

Size patterns through time: the case of the Early Jurassic ammonite radiation

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Abstract.—The shell size of 1236 ammonite species representing all known Early Jurassic faunas is analyzed. Size patterns are studied for the entire period and then at the biozone scale for the first four stages of the Jurassic (28 Myr), during which ammonites recovered from the crisis at the Triassic/Jurassic (T/J) boundary. Our analysis reveals that (1) a size continuum (normal distribution from “dwarfs” to “giants”) exists for all Early Jurassic ammonites; (2) although there are no sustained trends (e.g., no Cope’s rule), the succession is not monotonous and patterns may differ conspicuously from one biozone to the next; and (3) increases and decreases in size range are the most frequent evolutionary styles of size change. The only pattern that can be connected with a particular episode of Early Jurassic ammonite history is the initial increase in size disparity during the first four biozones attributable to phyletic radiation after the T/J crisis. Subsequent correlations with environmental constraints (e.g., sea-level changes), although suspected, cannot be shown.

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Introduction

The ammonoid clade first appeared in the Early Devonian and finally vanished at the Cretaceous/Tertiary (K/T) boundary. In upwards of 320 Myr of life history, the clade was affected by three major crises at the Devonian/Carboniferous, Permian/Triassic, and Triassic/Jurassic boundaries (House 1989). These crises were followed by radiations, phenomena that may be viewed as “natural experiments” (Jablonski 1999) in biodiversity at the macroevolutionary scale. Any of three standards may be used to characterize biodiversity over such an extended period: taxonomic richness, morphological disparity, or size disparity.

Taxonomic richness is the most comprehensive standard as it covers both shape and size and can be applied to the entire fossil record (for ammonites see Kennedy 1977; House 1989; Becker and Kullmann 1996; Wiedmann and Kullmann 1996). However, this standard is seriously biased by the subjective practice of systematics: currently accepted taxa are not necessarily monophyletic groups; and the same taxonomic rank does not represent an equivalent proportion of biodiversity for different periods, for different types of organ-

isms, or for different authors. This is particularly true of ammonoids because most of the seminal systematic studies were devised to provide a convenient biostratigraphic tool rather than to establish phylogenetic relationships. Examples of systematics in the service of biostratigraphy are to be found in the works of Quenstedt (1856–1858), Orbigny (1842–1851), Opper (1856–1858), Fucini (1899–1900), Simpson (1855), and Buckman (1887–1907), although some contemporary workers concentrated on phylogenetic constraints to establish the ammonoid taxonomic framework (Hyatt 1889). The upshot of this is that ammonoid taxonomy is a mix of phylogenetic and stratigraphic information that cannot readily be used as a measuring rod for biodiversity without critical revision. Examples of this confusion are that Liparoceratidae become Amaltheidae at the Carixian/Domerian boundary on the basis of morphological changes although both clearly belong to the same lineage (Dommergues and Meister 1999), whereas Dumortieriinae become Leioceratinae because of tiny morphological changes (Neige et al. 2001) but primarily because the lineage spans the Toarcian/Aalenian boundary. In both these examples, as in many other instances,

biodiversity might have been interpreted in radically different ways in terms of taxonomy.

Alternatively, to avoid such pitfalls, questions independent of taxonomy (e.g., adaptation, community structure) may be explored by using morphological disparity (for ammonites, see Raup 1967; Saunders and Swan 1984; Nikolayeva and Barskov 1994; Dommergues et al. 1996, 2001; Neige et al. 1997, 2001): this approach provides a quantitative signal that can be set against the environmental signals. One limitation on such studies is that they are only meaningful within the same bauplan. Similarly, body-size studies may be independent of taxonomy and to some extent of bauplan; disparity in body size is highly dependent on physiology and ecology, and it reflects features of life history rather than bauplan constraints. However, body sizes can hardly be compared between aquatic and terrestrial organisms for which the physical constraints (gravity vs. viscosity) are so different. Nevertheless, within a given environment (marine in our case), body-size studies can be expected to provide a signal depending on major environmental constraints: "favorability" and "predictability" of the habitat. Because these environmental constraints depend on major—more or less related—physical phenomena (e.g., eustasy, climatic changes, tectonics, volcanism) and because such phenomena are detectable in the rock record, it might be possible to correlate body-size disparity signals with physical signals. If so, the dramatic physical changes of post-crisis periods would make these propitious moments for comparing such signals.

The Triassic/Jurassic boundary crisis and the ensuing Jurassic–Cretaceous major eustatic rise can be viewed as "natural experiments." The crisis was followed by a spectacular recovery of morphological disparity (Dommergues et al. 1996) and provides a good opportunity to explore ammonoid body size throughout the 28 Myr of post-crisis (Early Jurassic) history.

Materials and Methods

Sampling.—This study is based on what we believe to be an exhaustive, worldwide compendium of published and illustrated Hettan-

gian–Toarcian ammonites (from Bruguière 1789 to Taylor 2000) containing some 3500 nominal species. First, poorly or incompletely preserved species (absence of information about fossil size) were removed from this compendium. Then forms were grouped into what we consider valid species, although for dimorphic species macroconchs and microconchs were processed separately so as to give two real mean adult sizes rather than some artificial value midway between the size ranges of micro- and macroconchs. However, the effect of dimorphism on variations in size pattern over time could not be examined more closely here because the phenomenon is not consistently recognized in the Early Jurassic, and specially from the Hettangian to the Pliensbachian (see Davis et al. 1996). The units of analysis (species or dimorphs) are here termed "operational size units" (OSU). By this procedure we built up a set of 1236 OSUs representing, we assume, a relevant sample of shell sizes of Liassic ammonite faunas worldwide. This type of large database is consistent with the approach developed by Benton (1999), who demonstrated the relevance of reusing published data in the context of large-scale studies of pattern in paleobiology. Part of the sample was controlled by our own field experience of Early Jurassic faunas.

Shell Size Characterization.—Because the body chamber is often missing or poorly preserved, body size was estimated here by size at the end of the adult phragmocone. The adult stage can be recognized from various features, namely septal approximation. Where species were widely illustrated or morphs had numerous specimens, we took the mean value of the size range; there was thus only one size datum per species or morph. At the broad time and space scale of the present study, which includes such different sizes as the "minute" *Cymbites* and the "huge" *Arietites*, the general size pattern was not altered by taking account only of mean values for OSUs. So as to divide the size data into convenient categories, size was expressed by the natural logarithm (\ln) of the volume of the smallest cylinder that could contain the adult phragmocone, from the equation:

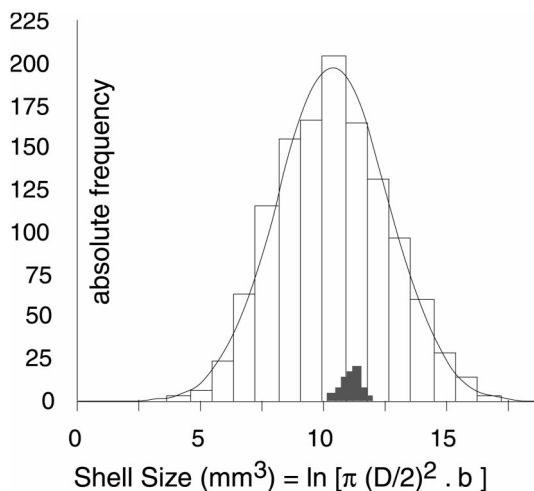


FIGURE 1. Shell size frequency distribution of operational size units (OSUs) for an exhaustive sample of Early Jurassic ammonites. The curve is the normal distribution. The small gray bars (in a bar chart) illustrate the frequency distribution in a case of intraspecific variation (see main text: *Productylioceras dawoei*, $n = 77$).

$$\text{Shell size} = \ln [\pi (D/2)^2 \cdot b]$$

where D is the shell diameter and b the whorl width (in mm). Volume is obviously a better estimator of a 3-D object and was therefore preferred to any simple linear measurement such as diameter.

Space and Time Scale.—The study covers all known ammonites worldwide over some 28 Myr of the Lower Jurassic. Although all paleogeographic areas are not known to the same degree, the extensive knowledge of such dispersed areas as northwestern Europe, Mediterranean Tethys, and the Western Ranges of America entitles us to consider that the available fossil record expresses a true global pattern. The Liassic period is divided here into 22 ammonite zones of the standard northwestern European scale proposed by *Groupe français d'étude du Jurassique* (1997). Correlations with other geographic areas are based on various published data (e.g., Hillebrandt 1988, 2000; Smith et al. 1988, 1994; Thomson and Smith 1992; Jakobs et al. 1994; Guex 1995; Taylor 1998, 2000; Pálffy et al. 1999, 2000).

Results

General Shell-Size Pattern.—If we consider the complete sample ($n = 1236$), size distribution (Fig. 1) can be adjusted to a normal dis-

tribution (Kolmogorov-Smirnov test not significant) and is not skewed (skewness is 0.120; t -test not significant). For the four Lower Jurassic stages worldwide there are no discrete categories for dwarf or giant forms, just a Gaussian continuum of ammonite sizes from smallest to largest. The mean adult phragmocone diameter of our sample is about 70 mm with a coefficient of variation of 0.86. As a comparison, intraspecific coefficient of variation is given by Howarth (1992) for various microconch (m) and macroconch (M) Toarcian Hildoceratid species: *Eleganticeras elegantulum*, 0.18 (m) and 0.16 (M); *Cleviceras exaratum*, 0.23 (m) and 0.21 (M); *Hildoceras bifrons*, 0.15 (m) and 0.18 (M). The mean size—by volume—of our complete sample is 10.33 mm^3 with a coefficient of variation of 0.21. By way of comparison (see Fig. 1) the intraspecific coefficient of variation of the Pliensbachian *Productylioceras dawoei* is 0.03 for a shell size of 11.13 mm^3 (same measurement protocol, and see Dommergues 1980 for the complete analysis of this population). This illustrates the stark contrast between intra- and interspecific variation as studied here. The smallest ammonite of our sample is *Eoderoceras tubellus* and the largest, *Arietites bucklandi*. The same two ammonites also have the smallest and largest adult phragmocone diameters at 5.3 mm and 480 mm, respectively. However, the relationship between volume and diameter is complicated by the effect of whorl width (Fig. 2): huge variability in whorl width is observed for the smallest diameters ($<60 \text{ mm}$) but is drastically reduced for the largest diameters ($>200 \text{ mm}$). This suggests that the larger the ammonite, the greater the constraints upon it. Accordingly, although diameter may be used as a proxy for size for ammonites of large diameter, the same does not hold for ammonites of small diameter. Indeed, for the latter the b/D ratio may vary from one to ten, leading to very different volumes for a similar diameter. As an example, *Catacoeloceras angustum*, which exhibits the highest b/D ratio ($b/D = 1$ for $D = 15 \text{ mm}$) is of similar diameter to *Gemmellaroceras gemmellaroi*, which has a very low b/D ratio ($b/D = 0.154$ for $D = 13 \text{ mm}$).

Temporal Pattern of Shell Size.—Changes in ammonite size pattern can be quantified from

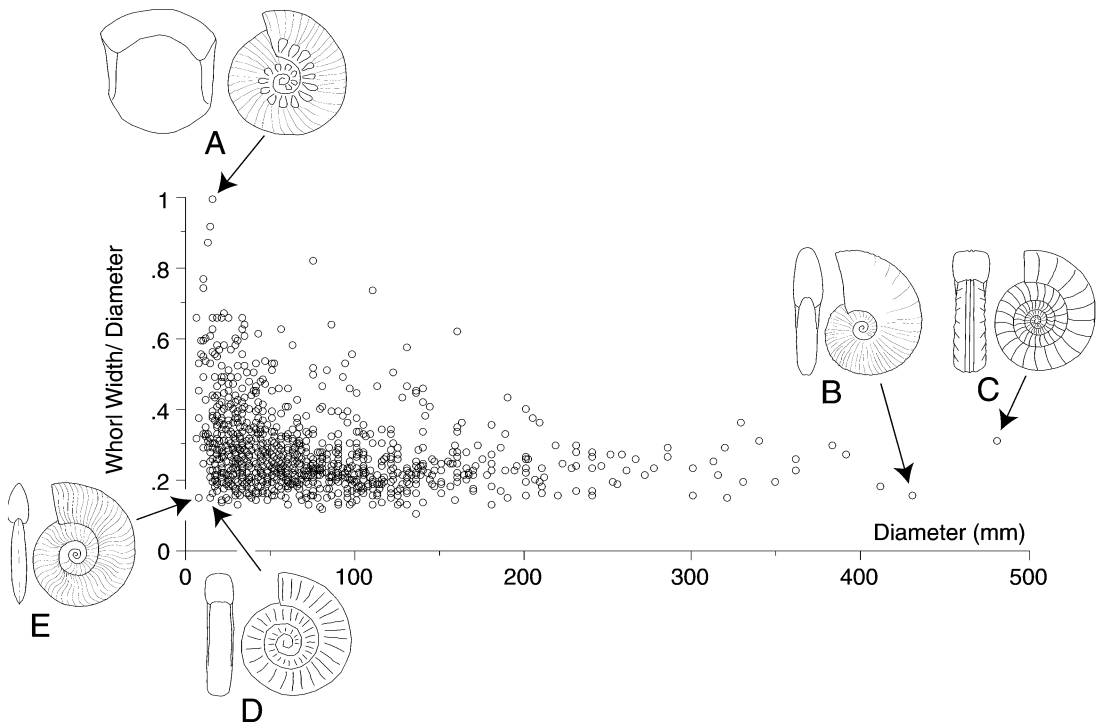


FIGURE 2. Whorl width/diameter ratio versus diameter for Early Jurassic ammonites. Several extreme morphologies are illustrated (no scale). A, *Catacoeloceras angustum*. B, *Charmasseiceras martinschmidti*. C, *Arietites bucklandi*. D, *Gemmellaroceras gemmellaroi*. E, *Polymorphites appenninicus*.

the first and last appearance data (FADs and LADs) of OSUs (Fig. 3). At first sight, the data exhibit no sustained trend through time of either minimum, median, or maximum size or range. However, trends and fluctuations are perceptible over shorter spans of time. For example, from the Planorbis to the Bucklandi zones, maximum size increases dramatically whilst minimum size decreases, leading to a sharp increase in size range. More-integrated data are provided by the coefficient of variation (Fig. 4) describing size disparity. The value first increases from the Planorbis to the Semicostatium zone and subsequently oscillates with a minimum value for the Tenuicostatium zone. A Spearman-rank correlation test was computed for the number of OSUs per zone versus range or coefficient of variation. The test proved not significant (Z-test on Spearman-rank correlation coefficient not significant for either range $p = 0.054$, or coefficient of variation $p = 0.89$), showing that range or coefficient of variation were independent of the number of OSUs per zone. Indeed,

noteworthy discordances occur between variation in size disparity (coefficient of variation) and variation in diversity (number of OSUs): increased size disparity associated with decreased diversity (five cases; see, for example, fluctuation from the Variabilis zone to the Thouarsense zone); decreased size disparity associated with increased diversity (a single case: from the Raricostatium zone to the Jamesoni zone). Two other cases involve a fairly stable size disparity associated first with increased diversity (from the Serpentinum zone to the Bifrons zone) and second with reduced diversity (from the Bifrons zone to the Variabilis zone). As Foote (1996) claimed, an increase in disparity (in his case trilobite morphological disparity) associated with stable or reduced diversity may be viewed as a consequence of nonselective extinction. The opposite case (a decrease in disparity associated with stable or increasing diversity) suggests the influence of constraints (e.g., phyletic, environmental). At the scale of our study (a worldwide analysis of size) phyletic and en-

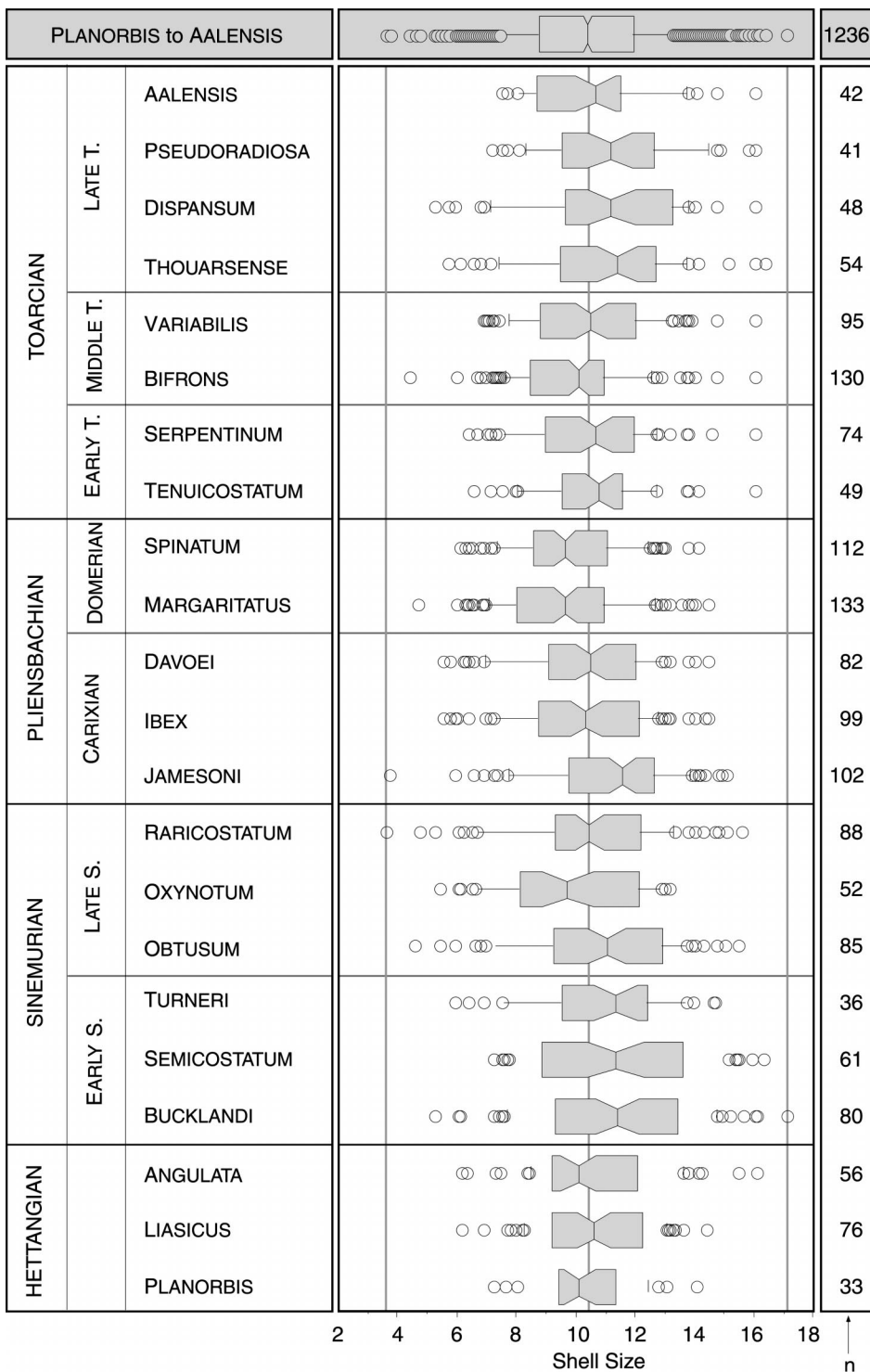


FIGURE 3. Comparison of size distribution over time (Planorbis to Aalensis zone) and for the entire Early Jurassic sample (top). Each box plot displays the 10th, 25th, 50th, 75th, and 90th size percentiles. All values below the 10th percentile or above the 90th percentile are plotted separately (open circles). The notch represents the 95% confidence interval around the median. The right-hand column indicates the number of OSUs per zone, and for the entire sample (top).

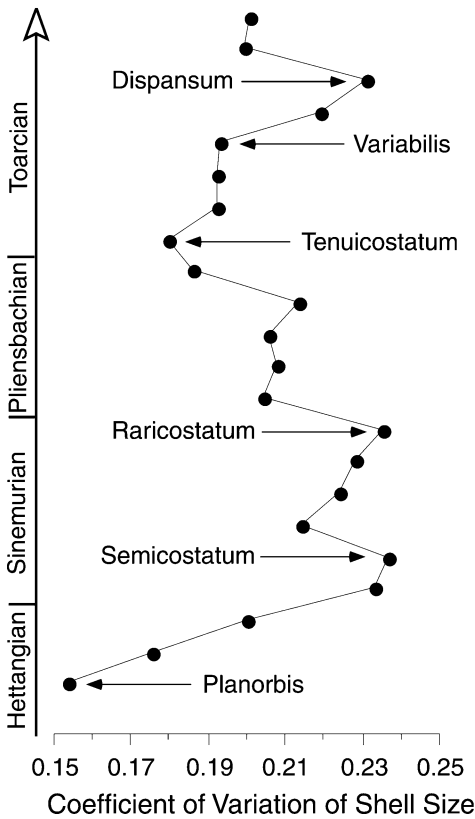


FIGURE 4. Coefficient of variation in ammonite shell size throughout the Early Jurassic.

environmental frameworks are not well enough documented to resolve this issue. We used two complementary methods to synthesize size variations over time: the first was derived from the method described by Jablonski (1996) for characterizing the different styles of size variation (Fig. 5A) between two consecutive samples in time (species, subgenera, or genera for Jablonski 1996, 1997; worldwide communities in the present work). This was done by using minimum and maximum size data only. The second method included these same parameters plus parameters for dispersion (range, variance) or position (interquartile, median, and mean), which were then processed by principal component analysis (PCA).

The plot of changes in minimum versus maximum size data (Fig. 5B) shows that changes are not equally distributed over the four quadrants. Point clusters (Fig. 5C; quadrants, axis, origin) reveal two marked frequen-

cies of evolutionary styles of size change: increase and decrease in size range (top left and bottom right, respectively). Two other frequencies are also well expressed, corresponding to decrease or increase in minimum size only (negative or positive x-axis, respectively). No other styles of size change are conspicuous.

PCA was performed with seven descriptive statistical parameters computed from data (shell size) for each of the 22 biozones (mean, minimum, maximum, range, variance, median, and interquartile). The first three axes represent 90% of variance (52%, 23%, and 15%, respectively).

Figure 6 shows the projection of biozones on the first two factorial planes (F1 vs. F2, and F1 vs. F3). The first axis is controlled mainly by variance, mean, median, and maximum; the second axis by minimum and range; the third axis by interquartile and maximum. Ordination was completed by clustering (ascendant hierarchical classification, or AHC) from the eigenvectors (of the first three axes) characterizing each biozone computed in the earlier PCA. A Euclidean distance algorithm (geometric distance in multidimensional space) was chosen to evaluate distances. Ward's method was chosen as a linkage rule, as it uses analysis of variance to evaluate distances between clusters (minimizing the sum of squares of any two hypothetical clusters that can be formed at each step). The dendrogram (Fig. 6) shows two first-order clusters (open vs. black symbols), subdivided into two in turn. Schematically, biozones characterized by open symbols express a narrow range associated with scarcity of small and large ammonites, low variance, mean, and median values. Black symbols express the opposite trend.

The previous four clusters are shown again in Figure 7 (same symbols as in Fig. 6) along with the styles of size variation (see Fig. 5) from one biozone to the next so that the temporal size pattern through the Early Jurassic can be examined. This new, more analytic, and more synthetic information supplements the row data analyzed previously (Figs. 3, 4). It expresses both the biozone size pattern (open and black symbols in Fig. 7) and the change between two successive patterns ("Jablonski's

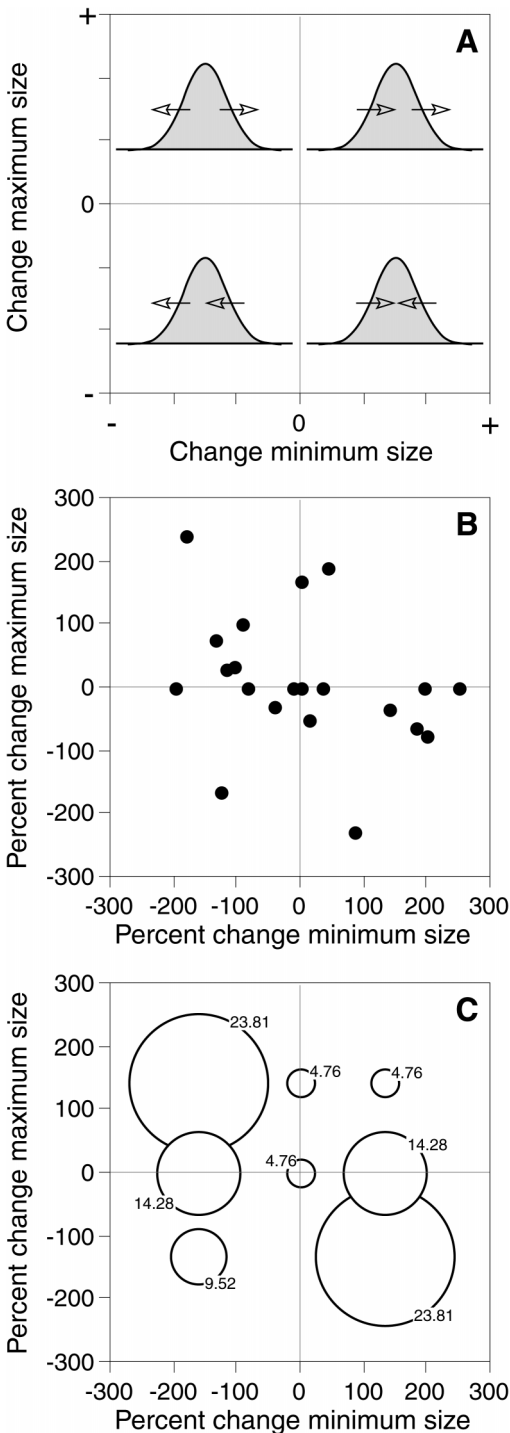


FIGURE 5. Styles of size change (“Jablonski’s target”) in Early Jurassic ammonites. A, Model derived from Jablonski 1996. The vertical axis shows the percentage change in maximum size between two successive sets of OSUs (corresponding to two successive zones). The horizontal axis shows the percentage change in minimum size between two successive sets of OSUs (corresponding to two successive zones). Thus, the top right quad-

target” in Fig. 7). No correlation is observed between these two synthetic signals, confirming the absence of any sustained trend as shown by row data. Only one phenomenon of note occurs between the *Ibex* and *Serpentium* biozones; otherwise the size pattern is relatively stable over this period, whereas the transition from one biozone to another remains highly variable. Despite the absence of any sustained trends, the succession is not monotonous and the patterns of two successive biozones may differ conspicuously (e.g., the changes from *Angulata* to *Bucklandi*, from *Obtusum* to *Oxynotum*, and from *Davoei* to *Margaritatus*).

Discussion

Various studies have concentrated on ammonite size variations at intraspecific, lineage, and macroevolutionary scale. Intraspecific studies (e.g., Elmi and Benshili 1987; Mignot et al. 1993) suggest a connection between miniaturization and a locally confined paleogeographic context. Miniaturization affected populations living in small isolated basins in part because of scarcity of nutriment. These small ammonites belong to species that are widespread and have larger individuals outside of the confined basins. This has been demonstrated for Toarcian and Bajocian ammonites by comparing Tethyan populations from small basins with populations from the northwest European platform. Such dwarfism is found experimentally in miniaturized (undernourished) cuttlefish (Boletzky 1974) although dwarf populations are unknown in the wild. Stevens (1988) suggests that environmental constraints could produce gigantism in adults; using recent squids as a model, he argues that these large specimens are assumed to prefer

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 rant corresponds to an increase in size, the bottom left quadrant to a decrease in size, the top left quadrant to an increase in size range, and the bottom right quadrant to a decrease in size range.

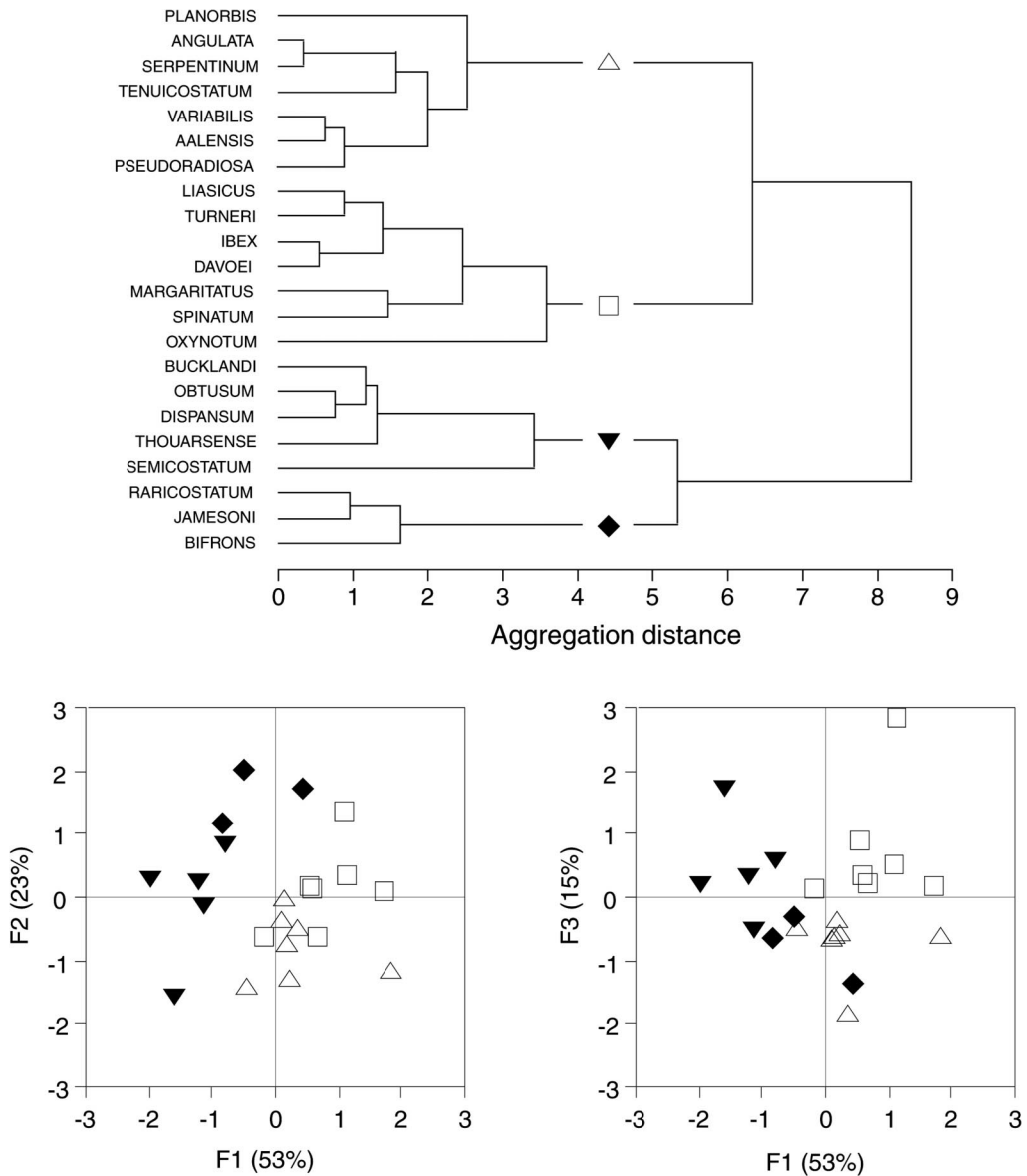


FIGURE 6. Bottom, plot of the first two factorial planes (F1 vs. F2 and F1 vs. F3) for seven descriptive statistical parameters (mean, minimum, maximum, range, variance, median, and interquartile). Each point corresponds to an ammonite zone (symbols are determined from the following AHC). Top, ordination completed by clustering (AHC) from the eigenvectors of the first three axes characterizing each biozone as computed in the earlier PCA (Euclidean distance algorithm chosen to evaluate distances; Ward's method chosen as a linkage rule).

deep-sea environments. As a consequence, they are more numerous in the fossil record during transgressive episodes. The same author also suggests that gigantism may be the outcome of pathological conditions; for example, when gonads are infected by parasites growth is not limited by sexual maturity (see Manger et al. 1999 for an illustration on Carboniferous cephalopods).

Such studies demonstrate that size is a highly variable parameter among populations within a species when subjected to specific environmental constraints. So as to exclude such "freak" populations or pathological specimens, our study uses the average size of available specimens (museum collections plus published illustrations) for each OSU.

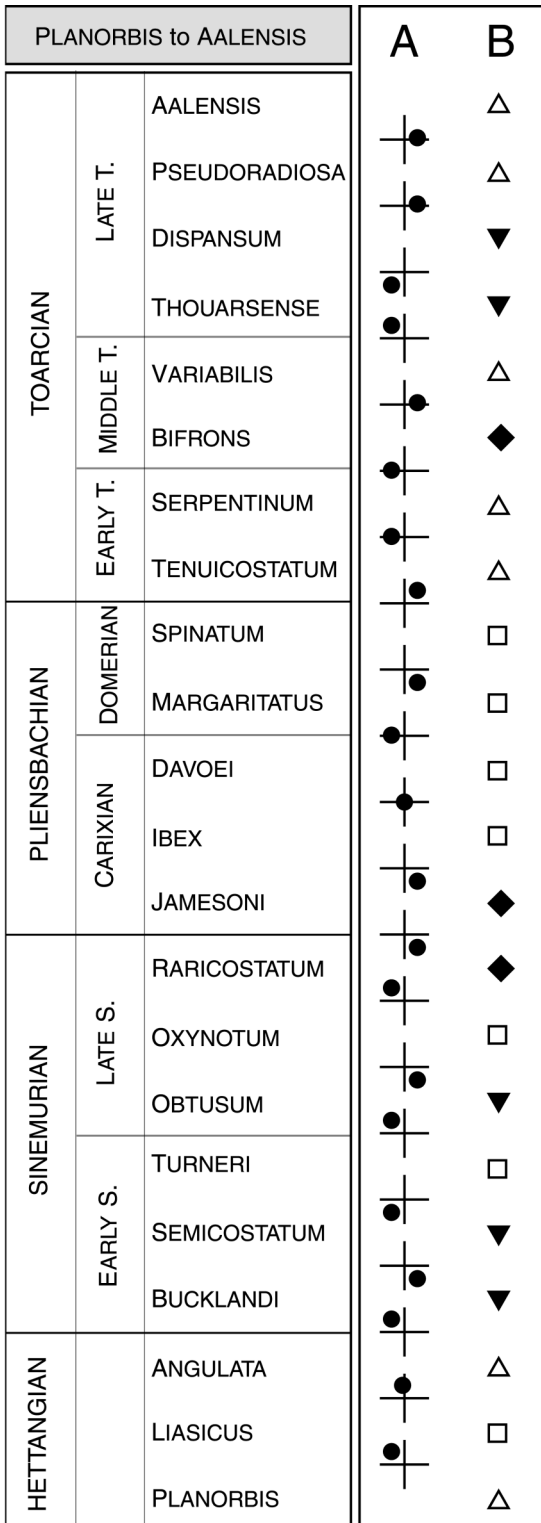


FIGURE 7. Temporal size pattern for Early Jurassic ammonites. A, Style of variation from one zone to the next ("Jablonski's target"; see Fig. 5). B, Size pattern for each zone (see Fig. 6 for symbols).

At lineage scale, most authors (as summarized in Kennedy 1977; Hallam 1975, 1990; Stevens 1988) report that giant forms tend to appear in the late stages of lineage development. This trend, with the sudden appearance of small initial species (paedomorphosis [Hallam 1975, 1990]) has been interpreted as an expression of Cope's rule (Newell 1949; Stanley 1973). Hallam (1990) suggests that size distributions may be affected by a change from r to K strategies during transgressive cycles. The opposite trend (progressive reduction in size within a lineage) appears to be rare (see Kennedy and Cobban 1976 for an example of heteromorphic Cretaceous ammonites, but see Wiedmann 1969 for an opposing view). One major difficulty when studying lineage size changes is in evaluating the robustness of a phylogenetic hypothesis. Indeed, the preconception that small species initiate a lineage implies that the probability of observing a size increase in the course of the lineage is high and that an abrupt reduction in size will be interpreted as the beginning of a new lineage. This pitfall could be avoided in principle at least by defining clades before analyzing size variation within the phylogenetic framework (i.e., within monophyletic groups). Alroy (2000) advocates using a resolved phylogeny in an ancestor-descendant comparison as the relevant way to understand the dynamics of trends within evolving lineages. However, as McShea (2000) points out, although the ancestor-descendant comparison approach may be useful, time-slice statistics independent of any phylogenetic framework still yield valuable results. Given the state of the art of ammonite phylogeny, this latter approach is the only working tool available.

The macroevolutionary scale (at which large space and/or time criteria and taxonomic data are considered) is seldom applied to ammonites. Quantitative data are provided by Stanley (1973) and more recently by Klug (1999). The first author gives size frequencies (shell diameter) for species for the early Hettangian, middle Hettangian, Bathonian, and Oxfordian. The author supposed these to be reasonably representative of the whole ammonoid pattern for the Jurassic. However, these data concern only northwest European faunas

(Germany for the Hettangian and England for the other stages), and the time sampling is too coarse and irregular to detect any overall trend. This is particularly so for the Hettangian data from Germany, where most ammonites are small whereas larger specimens occur at the same period in other paleogeographic areas (European Tethys, North and South America [see Guex 1995]). Recently Klug (1999) has studied the mean and maximum shell diameter from the later part of the Early Devonian to the Late Devonian (more than 1000 species over about 30 Myr). At global scale, Klug's data do not suggest Cope's rule. Klug does suggest links between some of the observed fluctuations and major global transgressions, but raw data do not support this claim.

Our data clearly represent the macroevolutionary scale (more than 1200 OSUs for about 28 Myr). The size patterns of Early Jurassic ammonites are similar to those of Devonian ammonites (Klug 1999). Again no Cope's rule is found (see Fig. 5), and the time-order fluctuations are similar (see Fig. 3). Our study uses a different method of data processing to attempt to decipher the significance of some of the major fluctuations with regard to environmental and phyletic phenomena. One of the most striking results is the fluctuations of the coefficient of variation of size over time (Fig. 4). This coefficient, quantifying size disparity, exhibits a contrasted pattern: (1) a drastic sustained increase from the Planorbis to the Semicostatum zone; (2) a relatively stable phase with marked size variation up to the Raricostatum zone; (3) a stepped decline until the Variabilis zone (with a minimum at the Tenuicostatum zone); and finally (4) an increase up to the Dispansum zone. The end of the pattern (from the Dispansum to the Aalensis zone) suggests a new phase of decrease, but this needs to be documented for subsequent times (Aalenian stage) before it can be confirmed. No parallelism between this pattern and the second-order global eustatic sea-level curve (Haq et al. 1988; Hallam 2001) is apparent. Because they are based on regional compilations, none of the more recently published sea-level curves (Haq et al. 1988; Hardenbol et al. 1998) are relevant for comparison with our

data. However, correlations may be sought between some of the observed size variations and phyletic and/or geological events.

First, the sustained initial increase in size disparity can be related to the post-Triassic crisis followed by the beginning of the major Jurassic transgression. This phenomenon provided new ecological niches, especially in the newly formed epicontinental seas. This increase in disparity also corresponded to a phyletic radiation, as all the earliest Jurassic ammonites derived from scarce ammonites of rather homogeneous and medium-sized species. Under such conditions, (few initial species and many new ecological niches), a sustained increase in size disparity seems rather predictable. Such a trend may be compared with a passive system (sensu McShea 1994) where there is no pervasive force or bias. The size disparity increased because changes were possible in both directions (toward smaller and larger extremes) because the ammonites were initially medium-sized.

Another noteworthy event is the occurrence in the Tenuicostatum zone of the lowest disparity in size of Early Jurassic times (except for the onset of the trend). This corresponds to the species-level extinction event documented for marine invertebrates by Little and Benton (1995). Nevertheless, this event is merely the end of a stepped decrease in size disparity that began at the start of the Pliensbachian, a decrease that could not be related to any global phenomenon.

The reduction in size disparity after the Dispansum zone can be related to the turnover of ammonite faunas. This led early authors (e.g., Haug 1892) to locate the Early Jurassic/Middle Jurassic (i.e., Toarcian/Aalenian) boundary after the Dispansum zone. However, to be properly demonstrated this faunal turnover should be reviewed within a more tightly constrained phylogenetic framework.

Finally, although the recovery phase (Hettangian and Early Sinemurian) following the T/J crisis exhibits an increase in size disparity that can be explained by two complementary processes—few founder species, all of medium size, and an increasing number of suitable environments—the size pattern during the post-recovery phase is more enigmatic. We

might suspect that biotic process regulation prevailed over abiotic factors (e.g., physical and chemical conditions).

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