf Max	0.166	0.253	-0.041	-0.137	-0.123	-0.283	-0.166	0.169	-0.234	

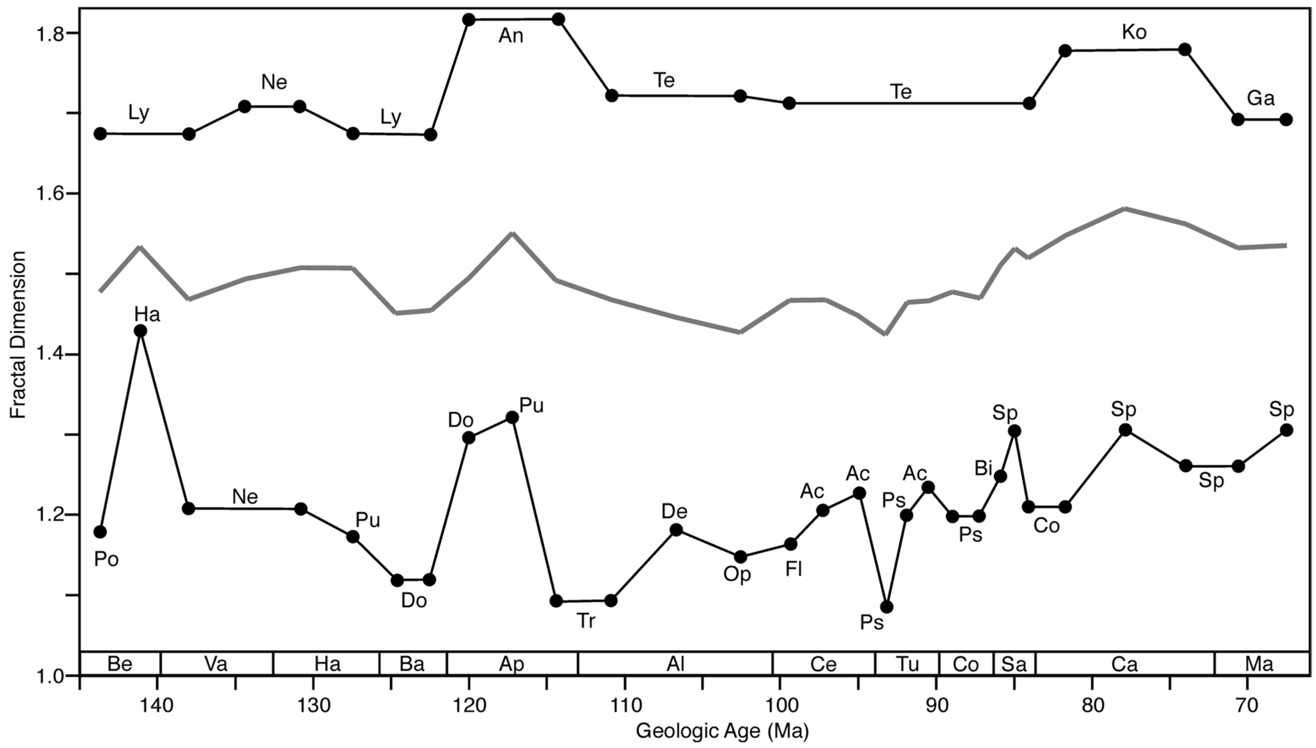

Fig. 1 Mean, maximum and minimum values of the fractal dimension of ammonoid sutures through geologic time for the Cretaceous substages analyzed. The two letters on the maximum and minimum values of each substage correspond to the initials of the families shown in Table 4

Cretaceous ($p > 0.6$ and $p > 0.4$, respectively). As shown in Table 3, both correlate strongly ($r = 0.945$, $p < 10^{-14}$) and show practically identical behavior with respect to the rest of the variables.

Figure 3 shows the diversity of the analyzed ammonoids together with the sampled-in-bin genera obtained from Paleobiology Database (McClennen et al., 2017). Since the chronostratigraphical stage is the temporal resolution of such a database, the ammonoid diversity of the substages of each stage has been averaged to make them equivalent. Although some parallels are observed between the two diversity estimates from the Berriasian to the Barremian and the Campanian to the Maastrichtian, the correlation between the two is not significant ($p > 0.3$). Comparison by simple visual inspection with other compilations based on the Paleobiology Database covering only mollusks, such as that by Freymueller et al. (2019), also reveals marked differences.

As seen in Table 3 there is a significant correlation between the diversity of genera of the families analyzed in each interval with both the mean, minimum and standard

Table 4 Genera corresponding to the minimum and maximum values of fractal dimensions in each substage analyzed

	Minimum value of Df			**Maximum value of Df**		
Substage	**Superfamily**	**Family**	**Genus**	**Superfamily**	**Family**	**Genus**
Early Berriasian	Perisphinctoidea	Polyptychitidae	*Garniericeras* (SPATH 1923)	Lytoceratoidea	Lytoceratidae	*Lytoceras* (SUESS 1865)
Late Berriasian	Haploceratoidea	Haploceratidae	*Neolissoceras* (SPATH 1923)	Lytoceratoidea	Lytoceratidae	*Lytoceras* (SUESS 1865)
Early Valanginian	Perisphinctoidea	Neocomitidae	*Neocomites* (UHLIG 1905)	Lytoceratoidea	Lytoceratidae	*Lytoceras* (SUESS 1865)
Late Valanginian	Perisphinctoidea	Neocomitidae	*Neocomites* (UHLIG 1905)	Perisphinctoidea	Neocomitidae	*Lytoceras* (SUESS 1865)
Early Hauterivian	Perisphinctoidea	Neocomitidae	*Neocomites* (UHLIG 1905)	Perisphinctoidea	Neocomitidae	*Lytoceras* (SUESS 1865)
Late Hauterivian	Pulchelliioidea	Pulchelliidae	*Pulchellia* (UHLIG 1883)	Lytoceratoidea	Lytoceratidae	*Lytoceras* (SUESS 1865)
Early Barremian	Douvelliceratoidea	Douvilleiceratidae	*Paraspiticeras* (KILIAN 1910)	Lytoceratoidea	Lytoceratidae	*Lytoceras* (SUESS 1865)
Late Barremian	Douvelliceratoidea	Douvilleiceratidae	*Paraspiticeras* (KILIAN 1910)	Lytoceratoidea	Lytoceratidae	*Lytoceras* (SUESS 1865)
Early Aptian	Douvelliceratoidea	Douvilleiceratidae	*Roloboceras* (CASEY 1954)	Ancyloceratoidea	Ancyloceratidae	*Ammonitoceras* (DUMAS 1876)
Middle Aptian	Pulchelliioidea	Pulchelliidae	*Subpulchellia* (HYATT 1903)	Ancyloceratoidea	Ancyloceratidae	*Ammonitoceras* (DUMAS 1876)
Late Aptian	Douvelliceratoidea	Trochleiceratidae	*Trochleiceras* (FALLOT & TERMIER 1923)	Ancyloceratoidea	Ancyloceratidae	*Ammonitoceras* (DUMAS 1876)
Early Albian	Douvelliceratoidea	Trochleiceratidae	*Trochleiceras* (FALLOT & TERMIER 1923)	Tetragonitoidea	Tetragonitidae	*Jauberticeras* (JACOB 1907)
Middle Albian	Desmoceratoidea	Desmoceratidae	*Silesitoides* (SPATH 1925)	Tetragonitoidea	Tetragonitidae	*Jauberticeras* (JACOB 1907)
Late Albian	Haploceratoidea	Oppeliidae	*Koloceras* (RICCARDI, AGUIRRE URRETA & MEDINA 1987)	Tetragonitoidea	Tetragonitidae	*Jauberticeras* (JACOB 1907)
Early Cenomanian	Acanthoceratoidea	Flickiidae	*Flickia* (PEVINQUIÈRE 1907)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Middle Cenomanian	Acanthoceratoidea	Acanthoceratidae	*Paracolinoceras* (KENNEDY & COBBAN 1990)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Late Cenomanian	Acanthoceratoidea	Acanthoceratidae	*Protacanthoceras* (SPATH 1923)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Early Turonian	Acanthoceratoidea	Pseudotissotiidae	*Eotissotia* (BARBER 1957)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Middle Turonian	Acanthoceratoidea	Pseudotissotiidae	*Pseudotissotia* (PERON 1897)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Late Turonian	Acanthoceratoidea	Acanthoceratidae	*Spathites* (KUMMEL & DEC KER 1954)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Early Coniacian	Acanthoceratoidea	Pseudotissotiidae	*Hemitissotia* (PERON 1897)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Late Coniacian	Acanthoceratoidea	Pseudotissotiidae	*Hemitissotia* (PERON 1897)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Early Santonian	Haploceratoidea	Binneyitidae	*Binneyites* (RESIDEE 1927)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)

Table 4 (continued)

Substage	Minimum value of Df			Maximum value of Df		
	Superfamily	**Family**	**Genus**	**Superfamily**	**Family**	**Genus**
Middle Santonian	Acanthoceratoidea	Sphenodiscidae	*Eulophoceras* (HYATT 1903)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Late Santonian	Acanthoceratoidea	Collignoniceratidae	*Haboroceras* (TOSHIMITSU 1988)	Tetragonitoidea	Tetragonitidae	*Gabbioceras* (HYATT 1900)
Early Campanian	Acanthoceratoidea	Collignoniceratidae	*Haboroceras* (TOSHIMITSU 1988)	Desmoceratoidea	Kossmaticeratidae	*Grossouvrites* (KILIAN & REBOUL 1909)
Middle Campanian	Acanthoceratoidea	Sphenodiscidae	*Manambolites* (HOURCQ 1949)	Desmoceratoidea	Kossmaticeratidae	*Grossouvrites* (KILIAN & REBOUL 1909)
Late Campanian	Acanthoceratoidea	Sphenodiscidae	*Lybicoceras* (HYATT 1900)	Desmoceratoidea	Kossmaticeratidae	*Grossouvrites* (KILIAN & REBOUL 1909)
Early Maastrichtian	Acanthoceratoidea	Sphenodiscidae	*Lybicoceras* (HYATT 1900)	Tetragonitoidea	Gaudryceratidae	*Gaudryceras* (GROSSOUVRE 1894)
Late Maastrichtian	Acanthoceratoidea	Sphenodiscidae	Manambolites (HOURCQ 1949)	Tetragonitoidea	Gaudryceratidae	*Gaudryceras* (GROSSOUVRE 1894)

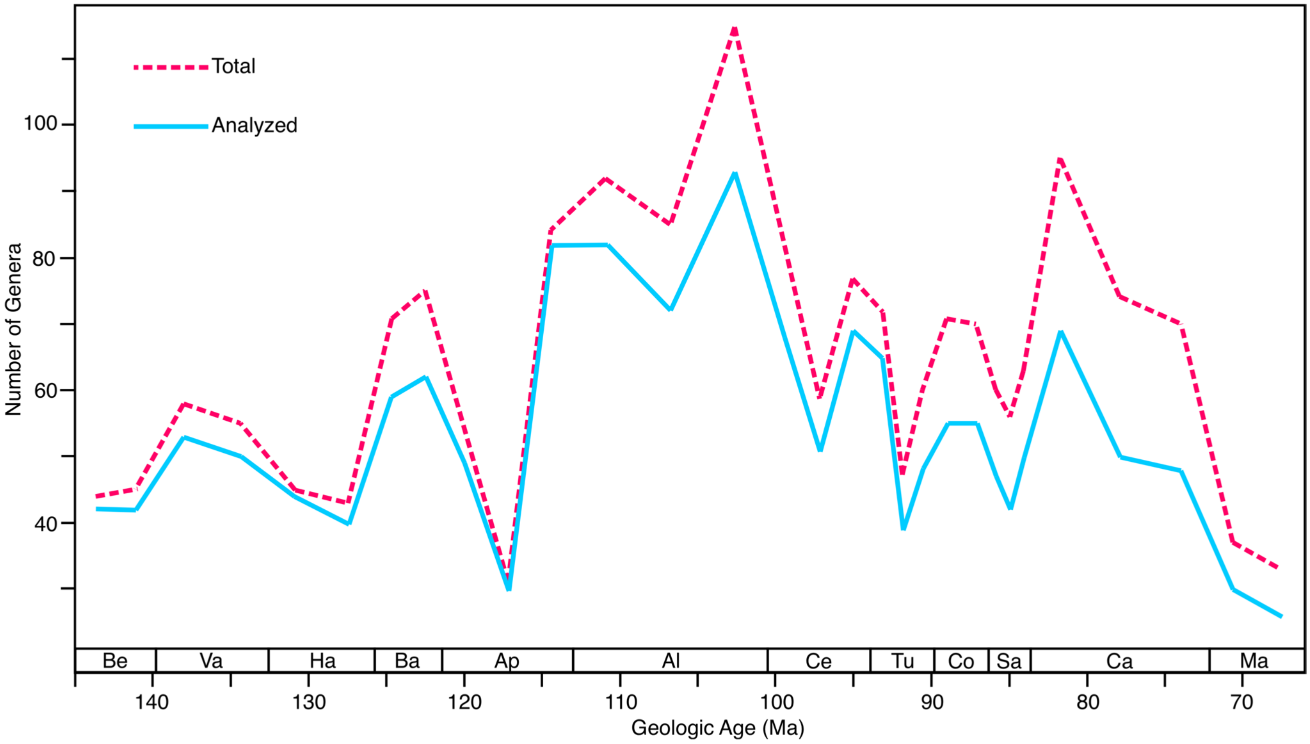

Fig. 2 Number of total ammonoid genera (Total) and number of planiespiral genera (Analyzed) in each Cretaceous substage

deviation values of the fractal dimension, although not with the maximum values (Fig. 4). In the case of the residuals of the fractal dimension versus fragmocone size there is also a correlation with the mean values, but not with the rest, although the direction of the correlation (positive or negative) is maintained. Figure 5 shows the mean values

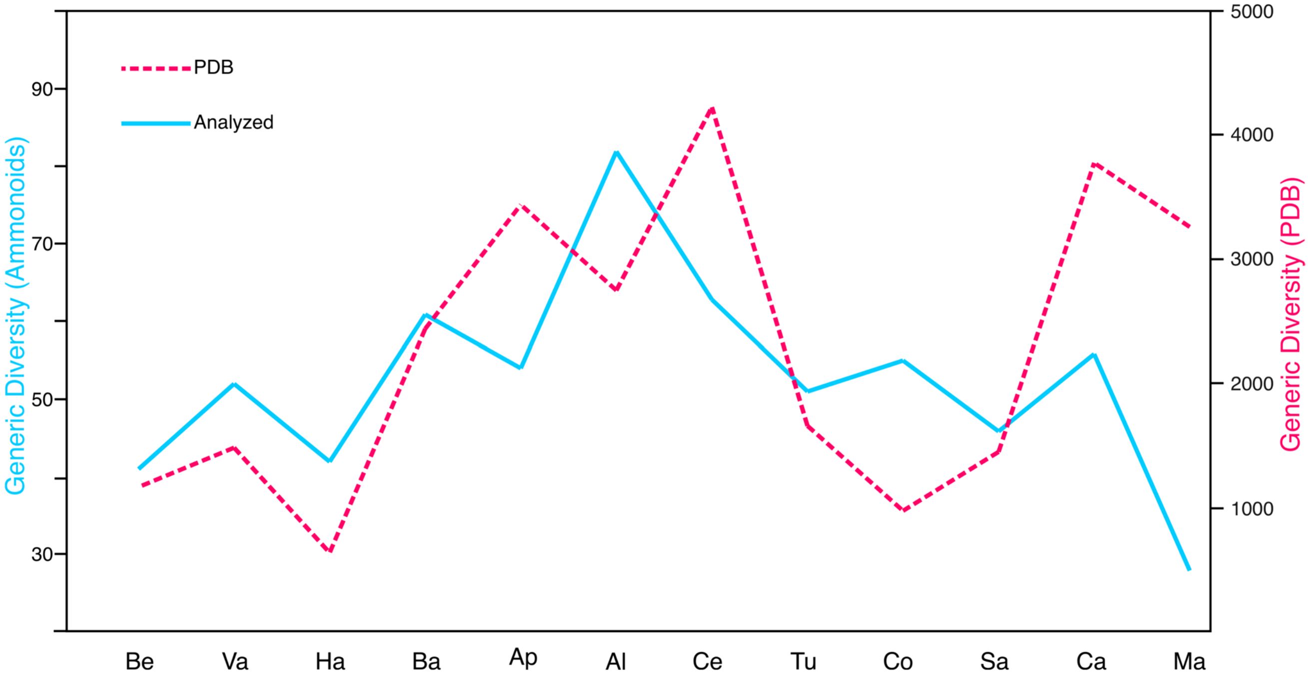

Fig. 3 Number of planiespiral ammonoid genera (Analyzed) and number of marine invertebrate genera (PDB) in each Cretaceous stage

of Df and generic diversity during the Cretaceous where the negative correlation between both variables is visually appreciated. In other words, the increase in diversity in each interval is linked to the appearance of genera with simple sutures and the contraction of diversity to the disappearance of such genera.

Since both standard deviation and Df values are significantly correlated with each other and with generic diversity, it is appropriate to analyze whether the partial correlations of both suture statistics with diversity remain significant. The correlations of the generalized differences between the minimum of Df and generic diversity in each interval controlling for Sd.Df remains significant ($r = -0.579$, $p = 0.001$) as does the correlation between standard deviation and generic diversity controlling for the minimum value ($r = 0.496$, $p = 0.006$). That is, the correlations of both statistics with diversity are independent of each other. Furthermore, the correlation between the minimum Df and Sd.Df controlling for the number of genera remains significant ($r = -0.705$, $p = 1.63\ 10^{-5}$).

An essential aspect for the present work that was addressed in Pérez-Claros and Bengtson (2018) is the normality of the distribution of Df values in the sample of 204 ammonoids analyzed (Fig. 6). In addition to the Kolmogorov-Smirnoff test presented by Pérez-Claros and Bengtson (2018), both the Lilliefors L test ($p = 0.115$) and the Jarque–Bera test ($p = 0.082$) show that the null hypothesis of normality of the sample cannot be rejected. It is important to note that the latter test analyzes whether the skewness and kurtosis of the sample deviates significantly from that expected for a normal distribution. Therefore, given that the distribution of Df values is symmetrical, it can be concluded that in the Cretaceous there are the same number of genera with Df below the mean as above it. Or, in other words, it is equally likely to randomly draw a genus with a simple suture as one with a complex suture. As will be discussed below, this result has important taphonomic and paleoecological implications.

The effect of anoxic events on the analyzed diversity (NGplan) is presented in Fig. 5 and Table 5. As can be seen in all cases there is a reduction in diversity over the substage following the anoxic event (except for OAE 1c, in which this cannot be determined). In four of the six quantified events such a reduction in diversity is associated with a decrease in the number of genera with simple sutures (Weissert event, OAE 1a, OAE 1b, OAE 1d and OAE 3). On the contrary in OAE 1b and OAE 2 the reduction in diversity is accompanied by an increase in the number of genera with simple sutures.

The effect that occurs in the interval itself in the case of OAE 1a is identical to that which occurs in the following interval for both diversity and septal complexity, but in the case of OAE 1b it is opposite to that which occurs in the following interval, increasing the number of genera. The effect of OAE 1c on the same interval where it occurs results in a strong increase in the number of genera and a decrease in the fractal dimension value. In other words, there is an increase of taxonomic and ecomorphological

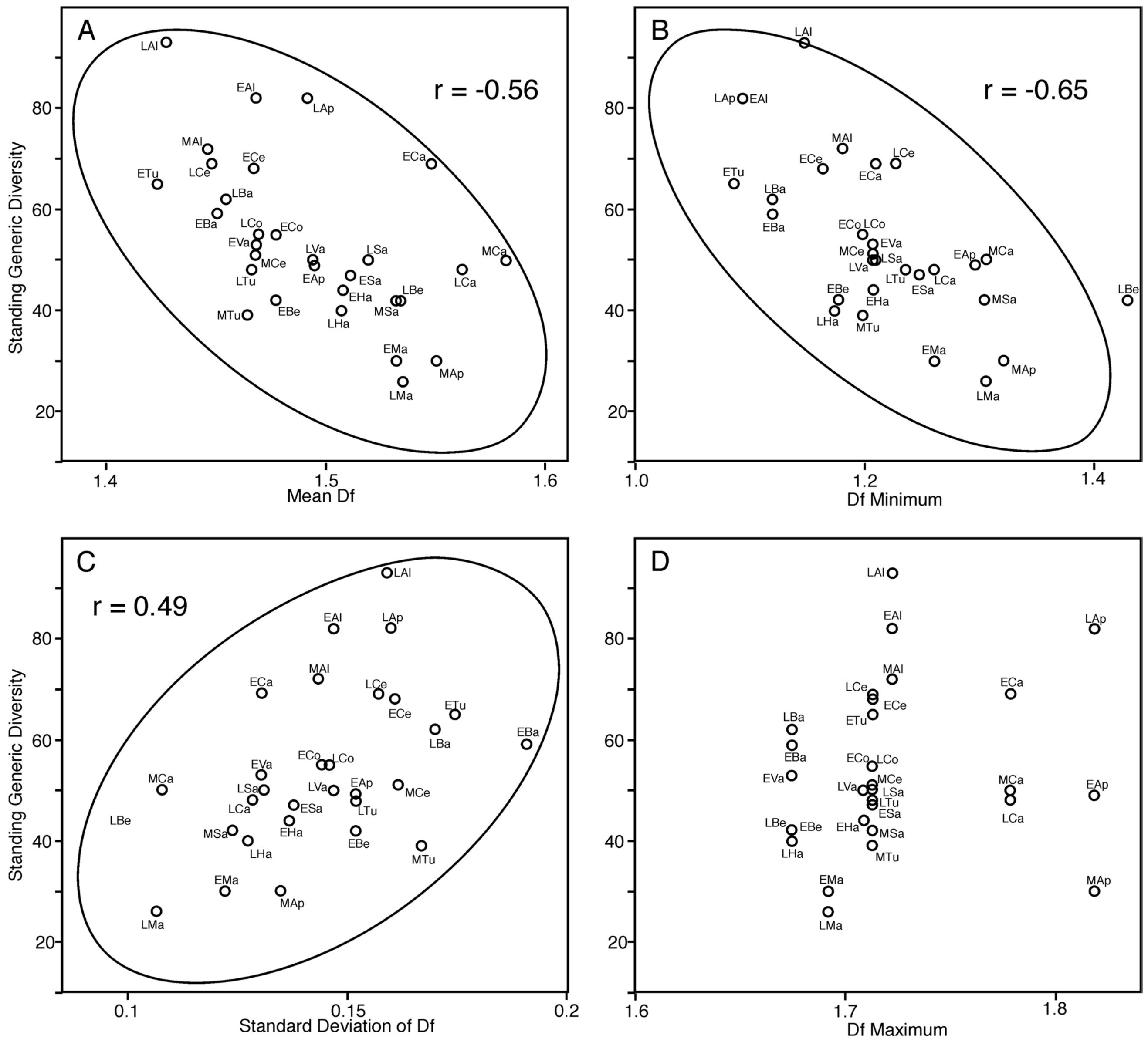

Fig. 4 Number of planiespiral ammonoid genera on the mean (**A**), minimum (**B**), standard deviation (**C**) and maximum (**D**) values of fractal dimension in each Cretaceous substage analyzed. The covariation ellipses (95%) and the values of correlation coefficients are shown for those significant relationships. Abbreviations for substages according to Table 2

diversification within the same intervals in which OAE 1b and OAE 1c events occur.

An interesting aspect to analyze is whether the magnitude of the effect of the six OAEs analyzed on the next substage to where the event occurs is greater than the changes in diversity and mean fractal dimension produced among the substages not affected by such events. Permutation tests indicate that for both planiespiral genus diversity and mean fractal dimension there are no significant differences between variations in both variables produced by anoxic events and those unaffected by them ($p = 0.068$ and $p = 0.230$, respectively).

4 Discussion

One of the first inferences to emerge from the relationship between generic diversity and sutural complexity is the absence of large preservation biases in the fossil record of Cretaceous ammonoids, i.e., the fossil record of Cretaceous ammonoids reflects reasonably well the actual diversity of the group in this period.

The support of the present work for such reasoning is straightforward: if the variation in the number of genera observed is due to preservation biases, as diversity in a substage contracts or expands, there would be the same

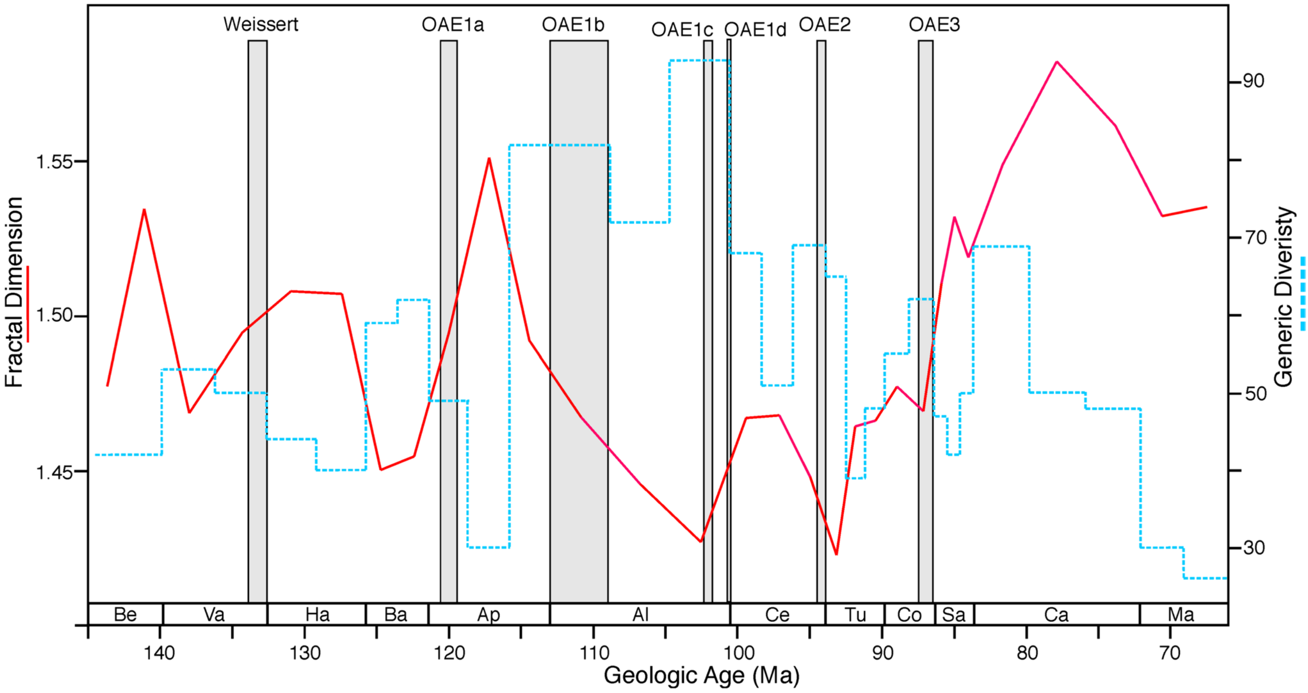

Fig. 5 Mean fractal dimension and number of planiespiral ammonoid genera through Cretaceous. Time occurrence and duration for the seven oceanic anoxic events analyzed according to Table 1

probability that such an event would occur through the elimination or incorporation of a simple suture genus as that of a complex suture genus. However, such a phenomenon does not occur: the dynamics of diversity are concentrated only in those genera of simple suture. It could be argued that this phenomenon could reflect the lower preservation potential of simple suture genera or simply that there are fewer simple suture genera than complex suture genera. However, the latter has to be ruled out since, as shown in Fig. 6, there is an equal probability of detecting a simple suture genus and a complex suture genus in the Cretaceous fossil record. That is, if one rules out the existence of specific taphonomic biases associated with suture complexity, one must admit that the dynamics of ammonoid diversity in the fossil record must reasonably well reflect the diversity that existed.

This reasoning can also be applied in the opposite direction: since there seem to be no differential taphonomic biases associated with suture complexity, apparitions or extintions of genera with simple sutures must correspond to real dynamics and not to a preservation artifact.

The dynamics of biological diversity over geological time has always attracted the interest of paleontologists. However, one of the major advances in this field was due to the compilations made by Sepkoski (1982, 2002), which allowed certain quantitative analyses that led to important conclusions regarding the dynamics of the planet's diversity throughout the Phanerozoic (e.g., quantifications of mass extinctions, periodicity of extinctions, etc.). However, since the 1990s, the extent to which recorded diversity is influenced by various preservation biases has been questioned (see review in Smith, 2007).

Several types of mega-biases have been proposed that make a literal reading of the fossil record difficult, such as the volume or continuity of the outcrop area of sedimentary rocks through time (e.g., Peters, 2005; Smith, 2001), although counterarguments have also been proposed (e.g., Benton et al., 2000). The results obtained here do not question the existence of such biases for most groups of marine organisms with preservation potential, but rather that the biological particularities of ammonoids make them less susceptible to such preservational biases. One result that supports the particularities of ammonoids, relative to all other marine groups, is the lack of correlation between ammonoid diversity with global marine diversity estimated from the Paleobiology DataBase. In fact, ammonoids have one of the highest probabilities of genus preservation per stratigraphic interval (Foote & Sepkoski, 1999). One of the elements that may be alluded to as a differential factor for preservation is the nektonic or necto-benthic mode of life of ammonoids, which makes them somewhat independent of the substrate, although other biological characteristics such as the capacity for biogeographic dispersal must have played a role.

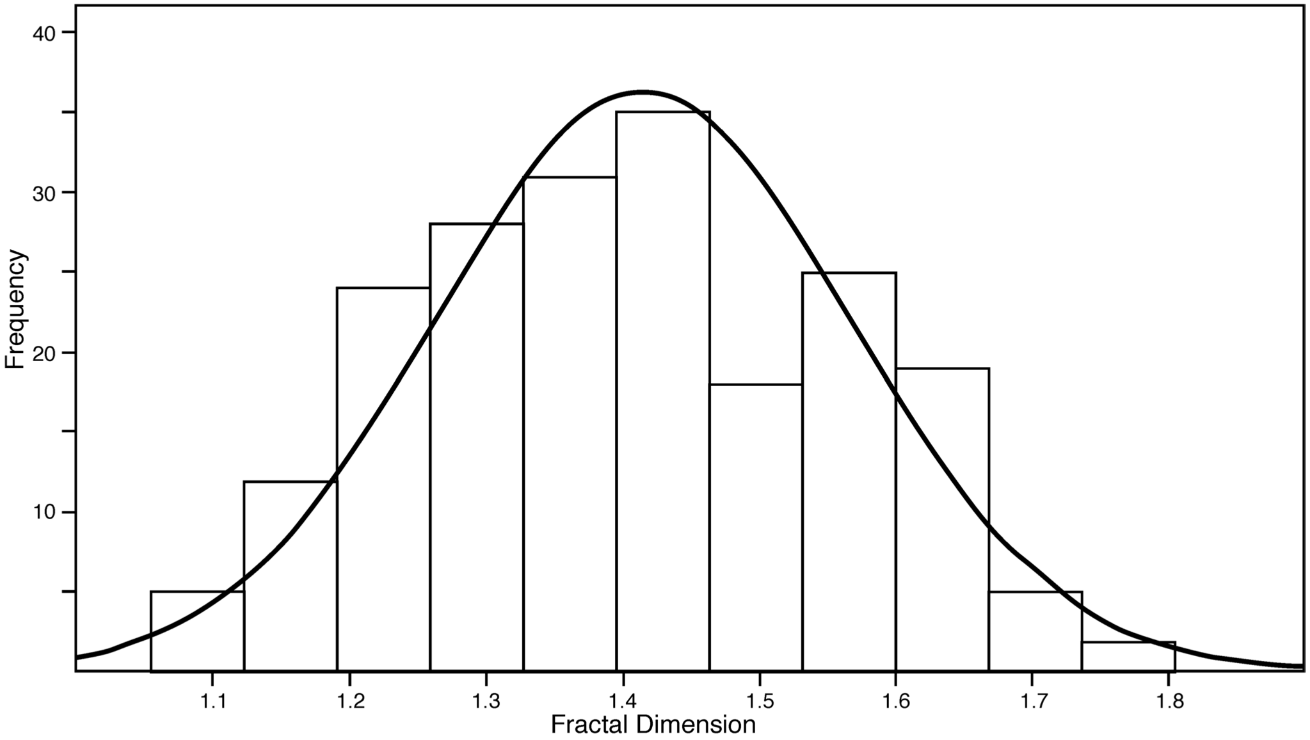

Fig. 6 Histogram and adjusted normal curve for fractal dimension values of all Cretaceous ammonoid genera analyzed

Table 5 Effects on ammonoid generic diversity and fractal dimension mean of the seven oceanic events analyzed

OAE	Ocurrence	Duration	Occurrence	Substage for the effect	Effect on Diversity	Effect on Df (Mean)
Weissert	~133.2	~1.3	Late Valanginian	Early Hauterivian	Reduction	Increase
OAE1a	~120	~1.0 to 1.3	Early Aptian	Early Aptian	Severe Reduction	Severe Increase
OAE1a	~120	~1.0 to 1.3	Early Aptian	Middle Aptian	Severe Reduction	Severe Increase
OAE1b	~111	~4.0	Early Albian	Early Albian	No Effect / Increase	Severe Reduction
OAE1b	~111	~4.0	Early Albian	Middle Albian	Reduction	Severe Reduction
OAE1c	~102	~0.56	Late Albian	Late Albian	Severe Increase	Reduction
OAE1c	~102	~0.56	Late Albian	Early Cenomanian	Not determinable	Not determinable
OAE1d	~100.7	~0.23 to 0.24	Late Albian	Early Cenomanian	Severe Reduction	Severe Increase
OAE2	~94.2	~0.6	Late Cenomanian	Early Turonian	Reduction	Severe Reduction
OAE3	~87	~1.0	Late Coniacian	Early Santonian	Reduction	Severe Increase

Another element on which the complexity and generic diversity data mutually support each other is the relationship obtained between the number of occupied niches (range of fractal dimension values) and biological diversity. Regardless of the biological role played by septal complexity, different degrees of complexity must reflect different adaptive strategies. Therefore, as generic diversity expands, it is expected that the range of values of septal complexity will also expand, widening the range of niches occupied by new genera. A possible exception to this relationship would be the existence of a high degree of provincialism that implies a high degree of endemism. In such a case, the same ecological role can be played by genera that play the same ecological role showing the same adaptations but would not compete because they are in allopatry.

As can be seen in Fig. 5 the greatest changes in diversity occur in the Aptian and Albian. In the Middle Aptian there is a sharp drop in generic diversity with respect to the Lower Aptian followed by a dramatic increase in diversity in the Upper Aptian with respect to the Middle Aptian. In fact, diversification continues practically until the end of the Albian (except for a small contraction in the Middle Albian).

From this point on, there are oscillations in diversity until reaching a relative maximum at the beginning of the Campanian, from which diversity begins to decline gradually until the end of the Cretaceous. It is possible that the maximum of diversity in the Lower Campanian is due to an increase in the number of endemisms (Ifrim et al., 2015) and not so much to a diversification linked to an adaptive radiation, hence the fractal dimension values remain high.

Another interesting aspect is the continuous drop in diversity from the Lower Campanian to the Upper Maastrichtian. This phenomenon highlighted decades ago (e.g., Kennedy & Cobban, 1976) is also observed in more recent work on a global (e.g., Yacubucci, 2005) or regional scale (e.g., Hirano et al., 2000; Toshimitsu et al., 2003), indicating (contrary to Ifrim et al. [2015]), that the group is experiencing a severe and continuous decline in diversity 15 Ma before the end-Cretaceous crisis. This decline in ammonoid diversity at the end of the Cretaceous seems to be linked to a high frequency of genera with complex septa, in fact, the absolute maximum of the Cretaceous in the number of genera with complex septa is observed in the Middle Campanian.

Given that the expansion of new niches is accomplished by the incorporation of simple septum genera and their contraction by the disappearance of such genera, it is worth asking whether the decline in ammonoid diversity observed at the end of the Cretaceous is due to environmental changes that decrease the rates of occurrence and/or increase the rates of extinction of simple septum ammonoids.

One of the environmental factors that a priori are good candidates for producing a response in the diversity and ecomorphology of septa are anoxic oceanic events. However, a relatively consistent effect is only seen in the time intervals following the events, and the changes are not significant compared to other periods where such effects do not occur. Even in the case of OAE 2, which is a paradigmatic example, although there is a slight decrease in the number of genera, this is not accompanied by a decrease in the number of genera with simple sutures. This result is consistent with those obtained by Monnet & Butcher (2007) and Yacobucci (2017) in which they do not detect significant drop in diversity at the Cenomanian/Turonian boundary.

Hirano et al. (2000) and Toshimitsu et al. (2003) have related declines in the diversity of Cretaceous ammonoids in Japan to anoxic events. However, like the results obtained in the present work, such a relationship does not seem to hold for all the events analyzed. Obviously, the geographic scope may partly explain the possible discrepancies between the results in a particular region and those obtained globally, both in the intensity of the event in the region analyzed and in the response of the fauna to it.

Another aspect to consider is the difference in intensity, geographic amplitude and other environmental conditions between the anoxic events themselves. Thus, the Weissert Event is marked by a deep global cooling (Cavalheiro et al., 2021) while OAE 2 occurs in the Cenomanian–Turonian Thermal Maximum (Scotese et al., 2021).

In summary, globally there does not seem to be a close relationship between ammonoid evolutionary dynamics and oceanic anoxic phenomena.

5 Conclusions

The increase in the number of Cretaceous planiespiral ammonoid genera is associated with the appearance of simple septal genera, while their decrease is associated with the extinction of such morphologies. This result confirms that simple suture forms are specialists or adapted to ephemeral environments while complex septa are either generalist forms or are adapted to environments that did not undergo major fluctuations over geologic time.

The simplest suture genera of each sub-stage are not ascribed to a particular family, while those of greater complexity generally belong to the suborder Lytoceratina.

The direct relationship between the number of genera and the range of septal complexity in each substage indicates that different degrees of septal complexity are distinct ecomorphological strategies of adaptation to the environment.

The generic diversity dynamics recorded for ammonoids is different from that of other marine invertebrates, reflecting paleobiological and/or taphonomic differences.

The symmetrical distribution of septal complexity values can be considered as an independent indicator of the relative fidelity of the Cretaceous ammonoid fossil record.

The maximum oscillations of generic diversity occur in the Aptian and Albian which are associated to corresponding variations in the number of genera with simple sutures. From the Middle Campanian there is a continuous loss of diversity until the end of the Maastrichtian, which corresponds to high values of complexity of the septa of the genera present in this final interval of existence of the group. The lack of net occurrence of simple suture genera may be linked to the continued decline of the ammonoids.

There is a systematic loss of diversity in the sub-stage following that in which anoxic events occur, however the effect of OAEs on diversity is not statistically distinguishable from diversity oscillations occurring in other intervals where OAEs are not recorded.

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Declarations

Conflict of interest The author has no relevant financial or non-financial interests to disclose.

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