Heterochronic differentiation of sexual dimorphs among Jurassic ammonite species

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Ontogenetic and then heterochronic approaches are used here to analyze sexual differentiation within two well-known Jurassic dimorphic species. This analysis compares two ways of determining the relative biological age of ammonites, one using size (diameter) and the other the number of septa as a proxy of age. The shape standard is established from factor analysis of morphological and growth parameters. Size-age-shape relationships are analyzed on the basis of a new heterochronic representation. When diameter is used as a proxy of age, microconch morphs are globally considered to be progenetic compared with macroconch morphs. When size and age are determined separately and shape is included, (1) *Ecbryxipiceras jactatuni* (microconch morph) has a shorter period of growth (progenesis) with acceleration of shape compared with its macroconch morph (*Morphoceras macrescens*), (2) *Cardioceras cordatum* (microconch morph) has a shorter period of growth (progenesis) coupled with a slower rhythm of growth (dwarfism) compared with its macroconch morph. These findings emphasize the complex relationship between supposed sexual dimorphs in ammonites when size and age standards can be separated, as well as the need for an ontogenetic approach.

ODimorphism, heterochrony, ontogeny, morphology, Ammonoidea, Jurassic.

Most studies of sexual dimorphism in ammonites have focused on differences between mature adults: microconchs and macroconchs (i.e. Makowski 1962; Callomon 1963; Tintant 1963; Westermann 1964; Callomon 1980; see Davis et al. 1996 for a review). Surprisingly, little work has been done on sexual dimorphism in the context of ontogenetic development (even though the heterochronic processes involved in differentiating ancestor-descendant relationships within lineages have been widely documented because ammonites record their entire ontogeny in their shells). In the most recent review of ammonoid dimorphism (Davis et al. 1996), only a few lines are devoted to the problem of dimorphism versus heterochronic processes.

Insofar as heterochronic processes are related to adaptive significance (Gould 1977), it would be particularly useful to understand these processes in the case of ammonoid sexual dimorphism (i.e. Gould 1977; Alberch et al. 1979; Fink 1982; Dommergues et al. 1986; McNamara 1986; McKinney 1988). This sort of study is still very rare for fossils and especially for ammonites. Moreover, in paleontological lineage studies, heterochronic processes have almost invariably been simplified by using only size (considered as a proxy of age) and shape standards; only a few studies attempt a three-standard approach (e.g., McNamara 1982; Dommergues 1988; Laurin & García-Joral 1990; David & Laurin 1991). This proxy, without the age standard, cannot reliably identify all cases of heterochrony, as demonstrated notably by Shea (1983) in primates, and by Jones (1988), Dommergues et al. (1986) and McKinney (1988) in a theoretical approach.

This paper investigates how to handle the heterochronic processes responsible for the similarities and differences between related ammonite dimorphs (as the dimorphic nature of these species has been demonstrated by various authors, it will not be done again here). The comparison is made first with two (size as a proxy of age, and shape) and then with three standards (size, age, and shape), and the results are compared.
Materials

Two species of phyletically unrelated ammonites were selected because of their well-known dimorphic pattern demonstrated by previous published studies, in which the two forms of each species were differentiated by morphological criteria. Specimens were selected so as to cover the full range of species variability, which meant that fewer specimens had to be submitted to the time-consuming and delicate preparation technique.

- *Morphoceras macrescens* Buckman (macroconch) and its microconch morph *Ebrayiceras jactatum* Buckman (Fig. 1; Ammonitina, Perisphinctaceae) were collected from a 5 cm thick, Lower Bathonian (Zigzag zone, Macrescens subzone) marly limestone bed at a single section near Nevers (Nièvre, France). The two morphs had been classified as separate species and genera before being paired by Mangold (1970), who clearly showed that these two morphs – whose stratigraphical range is only one subzone – belong to a single paleospecies. Thirteen representative specimens (eight macroconchs and five microconchs) were selected for this study.

- *Cardioceras cordatum* (Sowerby) (Fig. 2; Ammonitina, Stephanocerataceae) was collected from ferruginous marls of the Lower Oxfordian (Cordatum zone, upper part of the Cordatum subzone) near Neuviży (Ardennes, France). Compared with other European populations, the evolutionary steps of the ribbing pattern of the 29 specimens collected prove that they are isochronous (same subzone) and belong to the same paleopopulation. Moreover, the bed they come from is concentrated (numerous fossils of the same biostratigraphic unit) but not condensed (no successive biostratigraphic units mixed together). The dimorphic nature of this species has been established by the studies of Gygi & Marchand (1982), Callomon (1985) and Marchand (1986). Eight representative specimens (six macroconchs and two microconchs) were selected.

The material was prepared in a standardized manner to provide comparable measurements. Each ammonite was cut along the equatorial plane through the protoconch. This section was further cut along the axial plane and reconstructed by symmetry (Fig. 3). The septa were counted on the equatorial sections. Shell diameters were measured through the protoconch and the center of each chamber on magnified camera lucida drawings of the ammonites. This meant that the position of the protoconch – when absent – could be reconstructed with minimum error.

Characterization of the three standards

*Shape.* – In both cases, the shape of the ammonite shell was conveniently described by eight linear dimensions (Fig. 3B). Growth steps were measured every half whorl on each specimen, providing a record of ontogeny. Growth parameters (Raup 1966, 1967) were calculated: $D$ (relative distance between the generating curve and the axis of coiling), $W$ (whorl expansion rate), and $S$ (aspect ratio of the generating curve). Since the ammonites
For heterochronic analyses, shape can be expressed by a single parameter (or a small number of parameters). Earlier studies have demonstrated the effectiveness of multivariate analysis in providing simple values for shape (Saunders & Swan 1984; Tissot 1988; Laurin & Garcia-Joral 1990; Reyment & Kennedy 1991). Thus, in this study, a set of 10 values – T, d, a, b, p, f, D, W, S, DT – was then used to carry out a principal component analysis (PCA) for defining synthetic shape parameters.

**When size is a proxy of age.** – As in some earlier studies of ammonite heterochronies (e.g., Landman 1988; Marchand & Dommergues 1988; Korn 1992), diameter is used here as an age marker. Consequently, only two parameters can be compared: shape and age, assumed to be best represented by diameter. On this assumption, if the two sexual dimorphs of a single paleospecies are of different size (different diameter), the larger one is assumed to have had a longer period of growth.

**When size and age are separated.** – Features such as growth rings are commonly used for estimating the age of molluscs (Jones 1988), and extension of the technique to cephalopods has already led to paleontological data being reinterpreted (Doguzhaeva 1982; Bucher & Guex 1990). However, such lines were neither easily recognizable nor readily usable in the ammonites studied here because the specimens are preserved as internal molds. Studies of the recent *Nautilus* (Cochran & Landman 1984; Landman & Cochran 1987; Landman et al. 1989) suggest that the time between the secretion of two successive septa increases exponentially during ontogeny. By analogy, some authors have used the number of septa as an indicator of the relative age of ammonite specimens (Doguzhaeva 1982; Dommergues 1988; Mignot & Elmi 1990). As Landman (1983) pointed out, this assumption (1) provides neither the actual duration between the construction of two septa nor the true age of a specimen, and (2) must be used only on individuals assumed to belong to the same species. Satisfying these latter conditions, it may be proposed that septal density – the number of septa per whorl – may serve as a useful relative age standard for ammonites. Phragmocone diameter is then substituted as the size standard. On this assumption, if two specimens of a single paleospecies are of the same size but have a different number of septa, the more septate one is deemed to be the older. Conversely, if two specimens of a single paleospecies have the same number of septa but are of different sizes, the larger one is assumed to result from a higher rate of shell secretion. As tested by Dommergues (1988), relative age estimated on the one hand by septal density and on the other by size may vary by a ratio of 1:2. As a consequence, species that had previously been thought to be progenetic (no separation of age and size in the study) might be dwarfs, as revealed by septal density analysis. As the ammonites studied in this paper have been demonstrated to belong to

![Fig. 3. Selected measurements. □A. Equatorial view. A diameter of the shell passing through the protoconch (Pr) and the chamber center (Chc) is measured for each chamber. □B. Axial view. Measurements are pro parte defined by Raup (1967). D = d/d ; W = (d/e)^2 ; S = b/a ; DT = Pw^2/4πSa.](image-url)
Characterization of heterochronies

A heterochronic process results from the modification of the relationships between three standards – age, size and shape – which are assumed to be independent. They have been denoted as follows by Alberch et al. (1979): $s$ for size, $\sigma$ for shape, $\alpha$ and $\beta$ for age (respectively onset and offset of growth of a defined feature). In this study, when seeking to identify heterochronies, the macroconch is always arbitrarly considered as the reference morph and the microconch as the compared morph.

For heterochronic interpretations, specimens must have finished their growth (adult), so as to guarantee that complete ammonites are being compared. The clearest indicator that growth is completed is an increase in septal density (Makowski 1962; Callomon 1963). Other characteristics include (1) uncoiling of the umbilical seam, which is less marked in the macroconch, (2) the occurrence of lappets or a rostrum on the adult microconch, while the macroconch retains a slightly sinuous peristome, (3) a change in the ribbing pattern mainly on the macroconch body chamber, and (4) narrowing of the body chamber. These characteristics are used here to identify adult specimens.

Using size as a proxy of age. – In this case, the most widespread in paleontological literature, no size standard is identified. Thus, heterochronic interpretations are based on comparison of age versus shape. Four basic heterochronies that do not involve size-age dissociation can be identified: acceleration is defined as an increase in the rate of shape development; retardation (neoteny) as a decrease in the rate of shape development (in acceleration and retardation, compared and reference morphs differ only by the shape sequence); hypermorphosis is defined as an extension of ontogeny in terms of age; progenesis as a truncation of ontogeny in terms of age. The latter two heterochronies do not involve size-age dissociation: when ontogeny is extended (hypermorphosis), size is greater and the adult shape attains additional ontogenetic stages (generally with over-expression of allometries), and when ontogeny is shortened (progenesis), size is smaller and the adult shape results from cancellation of ontogenetic stages.

Separating size and age. – In this case, two further heterochronies resulting from a size-age dissociation can be identified in addition to the four set out above: giantism and dwarfism. Proportioned giantism is defined as more rapid size development with respect to the age-shape relationship; proportioned dwarfism as slower size development with respect to the age-shape relationship. Thus, each shape stage appears either at a greater size (giantism) or at a smaller one (dwarfism), but at the same age. Because the three standards are recognized, heterochronic results are presented in a three-dimensional heterochronic cartouche (Fig. 4C) constructed from size-age and size-shape graphs. Ontogenetic patterns are then
constructed directly from diagrams providing a quantitative view of heterochronies. In this kind of representation (Fig. 4C), a cartouche expresses size by the length of the size arrow, age by the length of the age segment, and shape by the sequence of stages in the box. In the reference morph, the age segment and the size arrow are of the same length (supposed to be the age of the adult at the end of growth), constructed from the size-age graph (Fig. 5). The growth of the compared morph is represented by the same rule: the length of the size arrow is found with respect to the adult size ratio between reference and compared morph, plotted on the age-size graph (Fig. 5). The ontogenetic shape sequence can be drawn inside the cartouche on the basis of the shape-size relationships. These two cartouches provide a comparison in terms of age, size and shape. Heterochronies are illustrated by this new mode of representation in Fig. 6.

Analysis of Morphoceras macrescens
Buckman – Ebrayiceras jactatum
Buckman

* M. macrescens*, considered as the macroconch, normally reaches 90 mm for a complete adult, with a 55 mm diameter phragmocone (adult without living-chamber), whereas *E. jactatum*, considered as the microconch, stops growing at 45 mm for a complete adult, with a 30 mm diameter phragmocone. The septa immediately following the protoconch could not be observed from the sections, so chamber numbering began when the diameter was 6.6 mm (which was the smallest common diameter observed for all specimens).
Shape/diameter (size).—Shape analysis revealed very close correlations between each linear dimension and the diameter ($0.85 < r < 0.99$). For a shape–size study, the use of shape indices provides an explanation of morphology that is free from the influence of the size factor. A series of characteristic trajectories (with diameter on the x-axis and shape index on the y-axis) reveals different ontogenetic patterns (Fig. 7). Type 1: simplest trajectory showing shape changing in the same direction from juveniles to adults. The whorl section ($S$) changed gradually from a circle to an elongated section, and $b/T$ decreased steadily throughout ontogeny. Type 2: morphological changes occurred mainly in juveniles, and thereafter shape was almost constant. This was particularly clear for $W$ and for $a/T$, $b/T$, $d/T$, and indicates large morphological change in juveniles up to 15 mm, which could be considered as a morphological crisis point, following a phase of instability. The method of measurement might be suspected of producing juvenile instability, but this instability was observed whatever the method used: linear measurements or image analysis processing (DT). Errors in determining the ammonite center (protoconch) when absent could not be suspected of producing this instability, as the latter was determined from parameters that are independent of center localization (DT, $S$). Moreover, similar instability has been observed in Liassic ammonites (Mignot & Elmi 1990) using methods based on interseptal angles. Type 3: a complex ontogenetic trajectory partly explained by high variability, but with dissociation between morphs. Thus for DT, juveniles had an increasingly complex circular section up to 15 mm. $D$, $a/T$, $p/T$ and $c/T$ were also characteristic of type 3. The amplitude of juvenile instability appears clearly on a $D$–$W$ graph where the studied specimens were digitized at three size stages (Fig. 8). The juvenile morphological space is very large but decreases drastically for specimens of more than 15 mm in diameter. This confirms the evidence of a growth crisis at 15 mm. To obtain a single value to express shape, multivariate analysis (PCA) was carried out on 10 parameters. Major contributions on the first axis express shell size (Table 1). The second axis (F2) is mainly representative of shell shape (major contributions for DT, $D$ and $W$). The F2 values were used for the size–shape study (Fig. 9). High juvenile instability appears...
clearly up to the morphological crisis point (15 mm). Thereafter both morphs show a difference in shape, both microconch and macroconch acquiring similar morphologies, but at very different sizes, as is brought out by the quadratic regression modeling the shape trajectory for each morph (Fig. 9B).

Diameter (size) / number of septa (age). – The rhythm of growth: the size–age correlation, was similar among specimens of each morph, as it was between macroconchs and microconchs (Fig. 10A). However, the microconchs had about 20 septa at the end of growth, whereas the macroconchs had about 35 septa. Thus the difference in adult

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**Table 1.** Eigenvalues, percentage of variance and relative weights of variables on the first two axes of the principal components analysis of *M. macrescens* and *E. jactatum* (bold values stress the most significant variable).

<table>
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<tr>
<th>Variable</th>
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<th>F2</th>
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<tr>
<td>Variance %</td>
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<td>15.3</td>
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<tr>
<td>S</td>
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<tr>
<td>d</td>
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<tr>
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Fig. 8. Morphological space (D–W) for three successive growth stages of *M. macrescens* and *E. jactatum*. Note the drastic decrease in variance after 15 mm in size, mainly attributable to W.

Fig. 9. **A.** Shape changes in axial sections for *M. macrescens* and *E. jactatum* (the number of each whorl section is used in Fig. 11 B). **B.** Shape ontogeny versus size in adults of each morph (phragmocone plus living-chamber), tested by quadratic regressions. Macroconch: $R^2 = 0.51$, highly significant *F*-test, microconch: $R^2 = 0.60$, highly significant *F*-test.
Diameter (size) / number of septa (age) / shape. – The size–age cartouche may be completed here with the shape data. Ontogenetic changes in shape are represented by quadratic regression. A size–age–shape cartouche was constructed as in Fig. 4C. The shape variation was divided into four parts, the part corresponding to the living chamber being added but without assumptions about age (Fig. 11). From the onset of growth to the morphological crisis, there was no morphologically stable stage. At the end of the phragmocone, the macroconch remained at shape stage 1, whereas the microconch reached shape stage 2. For the living chamber, the macroconch attained shape stages 1–3, whereas the microconch reached shape stages 2–4, which brings out the tendency of the microconch to acquire a more ogival section and a more involute shape more rapidly.

Heterochronic interpretation with size as a proxy of age. – The two ontogenetic patterns representing Macrinus macr...
(macroconch) and *E. jactatum* (microconch) can be interpreted in terms of heterochronies. The macroconch grows for a longer time (larger adult diameter) than the microconch (smaller adult diameter), and consequently the microconch appears to be progenetic compared with the macroconch. Shape changes are accelerated in the microconch, which passes from stages 1 to 4, while the macroconch only achieves stage 3, but at a greater size (Fig. 11). Thus the microconch presents characteristics of acceleration in comparison with the macroconch. We report then a set of two heterochronies explaining the differences between the two morphs. The results of the association of basic heterochronies (complex heterochronies) have been grouped in terms of both hyper-peramorphosis and hyper-paedomorphosis, and also as mimetic combinations when the association of two heterochronies looks like a single one (Dommergues et al. 1986). In the present case (progenesis plus acceleration), the association is a mimetic combination termed pseudo-dwarfism.

**Heterochronic interpretation when separating size and age.** Because no dissociation between size and age is recognized, the heterochronic interpretation when size and age are separated is the same as before. The macroconch grows for a longer time (more septa) than the microconch (fewer septa) with shape changes in the microconch being accelerated. Consequently, the microconch also appears to be progenetic and accelerated.

**Analysis of *Cardioceras cordatum* (Sowerby)**

The two morphs of the dimorphic species *C. cordatum* are of very different sizes. The macroconch can reach 200 mm on average for a complete adult, with a 140 mm diameter phragmocone, whereas the microconch stops growing at 80 mm for a complete adult, with a 50 mm diameter phragmocone. We have used incomplete macroconchs here but of sufficient size to avoid any ambiguity during comparison with microconchs. For size–age analysis, the chambers were numbered from 6 mm and upwards. No shape study was conducted because of a shortage of specimens (partly because of destruction during preparation).

**Diameter (size) / number of septa (age).** The two microconch phragmocones studied were about 40 mm in diameter, which is the top-end of the phragmocone size range described for this species. Thus, these two specimens could be considered as adults, even though there was no marked crowding of the last few septal sutures. The six macroconch specimens were not complete adults, but the three larger ones (diameter > 60 mm) could be used for studying the size/age relationship. The rhythm of size increase was similar for the two microconchs, whereas there was great variability among the macroconchs (Fig. 12A). The representative size–age relationship obtained by quadratic regression (Fig. 12B) showed that the two morphs did not increase in size at the same pace, the macroconchs having the higher rate. For example, the diameter was about 37 mm for 50 septa in the microconchs whereas it reached 57 mm for the same number of septa in the macroconchs. In addition, the microconchs (subadult) achieved their maximum number of septa (about 60), while the studied macroconchs were still juveniles, and consequently had still not acquired their maximum number of septa. Thus, the size–age difference between

![Fig. 12. Size–age relation in *C. cordatum*. □A. Ontogenetic trajectories (each line corresponds to an individual) for diameter $T$ (size) versus number of septa (= age). □B. Quadratic regression for adults of each morph. □C. Size–age framework for both morphs.](image-url)
these two morphs can be accounted for by two combined phenomena, the microconch being smaller than the macroconch because of a slower tempo and a shorter period of growth, as shown in the size-age cartouche (Fig. 12C).

Heterochronic interpretation when size is a proxy of age. – In C. cordatum, the two morphs become adults at a different size. In this case, where size is considered as a proxy of age, the microconch morph is simply interpreted as being progenetic compared with the macroconch.

Heterochronic interpretation when size and age are separated. – In this case, the difference in the size-age relationship is partly explained by a difference in the duration of growth. The microconch morph stops growing at about 60 septa, while the macroconch morph continues to grow. The final adult number of septa for the macroconchs could not be determined here, because the study specimens were incomplete phragmocones. Nevertheless, the difference in the duration of growth can be interpreted in terms of heterochronies, showing the progenetic nature of the microconchs (fewer septa than in the macroconchs). Moreover, comparison using the size-age cartouche (Fig. 12C) reveals a complex phenomenon of differentiation between the two morphs. The microconch is shorter than the macroconch at the same age (same number of septa), indicating dwarfism in the microconch. In this study, dwarfism is considered as the occurrence of a different size-age relationship between morphs (~dks). No shape data were needed to depict these heterochronies. Thus, microconch differentiation combined two phenomena: dwarfism and progenesis.

Conclusion

The accepted distinctive criteria in the literature for associating two ammonite morphs within a single dimorphic pair are based principally on the different diameters of adults (smaller for the microconch) and on morphological similarities at the juvenile stages. In heterochronous terms, using size as a proxy of age, this distinction would amount to considering the microconch morph as generally progenetic by definition. On the contrary, dissociating size (diameter) and age (here estimated by the number of septa) reveals two different ways for dimorphism to be acquired for the two studied cases: (1) in the case of the pair M. macrescens–E. jactatum, size-age relationships remain identical for both morphs. The microconch stops growing earlier and becomes, as a result, a developmental truncation of the macroconch: progenesis. Furthermore, the shape of the generating curve and the whorl section undergo modification more quickly in the microconch morph: progenesis is then associated with accelerated shape acquisition. As the shapes coincide but at different ages (or sizes), the similarity of the inner whorl (justifying the pairing of the two morphs) is thus not quite exact; (2) in the case of C. cordatum, and when size and age are separated, there is no absolutely identical size-age relationship between the two morphs. As with the previous case, the microconch stops growing earlier than the macroconch and thus is progenetic. Furthermore, at every age, the microconch is smaller than the macroconch. This slower pace of growth of the microconch can be interpreted as dwarfism. Thus, dimorphism among these two ammonite species appears as a complex phenomenon resulting from the association of basic heterochronies: progenesis plus acceleration in one case, and progenesis plus dwarfism in the other.

Once these heterochronic processes have been identified, one can speculate about the adaptive significance for each species of such different ways of acquiring dimorphism. Progenesis of microconchs, leading to precocious reproduction, would mean that males (if we accept the consensus assumption that the microconch is the male) could mate with immature females or with previous generation females. These two types of reproduction are known within coleoids (sister group of ammonites, Jacobs & Landman 1993): In many species, males mate with immature females and spermatozoa are stored for up to ten months (Mangold 1987, p. 164), whereas, in others, mature females are found more or less year-round and generations may overlap (Mangold 1987, p. 195). The case of dwarfism found in C. cordatum leads to a smaller mature male (microconch) than strict progenesis. It could be suggested that dwarfism provides the opportunity for the species to exploit two different ecological niches (one for the large macroconch, another for the small microconch). Anyway, as demonstrated by Boletzky (1986), no common reproductive strategies exist between the different recent cephalopod species, leading to a large variation in life-history patterns. Thus it is not surprising to find different ways for dimorphism to be acquired in ammonites, as demonstrated here. We should simply recall that the only relevant way to demonstrate such heterogeneity is to separate age and size data. Otherwise a microconch will invariably appear as a simple progenetic morph compared with the macroconch, which seems to be an oversimplification.

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References


Heterochronic differentiation of ammonite dimorpha


