INTRODUCTION

Macroevolutionary theory is concerned with both large-scale patterns and particular events, and with the processes that shaped those patterns and events. Numerous studies of macroevolutionary patterns have investigated diversity fluctuations, origination and extinction rates, morphologic novelities, and their relative success among clades (Raup and Sepkoski, 1982; Jablonski, 1999). They have shown that the fossil record exhibits nonrandom patterns in space and time (Jablonski, 2000). These macroevolutionary studies are conventionally based on the number of taxa, i.e., taxonomic diversity. A new measuring rod, morphological disparity, has been developed to provide a fresh take on biodiversity and its dynamics (Foote, 1993; Roy and Foote, 1997). When used as complementary metrics, taxonomic diversity and morphological disparity yield new information on radiations (Ehle, 2000) and on developmental or biogeographical constraints (Cianciaglione et al., 2001; Neige, 2003, respectively).

Like any other measurements based on biodiversity sampling, diversity and disparity are not free from bias. Such bias can be split into three (not wholly independent) categories: (1) the differential quality of the fossil record depending on stratigraphic context and age of fossil-bearing rocks (Benton et al., 2000; Holland, 2000; Jablonski et al., 2003); (2) the methods of characterizing biodiversity (i.e., taxonomic diversity and morphologic disparity), including the effect (or lack of effect) of the inclusion of many paraphyletic groups in fossil classification (Sepkoski and Kendrick, 1993; Patterson and Smith, 1987); and (3) the influence of paleontological practice (e.g., study effort, sampling intensity) on biodiversity fluctuations (e.g., see Signor, 1985; Foote, 1997). The argument is that as new discoveries are made, some of the species names attributed no longer correspond to coherent entities but can be included within the variability of others (Alroy, 2002). Thus, biodiversity estimates vary with the accumulation of knowledge and with taxonomic revisions over palaeontographical time (for cephalopod-based analyses, see Hewitt, 1989; Donovan, 1994). Discoveries of new taxa affect the morphological disparity metric as knowledge grows, but the relative fluctuation velocities of the two metrics (taxonomic diversity and morphologic disparity) are still poorly understood: from what point are biodiversity signals stable compared with the accumulation of knowledge? Do diversity and disparity fluctuate at the same rate for an identical increase in knowledge? These are particularly important questions, as the comparison between these two metrics may be used to exemplify the existence of macroevolutionary processes complementary to traditional microevolutionary Darwinian processes (Gould, 2002).

The pioneering study by Foote (1997) attempts to answer questions like this by evaluating morphological disparity fluctuations in palaeontographical time over nearly 150 yr. Foote used lists of species names (only one or a few species names per genus per stratigraphic interval) from palaeontological collections and from the literature. Biodiversity fluctuations over palaeontographical time, induced by revisions or by the accumulation of knowledge, are deciphered by comparisons of each metric and of the relationship between the two metrics for several key dates. Foote demonstrated that there is no preferential—early or late—description of either extreme or modal forms, and that the morphological disparity pattern is sensitive to the increase in sampling during palaeontographical time, but concluded that palaeontological patterns are now relatively stable. However, Foote’s sample choice underestimates the effects of taxonomic revisions at the species level (revalidations and invalidations) and their subsequent effect on the diversity/disparity relationship.

We have adopted a similar approach to Foote’s (1997) but at a higher resolution with the accompanying increase in details. Foote’s study of bias is an obvious reference for large-scale studies; this study is intended to supplement it for more detailed questions. This reduction in scale is fundamental for certain issues in biodiversity requiring exploration at this detailed level: short-lived clades, young clades (e.g., Pleistocene patterns and their relationships with modern biodiversity), high turnover groups such as ammonites or trilobites, and critical intervals around mass extinctions. In none of these cases is large-scale sampling a relevant way to clearly identify patterns and to suggest what processes...
may have shaped them. Our study uses a thorough species-level sample of a Lower Jurassic ammonite group. States of knowledge at various paleontographical times are analyzed. We first observe the fluctuation in morphological patterns and compare it with the fluctuation in taxonomic patterns over paleontographical time. We then assess changes in the diversity/disparity relationship during geological time at various historical dates.

DATA

We chose a clade of ammonites that are generally classified as two subfamilies—Hildoceratinae and Leukadiellinae—although a recent cladistic analysis has demonstrated that they form a single group (Rulèau et al., 2003). A total of 85 nominal species was studied, dated to the Toarcian (Lower Jurassic). The current view recognizes 35 valid species (i.e., species for which no reasoned invalidation based on new material or statistical analyses has been published); the others are invalid or synonyms. As our study is based on valid species only, it eliminates biases due to oversampling. The bibliographic compilation starts from Bruguèire (1789) and ends in 2002. We consider this sampling as exhaustive, and so not at risk from biases due to lesser-known journals. This group is useful in that it is the subject of 238 published studies over 214 yr yielding substantial knowledge of their morphology, species clusters, and stratigraphic occurrences, greatly increased by extensive statistical studies of intraspecific variations.

This provides an improved framework for the taxonomic and morphologic variations of the clade. In order to study diversity/disparity relationships for different states of knowledge (i.e., to reconstitute the state of knowledge of successive generations of paleontologists), we collated four databases, giving a picture of biodiversity of the studied group for four paleontographic periods with consistent paleontological practices: (1) 1789–1965, a period of increasing knowledge, when many species were named; (2) 1966–1980, when the first revisions (mostly invalidations) occurred; (3) 1981–1995, when new species were described and a second series of revisions made; and (4) 1996–2002, when more new species were described, although they have not yet been revised.

Diversity and Disparity Quantifications

Taxonomic diversity is represented by the number of valid species, as considered at the closing date of the four key periods. We use Foote’s method of assigning dates to species, taking the accepted date of publication as a proxy for the time the forms corresponding to the name were first known (Foote, 1997, p. 183).

Morphological descriptions of shell shape are based on the original description and on quantitative measurements (linear dimensions) and qualitative descriptions of the type material if available or of representative individuals if not. Two complementary aspects of shell shape were computed independently: shell geometry (section shape and coiling) and shell features (ribs, keel, umbilical wall, and ventral area). These two aspects are generally considered to vary independently, the second being of classificatory value at the species level. Shell geometry (from quantitative characters) was quantified by principal components analysis (PCA), and shell features (from qualitative characters) were quantified by principal coordinates analysis. Two disparity estimators (sum of range and sum of variance) were then calculated from the PCA scores (scaled by the square root of the eigenvalue) and the principal coordinates. Three axes (resulting from these multivariate analysis) were used for the two analyses, covering ~85% of cumulated variance. The extent of occupation of each univariate component was identified by the sum of range, the dispersion of the individuals within the morphospace by the sum of the variances (Eble, 2000). Error bars were calculated from bootstrap analyses (Foote, 1992). Disparity indices and error bars were computed using morphospace-disparity analysis (MDA package; Navarro, 2003).

Trends Through Paleontographical Time

A very general pattern for the two shape aspects (shell geometry vs. shell features) and for the two disparity descriptors can be traced through paleontographical time (Fig. 1): a first stage of increase in both sum of range and sum of variance followed by a plateau stage. However, the timing and intensity of increase are quite different for the two aspects of shell shape. Between 1789 and 1895, shell feature disparity increased greatly, whereas shell geometry disparity increased only slightly. Researchers concentrated on forms presenting very different shell features but with rather similar shell geometries. Thereafter (1895–1915) the indices displayed a sharp increase in shell geometry disparity and a constant increase in shell features disparity. The focus was still on shell features, but also on shell geometry when defining new species. From 1915 to 1965 the indices were relatively stable, demonstrating that no new extreme forms were described. From 1965 to 2002, disparity increased slightly for both shape aspects. However, this increase was only slight compared with the first stage of increase. Shell features were very important from the very beginning of ammonite paleontology. Taxonomists focused on forms with diversified shell features rather than on forms with different shell geometries. The disparity indices show a rapid saturation of morphospaces (Fig. 1).

Superimposition of the cumulated taxonomic diversity curve brings out the diversity/disparity relationships through paleontographical time (Fig. 2). Diversity fluctuations can be divided into four phases: (1) low level from 1789 to the late nineteenth century, (2) a sharp increase in the number of names up to 1920, (3) a second stagnation phase with few new names until 1965, and (4) a second sharp increase in the number of names up to 1987. Thereafter no substantial increase in names occurred except in 2001. This late increase is almost entirely attributable to a single publication whose new names have not yet been revalidated. The first stage of increased disparity is related to shell features. Increased disparity due to shell geometry occurs later but is clearly precocious compared with the increase in diversity. In any case, the morphological disparity of forms is perceived first: e.g., in 1915, the cumulative percentage of disparity relative to the maximum was 80%, whereas only 40% of the total number of valid species were named. Only by 1960 were 50%
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Bias Testing When Naming Species in Paleontology

Previously described patterns may be explained in comparison with a random sampling, which acts as a null hypothesis. The random model is computed using a random order of species naming. Using morphological data of the 35 valid species (as previously described), we were thus able to quantify disparity fluctuations for both shell geometry and shell features through a cumulated number of species (Fig. 3). We note that the random model and actual data (based on true order of naming) are generally not superimposed. The pattern of comparison is different for the two morphological aspects of the shell: (1) for shell geometry (both for sum of range and sum of variance), the random model predicts higher disparity than actually observed, at least for as many as ~20 named species, and (2) for shell features (both for sum of range and sum of variance), the random model predicts lower disparity after ~5 named species. We interpret these observations as reflecting bias. Shell geometry disparity seems to be underestimated for taxonomic purpose, while shell features seem to be overestimated as species diagnostic characteristics. In the latter case, this result indicates a tendency to sample extreme shapes when naming species (see Fig. 3). This contradicts Foote (1997), who reported no evidence of a general tendency to sample extreme species in either early or late stages. The underuse of shell geometry may be correlated to this tendency: in our example, the focus is on obvious morphological differences (i.e., shell features) to the detriment of shell geometry.

Trends Through Evolutionary Time

Diversity and disparity were compared over geological time (Fig. 4). To clearly investigate the effect of increasing knowledge over palentographical time, we made the comparison by using the closing date of each selected historical period (1965, 1980, 1995, and 2002). We used the northwest European zonation for the biostratigraphic framework, species coming from other areas being transposed to this framework. The subzone level was chosen for high precision. The total studied geological time represents 2 m.y. (1) In 1965, both diversity and disparity increased until the Falciferum subzone. This and the following Sublevisoni subzone represent a peak. Above, there is a steady decrease for both shell features and shell geometry. (2) For 1980 and for 1995, the observations are very similar to 1965 (except that the absolute values of diversity and disparity are slightly lower than before). An increase in biodiversity (diversity and disparity) in the Semipolitum subzone is also observable, particularly for 1995, and is much more marked for shell geometry than for shell features. (3) The present-day view presents a smoothing of the curves with a general decline in diversity and a lesser contrast between those subzones displaying maximum disparity and the others. Nevertheless, the maximum is still in the Falciferum subzone. We note a sharp decline in the number of species for the Sublevisoni subzone. This is mainly due to revisions invalidating many species of certain genera. An interesting point is that authors apparently selected fewer valid species, but ones representing more diverse morphologies.

CONCLUSIONS

The results show that fluctuations in morphological disparity and taxonomic diversity are not synchronous: disparity increases faster than diversity over palentographical time. Compared with a random model, our results demonstrate (for shell features) that there could be a trend in palentological practice to recognize and name extreme forms before intermediate ones. Also demonstrated here, as a possible by-product of this tendency, is the underuse of some other morphological variations that are less obvious (here, shell geometry) for taxonomic purposes. As suggested here, this observation contradicts Foote’s (1997) conclusions and may be due to the...
very different taxonomic and stratigraphic scales of the studies. The results imply that estimates of biodiversity are influenced by changes in knowledge over paleontographical time (an expected result), with different rates of variation for taxonomic diversity and morphological disparity (an unexpected result) and even within morphological disparity, depending on which characteristics are studied. However, biodiversity curves plotted against ammonite subzones remain relatively stable throughout paleontographical history. We consider that this relative stability may be explained by two factors: (1) revalidations/invalidations and new discoveries are randomly distributed within the subzones during paleontographical time so that their effects offset each other; and (2) because there is a tendency to identify extreme forms first, the naming of new species does not drastically change the level of disparity. Therefore, our study provides an alternative hypothesis about paleontological practices and the way they bias disparity patterns, compared with Foote (1997), who reported no tendency to sample more extreme species preferentially earlier or later during the study of a group. The next challenge will be to survey other groups in light of these alternatives. More data are now needed from the fossil record and from numerical experiments to test these alternatives and to properly interpret biodiversity patterns at all scales of the studies.

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