Ontogeny of the Oxfordian ammonite Creniceras renggeri from the Jura of France

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ABSTRACT

The complete ontogenetic development (protoconch to adult) of *Creniceras renggeri* (Oppel) is reconstructed by morphometrical studies of its shell (protoconch, ammonitella, whorl expansion rate, whorl height, siphuncle, septal spacing, crenulation and adult size). The embryonic stage is equated with egg-development. Hatching occurred at about 568 μm (end of ammonitella) where probably only two septa were secreted. No larval stage is assumed. Post-embryonic development exhibits no drastic morphological changes. This is interpreted as a constant mode of life from hatching to sexual maturity.

RESUME

Le développement ontogénétique complet (de la protoconque à l'adulte) chez *Creniceras renggeri* est reconstruit par une analyse morphométrique de sa coquille (protoconque, ammonitella, taux d'expansion spirale, hauteur du tour, siphon, espacement septal, crénulation et taille adulte). Le stade embryonnaire correspond au développement de l'oeuf. L'éclosion se produit à environ 568 μm (fin de l'ammonitella) où probablement deux cloisons seulement étaient sécrétées. Un développement sans stade larvaire est proposé. Le développement post-embryonnaire ne montre aucun changement morphologique majeur. Ceci est interprété comme le reflet d'un mode de vie constant depuis l'éclosion jusqu'à la maturité sexuelle.

Introduction

The ammonite shell is constructed by an accretionary process and provides a record of the animal's ontogenetic history. Morphological changes during growth can be observed by sectioning the shell. Workers have used such observations to propose an ontogeny common to all ammonoids (e.g. Druschits et al. 1977a; Kulicki 1979; Landman 1987; Kulicki & Doguzhaeva 1994). Most recognise two successive stages: embryonic (secretion of the ammonitella, Fig. 1), versus post-embryonic (secretion of the remainder of the shell). Between these two stages, the ammonite hatched and acceded to a stage of active life. This reconstitution is consistent with observation of living cephalopods (Mangold 1989). There is still debate about whether the exact moment of hatching was before the formation of the first varix (Druschits et al. 1977a) or after (Kulicki 1979). The number of septa formed by the time of hatching is undetermined, but it is claimed that the first septa was already secreted (Landman 1994). The caecum is thought to have been functional and to have enabled adjustment of buoyancy by secretion of cameral liquid, conferring on ammonites an active mode of life from the moment they hatched (but see Ebel 1992; Shigeta 1993). This mode of development, which is widely accepted by modern workers, is simpler than that envisaged by earlier scholars who supposed there had been a larval stage (e.g. Hyatt 1894; Smith 1901; Palframan 1967a). Study of the development of modern cephalopods indicates there is no larval stage (Boletzky 1974) and so refutes this hypothesis.

Detailed studies of ammonoid ontogeny have revealed similar embryonic structures throughout the group: a protoconch followed by a planispiral tube extending for about one whorl, together forming the ammonitella, although dimensions vary (Tanabe & Ohtsuka 1985). By contrast, the post-embryonic characters exhibit wide variations, as reported in a vast range of studies, and serve as a basis for species diagnosis. However, as Tanabe et al. (1979) remarked, the embryonic structures of a mere 2% of currently recognised species have been described. The taxonomic and paleobiological value of these is therefore very probably underestimated. Among extant cephalopods, for example, closely-related species of the same adult size may have eggs of very different sizes (corresponding to the embryonic phase): the ratio between egg size and man-

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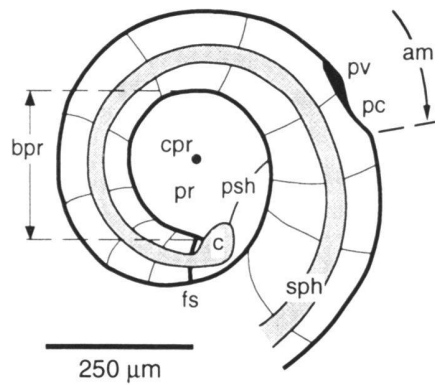
Fig. 1. Basic morphology of ammonoid internal shell structure in the median section. pr: protoconch, cpr: centre of protoconch, bpr: basal part of protoconch, psh: prosiphon, c: caecum, fs: first septum (sensu Landman 1985), sph: siphuncle, am: ammonitella, pv: primary varix, pc: primary constriction.

tle size of adult individuals is 15% for *Eledone moschata* and a mere 5% for *Eledone cirrhosa* (Boletzky 1992), although the adult mantle sizes of these two octopoda are similar.

The objective in this paper is to analyse the shell of *Creniceras renggeri* (Oppel) using morphometric methods. This analysis should further our understanding of the embryonic development of the species and the transition from the embryonic to the post-embryonic stage. The analysis should lead to a reconstruction of the ontogenetic process for the species and allow comparison of its development with that of other species.

Material

A population of 98 adult individuals of *C. renggeri* (Ammonitina, Haplocerataceae, Opeliidae, Taramelliceratinae, Fig. 2) was collected from the "Marnes à C. renggeri" Formation, dated to the Lower Oxfordian (Mariæ Zone, Praecordatum Subzone) at Pont du diable (Jura, France). The fauna is completely pyritised, the organisms being preserved as internal moulds. Embryonic characteristics are observed from sections along the median plane. All dimensions (Fig. 3) are measured from camera lucida drawings.

Comparison between *C. renggeri* and its supposed sexual dimorph *Taramelliceras richei* (see Palframan 1966, p. 308) will be made in the future but taking into account the different species and genera belonging to the Taramelliceratinae subfamily from the "Marnes à C. renggeri" Formation (e.g. *Scaphitodites scaphitoides,* Neige et al. 1997).

The material used in this study is housed at Centre des Sciences de la Terre, Université de Bourgogne.

Embryonic development

To measure the diameter of the protoconch and ammonitella, the centre of the spiral described by the shell must first be located. This point is difficult to fix as it does not correspond to any anatomical feature, but is merely a geometrical position. Here, it is located by convention at the centre of the circle inscribed in the base part of the protoconch (Fig. 1).

Protoconch

The mean maximum diameter (d1) is 327 µm and the mean minimum diameter (d2) is 242 µm (Tab. 1). The mean values of d1 and d2 are significantly different ($p < 0.001$): the protoconchs are elliptical. For the sake of comparison, for six *C. renggeri* specimens collected in England, Palframan (1966) recorded a mean maximum diameter of 290 µm.

Ammonitella

The mean diameter of the ammonitella (dA) is 568 µm (Tab. 1). Palframan (1966) recorded a mean ammonitella diameter of 540 µm. As with d1, this value is about 5% lower than that found here, and may result from the small number of individuals measured by that author (n = 3). The mean ammonitella angle (AA) is 264° (Tab. 1). The correlation coefficient of variables dA and AA is 0.43 (not significant), indicating there is no correlation between size and the ammonitella angle.

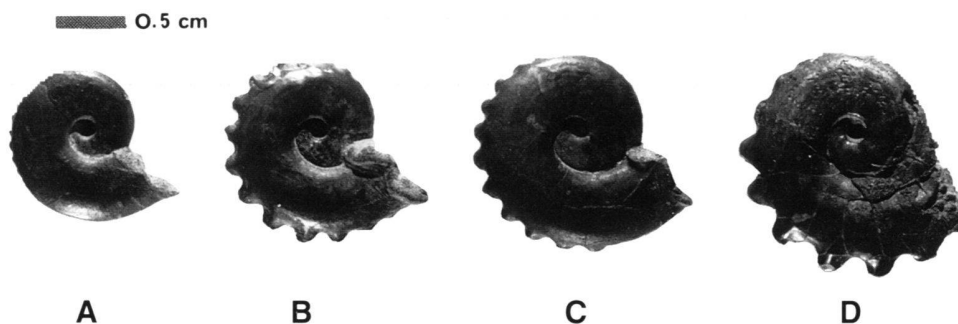

Fig. 2. A–D, *Creniceras renggeri*. A, small complete adult (PN-CR60). B, complete adult with lappets (PN-CR32). C, complete adult with lappets (PN-CR01). D, large adult specimen with incomplete body chamber (PN-CR80).
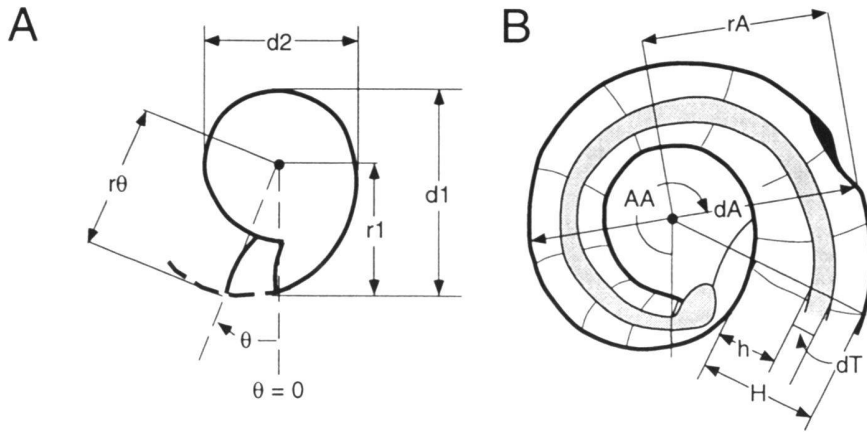
Fig. 3. Measurements of ammonoid shell structure in the median section. A, for protoconch, whorl radius and interseptal angle. B, for ammonitella, whorl height and siphuncle.

Tab. 1. Maximum (d1) and minimum (d2) diameter of protoconch, maximum diameter of ammonitella (dA) and ammonitella angle (AA) data for *Creniceras renggeri*.

	n	Mean	Range	Standard deviation
d1 (μm)	23	327	270–365	20
d2 (μm)	23	242	205–276	17
dA (μm)	18	568	526–604	23
AA(°)	18	264	250–281	8

Protoconch – ammonitella relationship

The ratio between the ammonitella diameter and the maximum protoconch diameter averages 1.74. The correlation between these two variables is 0.29 (not significant), indicating that protoconch size does not apparently affect ammonitella size.

Post-embryonic development

Whorl expansion rate

Planispiral ammonite coiling has long been compared with a logarithmic spiral (Moseley 1838; Thompson 1917; Raup 1966). This spiral is characterised by its expansion rate, which expresses the increase in radius versus the rotational angle. Expansion rate is usually studied by a single measurement on adult individuals (e.g. Raup 1967). The rare studies of whorl expansion rate changes during ontogeny include analyses of a few isolated individuals (Raup 1967; Raup & Chamberlain 1967) and of a population (Landman 1987). In these rare cases, the logarithmic spiral is studied from the ammonitella through to the end of growth, but rarely from the protoconch aperture.

The traditional formula (e.g. Raup 1967), and standardised dimensions (Fig. 3) for describing a logarithmic spiral are as follows:

$$r\theta = r1 . e^{k.\theta} \tag{1}$$

where k is the constant for whorl expansion. The angle origin

($\theta = 0$) is fixed conventionally at the protoconch aperture (Fig. 3). This constant (k) is related to parameter W (Raup 1966) by the equation (see Landman 1987):

$$W = e^{2k\pi} \tag{2}$$

In our analysis, spiral expansion rate is expressed by W, which is more widely used than k. W is calculated from the formula defined by McGhee (1980) and which can be used to calculate any rotational angle:

$$W = (r_x / r_{x-\Delta\theta})^{2\pi/\Delta\theta} \tag{3}$$

where $r_{x-\Delta\theta}$ is the ammonite radius at an angle $\Delta\theta$ before r_x.

The radii and corresponding angles of rotation were measured on average every 27° for 8 individuals. The radius – rotational angle relation is linear on a semilog scale (Fig. 4A), confirming that growth occurs as a logarithmic spiral. Variations do arise, however, especially in the early whorls. Growth may be analysed in more detail by analysing W, calculated from equation (3). The value of W oscillates through maxima for angles of rotation 0, 2π, 4π and 6π (Fig. 4B). Beyond 6π the oscillations are of lesser amplitude and W stabilises at about 2.5. Workers generally associate a change in the whorl expansion rate with the end of the embryonic phase (Kulicki 1979; Landman 1987). In *C. renggeri* the end of this stage is plainly marked by a change in the whorl expansion rate: W is less than 2 for the embryonic stage and greater than 2 for the post-embryonic stage (Fig. 4B). However, no biological explanation can be offered a priori to account for the peaks of W for angles of rotation 0, 2π, 4π and 6π. As already remarked by Landman (1987), these oscillations seem to result from the location of the protoconch centre and are therefore artificially induced. This can be clearly shown by modelling whorl growth from an elliptical protoconch similar to that of *C. renggeri* (Fig. 5). Landman (1987, p. 166) proposes a method of protoconch centre location whereby the artefacts are eliminated and then applies it to post-embryonic growth stages only. However, this method seems to mask in part the differences in whorl growth between embryonic and post-embryonic stages. For this reason
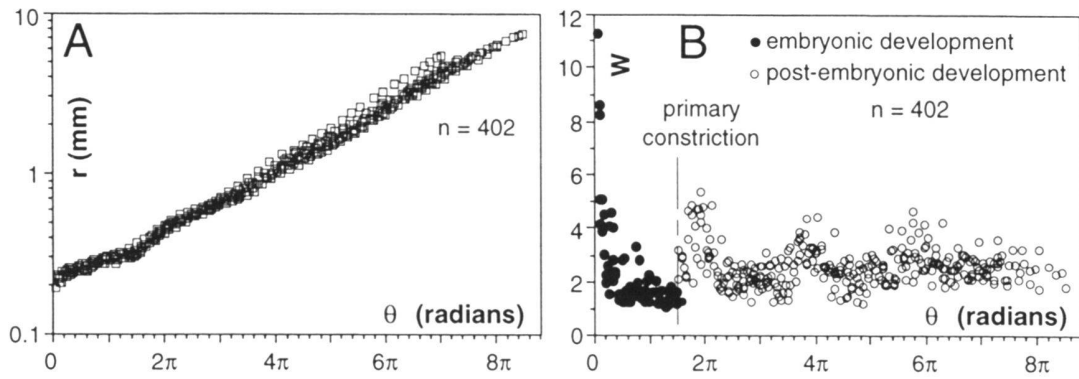
Fig. 4. A, plot of the radius of the spiral (r) versus total rotational angle (θ) for 8 specimens. B, plot of the whorl expansion rate (W) versus total rotational angle (θ) for 8 specimens. Note differences in W values before and after primary constriction, and artefact oscillation of W values at the beginning of each whorl.
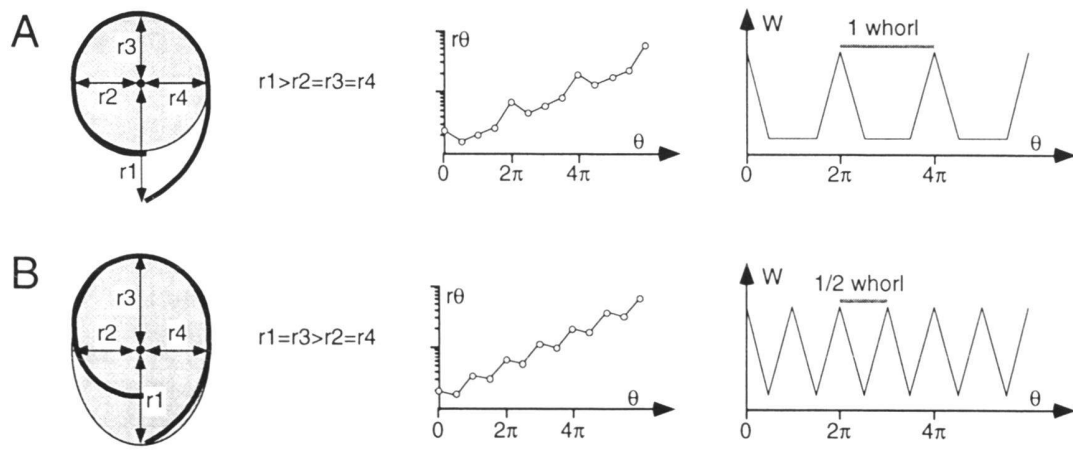

Fig. 5. Model of whorl growth from protoconch depending on the position of the protoconch centre. A, the protoconch centre is located at the centre of a circle inscribed in the basal part of the protoconch. This causes W to oscillate with a period of 2π. B, the protoconch centre is located at the centre of the ellipse circumscribing the protoconch. This causes W to oscillate with a period of π.

it is not used here, where W is studied right from the start of growth.

Whorl height

Whorl height (H) and the corresponding radius are measured every 90° on nine individuals from the protoconch to the end of growth. This measurement is not dependent on the location of the protoconch centre. Distribution on a logarithmic plot reveals a break in the slope between the embryonic and post-embryonic stages (Fig. 6). Linear adjustment over the variable logarithms is calculated for each stage (Fig. 6), so power functions can be calculated (sensu Gould 1966, and see Kant 1973). The power factor is tested with the Z-test defined by Hayami & Matsukuma (1970), which discriminates between (1) positive allometric (Z > 1.96), (2) negative allometric (Z < –1.96),

and (3) isometric (–1.96 < Z < 1.96) growth patterns (values shown for 95% significance limit). Application of this test indicates positive allometry for the embryonic stage (Z = 8.59 for n = 45) and for the post-embryonic stage (Z = 3.03 for n = 124). These analyses show then that H obeys a two-stage allometric growth pattern: two positive allometries (sensu Teissier 1948) of different intensity corresponding to the embryonic and post-embryonic stages, with the latter having very slight positive allometry (α = 1.04) and less than that of the first stage (α = 1.68).

Siphuncle

Siphuncle diameter (dT) and position (h) are measured for nine individuals. Siphuncle diameter is approximately 25 μm at the caecum outlet and reaches a maximum of 450 μm at the
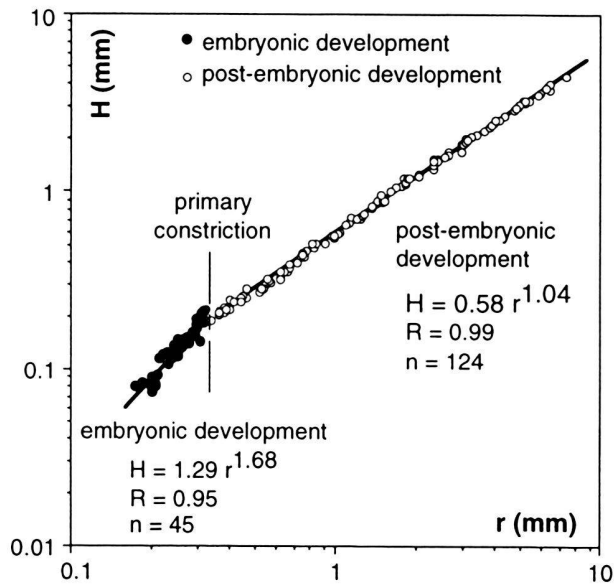
Fig. 6. Plot of whorl height versus shell radius for 9 specimens, and regression line. Power functions indicate positive allometric growth is greater for embryonic than for post-embryonic development.

end of the phragmocone. The increase in siphuncle diameter versus r or H is constant and exhibits no break in slope (Fig. 7). The mode of growth of dT versus r is described by a power function (Fig. 7A). The power factor is 0.85. The Z-test reveals negative allometry ($Z = -12.87$ for $n = 135$), indicating that siphuncle diameter increases ever more slowly for a constant increase in r. The patterns of growth of dT relative to H are described identically (Fig. 7B). The Z-test ($Z = -24.15$ for $n = 169$) also indicates negative allometry.

Parameter PS = (h+dT)/H expresses the relative distance from the ventral edge of the siphuncle to the ventral edge of the whorl (1 for a siphuncle in the ventral position, and 0 for a siphuncle in umbilical position). The siphuncle is initially in a central location and shifts abruptly to a ventral position with

the onset of growth (Fig. 8). The siphuncle adopts its final ventral position about one and a half whorls after the end of the protoconch, i.e. before attaining a radius of 1 mm.

Interseptal spacing

Eight individuals with their complete number of septa were analysed. The relation between the number of septa and the radius during ontogeny reveals a uniform first stage for the entire population (up to about 20 septa), followed by a stage that is specific to each individual (Fig. 9). The general shape of growth curves is very similar for all individuals. The end of the curves is systematically marked by an inflection produced by the reduced spacing of the final septa towards the end of growth.

The interseptal angle is particularly variable during ontogeny (Fig. 10A). Despite considerable criss-crossing of ontogenetic trajectories, several phases that are common to the set of individuals can be defined. A single representative individual is portrayed for a clear view (Fig. 10B). Each trajectory starts with a clearly unstable stage (stage 1), with the widest angles (up to 55°). This stage ends on average after 16 septa. There follows a stable stage (stage 2) with angles between 15° and 35° (although angles of more than 40° are found in one individual). The final stage (stage 3) exhibits a character that is peculiar to the end of growth: closer spacing of the septa where the narrowest angles are recorded.

Ornamentation

Ornamentation of C. renggeri is confined to ventral crenulations, consistently located on the final adult whorl. The occurrence of a smooth ventral edge after the final crenulation means that 18 individuals can be selected which are know to have all their crenulations (6–17 each). Earlier workers confined themselves to reporting their occurrence without describing their characteristics (e.g. Loriol 1902; Arkell 1939). Palframan (1966) provides some very general indications with no biometric information about their size and shape as well as the number per individual (on average 9 to 12, he claims, but vary-
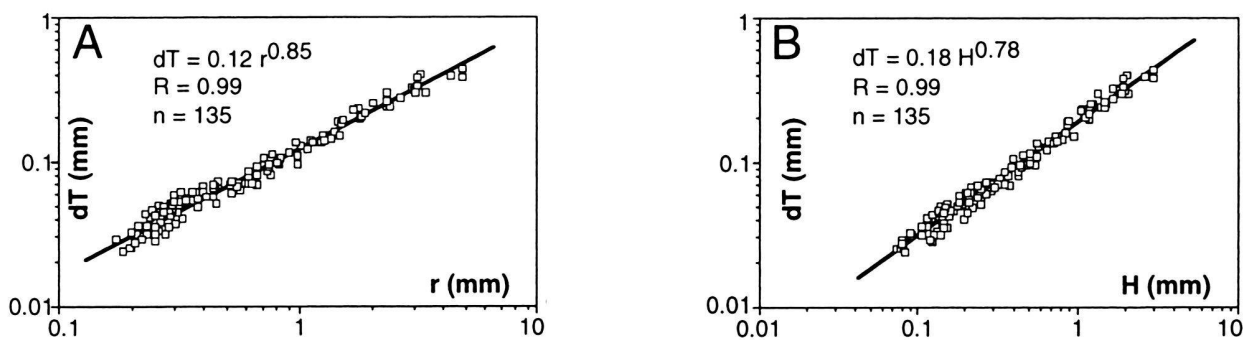

Fig. 7. A, plot of the diameter of the siphuncle versus shell radius for 9 specimens, regression line and power function. B, plot of the diameter of the siphuncle versus shell whorl height for 9 specimens, regression line and power function.

Tab. 2. Angle of crenulated ventral part data for *Creniceras renggeri*.

	n	Mean	Range	Standard deviation
Angle (°)	18	121	32–247	61

Tab. 3. Morphological co-ordinates of C' (transform from C Cartesian co-ordinates by baseline procedure: see main text).

	n	Mean	Standard deviation
XC	1160	0.50	0.05
YC	1160	0.27	0.11

Tab. 4. Adult phragmocone radius (rAd) data for *Creniceras renggeri*.

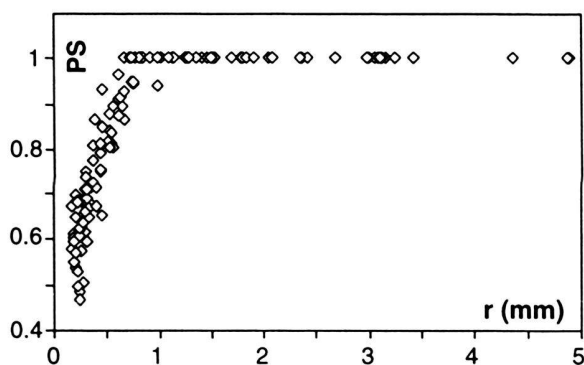|	n	Mean	Range	Standard deviation
rAd (mm)	98	5.14	3.81–8.03	0.81

A

Fig. 8. Plot of the relative position of the siphuncle versus shell radius for 9 specimens.

B

Fig. 10. A, plot of septal angle versus septal number for 8 specimens. B, detail of one specimen. Black star indicates position of septum number 28.
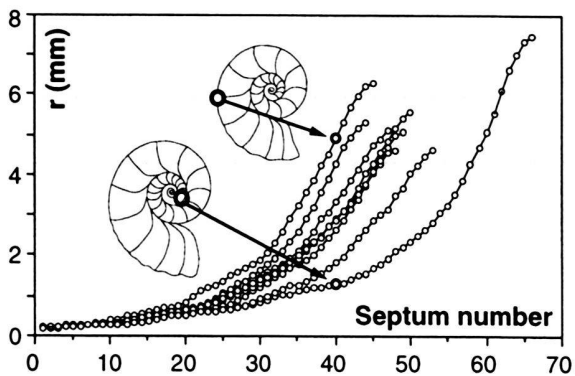
Fig. 9. Plot of shell radius versus septal number for 8 specimens. Notice the high variability near end of growth, illustrated here by the comparison of the position of septum number 40 for 2 specimens.
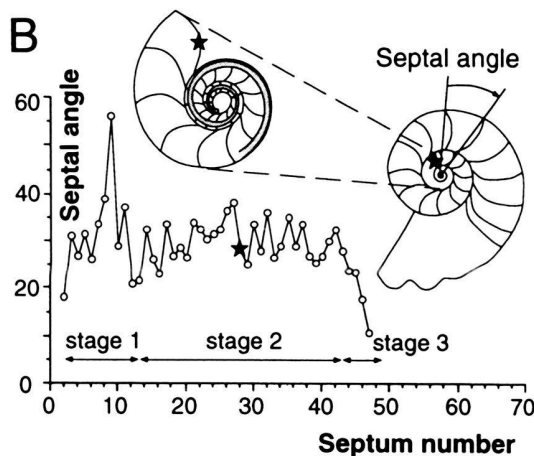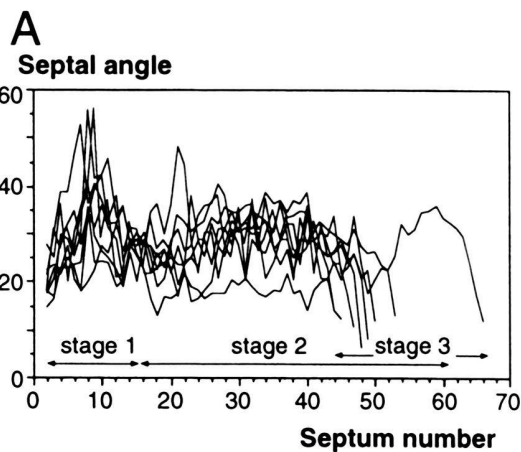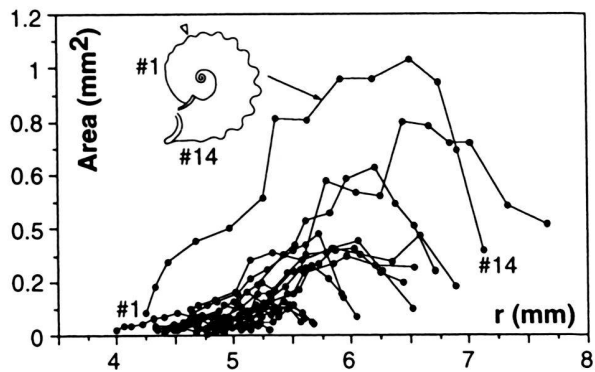
Fig. 11. Plot of the surface of crenulation versus shell radius for 18 complete specimens. Notice the decrease in surface area at the end of growth (triangle indicates end of phragmocone).
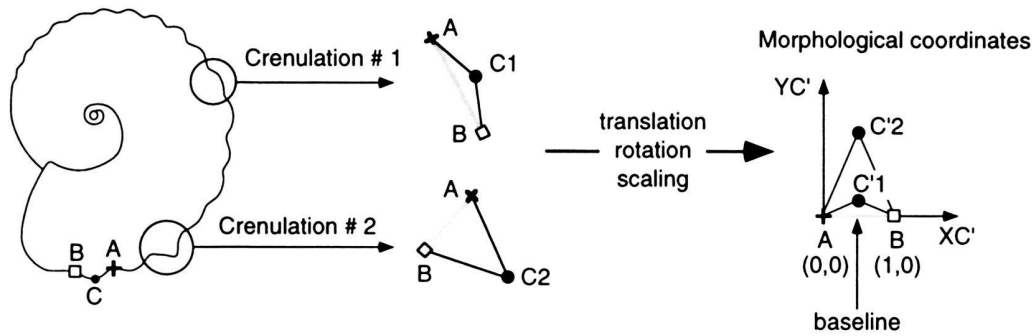
Fig. 12. Shape comparison of crenulations by the baseline method (see text).

ing from 0 to 24). Ziegler (1974) analyses just the relative height of crenulations in *C. renggeri* and *C. dentatum.*

The crenulation surface areas (measured in lateral view) decrease clearly for the final three crenulations at the end of ontogeny (Fig. 11). This feature was observed but not quantified by Palframan (1966, p. 307). The angle of the crenulated ventral part (between the first and last crenulations) is extremely variable, ranging from 32° to 247° (Tab. 2).

There is no link between the ammonite radius at the first crenulation and at the final crenulation (r = 0.14). The point at which the "crenulated venter" terminates does not depend on when it first appears. The first crenulation is on the phragmocone in 39% of cases and on the body chamber in 61% of cases. The final crenulation is invariably on the body chamber.

Crenulation shape is studied using a Procrustes type morphological adjustment method (Bookstein et al. 1985). These methods are used to analyse the shape of an object regardless of size and orientation. The baseline technique is used (Bookstein 1991; Neige & Dommergues 1995). Each crenulation is described by three points (A, B and C: Fig. 12). Segment [AB] is chosen as the baseline, i.e. its length is normalised to one for the entire population. The Cartesian co-ordinates of point C are then transformed into morphological co-ordinates: XC' and YC'. XC' represents the position of the top of the crenulation relative to the baseline, i.e. the shape of the crenulation: a right-angled triangle at A for XC' = 0, an isosceles triangle for XC' = 0.5 and a right-angled triangle at B for XC' = 1. The mean for XC' is close to 0.5 (Tab. 3). The t-test for comparing the mean of XC' to a theoretical mean (0.5) leads to accepting the equality of the mean for XC' as 0.5 (p = 0.25). The triangles are therefore isosceles, indicating rectiradial crenulations (sensu Palframan 1966). In this co-ordinate system where the base of the triangle is normalised as 1, the triangle height must be 0.87 for it to be equilateral (Pythagoras's theorem). With *C. renggeri* YC' is consistently less than 0.87 (Tab. 3). The crenulations are therefore on average isosceles triangles that are flatter than equilateral ones.
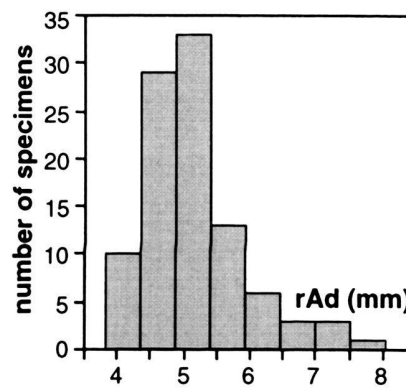
Fig. 13. Histogram of mature phragmocone radius for 98 specimens.

Mature stage

The adult stage is recognised in ammonites by distinctly reduced spacing of the septa marking the end of their secretion. The adult body chamber follows. This reduced spacing marking the end of growth is generally construed as the acquisition of sexual maturity but there is no way of telling how much time elapsed between this stage and the organism's death. The adult stage in *C. renggeri* is characterised by all the morphological modifications commonly observed in ammonoids (Makowski 1962): closer septal spacing, slight fall in the whorl overlap ratio, change of the adult peristome with the formation of lappets. No major change peculiar to the species is recognised. The five individuals with visible peristomal ridges have a body chamber of 215° on average.

Adult phragmocone size

The mean adult radius (rAd) measured at the end of the phragmocone at the location of the final septum is 5.14 mm (Tab. 4), giving a mean adult diameter of 8.3 mm. Palframan (1966) reported a quite comparable diameter of 8.4 mm for a

Fig. 14. A, histogram of maximum protoconch diameter for 102 ammonoid species (data from literature). B, histogram of maximum am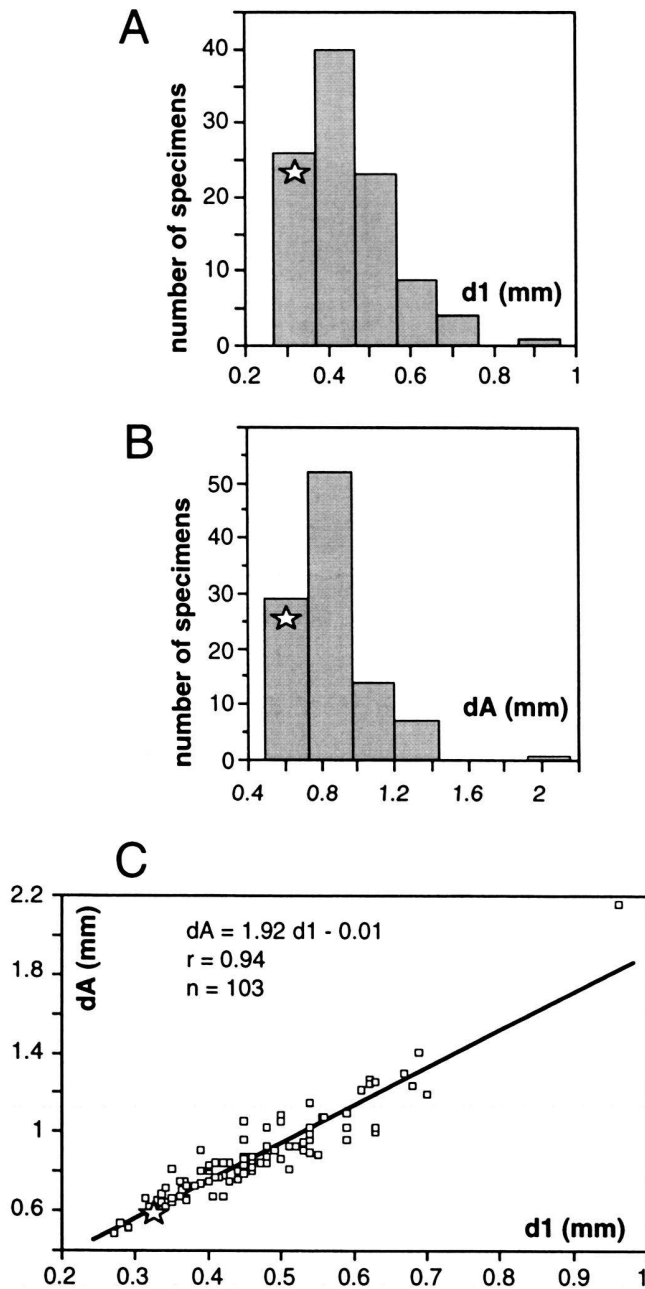monitella diameter for 102 ammonoid species. C, plot of maximum protoconch diameter versus maximum ammonitella diameter for 102 ammonoid species, and regression line. White star indicates data of *Creniceras renggeri* from this study.

population of more than 200 individuals. The distribution histogram for the mean adult radius is unimodal and slightly positively skewed (Fig. 13) indicating a shortage of large adults compared with a normal distribution.

To specify whether there is a link between ammonite size at hatching and the adult size, the radius of the ammonitella can be compared with that of the adult phragmocone. In the studied population there is no relation between these variables ($r = 0.04$): the adult size of the organism is not influenced by its size at hatching. Landman (1987) reported a similar finding for two species of the genus *Scaphites*. Similarly, there is no relation ($r = 0.26$) between the maximum protoconch radius (r1) and the adult radius (rAd).

Number of closely spaced septa

The mode of the number of closely spaced septa (calculated from a sample of 27 individuals) is three, with a minimum of two and a maximum of five. Spearman's rank correlation coefficient test shows that the number of narrowly spaced septa does not depend on the size of the adult phragmocone ($p = 0.71$). This result clearly expresses the originality of changes related to the end of growth that compound the post-embryonic development characteristics (Landman et al. 1991).

Discussion

The ontogeny described here for *C. renggeri* is compared with that of other ammonoids so the mode of development can be specified.

The Embryonic stage of *C. renggeri* compared with other ammonoids

To compare the embryonic dimensions of *C. renggeri* with those of ammonoids as a whole, values of d1 and dA for 102 species measured by different workers by protocols compatible with the one used here have been compiled (Bogoslovskaya 1959; Palframan 1966, 1967b, 1969; Druschits & Khiami 1970; Zakharov 1974; Druschits et al. 1977b; Tanabe & Ohtsuka 1985; Landman 1987; Landman & Waage 1993; Tanabe et al. 1994). Only the species *C. renggeri* is represented by two values: Palframan (1966) and that obtained for the work reported here. There are minor differences in the definition of the largest diameter of the protoconch. However, Landman (1987) showed that, for the same population, two series of measurements made using the two most commonly used protocols display no significant differences.

– *Protoconch.* The distribution histogram for d1 is unimodal (Fig. 14A), with a slight positive skew (skewness 1.20). *C. renggeri* ranks among the small protoconchs compared with the entire set of diameters observed. Very few data are available for comparing the minimum protoconch diameter (d2). Tanabe et al. (1979) and Landman (1987) report d2/d1 ratios ranging from 0.79 to 0.98 for Cretaceous ammonites (which indicates protoconchs ranging from elliptical to circular in median section), which indicates a more rounded protoconch than in *C. renggeri* (mean d2/d1 value of 0.74).

– *Ammonitella.* The histogram of the distribution of dA is unimodal (Fig. 14B) with a slight positive skew (skewness 2.06). As for d1, the ammonitella of *C. renggeri* is small compared with ammonoids as a whole.

– *Relations between the protoconch and ammonitella.* An intraspecific correlation between the size of the protoconch and that of the ammonitella was shown by Tanabe et al. (1979), Landman (1987) and Landman & Waage (1993). In all these cases a close adjustment to a linear model is proposed. The case of *C. renggeri* runs counter to these observations and no correlation between dA and d1 is found.

Within species, the ratio between the size of the ammonitella and the maximum diameter of the protoconch varies from 1.59 to 2.36. *C. renggeri* comes well within this range with a value of 1.74. These variables are positively correlated and are linked by a linear growth model with a slope of 1.92 (Fig. 14C). This result is very close to that of Tanabe & Ohtsuka (1985) and Shigeta (1993). This relation between the diameter of the ammonitella and that of the protoconch is usually interpreted as enabling the ammonite to have neutral buoyancy, i.e. to have a density close to that of sea water (Tanabe & Ohtsuka 1985; Landman 1987). At hatching, the gas-filled protoconch is thought to act as a float, and the planispiral tube of the ammonitella (containing the organism) as a counterweight. The fact that no correlation is found for *C. renggeri* raises a question about its mode of buoyancy. Further studies are required to investigate the relationship between these two parameters.

The embryonic – post-embryonic stage transition in
C. renggeri compared with other ammonoids

In *C. renggeri*, W does not have the same value in the embryonic stage (W < 2) and the post-embryonic stage (W > 2). To the best of our knowledge, the whorl expansion rate (W) has never been studied from the protoconch aperture through to the adult stage. However, other mathematically related parameters have been studied in detail. The results obtained for such parameters can therefore be compared with those for W. In particular, k (see equation 1) was studied by Landman (1987, Fig. 51 to 54) for three species of the genus *Scaphites* and one of the genus *Clioscaphites* which all exhibited changes in the values of this constant between the embryonic and post-embryonic stages. In addition, as W is directly related to the ammonite radius (see equation 3), the data about the increase in radius can be used for comparison. Dauphin (1978, Fig. 5A) studies the ontogeny of the shell radius of *Beudanticeras beudanti* relative to the number of chambers since the start of growth. After adjustment of the mean growth slopes that take oscillations into account (which are artefacts and so need to be eliminated: see Fig. 6), the data and conclusions of Dauphin (1978) are comparable with ours: change occurs in the whorl expansion rate at the primary constriction. Likewise in the analyses of Raup & Chamberlain (1967), regular oscillations at each whorl are detected, and are probably artefacts induced by the protocol for locating the protoconch centre.

Changes in whorl height between embryonic and post-embryonic stages comparable with those observed for *C. renggeri* have already been recognised by Dauphin (1978), Landman (1987) and Landman & Waage (1993).

Siphuncle ontogeny and interseptal spacing in *C. renggeri*
compared with other ammonoids

– *Siphuncle.* In *C. renggeri* the siphuncle diameter exhibits negative allometry compared with diameter and no change in the rhythm of growth is detected. This result is consistent with those of Westermann (1971) for different ammonites and for modern *Nautilus*, and with the results of Tanabe et al. (1979), Tanabe & Ohtsuka (1985) and Landman (1987) for different ammonites. By contrast, Trueman (1941) reports overall isometric growth (although without any statistical analysis) in *Dactylioceras commune* as does Chamberlain (1978) in living *Nautilus*. Negative allometric growth of the siphuncle demonstrated here may have had important repercussions on the mode of life of *C. renggeri*, and of other ammonoids with the same characteristic. The siphuncle is usually considered to be the organ with which cameral liquid could enter or leave the phragmocone chambers allowing the ammonite to maintain neutral buoyancy. If the rate of filling of the fluid were proportional to the size of the siphuncle, and therefore to its diameter (Ward 1982), negative allometric growth of the siphuncle compared with the whorl could be interpreted as a reduction in ability to maintain neutral buoyancy. However, Ward (1986) shows that in modern *Nautilus* the rate of filling of the cameral liquid is too slow to be involved in daily vertical movements, but on the contrary, filling is responsible for maintaining neutral buoyancy on an ontogenetic scale. It is probable then that the low negative allometry of the siphuncle, observed in *C. renggeri*, did not affect its capacity to regulate buoyancy but rather induced a deceleration in the emptying of cameral liquid during ontogeny. This could be interpreted as a downturn in the growth rate of the organism which had to "wait" to achieve perfect hydrostatic stability before secreting more shell.

The change in the position of the siphuncle in the whorl (from central to ventral) observed in *C. renggeri* is a well-known phenomenon described by many workers. This change seems to have been particularly abrupt and precocious in *C. renggeri* (1.5 whorls after the protoconch versus 2–3 whorls for the species studied by Tanabe et al. 1979).

– *Interseptal spacing.* A series of three stages are recognised in the ontogeny of *C. renggeri*: (1) variable interseptal spacing; (2) constant spacing; (3) reduced spacing marking the end of growth (see Fig. 10). Interseptal spacing is analysed in detail by Mignot (1993) on Jurassic ammonites, highlighting three stages in septa formation of *Hildoceras sublevisoni* (Mignot 1993, Fig. 29). These stages are identical to those observed in *C. renggeri*. Two differences must nevertheless be emphasised: (1) there is a slight tendency du-
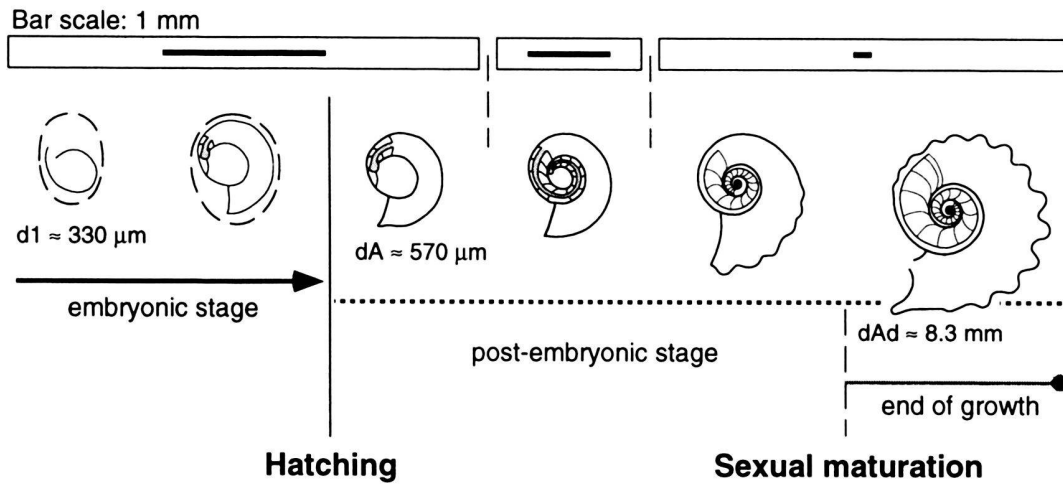
Fig. 15. Life history reconstruction of *Creniceras renggeri*. Two major stages are recognised: embryonic versus post-embryonic. Mature modifications are superimposed at the end of growth.

ring stage 2 to reduced septal spacing in *H. sublevisoni* that is not found in *C. renggeri* and (2) in *H. sublevisoni* the most closely spaced septa are not necessarily those marking the end of growth, whereas in *C. renggeri* the most closely spaced septa are invariably the final ones. Furthermore, the validity of the end of growth has been confirmed in *C. renggeri* by other independent characters: occurrence of lappets, cessation of crenulation. In *Sphaeroceras brongniarti*, an ammonite of mean adult diameter of 7 mm, stage 1 is not observed (Mignot 1993, Fig. 53). Similar results to those for *C. renggeri* were also reported by Kulicki (1974) and Landman (1987) for Jurassic and Cretaceous ammonites.

The significance of these three stages raises the question of whether they correspond to morphological changes of the shell. It has been seen that stage 3 is merely a change expressed at the end of growth. The transition from stage 1 to stage 2 requires clarification. The site of shell secretion (aperture of the body chamber) and the site of secretion of the corresponding septum (behind the body chamber) are separated by an angle equivalent to the angle of the chamber. To determine the radius of the ammonite where a morphometrical change is to be correlated with a change in septation, the value of one body chamber must therefore be added. For *C. renggeri* no juvenile individual was collected with its body chamber intact. It can be assumed that the angle is identical to that of the adult chamber, i.e. a mean value of 215°. If the offset of 215° is included, the morphological changes to be correlated with the end of stage 1 (located on average at 400°) would be at 615°, or a radius of 0.7 mm. Similarly, the morphological changes to be correlated with the maximum septal spacing of stage 1 (located on average at 200°) would be at 415°, or a radius of 0.5 mm. No

morphometric change has been demonstrated at these sizes. It is impossible therefore to be more specific about the phenomena inducing changes in septation. These results are not consistent with those of Landman (1987) who, by adopting an identical approach, correlated the maximum septal spacing with the site of the first varix and the end of stage 1 with substantial morphological changes (whorl expansion rate, umbilical diameter).

Conversely, to ascertain the number of septa secreted at the moment of hatching in *C. renggeri*, the angle of the juvenile body chamber (215°) must be subtracted from the primary constriction angle (264°). A phragmocone angle for the ammonitella of about 50° can be estimated, which corresponds to the position of the third septum. It must be assumed in this case that the first and second septa only were secreted by the end of the embryonic stage. It should be noticed that if hatching occurs after the primary constriction, the few degrees of coiling produced by constriction and the first varix mean that the third septum must already have been secreted.

Conclusions

Morphological data for *C. renggeri* and their comparison with more general data can be used to propose a reconstruction of its ontogenetic development (Fig. 15):

(1) A stage of embryonic development is recognised. This stage is characterised by an ammonitella comprising a small protoconch (d1 = 327 μm) relative to other ammonoids, followed by a planispiral tube of 264° on average. This embryonic stage is interpreted as characteristic of development inside a closed egg. At this stage the first two septa only seem to have been secreted, with the third being se-

creted only if hatching occurred after the formation of the primary constriction.

(2) Morphometric changes are recognised just after the end of the ammonitella (materialised by the primary constriction and primary varix). They relate to the whorl expansion rate (W) and the whorl height (H). These changes are interpreted as the transition to an active mode of life (hatching). The presence of a caecum maintained by the prosiphon suggests that the ammonite was able to regulate its buoyancy from the moment it hatched.

(3) A post-embryonic development stage occurred with no major morphometrical changes. When morphometrical changes are observed in development, they are interpreted as reflecting changes in mode of life (Landman 1987). In the absence of such changes in *C. renggeri*, it can be assumed that the ammonite had a relatively stable mode of life throughout this stage. Only changes in septal spacing, of which it has not been possible to determine the cause, are marked. The appearance and disappearance of crenulation occur towards the end of the post-embryonic stage.

(4) The end of growth (mature stage) is marked by characteristically reduced septal spacing, where interseptal angles are the narrowest during all of ontogenetic development, associated with a change of the peristome which developed lappets.

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