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Biodiversity dynamics and their driving factors during the Cretaceous diversification of Spatangoida (Echinoidea, Echinodermata)

L. Villier[a,b,*], N. Navarro[c]

[a]Institut für Paläontologie, Humboldt-Universität zu Berlin, Invalidenstrasse 43, 10115 Berlin, Germany
[b]Centre de Sédimentologie/Paléontologie, Université de Provence, Bâtiment de Sciences Naturelles, place Victor Hugo, 13331 Marseille cedex 3, France
[c]UMR CNRS 5561 Biogéosciences, Université de Bourgogne, Centre des Sciences de la Terre, 6 Bd. Gabriel, 21000 Dijon, France

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Abstract

Variations in recorded diversity over time present a scrambled signal that is modulated by a large number of variables: the potential of particular life forms to generate evolutionary innovations, external constraints induced by the environment in its broad sense, the heterogeneity of the fossil record and the analytical artefacts due to sampling bias. A key question is how to characterise and quantify the separate input of any given factor in the overall diversity signal. This paper explores the structure of diversity data for spatangoid heart urchins and the sensitivity of recorded diversity to different factors of analytical bias (length of geological periods, proportion of palaeogeographical realms explored, accessible area of outcrops and historical determinism). Unexpectedly, recorded diversity of spatangoids is not proportional to the duration of stages. Bias implied by time scale is negligible compared to bias of sampling or historical determinism. Diversity at any given time is dependent on its recent history (autocorrelation). For spatangoids, a high correlation between diversity at time t_i and t_{i-1} suggests that recorded diversity has an evolutionary significance. A nearly constant rate of diversification is hypothesised for the Cretaceous. A relative poor fossil record during the Turonian and the Coniacian interrupts the main trend of diversification. The number of species counted for a single time interval depends on the number of palaeogeographical realms considered. In conjunction with ecological and phylogenetic data, this relation suggests an evolutionary signal in which western Tethys acted as a centre of origination. Diversity at a single location is constrained ecologically and diversification is controlled by migration into new realms. Recorded diversity and available area of outcrop seem to be correlated, but alternative interpretations can be drawn, including large-scale bias in the fossil record or operation of similar causes (e.g., effect of sea-level fluctuation). Comparing recorded diversity with separate factors independently leads to conflicting results. A multivariate approach suggests that the main trend in recorded diversity might be partially related to evolutionary signal or biases connected with the heterogeneity of the fossil record. Results from

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* Corresponding author. Centre de Sédimentologie/Paléontologie, Université de Provence, Bâtiment de Sciences Naturelles, place Victor Hugo, 13331 Marseille cedex 3, France. Fax: +33 4 91 10 65 82.

E-mail address: lvillier@up.univ-mrs.fr (L. Villier).

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other approaches (phylogeny, morphological disparity) are consistent with and emphasise the evolutionary significance of the recorded diversity of spatangoids.

Keywords: Diversity; Spatangoida; Cretaceous; Robust regression

1. Introduction

It is widely accepted that the fossil record testifies to past life forms and evolution. However, we still do not fully understand the significance of diversity, as measured from the fossil record, and of changes in diversity through geological time. Variations in recorded diversity over time form a heterogeneous signal that is dependent on a large number of variables (e.g., Raup, 1976b; Benton, 1990). Although defined from an incomplete picture of the morphology, fossil taxa are assumed to be appropriate measures of past diversity. Therefore, changes in taxonomic richness should be determined primarily by the phylogenetic history of organisms (origination, speciation and extinction), and should be indicative of biological evolution (Newell, 1959; Valentine, 1969; Sepkoski, 1978, 1979, 1984). However, the completeness and heterogeneity of the fossil record, sampling bias and the taxonomic practices of workers alter and distort the initial diversity signal (Raup, 1972, 1976b; Peters and Foote, 2001; Smith, 2001; Smith et al., 2001). Statistical properties inherent to diversity metrics affect the time signal itself (e.g., Hurlbert, 1971; Signor, 1982, 1985; Gilinski, 1991; Foote, 2000). As an example, diversity metrics (e.g., standing diversity, origination or extinction rates) are scale- and self-dependent variables, which implies complex responses to evolutionary events.

The fossil record of past diversity encompasses the influence of all these factors and their likely complex interactions. But practically, any single factor may be primarily responsible for determining local changes as well as the main trends in measured diversity. The question thus arises as to how we can recognise, organise into a hierarchy and quantify the individual contributions of each factor to a given signal. Almost since diversity studies began, investigators have been aware of difficulties in extracting evolutionary signals from diversity data. A broad array of techniques has been developed in order to reduce the impact of analytical bias and to focus on the effect of a single factor (see Alroy et al., 2001; Connolly and Miller, 2001; Foote, 2001; Powell and Kowalewski, 2002 for recent developments). Despite refinements in the conceptual and analytical framework, most case studies raised various possible explanations given that all biases and factors were not controlled.

The aim of this paper is to determine to what extent measures of diversity derived from the palaeontological record might be sensitive to several, although not all types of putative factors of bias. Cretaceous spatangoid heart urchins are taken as a case study. Their palaeobiology is fairly well known since a wide array of approaches has been explored: functional morphology, palaeoecology, morphological disparity and phylogeny (e.g., Nichols, 1959; Néraudeau and Floquet, 1991; Eble, 2000; Villier et al., 2004). The impact of some factors can be predicted from previous analyses of the stratigraphic record (e.g., Néraudeau et al., 1997; Gale et al., 2000), which can aid us in interpretation of our results. We argue that spatangoids are good candidates for addressing the impact of biases on raw diversity estimates. Relationships between diversity and statistical properties of the diversity signal, variations in duration of time intervals, number of palaeogeographical realms sampled and amount of sediment available per time interval are explored. Practically, correlation is sought by calculating robust estimations (Rousseeuw and Leroy, 1987) to address separately the modality of the relationships between diversity and each factor. The consequence of correlation with evolutionary significance of the diversity signal is discussed. A multivariate approach attempts to quantify the relative contribution of each factor analysed to measured diversity.

2. Material and methods

2.1. The spatangoid heart urchins

The spatangoid heart urchins are the most diverse group of irregular echinoids in the Recent oceans. There are about 350 extant and 1700 fossil species, representing more than 25% of all echinoids with the same time range. Almost all spatangoids live buried in sandy to muddy sediment from superficial layers to more than 20 cm deep. They feed on detritus or by digesting organic matter from ingested sediment. Spatangoids are thus important elements of marine soft-bottom communities and contribute significantly to bioturbation. They are found at all depths and all latitudes, although they remain rare in shoreface environments and at high latitudes (Hyman, 1955). The relative frequency of spatangoids, compared to other echinoids, increased rapidly during the Cretaceous and has remained relatively stable, while the diversity of all other irregular groups (Holasteroida, Holectypoida, Cassiduloida) has declined. These later orders are almost all epibenthic, while burrowing mode of life was interpreted as the key innovation explaining the success of spatangoids (Kier, 1974). Principally, burrowing habit allows access to new food resources and escape from predators (Smith, 1984).

Data on the diversity of spatangoid were extracted from a compendium of Cretaceous nominal species established by Lambert and Thiéry (1912–1925) for species described before 1924, from Kier and Lawson (1978) for species published between 1924 and 1970, and from a survey of the major monographs published since 1970. This includes 807 species distributed among 54 genera. Most genera and families of spatangoids were initially defined as morphological clusters (implying numerous paraphyletic and polyphyletic taxa) but systematics is currently under review to fit a phylogenetic framework (Néraudeau, 1994; Smith, 2002–2004; Villier et al., 2004). When possible, we revised generic assignment of species, reducing the number of paraphyletic taxa and improved the relevance of stratigraphic ranges.

Diversity was analysed at the stage-level and measured at two taxonomic levels, i.e., the numbers of genera and species within stages (Table 1). Generally, the high heterogeneity and sometimes the low quality of the stratigraphic data prevented use of a more detailed temporal scale. Data were excluded when taxonomic occurrences of taxa were not available at the stage-level. The species-level diversity is a count of recorded species per stage and therefore mainly reflects monographic efforts to describe the fossil record. Almost all species are known from just a single stage. Irregular echinoids have a good potential of preservation and the high number of singletons reflects a relatively brief species longevity and/or a tendency for authors to split species names (Oyen and Portell, 2001). The stratigraphic range of genera is taken from their first and last occurrence in the fossil record. Although some genera have gaps in their fossil record, gaps were counted as occurrence (range-through method). Eight genera (*Aphelaster*, *Heterolampas*, *Jordaniaster*, *Menuthiaster*, *Nordenskjoeldaster*, *Polydesmaster*, *Somalechinus*, *Somaliaster*) are restricted to a single stage. They are all monospecific or poorly defined genera, but are included in the calculation of diversity.

Table 1
Summary of the data analysed

Stage	N. species	N. genera	SR. WE	SR. NA	Duration	Age
Maastrichtian	119	28	14	77	6.3	68.15
Campanian	92	27	49	83	12.2	77.4
Santonian	68	16	83	30	2.3	84.65
Coniacian	32	9	87	27	3.2	87.4
Turonian	80	17	104	29	4.5	91.25
Cenomanian	180	21	110	40	5.4	96.2
Albian	93	14	83	58	13.3	105.55
Aptian	49	8	48	26	8.8	116.6
Barremian	19	5	35	10	6	124.0
Hauterivian	23	3	36	8	5	129.5
Valanginian	7	2	30	10	5	134.5
Berriasian	3	1	17	8	7.2	140.6

SR. NA: estimation of sedimentary record focusing on North America, but recording from the rest of the world also taken into account. This is a compiled estimation of sedimentary record produce by counting the number of marine sedimentary formations (Peters and Foote, 2002). SR. WE: estimation of sedimentary record with number of geological maps in United Kingdom and France used as proxy for the number of sedimentary outcrops (Smith, 2001). Time scale from Gradstein et al. (1995). N. species: number of species with occurrences recorded within the time intervals. N. genera: number of genera within the time intervals, estimated using a range-through method. Duration: duration of stages.

A small number of European authors (Coquand, Cotteau, Desor, Fourtau, Gauthier, Lambert, de Loriol and d'Orbigny) described approximately half of the Cretaceous echinoid species during the nineteenth and the beginning of the twentieth century. As these authors were from the same 'taxonomic school', the way they recognised and defined species is roughly consistent from one study to the next. The most prolific workers Lambert and Cotteau, moreover, worked on material from all over the world and from all time intervals. In a series of papers, Lambert and Thiéry (1912–1925) attempted to list all published species as of the date of 1924 and to establish primary synonymies. Although the validity of several species may be questioned, any errors are expected to be randomly distributed in time and among groups. Therefore, we assume that, at the species-level, the effects of taxonomic practice can be disregarded and counting of the number of species per interval figures faithfully the diversity of spatangoids sampled from the fossil record. However, this assumption does not necessarily imply that the richness of fossil species is a face value of the true diversity. On the one hand, recent taxonomic reviews suggest a taxonomic splitting by the authors of the late nineteenth and early twentieth centuries regarding current species concepts (at a ratio of about 3 for 1). On the other hand, Néraudeau (1998) illustrated that various characters traditionally used by palaeontologists can be taxonomically uninformative or misleading for recognition of species.

Cladistic-based phylogenetic data highlight inconsistencies in the traditional systematic framework, showing that the classification contains both monophyletic and paraphyletic taxa (Jeffery, 1998, 1999; Villier et al., 2004). Such inconsistencies and uncertainties in the current classification of early spatangoids preclude any phylogeny-based estimations of diversity at genus- or family-level. Counting both monophyletic and paraphyletic taxa is indeed misleading when estimating diversity (Patterson and Smith, 1987, 1988; Smith and Patterson, 1988; Robeck et al., 2000). However, the number of genera provides a reliable approximation of diversity under certain assumptions (Raup and Boyajian, 1988; Sepkoski and Kendrick, 1993), and genera are taken as useful entities for diversity analyses.

Many species and some genera cannot be classified within a clade-based systematics. The time and place of origination is thus unclear for many spatangoid clades mainly due to the lack of a comprehensive phylogenetic framework. To address the influences of palaeogeography on diversity, species-level diversity for two monophyletic clades, the *Heteraster* clade (*Heteraster* and the derived taxa *Washitaster*, *Paraheteraster*, *Pseudowashitaster*) and the *Douvillaster*–*Macraster* clade was resolved. In these two groups, systematic, stratigraphic and geographic occurrences are of good and homogeneous quality (Neumann, 1996; Villier, 2001). The *Heteraster* clade appears during the Hauterivian, and diversity increases to a maximum during the Albian, just before extinction of the clade, early in the Cenomanian. The *Douvillaster*–*Macraster* clade has a similar history, but occurs later in time, with the first occurrence in the Aptian, a maximum diversity in the Cenomanian and extinction in the Turonian. Heterogeneous knowledge of other clades prevents exploration of much larger data sets.

2.2. Estimation of the sedimentary record

Many different techniques have been used to estimate the amount of sedimentary rocks available for sampling: the number of marine formations (Peters and Foote, 2001, 2002), direct estimates of outcrop area or sediment volume from maps (see Raup, 1972, 1976b; Walker et al., 2002), and the number of geographical bins as proxies for area (equal-area grids on geological maps or number of geological maps) (Hallam and Wignall, 1999; Peters and Foote, 2002; Smith et al., 2001; Smith, 2001). Crampton et al. (2003) suggests that outcrop area is the best metric, but no worldwide compendium is currently available for the stage-level. We compare here the diversity data of spatangoids against the data for Cretaceous stages provided by Smith (2001) and by Peters and Foote (2002) because they focused on different continents, Western Europe and North America, respectively (Table 1). Estimations provided by Peters and Foote (2002) and by Smith (2001) are not so well correlated for the Cretaceous, and three stages (Albian, Campanian and Maastrichtian) do indeed have a proportionally higher record in North America than in Western Europe. The differences between the two estimations reflect different tectonic and paleogeographical histories. Western Europe records one large-scale cycle with a maximum for the sedimentary record in the Cenomanian whereas North American data show a cycle reaching a maximum in the Albian and a second period of high sedimentary accumulation during the Campanian and Maastrichtian. In order to avoid artefacts in our estimation, we compared the diversity for both available data sets. However, the data from Peters and Foote (2002) cover a much wider area and are thus more representative of the worldwide sedimentary record.

The South Tethyan realm has yielded a significant number of fossil spatangoid species (about 25%) and palaeontological data suggest that important events in the history of early spatangoids occurred in this region. Pending precise estimation of the sedimentary record in North Africa, interpretation of a correlation with diversity should be treated with caution.

2.3. Definition of palaeogeographical framework

Fossils of the *Heteraster* and *Douvillaster–Macraster* clades occur mainly in lower shoreface and upper offshore environments of the Tethyan and Peri-Tethyan margins, from Japan to the western American coasts (Villier, 2001). The entire geographical range is divided into nine units (Fig. 1): East coast of Africa (Madagascar, Mozambique, Somalia), Far East (Japan), Central and North America (Honduras, Mexico, USA), South America (Colombia, Equator, Venezuela, Peru), Western Europe (England, France, Portugal, Spain, Switzerland), Northwest Africa (Algeria, Morocco, Tunisia), East Mediterranean (Egypt, Israel, Lebanon, Syria), Eastern Europe (Bulgaria, Hungary, Serbia), Central Asia (Afghanistan, Azerbaijan, Northern Iran, Turkmenistan). Units were established from palaeogeographical data (Peri-Tethys maps, Dercourt et al., 2000) and determined by their average areas and biogeographical provincialism.

The latitudinal range of *Heteraster* and *Douvillaster–Macraster* clades covers a relatively limited strip of tropical and equatorial waters. In this range, benthic marine organisms generally have a variable but high diversity (Crame, 2000), and we predict a reduced influence of latitudinal diversity gradients comparing the diversity recorded from two geographical units.

2.4. Statistical treatment of diversity data

The diversity signal is a composite function and is dependent on a large number of factors. A few of these factors consist of evolutionary information, while the others can be thought of as sampling artefacts. The aim of statistical processing of

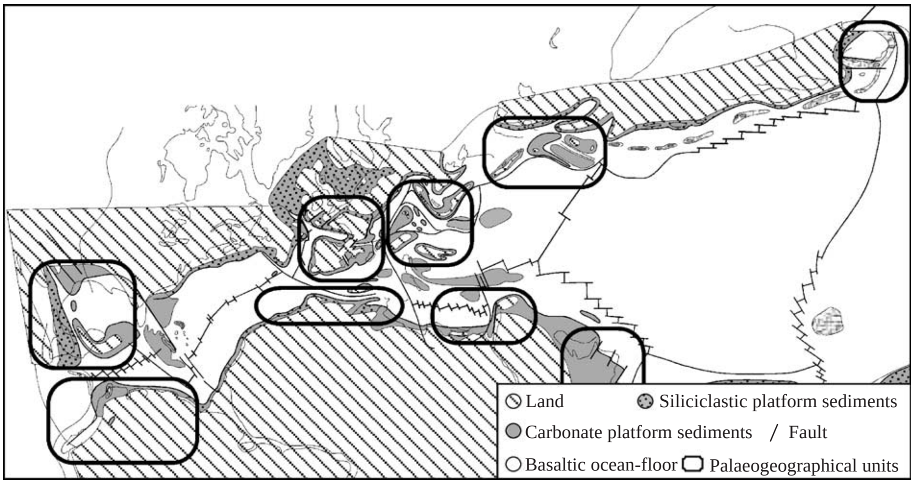

Fig. 1. Definition of the palaeogeographical units considered for estimation of diversity. Palaeogeographical background map is a simplified version of the Peri-Tethys map for the Early Aptian (Masse in Dercourt et al., 2000).

diversity data is generally to attempt to minimise the impact of sampling biases. Variations through time of diversity are sensitive to autocorrelation, which can obscure the influence of external factors. The effect of autocorrelation is generally removed by working with detrended signals. Diversity can also be standardised against variables suspected of involving artefacts, generally by dividing the diversity by the biasing factor (e.g., duration of time intervals). This assumes a restrictive linear relationship, which is not necessarily correct and does not remove all undesirable statistical properties of diversity estimates (sensitivity to completeness of the fossil record, duration of time intervals, edge effect, relative fluctuations of origination and extinction rates) (Foote, 1994, 2000). Regressions can be used to standardise data, and the analysis of residuals allows a corrected and detrended signal to be constructed. The accuracy of standardised data depends on the statistical robustness of the regression model. The least square regression (OLS) is the traditional and most popular method of seeking out relationships between variables (Saporta, 1990). However, this method is highly sensitive to outliers, showing a so-called "0% breakdown value" which means that "an arbitrary small percentage of bad observations change the OLS coefficients to any value at all" (Zaman et al., 2001, p. 2), implying restrictions on assumptions about data. The presence of a few outliers falling beyond the range of the model can greatly affect the results and obscure true relationships, even in large samples. Outliers can reflect analytical error, such as misestimates of diversity, or valid data that point to evolutionary events that fall outside the background conditions. In both cases, detection of outliers provides a key for understanding the evolutionary significance of the diversity signal. Removal of outliers in the standardisation of diversity data holds two main advantages. On the one hand, the quality of standardisation increases as fit of the regression model is improved, and on the other hand, events that may underlie evolutionary information are identified (the outliers). More generally, when the model of regression between diversity and sampling artefacts cannot predict outliers, they can be determined by independent factors and are potentially informative about evolution.

The processing of outliers is a domain where classic OLS fails, but it is the main domain of robust statistics (Zaman et al., 2001). Many alternative estimates exist, the best known and most widely used being the least median of squares (LMS) proposed by Rousseeuw (1984). At the same time, Rousseeuw proposed another technique known as the least-trimmed squares (LTS). This robust estimate is based on the analysis of subsets of the data matrix and its objective is to find the subset that minimises the trimmed sum of squared residuals (Rousseeuw and Hubert, 1997). In this case, the data excluded are outliers. In practice, OLS is calculated for random subsets of different sample sizes (h), sampled without replacement from n observations. An iterative procedure searches for the optimum subsets and for each value of h, in which the OLS possesses the lowest sum of squared residuals. LTS shows a high breakdown value equal to $(n-h+1)/n$, implying that results in standard applications are both robust and reliable. In the optimal case, LMS and LTS possess similar high breakdown values, but LTS is statistically more efficient. Its only shortcoming, considerable long computation time (Hawkins and Olive, 1999; Rousseeuw and Hubert, 1997), has been overcome by construction of a fast algorithm for LTS regression by Rousseeuw and van Driessen (1999: http://win-www.uia.ac.be/u/statis). The program computes the LTS estimate by the exact algorithm in the case of bivariate data (Rousseeuw and Leroy, 1987), whereas the fast algorithm is applied to multivariate data (Rousseeuw and van Driessen, 2000). The number (h) of points selected in subsets needs to be determined a priori. The optimal value of h is $(n+p+1)/2$, where p=number of variables, but h may be any integer within the interval $(n+p+1)/2 \leq h \leq n$ (Rousseeuw and Hubert, 1997). In the case study of spatangoid heart urchins, we computed the LTS for each value of h between $n/2$ and n, an interval that includes the optimal case. The sensitivity of the analysis to the h value is observed and characterised by variations of LTS parameters (scale estimate of the reweighted residuals, robust r^2, number of outliers detected). The value of h selected here was the highest value for which the number of outliers identified remained stable and increased the fit of the regression (Fig. 2).

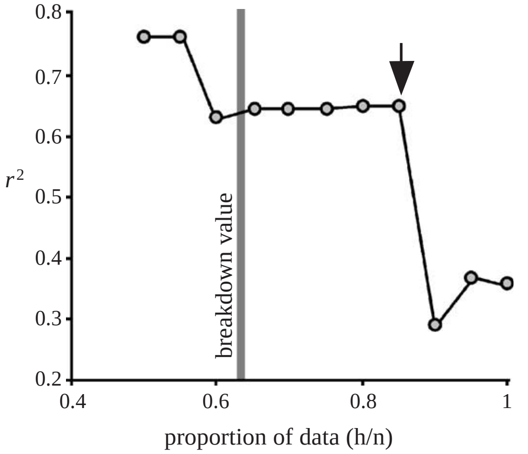

Fig. 2. Variation in the number of outliers identified by LTS when the size of the input matrix (h) varies between n and $n/2$. Example of correlation between the number of species at t_i and at t_{i-1}, reflecting self-dependence of the diversity signal. Arrow indicates the point at which the number of outliers becomes stable. Those values were selected for calculating the regressions.

After extraction of the outliers by LTS, a least square regression was carried out on the reduced sample and its coefficients were computed. This last step allowed direct comparison between the coefficients before and after removing outliers and permitted detection of improvements in the fit of data (Zaman et al., 2001). A notable change in coefficient values implies that outlying values have a strong impact on the OLS. The results of the LTS are thus better suited for analysis of diversity signals. Diversity data for the Cretaceous spatangoid heart urchins match the assumptions for the use of LTS. However, the data set is reduced to 12 time intervals, and such a small sample weakens the robustness of the regression. Exclusion of one or two outliers is expected to change notably the regression coefficient. As a consequence of a high-risk of type I error in the identification of outliers, we discussed neither regression parameters nor outliers individually. Only outliers that were recog-

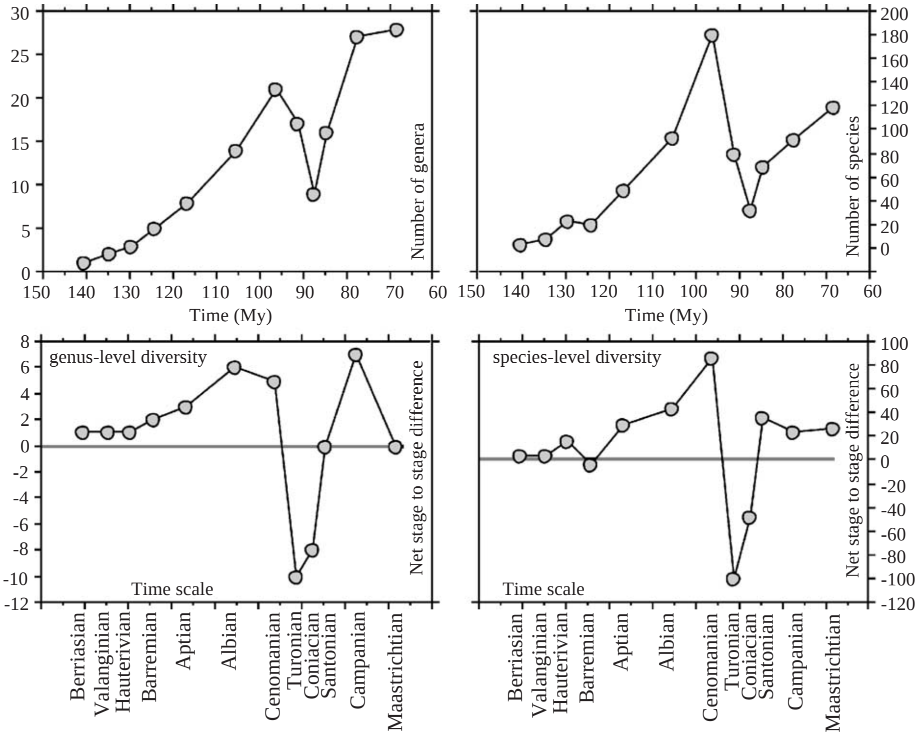

Fig. 3. Variation of spatangoid heart urchin's diversity during the Cretaceous.

Table 2
Relationships between diversity and the duration of time intervals

	Duration	Cst. term	r^2	% Data	Significance	Outliers
Standing diversity—genus-level						
All data	2.99	44.01	0.04	100	NS	
Outliers excluded	–	–	–	–	NS	–
Standing diversity—species-level						
All data	0.68	8.10	0.06	100	NS	
Outliers excluded	–	–	–	–	NS	–

Cst. term: constant term of the regression. Duration: duration of time intervals. Significance of the correlation: ***Highly significant ($p<0.001$); *significant ($p<0.01$); NS=non-significant correlation.

nised in various analyses have been considered in the discussion.

3. Diversity pattern of spatangoid heart urchins

Our data for the Cretaceous (Fig. 3) show slight differences from previous diversity patterns (Kier, 1974; Eble, 1998). The number of genera increases regularly from the Berriasian to the Cenomanian, drops to a low value in the Coniacian, while highest values are reached in the Campanian and Maastrichtian stages. The number of species increases steeply from the Berriasian to a maximum in the Cenomanian. It decreases during the Turonian and the Coniacian stages and increases again from the Coniacian to the Maastrichtian, but does not reach the high point observed in the Cenomanian. Trends for species-level and genus-level signals are relatively similar (Fig. 3). The number of genera is closely correlated with the number of species (Spearman rank correlation test, $r_s=0.904$, $p<0.001$). Considering the similarity of patterns, genus- and species-level data are likely to reflect the same factors. Although bias in the fossil record has been suggested, the diversity of spatangoids is generally accepted as documenting an evolutionary radiation during the Cretaceous (Smith, 1984; Eble, 1998, 2000). We predict therefore that evolutionary factors underlie the long-term trend and sampling biases explain at least part of the stage to stage fluctuations. Detrended signals are used below to analyse specific relationship between diversity and potential bias. Detrended diversity data was calculated as the net difference between consecutive stages. The main trend was removed, but the Turonian and Coniacian stages still have relatively low values at both the genus- and species-levels (Fig. 3).

4. Bivariate approach to relationship between diversity and potentially biasing factors

4.1. Impact of time scale

In the case of spatangoid heart urchins, diversity was estimated at stage-level. The duration of Cretaceous stages varies, ranging from 2.3 to 13.3 My, with a mean duration of 6.6 and a standard deviation of 3.34. Such a wide range of variation permits assessment of the influence of time scale on diversity. However, both OLS and LTS failed to found a correlation at either the species- or the genus-level (Table 2). A weak correlation was found by LTS using the detrended signal.

4.2. Impact of autocorrelation of diversity

Temporal variation in diversity is a cumulative and self-dependent variable. The diversity at time t_i depends on diversity at time t_{i-1}. It varies with the number of species present at t_{i-1}, some species being extinct, others surviving, with new ones appearing through speciation events. As an effect of the self-dependence of diversity metrics, the number of extinctions and originations is expected to be proportional to the number of taxa (Stanley, 1990). In a time series, diversity values are not statistically independent data, but imply autocorrela-

Table 3
Relationship between diversity at a given time (t_i) and diversity at the previous interval (t_{i-1})

	Nt_{i-1}	Cst. term	r^2	% Data	Significance	Outliers
Standing diversity—genus-level						
All data	0.91	3.21	0.71	100	***	
Outliers excluded	1.60	0.46	0.97	75	***	Turonian, Coniacian, Maastrichtian
Standing diversity—species-level						
All data	0.60	31.59	0.36	100	*	
Outliers excluded	1.52	6.69	0.65	85	***	Turonian, Coniacian

Nt_{i-1}: number of taxa at the previous time interval. Cst. term: constant term of the regression. Significance of the correlation: ***Highly significant (p<0.001); *significant (p<0.01); NS=non-significant correlation.

tion. This is analysed here by regressing diversity at t_i against diversity at t_{i-1}. In the case of autocorrelation, regression models can predict a value at a given time, if diversity is known for the previous or the next interval. Such a relationship is expected when a signal follows a random walk model, that is, when a signal has stable properties and evolves from one initial value by random variation at each step (see Sepkoski, 1994). In interpreting evolution, the slope of regression reflects the main trend for diversity (the slope should equal one when diversity is stable, but lies above or below one when diversity increases or decreases respectively).

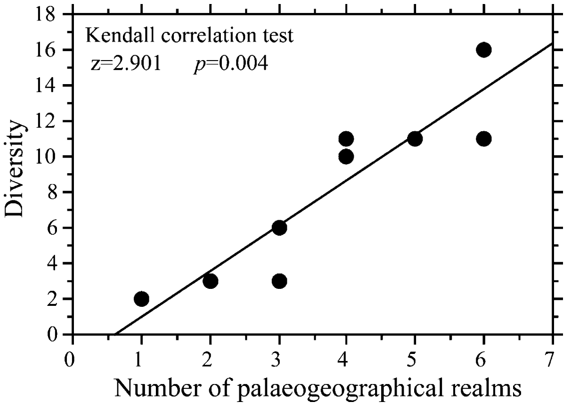

Fig. 4. Relationship between diversity and the number of palaeogeographical realms under consideration tested using a non-parametric test (Kendall correlation test), with a regression line plotted for guidance only. Diversity represented by the number of species for the *Heteraster* and *Macraster–Douvillaster* clades, each clade being counted separately. Each point represents data for a given time interval. One species can be counted in several palaeogeographical realms and time intervals, depending on its range.

In the example of spatangoid heart urchins, plots of diversity at t_i against t_{i-1} show a strong correlation (Table 3). The slope emphasises the expected diversification for spatangoids during the Cretaceous (slope 1.52 for species and 1.60 for genera). This main diversity trend through the Cretaceous suggests a biological explanation with a regular rate of diversification. Values in the Turonian and Coniacian form outliers in both species- and genus-level analyses with diversity lower than expected in the case of a regular diversification pattern.

4.3. Impact of the palaeogeographical framework

In the spatangoid clades *Heteraster* and *Douvillaster–Macraster*, the number of species counted for one time interval is correlated with the number of geographical realms considered—a Kendall rank correlation is highly significant (Fig. 4). Both clades analysed have a similar relationship to palaeogeography. The measured diversity of each clade is strongly linked to its geographical range as presence or absence from any palaeogeographical province affects diversity in a constant way. The correlation predicts co-occurrence of one to three species per paleogeographical province at one time, which is consistent with many examples from the Recent oceans (Hyman, 1955) and for other genera of Cretaceous spatangoids (Smith, 1992). This argues for the reliability of diversity measured at a regional scale, the number of sympatric species being stable through time and among groups (Table 4).

4.4. Impact of the sedimentary record

Our analysis revealed a link between the measured diversity of spatangoids and an estimation of the sedimentary record. However, comparisons with the two estimations of the sedimentary record available lead to the recognition of different outliers (Table 4). Three outliers are extracted when genus-level diversity is compared to data for Western Europe (Coniacian, Campanian and Maastrichtian), whereas correlation with data from Peters and Foote (2002) show a better fit and does not support extraction of outliers. This suggests that the main trend in diversity is linked to the sedimentary record (whatever the driving process). Species-level diversity is less well correlated with estimates of the sedimentary record. LTS failed to detect a correlation with data for Western Europe and identified one outlier for the North American data (Cenomanian). The difference between genus- and species-level analyses found here is counterintuitive. Using range-through method for estimation of genus-level diversity should smooth the signal and the volatility of species-level standing diversity should imply higher sensitivity to bias, including the sedimentary record.

Correlations are even less significant for analyses using detrended diversity and estimates of the sedimentary record. LTS found only one supported relationship between genus-level diversity and the estimates by Peters and Foote (2002), when three outliers are excluded (Cenomanian, Turonian and Coniacian). Three outliers represent 25% of the data, which is a high number close to the breakdown value and the reduced sample size suggests a weak statistical support. Therefore, a link between changes in standing diversity and changes in sedimentary record is plausible, but not well supported by the data.

5. Multivariate approach and hierarchy of factors

We attempted to build these factors into a hierarchy using multivariate stepwise regression (Table 5). Regression was performed after extraction of multivariate outliers by LTS. Multivariate approach leads to similar interpretation when

Table 4
Relationships between diversity and the amount of sediment available for sampling

Standing diversity—genus-level

	SR. WE	Cst. term	r^2	% Data	Significance	Outliers
All data	0.08	7.70	0.09	100	NS	
Outliers excluded	0.21	−3.21	0.95	75	***	Coniacian, Campanian, Maastrichtian

	SR. NA	Cst. term	r^2	% Data	Significance	Outliers
All data	0.33	1.49	0.83	100	***	
Outliers excluded	0.33	1.49	0.83	100	***	no outlier

Standing diversity—species-level

	SR. WE	Cst. term	r^2	% Data	Significance	Outliers
All data	0.81	16.56	0.27	100	NS	
Outliers excluded	–	–	–	–	NS	–

	SR. NA	Cst. term	r^2	% Data	Significance	Outliers
All data	1.30	10.05	0.44	100	NS	
Outliers excluded	1.30	10.05	0.80	95	***	Cenomanian

SR. NA: data focuses on North America, but records from the rest of the world are also taken into account. This is a compiled estimation of sedimentary record produce by counting the number of marine sedimentary formations (Peters and Foote, 2002). SR. WE: estimation with number of geological maps in United Kingdom and France used as proxy for the number of sedimentary outcrops (Smith, 2001). Significance of the correlation: ***Highly significant (p<0.001); *significant (p<0.01); NS=non-significant correlation.

Table 5
Mutivariate stepwise regression of spatangoid diversity against duration of time intervals, self-dependence and estimation of the sedimentary record

Standing diversity—species-level							
		Nsp.t_{i-1}	SR. WE	Duration	Cst. term	r^2	
All data	Step 1	0.60	–	–	18.73	0.36	
		Nsp.t_{i-1}	SR. WE	Duration	Cst. term	r^2	Outliers
Outliers excluded	Step 1	1.52	–	–	6.69	0.89	
	Step 2	1.13	0.56	–	−13.63	0.97	Turonian, Coniacian
		Nsp.t_{i-1}	SR. NA	Duration	Cst. term	r^2	
All data	Step 1	–	1.39	–	−16.61	0.48	
		Nsp.t_{i-1}	SR. NA	Duration	Cst. term	r^2	Outliers
Outliers excluded	Step 1	–	1.30	–	10.05	0.81	
	Step 2	0.21	1.12	–	5.41	0.87	Cenomanian
Standing diversity—genus-level							
		Ng.t_{i-1}	SR. WE	Duration	Cst. term	r^2	
All data	Step 1	1.92	–	–	3.21	0.71	
		Ng.t_{i-1}	SR. WE	Duration	Cst. term	r^2	Outliers
Outliers excluded	Step 1	1.15	–	–	2.73	0.90	
	Step 2	1.12	0.07	–	−0.65	0.93	Turonian, Coniacian
		Ng.t_{i-1}	SR. NA	Duration	Cst. term	r^2	
All data	Step 1	–	0.40	–	1.49	0.83	
	Step 2	–	0.40	−1.04	5.90	0.92	
		Ng.t_{i-1}	SR. NA	Duration	Cst. term	r^2	Outliers
Outliers excluded	Step 1	–	0.40	–	1.49	0.83	
	Step 2	–	0.40	−1.04	5.90	0.92	No outlier

Four analyses are presented, considering species- and genus-level data and the two estimates of the sedimentary record available. Duration: duration of time intervals. Ng.t_{i-1}: number of genera at the previous time interval. Nsp.t_{i-1}: number of species at the previous time interval. SR. WE: estimation of the sedimentary record after Smith (2001). SR. NA: estimation of the sedimentary record after Peters and Foote (2002). Cst. term: constant term of the regression.

applied on genus- and species-level diversity signals. Time scale properties have a minor effect. The relative influence of the sedimentary record and autocorrelation is balanced depending on the estimation of sedimentary record taken into account. When the estimation derived from North America is considered, the sedimentary record has a high explanatory power for the diversity data and no or only one outlier is detected (Table 6). On the contrary, estimations for Northwest Europe explain a low level of variance, lower than the autocorrelation. Thus, the sedimentary record and autocorrelation have similar powers to explain the main diversity trend, depending on the data analysed.

Low or non-significant multivariate correlation is found for detrended data, as LTS extracts outliers close to the “0% breakdown value”. Only genus-level data lead to significant results. The Cenomanian, Turonian and Coniacian stages are recognised as putative outliers whichever estimate of sedimentary record is used. Stepwise regression retains a single step supported correlation with duration of the time intervals. This may suggest that detrended data consist largely of noise or analytical bias.

6. Discussion

6.1. The reduced impact of the time scale

Diversity studies generally try to compare intervals of similar duration in order to obtain a homogeneous understanding of diversity, or to standardise diversity against time (Boucot, 1975; Raup, 1976a). No attempt was made here to reduce the analytical bias for raw diversity data. Taxa known from a single time interval (singletons) are widely recognised as distorting signals of standing diversity, origination and extinction (Gilinski, 1991; Foote, 1994; Alroy, 1996). It is expected that longer time intervals are likely to yield higher diversity values. A relationship nearly linear is expected between diversity and duration of time intervals in the case of constant turnover rate (Foote, 2000). Diversity values that deviate from the regression may be interpreted in terms of exceptionally low (deficit) or high record of diversity (excess). Such outlying values may result from heterogeneity in the fossil record or biological crises as well. In evolutionary terms, deficit corresponds to extinction and excess to diversification. An evolutionary explanation is likely when a particular clade is affected by a diversity crisis, independently of other clades overlapping in their ecological affinities.

The standing diversity of spatangoids does not seem to be related to the duration of time intervals. No correlation was found and the analytical relationship between diversity and the time scale cannot explain the main trends in the diversity pattern. This is surprising, because as discussed above, a link is expected when counting raw occurrences, without correcting for the ‘singleton’ effect, and considering that LTS increases statistical power by removing outliers. The most likely explanation for non-significance of the LTS is that the effect of heterogeneity in the time scale is negligible compared to the impact of other factors on the main diversity pattern.

6.2. Taxonomic levels and sampling bias

Although the variation through time of genus- and species-level signals has a similar pattern, the number of species only correlates weakly to the factors analysed. We found no significant correlation with the duration of time intervals and significant results only for autocorrelation and for sedimentary record of North America when outliers are excluded. In contradiction to our results, it is generally assumed that the number of species is highly sensitive to systematic bias and stratigraphical ranges that are generally shorter than stages. Systematic bias is supposedly randomly distributed in Cretaceous spatangoid heart urchins and thus should have a reduced impact. ‘Singleton’ effects should have strengthened links between diversity and the duration of time intervals, but this is not the case.

Smith (1992) has shown that current knowledge of Cenomanian diversity in terms of species richness of echinoids is generally well correlated with the number of specimens available. Many of the recently published monographs focus on Cenomanian and Maastrichtian while early Cretaceous is underrepresented. It is thus likely that heterogeneous sampling effort of time intervals explains some fluctuations of species-level diversity. Using range-through method at the genus-level probably smoothes the sampling biases and means that the number of genera is a more reliable signal, although the main trends are similar at the species- or genus-level.

6.3. The difficulty of analysing relationship to the sedimentary record

Most of the uncertainty in the interpretation of the relationship between spatangoid diversity and the sedimentary record results from a lack of estimation of sedimentary record at global scale. However, the most inclusive estimation (Peters and Foote, 2001, 2002) is capable on its own of explaining the main trend of increasing diversity in the Cretaceous. To the current knowledge, the putative correlation between sedimentary record and measured diversity of spatangoids supports either interpretation of sampling bias or evolutionary signal.

Several empirical studies have shown a close correlation between diversity and estimates of the volume of the sedimentary record, and numerous models predict such a relationship (Raup, 1972, 1976b; Sepkoski, 1976; Smith, 2001; Peters and Foote, 2001, 2002; Crampton et al., 2003). On the one hand, correlation may result from a simple artefact: the more sediment is preserved the more fossils and taxa are preserved. On the other hand, other

Table 6
Comparison between first occurrence dates for spatangoid clades in Western Tethys (Europe and North Western Africa) and the American Continent

Taxon	Western Tethys	American continent
Toxaster (paraphyletic)	*Toxaster rochi*, Berriasian	*Toxaster colombianus*, Hauterivian
Heteraster clade	*Heteraster corvensis*, Hauterivian	*Heteraster alencasterae*, Upper Aptian
Douvillaster clade	*Douvillaster convexus*, Aptian	*Macraster solitariensis*, Lower Albian
Micrasterina	*Epiaster polygonus*, Upper Aptian	*Epiaster dartoni*, Upper Aptian (?)
Hemiasterina	*Hemiaster minimus*, Upper Aptian	*Palhemiaster comanchei*, Lower Albian

A delay for all cases suggests an earlier appearance in Western Europe and later migration to America. Clades are defined after Villier et al. (2004).

models explain the correlation through evolutionary models, diversity and sedimentary record being sensitive to mutual causes (e.g., sea-level fluctuations).

At the scale of the outcrop or regional section, taphonomic bias, type of sediment recorded, pattern of sedimentary deposits and ecology of taxa determine the preserved diversity. Preservation and environmental conditions vary according to sea-level fluctuations, which is therefore considered as a principal factor controlling the fossil record (Brett, 1995, 1998; Holland, 1995, 2000; Schaaf, 1996; Gale et al., 2000; Smith, 2001). This has been largely documented in echinoids and underpins sampling bias and evolutionary mechanisms (Néraudeau et al., 1997; Smith et al., 2001).

At a wider scale, sea-level fluctuations modify the surface of shelves with shallow marine conditions. Given that most marine organisms live on shelves, sea-level rise increases the surface available for the marine fossil record and the surface inhabitable by shallow marine benthic communities (and consequently diversity). Recorded diversity is therefore likely to vary in proportion to the area of the shelf covered by the sea (Flessa and Sepkoski, 1978; Sepkoski, 1987, 1991). This could be the case for spatangoids that are most diverse on shelves and continental slopes (Durham, 1966). The relationship between recorded diversity and sea-level fluctuations is dual and reflects the joint effect of sampling bias and ecological constraints, but their respective contribution to the signal remains unknown. As an example, the same kind of data has been previously interpreted as an evolutionary signal (Sepkoski, 1976; Benton, 1990; Foote, 2003) or as a probable sampling bias (Raup, 1972; Smith, 2001; Smith et al., 2001; Peters and Foote, 2001, 2002).

6.4. Relationship to palaeogeography

The relationship between diversity and the number of geographical domains represented can reflect either a heterogeneous record among domains (true or by lack of collection), or an evolutionary signal, in which faunal migrations are associated with diversification events.

Heterogeneity of sampling among provinces is likely to distort the relationship, the diversity within a province fluctuating from high diversity when it is well-explored to weak diversity when under-explored. It is obvious that worldwide, all potential outcrops or accessible areas have not been sampled with the same intensity. For historical reasons, Europe, North Africa and North America have been more extensively and intensively studied than Asia or South America. About 30% of Cretaceous spatangoid species were reported from the Western Europe whereas only 10% were reported from Japan or the Caribbean. Such asymmetry in the sampling effort is likely to have curtailed estimation of the diversity preserved in the fossil record. However, heterogeneity of shallow marine sedimentary record is also likely to lead to an heterogeneity of diversity among provinces.

In evolutionary terms, geographical history is expected to have a significant impact on the history of diversity. Sporadic connections between geographical domains induce migration and faunal exchanges. Separation of species or population habitats is likely to result in allopatric speciation (model of vicariance). Positive correlation between diversity and the number of geographical domains is expected, assuming a diversification event constrained by palaeogeography. When a lineage settles in a new, unoccupied area, it may experience origination. In the case of successive settlements of new domains, each step is associated with diversification events. Such a pattern of clade dispersal and diversification should be obvious in the fossil record and consistent for different groups and at different times, which is the case in spatangoids.

The most primitive *Heteraster* species are from the Hauterivian of Portugal. The genus is recorded from all northern Tethyan units during the Barremian, colonise the southern Tethyan margins during the Late Aptian and in the American continent during the Late Albian (Villier, 2001). The *Douvillaster–Macraster* clade occurs only on the North African margin during the Aptian and expanded its geographical distribution during the Albian, which is attested by records from Europe, Africa, and Central and North America (Neumann, 1996). A similar pattern is evident at a larger taxonomic scale. The earliest known spatangoids are from the Middle Berriasian of Morocco (Devriès, 1960). According to the data of Fischer (1966), all spatangoid families, save one, with a fossil record from the Cretaceous have their earliest occurrence in Europe even if they have been found on other continents. In the preliminary phylogenetic scheme proposed for primitive spatangoids (Villier et al., 2004), the most primitive members of clades are known from the western Tethyan realms. This supports the hypothesis of a single place of origination for the Cretaceous families of spatangoids (the shelves of the western Tethys) and several phases of dispersion each associated with diversification events. As an example, the first occurrence of spatangoid clades in America is always delayed when compared to the Western Tethyan realms (Table 6). This delay cannot be explained by a deficit of record in America since various echinoids are known continuously through the Cretaceous in the Andean basin (Néraudeau and Mathey, 2000).

6.5. Interpretation of the main diversity trend

Heart urchins of the order Spatangoida first appear in the fossil record during the middle Berriasian. The number of families and genera gradually increases in the Cretaceous reaching a maximum during the Eocene, but later decreases (Eble, 1998). The number of species reaches a high point in the Cenomanian and fluctuates subsequently. Kier (1974) suggested that fluctuations of standing diversity mainly reflect variable duration of time intervals and by amount of sediment available for sampling, but our analyses do not fully support his hypothesis.

At a large scale, the temporal evolution of the diversity signal and the correlation between diversity and other data sources remains difficult to understand. The main diversity trend can be accurately estimated from the variables analysed (sedimentary record, self-dependence). Links to the sedimentary record and autocorrelation of the diversity signal can both explain the main trend of diversity increase through the Cretaceous. The sedimentary record is the primary factor when the estimate proposed by Peters and Foote (2002) is taken into account. Alternatively, autocorrelation seems to drive trends when the data published for Western Europe is considered (Smith, 2001).

Considering relationships between diversity and individual variables, an evolutionary signal is favoured. A non-significant relationship with time scale properties eliminates a potential analytical bias. Autocorrelation supports the interpretation of diversification at a regular rate and potentially linked to intrinsic determinism. A strong link with the palaeogeographical framework at a low taxonomic level (*Heteraster* and *Douvillaster–Macraster* clades) suggests that diversification events were connected to geographical dispersal from a main centre of origination.

Results from methods of analysis that are weakly sensitive to ‘geological bias’ (phylogeny, morphological disparity) suggest a more robust evolutionary pattern than statistical treatment of diversity alone. Phylogenetic trees imply a progressive diversification of Spatangoida, and origin of the modern families from a burst of basal lineages representing various character associations (Villier et al., 2004). Similarly, temporal changes in disparity reveal constant diversification during the Cretaceous with a progressive deceleration in morphological innovation (Eble, 1998, 2000). This disparity pattern closely fits the models of evolutionary radiation (see, e.g., Foote, 1993). Evolutionary hypotheses grounded in phylogeny, functional analysis, or disparity curves may thus be compared against diversity data. Exploring this aspect, Eble

(1998) found consistency between patterns. Among the alternative interpretations of the correlations found in our analysis, the hypothesis of evolutionary significance is therefore reinforced.

6.6. Dynamics of spatangoid diversification and interpretation of outliers

Autocorrelation of diversity data supports the hypothesis of a constant diversification dynamic, obscured or interrupted by apparent low diversity during the Turonian and Coniacian stages. The substantial drop in diversity between the Cenomanian and the Turonian suggests some kind of crisis at this time. Eight nominal genera have their last record in the Cenomanian (*Heteraster*, *Jordaniaster*, *Macraster*, *Physaster*, *Polydesmaster*, *Pliotoxaster*, *Somalechinus* and *Toxaster*). *Somalechinus* is so poorly described that it cannot be usefully discussed and the phylogenetic status of *Physaster* is not yet resolved. *Heteraster* last appears in the Lower Cenomanian of France and Texas, its disappearance recording the extinction of a clade, but this cannot be directly related to an end-Cenomanian event. *Macraster* and *Douvillaster* are probably synonymous and form a monophyletic group that survived into the Turonian. *Toxaster* and *Pliotoxaster* are generic names for paraphyletic stem spatangoids. Similarly, *Jordaniaster* and *Polydesmaster* are characterised by plesiomorphic character states of Hemiasterina. Therefore, the apparent 'crisis' event may be misleading. It is difficult to measure how apparent extinctions reflect extinction of lineages or morphological changes in evolving lineages because the decrease in recorded taxon names could be linked partially to phylogenetic and systematic imprecision.

A sampling bias is the most likely explanation for the low diversity in the Turonian and Coniacian stages. Most of the corrections of diversity by the 'range-through method' affect the Turonian and Santonian. The Coniacian is thus surrounded by intervals with a poor fossil record. In such a case, 'range-through method' may not be appropriate for calculating a reliable estimation of Coniacian diversity. The Turonian, Coniacian and Santonian are also the three shortest stages of the Cretaceous and have a relatively low sedimentary record compared to other Late Cretaceous stages. This suggests a high deficit of sampling in the interval from the Turonian to the Santonian.

The end Cenomanian crisis had a much more reduced impact on spatangoid diversity than suggested by the fossil record. Smith et al. (2001) drew a similar conclusion for the echinoid order Cassiduloida, explaining the end Cenomanian decrease in recorded diversity as a conjunction of two main factors: (1) inconsistencies between systematic and phylogenetic history, and (2) poor fossil record during the Turonian.

7. Conclusion

Statistical processing of diversity data is generally used to distinguish quantitatively between analytical bias, impact of the fossil record and evolutionary signal. Search for correlation between the diversity of spatangoid heart urchins and putative factors of bias does not clearly decipher the respective contribution of sampling bias and evolutionary signal in the raw data. Nevertheless, the use of robust estimation allows the identification of significant correlations where standard correlation fails, and rationalises the identification and understanding of the outliers. The case study of spatangoid heart urchins demonstrates that the influence of variation in duration of stratigraphical units is reduced compared to other factors. The main diversity trend can be explained by several hypotheses all supporting an evolutionary interpretation—a diversification through the Cretaceous. Assuming an evolutionary signal, the nature of the correlation with the diversity signal that we found helps in measuring its properties from parameters of regressions. Linear autocorrelation suggests a relatively constant rate of diversification. The stability in the number of species per paleogeographical provinces successfully predicts the expected number of sympatric species in a genus. Recognised as recurrent outlying values, the low diversity during the Turonian/Coniacian interval suggests impact of a Cenomanian/Turonian crisis. This crisis was reported for many different groups of marine organisms, but at least in spatangoids, this crisis appears to be misleading and reflects sampling heterogeneity and immature systematics. Thus, the overall pattern of spatangoid diversity is not determined by a single predominant factor throughout the entire Cretaceous. Although the diversification was strong enough to sustain the main trend, periods associated with high sampling bias obviously impact the measured diversity.

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