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Nautilus pompilius in captivity: a case study of abnormal shell growth

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Abstract: The abnormal shell growth in two individuals of *Nautilus pompilius* reared in the aquarium tank of the Jura-Museum Eichstätt (southern Germany) is described. Analysis of etiology focusses on the control of shell growth, subject of controversial discussion to which additional facts and interpretations are contributed to. The shell anomaly is characterized by protuberant apertural growth having formed a ventro-lateral bulgy fold, and creation is evidently correlated with temporary change of water chemistry triggering off retarded calcification of the periostracum. Due to the constructional problems, apertural growth hardly progressed in respect to body chamber length. On the other hand speed of septal formation also decreased, however, not to the same degree as apertural growth. In consequence, the body chamber successively became shorter. Subsequently, the soft body increasingly projected over the aperture, although the animal attempted to maintain functionality, which is featured by allometric growth of soft parts, reducing the volume of the posterior body. This extreme situation demonstrates clearly that feedback between apertural growth and chamber formation is of very limited flexibility, i.e., is easily unbalanced. It is evident that immature individuals of *Nautilus* can slow down septal formation, but even when drifting towards lethal morphological disproportion chamber formation cannot be stopped. Comparable shell anomalies have been described in literature for Cenomanian nautili and for a Bathonian perisphinctid ammonite, indicating that our aquarium tank scenario may be performed also under natural conditions. The shell anomalies described here are attributed to the newly coined forma aegra *complicata*.

Zusammenfassung: Zwei abnormal gewachsene Individuen von *Nautilus pompilius* aus dem Aquarium des Jura-Museums Eichstätt werden beschrieben, ätiologisch gedeutet und hinsichtlich ihrer Bedeutung für das bis heute kontrovers diskutierte Verständnis des Gehäusebaues bei Nautiliden interpretiert. Die anomal nach außen gewachsene Gehäusemündung, die mit der Bildung eines ventro-lateralen Faltenwurfes verbunden ist, wird auf verzögerte Verkalkung des Periostracums infolge einer artifiziell veränderten Wasserchemie zurückgeführt. Der zwar verlangsamte, aber nicht völlig eingestellte Einbau von Septen führt durch das weitgehende Fehlen eines effektiven Gehäusevorbaues zur sukzessiven Verkürzung der Wohnkammer, die schließlich zu einem allometrischen Wachstum des Weichkörpers und seinem zunehmenden Hinausdrängen aus dem Gehäuse führt. Es wird daraus ersichtlich, daß Vorbau der Conothek und Septeneinbau nur mittels einer eng begrenzten Rückkoppelungsfähigkeit aufeinander abgestimmt werden können. Immature Individuen von *Nautilus* können ihren genetischen Drang zum Einbau von Septen nur drosseln, nicht aber unterbinden. Vergleichbarer abnormaler Gehäusewuchs wurde für cenomanische Nautili und einen perisphinctiden Ammoniten aus dem Bathonium beschrieben, so daß offensichtlich auch unter natürlichen Bedingungen ähnliche Szenarien wie im Aquarium möglich sind. Für die hier beschriebene Gehäuseanomalie wird die Bezeichnung forma aegra *complicata* eingeführt.

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Introduction

The importance of anomalous shell growth for interpreting the functional morphology of taxa is very often underrated. However, great emphasis should be laid on the study of such abnormally growing taxa, which in many cases reveal certain bioconstructional limits, actually allowing to falsify the "normal" condition. Anomalies generally can be used to approach a better understanding of what is "normality" (Engel, 1894; Keupp, 1984) and very often not only document individual pathology but reflect synecological interactions (predation, parasitism, commensalism, etc.) or physical conditions (water energy, pressure, temperature, etc.), allowing to correlate part of the environmental network. In addition, diagnosis of anomaly uncovers morphological patterns beyond taxonomic characters, i.e., a fair amount of taxa could already be eliminated from ammonoidean classification schemes, which have been coined on the basis of misinterpreted pathologic phenomena (cf. Keupp, 1992a).

The tradition of studying pathologic Ammonoidea was already well established in the last century (e.g. Fraas, 1863; Quenstedt, 1885-1888; Engel, 1894) and has been continued by several authors (among others Bayer, 1970; Bond & Saunders, 1989; Bülow, 1918; Fernández López, 1987; Géczy, 1966; Guex, 1967, 1968; Heller, 1958, 1964; Hengsbach, 1979, 1987, 1990, 1991; Hiltermann 1962; Hölder, 1956, 1970, 1973, 1977; Hollmann, 1961; Jessen, 1959; Keupp, 1973, 1976, 1977, 1984, 1985, 1992, 1993, 1994, 1995; Keupp & Dietze, 1987; Keupp & Ilg, 1992, 1994; Kolb, 1955; Landman & Waage, 1986; Lange 1932; Lehmann, 1974, 1975; Malecki, 1986; Morton, 1983; Müller, 1954, 1970, 1976, 1980; Pockrandt 1970; Rein, 1989, 1991, 1994; Rieber, 1963; Schindewolf, 1934; Thiermann, 1964; Wagenplast, 1976; Wenger, 1956). On the other hand the pathology of fossil and Recent nautiloids has been somewhat neglected. Only few reports on abnormal shell growth in fossil Nautiloidea could be recognized (e.g. Loesch, 1912; Kieslinger, 1926; Sornay, 1955; Teichert, 1964; Ansorge & Koppka, 1994), however, some more data have been compiled on shell anomalies in Recent *Nautilus* (among others Meenakshi et al., 1974; Mapes et al., 1979; de Graaf, 1981, Landman, 1983; Arnold, 1985, Saunders et al., 1987; Ward 1987) of which some are pathologic.

The predominant role of *Nautilus* for the interpretation of the paleobiology of ectocochliate cephalopods in general, has been discussed contrarily several times (see Jacobs & Landman, 1993 and references therein) and although many generalized conclusions have to remain speculative, some gaps of knowledge still can be filled, e. g., with the aid of morphological details extracted from shell anomalies in Ammonoidea and Nautiloidea, which have been overlooked in respect to the interpretation of functional morphology and ecology.

Recent *Nautilus* has been observed in surface waters and trapped as deep as 600 m (Ward & Martin, 1980), but most commonly can be found in water depths of 100-300 m (see Ward, 1987). Thus direct observation of living *Nautilus* by scuba divers is more-or-less an exception, which means that most of our knowledge of functional morphology and behaviour of nautili has derived from individuals reared in aquarium tanks. Artificial conditions, such as close-quartered rearing, permanent low pressure, light, unusual water chemistry, etc., certainly have influence on the development of the *Nautilus*, but as long as the cephalopod can manage the situation, the feedback with the environment cannot be beyond the nautili biological limits and thus "aquarium-research" always reflects objective aspects of life, which potentially are also produced under natural conditions.

This study represents the analysis of abnormal shell growth in two aquarium-reared individuals of *Nautilus pompilius*. A similar shell anomaly in *Nautilus pompilius* was figured and described by de Graaf (1981), but discussed only very briefly: "What caused the abnormal shell growth is still a mystery". Arnold (1985) figured comparable anomalous apertural shell growth from *Nautilus belauensis* in captivity. He concluded that more-or-less continuous contact with the walls of the aquarium tank may have caused such abnormal growth. Whatever the causes were (see discussion), it is the consequence for the life of the *Nautilus*, i.e., for the "feedback system" controlling shell growth, on which emphasis should be laid. We will demonstrate that this avenue of research is very fruitful to understand aspects of the functional morphology of *Nautilus*. Finally a brief comparison with a similar shell abnormality in a Jurassic ammonite (see Schairer, 1989) bridges between the two evolutionary lines of ectocochliates.

Methods and materials

All specimens of *Nautilus pompilius* examined here originate from the Philippines. The pathological shells of which one contained the soft parts (Specimen 1), both derived from the Jura-Museum in Eichstätt, southern Germany. These two individuals have been reared in the aquarium tank from September 1990 to September 1993 and to about early 1993 respectively, in case of the specimen without the soft parts preserved (Specimen 2). This is a comparatively long period of life in captivity (see de Graaf, 1981; Ward, 1987). Thus the tank conditions must have been not too bad. The tank has a capicity of 1500 litres. The water temperature usually varied from about 16 to 18º C but may have reached 21º C in summer. The nautili were fed shrimps every second day. One remark on the water chemistry has to be made. The water was enriched with calcium hydroxide for a few months during the first year of rearing the nautili (see discussion).

Conch characters have been compared and correlated with the shells of nineteen nautili, which were not reared in an aquarium tank. The body chamber angle was measured sensu Ward (e. g. 1980). The ultrastructure of the shells was examined using a light microscope for the acetate peel and a scanning electron microscope (Cambridge) for freshly broken pieces of the body chamber and septal shell.

Comparison of the gross anatomy (aside from literature data) was possible with the aid of an individual, which was reared in the aquarium tank of Hagenbecks Tierpark (Zoo of Hamburg) only for a very short period. The buccal mass of the pathologic animal was removed and soaked in 15 % cold KOH for about one hour and then jaws and radula were extracted.

The two pathological specimens of *Nautilus* are deposited at the Institut Für Paläontologie, Freie Universität Berlin.

Description of the pathologic specimens

Specimen 1, with soft parts: The shell has a maximum diameter of 10.9 cm (Pl. 1, figs. 2-4). Thirty-four septa form the phragmocone which measures 9.3 cm across (Pl. 2, fig. 1). The diameter at 30 septa is 8.3 cm, at 25 septa 6.6 cm, at 20 septa 5.1 cm, at 15 septa 3.7 cm and at 10 septa 2.5 cm. Aside from the approximation between septa 7 and 8, which indicates hatching (see Arnold et al., 1987; Landman et al., 1989), the formation of the first twenty-six septa had been very regularly, in distance as well as in shape and thickness. Septum 27, with a maximum thickness of 1.2 mm, is about twice as strong as the preceding septum. The distances between the following septa vary considerably from 4 to 8 mm (Pl. 2, figs. 1,4). The thirty-fourth septum had been in the early process of secretion and is only 50 µm thin. This last septum is neighbouring the 13th septum in the radial direction.

The body chamber has an angle of 40º and a maximum length of 5.9 cm. The convex fronts of the muscle attachment scars run in a maximum distance of 2.2 cm to the last septum. The anterior ventral aponeuric band had been attached about 2.5 mm in front of the last septum while the posterior aponeuric band runs along the basis of this newly secreted septum. The venter is characterized by a second shell wall underlaying the normal shell. The normal "outer" wall performs a large ventral bulge of about 1 cm depth and 1.5 cm length, commencing at a distance of 3 cm to the last septum. The formation of the bulge became evident after the animal had lived in the aquarium tank for about half a year (Pl. 1, fig. 1). The bulge is restricted to the ventral almost apertural shell while the lateral shell is bended outwardly (Pl. 1, figs. 2-4; Pl. 2, fig. 3), which, however, is less pronounced on the left side. The bulge does not follow the exact symmetry of earlier whorls but forms an angle of 80º (right side) or 100º (left side) respectively, instead of 90º. Thus the body chamber is a little bit shorter on the right side.

The "inner" shell wall sets in at a distance of about 1 cm to the last septum, regularly underpinning the "outer" shell for 1.5 cm, but then performing an irregular fold, which reduces the diameter of the body chamber for 5 mm at maximum (Pl. 2, fig. 1; Pl. 3, fig. 1). The fold of the "inner" shell is mainly pronounced ventrally and there reaches a thickness of 3 mm. The bulge of the "outer" shell is not underlaid but separated from the body chamber by the "inner" shell leaving a ventral waterfilled space (Pl. 3, fig. 1). The first layers of the "inner" shell form an angle of about 13º to the outer shell and terminate at a distance of about 1 mm to the internal layer of the outer shell. This first attempt of compensating the bulge was followed by a second series of layers forming an angle of about 16º to it, again terminating at close range to the "outer" shell. A third series of shell layers then succeeded in dividing off the bulge from the body chamber in joining the "outer" shell wall for the last portion of apertural shell, which shows the normal growth direction (Pl. 3, fig. 1). The irregularly grown ("outer" and "inner") shell shows marked intercalations of black organic layers.

The shell microstructure of the unusual growth zone could be roughly correlated with the aid of an acetate peel (Pl.3, figs.1A-E), which under the light microscope already shows very clearly the irregular thickening of the prismatic layers. The electron microscope revealed that the two series of shell layers which project into the bulge and also the third series of shell layers which finally joins the "outer" shell are largely prismatic (Pl. 3, fig. 3). The outer portions of these shell sections consist always of irregular aragonite crystal aggregates, which are more-or-less strengthened by layers of regular aragonitic needles. The bulge itself in its main part is formed by outer prismatic and inner nacreous layers. A closer view reveals considerable variation of structural differentiation. A one milimeter thick shell section of the middle part of the bulge consists of about 300 µm irregular crystal aggregates, underlain by 180 µm aragonitic needles (Pl. 3, fig. 4). This prismatic portion of the shell is underpinned by 270 µm of nacreous shell, another regular prismatic intercalation which is 30 µm thick, and the inner nacreous layers measuring 180 µm across. The terminal portion of the bulge - from outside to inside - consists of 40 µm regular prismatic crystals, 65 µm nacre, another 22 µm of aragonitic needles and 45 µm of nacreous layers. The non-bulgy, apertural portion of the "outer shell" like its inner counterpart lacks nacre and consists mainly of regular prismatic layers with intercalation of comparatively thin layers of irregular crystal aggregates.

There are no microstructural differences between septal shell of early ontogenetic (wild living) and late ontogenetic chambers (in captivity). Septal necks and connecting rings have not been examined. The pellicle of a septum consists of about half a dozen organic layers which together are 1.5-2.0 µm thick (Pl. 3, fig. 2). The surface of this organic septal shell is covered by minute irregularly shaped "blebs" (compare Ward, 1987). The pellicle is underlaid by a few micrometer of spherulitic prismatic aragonite, while the remaining 95-98 % of septal shell consist of nacre which is interbedded with sheets of conchiolin. The newly secreted last septum shows perfectly the pagodiform growth fronts of the nacre (Pl. 3, fig. 5).

The anatomy has been examined with respect to a few features only, i.e., to the spatial arrangement of the soft parts within the body chamber. The body chamber is apparently too short to house the complete body, i.e. the hood by far cannot close the aperture (Pl. 2, fig. 4). The animal is an immature male, indicated by the gonads and the spadix, which both are not well developed (compare Haven, 1977; Arnold, 1987; Ward, 1987). The mantle cavity is comparatively short, judging from the gills, which project from it for some milimeters and terminate exactly where the bulge of the shell had been formed (Pl. 2, fig. 4). The mantle margin is relatively thick, while the posterior mantle is more-or-less thin and normal transparent (see comparison). The ventral mantle edge lies closely but anterior to the internal fold of the body chamber. The dorsal mantle edge lies in a distance of about 1 cm to the tissue of the "mantle fold" (sensu Stenzel, 1964) forming the rear of the hood. The hood is only scarcely pigmented (Pl. 2, fig. 4). From the alimentary tract the buccal mass with jaws and radula have been extracted. The buccal mass has a maximum length of 3 cm and measures maximally 2 cm in width. The radula has been described and figured by several authors (e.g. Solem & Richardson, 1975; Saunders et al., 1978; Tanabe et al., 1990). Thus another description is unnecessary and only some measurements and additional photographs are provided (Pl. 4, figs. 1-8). The radula of this specimen has a length of 18 mm, the membrane bearing about 35 rows of teeth. The membrane of the functional part of the radula has a width of 4.5 mm.

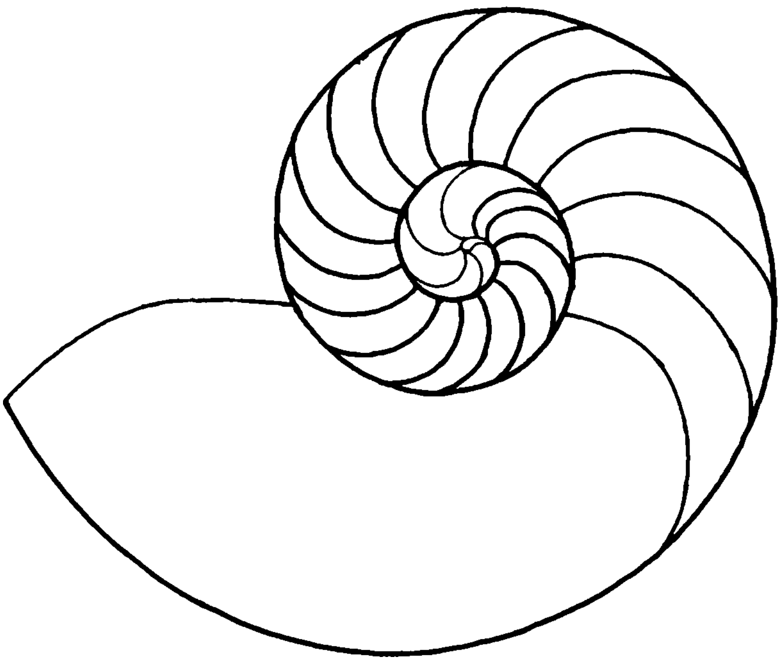
Some more measurements are given, which are rated in the next chapter. The animal has a total length of 7.6 cm, measured from the anterior tip of the hood (thus excluding the retractable tentacles) to the most posterior portion of the testis. The hood itself has a maximum length of 5.4 cm. The distance between the ventral mantle margin and the siphuncle amounts to 5.4 cm. The width of the soft parts is 3.7 cm, measured right in front of the dorsal mantle margin and amounts to 4.2 cm across the largest dimension of the retractor muscles.

Specimen 2, without soft parts: The shell measures 11.0 cm across (Pl. 1, figs. 5-6). The phragmocone consists of thirty-seven chambers and has a diameter of 9.2 cm (Pl. 2, fig. 2). The diameter at 30 septa is 7.7 cm, at 25 septa 6.2 cm, at 20 septa 4.5 cm, at 15 septa 3.5 cm and at 10 septa 2.4 cm. The normal approximation between the 7th and 8th septum marks the end of embryonic development. The following septa inclusive the 26th septum had been secreted in regularly increasing distances, with constant increase of septal thickness. The 27th septum has a maximum thickness of 1.1 mm, which is more than twice as much as the preceding septum (about 0.5 mm). The distances between the following ten septa do not increase and vary only little between 3.5 and 4.5 mm (Pl. 2, fig. 2). The 37th septum neighbours the 15th septum in radial direction whereas the 13th septum is joined by the 34th septum, which is the same as in Specimen 1.

The body chamber has an angle of 65º, the maximum ventral length is 7.5 cm (Pl. 2, fig. 2). The fronts of the muscle attachment scars have a maximum distance of 2.5 cm to the last septum. The posterior aponeuric band runs along the suture zone. The anterior ventral aponeuric band documents muscle attachment in a distance of about 2.5 mm to the septal basis. The venter shows the same unusual characteristic features as in Specimen 1, which, however, are pronounced differently (Pl. 1, figs. 5-6; Pl. 2, fig. 2). Intercalations of black organic layers are visible externally on the whole body chamber wall.

The two shell walls, which had been secreted, as in the other specimen are designated "outer" and "inner" wall. The "outer" shell wall shows a bulge of 0.8 cm depth and 1.5 cm length, which is formed in a distance of 1.1 cm to the last septum. The bulge is pronounced ventrally while the lateral shell of this body chamber section is more-or-less bended outwardly. This abnormal growth zone produces a slight asymmetry of the body chamber. The growth of the "outer" shell had ceased in a distance of 5 cm to the last septum (which by that time of course had not been secreted). The suture zone of the last septum covers the initial portion of the "inner" shell, which means that the compensation of the bulge began 1.5 cm posterior to it. The "inner" shell divides off the bulge of the "outer" shell, however, producing another bulge which is less pronounced. The cavity between "outer" and "inner" shell actually represents an axial tube, which is open at both ends. The "inner" shell underpins all of the non-bulgy "outer" shell and becomes the functional outer wall for the last 3 cm of the venter, substituting the original "outer" wall, which had ceased to be secreted. The internal fold of the shell, which is pronounced ventrally in the other specimen, is here restricted to the right side of the body chamber. The fold forms right in front of the muscle attachment scar and reaches a maximum height of 3 mm.

The shell microstructure of this specimen has been examined only briefly. There is an obvious dominance of prismatic aragonite forming the body chamber wall, i.e., where the bulge is pronounced.



Textfig.1: Ratio between body chamber length and number of septa in the specimen with preserved soft parts before unusual growth commenced. Maximum diameter of shell 9.7 cm.

Comparison with regularly grown nautili

The shells: Fully grown specimens of *Nautilus pompilius* have a maximum shell diameter in a range of about 15 to 18 cm (Saunders, 1981b; pers. observation). The phragmocone is usually divided into 30-33 chambers (compare Ward, 1987), however, in one specimen 38 septa have been counted (Saunders, 1981a). An individual of *N. pompilius*, having the same diameter (about 11 cm) as the two pathologic specimens, would have secreted 27-28 chambers under natural conditions. Thus it appears that about 6-9 septa too much had been secreted (compare Textfig. 1) within the two shells described here (see discussion). The ratio of diameter and number of septa of the first twenty-six chambers lies within the range of what could be measured from wild living specimens. Thus unusual growth began with the twenty-seventh septum, which is as thick as the latest septum in the ontogeny of normally grown nautili. Aside from a possible approximation of the last two or three septa (documenting maturity), the distances between the septa under natural conditions regularly increase during post-embryonic ontogeny, while it had more-or-less stagnated in the pathologic shells.

The body chamber has an angle of about 130º-135º in adult nautili. Juveniles have a relatively shorter body chamber, which is more significant in the early post-embryonic phase where an angle of only 80-90º (pers. observ.; compare Ward, 1987) occurs in case a septum has been newly secreted. A new septum reduces the angle of the body chamber temporarily for almost 30º in early juveniles and for about 20-25º in late juveniles. These data indicate that the body chambers of the two pathologic specimens are too short for about 60-70º, which in absolute numbers means that the ventral portion of the body chambers should be 5.5 to 7 cm longer.

The microstructure of the shell of nautili, which had not been reared in an aquarium tank has been examined by several authors (e.g. Blind, 1976, 1988; Bandel & Boletzky, 1979; Ward, 1987) and personally. As was expected, the composition of aragonite differs from the normal pattern only where the unusual shell growth can already be recognized macroscopically. It is evident that shell repair potentially requires large amounts of prismatic aragonite, which is comparatively promptly available to the animal.

The soft parts: The anatomy of mature individuals of *Nautilus* has been documented by a fair amount of authors (e.g. Haven, 1977; Ward, 1987) and a superficial comparison with these literature data gives already evidence that the soft parts of the pathologic specimen reflect the short body chamber. The measurements given in the preceding chapter could be roughly rated with the aid of the body of an immature *Nautilus pompilius*, bearing a shell, which measures 9.3 cm across. Although the shell is smaller compared to that of the pathologic specimen, the body is longer (8.3 cm). However, the hood is about 4 mm shorter, having a length of 5 cm. The distance between the ventral mantle margin and the siphuncle amounts to 7.2 cm. The width of the soft parts is 3.2 cm and 3.7 cm respectively. The dorsal mantle margin lies closely to the rear of the hood ("mantle fold"). The gills terminate inside the mantle cavity, in a distance of about 1.5 cm to the mantle edge.

This brief comparison shows clearly that the soft parts of the pathologic specimen are significantly disproportionate (see Pl. 2, fig. 4). While the anterior body (hood, tentacles, buccal mass, etc.) has normal proportions, the posterior soft parts on one hand are too short and on the other hand too wide.

Discussion and conclusions

Several authors have pointed out the differences in shell growth between aquarium reared individuals and wild living nautili (among others, Martin & Ward, 1978; Bandel & Spaeth, 1983; Arnold, 1985; Spaeth, 1986; Spaeth & Hoefs, 1986; Ward, 1987). The apertural shell of *Nautilus* in captivity usually shows intercalation of black organic layers, which manifest disturbation of growth. Aside from this well-known artefact, the two specimens of *Nautilus pompilius* which are described here have performed an abnormal apertural shell growth uncovering important aspects of functional morphology.

The etiology of anomaly is of secondary importance and is only briefly discussed. The formation of the bulge is considered to be primarily correlated with the water chemistry. In the early phase of rearing the nautili, for a few month calcium hydroxide had been added to the tank water, in respect to supply the animals with sufficient carbonate for a better mineralization of their shells. However, calcium hydroxide precipitates dissolved carbonate and thus reduces available anorganic shell material. In consequence, the periostracum which is secreted continuously cannot be mineralized as usual, i.e., calcification is retarded. The flexible (since predominantly organic) apertural shell is then affected by the hyponome as well as by the tentacles, their movements forcing the shell to bend outwards. Once the water chemistry is normalized the usual growth direction of apertural shell can be held.

Both specimens were able to continue ventral growth, the return to normal growth direction conditioning the formation of the bulge. In contrast, lateral apertural shell had been bended outwards to such a degree (slightly backward) that the mantle edge was finally unable to add new periostracum, which means that lateral growth had stopped (except for thickening). Consequently, to regain functionality, this dead end had to be left. The mantle margin was retracted posterior to the protuberant shell and secreted another series of shell layers, enabling the *Nautilus* to produce progressive apertural shell growth. The separation of the ventral bulge from the body chamber thus represents a coincidental conchological character and not the attempt to repair a presumed hole.

Growth rates in general or chamber formation cycles have been studied by several authors (e.g. Cochran et al., 1981; Landman et al., 1989; Saunders, 1983; Spaeth, 1986; Ward, 1985, 1987; Ward et al., 1981). However, there is very little evidence to account for the interaction and coordination between apertural shell growth and chamber formation. The main problem is that normal shell growth always produces a synchronization of certain factors, which can be also interpreted to represent a feedback system. It sounds like circular reasoning to maintain that apertural growth controls septal spacing because the former precedes the latter. The statement that the length of the soft parts, i.e., the distance between mantle margin and the septal mantle epithelium controls the length of the body chamber is trivial, however, focusses on the fact that feedback is not necessary between two different organs but between two sections of one continuous mantle. Thus nervous control is presumingly of limited complexity.

Ward (1987) more-or-less summed up the knowledge on the control of new chamber formation in *Nautilus:* "..., and because of the evidence of abnormal approximation in those specimens with shell breaks, it appears that the signal for a new chamber formation may be related to apertural shell growth, or perhaps chamber volume increases, perhaps in conjunction with liquid level". Ward (1985, 1987) found out that late ontogenetic chambers take longer to be formed than early ontogenetic chambers and because the chambers of *Nautilus* usually increase in size during ontogeny he correlated inreasing time of chamber formation events with increasing volume of chambers. Large volumes of liquid are supposed to need a longer time to be removed than low volumes. The problem is, however, that there is no obvious reason why speed of liquid removal should remain constant (even under unchanging physical conditions). The approximation of septa has usually been interpreted to reflect deceleration of shell growth (e.g. Lehmann, 1990). Thus in consequence it must be concluded that low volume chambers can be emptied very slowly.

Septal approximation is here described for the two pathologic specimens of *Nautilus pompilius* (see description chapter). Size, angle of body chamber and number of septa at the moment of capture can be well correlated when retracting from the length the portion of apertural shell with intercalated black layers on one hand and number of approximated septa on the other hand (Textfig. 1). In comparison with the shells having grown for three years in captivity it is evident that the proportions have extremely changed (see Pl. 2, figs. 1-2, 4). Six and nine septa respectively had been formed, which means a comparatively low number of 2-3 per year (in average). The body chamber of the two specimens had become increasingly shorter during this period, which obviously had to do with the apertural growth problems. The decreasing number of annual chamber formations indicates that the signal triggering off deceleration of growth, comes from the mantle margin. The body chamber of the specimen with preserved soft parts had become extremely short with the consequence that the soft parts already grew allometric (see comparison chapter). Thus it must be considered that the *Nautilus* would have seized its opportunity to stop chamber formation if it could. The newly secreted septum in one of the pathologic specimens (Specimen 1) demonstrates that even in this extreme situation chamber formation continued, actually pushing the animal out of its shell. This shows clearly that chamber formation cannot be stopped (not even temporarily) before the *Nautilus* has reached maturity. The minimum annual number of septa is considered to be not higher than two but possibly only one chamber has to be formed.

Although it makes no difference for analysis of functional morphology if the pathology described here is strictly correlated to tank conditions or perhaps occurs also under natural conditions, because performance of life is always somehow objective, it may be of some interest if a similar scenario can also be enacted in the wild. A short body chamber can be produced by predators breaking off apertural shell. However, such a loss of body chamber shell is a matter of moments and if too much shell is broken off, the *Nautilus* being attacked is not able to compensate the sudden loss of weight and will ascend to the surface. On the other hand, the loss of small pieces of shell will not produce a strongly disproportionate growth as documented here. In case the *Nautilus* is repeatedly attacked in more-or-less regular sequences, a series of minor shell breakages will also sum up to a degree at which the loss of weight finally cannot be tolerated any longer. The two pathologic specimens have an extremely short body chamber, however, it has to be emphasized that in contrast to shell breakage there was no evident loss of weight. The nautili actually had continuously secreted apertural shell, if not in length, but in thickness. Thus it appears that physical forces cannot produce the desired scenario but solely chemical conditions.

We could find in the literature two examples of fossil ectocochliates (usually not reared in aquarium tanks), which demonstrate that a similar chemically controlled disturbation of shell growth actually may occur under natural conditions. Sornay (1955) figured a Cenomanian *Nautilus* and described three more specimens, which all show protuberant shell growth, the bulgy shell deformation divided off from the body chamber by another series of shell layers.

Schairer (1989) described a specimen of the Bathonian perisphinctid ammonite *Morrisceras sknipum* (Buckman, 1921) forma *inflata* Keupp, 1976 (Pl. 2, figs. 5-6). The anomalous shell growth is preceded by the repair of a major shell breakage and is mainly characterized by an asymmetrical ventral bulge - with displacement of the centre of gravity to the right - of which the shell of the initial phase of formation was bended backward, comparable to the lateral protuberant shell in the two Recent pathologic specimens of *Nautilus*. However, while the nautili were not able to produce progressive apertural shell growth in case of backwardly bended shell and thus had to secrete another body chamber wall (see description) to regain normal growth direction, the ammonite could still add apertural periostracum recovering more-or-less functional growth without underpinning the protuberant shell. Consequently, in contrast to the nautili, the body chamber of the ammonite was only slightly reduced in length, probably not triggering pathology of soft parts. The *Morrisceras* in later ontogeny was able to secrete a septum perfectly fitting in the complicated shape of the anomalous grown shell section (Pl. 2, fig. 5).

Finally it is proposed that the Jurassic *Morrisceras sknipum* should not be attributed to forma aegra *inflata,* a term which can be restricted to more-or-less simple protuberances, triggered off by parasites swelling up the soft parts and thus secondarily enlargening the volume of the body chamber (see Keupp, 1995 and references therein). In addition, the forma aegra *complicata* n.f. is introduced here to describe (bio-) chemically controlled anomalous shell growth (including retarded calcification), producing folds in connection with movements of tentacles and hyponome, i.e., apertural shell temporarily grows backward.

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Plate 1

Fig.1: *Nautilus pompilius* in the aquarium tank of the Eichstätt Museum. The attention is drawn to the apertural shell. The onset of intercalation of black organic layers marks the beginning shell growth in captivity. The shell margin is already slightly bended outwardly, marking the initial phase of the formation of the bulge. The creamy white margin is not the inside of the outwardly bended shell but the mantle edge. The photograph was taken after having reared the *Nautilus* for about half a year (photograph by courtesy of the Eichstätt Museum).

Figs.2-4: Same specimen as in fig.1, which died and was preserved after three years in captivity: in lateral, semi-lateral and ventral view. Maximum diameter of shell about 10.9 cm (excluding the bulge).

Figs.5-6: Left and right lateral view of second pathologic specimen, which died about a few month earlier than the other individual. The soft parts have not been preserved. The intercalated black organic layers indicate shell formation in captivity. The aperture of the shell was damaged during transport. Maximum diameter of shell about 11.0 cm.


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Plate 2

Figs.1-2: Median sections of pathologic specimens, revealing the pattern of chamber formation and length and macroscopic shell structure of the body chamber. Not to scale.

Fig.3: Shell of pathologic specimen with preserved soft parts in semi-lateral view. Not to scale.

Fig.4: The spatial arrangement of soft parts, which are evidently disproportionate. The hypothetical normal length of the body chamber is indiacted by an arrow. Scale bar = 5 cm.

Abbreviations: e = eye, g = gills, h = hood, hy = hyponome, me = mantle edge, r = retractor muscle, s = spadix, si = siphuncle, t = tentacles, te = testis.

Fig.5: Moulding of pathologic specimen of the Jurassic perisphinctid ammonite *Morrisceras sknipum* in right semi-lateral view, demonstrating shape and dimension of abnormal shell growth. For scale see fig. 6.

Fig. 6: *Morrisceras sknipum*; original of same specimen as in fig. 5 (by courtesy of G. Schairer). Maximum diameter about 3.6 cm.

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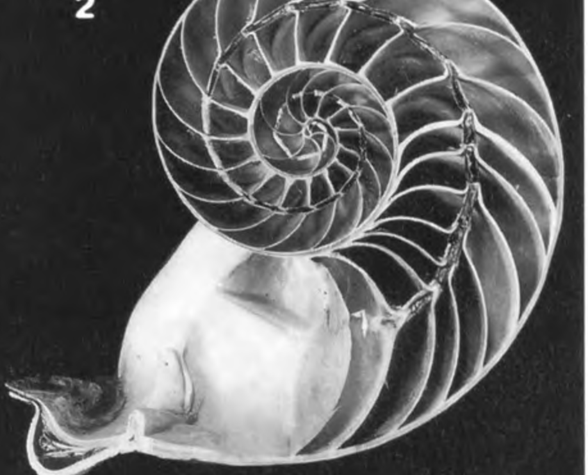

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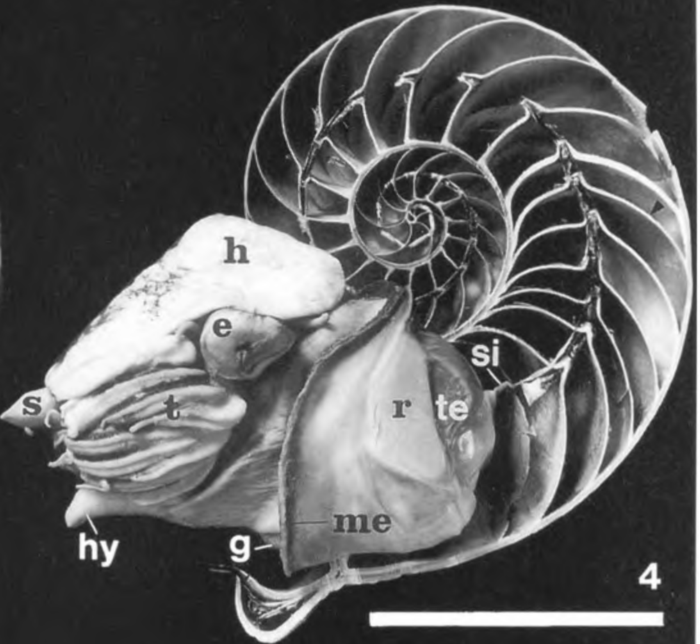

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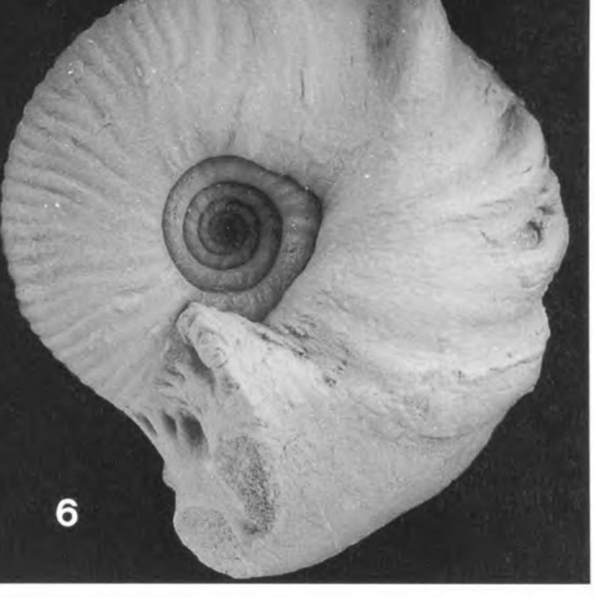

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Plate 3

Figs.1-5: Shell microstructure of pathologic specimen with preserved soft parts.

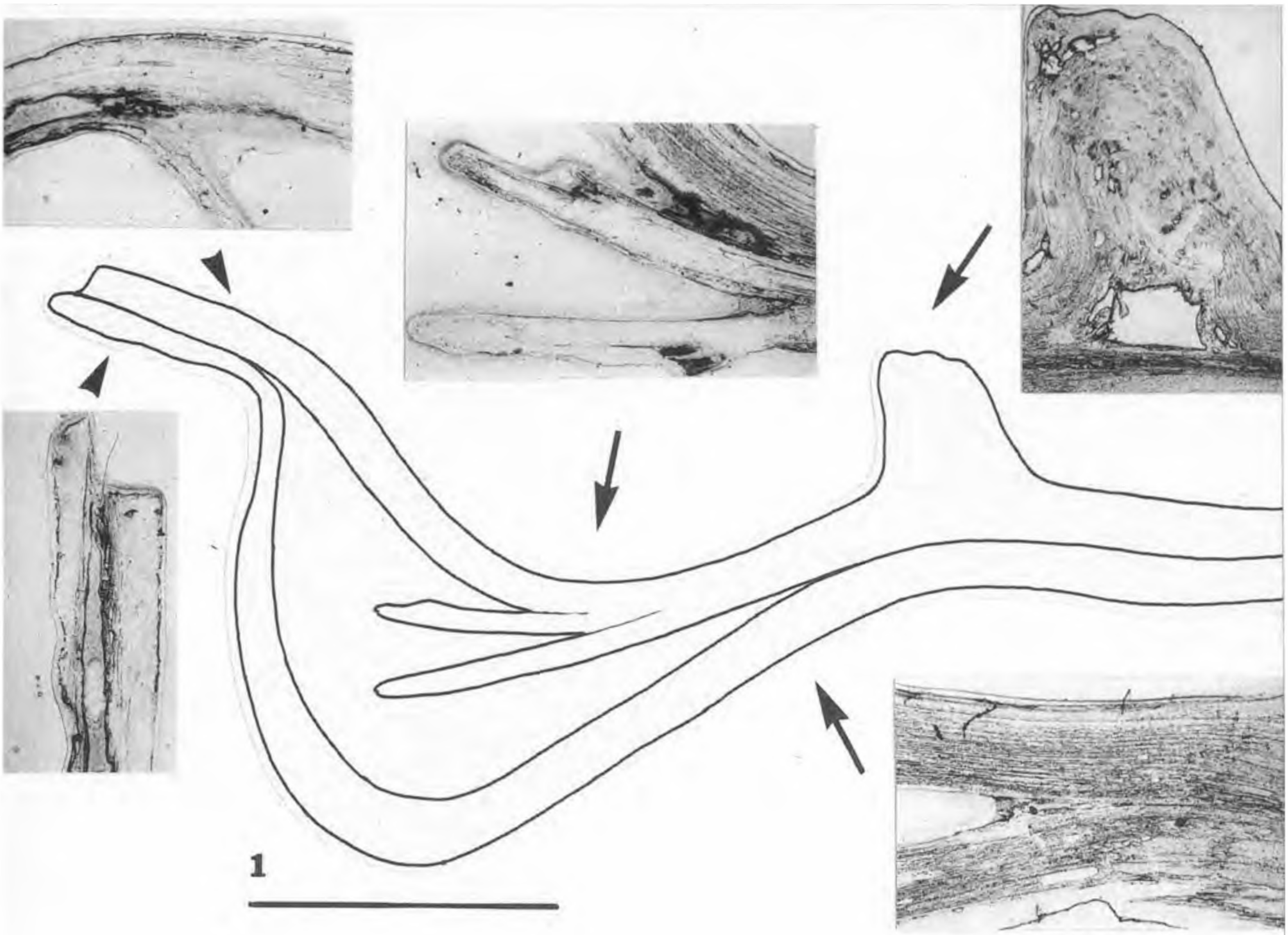
Fig.1: Sketch of acetate peel of median section of the unusual growth zone. Photographs with focus on spectacular sections: A: internal fold, B: angle between "outer" and "inner" shell, C: two shell layers which terminate inside the cavity of the bulge, D: the "inner" shell joins the "outer" shell, E: the apertural shell. Scale line for sketch = 1 cm.

Fig.2: The pellicle of septal shell consists of several organic layers; the surface is covered by "blebs". Scale bar = 5 µm.

Fig.3: The abnormal growth zone is characterized by comparatively large amounts of spherulitic aggregates of aragonite. Scale bar = 50 µm.

Fig.4: Section of the ventral bulge showing the unusual intercalation of prismatic aragonite between the nacreous layers of the shell. Scale bar = 20 µm.

Fig.5: The pagodiform growth fronts of nacre could be well recognized in the latest septum.
Scale bar = 10 µm



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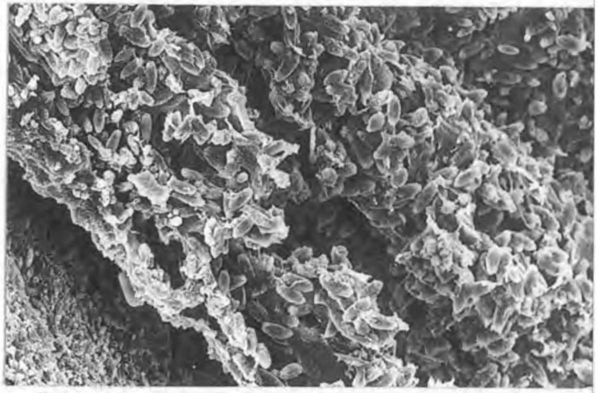

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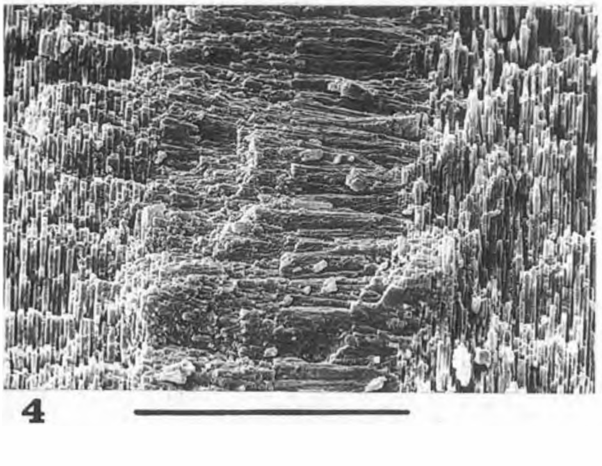

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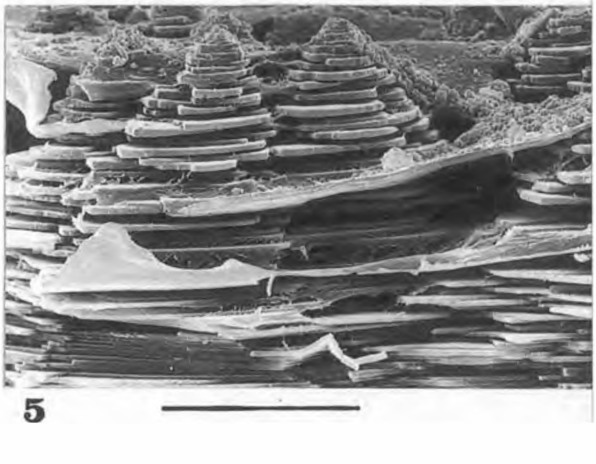

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Plate 4

Figs.1-8: Radular teeth of pathologic *Nautilus pompilius.*

Fig.1: General view. Scale bar = 4 mm.

Fig.2: Magnification of section from inside the radula sac. Scale bar = 2 mm.

Fig.3: Magnification of functional part. Scale bar = 2 mm.

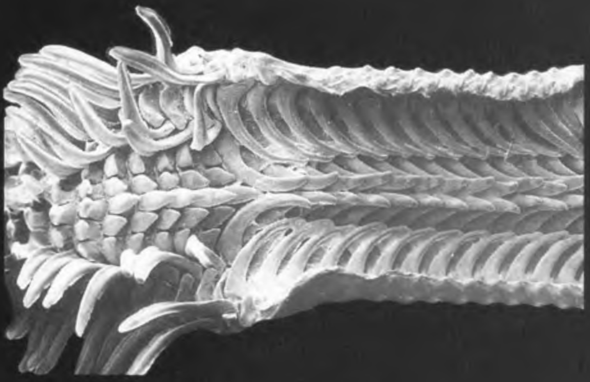
Fig.4: Magnification of central and lateral teeth. Scale bar = 0.5 mm.

Fig.5: Close-up of central teeth. Scale bar = 0.5 mm.

Fig.6: Magnification of cutting edge of central tooth. Scale bar = 0.05 mm.

Fig.7: Marginal teeth. Scale bar = 1 mm.

Fig.8: Close-up of marginal tooth. Scale bar = 0.5 mm.



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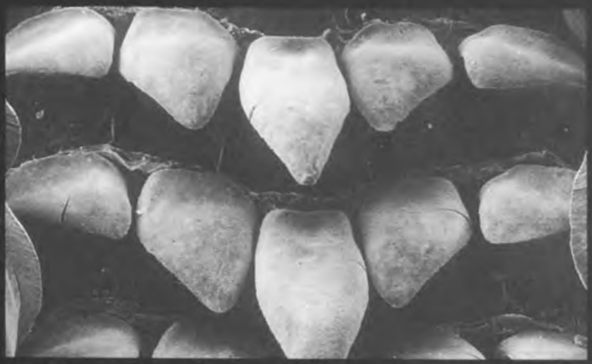

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