Chapter 12

Mode and Rate of Growth in Ammonoids

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1. Introduction

In this chapter we discuss the mode and rate of growth in ammonoids, focusing primarily on postembryonic growth. We first discuss the general mode of growth and then describe the ontogenetic sequence of growth stages. These stages are recognized on the basis of changes in morphology. For example, a graph of the increase in size of whorl width versus shell diameter in an individual reveals changes through ontogeny that pinpoint the end of one growth stage and the beginning of another. We next discuss the overall rate of growth through ontogeny and establish a generalized growth curve. In this discussion, we refer to other cephalopods whose rate of growth is known. Fluctuations in the rate of growth that are superimposed on this growth curve are indicated in ammonoids by the presence of such shell features as varices and constrictions.

The absolute rate of growth in ammonoids depended on a variety of factors, including temperature, food availability, and injuries to the individual animal. In addition, ambient pressure and the permeability of the siphuncle governed the rate at which cameral liquid was removed and, hence, the growth rate. Most methods to determine the actual rate of growth in ammonoids assume that particular morphological features were secreted at a known rate or periodicity. Other methods attempt to identify an environmental signal that was captured in the morphology or chemistry of the shell. It is also possible to study epizoans that grew on the shell of an ammonoid while the ammonoid was alive. In this method, the epizoans are used as chronometers to measure the rate of ammonoid growth. We compile the data from these various methods to arrive at some general estimates of the age at maturity, especially for shallow-water taxa.

Specimens illustrated in this chapter are reposited at the University of Lausanne (here indicated by the prefix HB), the American Museum of Natural History (AMNH), the Yale Peabody Museum (YPM), the United States Geological Survey (USGS), and the British Museum (Natural History) [BM(NH)].

2. Mode of Growth

In this section, we describe the overall mode of growth of ammonoids with reference to *Nautilus*, the only externally shelled cephalopod that is still extant. Ammonoids are, in fact, phylogenetically more closely related to coleoids than they are to *Nautilus* (Engeser, 1990; Jacobs and Landman, 1993; Chapter 1, this volume). However, the retention of an external shell in ammonoids implies that these extinct forms shared with *Nautilus* basic similarities in their processes of growth, although not necessarily a similarity in their rate of growth or age at maturity.

Therefore we begin our discussion by briefly reviewing the mode of growth of *Nautilus*. We are primarily interested in three aspects: (1) secretion of shell material at the apertural margin as the soft body increases in size, (2) secretion of additional shell layers on the inside surface of the body chamber, and (3) secretion of septa at the rear of the body, thereby forming chambers.

The cycle of chamber formation in *Nautilus* consists of several steps: secretion of a septum, formation of a siphuncular segment, removal of cameral liquid, and forward movement of the body to the position of the next septum (translocation) (Ward, 1987; Ward *et al.*, 1981; Ward and Chamberlain, 1983). Most of the time involved in chamber formation (approximately 90%) is devoted to septal secretion with the rear of the soft body fixed against the face of the septum being secreted. Removal of cameral liquid begins when the septum reaches approximately 60% of its final thickness. When the septum is completed, the soft body moves forward to the position of the next septum. Throughout the chamber formation cycle, growth of the shell at the apertural margin is continuous (see references cited above).

The rate of weight increase of the shell and soft body is coordinated with the rate of chamber formation to achieve near-neutral buoyancy as the animal grows (Denton and Gilpin-Brown, 1966; Ward, 1987). In other words, the rate at which chambers form and at which cameral liquid is removed balances the rate of weight increase of the shell and soft body. This system of coordinated balances also entails maintaining a balance between the volumetric increase of the body chamber and soft body and the volumetric increase of new buoyancy chambers.

This system is flexible enough to withstand a certain amount of perturbation. The system responds to perturbations by modifying the rate of removal, and sometimes the direction of flow, of cameral liquid and the volume of buoyancy chambers. For example, in the case of shell breakage at the apertural margin, the animal responds to the increase in positive buoyancy by reducing the rate of cameral liquid removal, even possibly refilling a previously emptied chamber, reducing the volume of the succeeding chamber (septal approximation), and repairing the injury at the apertural margin (Ward, 1986). Changes in cameral volume and the rate of cameral liquid removal also occur at maturity in association with an overall decrease in the rate of growth, a change in shell shape, and the development of the reproductive organs (Collins *et al.*, 1980).

This overall mode of growth was probably also characteristic of ammonoids. In ammonoids, growth occurred at the apertural margin and commonly involved the formation of ribs and other ornamental features. Additional shell layers were secreted on the inside surface of the body chamber (Chapter 4, this volume). The cycle of chamber formation probably consisted of septal and siphuncular secretion, removal of cameral liquid or possibly gel (Hewitt and Westermann, 1987), and movement of the soft body to the position of a new septum (Chapters 6 and 9, this volume). On the basis of the location and shape of muscle scars, we can infer that the rear of the soft body of the ammonoid was fixed against the septum during most of the chamber formation cycle (Tanabe and Landman, in prep.). It is likely that translocation occurred in incremental steps to judge from observations of closely spaced pseudosutures between actual sutures (Zaborski, 1986; Hewitt *et al.*, 1991; Weitschat and Bandel, 1991, 1992; Westermann, 1992; Landman *et al.*, 1993; Lominadzé *et al.*, 1993). During the chamber formation cycle, growth of the soft body and of the shell margin was probably continuous.

The time of chamber formation and the volumetric increase in chamber volume within an individual ammonoid were, no doubt, also coordinated with growth at the aperture to insure near-neutral buoyancy as the animal grew. As in *Nautilus*, we suspect that this system did not function as a means to regulate the depth of the animal in the water column but, rather simply, to maintain near-neutral buoyancy during growth (Chapter 7, this volume). Variation in the spacing between septa (chamber volume) and the time of chamber formation within an individual ammonoid may have represented a response to variation in the overall rate of growth (e.g., more rapid growth because of favorable conditions), changes in the shape of the shell (which were generally more marked than those in *Nautilus*), and modifications in the volume and density of the hard and soft tissues (Westermann, 1971, 1975).

3. Growth Stages

The growth program of ammonoids consisted of several stages. We recognize these stages on the basis of more or less abrupt changes in the shape, position, and size of individual morphological features. These morphological features include, for example, the umbilicus, the pattern of ornamentation, and the suture. In some specimens, the growth of these and other features was gradual, and, therefore, it is difficult to identify when and where changes occurred. As a result, the transition from one stage to another is unclear. In other instances, however, changes in morphology were abrupt (called critical points; "*Knickpunkte*" of Kullmann and Scheuch, 1972) and occurred in nearly all specimens within a species, indicating that growth was polyphasic (Gould, 1966). For example, in the shells of some planispirally coiled ammonoids, there are several changes in the pattern of coiling, each of which occurs at a consistent number of whorls; these are recognized on the basis of measurements of the spiral radius versus the angle of rotation (whorl number) (Currie, 1942, 1943, 1944; Obata 1959, 1960; Kant and Kullmann, 1973; Landman, 1987). Commonly, changes in a number of morphological features occurred at the same time in ontogenetic development and, thereby, delimit the boundaries of a growth stage.

The first stage in all ammonoids was the embryonic stage (Fig. 1A; Chap. 11, this volume). The embryonic shell is called the ammonitella. (This term is also used to describe the embryonic animal as a whole.) The ammonitella extends adaperturally to the primary constriction and accompanying varix. The ornamentation of the ammonitella, if present, ends at this point, and a new ornamentation begins. Commonly, there is also a change in shell shape

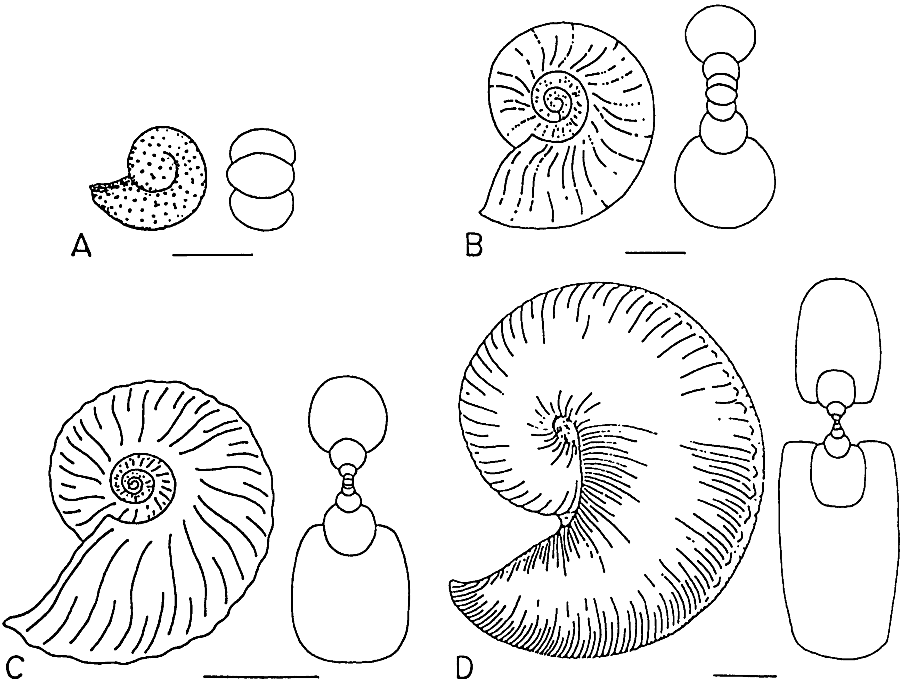


FIGURE 1. Schematic drawings of four growth stages in the ontogeny of *Hoploscaphites nicolletii*, macroconch (Late Cretaceous), in lateral and transverse cross-sectional views. (A) Ammonitella. Scale bar, 500 μm. (B) Neanoconch. Scale bar, 1 mm. (C) Juvenile. Scale bar, 5 mm. (D) Adult. Scale bar, 1 cm.

at this point (Currie, 1942, 1943; Lehmann, 1966, Fig. 1; Kulicki, 1974, 1979; Landman, 1987, 1988; Maeda, 1993); this change is particularly dramatic in heteromorph ammonoids (Bandel *et al.*, 1982, Fig. 1C). On the basis of discoveries of preserved ammonitellas, we know that as few as one septum, i.e., the proseptum, formed during embryogenesis (Chap. 11, this volume).

The rest of growth was, by definition, postembryonic. The first postembryonic stage is called the neanic stage (Westermann, 1958), and the animal or shell that formed during this stage is called the neanoconch (Fig. 1B; Chap. 16, this volume). This stage is equivalent to the late nepionic plus early neanic stages of Hyatt (1894) and Smith (1898), the larval stage of Zell *et al.* (1979), "the pseudolarval stage" of Kulicki (1979), the "goniatitic growth phase" of Hewitt (1985), the *phase juvénile* of Mignot (1993), and the stage up to the "neanic–ephibic developmental rupture" of Checa and Sandoval (1989, abbreviated NEDR). ("Ephibic" is spelled "ephebic" by Hyatt, 1894, and elsewhere.)

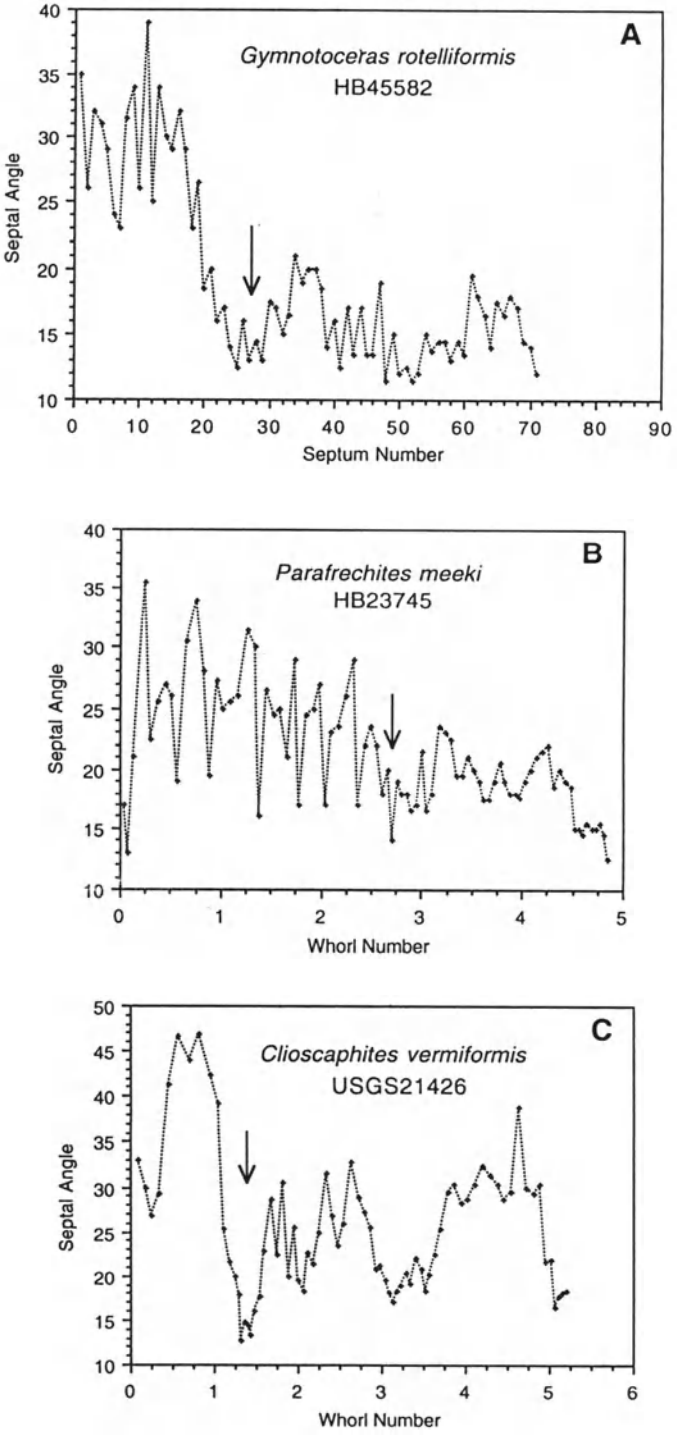
The neanoconch is commonly planorbiconic or cadiconic in planispiral ammonoids and displays little or no ornamentation. It extends adaperturally up to approximately two whorls beyond the end of the ammonitella, corresponding to a shell diameter of 3–5 mm. In general, it shows an interval of widely spaced septa. In many taxa, there is an abrupt increase in septal spacing at the beginning of the neanoconch, leading to a maximum midway through, followed by an equally abrupt decrease at the end (e.g., in Middle Jurassic *Quenstedtoceras*, Kulicki, 1974, Fig. 8; Middle Triassic *Gymnotoceras*, Fig. 2A; and Late Cretaceous *Clioscaphites*, Fig. 2C). In other taxa, this pattern is not as well developed (e.g., in Middle Triassic *Parafrechites*, Fig. 2B). In still other taxa, as noted by Mignot (1993), an interval of wide septal spacing is absent altogether (e.g., in Middle Jurassic *Sphaeroceras*).

The end of the neanic stage was marked by changes in several other features in addition to septal spacing, including whorl shape, degree of whorl overlap, ornamentation, and sutural complexity (Currie, 1942, 1943, 1944; Westermann, 1954; House, 1965, Figs. 17–19; Obata, 1965; Palframan, 1966, 1967; Kullmann and Scheuch, 1970, 1972; Kant, 1973a–c; Kulicki, 1974; Tanabe, 1975, 1977; Zell *et al.*, 1979; Landman, 1987; Checa and Sandoval, 1989; Maeda, 1993). In heteromorph ammonoids in which the early whorls are uncoiled, the end of the neanic stage may have corresponded to the first appearance of ornamentation (Tanabe *et al.*, 1981, Pl. 37, Fig. 3, Pl. 38, Fig. 2b; Matsukawa, 1987, Figs. 2, 3). These morphological changes imply further changes in the mechanical strength of the shell (Hewitt, 1988) and its hydrodynamic efficiency (Landman, 1987; Jacobs, 1992; Chapter 7, this volume). During the neanic stage, the ammonoid may have lived in the plankton, and, at the end of this stage, it may have assumed another mode of life in a different habitat (Westermann, 1958; Zell *et al.*, 1979; Landman, 1987, 1988; Checa and Sandoval, 1989; Shigeta, 1993; Chapter 16, this volume).

The next growth stage is referred to as the juvenile stage and the animal or shell as the juvenile (Fig. 1C; Chapter 16, this volume). This stage included all of the remaining whorls up to the start of the mature body chamber and is equivalent to the late neanic plus early ephebic stages of Hyatt (1894), the later part of the juvenile stage of Westermann (1954) and Landman and Waage (1993), and the early part of the *phase submature* of Mignot (1993). Some authors also distinguish among early, middle, and late juvenile stages, mainly on the basis of shell size (e.g., Morton, 1988, described small, medium, and

→

FIGURE 2. (A) Plot of septal angle (in degrees) versus septum number in a juvenile specimen of *Gymnotoceras rotelliformis* (Middle Triassic, Nevada, HB 45582). The end of the neanoconch is marked by a minimum in septal spacing around septum 25 (arrow). The first few septa in this specimen were not preserved, and so the septum number is an approximation. The septal angle is defined as the angle between septa n and $n-1$. (B) Plot of septal angle (in degrees) versus whorl number in a juvenile specimen of *Parafrechites meeki* (Middle Triassic, Nevada, HB 23745). The arrow indicates a change in the pattern of septal spacing, which correlates with the end of the neanoconch. (C) Plot of septal angle (in degrees) versus whorl number in a mature specimen of *Clioscaphites vermiformis* (Upper Cretaceous, Montana, USGS 21426). The end of the neanoconch is marked by a minimum in septal spacing (arrow). The septal approximation at the end of ontogeny indicates the attainment of maturity (modified from Landman, 1987, Fig. 59).


A
Gymnotoceras rotelliformis
HB45582
Septal Angle
40
35
30
25
20
15
10
0
10
20
30
40
50
60
70
80
90
Septum Number
B
Parafrechites meeki
HB23745
Septal Angle
40
35
30
25
20
15
10
0
1
2
3
4
5
Whorl Number
C
Clioscaphites vermiformis
USGS21426
Septal Angle
50
45
40
35
30
25
20
15
10
0
1
2
3
4
5
6
Whorl Number

large juveniles of Middle Jurassic *Graphoceras*). Another term in the literature, adolescent, also refers to a late juvenile stage (Hyatt, 1894; see Collins and Ward, 1987, for the use of this term as applied to *Nautilus*).

In general, the juvenile shell is more compressed and involute than the neanoconch, and ornamentation is almost always present (Westermann, 1954; Landman, 1987). In the juvenile shells of many taxa, there is a phase of more or less uniform septal spacing, punctuated by occasional fluctuations (Fig. 2; corresponds to the interval between depressions II and III in Kulicki, 1974, Fig. 8). There is some variation in the number of septa that formed during the juvenile stage among individuals within the same species (Lehmann, 1966; Kulicki, 1974; Mignot, 1993).

Maturity or adulthood is the next stage, and the animal or shell is called the adult (Fig. 1D; Callomon, 1963; Makowski, 1962). This stage is demarcated by a number of morphological changes, most of which affected the final body chamber and last few septa. It is also common to describe a subadult or submature stage in which the sequence of morphological changes culminating in maturity has only just begun or is in progress (e.g., Mignot, 1993). In contrast, an immature stage lacks any sign of maturity (Howarth, 1992) and is equivalent to the neanic and juvenile stages.

The morphological changes associated with maturity are described briefly below (but see Chapter 13, this volume, for a more complete discussion). The pattern of septal spacing generally changed in late ontogeny and showed an initial increase followed by a final decrease (Fig. 2C; Oechsle, 1958; Rieber, 1963; Lehmann, 1966; Clausen, 1968; Bayer, 1972a,b, 1977; Kulicki, 1974; Druschits *et al.*, 1977; Blind and Jordan, 1979; Checa, 1987; Dommergues, 1988; Bucher and Guex, 1990; Mignot, 1993). The closer spacing or approximation of the last few septa is widely interpreted as indicating the onset and attainment of maturity (Callomon, 1963; Crick, 1978). Microconchs showed septal approximation in the last one or over the last two chambers, whereas macroconchs showed progressively reduced septal spacing over many more chambers (Chapter 13, this volume; Makowski, 1962; Crick, 1978; Lehmann, 1981; Landman and Waage, 1993). Commonly, but not invariably, there were also concurrent changes in the shape and length of the body chamber including a reduction in angular length, a change in the pattern of coiling, an increase in whorl width, either an appearance or strengthening of ornamentation or, conversely, an attenuation or even disappearance of ornamentation, and modifications in the shape and thickness of the apertural lip.

As indicated, these changes are interpreted as reflecting sexual maturation in analogy with present-day *Nautilus* (Makowski, 1962; Callomon, 1963). However, it is important to note that the exact timing of these changes relative to the growth of the reproductive organs is unclear. In *Nautilus*, for example, the secretion of the last septum begins before the complete development of the reproductive organs (Collins and Ward, 1987). The final thickening of the apertural lip, however, coincides with the attainment of full sexual maturity.

All of these morphological changes in the ontogeny of ammonoids indicate that growth was determinate and that maturity occurred at a more or less prescribed size for each species (Makowski, 1962; Callomon, 1963). As mentioned, many of these changes were initiated before the final size was reached in order to achieve the desired adult shape, an inevitable consequence of accretionary growth (Callomon, 1963). Thus, it is reasonable to interpret these changes in terms of the mode of life of the adult (Chapter 16, this volume: Seilacher and Gunji, 1993). For example, development of a hook-like body chamber in some Cretaceous heteromorph ammonoids culminated in an upturned aperture, which has been interpreted as an adult adaptation facilitating vertical locomotion (Chapter 16, this volume).

In many modern cephalopods, the release of a hormone from the optic gland system induces sexual maturation (Wells and Wells, 1959; Richard, 1970; Boyle and Thorpe, 1984; Mangold, 1987). When the gonads are large enough to respond to this hormone, the maturation program takes over, entraining a sequence of morphological modifications leading to the attainment of the final mature size, and, ultimately, the completion of the life cycle. Such a sequence of morphogenetic events has been referred to as a "countdown" terminating in the cessation of growth (Seilacher and Gunji, 1993). In some large ammonoids, late ontogenetic modifications are absent, suggesting that growth may have been more or less indeterminate in these forms (Westermann, 1971; Stevens, 1988).

In the 19th century, the morphological features we now recognize as indicating maturity were considered to have formed during a stage following maturity and indicative of old age. This stage is referred to as the senescent, senile, or gerontic stage (Hyatt, 1894). This stage of life in many modern cephalopods is characterized by a deterioration in locomotor performance, an inability to heal injuries, a decrease in weight, and a reduction in metabolic activity (Van Heukelem, 1978). These phenomena may also have characterized the postreproductive life of ammonoids. However, such a stage is unlikely to have been expressed in shell secretory products, so it is probably never directly observable in fossil material (see also discussion in Miller *et al.*, 1957, p. L14, and Matyja, 1986, p. 42).

4. Growth Curve

In this section, we discuss the overall pattern of growth through ontogeny, identifying those periods when the rate of growth accelerated, decelerated, or remained the same. These changes were controlled by the organism's internal clock, but also may have been affected by external factors (see Section 6). At the end of this section, we present a generalized growth curve for all ammonoids, although, given their diversity, this curve will not necessarily apply to every taxon.

The rate of growth of an organism is defined as the change in its overall size through time. It is, therefore, important to choose an appropriate measure of size. In studies of modern coleoids, the variables "weight" and "mantle length" are usually chosen (Mangold, 1983; Forsythe and Van Heukelem, 1987). Because soft parts are not preserved in ammonoids, this metric is unavailable to us. Instead, the diameter of the shell, the number of whorls, or the number of septa is generally used as a measure of size (Matyja, 1986). These same parameters are also employed in studies of the rate of growth of present-day *Nautilus* (Saunders, 1983; Ward, 1985; Landman and Cochran, 1987). The volume of the body chamber or its cube root is, perhaps, a more accurate measure of size in ammonoids, especially if there were significant modifications in the shape of the shell during ontogeny, as there were in heteromorph forms (R.A. Hewitt, personal communication, 1994). However, the volume of the body chamber is seldom used in the literature, and in order to facilitate comparisons with other studies, the standard parameters are used in this chapter.

In practice, determination of the ontogenetic pattern of growth in ammonoids depends on reference to *Nautilus*, whose rate of growth is relatively well known. As explained earlier (Section 2), the fact that both *Nautilus* and ammonoids share an external shell implies basic similarities in their processes and patterns of growth. Therefore, we will begin with a short review of what is known about the ontogenetic pattern of growth in *Nautilus*.

In *Nautilus*, the length of time required for chamber formation (referred to simply as the time of chamber formation in the rest of the chapter) generally increases throughout ontogeny. This is because cameral volume increases faster than the surface area of the siphuncle during ontogeny, requiring increasingly longer times to pump out larger chambers (Chamberlain, 1978; Ward, 1982, Fig. 2). In addition, septa become thicker throughout ontogeny, and, assuming a constant rate of carbonate secretion, it takes increasingly longer times to secrete thicker septa (Westermann, 1990).

The increase in the time of chamber formation appears to be exponential throughout most of ontogeny, judging from growth studies of *Nautilus pompilius* and *N. macromphalus* in aquaria (Ward, 1985; Landman and Cochran, 1987). This increase in time corresponds with a more or less exponential increase in chamber volume, expressed by septa spaced at equal angular intervals. Departures from this pattern of uniform septal spacing, for example, at maturity (see below), indicate variation in the time of chamber formation. Such variation, which also occurs in *Sepia*, as described by Wiedmann and Boletzky (1982), reflects changes in the overall rate of growth and in the shape of the shell and soft body.

Consistent with the exponential increase in the time of chamber formation in *Nautilus*, the rate of growth of the venter at the apertural margin is more or less constant during most of ontogeny (Saunders, 1983; Ward, 1985; Carlson *et al.*, 1992). As a result, the diameter of the shell generally increases as a linear function of time, whereas the number of whorls increases as a negatively logarithmic function of time.

These general patterns also probably characterized the rate of growth of ammonoids because similar physiological processes operated in these animals as well. The same ontogenetic relationships between cameral volume and the surface area of the siphuncle and between septal thickness and shell diameter also existed in most ammonoids (Chamberlain, 1978; Ward, 1982; Westermann, 1990). In addition, in many ammonoids, the diameter of the siphuncle grew with a strong negative allometry (Westermann, 1971, 1990; Tanabe, 1977; Landman, 1987). All of this evidence suggests that the time of chamber formation in ammonoids increased exponentially throughout most of ontogeny. Between any two adjacent chambers, the time of formation may have been only slightly different, but between chambers at the beginning and at the end of ontogeny, the difference in time of formation was undoubtedly significant. The exact rate of increase in the time of chamber formation probably varied among individuals within the same species and especially among individuals of different species.

An exponential increase in the time of chamber formation in ammonoids correlated with a nearly exponential increase in chamber volume, which is expressed by the fact that septa are spaced at approximately equal angular intervals (Fig. 3). However, as we have seen, septal spacing in ammonoids is very variable and much less uniform than it is in *Nautilus*. As in *Nautilus*, it

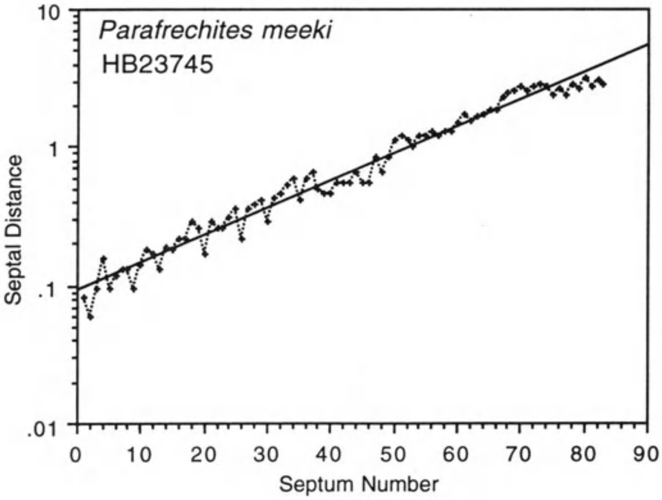


FIGURE 3. Semilog plot of the distance between septa (mm) versus septum number in a juvenile specimen of *Parafrechites meeki* (Middle Triassic, Nevada, HB 23745). The septal distance is defined as the distance between septa n and $n-1$. For consistency, this distance is measured at one-third the whorl height from the venter on a median cross section. Note that the distance between septa increases exponentially over ontogeny (same specimen as in Fig. 2B.)

is likely that fluctuations in septal spacing were related to variations in the overall rate of growth and in the shape of the shell and soft body.

An exponential increase in the time of chamber formation in ammonoids implies that the rate of growth of the venter at the apertural margin was probably constant during most of ontogeny, with shell diameter increasing as a linear function of time. Increase in angular length (whorl number), in contrast, was probably a negatively logarithmic function of time, with equal angular increments taking increasingly longer to form.

Departures from this general pattern of growth occurred during the neanic and mature stages. The neanic stage, as noted, was characterized by an interval of wide septal spacing. In addition, in many ammonoids, the beginning of this stage was marked by a pronounced increase in whorl width. These observations both suggest that there may have been an acceleration in the rate of growth during this time interval.

In contrast, the rate of growth probably decelerated at the approach of maturity (Callomon, 1963). Observations of this stage in *Nautilus* indicate a rapid decrease in the rate of growth of the shell at the apertural margin (Ward, 1985). This decrease coincides with the formation of a number of morphological features, including thickening of the apertural margin and approximation of the last few septa (Davis, 1972; Collins and Ward, 1987).

The explanation of septal approximation at maturity is not entirely clear. In *Nautilus*, this feature is associated with, among other changes, a decrease in the rate of growth at the apertural margin, a reduction in the forward movement of the soft body, an enlargement of the reproductive organs, and a change in the shape of the shell. It is possible that the reduced spacing and extra thickness of the last few septa serve to provide additional weight necessary to compensate for a decrease in the density of the soft body as a result of the growth of the reproductive organs, which are presumably composed of fatty tissue. Ward (1987) has also suggested that septal approximation in *Nautilus* allows for a final trimming of buoyancy.

The presence of many of the same morphological features in ammonoids as in *Nautilus* also indicates that there was probably a deceleration in the rate of growth of ammonoids at the approach of maturity. In many ammonoids the final apertural lip is thickened and bears ventral and lateral lappets. The adult body chamber commonly shows a change in shape and a reduction in angular length. In addition, ribs and other ornamental features tend to become more closely spaced toward the aperture (Matyja, 1986). All of this evidence suggests a deceleration in the rate of growth and, ultimately, the cessation of growth at a more or less prescribed size. However, the time interval over which the rate of growth decelerated may have varied depending on the taxon and dimorph (possibly indicated by differences in the patterns of septal approximation).

Additional information about the overall pattern of growth in ammonoids comes from a study of growth increments on the lower jaws of Mesozoic ammonoids. In this study, Hewitt *et al.* (1993) investigated several specimens

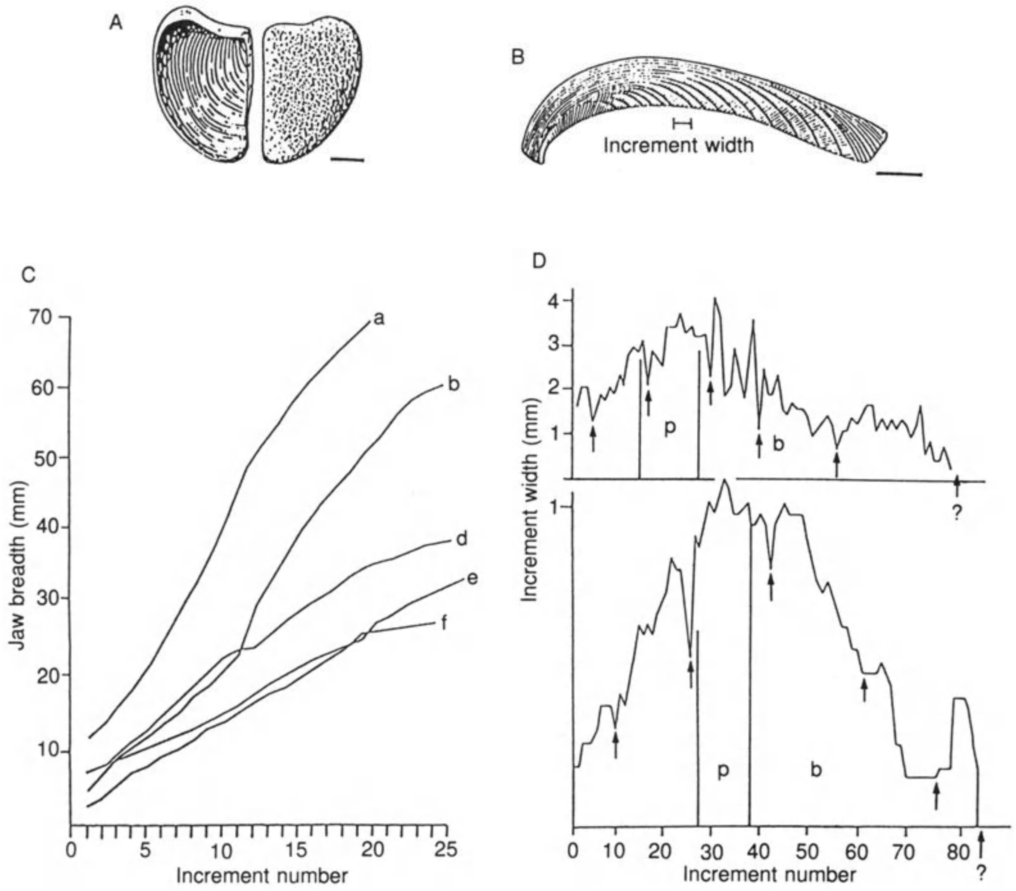


FIGURE 4. (A) View of the concave inner and convex outer surfaces of the two valves composing a specimen of *Laevapytchus*, here interpreted as a lower jaw. The concave surfaces of these valves are marked with concentric ridges called growth increments. Scale bar, 1 cm. (After Lehmann, 1981, Fig. 73.) (B) Longitudinal cross section through one of these valves showing the internal lamellae that correspond to the growth increments. Note the measurement of increment width. Scale bar, 5 mm. (After Schindewolf, 1958, Fig. 2.) (C) Plot of the ontogenetic increase in jaw breadth with respect to increment number in five specimens of *Lamellaptychus*, also interpreted as lower jaws. The three smallest specimens (d,e,f) show a nearly constant increase in jaw breadth with a slight decrease near the end of ontogeny; the two largest specimens (a,b) show a more sigmoidal pattern. Jaw breadth is measured across the jaw (perpendicular to the straight edges of the valves) when the two valves are folded into a U-shape, approximating their position in life. (After Hewitt *et al.*, 1993, Fig. 1.) (D) Plot of increment width versus increment number through ontogeny in two specimens of *Laevaptychus*. There is an increase in increment width followed by a decrease starting at the point of the jaw corresponding to the formation of the middle or the end of the penultimate whorl (p) and continuing through the part of the jaw corresponding to the formation of the mature body chamber (b). The arrows indicate possible winter events characterized by reductions in increment width. According to this interpretation, the animals in which these jaws once occurred attained maturity in about 6 years. However, the decrease in increment width at the end of ontogeny may simply be related to the attainment of maturity. (After Hewitt *et al.*, 1993, Fig. 2.)

of *Lamellaptychus* and *Laevaptychus*, here interpreted as lower jaws, belonging to Late Jurassic oppeliids and Late Jurassic and Early Cretaceous aspidoceratids, respectively. The growth of these jaws was related to the growth of the entire animal because they were located within the body chamber. For example, measurements of specimens of *Lamellaptychus* indicate that the length of these jaws approximately equals the whorl height at the aperture, so, if the whorl height at the aperture doubled in, for example, 5 years, then half the length of the jaw would have formed in that same time interval (Hewitt *et al.*, 1993).

The concave, chitinous surfaces of these lower jaws are marked with concentric ridges (growth increments) that correspond to internal lamellae (Fig. 4A,B). Hewitt *et al.* (1993) plotted jaw breadth versus the number of growth increments on the surface of the jaw in several specimens of *Lamellaptychus* (Fig. 4C). Smaller specimens (labeled d, e, and f on Fig. 4C, possibly belonging to microconchs) showed a nearly constant increase in jaw breadth versus increment number, with a slight decrease in the slope of the curve near the end of ontogeny. Larger specimens (a and b on Fig. 4C, possibly belonging to macroconchs) showed a more sigmoidal pattern consisting of two phases, an early phase of increasing slope and a later phase of decreasing slope. Hewitt *et al.* (1993) also plotted increment width versus increment number in several specimens of *Laevaptychus* (Fig. 4D). They detected an increase in increment width in early ontogeny followed by a decrease in later ontogeny. According to their calculations, the point at which this change occurred corresponded to the end of the penultimate whorl and the beginning of the adult body chamber in the ammonoids in which these jaws grew.

Assuming that these growth increments were secreted at equal time intervals, plots of increment width versus increment number and jaw breadth versus increment number indicate that the rate of growth in these ammonoids was constant or accelerated up to the end of the penultimate whorl and then decelerated at the start of the mature body chamber. This suggests that a major portion of the life span of these ammonoids involved a protracted period during which the rate of growth decreased, beginning with the onset of maturity.

In summary, we present a generalized growth curve for all ammonoids (Fig. 5). We postulate that the rate of growth accelerated during the neanic stage, was more or less constant during the juvenile stage, and decelerated at the approach of maturity. However, given the wide diversity of ammonoids, this curve represents only an approximation. Differences in the slope of this curve probably resulted from variation in those features affecting the rate of cameral liquid removal and shell secretion, namely, the diameter of the siphuncle, the length of the septal necks, and the thickness of the shell wall and septa as well as from variation in environment and mode of life (Westermann, 1990). In some ammonoids there may also have been variation in the duration of the juvenile and adult stages, with some forms showing indeterminate growth (Ivanov, 1975).

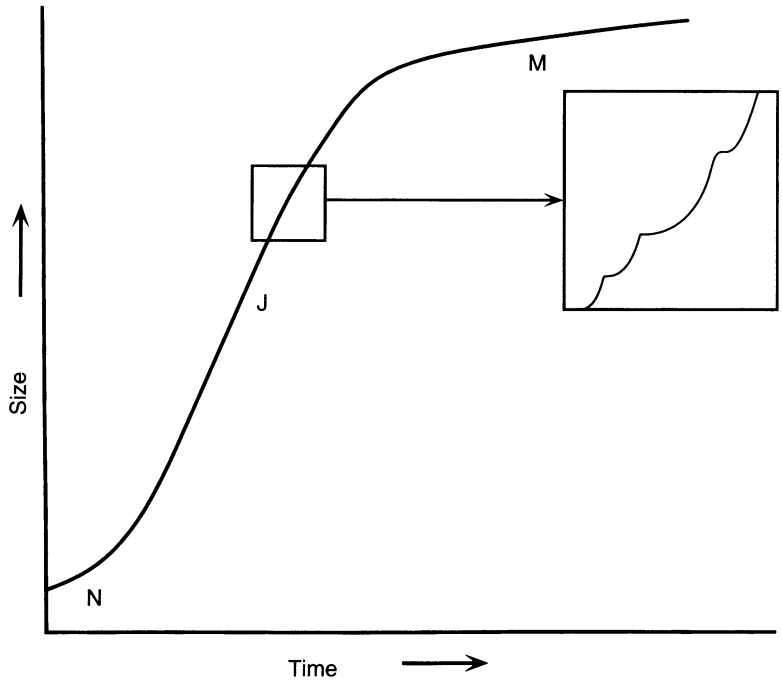


FIGURE 5. Generalized growth curve for ammonoids showing the ontogenetic pattern of growth through ontogeny. Size is usually expressed as shell diameter or whorl number. The cube root of the volume of the body chamber is a more accurate measure of size, especially if there were pronounced changes in the shape of the shell during ontogeny (R.A. Hewitt, 1994, personal communication). The enlarged view on the right reveals numerous fine-scale fluctuations in the rate of growth. Abbreviations: N, neanic stage; J, juvenile stage; M, mature stage.

5. Intrinsic Fluctuations in the Rate of Growth

Superimposed on the ontogenetic growth curve were short-term fluctuations in the rate of growth, which are indicated by the presence of certain shell features. Such fluctuations were probably an intrinsic part of the growth program, although there also may have been an environmental component. These fluctuations indicate that, on a finer scale, the growth curve of ammonoids was never as smooth as it is shown in Fig. 5.

5.1. Growth Lines, Lirae, and Ribs

Growth lines represent discontinuities in secretion and indicate that growth was intermittent at some time scale (Vermeij, 1993). Growth lines appear in the periostracum and on the shell surface (Checa, 1994). Okamoto (1989, Fig. 1) illustrated growth lines spaced at intervals of approximately 100 μm in a specimen of Late Cretaceous nostoceratids. We have observed still finer growth lines on a number of other species (Fig. 6). These lines appear on the surface of the outer prismatic layer but are not visible in cross section (compare with growth lines in *Nautilus*, Fig. 7). The smallest such growth lines measure 1 μm in width, suggesting that they reflect intermittent growth at the cellular level (G.R. Clark, II, personal communication, 1993).

The distinction between growth lines and lirae is somewhat arbitrary, and these two terms have been used interchangeably by many authors (Doguzhaeva, 1982; Korn and Price, 1987). However, the general sense is that lirae are larger and more widely spaced than growth lines—they characteristically occur at intervals of 0.1 to 1.0 mm, although their precise spacing depends on where they occur on the shell (Fig. 8). Lirae may uniformly cover the shell surface or show variations in spacing throughout ontogeny (Doguzhaeva, 1982).

On the next coarser scale are ribs. In most ammonoids, ribs and lirae tend to parallel growth lines, indicating that both of these features mark former positions of the apertural margin (Fig. 6D,E; see Chapter 8, this volume, for a discussion of how the orientation of the living ammonoid may have influenced rib direction; Checa and Westermann, 1989; Okamoto, 1989; Checa, 1994). However, in some ammonoids, ribs intersect growth lines at low angles (Arkell *et al.*, 1957; Cowen *et al.*, 1973). In general, ribs represent plications (corrugations) of the shell wall and, therefore, are expressed on the steinkern.

The formation of ribs was probably controlled mostly by the growth program rather than by the environment. Rib formation may have involved a system of activation and inhibition at the mantle edge, similar to that which produces color patterns in living gastropods and bivalves (Meinhardt and Klinger, 1987). Checa (1994) proposed that, in many ammonoids, an entire rib may have formed during a single secretory event (see Section 5.6). This would have produced episodic advances in the growth of the apertural margin. There is some evidence suggesting that such a process may have been reflected in septal spacing. Checa (1987, Fig. 2) and Dommergues (1988, Figs. 2–8)

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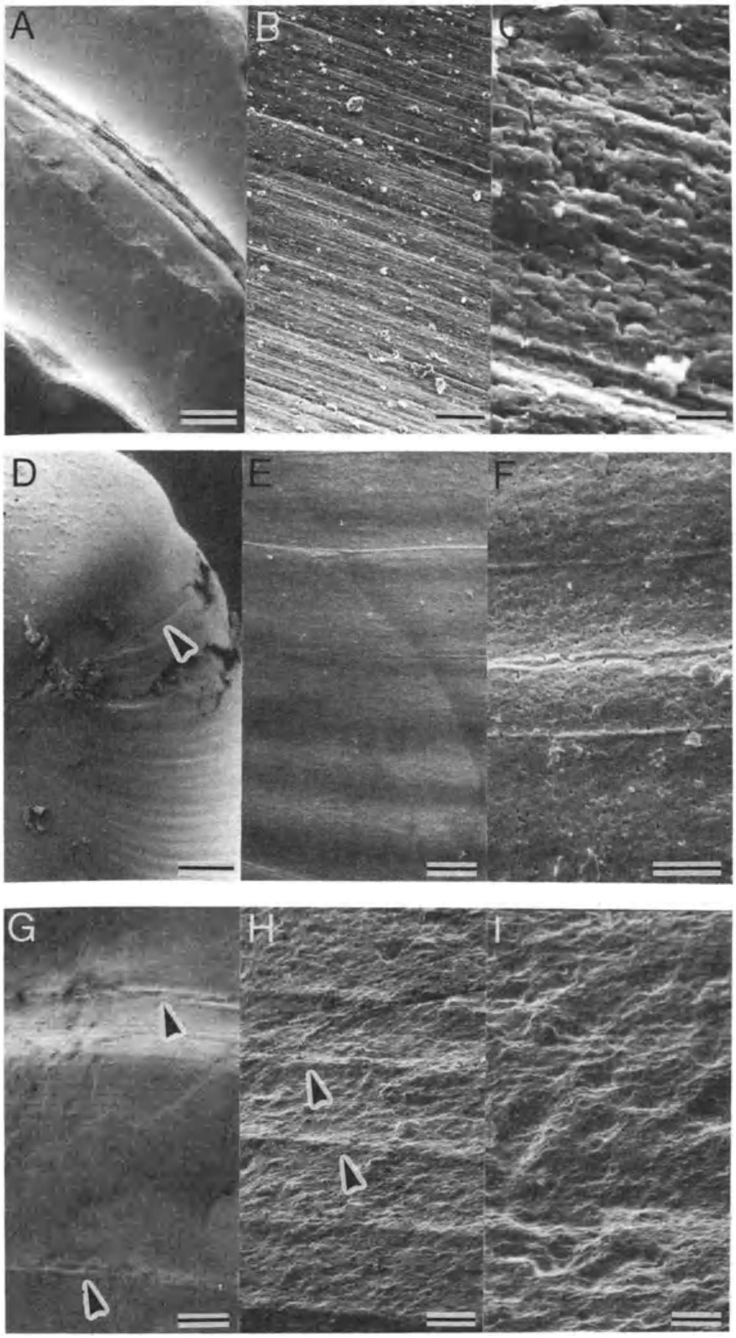
FIGURE 6. Ammonoid ribs, lirae, and growth lines. (A–C) Ventral view of part of the mature body chamber of a specimen of *Scaphites carlilensis*, Upper Cretaceous, Kansas, USGS loc. D5140. (A) The body chamber is marked by strong ribs. The adoral direction is toward the lower left-hand corner of the photo. Scale bar, 500 μm. (B) Close-up of a well-preserved portion of this shell reveals the existence of growth lines. Scale bar, 20 μm. (C) These growth lines occur at intervals of approximately 1 μm. Scale bar, 2 μm. (D–F) Lateral view of part of the ammonitella and first whorl of the neanoconch of a specimen of *Scaphites whitfieldi*, Upper Cretaceous, South Dakota, AMNH 44833. (D) The arrow indicates the end of the ammonitella. Scale bar, 50 μm. (E) Close-up of ribs and growth lines on the neanoconch shows that ribs parallel growth lines. Scale bar, 10 μm. (F) A further enlargement reveals that the growth lines occur at intervals of approximately 1 μm. Scale bar, 5 μm. (G–I) Lateral view of part of the mature body chamber of a specimen of *Parafrechites meeki*, Middle Triassic, Nevada, AMNH 44994. (G) Ribs, lirae, and megastriae (arrows) are visible. The adoral direction is toward the bottom of the photo. Scale bar, 200 μm. (H) Close-up showing lirae (arrows) and growth lines between them. Scale bar, 20 μm. (I) The growth lines appear to be spaced at intervals of about 1 μm. Scale bar, 5 μm.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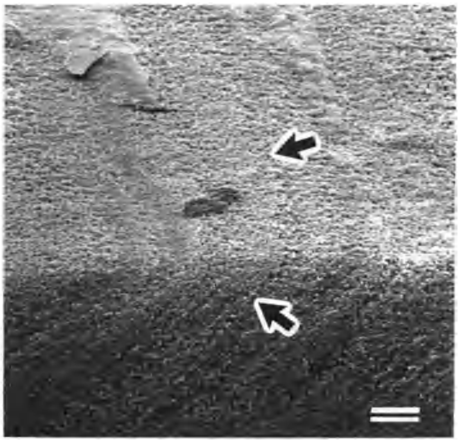


FIGURE 7. Growth lines along the venter of the mature body chamber of a specimen of *Nautilus belauensis*, Palau, AMNH 45073. A piece of the shell was broken off near the apertural margin and sectioned perpendicular to the growth lines. It was photographed at an angle so that the surface of the shell (lighter area on top) as well as the cross section through the spherulitic prismatic layer (darker area on bottom) are visible. The growth lines (arrows) appear both on the surface and in cross section. The visibility of the growth lines was enhanced by etching with acid (EDTA). The adoral direction is toward the right. Scale bar, 20 μm.

observed a positive correlation between septal spacing and rib spacing in many Jurassic ammonoids. This correlation suggests that septal spacing may have responded to the growth spurts and concomitant changes in shell shape associated with rib formation.

5.2. Constrictions, Varices, and Stretch Pathology

Constrictions are defined as grooves on the surface of the shell and may be rectiradiate, prorsiradiate, sigmoid, or angular (Fig. 9; Arkell *et al.*, 1957). They generally represent flexures in the shell wall and hence form corresponding grooves on the steinkern. They are sometimes accompanied by a varix, that is, a thickening of the shell wall, caused primarily by an increase in the thickness of the nacreous layer (Birkelund, 1981; see Arkell *et al.*, 1957, for a description of the different kinds of varices, for example, labial ridges). Varices may also occur without an associated constriction; such varices have been called internal ridges or pseudo-constrictions (Westermann, 1990) and appear as grooves on the steinkern.

Constrictions have generally been interpreted as reflecting discontinuities in growth (Simoulin, 1945; Arkell *et al.*, 1957; Kulicki, 1974; Kennedy and Cobban, 1976; Obata *et al.*, 1978; Bogoslovsky, 1982; Westermann, 1990; see Section 5.6). This interpretation is supported by a number of observations: (1) the association of constrictions with varices, (2) the change in direction of

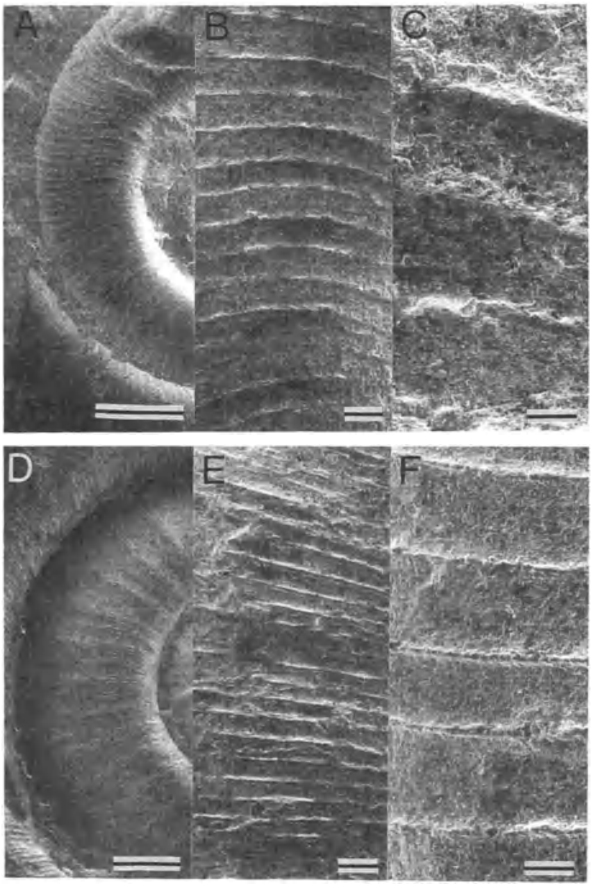


FIGURE 8. Ammonoid lirae. (A–C) Lateral view of part of the juvenile whorls of a specimen of *Ussurites* sp., Triassic, Greece, AMNH 45072. (A) Lirae are visible on the whorl flanks. Coiling is counterclockwise. Scale bar, 2 mm. (B) Enlarged view of A. Scale bar, 200 μm. (C) Enlarged view of B. Scale bar, 50 μm. (D–F) Lateral view of part of the juvenile whorls of a specimen of *Clymenia undulata*, Devonian, Germany, YPM 2513. (D) Lirae are visible on the whorl flanks. Coiling is clockwise. Scale bar, 2 mm. (E) Enlarged view of D. Scale bar, 200 μm. (F) Enlarged view of E. Scale bar, 100 μm.

ribbing following a constriction (Fig. 9; Simoulin, 1945; Arkell *et al.*, 1957; Checa and Westermann, 1989; Maeda, 1993), (3) the pronounced increase in whorl height following a constriction, as shown in many perisphinctids (Arkell *et al.*, 1957), and (4) the disappearance of repaired shell injuries at a constriction (Simoulin, 1945).

In contrast to varices and constrictions, a stretch pathology refers to a portion of a shell characterized by a decrease in whorl width and height, an attenuation of ornamentation, and a thinning of the shell wall (Landman and Waage, 1986). Stretch pathologies are common in macroconchs of some Late

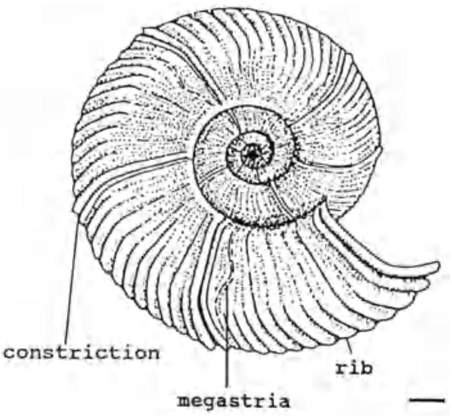


FIGURE 9. Sketch of a macroconch of *Yokoyamaoceras ishikawai*, Late Cretaceous, Japan, showing ribs, constrictions, and megastriae (after Maeda, 1993, Fig. 2). Scale bar, 10 mm.

Cretaceous scaphitid ammonoids and occur at the point where the shell uncoils from the phragmocone into the shaft of the adult body chamber. This phenomenon may indicate a period of rapid growth just prior to the onset of maturity or, alternatively, may record a diversion of resources toward the development of the reproductive organs. A period of rapid growth would explain the extreme rarity of submature specimens of these ammonoids in which the hook-like body chamber is only half-formed (Landman and Waage, 1993).

5.3. Spines

The presence of spines may indicate that there were variations in the rate of forward growth of the apertural margin. For example, on the basis of the pattern of growth lines, Checa and Martin-Ramos (1989) reconstructed the formation of long, hollow spines in Late Jurassic *Aspidoceras*. They concluded that the mantle must have remained in a more or less stationary position until each spine was completed, implying occasional pauses in forward growth of the apertural margin. In other instances, however, the process of spine formation may have occurred without any interruptions in forward growth. For example, in Late Jurassic *Orthaspidoceras*, the formation of mammiform spines probably occurred as the mantle continuously moved forward (Checa and Martin-Ramos, 1989).

It is possible that some spines, depending on their location on the shell, may have been resorbed during ontogeny. This is because in closely coiled ammonoids, the dorsum of one whorl is secreted against the venter of the preceding whorl, and, therefore, the ventral surface of the preceding whorl had to have been relatively smooth. In Early Triassic *Monacanthites*, spines are present on the venter of the last whorl of mature specimens but are absent on the venter of earlier whorls where parabolic nodes occur instead (Tozer, 1965). If these nodes were once the site of spines, the spines would have had to have been resorbed before secretion of the next whorl, in a process similar to that which occurs in some gastropods (Carriker, 1972; Vermeij, 1993). An alternative explanation is that spines developed only on the last whorl of mature specimens (Tozer, 1965).

In other ammonoids, spines may have been retained throughout ontogeny even though they evidently interfered with the secretion of succeeding whorls. In Late Cretaceous *Euomphaloceras septemseriatum*, ventrolateral tubercles form the septate bases of long spines (Kennedy, 1988, Pl. 8, Figs. 4, 6, 9; Pl. 9, Fig. 11). These spines are accommodated in radial grooves along the flanks of the succeeding whorls. In some instances, the spines are almost entirely concealed within these grooves. In other instances, the spines are missing altogether and may have broken off during life, leaving only the ventrolateral tubercles behind.

Seilacher and Gunji (1993) described another example in which ornamental features may have been discarded during ontogeny. In Early Jurassic *Lytoceras lythense*, the apertural margin displays a crenulated flare. These apertural flares have been found as isolated fragments in the Posidonia Shale of Germany. One explanation is that the animal purposely shed these flares during ontogeny. Alternatively, these features may have simply broken off soon after they were formed.

5.4. Megastriae

Megastriae are defined as distinctive thick lines, different from growth lines and lirae, that extend continuously around the flanks and venter (Figs. 6G, 9; Bucher and Guex, 1990). This term is used to refer to all such features that have previously been referred to by different terms: *alte Mundränder* (Pompeckj, 1884; Teisseyre, 1889; Mojsisovics, 1886; Wähner, 1894; Diener, 1895), demarcation lines (Matsumoto *et al.*, 1972; Obata *et al.*, 1978), parabolic lines (Arkell *et al.*, 1957; Matsumoto, 1991; Maeda, 1993), and transitional mouth borders (Tozer, 1991). Megastriae highlight the discontinuous nature of shell secretion in that they represent intrinsic pauses in growth superimposed on the overall growth curve. There are many different kinds of megastriae, and they occur in a wide variety of taxa (Fig. 10).

Microstructural studies of megastriae reveal that these features represent actual breaks in secretion. In median cross section, a megastria is seen to result from the overlap of two consecutive shell segments (Fig. 11). The old segment may either wedge out gradually or end abruptly as a thickening or an upturned flare visible on the surface of the shell (Fig. 6G). The new segment appears beneath the previous one and thickens progressively until it outgrows the former apertural margin. Secretion of this new segment involved both the

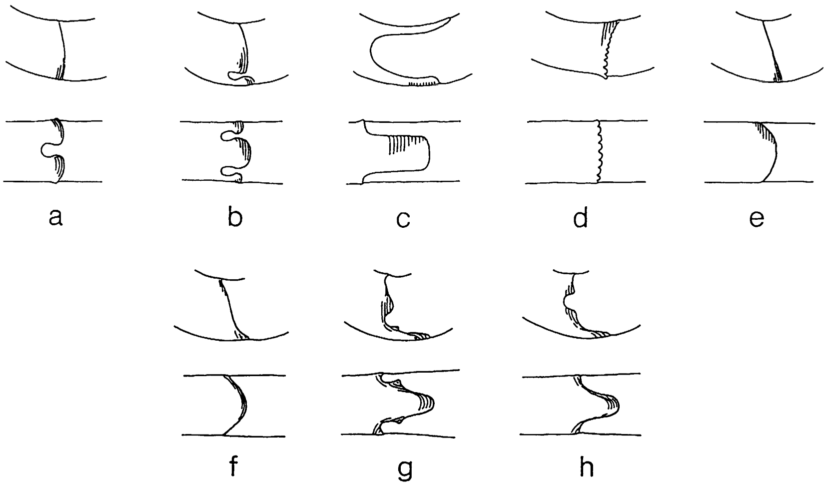


FIGURE 10. Types of megastriae shown in lateral (above) and ventral view (below). The adoral direction is toward the right. Some representative taxa are listed for each type of megastriae: (a) parabolic, *Keyserlingites, Monacanthites* (both Early Triassic); (b) parabolic, *Nordophiceras* (Early Triassic), *Ussurites* (Middle Triassic), *Perisphinctes* (Late Jurassic); (c) concave, *Pleuroacanthites* (Early Jurassic); (d) crinkled and flared, *Lytoceras* (Early Jurassic); (e) straight, *Pachylytoceras* (Middle Jurassic); (f) sigmoidal, *Eotetragonites* (Cretaceous); (g, h) subparabolic, *Anagymnotoceras, Eogymnotoceras, Gymnotoceras, Parafrechites* (all Middle Triassic).

FIGURE 11. Median cross section through a specimen of *Anagaudryceras limatum*, Upper Cretaceous, Hokkaido, AMNH 44374, showing the arrangement of shell layers in a megastria. The old shell segment stops abruptly, and the new shell segment appears beneath it. The arrow indicates the adoral direction. The exterior is toward the top of the photo. When the relief created by a megastria is strong enough, the inner prismatic layer of the new shell segment may not perfectly line the inside surface of the shell wall. Abbreviations: OP, outer prismatic layer; NA, nacreous layer; IP, inner prismatic layer. Scale bar, 10 μm.

outer prismatic and nacreous layers, implying a retreat of the secreting edge of the mantle (see Kulicki, 1979, Pl. 47, Fig. 7; compare to Bucher and Guex, 1990, Fig. 4). In contrast, the inner prismatic layer (= preseptal layer of Guex, 1970) is perfectly continuous, indicating that it was laid down subsequently. Thus, the structural relationships in megastriae appear to be analogous to those of apertural shell repairs (for example, in pelecypods, Tevesz and Carter, 1980, Figs. 6, 7).

Megastriae are associated with particular morphological features and occur more commonly on certain portions of a shell than others. In general, there are more megastriae on juvenile than on mature whorls. In Middle Triassic *Parafrechites meeki*, the juvenile whorls display numerous, variably spaced megastriae (Fig. 12). However, these features are generally absent on the adult body chamber, implying that there were more growth pauses in early than in later ontogeny. In only a few ammonoid groups, e.g., some lytoceratids, did megastriae persist to maturity.

Megastriae are commonly associated with ribs, suggesting a relationship between pauses in secretion and rib formation (see also Checa, 1994). For example, on the juvenile whorls of *Parafrechites meeki*, megastriae occur on the adapical sides of ribs (Fig. 12A). On later whorls, where there are bifurcating ribs, a megastria always occurs on the adapical side of the more adoral rib of the bifurcating pair (Fig. 12C). This megastria cuts across the whorl at the point of bifurcation. The presence of closely spaced megastriae results in composite ribs consisting of a number of juxtaposed elements (Fig. 12D).

In many ammonoids, open spines also are associated with megastriae. For example, in Early Jurassic *Analytoceras articulatum*, megastriae occur in association with hollow ventrolateral spines on the adult body chamber

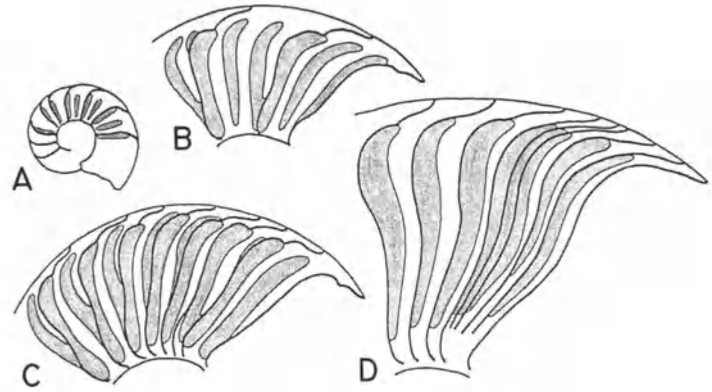
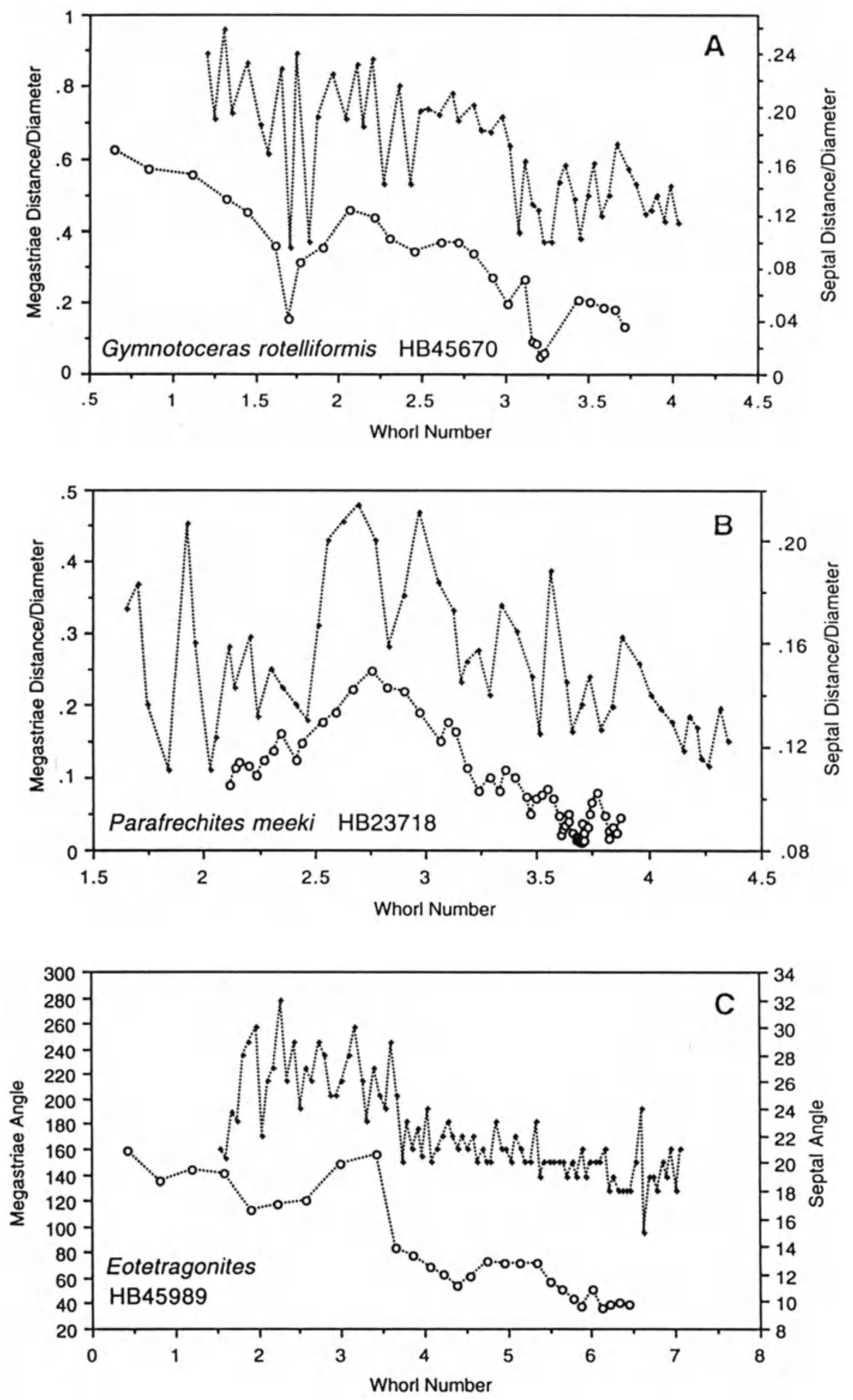


FIGURE 12. The relationship between megastriae and ribs shown diagrammatically in lateral view at successively later ontogenetic stages (A–D) of *Parafrechites meeki*, Middle Triassic, Nevada. The shaded areas represent ribs, the dark lines, megastriae. Coiling is clockwise. (Modified from Bucher and Guex, 1990, Fig. 3.)

(Wähner, 1894). This suggests that secretion of this kind of spine coincided with a pause in forward growth of the apertural margin (see Section 5.3).

In addition to growth pauses, megastriae also imply that some resorption of the shell may have occurred because these features demarcate angular discontinuities that affect growth lines and ribs. In some lytoceratids, megastriae cut sharply and obliquely across roughly parallel ribs at the umbilical margin. In areas of the shell not covered by subsequent whorls, the only possible opportunity for creating this type of discontinuity was during the growth break itself. Similarly, in Middle Triassic *Parafrechites* and *Gymnotoceras*, subparabolic megastriae cut sharply across growth lines, implying that partial resorption occurred, especially along the ventrolateral shoulder and, to a smaller extent, on the flanks (Fig. 10g; Bucher and Guex, 1990, Fig. 2A). There is also evidence of shell resorption in some Jurassic perisphinctids. In *Grossouvria*, for example, parabolic megastriae swing backward along the ventrolateral shoulder cutting across preexisting growth lines to form notches on each side of the venter (Fig. 10b; Arkell *et al.*, 1957, Fig. 140, 1a, b). However, in other perisphinctids such as *Dichotomoceras*?, there is a gradual change in the shape of growth lines that culminates in the formation of a parabolic margin at megastriae (R. Enay, personal communication, 1995). This suggests that the shape of the aperture at these points was the result of normal growth processes rather than secondary resorption.

FIGURE 13. Plots of septal spacing (crosses) and megastriae spacing (open circles) versus whorl number in three ammonoid species. Curves of septal spacing have been translated to the right with respect to those of megastriae spacing to compensate for the known length of the body chamber so that the megastriae and septa that formed at approximately the same time appear near one another. (A) *Gymnotoceras rotelliformis*, Middle Triassic, Nevada, HB 45670. The patterns of septal spacing and megastriae spacing are broadly similar. The ratio of the number of megastriae to that of septa averages approximately 1.5 between whorls 1.5 and 3.25. The distance between septa (septal distance) and the distance between megastriae (megastriae distance) were measured at one-third the whorl height from the venter. The diameter used to calculate each of the ratios on the *y*-axes was measured at a point midway between successive septa or megastriae, depending on the particular ratio. The early whorls of this specimen were not preserved, and hence, the whorl number is an approximation. The septal curve has been translated 0.5 whorls to the right. (B) *Parafrechites meeki*, Middle Triassic, Nevada, HB 23718. Both curves show a peak in spacing between whorls 2.5 and 3.0. The ratio of the number of megastriae to that of septa averages approximately 3.0 for the episode of megastriae crowding at 3.7 whorls. The diameter, septal distance, and megastriae distance are defined as in A. The early whorls of this specimen were also not preserved, and hence, the whorl number is an approximation. The septal curve has been translated 0.6 whorls to the right. (C) *Eotetragonites* sp., Upper Cretaceous, Madagascar, HB 45989. The pattern of septal spacing covaries with that of megastriae spacing. The ratio of the number of megastriae to that of septa equals 0.2 between whorls 1.5 and 3.5. Septal spacing and megastriae spacing are measured in degrees as indicated on the *y*-axes. The number of whorls is counted starting at the primary constriction. The amount of translation of the curve of septal spacing, 230°, was determined graphically so that the patterns of megastriae spacing and septal spacing matched. However, this value is a good approximation of the angular length of the body chamber in this species (see Okamoto, Chapter 8, this volume, Fig. 3 for an estimate of the angular length of the body chamber in a species of the closely related genus *Tetragonites*).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Gymnotoceras rotelliformis HB45670
Megastriae Distance/Diameter
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The pauses in growth associated with megastriae appear to be reflected in septal spacing. We investigated the relationship between the spacing of septa and the spacing of megastriae in specimens of Middle Triassic *Gymnotoceras* and *Parafrechites* and Late Cretaceous *Eotetragonites* (Fig. 13). After the angular length of the body chamber had been taken into account, a marked similarity in the patterns of septal and megastriae spacing within each specimen was observed. Bucher and Guex (1990) also observed a correlation

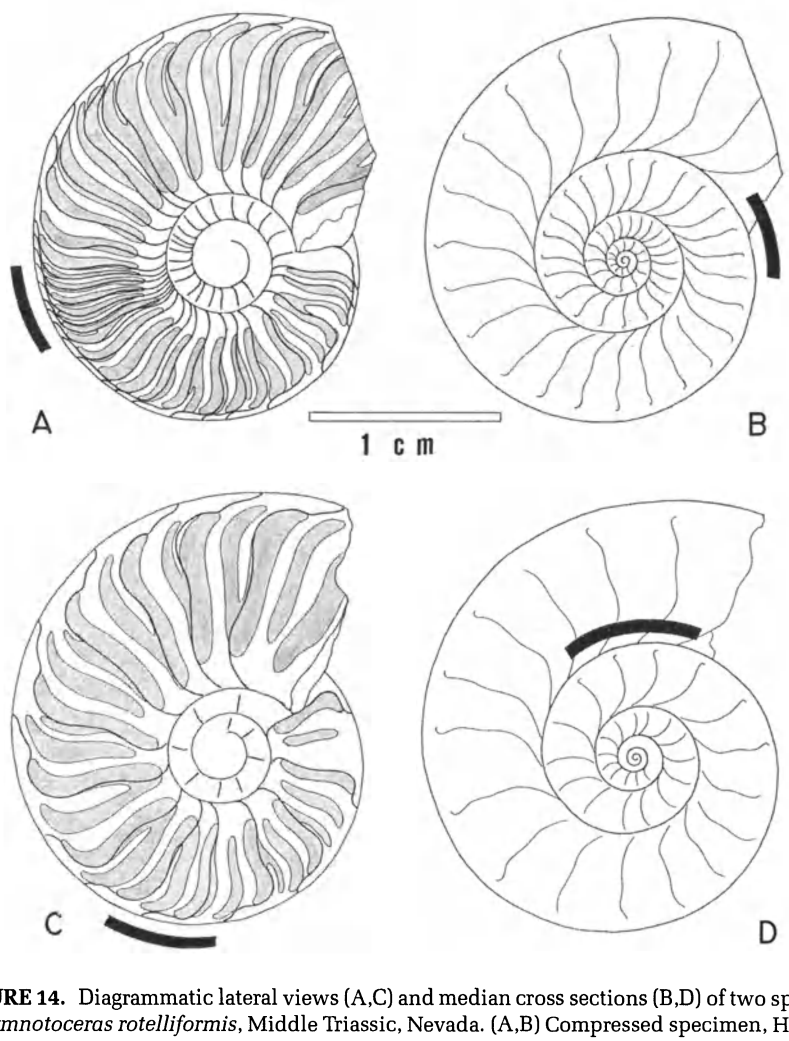

FIGURE 14. Diagrammatic lateral views (A,C) and median cross sections (B,D) of two specimens of *Gymnotoceras rotelliformis*, Middle Triassic, Nevada. (A,B) Compressed specimen, HB 45582. (C,D) Depressed specimen, HB 45663. In lateral view, the shaded areas represent ribs, the dark lines, megastriae. In median cross section, the siphuncle is omitted for simplicity, and only the septa are shown. Megastriae, ribs, and septa are all more closely spaced in the more compressed specimen. The black arcs indicate intervals of closely spaced megastriae (A,C) that correspond in time of formation with intervals of closely spaced septa (B,D) within each specimen. (From Bucher and Guex, 1990, Fig. 6.)

between the spacing of septa and that of megastriae, on the one hand, and the degree of shell compression, on the other hand, among individuals within a single species of *Gymnotoceras*. According to them, septa and megastriae are more closely spaced in more compressed specimens, suggesting that pauses in growth were more numerous, with respect to angular length, in these specimens than in more depressed specimens (Fig. 14).

It has been suggested that, during the pause in growth represented by a megastria, the animal moved forward preparatory to forming a new septum (Tozer, 1991). However, the number of megastriae that corresponded in time of formation with that of a single septum usually does not equal one. For example, the ratio of the number of megastriae to the number of septa that formed at approximately the same time averages 1.5 in *Gymnotoceras rotelliformis* (Fig. 13A), 3.0 in *Parafrechites meeki* (Fig. 13B), and 0.2 in *Eotetragonites* sp. (Fig. 13C). Thus, although the spacing of septa appears to mimic the spacing of megastriae within a specimen, there is clearly no one-to-one correspondence between the number of megastriae and the number of septa. This suggests that translocation to the site of a new septum probably did not coincide with the pause in growth associated with a single megastria.

There are several lines of evidence suggesting that the formation of megastriae was intrinsic in origin and was not the result of injuries or other external factors: (1) the association of megastriae with open spines and ribs, which were themselves presumably intrinsic in origin, (2) the presence of megastriae in some taxa (e.g., berychitids, lytoceratids, and perisphinctids) but not others (e.g., arcestids, paraceratids, and baculitids), (3) consistent changes in the spacing of megastriae through ontogeny, and (4) the correlation between megastriae spacing and the degree of shell compression in certain species. Additional support for an intrinsic origin of megastriae comes from study of a sample of Middle Triassic *Parafrechites meeki* thought to represent a census population (Bucher and Guex, 1990). If megastriae were caused by the environment, and if all the specimens in the sample experienced this same environment, one might expect to observe a similarity in the pattern of megastriae spacing among individuals within any given size class. However, no such similarity appears.

5.5. Pseudosutures

Suture-like lines called pseudosutures occur between sutures and follow the general outline of the sutures (Fig. 15). Pseudosutures have been observed in many ammonoids and have been interpreted as imprints of the adapical end of the soft body (Zaborski, 1986; Hewitt *et al.*, 1991; Weitschat and Bandel, 1991, 1992; Westermann, 1992; Landman *et al.*, 1993; Lominadzé *et al.*, 1993; Chapter 6, this volume). The spacing of pseudosutures provides some information on variations in the rate at which the body moved forward, provided that these features formed at equal intervals of time (see Section 7.1 for actual

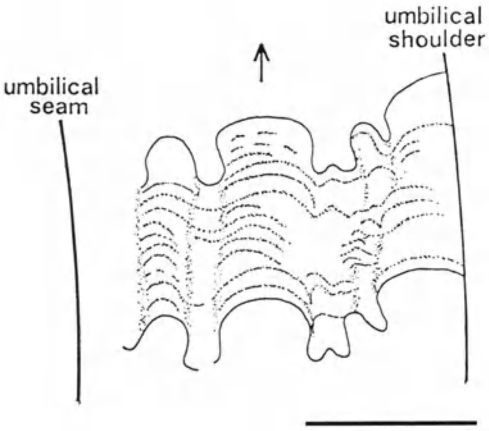

FIGURE 15. Specimen of *Paravascoceras cauvini*, Upper Cretaceous, Nigeria, BM(NH) C.90409, showing approximately 15 pseudosutures between two successive sutures. The arrow indicates the adoral direction. (After Zaborski, 1986, Text-Fig. 4.)

estimates of the periodicity of pseudosutures). For example, Hewitt *et al.* (1991) observed that pseudosutures in Late Cretaceous vascoceratids are evenly spaced along the venter, suggesting a constant rate of translocation. In contrast, Lominadzé *et al.* (1993) noted that pseudosutures in phylloceratids and lytoceratids are more closely spaced near the actual septum, indicating a decrease in the rate of translocation at that point. However, both of these inferences rely on the untested assumption that the formation of pseudosutures was periodic.

5.6. Episodic Growth

Many of the fluctuations in the rate of growth described above are related to secretion of portions of a whorl as distinct units. We refer to this type of growth as episodic. Arkell *et al.* (1957) used the term “segmental growth” to describe this same phenomenon. (Note, however, that this term is also used in ontogenetic studies of arthropods, but in a completely different sense.) It is important to bear in mind that such whorl “segments” did not necessarily form with any particular temporal regularity. Secretion of any one portion of a whorl may have been rapid and may have been followed by a long interval of no apertural growth except perhaps for a thickening of the apertural lip.

One example in which episodic growth may have occurred was in rib formation. On the basis of a study of growth lines and ribs in Jurassic and Cretaceous ammonoids, Checa and Westermann (1989, Fig. 1) postulated that, in the formation of branching ribs, secretion proceeded by adding alternately wedge-shaped and parallel-sided whorl segments. Checa (1994) also analyzed the microscopic sculptural features on the shell surfaces of these ammonoids and, on the basis of these new data, argued that the formation of an entire rib may have occurred during a single secretory event. According to him, the free edge of the mantle initially extended completely beyond the apertural margin to the position of a new rib while, at the same time, secreting a periostracum. Subsequently, the mantle retracted, producing a rib-like fold in the periostracal layer (which was presumably attached to the mantle). Calcification of this fold occurred just before or at the time of initiation of a new episode of mantle extension. This reconstruction is supported by the fact that ribs are sometimes bound, at least on one side, by megastriae, indicating pauses in secretion.

Constrictions, along with their accompanying varices, also mark off distinct portions of a whorl, implying "segmental" or episodic growth (Arkell *et al.*, 1957). The discordant nature of constrictions, noted earlier, as well as the fact that megastriae occur on the adoral sides of some constrictions (Maeda, 1993; Checa, 1994) are consistent with this notion. Seilacher and Gunji (1993) interpreted the process of shell secretion leading to the formation of constrictions as representing "iterative countdown cycles" superimposed on the overall growth pattern. In addition, Checa (1994) proposed that the whorl "segments" bounded by constrictions may have formed as single units, implying an episodic pattern of shell formation comparable to that in many gastropods (Mackenzie, 1960; Linsley and Javidpour, 1980; Vermeij, 1993). However, the relative time of formation of the whorl "segment" between constrictions versus that of the constriction itself is unknown. This relationship may have been similar to that in many gastropods, in which the time interval between the formation of varices is much shorter than the time of formation of the varix itself (Seilacher and Gunji, 1993; Vermeij, 1993).

This process of "segmental growth" may have necessitated occasional readjustments in the shape of the shell. These readjustments seem to have occurred at the sites of constrictions and megastriae. As we noted earlier, these features demarcate angular discontinuities that affect growth lines and ribs, thereby implying changes in the trajectory of shell secretion. Such readjustments served to maintain the shape of the shell and the orientation of the apertural margin throughout ontogeny (Seilacher and Gunji, 1993, Fig. 2; Checa, 1994). In some taxa, these readjustments in shell shape were pronounced, resulting in a polygonal outline (e.g., Early Jurassic *Lytoceras cornucopiae* and Late Devonian *Wocklumeria sphaeroides*). The magnitude of the readjustment appears to have covaried with the angular distance between constrictions (Checa, 1994) or megastriae.

The pattern of growth in heteromorph ammonoids was similar, in some respects, to "segmental growth." In these forms, there were marked changes in the shape of the shell during ontogeny. For example, Okamoto (1993; Chapter 8, this volume) has described changeovers from one mode of coiling to another in Late Cretaceous *Nipponites* and related genera. Seilacher and Gunji (1993) speculated that these changeovers in mode of coiling occurred rapidly and were followed by long intervals of slower growth. They described this pattern as consisting of a series of morphogenetic countdowns leading to iterative changes in shell shape.

6. Environmental Control on the Rate of Growth

Many environmental factors affect the rate of growth of marine organisms, including temperature, food availability, light intensity, pressure, dissolved oxygen, day length, and the abundance and kind of predators. As an introduction to this section, we present several examples of the effects of the environment on the rate of growth of modern cephalopods.

Temperature is one of the main factors affecting the rate of growth of cephalopods. For example, specimens of *S. officinalis* from the English Channel experience a lower temperature during the winter months when they migrate to an offshore habitat (Boletzky, 1983). This decrease in temperature is reflected in a deceleration in the rate of growth, a reduction in septal spacing, and an increase in the time of chamber formation (Hewitt and Stait, 1988). Food is another important factor affecting growth. Wiedmann and Boletzky (1982) demonstrated that lack of food during the life cycle of *S. officinalis* results in lower rates of growth and closer septal spacing. Indeed, temperature and food are interrelated because feeding rate is usually a function of temperature (Boletzky, 1983; Mangold, 1983; Hewitt and Stait, 1988).

The developmental program in many cephalopods is extremely plastic and can be modified easily by the environment, leading to variation in the age and size at maturity within a single species (Mangold, 1987). For example, certain environmental conditions (e.g., undernutrition, short day length) tend to promote early maturation at a small size whereas others (e.g., long day length, high light intensity) tend to promote late maturation at a large size (Mangold, 1987, table, p. 189). The outcome also depends on when during the life cycle the particular conditions prevail, that is, before or after the gonads attain the size at which they are receptive to the growth hormone (Richard, 1970; Mesnil, 1977). As a result, individuals within the same population that experience different environmental conditions (perhaps during migrations) at different points in their ontogeny mature at different ages and sizes (Wells and Wells, 1977; Zuev, 1975). One example of this phenomenon in ectocochliate cephalopods is shown by a study of *Nautilus* in an aquarium. In this study, several specimens achieved maturity at one-half their normal size in approximately 3 years as compared to an estimated age at maturity of 10 years in nature (Ward, 1985). This case of precocious maturation probably resulted from a favorable combination of low water pressure (because of the shallowness of the aquarium) and abundant food (provided by the aquarist).

Many of these same environmental factors (temperature, nutrition) may also have influenced the rate of growth of ammonoids. Ammonoids, in comparison with *Nautilus*, show much more variation in septal spacing. Some of this variation has been attributed to seasonality, with episodes of closer septal spacing interpreted as slowdowns in growth associated with colder temperatures, etc. during the winter (Westermann, 1971; Zakharov, 1977; Kulicki, 1974). Other variations in septal spacing may have been caused by changes in habitat during ontogeny. Hewitt (Chapter 10, this volume) and Westermann (Chapter 16, this volume) have argued that animals at different growth stages may have lived in different environments. In addition, some species may have undergone seasonal onshore–offshore migrations (Morton, 1988) as well as daily vertical migrations (Westermann, 1990). These changes in habitat may also have affected the rate of growth and been reflected in septal spacing.

Injuries to the individual animal clearly reduced the rate of growth. Injuries in ammonoids are identified by scars on the shell surface and, sometimes, in addition, by a reduction in septal spacing (septal approximation) at an angular distance of approximately one body chamber length adapical of the scar (Chapter 15, this volume; Lehmann, 1966; Bayer, 1977; Landman and Waage, 1986). Experimental observations on *Nautilus* help explain why septal approximation is associated with an injury. During the repair of an injury in *Nautilus*, the rate of cameral liquid removal from the most recently formed chamber decreases, or this process stops altogether, effectively allowing liquid to flow back into the chamber (Ward and Greenwald, 1982). As a result, there is a delay in the formation of the next septum, which is eventually secreted at a reduced distance from the preceding septum (Ward, 1985). The resultant septal approximation appears to be a result of (1) the cessation of forward movement of the soft body coincident with the injury, (2) the interruption in the normal cycle of chamber formation, and (3) the need for additional weight to counteract the effect of positive buoyancy resulting from the breakage of shell material at the apertural margin.

Hydrostatic pressure, which covaries with water depth, must also have affected ammonoid growth rates. In *Nautilus*, there is a strong negative correlation between the rate of cameral liquid removal, thus the rate of growth, and hydrostatic pressure (Ward, 1982). We can therefore infer that ammonoids that lived in deep water grew more slowly than those that lived in shallow water. In addition, many deep-water ammonoids (some lytoceratids, phylloceratids, and desmoceratids) show thicker septa and narrower but thicker-walled siphuncles than do many shallow-water forms, implying additional differences in rates of cameral liquid removal and septal secretion and, therefore, rate of growth (Doguzhaeva, 1988; Westermann, 1990; Tanabe *et al.*, 1993). Moreover, in some deep-water ammonoids, the development of long septal necks further decreased the ratio of siphuncular surface area to chamber volume through ontogeny, thus depressing even more the rate of cameral liquid removal (Tanabe *et al.*, 1993).

Several studies have also suggested that environmental factors may have controlled the size at maturity within an ammonoid species. Matyja (1986) reported that in some Jurassic ammonoids there are three adult morphs, which are distinguished primarily on the basis of their size. He argued that the size at which maturity occurred depended on the particular environmental conditions. In a study of Early Jurassic liparoceratids from England, Hewitt and Hurst (1977) documented changes in the size of adults over geological time. They attributed these changes to fluctuations in climatic conditions, which, according to them, also affected feeding rates. Elmi and Benshili (1987) reported differences in adult size among populations of a single species of Early Jurassic *Hildoceras* from Northwest Europe and North Africa. They related these differences in size to differences in environmental conditions, namely water depth, oxygen content, and abundance of nutrients. Mignot *et al.* (1993) further suggested that the small adult size of this species in some areas was an adaptive response (paedomorphism) to a less than optimal environment. Mancini (1978) suggested this same interpretation to explain a fauna of dwarfed ammonoids from the Lower Cretaceous of Texas. In contrast, Stevens (1988), in analogy with what we know about giant squids, speculated that gigantism in ammonoids was related to life in cold deep-water environments. Such animals may have grown slowly but may have lived for a long period of time. Along these same lines, Kemper and Wiedenroth (1987) observed that in the Lower Cretaceous of Northwest Germany, ammonoids that lived in the Boreal Realm tended to be larger than those that lived in the warmer water of the Tethyan Realm. (See also Landman and Waage, 1993, p. 230, for an additional example of variation in adult size within a single species, possibly related to differences in the environment.)

Environmental factors may also have affected the shape of the ammonoid shell, notably how robust it was (Chapter 10, this volume). Such variation in shape as a result of environmental conditions is common in gastropods (Vermeij, 1980, 1993). In ammonoids, this may have produced a wide range of intraspecific variation (Kennedy and Cobban, 1976; Callomon, 1985; Landman and Waage, 1993). However, in some instances at least, the degree of whorl compression appears to have been controlled by selection for hydrodynamic efficiency (Jacobs *et al.*, 1994; Chapter 7, this volume).

If ammonoids showed as much developmental plasticity in response to environmental conditions as do modern cephalopods, this would explain the high incidence of heterochrony in ammonoid evolution (Landman, 1988). Heterochrony depends on the dissociablility of three processes: size increase, morphological differentiation, and maturation (Gould, 1977). If the environment affected this dissociability in ammonoids, it could have produced an acceleration or retardation in the program of growth. Although the literature on heterochrony in ammonoids is enormous, we present one example that bears on the question of the time of maturation. There are a number of scaphitid species in the Upper Cretaceous of North America that develop all of the morphological features characteristic of maturity at a diameter of only approximately 10 mm (Cobban, 1951). Landman (1989) interpreted these forms as progenetic offshoots of larger cooccurring species. It is unclear if the environment was responsible for this acceleration in maturation. However, what is interesting about this study is that the formation of the mature body chamber in these progenetic species began exactly at the end of the neanic stage. This may indicate the earliest point in ontogeny when maturation could have occurred with all of the ensuing implications about the time of initiation of gonad development.

7. Determination of the Actual Rate of Growth

Now that we have described the overall growth curve and the fluctuations in it caused by internal and external factors, we are ready to introduce actual numbers into our discussion. There are several ways to determine the actual rate of ammonoid growth, each of which is described below. Following the description of these methods, we synthesize the data and provide an estimate of the age at maturity of various taxa (Table I).

7.1. Assumptions about the Periodicity of Shell Secretion

It has commonly been assumed that ammonoid lirae, ribs, and septa formed with a constant periodicity (see general discussions in Checa, 1987, and Dommergues, 1988). Specific estimates of the time of septal formation range from 1 day to 1 month. For example, Ivanov (1971) suggested that ammonoid septa formed every lunar month. (See Kahn and Pompea, 1978, for a similar assumption about the time of septal formation in nautilids.) Doguzhaeva (1982) hypothesized that ammonoid septa formed with a fortnightly periodicity, yielding an estimated age at maturity of 2.5 to 4.5 years, depending on the number of septa present (Table I). Weitschat and Bandel (1991) suggested that septa formed every 1 to 2 days, similar to that in *Sepia*, and estimated an age at maturity in ammonoids of 1 to 2 years (Table I).

The time of formation of other morphological features has also generally been assumed to have been constant. Doguzhaeva (1982) suggested that in some ammonoids the formation of lirae occurred daily. Hirano (1981) hypothesized that constrictions in Late Cretaceous *Gaudryceras denseplicatum* formed every year and calculated an age at maturity of 20 years for this species (Table I). Hewitt *et al.* (1991) assumed that pseudosutures in Late Cretaceous *Vascoceras* formed diurnally or semidiurnally and estimated an age at maturity of 6 years for species within this genus (Table I; see also Seilacher, 1988). Although they did not postulate a specific time of pseudosuture formation, Lominadzé *et al.* (1993) nevertheless argued that, on the basis of the number of pseudosutures per chamber, the time of chamber formation was longer in phylloceratids and lytoceratids than in other ammonoids.

All of these assumptions about periodicity of shell secretion are unconfirmed. As discussed earlier (Section 4), the time of septal formation in ammonoids probably increased exponentially through most of ontogeny. Therefore, it is not possible to multiply the number of septa by some constant

Table I. Estimate of Age at Maturity of Various Ammonoids Based on the Methods Described in the Text

Method	Source	Taxon	Adult size/number of whorls[a]	Age at maturity (years)
Assumption of periodicity (septa)	Doguzhaeva (1982)	Ammonoidea	6 whorls	2.5–3.6
			7 whorls	3.4–3.7
			8 whorls	3.8–4.5
Assumption of periodicity (septa)	Weitschat and Bandel (1991)	Ammonoidea	—	1–2
Assumption of periodicity (constrictions)	Hirano (1981)	*Gaudryceras denseplicatum*	140 mm/7 whorls	20
Assumption of periodicity (pseudosutures)	Hewitt *et al.* (1991)	*Vascoceras* spp.	100 mm	6
Seasonality (shell volume)	Trueman (1941)	*Dactylioceras commune*	50 mm	4
Seasonality (rate of whorl expansion)	Westermann (1971)	*Hammatoceras insigne*	70 mm/4.5 whorls[b]	4–6
		Paracravenoceras ozarkense	25 mm/8.5 whorls[b]	4–6
Seasonality (septal spacing)	Westermann (1971)	*Leioceras* spp.	50 mm	4–6
		Ludwigia spp.	70 mm	4–6
		Sonninia spp.	100 mm	4–6
Seasonality (septal spacing)	Zakharov (1977)	*Pinacoceras* aff. *regiforme*	40 mm[b]	7
Seasonality (septal spacing)	Kulicki (1974)	*Quenstedtoceras* spp.	50 mm/5.5 whorls (♂)	2
			130 mm/7.5 whorls (♀)	3
Seasonality (jaw increments)	Hewitt *et al.* (1993)	Aspidoceratids	300 mm	5–6
		Oppeliids (♂,♀)	50 mm	1
Seasonality (oxygen isotopes)	Jordan and Stahl (1970)	*Staufenia staufensis*	100 mm[b]	4[c]
		Quenstedtoceras sp.	80 mm[b]	5[c]
Size classes	Trueman (1941)	*Promicroceras marstonense*	25 mm	5
Size classes	Landman and Klofak (in prep.)	*Hoploscaphites nicolletii* (♂)	50 mm	6
Size classes	This chapter	*Schreyerites* n. sp.	55 mm/6 whorls	6
Epizoans (*Serpula*)	Schindewolf (1934)	*Arietites* cf. *kridion*	40 mm[b]	3.5[c]
Epizoans (*Nanogyra nana*)	Hirano (1981)	*Leioceras opalinum*	60 mm	1–7.5[c]
Epizoans (*Liostrea*)	Merkt (1966)	*Euagassiceras* sp.	30 mm[b]	3–4.5[c]
Epizoans (*Placunopsis ostracina*)	Meischner (1968)	*Ceratites semipartitus*	370 mm[b]	7[c]

[a] These values represent gross estimates based on many specimens unless the author provided size data for a single specimen.

[b] Data based on a single specimen.

[c] The age at maturity is calculated on the basis of the time of formation of a certain number of whorls at the end of ontogeny, as cited in this chapter, and the observed rate of whorl expansion (Raup's *W*), using equation 10 in the Appendix. This method assumes a constant rate of growth of the venter at the apertural margin. Because the rate of growth is not constant throughout ontogeny and, notably, decreases at maturity, this calculation yields only an estimate. Values are approximated to the nearest half-year.

value to obtain an absolute age at maturity (Landman, 1983, 1986). Similarly, there is no evidence to suggest that the time interval between the formation of successive lirae, ribs, or constrictions was constant during ontogeny, especially if, as supposed in some ammonoids, growth at the apertural margin was episodic. The spacing of such features on the shell was probably controlled by the growth program, although it may have been subject to some environmental influence.

On the basis of a study of the spacing of lirae and septa in various ammonoids, Doguzhaeva (1982) documented that in some ammonoids a nearly constant number of lirae on the outer shell corresponded in time of formation with that of a chamber at the back of the body. However, this does not imply a constant period of chamber formation. If anything, the time interval between the formation of successive lirae probably increased during ontogeny, implying a concomitant increase in the time of chamber formation.

7.2. Detection of Seasonal Signals in Morphology

There have been several attempts to identify seasonal signals in the morphology of ammonoid shells and jaws. These studies presume that the environment was seasonal, that the rate of ammonoid growth was fast enough to record seasonal changes, and that one can differentiate seasonal signals from intrinsic fluctuations in the rate of growth.

Trueman (1941, Fig. 5) noted ontogenetic changes in shell volume in several specimens of Early Jurassic *Dactylioceras commune* at shell diameters of 12–15 mm, 25 mm, and 40–50 mm. He speculated that these changes may have been seasonal in origin, suggesting an age at maturity of approximately 4 years for this species (Table I). Westermann (1971) observed ontogenetic fluctuations in the rate of whorl expansion in a specimen of Early Jurassic *Hammatoceras insigne* and in a specimen of Pennsylvanian *Paracravenoceras ozarkense* (illustrated in Raup and Chamberlain, 1967, Fig. 2, and Raup, 1967, Fig. 10, respectively). He also interpreted these fluctuations as seasonal, suggesting an age at maturity of 4 to 6 years in these ammonoids (Table I).

Studies of septal spacing have also provided evidence of seasonality. Westermann (1971) identified four to six possible annual cycles in graphs of septal spacing in several species of Middle Jurassic *Leioceras, Ludwigia*, and *Sonninia* (Table I) (see Rieber, 1963, Figs. 9, 10, and Oechsle, 1958, Fig. 7, for illustrations of the original graphs). Zakharov (1977, Fig. 3) recognized six episodes of reduced septal spacing in a specimen of Late Triassic *Pinacoceras* aff. *regiforme* with about 80 septa. He therefore estimated an age at maturity of 7 years in this species (Table I). Kulicki (1974, Fig. 8) investigated the pattern of septal spacing in several specimens of Middle Jurassic *Quenstedtoceras*. He (p. 218) argued that "the termination of the last sexual cycle," as indicated by a decrease in septal spacing at the end of ontogeny, occurred in the autumn or winter. On the basis of this assumption, he concluded that microconchs (males?) reached maturity in 2 years, and macroconchs (females?) in 3 years (Table I).

In a study of growth increments on two specimens of *Laevaptychus*, here interpreted as lower jaws, Hewitt *et al.* (1993) hypothesized that fluctuations in increment width reflected seasonal changes. As we have already observed, a plot of increment width versus increment number in these specimens shows an increase in width in early ontogeny followed by a decrease in later ontogeny (Fig. 13D). However, superimposed on this overall ontogenetic pattern are several episodes of reduced increment width, which Hewitt *et al.* interpreted as marking winter events (indicated by arrows on Fig. 13D). There is some uncertainty as to the exact number of such events, although the best estimate seems to be five or six. (One complication is that the episode of reduced increment width at the end of ontogeny may simply be related to a deceleration in the rate of growth associated with maturity). Hewitt *et al.* (1993) concluded that the ammonoids in which these jaws once occurred, probably Late Jurassic and Early Cretaceous aspidoceratids, reached maturity in 5 to 6 years.

On the basis of this figure, Hewitt *et al.* (1993) also calculated the rate at which these growth increments formed. Using this value, they determined the age of several specimens of *Lamellaptychus*, here also interpreted as lower jaws, for which they had already counted the number of growth increments (Fig. 13C). They estimated that the ammonoids in which these jaws once occurred, most probably Late Jurassic oppeliids, attained maturity in approximately 1 year.

7.3. Detection of Seasonal Signals in Isotopic Data

A number of studies have investigated the record of oxygen isotopes in ammonoid shells to learn about the rate of growth. This method assumes that the growing shell recorded fluctuations in water temperature that were related to seasonal changes in the environment. However, the isotopic composition of biogenic $CaCO_3$ depends on a number of factors other than the temperature during secretion, including the isotopic composition of the ambient water (Grossman and Ku, 1986; Geary *et al.*, 1992), species-specific effects related to the growth of the particular organism (McConnaughey, 1989a,b), and the state of preservation of the sampled shell material (Stahl and Jordan, 1969; Jordan and Stahl, 1970; Buchart and Weiner, 1981). These factors influence the extent to which the isotopic data faithfully reproduce a seasonal temperature signal.

Oxygen isotopic analyses have been performed on several well-preserved specimens of *Baculites* from the Upper Cretaceous of North America (Tourtelot and Rye, 1969; Forester *et al.*, 1977; Rye and Sommer, 1980; Whittaker *et al.*, 1987). Samples taken along the shell length revealed cyclic fluctuations

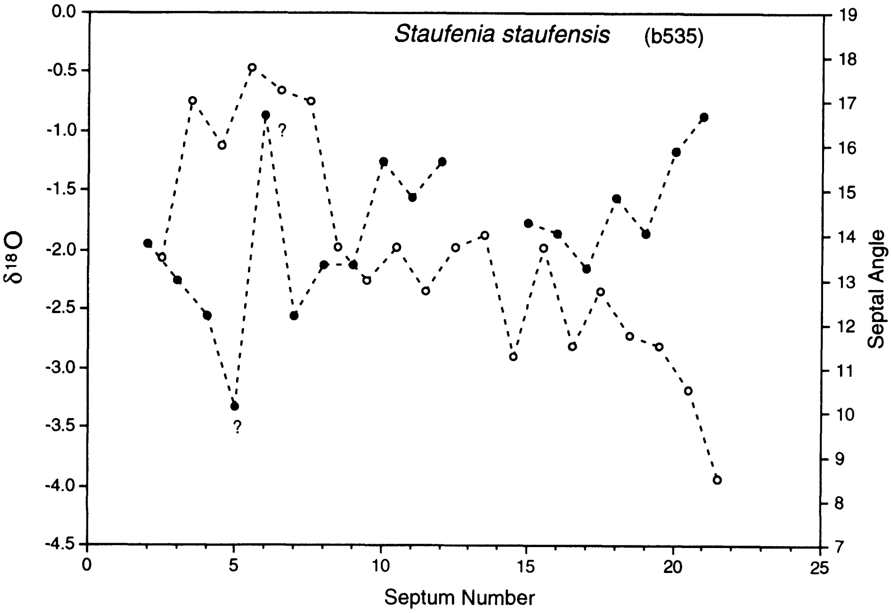

FIGURE 16. Plots of $\delta^{18}O$ (in parts per thousand) of septa (filled circles) and of the angular spacing between septa (in degrees; open circles) versus septum number in a mature specimen of Middle Jurassic *Staufenia staufensis* from Germany. (Values of $\delta^{18}O$ are from Jordan and Stahl, 1970, p. 48; values of the septal angle were measured from their Fig. 5A; the specimen is referred to there as b535.) These authors questioned the $\delta^{18}O$ values of septa 5 and 6 because of the small size of the samples; they did not analyze septa 1, 13, and 14 for the same reason. The angle between two successive septa is plotted at the midpoint between their respective septum numbers. Septa are numbered starting from the last, most recently formed septum (1).

in $\delta^{18}O$, but there are too few data points to permit an interpretation in terms of rate of growth.

The most complete isotopic data set for determination of the rate of growth of ammonoids appears in a study by Jordan and Stahl (1970). These authors measured the oxygen isotopic composition of the seven most recently formed septa of an adult specimen of Middle Jurassic *Quenstedtoceras* sp. and the 21 most recently formed septa of an adult specimen of Middle Jurassic *Staufenia staufensis*. These authors interpreted the isotopic values in both specimens as reflecting seasonal temperature signals. Based on this interpretation, they inferred that the specimen of *Quenstedtoceras* sp. formed five septa (0.3 whorls) in 1 year, that the specimen of *S. staufensis* formed 17 septa (0.6 whorls) in 1.5 years, and that septa formed at a constant, albeit different, periodicity in each specimen (Table I).

If one accepts that the cyclic pattern in the *S. staufensis* data is seasonal in origin, it is interesting to investigate the relationship between septal spacing and the values of $\delta^{18}O$. The spacing between septa shows a slight decrease at the end of ontogeny (Jordan and Stahl, 1970, Fig. 5A), which is associated with an increase in $\delta^{18}O$ (Fig. 16). If septal spacing provides a measure of variation in rate of growth, this negative correlation between septal spacing and $\delta^{18}O$ suggests that a decrease in the rate of growth corresponded to a decrease in temperature, which is consistent with the temperature–growth rate relationship observed in *Sepia* (see Boletzky, 1983). However, the decline in septal spacing in *S. staufensis* corresponds to the attainment of maturity and may not be related to the environment.

There is, however, some uncertainty whether the isotopic data record a seasonal signal. Theoretically, as long as the time of septal formation is rapid, that is, considerably shorter than a year, the isotopic composition of a septum will accurately reflect the temperature at a discrete point in time. As the time of septal formation becomes longer, however, the isotopic composition of a septum will reflect a temperature value that is averaged over a longer and longer time interval (see Section 7.6). As a result, the isotopic pattern will represent a distorted version of the original signal (Fig. 17; Landman, 1987). This may apply to the isotopic pattern in *S. staufensis* because the data were derived from septa in the submature to mature stages of ontogeny when the

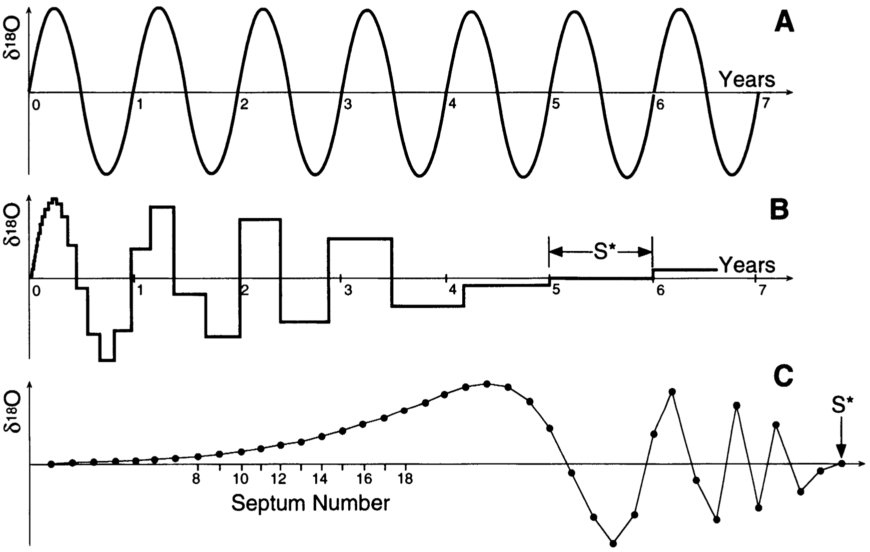

FIGURE 17. Pattern produced by nonperiodic sampling of a seasonal signal of $\delta^{18}O$. (A) Idealized seasonal signal of $\delta^{18}O$ shown over time (years). (B) Distortion of the original signal resulting from increasingly longer intervals of septal formation; same axes as in A. Each horizontal step represents the average value of the signal during the time of formation of a single septum. In this simulation, we assumed 41 septa and an exponential increase in the time of septal formation. Only a single septum (S^*) is formed during the sixth year. (C) Plot of $\delta^{18}O$ versus septum number. The signal is dilated for rapidly formed septa (left side) and contracted for slowly formed septa (right side). The value of $\delta^{18}O$ for any particular septum is the same as its value plotted in B.

time of septal formation was relatively long. If this is the case, the isotopic pattern in this specimen does not faithfully record a seasonal signal and is much more difficult to interpret in terms of time.

Another explanation for the pattern of $\delta^{18}O$ in *S. staufensis* is that it reflects some sort of migrational behavior (Kennedy and Cobban, 1976). It is well established that the $\delta^{18}O$ values of *Nautilus* septa record a change in temperature after hatching, reflecting a migration to colder, deeper water at this point (Oba *et al.*, 1992; Landman et al., 1994). If the isotopic pattern in *S. staufensis* results from migration, there is little hope of deriving any information from it about rate of growth, unless the migrations themselves corresponded to seasons.

7.4. Size Classes

The use of size classes to determine the rate of growth of ammonoids is possible if the particular ammonoid species bred (and spawned) at a definite time of the year and if this periodicity resulted in distinct age classes or cohorts (Rounsefell and Everhart, 1953). In a census population, as represented in the fossil record by a single mass-mortality event (Deevey, 1947; Fagerstrom, 1964; Hutchinson, 1978; Brett and Seilacher, 1991; Kidwell and Bosence, 1991), such behavior ideally produces a polymodal size–frequency histogram in which the succession of modes corresponds to the succession of year classes (see, for example, Boucot, 1953; Sheldon, 1965; Speden, 1970; Surlyk, 1972; Richards and Bambach, 1975).

Trueman (1941, p. 367) identified size classes in a sample of Early Jurassic *Promicroceras marstonense* from England. These size classes ranged in diameter from 1.5 mm (ammonitellas) to 25 mm (adults). If these size classes represented the young of five successive annual breeding seasons, then this species reached maturity in 5 years (Table I). Trueman (1941, p. 367) also identified size classes in a sample of Early Jurassic *Arnioceras* sp. from England, but the largest individuals were only 7 mm in shell diameter, which precluded an estimate of the age at maturity.

We have obtained preliminary results from analysis of samples of *Hoploscaphites nicolletii* from the Upper Cretaceous of South Dakota (Landman and Klofak, in prep.). Juveniles and adults of this species are sometimes preserved together in concretions, which have been interpreted as resulting from mass mortality events followed by rapid burial (Waage, 1968; Landman and Waage, 1993). We measured the shell diameters of all the specimens in each of three concretions, totaling more than 1000 specimens, and identified what appear to be the same six size classes in each concretion, ranging in shell diameter from 5 mm (neanoconchs) to 50 mm (adults). If it had an annual breeding cycle, this species may therefore have reached maturity in 6 years (Table I). A comparable number of size classes also have been observed in a study of Middle Triassic *Schreyerites* n. sp. from the Fossil Hill Formation of Nevada

(Table I). This sample consisted of several hundred individuals and probably represented a census population (H. Bucher, unpublished data).

These size-class studies clearly rely on a number of assumptions. Breeding (and spawning) is assumed to have been periodic, usually annual, and the duration of the breeding (and spawning) season is assumed to have been relatively short. In present-day cephalopods, however, the period of spawning is variable, ranging from seasonal to year-round, depending on the species and its environment (Mangold, 1987, Table 9.7). In addition, these studies assume that all ontogenetic stages were present in the population sample, although it is possible that animals at different ontogenetic stages lived in different environments (Chapter 16, this volume). Given these and other assumptions, it is probably best to regard age estimates from these studies as approximations.

7.5. Epizoans

The rate of ammonoid growth can also be estimated by studying epizoans that grew on the shell of an ammonoid while the ammonoid was still alive. This method depends on working out the relationship between the rate of growth of the epizoan and that of the ammonoid. In general, we assume that the rate of growth of the epizoan species was identical to that of the same species today, or of a closely related living form if the epizoan species is extinct. If performed properly, this method can provide reliable estimates of the rate of ammonoid growth.

Several examples have been described of Early Jurassic ammonoids encrusted by serpulids (Lange, 1932; Schindewolf, 1934; Merkt, 1966; Seilacher, 1982). The serpulids grew along the venter of the ammonoid, supposedly in synchronism with the ammonoid. To the extent that this was true, one can calculate the rate of growth of the ammonoid on the basis of the growth rate of the serpulid. Schindewolf (1934) used this approach to estimate the time of formation of the last whorl of a small adult specimen of *Arietites* encrusted by a serpulid. On the basis of the rate of growth of several species of modern serpulids, he calculated a range in the time of formation of this whorl from 0.5 to 3.0 years. We favor the midway figure of 1.5 years because this is based on the rate of growth of the modern species of *Serpula* that is most closely related to the fossil form (Table I).

Ammonoids encrusted by bivalves provide additional evidence of the rate of ammonoid growth. Hirano (1981) described a specimen of Middle Jurassic *Leioceras opalinum* encrusted by the oyster *Nanogyra nana*. On the basis of the age of the oyster and where it settled relative to the apertural margin of the ammonoid, he estimated that the last whorl of this ammonoid formed in 0.5 to 4.0 years (Table I). Merkt (1966) described an adult specimen of Early Jurassic *Euagassiceras* sp. encrusted by the oyster *Liostrea* sp. He argued that in the last 2 to 3 years of the oyster's life it attained a size large enough to affect the formation of the last 1.5 whorls of the ammonoid, as indicated by a marked whorl asymmetry. This suggests that these 1.5 whorls formed in 2 to 3 years (Table I).

Meischner (1968) described a complex case of encrustation of an adult specimen of Middle Triassic *Ceratites semipartitus* by the bivalve *Placunopsis ostracina*. The bivalves occur on approximately the last two-thirds of the final whorl. Meischner hypothesized that the bivalves represented six annual spatfalls on the basis of their orientation, size, and distribution on the ammonoid shell and the probable orientation of the ammonoid during life. According to this author, four of the spatfalls settled on the ammonoid while it was still alive, implying that the last two-thirds of the final whorl formed in about 3 years (Table I). The other two spatfalls settled after the ammonoid died, suggesting that this individual did not live more than 1 year after reaching maturity.

Seilacher (1960) also presented an estimate of the number of years between the attainment of maturity and death in an adult specimen of Late Cretaceous *Buchiceras bilobatum* encrusted by *Ostrea* sp. The orientation and distribution of the oysters suggest that they may have grown after the ammonoid was mature but before its death (but see Heptonstall, 1970, and Westermann, 1971, for another interpretation). On the basis of the age of the oysters, this specimen may have lived 1/2 to 3 years after reaching maturity.

7.6. Estimates of the Age at Maturity

Estimates of the age at maturity of various ammonoids, derived from the methods discussed above, are presented in Table I (see Chapter 11, this volume, for the duration of the embryonic stage). Most of the species listed are Mesozoic except for *Paracravenoceras ozarkense*, which is Pennsylvanian. In addition, most of the species described lived in shallow water, with the possible exception of the aspidoceratids and *Gaudryceras denseplicatum*. The estimates of the age at maturity vary in their reliability, depending on the method used. The most reliable estimates are probably those derived from studies of epizoans. The least reliable estimates are probably those derived from studies assuming periodic shell secretion because this method lacks an independent means of determining time.

Many of these studies provide an estimate of the time of formation of only one or two whorls at the end of ontogeny. In order to calculate the age at maturity in these cases, a constant rate of growth of the venter at the apertural margin throughout ontogeny was assumed. We used the value of the time of formation of the portion of the whorl given in a particular study and, on the basis of the whorl expansion rate of the shell (Raup's W, measured from photos or actual specimens), calculated the age at maturity according to equation 10 in the Appendix. Because the rate of growth was not constant throughout ontogeny and, notably, decelerated at the onset of maturity, this calculation only yields an estimate. To obtain a more precise result, one would have to take into account variation in the rate of growth throughout ontogeny, but, inasmuch as the data are so sparse, only a general estimate is practical now.

The age at maturity of the ammonoids listed in Table I averages about 7 years or less. For example, studies of epizoans yield estimates ranging from 1 to 7.5 years. Studies based on identifying a seasonal signal in patterns of septal spacing yield estimates ranging from 2 to 7 years. The highest estimate of the age at maturity (20 years) is given for *Gaudryceras denseplicatum*. This species lived in an offshore environment (Tanabe, 1979) in which the rate of growth may well have been low. However, this estimate is based on the unproven assumption that constrictions formed with an annual periodicity and is probably unreliable. There are two estimates of the age at maturity of *Quenstedtoceras* spp. based on two different methods, septal spacing and oxygen isotopes. The two estimates are comparable, ranging from 2 to 5 years.

A few other estimates of the age at maturity of ammonoids have been published in the literature and are similar to those in Table I. Westermann (1990, 1992; Chapter 16, this volume) suggested that small shallow-water ammonoids reached maturity in 1 to 2 years, whereas midshelf forms of average size reached maturity in 3 to 5 years. In addition, Ward (1982, 1992) argued that the rate of growth of shallow-water ammonoids was higher than that of *Nautilus* on the basis of the value of the ratio of siphuncular area to chamber volume through ontogeny. (Note, however, that the rate of growth of some Paleozoic nautiloids may have been more rapid than that of *Nautilus*: Hewitt and Watkins, 1980; Hewitt and Hurst, 1983). There is also a general consensus that deep-water ammonoids reached maturity later than shallow-water forms. Westermann (1990, 1992) estimated that the age at maturity of large specimens of *Lytoceras* may have equaled as much as 50 years.

If 5 years is accepted as a reasonable estimate of the age at maturity of a shallow-water ammonoid, the duration of each growth stage in ontogeny can be calculated using equation 10 in the Appendix, assuming that the rate of growth was constant throughout ontogeny. For example, in an ammonoid with W of 2, the neanic stage, represented by the first two postembryonic whorls, would have lasted about 0.5 years, the juvenile stage, represented by the next two whorls, about 2 years, and the submature to mature stage, represented by the last whorl, about 2.5 years. The time of chamber formation in this ammonoid can also be calculated using equation 12 in the Appendix, assuming that the time of chamber formation increased exponentially through ontogeny. For example, if there were 90 chambers in this ammonoid, and the time of formation of the first postembryonic chamber is assumed to have been 1 day based on estimates of the time of chamber formation in *Sepia*, then the time of formation of the last chamber (90) would have been about 95 days. If there were only 70 chambers in this ammonoid, then the time of formation of the last chamber would have been about 135 days. However, it is important to remember that all of these estimates assume a constant rate of growth.

Table I indicates differences in the age at maturity of dimorphs within the same species ("antidimorphs" of Davis, 1972). In ammonoids, microconchs are generally smaller and have fewer whorls than do macroconchs (Makowski, 1971). Kulicki (1974) suggested that microconchs of Middle Jurassic *Quenstedtoceras* reached maturity earlier than did macroconchs (see also Guex, 1970; Makowski, 1962, 1971; Westermann, 1990). This is consistent with observations in present-day cephalopods in which males tend to mature earlier and usually at a smaller size than do females (Mangold, 1987). In contrast, Hewitt *et al.* (1993) suggested that macroconchs of oppeliids reached maturity at the same age as the smaller microconchs because they grew more rapidly. Matyja (1986) has also pointed out that, in some species of Jurassic ammonoids, there are three adult morphs, each of a different size and, presumably, age.

There is little information about the length of time that ammonoids lived after reaching maturity. This may have varied widely. Studies of ammonoids encrusted by epizoans suggest that some species of Ceratitina and Ammonitina did not live longer than 1 to 2 years after reaching maturity (Meischner, 1968; Seilacher, 1960, respectively). This is consistent with speculations that the formation of the mature body chamber was designed for a single egg-laying episode followed by death. In contrast, Kulicki (1974) hypothesized that some macroconchs of Middle Jurassic *Quenstedtoceras* experienced two "sexual cycles" separated by a year. Westermann (1971) suggested that the pronounced modifications of the adult body chamber in many ammonoids indicate that these animals lived a long time after reaching maturity. Callomon (1963) made a similar suggestion on the basis of his observation that specimens of adult shells are far more common in the fossil record than those of immature shells, implying that the long duration of the adult stage increased the chances of fossilization. However, these deposits may equally reflect age segregation, postspawning mortality, migrations, or hydrologic accumulations (Chapter 16, this volume).

8. Summary

Changes in shell shape, ornamentation, septal spacing, and other morphological features in the ontogeny of ammonoids indicate the presence of three stages in postembryonic growth: a neanic stage immediately after hatching, a juvenile stage, and a mature stage. Growth was determinate in most ammonoids, and maturity occurred at a more or less prescribed size for each species.

The generalized growth curve shows that the rate of growth accelerated during the neanic stage, was nearly constant during the juvenile stage, and decelerated at the onset of maturity (Fig. 5). As in present-day *Nautilus*, the time of chamber formation probably increased more or less exponentially over most of ontogeny. Microconchs, with generally fewer whorls than macroconchs, may have reached maturity earlier.

Observations of several morphological features support this generalized growth curve. The neanic stage was characterized by an interval of wide septal spacing. It also coincided, as shown in some ammonoids, with the formation of widely spaced increments on the lower jaw. These features both suggest that there was an acceleration in the rate of growth during this stage. In contrast, at the approach of maturity, the rate of growth decelerated, as shown by a thickening of the apertural margin and the approximation of the last few septa.

Superimposed on this generalized growth curve were fluctuations in the relative rate of growth, many of which were caused by intrinsic processes. Such fluctuations are indicated by the presence of ribs, constrictions, varices, and megastriae. Although many of these features are regularly spaced with respect to their angular distance on the shell, there are no data to suggest that they were periodic with respect to their time of formation. In some ammonoids, the growth of the shell was episodic, meaning that successive portions of a whorl were secreted as separate units.

In present-day cephalopods, the environment affects how quickly animals grow and how soon they reach maturity (Mangold, 1987). Environmental factors must also have affected the rate of growth of ammonoids and their age at maturity. These factors included light, temperature, pressure, dissolved oxygen, and food availability. Pressure (depth) may have played an especially important role because it controlled the rate at which cameral liquid was removed and, hence, the rate of growth.

As a result of intrinsic and extrinsic factors, the absolute rate of growth varied within and among species. Growth was rapid in most shallow-water ammonoids; they probably attained maturity in about 5 years. This is consistent with the fact that in many of these forms, the wall of the siphuncle was thin, permitting rapid removal of cameral liquid (Westermann, 1990). The growth rate of these ammonoids may have approached that of coleoids, most of which grow rapidly and reach maturity in 1 to 2 years (Mangold, 1983; Wells, 1983). In contrast, the rate of growth of deep-water ammonoids may have been more similar to that of *Nautilus*, which grows slowly and reaches maturity in 10–15 years (Saunders, 1983; Landman and Cochran, 1987).

The length of time an ammonoid lived after reaching maturity probably varied among taxa in accordance with whether reproduction was semelparous or iteroparous. The presence of distinctive monospecific assemblages consisting of nearly all adults in shallow-water deposits of the Mesozoic (Callomon, 1981; Landman and Waage, 1993) suggests that some species may have been semelparous and died soon after spawning. (However, there are many other explanations for these occurrences; see Chapter 16, this volume.) Deep-water forms, however, may have been iteroparous and may have lived for several years after reaching maturity.

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Appendix

A.1. Calculation of the Age of an Ammonoid When the Time of Formation of the Last Whorl is Given

If the rate of growth along the venter of an ammonoid was constant through ontogeny, then

$$A = cL \tag{1}$$

where A is the age of the ammonoid, c is a constant expressed in units of time per unit length along the venter, and L is the total length along the venter. The ratio of the age of the whole ammonoid to the time of formation of a portion of the shell at the end of ontogeny (A_{p}) is expressed as

$$A/A_{\mathrm{p}} = L/L_{\mathrm{p}} \tag{2}$$

where L_{p} is the length along the venter of the portion of the shell at the end of ontogeny. Therefore,

$$A = \left(\frac{L}{L_{\mathrm{p}}}\right) A_{\mathrm{p}} \tag{3}$$

In a planispirally coiled ammonoid in which shell shape did not change during ontogeny, the length along the venter (L) is defined as

$$L = r\sqrt{(1/k^2) + 1} \tag{4}$$

where r is the radius of the spiral and k is the rate of spiral expansion (Thompson, 1917, p. 810; Hewitt, 1986, p. 338; Landman, 1987, p. 212). The ratio of the length along the venter of the whole ammonoid to that of a portion of the shell at the end of ontogeny is equal to

$$L/L_p = \frac{r_\theta}{r_\theta - r_{\theta-n\pi}} \tag{5}$$

where r_θ is the radius at angle θ, and $r_{\theta-n\pi}$ is the radius at angle $\theta - n\pi$, and n is some multiple of π (e.g., 2π radians = 1 whorl). Substituting

$$r = ae^{k\theta} \tag{6}$$

where a is the value of r when $\theta = 0$

$$\frac{L}{L_p} = \frac{ae^{k\theta}}{ae^{k\theta} - ae^{k(\theta-n\pi)}} = \frac{ae^{k\theta}}{ae^{k\theta}(1 - e^{-nk\pi})} = \frac{1}{1 - \dfrac{1}{e^{nk\pi}}} = \frac{e^{nk\pi}}{e^{nk\pi} - 1} \tag{7}$$

Substituting

$$W = e^{2k\pi} \tag{8}$$

where W is the rate of whorl expansion (Raup, 1967),

$$L/L_p = \frac{W^{n/2}}{W^{n/2} - 1} \tag{9}$$

Therefore,

$$A = \left(\frac{W^{n/2}}{W^{n/2} - 1}\right)A_p \tag{10}$$

If A_p is the time of formation of the last whorl ($n = 2$), and if $W = 2$, this expression becomes

$$A = \left(\frac{W}{W - 1}\right)A_p = 2A_p \tag{11}$$

In this case, the age of the whole ammonoid is equal to twice the time of formation of the last whorl. Because the rate of growth was probably not constant throughout ontogeny, and, notably, decreased at maturity, this calculation yields only an estimate.

A.2. Calculation of the Time of Chamber Formation When the Age of an Ammonoid Is Given

If the time of chamber formation increased exponentially through ontogeny, then

$$y = fe^{b(x-1)} \tag{12}$$

where y is the time of chamber formation, x is the chamber number, f is the time of formation of the first postembryonic chamber (x = 1), and b is a constant that is inversely proportional to the total number of chambers in the ammonoid.

The integral of this equation is

$$A = \frac{f}{b}\left[e^{b(x-1)} - 1\right] \tag{13}$$

where A is the age of the ammonoid at any value of $x \geq 2$ (if x = the chamber number of the last chamber = the total number of chambers in the ammonoid, then A is the age of the whole ammonoid). If A, f, and the total number of chambers are given, this equation can be solved for b. For example, if $A = 1865$ days (5 years), $f = 1$ day, and the total number of chambers = 90, then $b = 0.051$. Using this value of b, the time of chamber formation (y) can be calculated for any value of $1 \leq x \leq 90$. Note that this method yields only an estimate because, in fact, the rate of growth was not constant during ontogeny.

References

Arkell, W. J., Kummel, B., and Wright, C. W., 1957, Mesozoic Ammonoidea, in: *Treatise on Invertebrate Paleontology*, Part L, *Mollusca 4* (R. C. Moore, ed.), Geological Society of America and University of Kansas Press, Lawrence, KS, pp. 80–465.

Bandel, K., Landman, N. H., and Waage, K. M., 1982, Micro-ornament on early whorls of Mesozoic ammonites: Implications for early ontogeny, *J. Paleont.* **56**(2):386–391.

Bayer, U., 1972a, Zur Ontogenie und Variabilität des jurassischen Ammoniten *Leioceras opalinum*, *N. Jb. Geol. Paläont. Abh.* **140**:306–327.

Bayer, U., 1972b, Ontogenie der liassischen Ammonitengattung *Bifericeras*, *Paläontol. Z.* **46**:225–241.

Bayer, U., 1977, Cephalopoden-Septen. Teil 2. Regelmechanismen im Gehäuse- und Septenbau der Ammoniten, *N. Jb. Geol. Paläont. Abh.* **155**:162–215.

Birkelund, T., 1981, Ammonoid shell structure, in: *The Ammonoidea*, Systematics Association Spec. Vol. 18 (M. R. House and J. R. Senior, eds.), Academic Press, London, pp. 177–214.

Blind, W., and Jordan, R., 1979, "Septen-Gabelung" an einer *Dorsetensia romani* (Oppel) aus dem nordwestdeutschen Dogger, *Paläontol. Z.* **53**:137–141.

Bogoslovsky, B. I., 1982, An interesting form of apertural formation in the shell of clymeniids, *Dokl. Akad. Nauk SSSR* **264**(6):1483–1486 (in Russian).

Boletzky, S. v., 1983, *Sepia officinalis*, in: *Cephalopod Life Cycles*, Vol. I (P. R. Boyle, ed.), Academic Press, New York, pp. 31–52.

Boucot, A. J., 1953, Life and death assemblages among fossils, *Am. J. Sci.* **251**:25–40.

Boyle, P. R., and Thorpe, R. S., 1984, Optic gland enlargement and female gonad maturation in a population of the octopus *Eledone cirrhosa*: A multivariate analysis, *Mar. Biol.* **79**:127–132.

Brett, C. E., and Seilacher, A., 1991, Fossil Lagerstätten: A taphonomic consequence of event sedimentation, in: *Cycles and Events in Stratigraphy* (G. Einsele, W. Ricken, and A. Seilacher, eds.), Springer-Verlag, New York, pp. 283–297.

Buchardt, B., and Weiner, S., 1981, Diagenesis of aragonite from Upper Cretaceous ammonites: A geochemical case-study, *Sedimentology* **28**:423–438.

Bucher, H., and Guex, J., 1990, Rythmes de croissance chez les ammonites triasiques, *Bull. Soc. Vaudoise Sci. Nat.* **80**(2):191–209.

Callomon, J. H., 1963, Sexual dimorphism in Jurassic ammonites, *Trans. Leicester Lit. Phil. Soc.* **57**:21–56.

Callomon, J. H., 1981, Dimorphism in ammonoids, in: *The Ammonoidea*, Systematics Association Spec. Vol. 18 (M. R. House and J. R. Senior, eds.), Academic Press, London, pp. 257–273.

Callomon, J. H., 1985, The evolution of the Jurassic ammonite family Cardioceratidae, *Spec. Pap. Palaeont.* **33**:49–90.

Carlson, B., Awai, M., and Arnold, J., 1992, Waikiki Aquarium's Chambered *Nautilus* reach their first "Hatch-day" anniversary, *Hawaiian Shell News* **40**(1):1,3–4.

Carriker, M. R., 1972, Observations on removal of spines by muricid gastropods during shell growth, *Veliger* **15**:69–74.

Chamberlain, J. A., Jr., 1978, Permeability of the siphuncular tube of *Nautilus*: Its ecologic and paleoecologic implications, *N. Jb. Geol. Paläont. Mh.* **3**:129–142.

Checa, A., 1987, Morphogenesis in ammonites—differences linked to growth pattern, *Lethaia* **20**:141–148.

Checa, A., 1994, A model for the morphogenesis of ribs in ammonites inferred from associated microsculptures, *Palaeontology (Lond.)* **37**(4):863–888.

Checa, A., and Martin-Ramos, D., 1989, Growth and function of spines in the Jurassic ammonite *Aspidoceras, Palaeontology (Lond.)* **32**:645–655.

Checa, A., and Sandoval, J., 1989, Septal retraction in Jurassic Ammonitina, *N. Jb. Geol. Paläont. Mh.* **4**:193–211.

Checa, A., and Westermann, G. E. G., 1989, Segmental growth in planulate ammonites: Inferences on costal function, *Lethaia* **22**:95–100.

Clausen, C.-D., 1968, Oberdevonische Cephalopoden aus dem Rheinischen Schiefergebirge. I. Orthocerida, Bactritida, *Palaeontogr. Abt. A* **128**:1–86.

Cobban, W. A., 1951, Scaphitoid cephalopods of the Colorado group, *U.S. Geol. Surv. Prof. Pap.* **239**:1–42.

Collins, D., and Ward, P. D., 1987, Adolescent growth and maturity, in: *Nautilus—The Biology and Paleobiology of a Living Fossil* (W. B. Saunders and N. H. Landman, eds.), Plenum Press, New York, pp. 421–432.

Collins, D., Ward, P. D., and Westermann, G. E. G., 1980, Function of cameral water in *Nautilus, Paleobiology* **6**:168–172.

Cowen, R., Gertman, R., and Wright, G., 1973, Camouflage patterns in *Nautilus* and their implications for cephalopod paleobiology, *Lethaia* **6**:201–213.

Crick, R. E., 1978, Morphological variations in the ammonite *Scaphites* of the Blue Hill Member, Carlile Shale, Upper Cretaceous, Kansas, *Univ. Kans. Paleontol. Contrib. Pap.* **88**:1–28.

Currie, E. D., 1942, Growth changes in the ammonite *Promicroceras marstonense* Spath, *Proc. R. Soc. Edinb. Sect. B* **61**:344–367.

Currie, E. D., 1943, Growth stages in some species of *Promicroceras, Geol. Mag.* **80**:15–22.

Currie, E. D., 1944, Growth stages in some Jurassic ammonites, *Trans. R. Soc. Edinb.* **61**:171–198.

Davis, R. A., 1972, Mature modification and dimorphism in selected Late Paleozoic ammonoids, *Bull. Am. Paleont.* **62**(272):27–130.

Deevey, E. S., 1947, Life tables for natural populations of animals, *Q. Rev. Biol.* **22**:283–314.

Denton, E., and Gilpin-Brown, J., 1966, On the buoyancy of the pearly *Nautilus*, *J. Mar. Biol. Assoc. U.K.* **46**:723–759.

Diener, C., 1895, Himalayan fossils—the Cephalopoda of the Muschelkalk, *Palaeont. Indica Ser. 15, II* **2**:1–118.

Doguzhaeva, L., 1982, Rhythms of ammonoid shell secretion, *Lethaia* **15**:385–394.

Doguzhaeva, L. A., 1988, Siphuncular tube and septal necks in ammonite evolution, in: *Cephalopods—Present and Past* (J. Wiedmann and J. Kullmann, eds.), Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 291–302.

Dommergues, J.-L., 1988, Can ribs and septa provide an alternate standard for age in ammonite ontogenetic studies?, *Lethaia* **21**:243–256.

Druschits, V. V., Doguzhaeva, L. A., and Mikhailova, I. A., 1977, The structure of the ammonitella and the direct development of ammonites, *Paleontol. J.* **11**(2):188–199.

Elmi, S., and Benshili, K., 1987, Relation entre la structuration tectonique, la composition des peuplements et l'évolution; exemple du Toarcien du Moyen-Atlas méridional (Maroc), *Boll. Soc. Paleontol. Ital.* **26**:47–62.

Engeser, T. S., 1990, Major events in cephalopod evolution, in: *Major Evolutionary Radiations*, Systematics Association Spec. Vol. 42 (P. D. Taylor and G. P. Larwood, eds.), Clarendon Press, Oxford, pp. 119–138.

Fagerstrom, J. A., 1964, Fossil communities in paleoecology: Their recognition and significance, *Geol. Soc. Am. Bull.* **75**:1197–1216.

Forester, R. W., Caldwell, W. G. E., and Oro, F. H., 1977, Oxygen and carbon isotopic study of ammonites from the Late Cretaceous Bearpaw Formation in southwestern Saskatchewan, *Can. J. Earth Sci.* **14**:2086–2100.

Forsythe, J. W., and Van Heukelem, W. F., 1987, Growth, in: *Cephalopod Life Cycles*, Vol. II (P. R. Boyle, ed.), Academic Press, New York, pp. 135–156.

Geary, D. H., Breiske, T. A., and Bemis, B. E., 1992, The influence and interaction of temperature, salinity, and upwelling on the stable isotopic profiles of strombid gastropod shells, *Palaios* **7**:77–85.

Gould, S. J., 1966, Allometry and size in ontogeny and phylogeny, *Biol. Rev.* **41**:587–640.

Gould, S. J., 1977, *Ontogeny and Phylogeny*, Belknap Press, Harvard University, Cambridge, MA.

Grossman, E. L., and Ku, T. L., 1986, Oxygen and carbon isotope fractionation in biogenic aragonite: Temperature effects, *Chem. Geol.* **59**:59–72.

Guex, J., 1970, Sur les moules internes des Dactyliocératides, *Bull. Lab. Geol. Mineral. Geophys. Mus. Geol. Univ. Lausanne* **70**(182):1–7.

Heptonstall, W., 1970. Buoyancy control in ammonoids, *Lethaia* **3**:317–328.

Hewitt, R. A., 1985, Numerical aspects of sutural ontogeny in the Ammonitina and Lytoceratina, *N. Jb. Geol. Paläont. Abh.* **170**(3):273–290.

Hewitt, R. A., 1986, Terminology of ammonoid coiling equations, *Lethaia* **19**:338.

Hewitt, R. A., 1988, Significance of early septal ontogeny in ammonoids and other ectocochliates, in: *Cephalopods—Present and Past* (J. Wiedmann and J. Kullmann, eds.), Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 207–214.

Hewitt, R. A., and Hurst, J. M., 1977, Size changes in Jurassic liparoceratid ammonites and their stratigraphical and ecological significance, *Lethaia* **10**:287–301.

Hewitt, R. A., and Hurst, J. M., 1983, Aspects of the ecology of actinocerid cephalopods, *N. Jb. Geol. Paläont. Abh.* **165**(3):362–377.

Hewitt, R. A., and Stait, B., 1988, Seasonal variation in septal spacing of *Sepia officinalis* and some Ordovician actinocerid nautiloids, *Lethaia* **21**:383–394.

Hewitt, R. A., and Watkins, R., 1980, Cephalopod ecology across a late Silurian shelf tract, *N. Jb. Geol. Paläont. Abh.* **160**(1):96–117.

Hewitt, R. A., and Westermann, G. E. G., 1987, Function of complexly fluted septa in ammonoid shells, II, Septal evolution and conclusions, *N. Jb. Geol. Paläont. Abh.* **174**(2):135–169.

Hewitt, R. A., Checa, A., Westermann, G. E. G., and Zaborski, P. M., 1991, Chamber growth in ammonites inferred from color markings and naturally etched surfaces of Cretaceous vascoceratids from Nigeria, *Lethaia* **24**:271–287.

Hewitt, R. A., Westermann, G. E. G., and Checa, A., 1993, Growth rates of ammonites estimated from aptychi, *Geobios Mem. Spec.* **15**:203–208.

Hirano, H., 1981, Growth rates in *Nautilus macromphalus* and ammonoids: Its implications, in: *International Symposium on Conceptions and Methods in Paleontology, Barcelona* (J. Martinell, ed.), University of Barcelona, Barcelona, pp. 141–146.

House, M. R., 1965, A study in the Tornoceratidae: The succession of *Tornoceras* and related genera in the North American Devonian, *Phil. Trans. R. Soc. Lond. B* **250**(763):79–130.

Howarth, M. K., 1992, The ammonite family Hildoceratidae in the Lower Jurassic of Britian, Part 1, *Palaeontologr. Soc. Monogr. (Lond.)* **145**:1–106.

Hutchinson, G. E., 1978, *An Introduction to Population Ecology*, Yale University Press, New Haven.

Hyatt, A., 1894, Phylogeny of an acquired characteristic, *Proc. Am. Philos. Soc.* **32**(143):349–647.

Ivanov, A. N., 1971, On the problem of periodicity of the formation of septa in ammonoid shells and in that of other cephalopods, *Uch. Zap. Yarvsl. Pedagog. Inst. Geol. Paleontol.* **87**:127–130 (in Russian).

Ivanov, A. N., 1975, Late ontogeny in ammonites and its characteristics in micro-, macro- and megaconchs, *Yarosl. Pedagog. Inst. Sb. Nauchn. Tr.* **142**:5–57 (in Russian).

Jacobs, D. K., 1992, Shape, drag, and power in ammonoid swimming, *Paleobiology* **18**(2):203–220.

Jacobs, D. K., and Landman, N. H., 1993, *Nautilus*—a poor model for the function and behavior of ammonoids? *Lethaia* **26**:101–111.

Jacobs, D. K., Landman, N. H., and Chamberlain, J. A., Jr., 1994, Ammonite shell shape covaries with facies and hydrodynamics: Iterative evolution as a response to changes in basinal environment, *Geology* **22**:905–908.

Jordan, R., and Stahl, W., 1970, Isotopische Paläotemperatur-Bestimmungen an jurassischen Ammoniten und grundsätzliche Voraussetzungen für diese Methode, *Geol. Jb.* **89**:33–62.

Kahn, P. G. K., and Pompea, S. M., 1978, Nautiloid growth rhythms and dynamical evolution of the Earth–Moon system, *Nature* **275**:606–611.

Kant, R., 1973a, "Knickpunkte" im allometrischen Wachstum von Cephalopoden-Gehäusen, *N. Jb. Geol. Paläont. Abh.* **142**(1):97–114.

Kant, R., 1973b, Allometrisches Wachstum paläozoischer Ammonoideen: Variabilität und Korrelation einiger Merkmale, *N. Jb. Geol. Paläont. Abh.* **143**(2):153–192.

Kant, R., 1973c, Untersuchungen des allometrischen Gehäusewachstums paläozoischer Ammonoideen unter besonder Berücksichtigung einzelner "Populationen," *N. Jb. Geol. Paläont. Abh.* **144**(2):206–251.

Kant, R., and Kullmann, J., 1973, "Knickpunkte" im allometrischen Wachstum von Cephalopoden-Gehäuse, *N. Jb. Geol. Paläont. Abh.* **142**:7–114.

Kemper, E., and Wiedenroth, K., 1987, Klima und Tier-Migrationen am Beispiel der frühkretazischen Ammoniten Nordwestdeutschlands, *Geol. Jahr. A* **96**:315–363.

Kennedy, W. J., 1988, Late Cenomanian and Turonian ammonite faunas from north-east and central Texas, *Spec. Pap. Palaeontol.* **39**:1–131.

Kennedy, W. J., and Cobban, W. A., 1976, Aspects of ammonite biology, biogeography, and biostratigraphy, *Spec. Pap. Palaeontol.* **17**:1–94.

Kidwell, S. M., and Bosence, D. W. J., 1991, Taphonomy and time-averaging of marine shelly faunas, in: *Taphonomy—Releasing the Data Locked in the Fossil Record* (P. A. Allison and D. E. G. Briggs, eds.), Plenum Press, New York, pp. 115–209.

Korn, D., and Price, J. D., 1987, Taxonomy and phylogeny of the Kosmoclymeniinae subfam. nov. (Cephalopoda, Ammonoidea, Clymeniida), *Cour. Forschungsinst. Senckenb.* **92**:5–75.

Kulicki, C., 1974, Remarks on the embryogeny and postembryonal development of ammonites, *Acta Palaeontol. Pol.* **19**:201–224.

Kulicki, C., 1979, The ammonite shell: Its structure, development and biological significance, *Palaeontol. Pol.* **39**:97–142.

Kullmann, J., and Scheuch, J., 1970, Wachstums-Änderungen in der Ontogenese paläozoischer Ammonoideen, *Lethaia* **3**:397–412.

Kullmann, J., and Scheuch, J., 1972, Absolutes und relatives Wachstum bei Ammonoideen, *Lethaia* **5**:129–146.

Landman, N. H., 1983, Ammonoid growth rhythms, *Lethaia* **16**:248.

Landman, N. H., 1986, Developmental criteria for comparing ammonite ontogenies, *Geol. Soc. Am. Abst. Prog.* **18**(6):665.

Landman, N. H., 1987, Ontogeny of Upper Cretaceous (Turonian–Santonian) scaphitid ammonites from the Western Interior of North America: Systematics, developmental patterns, and life history, *Bull. Am. Mus. Nat. Hist.* **185**(2):117–241.

Landman, N. H., 1988, Early ontogeny of Mesozoic ammonites and nautilids, in: *Cephalopods—Present and Past* (J. Weidmann and J. Kullmann, eds.), Schweitzerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 215–228.

Landman, N. H., 1989, Iterative progenesis in Upper Cretaceous ammonites, *Paleobiology* **15**(2):95–117.

Landman, N. H., and Cochran, J. K., 1987, Growth and longevity of *Nautilus*, in: *Nautilus—The Biology and Paleobiology of a Living Fossil* (W. B. Saunders and N. H. Landman, eds.), Plenum Press, New York, pp. 401–420.

Landman, N. H., and Klofak, S. M., Size frequency studies in Late Cretaceous ammonoids: Evidence for rate of growth, in prep.

Landman, N. H., and Waage, K. M., 1986, Shell abnormalities in scaphitid ammonites, *Lethaia* **19**:211–224.

Landman, N. H., and Waage, K. M., 1993, Scaphitid ammonites of the Upper Cretaceous (Maastrichtian) Fox Hills Formation in South Dakota and Wyoming, *Bull. Am. Mus. Nat. Hist.* **215**:1–257.

Landman, N. H., Tanabe, K., Mapes, R. H., Klofak, S. M., and Whitehill, J., 1993, Pseudosutures in Paleozoic ammonoids, *Lethaia* **26**:99–100.

Landman, N. H., Cochran, J. K., Rye, D. M., Tanabe, K., and Arnold, J. M., 1994, Early life history of *Nautilus*: Evidence from isotopic analysis of aquarium-reared specimens, *Paleobiology* **20**(1):40–51.

Lange, W., 1932, Über Symbiosen von *Serpula* mit Ammoniten im unteren Lias Norddeutschlands, *Z. Dtsch. Geol. Ges.* **84**:229–234.

Lehmann, U., 1966, Dimorphismus bei Ammoniten der Ahrensburger Lias-Geschiebe, *Paläontol. Z.* **40**:26–55.

Lehmann, U., 1981, *The Ammonites: Their Life and Their World*, Cambridge University Press, Cambridge.

Linsley, R. M., and Javidpour, M., 1980, Episodic growth in Gastropoda, *Malacologia* **20**:153–160.

Lominadzé, T. A., Sharikadzé, M. Z., and Kvantaliani, I. V., 1993, On mechanism of soft body movement within body chamber in ammonites, *Geobios Mem. Spec.* **15**:267–273.

Mackenzie, C. L., Jr., 1960, Interpretation of varices and growth ridges on shells of *Eupleura caudata, Ecology* **41**(4):783–784.

Maeda, H., 1993, Dimorphism of Late Cretaceous false-puzosiine ammonites, *Yokoyamaoceras* Wright and Matsumoto, 1954 and *Neopuzosia* Matsumoto, 1954, *Trans. Proc. Palaeont. Soc. Jpn. N.S.* **169**:97–128.

Makowski, H., 1962, Problem of sexual dimorphism in ammonites, *Palaeontol. Pol.* **12**:1–92.

Makowski, H., 1971, Some remarks on the ontogenetic development and sexual dimorphism in the Ammonoidea, *Acta Geol. Pol.* **21**(3):321–340.

Mancini, E. A., 1978, Origin of micromorph faunas in the geologic record, *J. Paleontol.* **52**(2):311–322.

Mangold, K., 1983, Food, feeding and growth in cephalopods, *Mem. Natl. Mus. Victoria* **44**:81–93.

Mangold, K., 1987, Reproduction, in: *Cephalopod Life Cycles*, Vol. II (P. R. Boyle, ed.), Academic Press, London, pp. 157–200.

Matsukawa, M., 1987, Early shell morphology of *Karsteniceras* (ancyloceratid) from the Lower Cretaceous Choshi Group, Japan and its significance to the phylogeny of Cretaceous heteromorph ammonites, *Trans. Proc. Palaeont. Soc. Jpn. New Ser.* **148**:346–359.

Matsumoto, T., 1991, The Mid-Cretaceous ammonites of the family Kossmaticeratidae from Japan, *Palaeont. Soc. Jpn. Spec. Pap.* **33**:1–143.

Matsumoto, T., Muramoto, T., and Inoma, A., 1972, Two small desmoceratid ammonites from Hokkaido, *Trans. Proc. Palaeont. Soc. Jpn. New Ser.* **87**:377–394.

Matyja, B. A., 1986, Developmental polymorphism in Oxfordian ammonites, *Acta Geol. Pol.* **36**(1–3):37–68.

McConnaughey, T., 1989a, ^{13}C and ^{18}O isotopic disequilibrium in biological carbonates, *I.* Patterns, *Geochim. Cosmochim. Acta* **53**:151–162.

McConnaughey, T., 1989b, ^{13}C and ^{18}O isotopic disequilibrium in biological carbonates. II. *In vitro* simulation of kinetic isotope effects, *Geochim. Cosmochim. Acta* **53**:163–171.

Meinhardt, H., and Klinger, M., 1987, A model for pattern formation on the shells of molluscs, *J. Theor. Biol.* **126**:63–89.

Meischner, D., 1968, Perniciöse Epökie von *Placunopsis* auf *Ceratites*, *Lethaia* **1**:156–174.

Merkt, J., 1966, Über Austern und Serpeln als Epöken auf Ammonitengehäusen, *N. Jb. Geol. Paläont. Abh.* **125**:467–479.

Mesnil, B., 1977, Growth and life cycle of squid, *Loligo pealei* and *Illex illecebrosus*, from the Northwest Atlantic, *ICNAF Sel. Papers* **2**:55–69.

Mignot, Y., 1993, Un problème de paléobiologie chez les ammonoïdes (Cephalopoda): Croissance et miniaturisation en liaison avec les environnements, *Docum. Lab. Geol. Lyon* **124**:1–113.

Mignot, Y., Elmi, S., and Dommergues, J.-L., 1993, Croissance et miniaturisation de quelques *Hildoceras* (Cephalopoda) en liaison avec des environnements contraignant de la Téthys toarcienne, *Geobios Mem. Spec.* **15**:305–312.

Miller, A. K., Furnish, W. M., and Schindewolf, O. H., 1957, Paleozoic Ammonoidea, in: *Treatise on Invertebrate Paleontology*, Part L, *Mollusca 4* (R. C. Moore, ed.), Geological Society of America and University of Kansas Press, Lawrence, KS, pp. 11–80.

Mojsisovics, E. v., 1886, Arktische Triasfaunen, *Mem. Acad. Imp. Sci. St. Petersbourg* **7**:33.

Morton, N., 1988, Segregation and migration patterns in some *Graphoceras* populations (Middle Jurassic), in: *Cephalopods—Present and Past* (J. Wiedmann and J. Kullmann, eds.), Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 377–385.

Oba, T., Kai, M., and Tanabe, K., 1992, Early life history and habitat of *Nautilus pompilius*, *Kagoshima Univ. Res. Center S. Pac. Occas. Pap.* **1**:26–29.

Obata, I., 1959, Croissance relative sur quelques espèces des Desmoceratidae, *Mem. Fac. Sci. Kyushu Univ., Ser. D Geol.* **9**(1):33–45.

Obata, I., 1960, Spirale de quelques ammonites, *Mem. Fac. Sci., Kyushu Univ., Ser. D Geol.* **9**(3):151–163.

Obata, I., 1965, Allometry of *Reesidites minimus*, a Cretaceous ammonite species, *Trans. Proc. Palaeont. Soc. Japan, New Ser.* **58**:39–63.

Obata, I., Futakami, M., Kawashita, Y., and Takahashi, T., 1978, Apertural features in some Cretaceous ammonites from Hokkaido, *Bull. Natl. Sci. Mus. Ser. C (Geol.)* **4**(3):139–155.

Oechsle, E., 1958, Stratigraphie und Ammonitenfauna der Sonninien-Schichten des Filsgebiets unter besonderer Berücksichtigung der Sowerbyi-Zone (Mittlerer Dogger, Württemberg), *Palaeontogr. Abt. A* **111**:47–129.

Okamoto, T., 1989, Changes in life orientation during the ontogeny of some heteromorph ammonoids, *Palaeontology (Lond.)* **31**(2):281–294.

Okamoto, T., 1993, Theoretical modelling of ammonite morphogenesis, *N. Jb. Geol. Paläont. Abh.* **190**(2/3):183–190.

Palframan, D. F. B., 1966, Variation and ontogeny of some Oxfordian ammonites: *Taramelliceras richei* (de Loriol) and *Creniceras renggeri* (Oppel), from Woodham, Buckinghamshire, *Palaeontology (Lond.)* **9**(2):290–311.

Palframan, D. F. B., 1967, Mode of early shell growth in the ammonite *Promicroceras marstonense* Spath, *Nature (Lond.)* **216**:1128–1130.

Pompeckj, J. F., 1884, Über Ammonoideen mit anomaler Wohnkammer, *J. Ver. Vaterl. Naturk. Wurtt.* **49**:220–290.

Raup, D., 1967, Geometric analysis of shell coiling: Coiling in ammonoids, *J. Paleontol.* **41**:43–65.

Raup, D., and Chamberlain, J. A., Jr., 1967, Equations for volume and center of gravity in ammonoid shells, *J. Paleontol.* **41**:566–574.

Richard, A., 1970, Analyse du cycle sexual chez les céphalopodes mise en évidence expérimentale d'un rythme conditionné par les variations des facteurs externes et internes, *Bull. Soc. Zool. Fr.* **95**:461–469.

Richards, R. P., and Bambach, R. K., 1975, Population dynamics of some Paleozoic brachiopods and their paleoecological significance, *J. Paleontol.* **49**(5):775–798.

Rieber, H., 1963, Ammoniten und Stratigraphie des Braunjura β der Schwaebischen Alb., *Palaeontogr. Abt. A* **122**:1–89.

Rounsefell, G. A., and Everhart, W. H., 1953, *Fishery Science—Its Methods and Applications*, John Wiley & Sons, New York.

Rye, D. M., and Sommer, M. A., 1980, Reconstructing paleotemperature and paleosalinity regimes with oxygen isotopes, in: *Skeletal Growth of Aquatic Organisms* (D. C. Rhoads and R. A. Lutz, eds.), Plenum Press, New York, pp. 169–202.

Saunders, W. B., 1983, Natural rates of growth and longevity of *Nautilus belauensis*, *Paleobiology* **9**(3):280–288.

Schindewolf, O. H., 1934, Über Epöken auf Cephalopoden-Gehäusen, *Palaeontol. Z.* **16**:15–31.

Schindewolf, O. H., 1958, Über Aptychen (Ammonoidea), *Palaeontogr. Abt. A* **111**:1–46.

Seilacher, A., 1960, Epizoans as a key to ammonoid ecology, *J. Paleontol.* **34**:189–193.

Seilacher, A., 1982, Ammonite shells as habitats in the Poseidonia Shales of Holzmaden—floats or benthic islands? *N. Jb. Geol. Paläont. Abh.* **159**:98–114.

Seilacher, A., 1988, Why are nautiloid and ammonite sutures so different? *N. Jb. Geol. Paläont. Abh.* **177**:41–67.

Seilacher, A., and Gunji, P. Y., 1993, Morphogenetic countdowns in heteromorph shells, *N. Jb. Geol. Paläont. Abh.* **190**(2/3):237–265.

Sheldon, R. W., 1965, Fossil communities with multi-modal size–frequency distributions, *Nature* **206**(4991):1336–1338.

Shigeta, Y., 1993, Post-hatching early life history of Cretaceous Ammonoidea, *Lethaia* **26**(2):133–145.

Simoulin, E., 1945, Observations sur la croissance de la coquille chez quelques Stéphanocératides, *Ann. Soc. Géol. Nord* **65**:9–19.

Smith, J. P., 1898, The development of *Lytoceras* and *Phylloceras*, *Proc. Calif. Acad. Sci. (Geol.)* **1**(4):129–161.

Speden, I. G., 1970, The type Fox Hills Formation, Cretaceous (Maestrichtian), South Dakota, Part 2, Systematics of the Bivalvia, *Peabody Mus. Nat. Hist. Yale Univ. Bull.* **33**:1–222.

Stahl, W., and Jordan, R., 1969, General considerations on isotopic paleotemperature determinations and analyses on Jurassic ammonites, *Earth Planet. Sci. Lett.* **6**:173–178.

Stevens, G. R., 1988, Giant ammonites: A review, in: *Cephalopods—Present and Past* (J. Wiedmann and J. Kullmann, eds.), Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 141–166.

Surlyk, F., 1972, Morphological adaptations and population structures of the Danish Chalk brachiopods (Maastrichtian, Upper Cretaceous), *K. Dan. Vidensk. Selsk. Biol. Skr.* **19**(2):1–57.

Tanabe, K., 1975, Functional morphology of *Otoscaphites puerculus* (Jimbo), an Upper Cretaceous ammonite, *Trans. Proc. Palaeontol. Soc. Jpn, New Ser.* **99**:109–132.

Tanabe, K., 1977, Functional evolution of *Otoscaphites puerculus* (Jimbo) and *Scaphites planus* (Yabe), Upper Cretaceous ammonites, *Mem. Fac. Sci. Kyushu Univ. Ser. D (Geol.)* **23**:367–407.

Tanabe, K., 1979, Palaeoecological analysis of ammonoid assemblages in the Turonian *Scaphites* facies of Hokkaido, Japan, *Palaeontology (Lond.)* **22**(3):609–630.

Tanabe, K., and Landman, N. H., Translocation of the soft body in Mesozoic ammonoids, in prep.

Tanabe, T., Obata, I., and Futakami, H., 1981, Early shell morphology in some Upper Cretaceous heteromorph ammonites, *Trans. Proc. Palaeontol. Soc. Jpn. New Ser.* **124**:215–234.

Tanabe, K., Landman, N. H., and Weitschat, W., 1993, Septal necks in Mesozoic Ammonoidea: Structure, ontogenetic development, and evolution, in: *The Ammonoidea: Environment,* *Ecology, and Evolutionary Change*, Systematics Association Spec. Vol. 47 (M. R. House, ed.), Clarendon Press, Oxford, pp. 57–84.

Teisseyre, L., 1889, Über die systematische Bedeutung der sog. Parabeln der Perisphincten, *N. Jb. Miner. Geol. Paläont.* **6**(1):570–643.

Tevesz, M. J. S., and Carter, J. G., 1980, Environmental relationships of shell form and structure of unionacean bivalves, in: *Skeletal Growth of Aquatic Organisms* (D. C. Rhoads and R. A. Lutz, eds.), Plenum Press, New York, pp. 295–322.

Thompson, D. W., 1917, *On Growth and Form*, Cambridge University Press, London.

Tourtelot, H. A., and Rye, R. O., 1969, Distribution of oxygen and carbon isotopes in fossils of Late Cretaceous age, Western Interior region of North America, *Geol. Soc. Am. Bull.* **80**:1903–1922.

Tozer, E. T., 1965, Latest Lower Triassic ammonoids from Ellesmere Island and northeastern British Columbia, *Geol. Surv. Can. Bull.* **123**.

Tozer, E. T., 1991, Relationship between spines, parabolic nodes, rhythmic shell secretion and formation of septa in some Triassic ammonoids, in: *The Ammonoidea: Evolution and Environmental Change*, Systematics Association Symp. London Prog. Abstr., pp. 23–24.

Trueman, A. E., 1941, The ammonite body-chamber, with special reference to the buoyancy and mode of life of the living ammonite, *Q. J. Geol. Soc. Lond.* **96**:339–383.

Van Heukelem, W. F., 1978, Aging in lower animals, in: *Biology of Aging* (J. A. Behnke, C. E. Finch, and B. C. Moment, eds.), Plenum Press, New York, pp. 115–130.

Vermeij, G. J., 1980, Gastropod shell growth rate, allometry, and adult size—environmental implications, in: *Skeletal Growth of Aquatic Organisms* (D. C. Rhoads and R. A. Lutz, eds.), Plenum Press, New York, pp. 379–394.

Vermeij, G. J., 1993, *A Natural History of Shells*, Princeton University Press, Princeton.

Waage, K. M., 1968, The type Fox Hills Formation, Cretaceous (Maestrichtian), South Dakota, Part 1, stratigraphy and paleoenvironments, *Peabody Mus. Nat. Hist. Yale Univ. Bull.* **27**:1–175.

Wähner, F., 1894, Beiträge zur Kenntniss der tieferen Zonen des unteren Lias in der nordöstlische Alpen, *Beitr. Paläontol. Österr. Ungarns. Orients* **9**(I–II):1–54.

Ward, P. D., 1982, The relationship of siphuncle size to emptying rates in chambered cephalopods: Implications for cephalopod paleobiology, *Paleobiology* **8**:426–433.

Ward, P. D., 1985, Periodicity of chamber formation in chambered cephalopods: Evidence from *Nautilus macromphalus* and *Nautilus pompilius*, *Paleobiology* **11**:438–450.

Ward, P. D., 1986, Rates and processes of compensatory buoyancy change in *Nautilus macromphalus*, *Veliger* **28**:356–368.

Ward, P. D., 1987, *The Natural History of Nautilus*, Allen and Unwin, Boston.

Ward, P. D., 1992, *On Methuselah's Trail*, W. H. Freeman, New York.

Ward, P. D., and Chamberlain, J. A., Jr., 1983, Radiographic observation of chamber formation in *Nautilus pompilius*, *Nature (Lond.)* **304**:57–59.

Ward, P. D., and Greenwald, L., 1982, Chamber refilling in *Nautilus*, *J. Mar. Biol. Assoc. U.K.* **62**:469–475.

Ward, P. D., Greenwald, L., and Magnier, Y., 1981, The chamber formation cycle in *Nautilus macromphalus*, *Paleobiology* **7**(4):481–493.

Weitschat, W., and Bandel, K., 1991, Organic components in phragmocones of Boreal Triassic ammonoids: Implications for ammonoid biology, *Paläontol. Z.* **65**:269–303.

Weitschat, W., and Bandel, K., 1992, Formation and function of suspended organic cameral sheets in Triassic ammonoids: Reply, *Paläontol. Z.* **66**:443–444.

Wells, M. J., 1983, Cephalopods do it differently, *New Sci.* **100**:332–338.

Wells, M. J., and Wells, J., 1959, Hormonal control of sexual maturity in *Octopus*, *J. Exp. Biol.* **36**:1–33.

Wells, M. J., and Wells, J., 1977, Cephalopoda: Octopoda, in: *Reproduction of Marine Invertebrates*, Vol. IV (A. C. Giese and J. S. Pearse, eds.), Academic Press, New York, pp. 291–336.

Westermann, G. E. G., 1954, Monographie der Otoitidae (Ammonoidea), *Geol. Jahrb. Beih.* **15**:1–364.

Westermann, G. E. G., 1958, The significance of septa and sutures in Jurassic ammonite systematics, *Geol. Mag.* **95**(6):441–455.

Westermann, G. E. G., 1971, Form, structure, and function of shell and siphuncle in coiled Mesozoic ammonoids, *Life Sci. Contr. R. Ont. Mus.* **78**:1–39.

Westermann, G. E. G., 1975, Architecture and buoyancy of simple cephalopod phragmocones and remarks on ammonites, *Paläontol. Z.* **49**:221–234.

Westermann, G. E. G., 1990, New developments in ecology of Jurassic–Cretaceous ammonoids, in: *Atti del secondo convegno inernazionale, Fossili, Evoluzione, Ambiente, Pergola, 1987* (G. Pallini, F. Cecca, S. Cresta, and M. Santantonio, eds.), Tectnostampa, Ostra Vetere, Italy, pp. 459–478.

Westermann, G. E. G., 1992, Formation and function of suspended organic cameral sheets in Triassic ammonoids—discussion, *Paläontol. Z.* **66**(3/4):437–441.

Whittaker, S. G., Kyser, T. K., and Caldwell, W. G. E., 1987, Paleoenvironmental geochemistry of the Clagett marine cyclothem in south-central Saskatchewan, *Can. J. Earth Sci.* **24**:967–984.

Wiedmann, J., and Boletzky, S. v., 1982, Wachstum und Differenzierung des Schlups von *Sepia officinalis* unterkünstlichen Aufzuchtbedingungen—Grenzen der Anwendung im palökologischen Modell, *N. Jb. Geol. Paläont. Abh.* **164**(1/2):118–133.

Zaborski, P. M. P., 1986, Internal mould markings in a Cretaceous ammonite from Nigeria, *Palaeontology* **29**:725–738.

Zakharov, Y. D., 1977, Ontogeny of ceratites of the genus *Pinacoceras* and developmental features of the suborder Pinacoceratina, *Paleontol. J.* **4**:445–451.

Zell, H., Zell, I., and Winter, S., 1979, Das Gehäusewachstum der Ammonitengattung *Amaltheus* De Montfort während der frühontogenetischen Entwicklung, *N. Jb. Geol. Paläont. Mh.* **10**:631–640.

Zuev, G. V., 1975, Physiological variation in female squids *Symplectoteuthis pteropus* (Steenstrup), *Biol. Moyra* **38**:55–62.