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RAPID COMMUNICATIONS

Ammonoid morphological signal versus sea-level changes

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Abstract

The morphological diversity, considered as a biological signal, of a series of four Upper Callovian (Middle Jurassic) ammonite populations of Côte-d'Or (France) is quantified. These populations fall within two third-order sequences of a second-order transgression. A sampling method that adheres as closely as possible to the morphological characteristics of the populations is established. It is valuable in that it eliminates the subjectivity related to taxonomy to allow more objective comparisons between the biological signal (shell morphology) and the physical signal (eustasy).

1. Introduction

The use of ammonites in biostratigraphy may give the impression that these fossil cephalopods serve only to establish chronological units. However, workers investigating their ecology have suggested a correlation between shell morphology and environment (e.g. Ziegler, 1963, 1967; Marchand, 1992, for a review). Others have suggested that sea-level variations, by giving rise to new ecological niches, are one of the engines of morphological change (e.g. Enay, 1980; Donovan, 1985; Marchand & Thierry, 1986; Hantzpergue, 1995). If such correlations between morphology and eustatic variations could be generalized ammonites might then be used as palaeoenvironmental markers. In practice, establishing correlations runs up against a major difficulty posed by sample selection.

In this work we adopt a new approach to test for correlations between morphology and environment in a series of four Upper Callovian (Middle Jurassic) populations from Côte-d'Or (Burgundy, France). This approach is based on minimizing taxonomic constraints when forming samples for analysis. It allows morphodiversity to be read directly without interference from taxonomic subjectivity. In addition, the choice of a comparatively restricted geographic range seems essential during the development stage of the method.

2. Environmental information

The studied deposits are from the southeastern border of the Paris Basin (Fig. 1). The Lower Callovian deposits are bioclastic limestones indicative of strong hydrodynamic activity. The occurrence of Middle Callovian deposits in the study region has never been proven in terms of palaeontology, although they do occur to the north and south of the area. As is commonplace in Western Europe, Upper Callovian sedimentation resumed with ammonite-rich, argillaceous limestones (weak hydrodynamic activity).

The Upper Callovian (Fig. 2) is located at the end of the second-order transgressive cycle (Hardenbol *et al.* 1996), the peak transgression of which is located at the base of the Oxfordian (*mariae* Zone, *scarburgense* Subzone). The third-order sequential division (*sensu* Vail *et al.* 1987) shows that the *athleta* Zone corresponds to the end of the Call5 sequence and the *lamberti* Zone to the end of the Ox0 sequence (Hardenbol *et al.* 1996). A series of two zones and four subzones is recognized (Fig. 2) representing some two million years.

3. Quantifying morphological diversity

The analysis is based on collections of more than 8000 ammonites (belonging to 6 families, 14 genera, and at least 30 species). The taxonomic characteristics of the populations collected were analysed by Bonnot & Marchand (1991, 1994); they will not be detailed here. Many individuals have intact lappets and tubercles. The occurrence of such fragile structures and the absence of intra-thalamic epizoans are interpreted as a good indication that there was little post-mortem transportation of the shells (Tintant, 1982).

As it was impractical to analyse all of the individual fossils, a sample of the collected material was taken. By contrast with the most commonly used method (selecting a few individuals per species or per genus, e.g. Raup, 1967; Dommergues, Laurin & Meister, 1996) we used a method which reflects the structure of the original populations as accurately as possible (diversity and proportion of morphologies within the ammonoid assemblages): individuals within the different families collected were selected at random in keeping with the relative proportions of the families. Measurements were made (at the end of the phragmocone) of 52 individuals in the *trezeense* Subzone, 62 in the *collotifomris* Subzone, 47 in the *poculum* Subzone and 63 in the *lamberti* Subzone, making a total of 224 individuals.

W, *D* and *S* parameters as defined by Raup (1967), which are especially effective for quantifying the overall shape of ammonites (e.g. Ward, 1980), were calculated for each individual (Fig. 3). From these parameters, morphological spaces *D* versus *W*, and *D* versus *S*, were used to quantify and visualize morphological diversity. *D*–*W* describes the coiling characteristics of the shell (degree of involution versus whorl expansion) whereas *D*–*S* describes the characteristics of the shell section (degree of involution versus cross-sectional shape).

4. Results

The morphological space *D*–*W* was calculated for the four subzones (Fig. 4). If predominances are disregarded, for each subzone, the morphospace envelope is similar overall, with a

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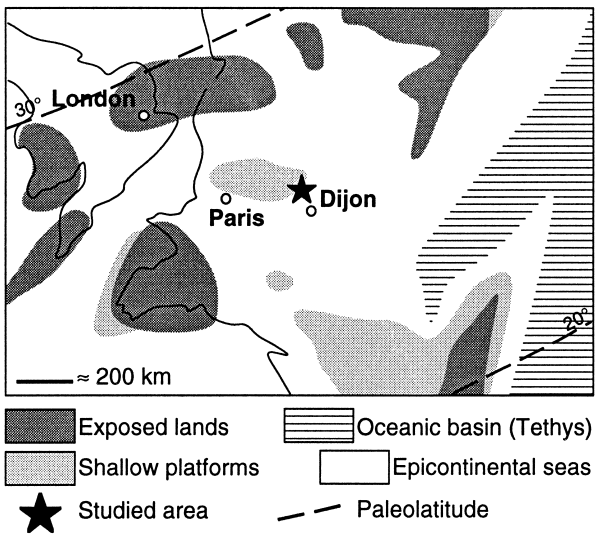


Figure 1. Palaeogeographic sketch map of western Tethys during Callovian time (modified from Enay *et al*. 1993).

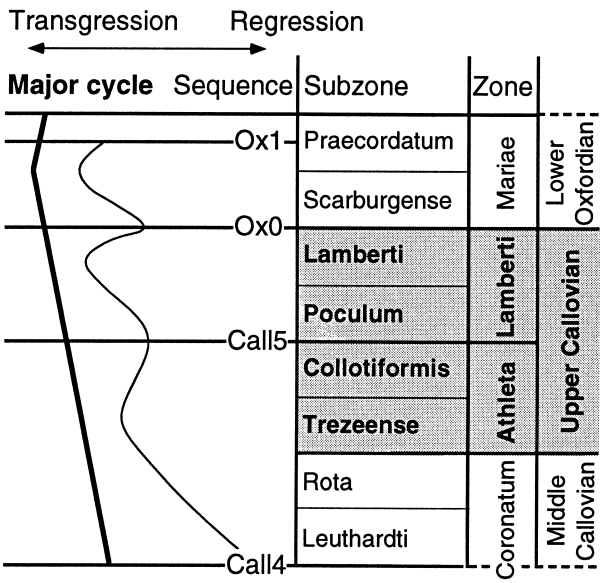


Figure 2. Middle Callovian (part) to Upper Callovian second- and third-order eustatic signals (modified from Hardenbol *et al*. 1996). The studied period is in bold print.

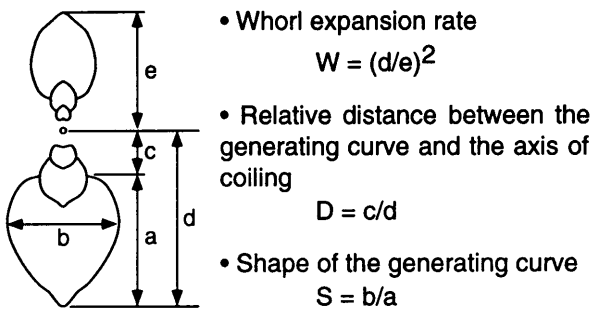


Figure 3. Linear dimensions measured for the calculation of *W*, *D* and *S*, and definitions of these shape parameters (modified from Raup, 1967).

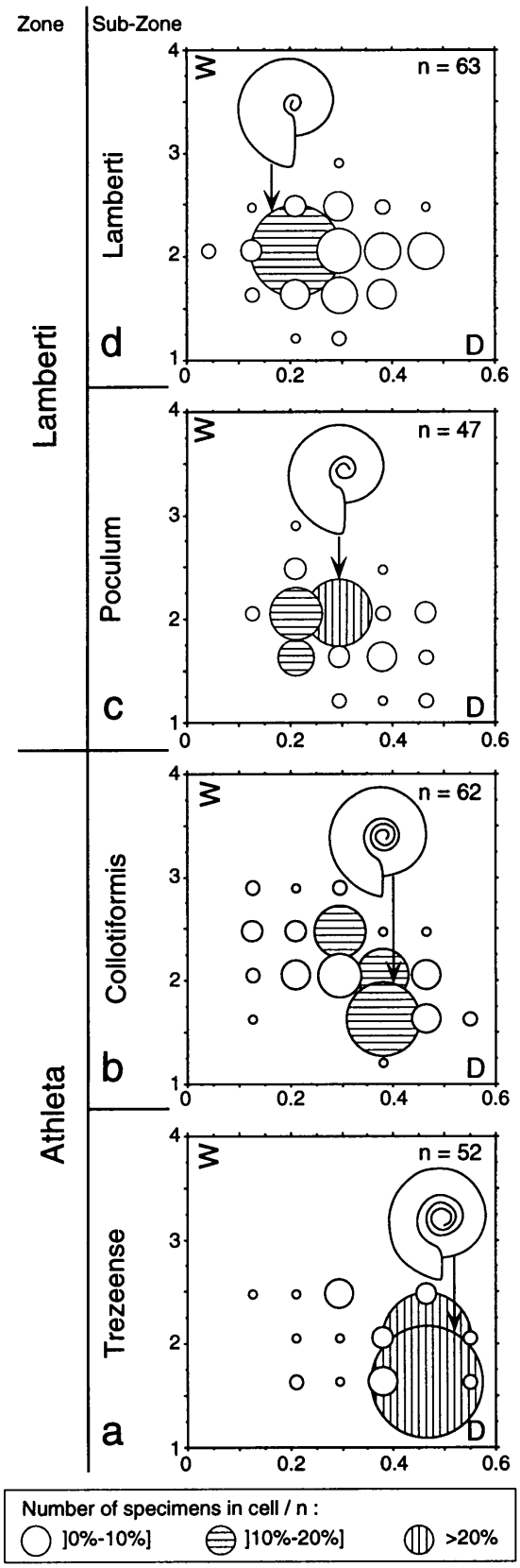


Figure 4. Variation of morphospace *D* versus *W* for the four sub-zones of the Upper Callovian in the studied area. Cell clusters have been constructed using StatView II™/F software (circle size is proportional to the number of specimen in the cell). Ilustrated shapes are those localized at the centre of the arrowed cell.

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slight shift over time towards more involute forms (reduction of *D*). By contrast, the predominant morphological type changes very clearly over time. For the *trezeense* Subzone (Fig. 4a), evolute ammonites ($D \approx 0.5$) with low whorl expansion rates ($W \approx 1.5$) are clearly predominant. In the next subzone (*collotiformis*, Fig. 4b) this predominance declines and there is a more uniform distribution of morphologies, although there are more numerous evolute samples ($D \approx 0.4$) with moderate whorl expansion rates ($W \approx 1.5$–2). In the following subzone (*poculum*, Fig. 4c) there is a shift towards predominantly involute forms ($D \approx 0.3$) with high whorl expansion rates ($W \approx 0.2$). In the final subzone (*lamberti*, Fig. 4d) this domination becomes more acute, though for increasingly involute morphologies ($D \approx 0.2$).

For morphospace *D*–*S* (Fig. 5), the first two subzones (Fig. 5a,b) are characterized above all by abundant forms of quadrate section ($S \approx 1$), which are very dominant in the first subzone. The last two (Fig. 5c,d) are mainly characterized by compressed sections ($S \approx 0.8$–0.7) which are clearly predominant in the most recent of the subzones. Finally, as with *D*–*W*, it can be seen that if predominance is disregarded, the morphologies expressed for each subzone exhibit only minor differences.

By combining the two morphospaces (*D*–*W* and *D*–*S*), the oldest population is dominated by what we shall call subserpenticone forms with large umbilici and quadrate sections, whereas the most recent population is dominated by what we shall term suboxycone forms with relatively narrow umbilici and rather compressed sections. It could be noted that similar evolutionary changes (from serpenticone to oxycone shells) have been claimed for Lower Jurassic ammonites (Donovan, 1994).

5. Implications

The quantitative morphospaces proposed here cover both the diversity and the frequency of morphological types as they appear in the populations. This method can therefore be used to compare the morphological signal of ammonites with other physical or chemical signals.

Thus comparison of the morphological signal with eustatic cycles (physical signal) can be viewed more objectively (deliberately excluding taxonomy). The biological signal is very clearly correlated with the major second-order transgression (Fig. 2) by a change in the predominant morphotype (subserpenticone versus suboxycone). With regard to the third-order sequences, the two maximum transgression periods (*trezeense* Subzone and *lamberti* Subzone) share the very clear predominance of a single morphological type, which is clearly apparent in the *D*–*S* morphospace: evolute forms with quadrate section for the most ancient and involute forms, with compressed sections for the most recent. The boundary between the two sequences (Call5) is marked above all by a reversal of the predominant morphological pole: subserpenticone before and suboxycone after.

It seems that, at the onset of late Callovian times, the subserpenticone morphologies corresponded to a nektopelagic mode of life (if we refer to the models of Tintant, Marchand & Mouterde, 1982) and were probably better suited to massive colonization (*r* strategy?) of the shallow platforms which were becoming widespread at the start of the transgression. However, suboxycone morphologies, which are thought to correspond to a nektobenthic mode of life (because more frequent in shallow sedimentary deposits: see Marchand, 1992), may have been better suited to a stable biotope (*K* strategy?) as these forms gradually came to predominate during the transgression (Fig. 4).

As conducted here, this approach involves multi-disciplinary data (morphology versus eustasy) providing signals for comparison. It should enable the testing (by quantification) of

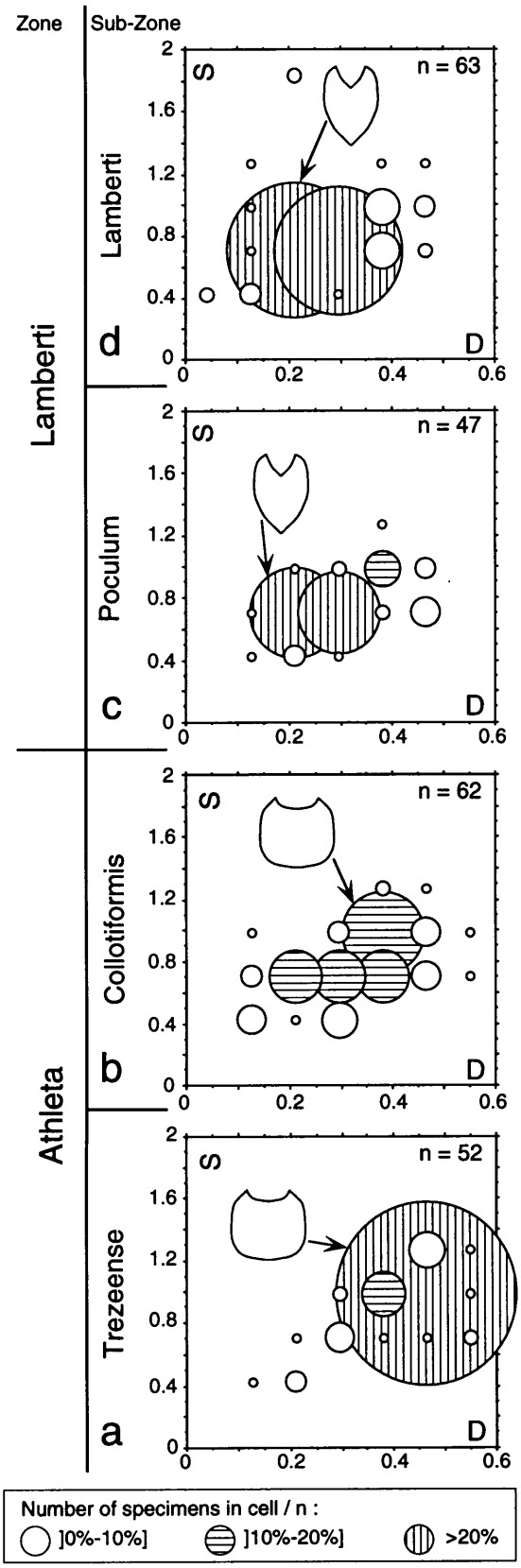


Figure 5. Variation of morphospace *D* versus *S* for the four subzones of the Upper Callovian in the studied area. Cell clusters have been constructed using StatView II™/F software (circle size is proportional to the number of specimen in the cell). Ilustrated shapes are those localized at the centre of the arrowed cell.

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palaeoecologic models (as proposed by Tintant, Marchand & Mouterde, 1982; Batt, 1989; Westermann, 1990; Marchand, 1992) for ammonoids on a larger scale. It should also, in return, refine the use of such organisms as palaeodepth indicators. Further comparisons between biological signals (including ornamentation, septal line and shell ontogeny as suggested by Westermann, 1990), and physico-chemical signals are now required if we are to make headway with decrypting the morphological message of lifeforms.

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References

BATT, R. J. 1989. Ammonite shell morphotype distributions in the Western Interior Greenhorn Sea and some paleoecological implications. *Palaios* **4**, 32–42.

BONNOT, A. & MARCHAND, D. 1991. Biostratigraphie de la zone à Athleta (Callovien supérieur) en Côte-d'Or. *Bulletin Scientifique de Bourgogne* **44**, 23–31.

BONNOT, A. & MARCHAND, D. 1994. Le contact Dogger–Malm en Côte-d'Or (France). III. La coupe de Chaignay : interprétation biostratigraphique. *Bulletin Scientifique de Bourgogne* **46**, 43–50.

DOMMERGUES, J.-L., LAURIN, B. & MEISTER, C. 1996. Evolution of ammonoid morphospace during the Early Jurassic radiation. *Paleobiology* **22**, 219–40.

DONOVAN, D. T. 1985. Ammonite shell form and transgression in the British Lower Jurassic. In *Sedimentary and Evolutionary Cycles*, vol. 1 (eds U. Bayer and A. Seilacher), pp. 48–57. Berlin: Springer-Verlag.

DONOVAN, D. T. 1994. Evolution in some early Jurassic ammonites: Asteroceratinae, Oxynoticeratidae and related forms. *Palaeopelagos Special Publication* **1**, 383–96.

ENAY, R. 1980. Paléobiogéographie et ammonites jurassiques : "rythmes fauniques" et variations du niveau marin ; voies d'échanges, migrations et domaines biogéographiques. *Mémoires Hors Série de la Société géologique de France* **10**, 261–81.

ENAY, R., CARIOU, E., BELLION, Y., GUIRAUD, R., MANGOLD, C. & THIERRY, J. 1993. Callovian paleoenvironments (162–158 Ma). In *Atlas Tethys Palaeoenvironmental Maps. Maps* (eds J. Dercourt, L. E. Ricou and B. Vrielynck). Rueil-Malmaison: BEICIP-FRANLAB.

HANTZPERGUE, P. 1995. Faunal trends and sea-level changes: biogeographic patterns of Kimmeridgian ammonites on the Western European Shelf. *Geologische Rundschau* **84**, 245–54.

HARDENBOL, J., THIERRY, J., FARLEY, M. B., JACQUIN, T., GRACIANSKY, P .C. de & VAIL, P. R. 1996. Jurassic chronostratigraphy. In *The Mesozoic–Cenozoic Chronostratigraphic Framework; Sequence Stratigraphy of European Basins* (eds P. C. de Graciansky, J. Hardenbol, T. Jacquin, P. R. Vail & M. B. Farley). Seminar Volume SEPM, Special Publication (in press).

MARCHAND, D. 1992. Ammonites et paléoprofondeur : les faits, les interprétations. *Paleovox* **1**, 49–68.

MARCHAND, D. & THIERRY, J. 1986. Relations entre les évènements calloviens et l'évolution des peuplements d'ammonites en Europe occidentale. *Bulletin du Centre de Recherche Elf Aquitaine* **10**, 383–92.

RAUP, D. M. 1967. Geometric analysis of shell coiling: coiling in ammonoids. *Journal of Paleontology* **41**, 43–65.

TINTANT, H. 1982. Autochtonie ou allochtonie chez les céphalopodes. *Mémoire Géologique de l'Université de Dijon* **7**, 257–71.

TINTANT, H., MARCHAND, D. & MOUTERDE, R. 1982. Relations entre les milieux marins et l'évolution des Ammonoïdés : les radiations adaptatives du Lias. *Bulletin de la Société géologique de France* **7**, 951–61.

VAIL, P. R., COLIN, J. P., CHENE R. J. du, KUCHLY, J., MEDIAVILLA, F. & TRIFILIEFF, V. 1987. La stratigraphie séquentielle et son application aux corrélations chronostratigraphiques dans le Jurassique du bassin de Paris. *Bulletin de la Société géologique de France* **8**, 1301–21.

WARD, P. D. 1980. Comparative shell shape distributions in Jurassic–Cretaceous ammonites and Jurassic–Tertiary nautilids. *Paleobiology* **6**, 32–43.

WESTERMANN, G. E. G. 1990. New developments in ecology of Jurassic–Cretaceous ammonoids. In *Fossili, Evoluzione, Ambiente* (eds G. Pallini, F. Cecca, S. Cresta and M. Santantonio), pp. 459–78. Pergola: Atti del secondo Convegno internazionale.

ZIEGLER, B. 1963. Ammoniten als Faziesfossilien. *Paläontologische Zeitschrift* **37**, 96–102.

ZIEGLER, B. 1967. Ammoniten-Ökologie am Beispiel des Oberjura. *Geologische Rundschau* **56**, 439–64.

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