

## Ontogeny and covariation in the Toarcian genus *Osperleioceras* (Ammonoidea)

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*Key words.* – Covariation, Ornamentation, Shell shape, Ontogeny, Stress-induced variability, Ammonoidea, Toarcian

*Abstract.* – Starting from embryonic (protoconch-ammonitella) and early juvenile shells, which are indistinguishable at the species level, growth curves of *Osperleioceras* from the Reynesi Subzone (Upper Toarcian) of the Causses Basin (Aveyron, France) show a continuous radiating range of correlated variation in dimensional and ornamental characters, such as involution, whorl compression, rib strength and rib density. This covariation pattern can be observed among single-horizon assemblages, as well as during individual ontogenetic development.

The existence of a continuous intergradational series of shells, ranging from stout coarsely ribbed to smooth suboxycone morphologies, rules out functional or ecological selectivity to explain this non-random variability pattern. The complex interdependence of shape and sculpture can be simulated by a model in which sculpture intensity depends on mantle curvature [Guex, 1999].

The expression of covariation in subadult specimens since the base of Upper Toarcian reveals a rise in variability, concomitant with a size decrease, both contemporaneous with environmental instability. It developed in successive bursts from a fairly long low variability period spanning the whole Middle Toarcian.

### Ontogenèse et covariation chez le genre toarcien *Osperleioceras* (Ammonoidea)

*Mots clés.* – Covariation, Ornementation, Ontogenèse, Variabilité morphologique, Stress environnemental, Toarcien, Ammonoidea

*Résumé.* – Les courbes de croissance des *Osperleioceras* de la sous-zone à Reynesi (Toarcien supérieur) du bassin des Causses (Aveyron, France) sont toutes confondues du stade de la protoconque et de l'ammonitelle, jusqu'à un diamètre de 7-8 mm. Elles forment ensuite un éventail de trajectoires résultant en un continuum morphologique allant de formes évoluées à tours larges et ornementation forte (*O. reynesi*) jusqu'à des formes involutes, comprimées et faiblement ornées (*O. lapparenti*). La covariation de divers paramètres morphologiques et ornementaux est observable tant au sein d'assemblages provenant d'horizons uniques qu'au cours des développements ontogénétiques individuels.

Il n'est pas possible d'interpréter cette série continue et contemporaine, passant insensiblement des morphologies de type *reynesi* à celles de type *lapparenti*, comme étant une tendance évolutive due à des contraintes fonctionnelles ou à des adaptations différentielles. L'interdépendance complexe de la forme de la coquille (involution, section du tour) et de son ornementation (force, densité et flexuosité de la costulation) peut être simulée par un modèle où l'intensité de l'ornementation dépend de la courbure du manteau [Guex, 1999].

La covariation observée chez les *Osperleioceras* dès la base du Toarcien supérieur trahit une augmentation de variabilité, concomitante d'une réduction de taille, suite à des instabilités environnementales. Elle se fait en plusieurs poussées à partir d'un stock de formes ayant très peu varié au cours du Toarcien moyen.

## INTRODUCTION

First observed by Buckman in *Sonninia* and *Amaltheus* [Buckman, 1887-1907] and addressed later by Westermann [Westermann, 1966], covariation was originally described as follows: "Roughly speaking, inclusion of the whorls correlate with the amount of ornament – the most ornate species being the more evolute [= loosely coiled] and having almost circular whorls..." (two such covariation series are illustrated in figure 1). It is now known that covariation depends on internal shell geometry, namely the lateral and ventral curvature of the shell which controls the thickness of the mantle and the concentration of morphogens present in that shell-secreting epithelium [Guex, 1999; 2001a]. The most salient ornamentation is present where the whorls are the most curved. Shells with slight angular bulges are often

spinose or carinate whereas flat ones are almost smooth. These observations have recently been tested by André Koch [in Guex *et al.*, 2003] within the conceptual framework of Meinhardt's reaction-diffusion models [Meinhardt, 1995]. Koch simulated the distribution of morphogens in a triangular body chamber and demonstrated that morphogen maxima are located in those parts of the mantle situated in the angular parts of the shell.

Covariation patterns linking evolute, wide-whorl, strongly ornate to involute, compressed, smooth shells, through all intermediate and intergradational forms have been found in many Mesozoic groups (table I). Ornamental covariation has scarcely been reported in Paleozoic ammonoids [Kaplan, 1999], although morphological parameters may covary.

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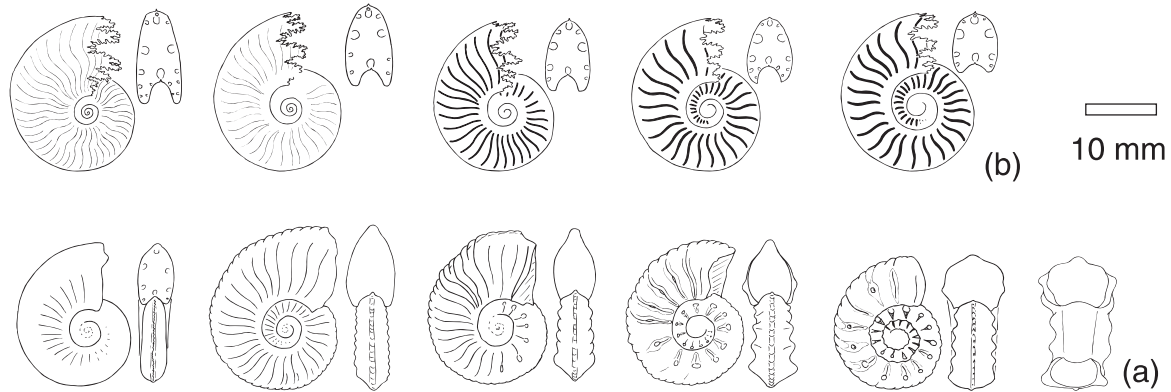


FIG.1. – Two examples of covariation in ammonoid shells from the Causses Basin (all specimens are of equivalent size) : (a) Domerian *Amaltheids* (see also plate 1 in Mattei [1985] for a similar series of intergradational forms) ; (b) Upper Toarcian *Osperleioceras* species.

FIG.1. – Exemples de covariation chez deux genres d'ammonites du bassin des Causses (spécimens de tailles équivalentes) : (a) *Amaltheus* du Domérien ; (b) *Osperleioceras* du Toarcien supérieur.

TABLE I. – Examples of covariation patterns in ammonoids of various ages. The spectrum of variability is more or less wide and its exact morphological expression depends on specific characteristics.

TABLE I. – Quelques exemples de covariation chez les ammonites au cours des temps géologiques.

group	age	morphological range	bibliographic references
<i>Neogastrolites</i>	Cretaceous	compressed, costate stout nodose subglobose spinose	COBBAN & REESIDE 1960, plates 5-7
diverse species	Malm		OLORIZ et al. 1999
Kosmoceratids	Callovian		TINTANT 1963 : "variations corrélatives"
<i>Sonninia</i>	Bajocian		BUCKMAN 1887-1907; WESTERMANN 1966
<i>Poecilomorphus</i>	Bajocian	"the stouter the whorls, the stronger the ribbing"	STURANI 1971 : covariation
<i>Osperleioceras</i>	Toarcian	involute, flat-topped midvolute, falcoid evolute, sigmoid	this paper
<i>Amaltheus</i>	Domerian	involute, lenticular, smooth compressed, costate evolute, spinose	BUCKMAN 1887-1907 ;ZELL et al. 1979 ;MATTEI 1985, plate 1 : "consécution morphologique"
<i>Czekanowskites</i>	Trias	smooth oxycone straight-ribbed platycone rough, subnodose cadicone	DAGYS & WEITSCHAT 1993 ; CHECA et al. 1996
<i>Trachyceras</i>	Trias	compressed, delicately strigate robust, coarsely ornate	SILBERLING 1956
Medicottiaceae, <i>Clymeniina</i>	Palaeozoic		KAPLAN 1999

The Toarcian genus *Osperleioceras* KRIMHOLZ & TAZIKHIN, 1957 serves as a striking example to illustrate ontogenetic and phylogenetic aspects in the development of such non-random continuous variability through morphometric comparisons, both in terms of shape and sculpture.

## MATERIAL AND METHODS

The wealth of well-preserved, finely pyritized, ammonites of the Middle to Upper Toarcian from the Causses Basin (Aveyron, France), is particularly well suited for studies of early growth stages. However, most of the material (mainly internal moulds) consist of incomplete phragmocones, or shells of indeterminate developmental stage, with the body chamber marked either as a flattened impression in the marly sediment, or as a bloated concretion at the end of the phragmocone. A number of criteria (septal approximation, ornamental differentiation, change in coiling parameters)

tend to indicate a subadult stage at a shell diameter of 15-20 mm or more. In spite of the lack of indisputable adult morphologies, much information can be gained with simple meticulous preparation techniques.

The samples were gathered from the Reynesi Subzone [Guex, 1973] (approximately equivalent to the Gruneri Subzone [Elmi *et al.*, 1997]), as this period of time corresponds to the largest range of morphological diversity attained by *Osperleioceras* [Mattei, 1969 ; Guex, 1975 ; Guex, 1992]. Indeed, the first representatives of this genus – mainly *Osperleioceras bicarinatum* (ZIETEN) – remained remarkably stable during the Middle Toarcian, before a first increase in variability at the base of the Upper Toarcian (*O. beauliziense* and *O. rivierense*). A further radiation occurred in at least two distinct bursts, although each successive horizon displays a continuous range of intergradational and overlapping morphologies. The Speciosum Subzone [Guex, 1973] (approximately equivalent to the Insigne Subzone [Elmi *et al.*, 1997]) is characterised by *O. wunstorfi*

(MONESTIER) variants (*O. subcostulatum*, *O. alternans*) with widely spaced ribs in juvenile forms. Contemporaneous involute finely ribbed morphotypes are also found (*O. carezi* and *O. pervinquieri*). The following Reynesi Subzone represents the final diversification of the genus with an evolute pole (*O. reynesi*) coexisting with involute forms (*O. authelini*, *O. lapparenti* and less commonly *O. suessi*) [Guex, 1992]. It should be noted here that *O. bicarinatum* and *O. beauliziense-rivierense* specimens are larger on average than later representatives.

We prepared and measured about 300 *Osperleioceras* specimens. The internal structures were not always preserved and some material was also broken during preparation, which left us with 48 polished sagittal sections and 28 dissected protoconchs adequately preserved. The parame-

ters, measured either directly with an unequal-branch calliper or on accurate camera-lucida drawings, are defined on corresponding illustrations.

We concentrated our measurements on extreme morphotypes so that possible differences would appear more clearly. However, preparations were also made on intermediate forms in order to constrain the range and the continuity of the variation pattern. Moreover, a few specimens were also prepared from successive stratigraphically allocated assemblages spanning the evolutionary radiation of the genus.

Measurements were initially made in order to test a hypothetical correlation between the size and proportions of the protoconch and the coiling, involution or whorl proportion of the subterminal phragmocone. As no significant

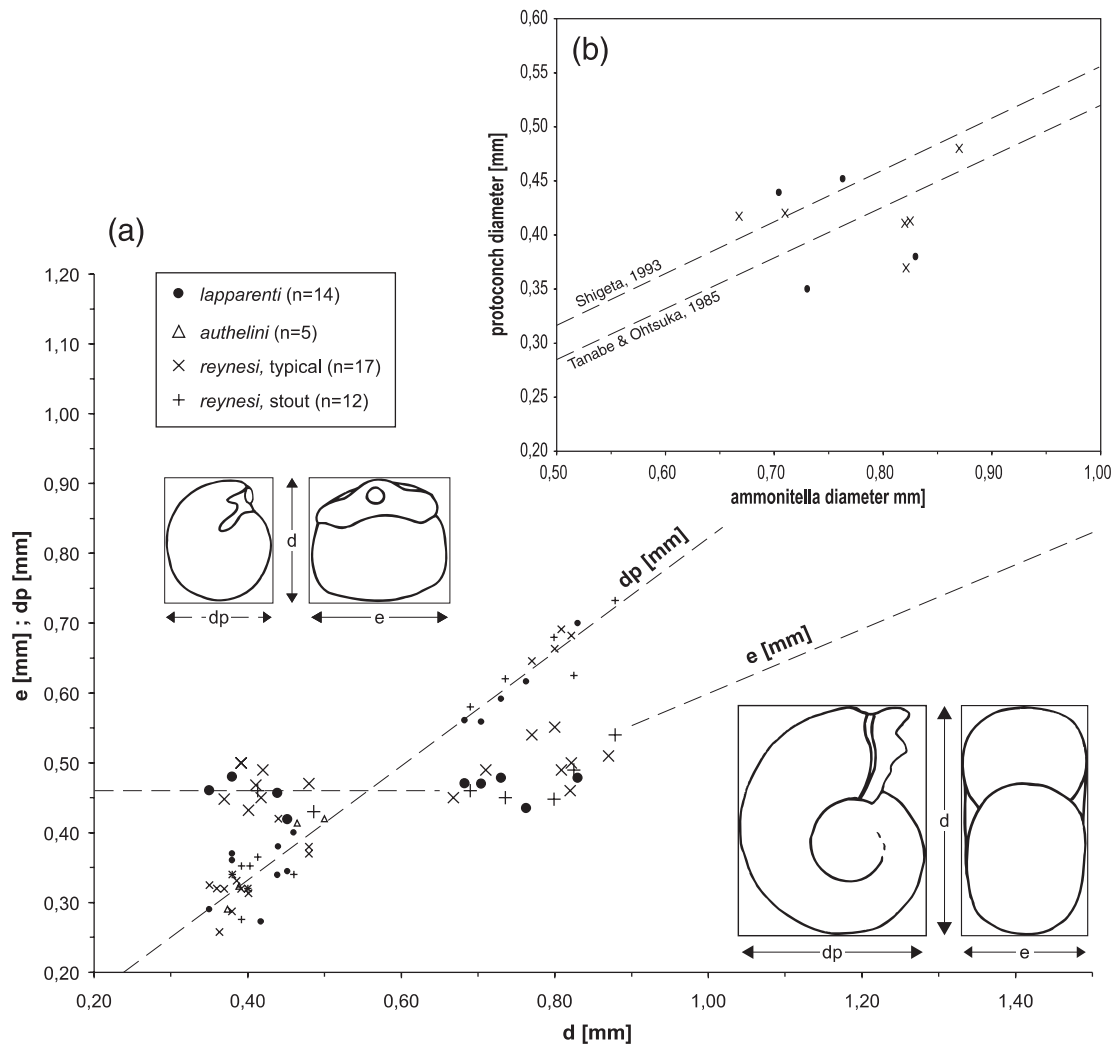


FIG. 2. – (a) Comparison of growth curves based on three orthogonal morphological parameters in the early stages of *Osperleioceras* specimens from the *Reynesi* horizon (Upper Toarcian). Evolute (*reynesi*), midvolute (*authelini*) and involute (*lapparenti*) morphotypes have indistinguishable protoconch and ammonitella sizes. The respective proportions (dp/d and e/d) do not show any significant differences either. Note the constant shell width from the protoconch to the ammonitella. The regression curves were drawn from measurements on later stages only. (b) Correlation between protoconch and ammonitella sizes could not be statistically confirmed from our data. However, our measurements lie close to published regression curves calculated from comparisons of several ammonoid orders [Shigeta 1993 ; Tanabé and Ohtsuka 1985].

FIG. 2. – (a) Comparaison des courbes de croissance pour les stades précoces d'*Osperleioceras* de l'horizon à *Reynesi*. La taille et la forme des protoconques et ammonitelles sont indistingables. (b) Corrélation entre les tailles de la protoconque et de l'ammonitelle d'après les courbes de Shigeta 1993 ; Tanabé and Ohtsuka 1985.

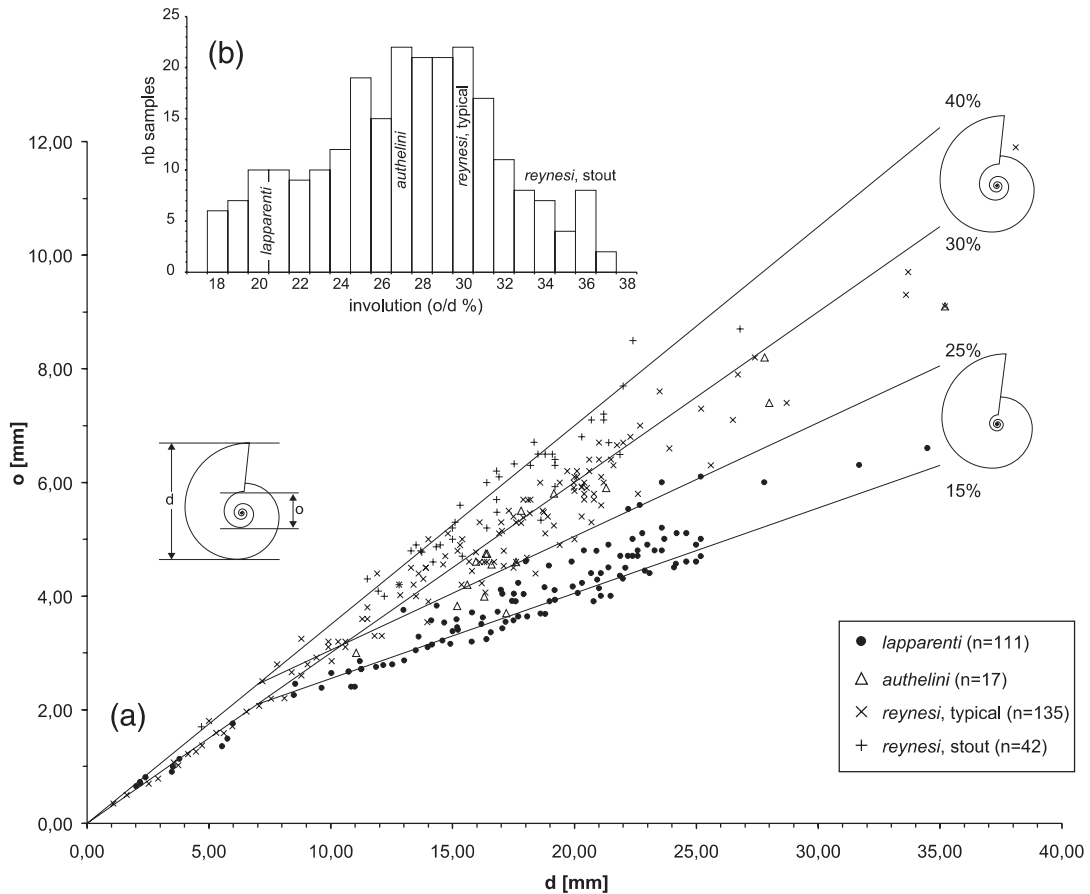


FIG. 3. – (a) Growth curves for umbilical diameter in function of ventral diameter. Early growth stages are rather evolute and do not show any significant differences (see also fig. 2). But from 7-8 mm ventral diameter, a continuous fan of divergent morphologies develops. Two major trends are outlined by lines of equal involution :  $o/d = 15-25\%$  for involute shells ;  $o/d = 30-40\%$  for evolute ones. Intermediate (midvolute) shells are numerous and group together *authelini* morphotypes, as well as specimens attributed to either *reynesi* or *lapparenti* morphotypes on ground of ribbing pattern and/or whorl section. (b) Histogram for the involution of specimens larger than 15mm diameter. Although some taphonomical and methodological selection inevitably occurred, this represents quite well the predominance of *reynesi-authelini* morphologies in these levels, with a non-negligible proportion of more involute and compressed shells (*lapparenti*) and some very evolute *reynesi* variants with stout equidimensional whorl section.

FIG. 3 – (a) Courbes de croissance du diamètre ombilical en fonction du diamètre ventral. Deux trajectoires extrêmes sont soulignées au sein d'un spectre continu. (b) Histogramme du degré d'involution pour des spécimens de plus de 15mm de diamètre.

differences could be ascertained [Morard, 1997], we carried our investigations further on with a few complete individual growth curves of representative morphotypes.

**TAXONOMIC REMARK**

We refer to Monestier [1921], Mattei [1969] and Guex [1973, 1975] for taxonomic descriptions. The results obtained here accord fairly well with Monestier's initial "specific" nomenclature, although his types were originally distributed among several different genera. Moreover, he already acknowledged a certain amount of variability, giving two or three illustrations of each group, spanning the range of variability he considered of specific value. Although a revision of the genus in the light of new population and morphometric data might be undertaken, we believe it would change neither the stratigraphical resolution, nor the phylogenetic inferences dramatically. Furthermore, a population approach would probably result in the grouping of all intergradational morphologies from a single level into only one "species" [see discussion in Callomon, 1963].

**RESULTS**

Three major growth stages were recognised in the development of *Osperleioceras* individuals, on grounds of allometric parameters and ornamental changes.

**Protoconch, ammonitella, early juvenile**

When breaking down specimens of different *Osperleioceras* morphotypes, it rapidly became apparent that early growth stages tended to be almost indistinguishable for shells of less than 5 mm diameter. The first whorls are little overlapping and subcircular in section. Ornamentation is not yet perceptible. This impression was confirmed by morphometric measurements, as the growth curves are all superimposed whatever the later morphology of the shell (figures 2 and 3).

The comparison of protoconch data belonging to extreme morphotypes did not show any significant differences, either in size (diameter, width), or in shape (lateral and frontal projections). The ammonitellas are identical as well, corresponding approximately to one whorl. Though

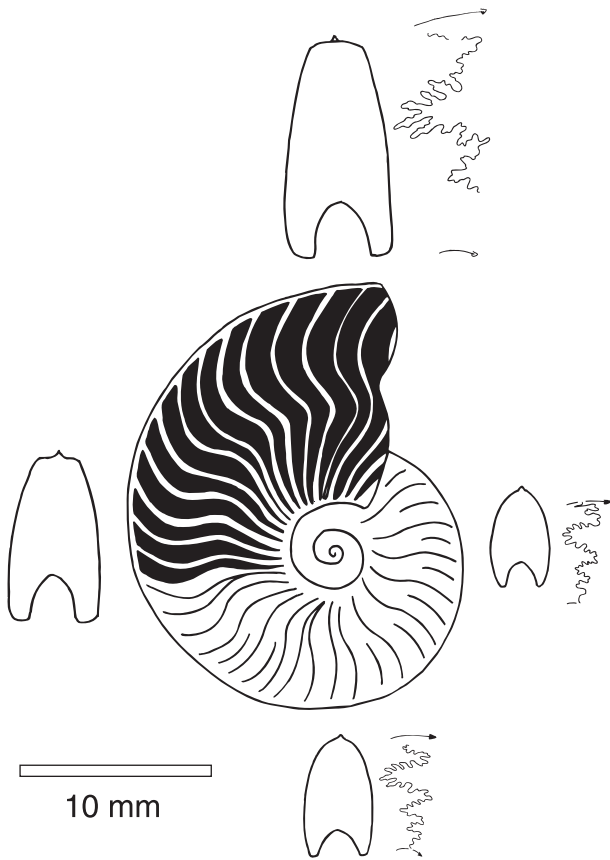


FIG. 4. – Simultaneous changes in flank curvature, venter profile and rib type in *Osperleioceras bicarinatum* (ZIETEN) from the Middle Toarcian of the Causses Basin (France). The acquisition of a typical tabulate whorl section is concomitant to the development of flat-topped ribs bridging two asymmetrically spaced single ribs.

FIG. 4. – Changements simultanés entre la courbure des flancs, le profil ventral et l'ornementation chez *Osperleioceras bicarinatum* (ZIETEN).

scarce, our measurements fall close to the regression lines obtained on a bivariate plot of protoconch versus ammonitella sizes when comparing species from different ammonoid orders (fig. 2) [Tanabe and Ohtsuka, 1985 ; Shigeta, 1993]. This large-scale correlation of ammonitella and protoconch sizes was interpreted in terms of buoyancy of the newly-hatched ammonite and seems to indicate a juvenile planktic mode of life [see Landman *et al.*, 1996 for a review].

In addition, note that from the protoconch to the first (nepionic) constriction there is no increase in width (parallel to the coiling axis). This constant embryonic shell width

seems to be common among ammonites [see for example the curves in Zell *et al.*, 1979 ; other references in Landman *et al.*, 1996]. Moreover, the umbilicus is geometrically undefined until the end of the first whorl.

The subsequent whorl is still qualitatively and quantitatively similar in all morphotypes, resulting in a shell of approximately 5 mm diameter (fig. 3). From this stage onwards the divergence of growth trajectories becomes more and more visible, simultaneously with the inception of ribbing. However it should be noted that there is no definite turning point, but rather a transition period of 1/2 whorl from 3-8 mm diameter. This change in growth parameters is both progressive in individual trajectories and slightly variable between individuals.

**First divergence and inception of ornamentation**

The increasing range of variability is difficult to separate objectively in the following stage as a complete intergradation of forms is observed.

The divergence of growth trajectories is particularly visible on a graph with umbilical diameter represented as a function of ventral diameter (fig. 3). Not only does the umbilical spiral expand more slowly in involute than in evolute shells (o/d ≈ 20 %, respectively 30 %), but the ventral spiral is also slightly more openly coiled (W = 2.58 and 2.34 respectively, table II). The difference in whorl width is much smaller.

In the meantime, ornamentation starts as low rounded undulations rapidly gaining in strength in evolute forms, whereas they remain faint tending to become finer and denser on involute shells. Involute and evolute forms are thus rapidly distinct, though variability is huge and all transitions can be observed in many traits (rib density, sinuosity, and strength ; involution, whorl proportions, flank profile).

Almost all shells tend to increased involution, compression and development of more flexuous, denser and finer ribs during ontogeny. However, evolute shells soon attain an overall stable morphology (subisometric growth). In contrast, involute shells continue to change shape as they grow.

**Subadult differentiation : (d ≥ 15-20 mm)**

Within the *reynesi-authelini-lapparenti* series, juvenile representatives are difficult to classify, as the range of variability does not show any clear-cut discontinuity. However, the morphotypes defined by Monestier [1921] represent a few typical morphologies judiciously selected to describe this range of variability. Some of their diagnostic characters may be due to subadult maturation.

TABLE II. – Parameters for spiral growth of representative specimens. Shell parameters were measured every 15° for diameter (d), umbilicus (o) and whorl height (h), every 180° for whorl width. When expressed in function of polar angle, the best fits for growth curves is obtained with exponential equations. TABL. II. – Paramètres de croissance pour deux spécimens représentatifs. En coordonnées polaires, les mesures peuvent être approximées par une équation exponentielle.

	involute ( <i>O. lapparenti</i> )	evolute ( <i>O. reynesi</i> )
<b>ventral diameter</b>	$d = 0.403 e^{0.151\phi}$	$d = 0.431 e^{0.136\phi}$
=> ventral expansion rate	W = 2.58	W = 2.34
<b>umbilical diameter</b>	$o = 0.210 e^{0.108\phi}$	$o = 0.143 e^{0.133\phi}$
=> involution	o/d decreases with growth, down to 15%	o/d ~ constant around 30%
<b>whorl height</b>	$h = 0.151 e^{0.164\phi}$	$h = 0.185 e^{0.134\phi}$
<b>whorl width</b>	$e = 0.366 e^{0.101\phi}$	$e = 0.265 e^{0.111\phi}$
=> whorl compression	h/e increases more steeply up to 200%	h/e gently increases up to 150%

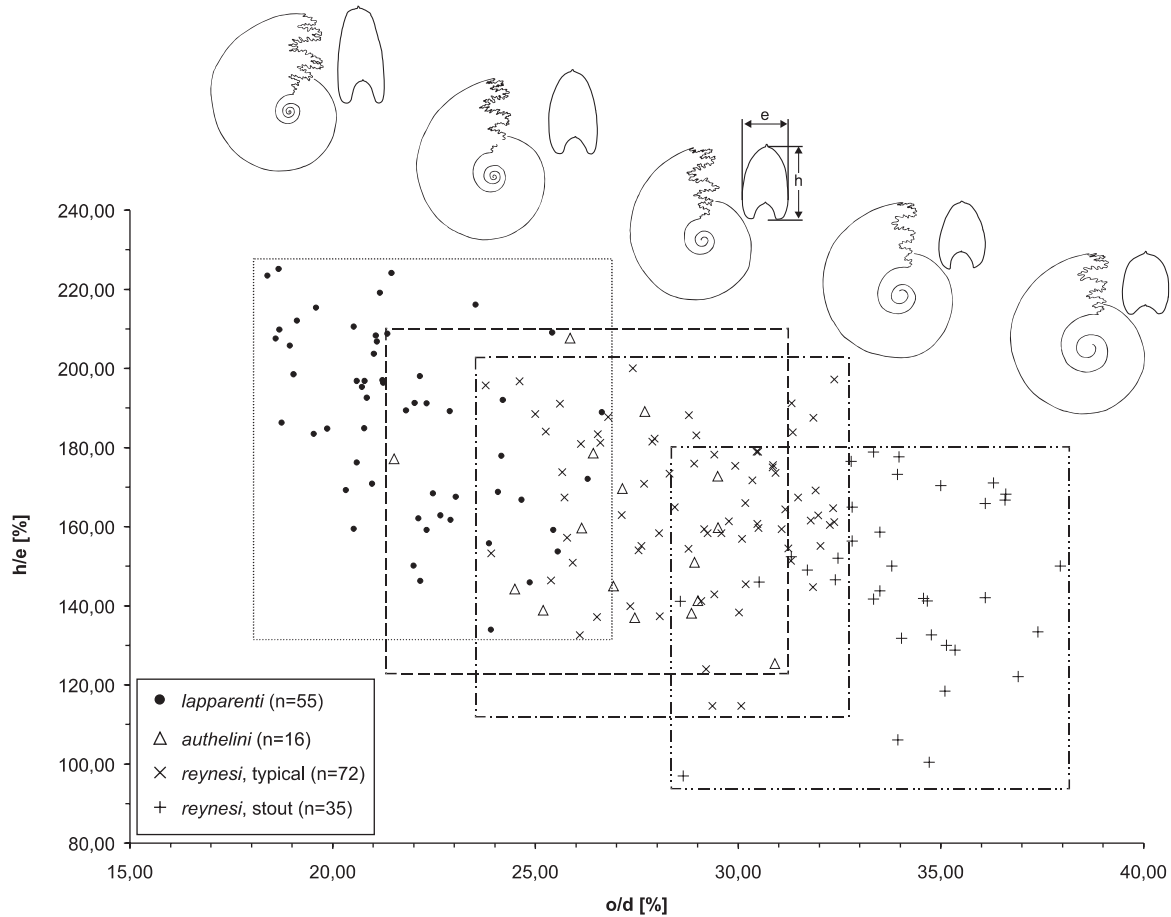


FIG. 5 – Interdimensional covariation of involution and whorl proportions for shells larger than 15 mm. Involute shells are relatively more compressed than evolute ones. This is partly due to the inverse relationship between whorl height and umbilical diameter, as they are interdependently defined. Ventral diameter and whorl width show less differences between extreme morphotypes during growth, although involute shells tend to be slightly more openly coiled. Selected specimens forming an ideal series of intergradational forms of equal size ( $d=18$  mm) are also represented.

FIG. 5 – Covariation interdimensionnelle entre le degré d'involutions et les proportions du tour pour des spécimens de plus de 15 mm.

Though extreme morphologies diverge already at 3-8 mm diameter, a further differentiation occurs in some midvolute to involute morphologies. This fairly rapid ornamental transition (“alternance”) occurs between 15-20 mm shell diameter. Ribbing becomes markedly denser, finer and slightly more flexuous, with possible intercalation of peripheral ribs in the upper half of the flanks.

A close correspondence exists between the modification of the ribbing pattern and the adoption of a tabulate whorl section. A noticeable rise in rib density appears quite suddenly (spanning 1/4 whorl) together with a decrease in strength and an increase in flexuosity. This is most visible among *Osperleioceras wunstorfi* variants (*sucostulatum-alternans* particularly). The appearance of flat-topped ribbing in *Osperleioceras bicarinatum* corresponds to the same change in whorl section (fig. 4). This peculiar pattern is due to the junction of pairs of asymmetrically spaced flexuous ribs.

### SYNTHESIS OF GROWTH TRAJECTORIES

Whereas “stout *reynesi*” morphotypes tend to grow almost isometrically, keeping their overall proportions and ribbing pattern as they grow, all other variants tend to increased involution, compression of the whorl and development of denser and finer ribs.

A smooth phase was observed up to the third whorl, followed by a wide diversification (4<sup>th</sup>-5<sup>th</sup> whorls) and a final convergence by sculptural weakening in the last half whorl. Amaltheids also show these three stages in ontogeny: identical almost unornamented embryonic stages, an explosive burst of juvenile variability, and a final parallelism by compression of the whorl and development of finer, denser ribs. It would be tempting to interpret the subadult differentiation as a case of sexual dimorphism (or another kind of discrete polymorphism) were it not for the clear absence of any bimodal size repartition and the perfectly continuous variability in both magnitude and timing of these changes.

We can somewhat arbitrarily separate a few typical morphotypes in the stratigraphically successive populations. Typical coiling parameters are given in table II for “average” *reynesi* and *lapparenti* morphotypes.

### CHARACTER COVARIATIONS

Extreme morphotypes differ in a large number of characters. However, these do not vary independently from one another. Covariation patterns, as defined in the introduction, are observed both among adult morphologies and in ontogenetic series.

**Interdimensional covariation (fig. 5 ; involution-compression)**

In *Oesperleioceras*, involute shells are relatively more compressed than evolute ones (fig. 5). This is mainly due to the inverse relationship between whorl height and umbilical diameter, as they are interdependently defined, whereas whorl width shows but little difference between extreme morphotypes during growth. Involute shells also tend to be slightly more openly coiled, which means that growth rate of the ventral diameter [W as defined in Raup, 1967] is somewhat greater (table II).

**Sculpture-whorl shape covariation (fig. 6)**

Several methodological difficulties arise when considering the relation between whorl shape and rib strength.

In the first place, the prominence of the ribs will influence the measurement of whorl proportions, even on internal moulds. For practical reasons, whorl width measurements included rib relief. Although inter-rib width would have been more appropriate, this would have implied inextricable practical complications. However rib prominence does not suffice to explain the covariation patterns observed, as can be proved from similar measurements in *Amaltheus* that displays a greater range of rib variability

(from stoutly spinose to almost smoothly and densely flexuous ; fig. 1). In this genus, whorl proportions can be measured between ribs. Sculpture prominence clearly adds to and reinforces existing differences in whorl proportions.

In the second place, simple whorl proportions do not precisely describe flank curvature. Indeed one can easily imagine different whorl outlines inscribed in the same rectangle. However, in *Oesperleioceras*, whorl section can be roughly approximated to a semi-ellipse whose short and long axes correspond to whorl width and half whorl height respectively. At equal whorl width, mean flank curvature increases with a decrease in whorl height, whereas ventral curvature decreases concomitantly.

In spite of these methodological limitations, a significant covariation appears qualitatively between rib strength and whorl section. Now, as rib strength is also difficult to quantify, we measured rib density (number of ribs per half whorl) and plotted it in relation to involution, a measurement not directly influenced by sculpture pattern (fig. 6). The correlation is clearly visible. Extreme morphologies do not overlap, although no discontinuity can be viewed when considering the whole range of variability. The only perceptible differences occur in the uneven frequency distribution of characters (fig. 3).

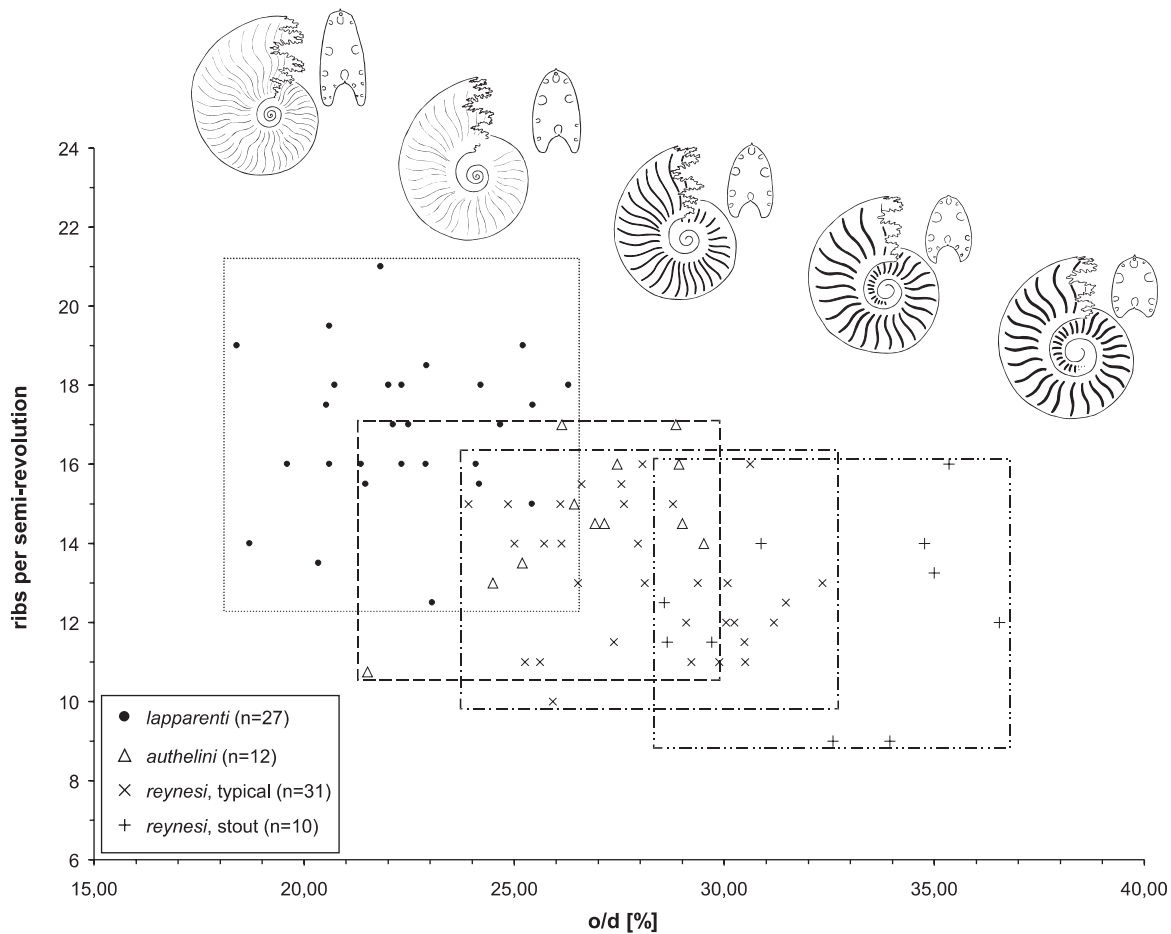


FIG. 6 – Shape-sculpture covariation of involution and rib density for shells larger than 15 mm. Involute shells are more densely ribbed. Their ornamentation is also less prominent and more flexuous. As in figure 4, the same series of intergradational forms of equal size (d=18 mm) was used to illustrate the continuous range of variability.

FIG. 6 – Covariation entre forme et ornementation pour des spécimens de plus de 15 mm.

### Suture-whorl shape covariation

Fractal analyses of suture lines have shown that sutural complexity correlates on a large scale with shell geometry [Oloriz *et al.*, 1999]. Only qualitative differences were observed in *Osperleioceras*: sutural elements tend to be more finely fringed in involute morphotypes. In these shells the lateral saddle also lies proportionally a little lower on the flanks (fig. 6).

It should be noted that sculpture probably does not influence suture complexity directly, even though there is some internal irregularities to accommodate in the shell tube. We rather think that sculptural and sutural elements both depend on a common third factor, namely whorl shape [Guex, 1999, 2001b].

### DISCUSSION

Though data on embryonic shells are quite numerous, few authors have studied their variability within a single species or genus. The identity of the protoconch both in absolute size and relative proportions in *Osperleioceras* has also been observed in *Amaltheus* species [Zell *et al.*, 1979]. Significant differences in protoconchs only appear at the order or family level [Drushchits and Doguzhaeva, 1974; Zakharov, 1974]. The functional correlation between protoconch and ammonitella sizes [Tanabe and Ohtsuka, 1985; Shigeta, 1993] could not be ascertained within *Osperleioceras* due to a much more restricted range of variation. A further limitation should be taken into consideration: the imprecision on the measurements at such small sizes is far from negligible. Although the use of a scanning-electron microscope could improve the magnification factor and thus lessen the problem, imprecision in the orientation or sagittal position of the section (respectively projection of dissected specimens) will remain.

Growth curves display remarkable ontogenetic changes, particularly visible in involution, whorl compression and ornamentation. These characters show significant correlations, producing a morphological spectrum ranging from evolute shells with strong regular ornamentation to involute, densely and finely ribbed conchs, through a continuous series of intermediate forms. The rise in variability observed since the transition from Middle to Upper Toarcian in *Osperleioceras* developed in successive bursts from a fairly long low variability period spanning the whole Middle Toarcian. Environmental instability, documented in the Causes Basin by sedimentary changes interpreted in terms of sea-level fluctuations, favoured a stress-induced rise in variability [Guex, 1992], concomitant with size decrease. Competition for ecological niches was also partly lessened, since few platycone to oxycone ammonite genera survived up to the Reynesi subzone. However, no ecological selectivity for particular morphotypes could be ascertained as the whole covariation series occurs in the same beds.

In summary, we noted a conspicuous relation between shell shape and ribbing pattern (fig. 6). This covariation can be explained by an integrated model of shell secretion, combining both local geometrical constraints on the shape of the shell and a dynamic reaction/diffusion regulation of ornamental production [Guex, 1999, 2001a]. Starting from Meinhardt's work on colour patterns in molluscan shells [Meinhardt, 1995], Hammer and Bucher proposed a reaction/diffusion process to simulate ammonoid rib trajectory [Hammer and Bucher, 1999]. However, wrapping these 2D patterns on the surface of 3D shells implies more complex interactions between morphogen concentration and mantle curvature [Guex, 1999]. This local expression, controlled by geometrical and biological interactions, does not imply genomic integration of numerous minute controls [Kaplan, 1999], but rather a single genetic signal followed by epigenetic mechanistic consequences [Hammer and Bucher, 1999]. As sculpture is formed by shell undulations and/or thickening, pattern formation is definitely very tightly connected to shell secretion mechanisms. This is a case of developmental integration [Klingenberg and Zaklan, 2000] in the sense that the relationships between shell shape and ornamentation result from a common developmental process.

Interdimensional covariation tends to support a complex dynamic interdependence, probably under constructional (geometrical constraints, shell secreting mechanisms) and metabolic controls (resource availability and allocation). In that sense, it would be very interesting to test if both extreme morphologies imply similar energetic demands for shell building. Considering the number of parameters that intervene in such calculations, this question could not be resolved in this study. However, the investigation of the relations between linear, surface and volumetric parameters [Guex, 2001b] shows that at a constant ventral growth rate, similar septal spacing, and a given volume, the more involutely coiled shells will have more compressed whorls. As a corollary, phyletic size increase in spirally coiled organisms might be concealed by coiling modifications [Guex, 2001b]. The problem is to know which parameters are of most significance.

Covariation in ammonoids should not be viewed as a strict compliance to genetic determinants but rather as a conformation to a general building plan in response to complex and dynamic metabolic interactions under hereditary and/or environmental controls. While its morphological expression is modulated by the basic characteristics of the studied taxon (table I), the overall pattern observed will be the same.

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