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REMARKS ON THE EMBRYOGENY AND POSTEMBRYONAL
DEVELOPMENT OF AMMONITES

Abstract.— Previous views on the type of embryogeny in ammonites are discussed by the present writer who also points out some morphological characters of the initial chamber, along with the first whorl, which are indicative of a non-larval type of embryogeny. The swelling of shell wall on the nepionic constriction is analyzed in detail and the manner of forming this swelling explained, together with the hypothesis on an adaptative character of the swelling.

The diagrams of a relative density of septa in the genus *Quenstedtoceras* are analyzed and used as a basis for showing certain similarities in the postembryonal development of ammonites and the development of the Recent Decapoda. The occurrence of the morphological hiatus—lack of one whorl—characteristic for the sexual dimorphism of type “A” is explained, on the basis of the *Quenstedtoceras*, by the difference of one whorl in the ending of the only sexual cycle in males and the first sexual cycle in females.

INTRODUCTION

The works of Denton & Gilpin-Brown (1961, 1966), concerning the buoyancy of the cuttlefish and the pearly nautilus, make up a basis for interpreting the function of shell in ammonites mostly as a hydrostatic organ. In the ontogenetic development of all ammonites, differences observed in the proportions of the size of a hydrostatic organ to the size of the ammonite body, as well as in the proportions of the diameter of siphon to the height and width of whorls. Particularly large is the difference in the two proportions between the initial chamber and subsequent phragmoconal chambers. This allows one to interpret the initial chamber, together with caecum, as a particularly well-developed hydrostatic organ, representing an adaptation to the planktonic mode of life of juvenile forms. A certain discrepancy is observed between the interpretation of the role of initial chamber and the theory of larval embryogeny in ammonites, particularly developed by Erben (1964). According to this author initial chamber is distinguished, on the basis of morphological and microstructural differences, as a separate, embryonal stage in the ontogenetic development of shell, homological of the trochophore shell of other mol-

luses, while the first whorl, up to the termination of the nepionic constriction, is supposed to correspond to the living chamber of a free-floating larva of the *veliger* type. The stability of the places in which microstructural changes occur in ammonite shell, coinciding with Erben's "I and II Wachstums-Änderung", recorded by Birkelund (1967), Birkelund & Hansen (1967) and Erben, Flajs & Siehl (1968, 1969), is difficult to explain in the light of the theory of the direct development of ammonites. On the other hand, the homologization of the initial chamber with the shell of trochophore of other molluscs is rather doubtful. The size of Recent trochophores amounts to nearly 0.2 mm, while that of initial chambers in primitive ammonites varies between 0.60 and 0.70 mm (Erben, 1964), and decreases in the process of evolution (Ruzhentsev & Shimanskij, 1954).

The distances between septa were studied by several authors, e.g., Oechsle (1958), Rieber (1963), Lehmann (1966), Bayer (1972) and the results of these studies applied to taxonomic considerations and those concerning sexual dimorphism. The interpretation of the diagrams of relative density of septa in the representatives of the genus *Quenstedtoceras*, preserved complete, allows one to show certain analogies in the postembryonal development of this genus and of the Recent Decapoda.

In the present paper, the terminology is used after Erben, Flajs & Siehl (1969), except for the term "II Wachstums-Änderung", for which Hyatt's definition "nepionic constriction" has been kept and the term protoconch, replaced by the definition "initial chamber".

The collection described is housed at Palaeozoological Institute of the Polish Academy of Sciences (abbr. Z. PAL.). The present writer feels indebted to Mr. Z. Strąk for making thin sections, to Miss M. Wąsak and Miss E. Mulawa for taking photographs.

MATERIAL AND METHOD

Specimens of the genus *Quenstedtoceras* Hyatt, abundantly occurring at Łuków, eastern Poland, are the basis of the present paper. The Jurassic deposits, occurring in the environs of Łuków, form erratic masses of considerable size embedded in Quaternary sediments. These are black and dark-gray clays with calcareous and sideritic concretions. The macrofauna mostly accumulated in these concretions determines the age of the Łuków deposits as Middle Callovian and the lowermost part of Upper Callovian (Makowski, 1952).

The Łuków ammonites are very well preserved. The mineral substance of their shells does not differ from that of the shells of Recent molluscs. The living chamber is frequently preserved in shells which are in various stages of the ontogenetic development. In most specimens, the living chamber and the last phragmoconal chambers are filled with deposit. The remaining part of phragmocone may be filled partly or completely with

pyrite, siderite, calcite, or it may be quite empty, without any traces of mineralization. Specimens with an empty phragmocone were sectioned after filling empty spaces with epoxy resin or Canada balsam.

Sectioned specimens, examined through the Stereoscan JSM-2 electron microscope, were previously polished with aluminum oxides and then etched for 15 minutes in a 2-per-cent solution of EDTA. For the purposes of observation, all specimens were covered with carbon and, subsequently, gold.

The measurements of a relative density of septa were taken in the medial plane and on the sectioned surface of specimens. The relative density of septa is expressed by the magnitude of an angle between two septa adjoining each other. The apex of such an angle is situated in the middle of the initial chamber, while its arms run through the medial points of successive septa.

More than 50 specimens were studied on medial sections. Angles were measured by means of microscope with a revolving object stage.

THE TYPE OF EMBRYOGENY IN AMMONITES

Previous views

Two or three ontogenetic stages are distinguished in the development of ammonites by the authors who deal with the ontogeny of this group. Erben (1962, 1964), Erben, Flajs & Siehl (1968, 1969), Makowski (1971) and others distinguish the following three stages: (1) an embryonal, (2) a free-floating larva of the veliger type and (3) a postlarval stage. Only two, that is, (1) an embryonal and (2) a postembryonal stage, are distinguished by Ruzhentsev & Shimanskij (1954), Druzcic (1956), Druzcic & Khiami (1970), Druzcic, Doguzhaieva & Mikhailova (1973).

The followers of the former conception assume, as a boundary between the embryonal and larval stage, a constriction of shell at the anterior end of the initial chamber (protoconch), at which the microstructure of wall also changes from subprismatic to prismatic (Birkelund, 1967; Birkelund & Hansen, 1968; Erben, Flajs & Siehl, 1968, 1969). According to Erben (1962, 1964), the shell in the embryonal stage would correspond to that secreted by the trochophore of other molluscs, and in the second stage to the *veliger* larva. It would include the first whorl up to the termination of the nepionic constriction, as well as prosiphon, caecum and proseptum. The difference between the second and third ontogenetic stage is expressed in changed growth of whorl, the appearance of growth lines, and of sculpture (Erben, 1962) and of a pearly layer characteristic of the shell proper (Erben, Flajs & Siehl, 1968, 1969). The metamorphosis of larva would result in a swelling of shell at the nepionic constriction, a change in the shape of the posterior part of the ammonite body expressed in an inver-

sion of the suture between the first and second septum (Erben, 1962) and in a change in the arrangement of mantle expressed in a different relation of the first septum to the inner surface of shell (Erben, Flajs & Siehl, *l.c.*). Makowski (1971, p. 328) believes that the larval metamorphosis results in the appearance, behind the nepionic constriction, of "a quite new element in the structure of shell, that is, a prismatic layer which appears simultaneously with growth lines, sculpture and colour". He compares differences between the protoconch and taleoconch of prosobranchiate gastropods with those between the second and third ontogenetic stage in ammonites. In connection with the analogies existing, Makowski (1971) suggests to extend the concept of protoconch and include in it all larval elements, that is, prosiphon, caecum and proseptum as concerns internal elements, as well as the initial chamber, along with the first whorl up to the termination of the nepionic constriction.

The followers of the direct development of ammonites (*l. c.*) base their view on an analogy to the simple development of all the Recent cephalopods. The shell up to the termination of the nepionic constriction, but to the exclusion of the swelling of pearly layer, is assigned by Druzczic & Khiami (1970) to the embryonal stage. In their opinion, also the second septum may belong to this stage.

Observations

At the nepionic constriction, the prismatic layer becomes gradually thinner and thinner up to the end of constriction. The distance, over which a decrease in the thickness of prismatic layer takes place, may be accurately determined and it probably corresponds to the width of the pallial zone in which took place the secretion of mineral substances of the prismatic layer. As seen in a juvenil *Quenstedtoceras henrici* (Pl. V, Fig. 1a, b; Text-fig. 1) and *Kosmoceras (Spinikosmoceras)* sp., illustrated by Erben, Flajs & Siehl (1969, Pl. 8, Fig. 4), beginning with the termination of the nepionic constriction, the prismatic layer changes its direction of growth and continues towards the posterior part of shell and towards its inner surface, where it disappears. The prismatic layer of this zone of shell has its microstructure in a complete conformity with that of the outer part of the prismatic layer of shell before the termination of the nepionic constriction.

The arrangement of the laminae of nacreous layer, which mostly forms the swelling of shell at the nepionic constriction, is as follows. The first, outer laminae are relatively short and tapering posteriorly near the end of constriction under the prismatic layer. Further laminae of nacreous layer, becoming longer and longer, taper under the prismatic layer further towards the end of the nepionic constriction than the first ones (Pl. V, Fig. 1a, b; Text-fig. 1 and Erben, Flajs & Siehl, 1969, Pl. 8, Figs 4 and 5;

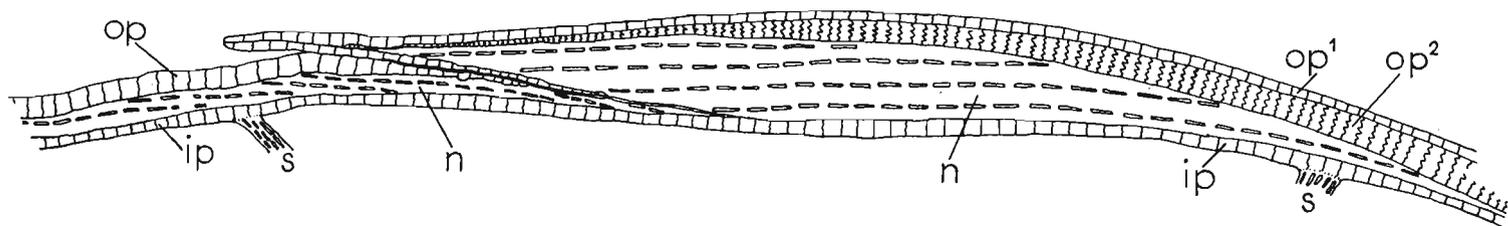


Fig. 1. *Quenstedtoceras henrici* R. Douv. A longitudinal section of the ventral wall of shell at the nepionic constriction. The same specimen and section as on Plate V, Figs 1a, b; explanations as on Text-fig. 3.

Pl. 9, Figs 1—5). The drawings, presented by Erben *et al.* (*l. c.*, Pl. 9a), illustrate a different arrangement of the laminae of nacreous layer and are not in conformity with photographs on the basis of which they were drawn. The structure of the swelling of shell at the nepionic constriction described above may be explained only by a withdrawal of the margin of mantle with a simultaneous secretion of the prismatic layer and by a secretion of a quite new structural element, that is, the nacreous layer. The swelling of shell at the nepionic constriction is separated from the further part of shell by a sharply outlined boundary which, viewed in the medial section (Pl. V, Fig. 1a, b; Text-fig. 1), runs from the end of the swelling up to the inner prismatic layer.

Studying relative spacing of septa in the genus *Quenstedtoceras*, expressed by the value of a median angle between septa, the present writer found a reduction in a relative distance between septa 3 and 4, 4 and 5 and 5 and 6 (Text-fig. 2b, c, d, h, i, j).

The decreased distance between the proseptum and the second septum, shown in diagrams (Text-fig. 2g), is caused by an "inversion" of medial elements of the posterior part of body prior to the formation of the second septum. For this reason, in the medial section, the distance is measured between the middle of proseptum, which, in this plane, is strongly bent anteriorly and the middle of the second septum, which, in this same plane, is bent posteriorly. In the parallel section, but running through saddle E/L of the second septum and through lobe 1 which corresponds to it on proseptum, the first two septa are considerably widely spaced. A different shape of proseptum precludes the possibility of comparable results obtained by this method.

In the genus *Quenstedtoceras*, the relative length of the living chamber displays a considerable degree of stability. The shell of juvenile individuals of *Quenstedtoceras* have living chambers 195° to 240° and mostly 225° long. Similar is the case of specimens, whose sex may already be determined but which do not yet display gerontic characters.

The male and female specimens, which do display gerontic stage have living chambers 160° to 175° long. The length of a part of whorl between the proseptum and the termination of the nepionic constriction amounts, in three specimens of *Q. sp. juv.* respectively 275° , 283° and 335° . A sector of whorl, measured from the nacroseptum preceding the reduced phragmoconal chamber (the second or third nacroseptum) to the termination of the nepionic constriction is, in the same specimens, 225° , 225° , and 236° long, which represents identical values with those in juvenile individuals.

The initial chamber, together with the first whorl up to the termination of the nepionic constriction, is marked in the investigated representatives of *Quenstedtoceras* and *Kosmoceras* by a peculiar microornamentation which, except for the nepionic constriction (Pl. IV, Figs 1, 2), is not

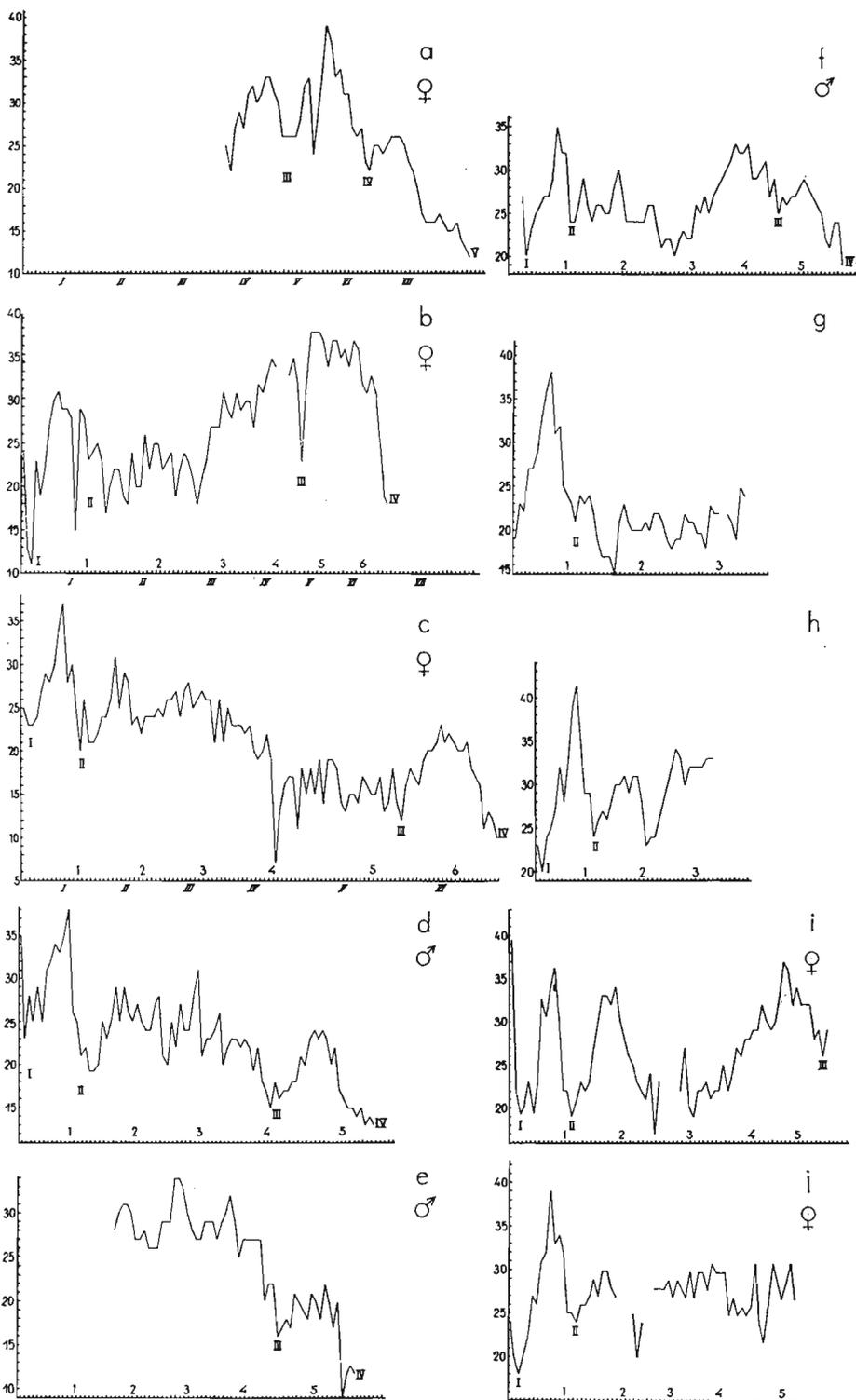


Fig. 2. Diagrams of relative density of septa in the following representatives of the genus *Quenstedtioceras* from Łuków: a *Q. vertumnum* (Leck.) ♀, Z. PAL. No. Am. 1/9, b *Q. vertumnum* (Leck.) ♀, Z. PAL. No. Am. 1/16, c *Q. henrici* R. Douv. ♀, Z. PAL. No. Am. 1/17, d-f *Q. henrici* R. Douv. ♂, Z. PAL. No. Am. 1/104, 107, 335, g *Q. sp. juv. non henrici*, Z. PAL. No. Am. 1/5, h *Q. henrici* R. Douv. juv., Z. PAL. No. Am. 1/18, i *Q. mariae* (d'Orb.) ♀ juv., Z. PAL. No. Am. 1/501, j *Q. vertumnum* (Leck.) ♀, juv., Z. PAL. No. Am. 1/159.

observed on the shell. Small nodes, covering the surface of the initial chamber and the first whorl, are the main element of this microornamentation. The distribution of the nodes is irregular.

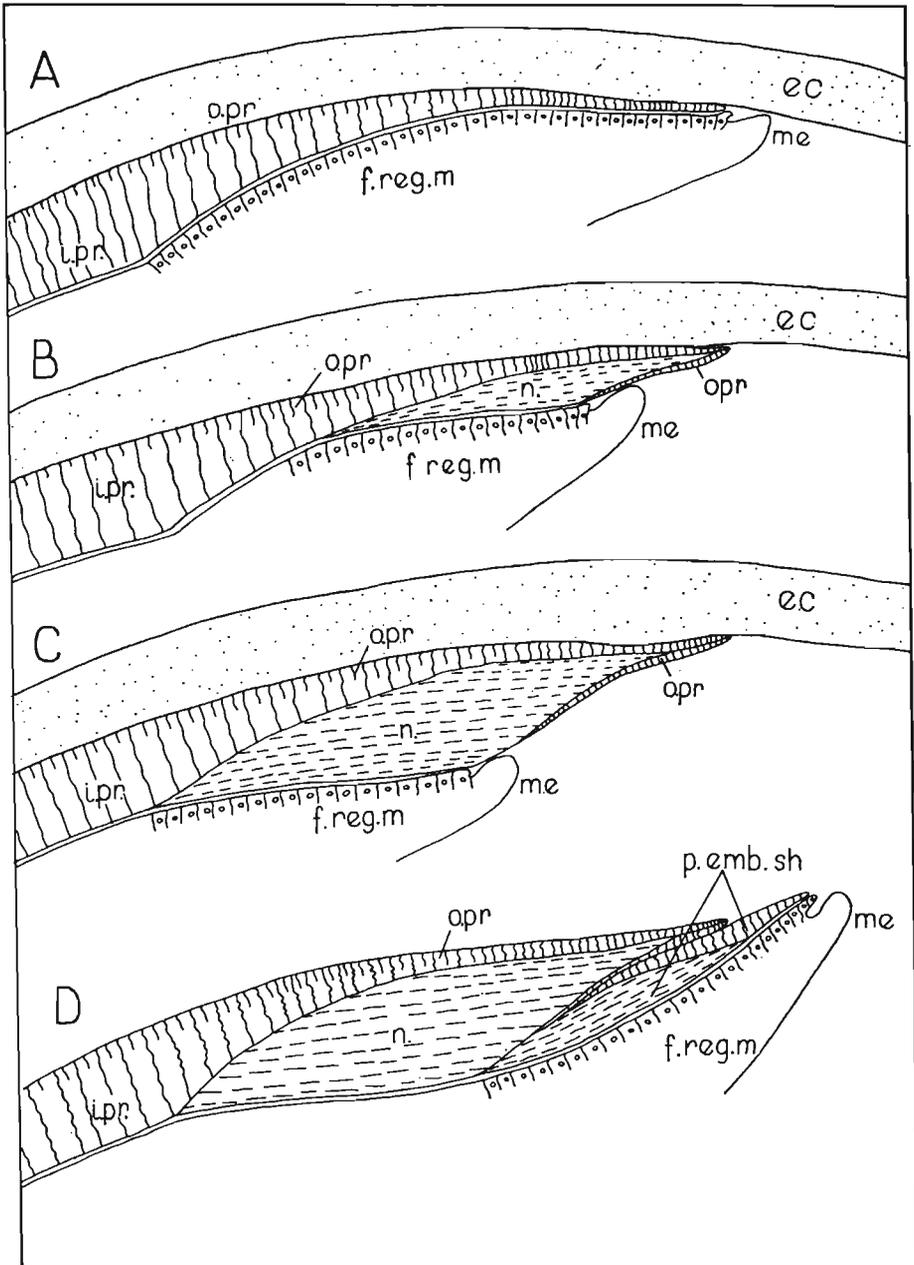


Fig. 3. A diagram of the formation of the swelling of shell at the nepionic constriction; successive stages of the thickening: A-D. e. c. eggs envelope; o. pr. outer part of prismatic layer; i. pr. inner part of prismatic layer; n. pearly layer of the swelling of shell; m. e. pallial margin; f. reg. m. physiologically active zone of mantle (the zone of shell wall secretion); p. em. sh. postembryonal shell.

No growth lines and other boundaries of discontinuity were found on the surface of shell before the end of the nepionic constriction.

The origin of growth lines is complex. Partly these are growth discontinuities, marked in transverse section in all layers forming the wall of shell and partly rollers and furrows forming a microornamentation,

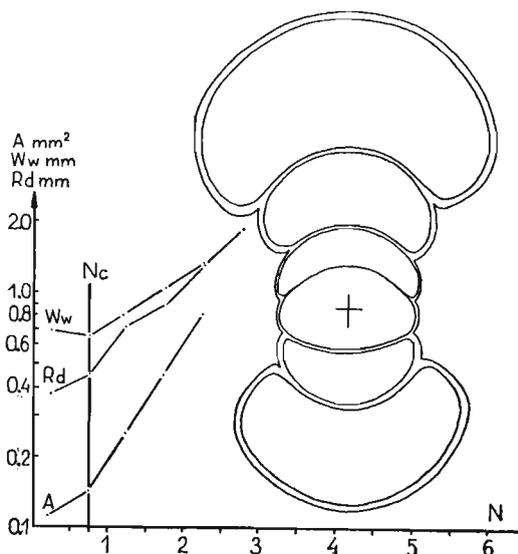


Fig. 4. An increase in some parameters of shell on the first whorls of *Q. vertumnum* (Leck.) ♂, Z. PAL. No. Am. I/316. Ww—width of whorl; Rd shell radius; A area of transverse section of whorl; Nc nepionic constriction; N number of whorls.

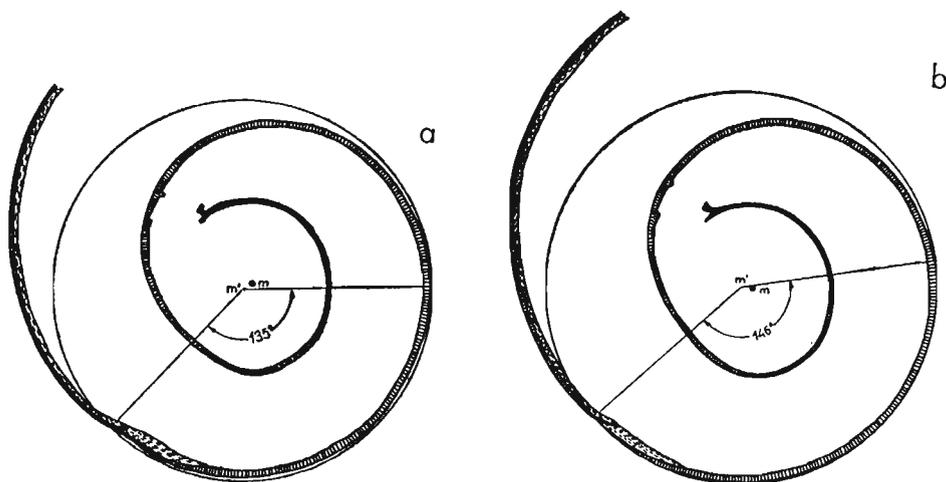


Fig. 5. A schematic drawing of the coiling of shell in two representatives of *Quenstedtoceras*, Z. PAL. No. Am. I/3, 6 shown in medial section. It is visible that considerable part of the terminal sector of the embryonal shell does not display a decrease in spiral radius. m the middle of initial chambers; m' the middle of a circle.

independent of macroornamentation but not marking the discontinuity of the structure of layers in the section through shell walls. Behind the nepionic constriction, the ammonite shell is covered with growth lines of both types, the second type being predominant. The growth lines of the first type may be compared with the boundaries of laminae of subprismatic and prismatic layers (see Erben *et al.*, 1969, Pl. 3, Fig. 12, Text-fig. 5), occurring on shell before the nepionic constriction.

Before the nepionic constriction, the ammonite shell also displays certain geometrical features, which distinguish it from the remaining part of shell. In medial section, considerable part of the terminal sector of the first whorl (about 140°) does not display an increase in the radius of spiral (Text-fig. 5a, b). Beginning with the nepionic constriction, an increase occurs in the width of whorl and the surface of transverse section also begins to increase more rapidly (Text-fig. 4). Irregularities in growth, consisting in a rapid increase in the radius of spiral behind

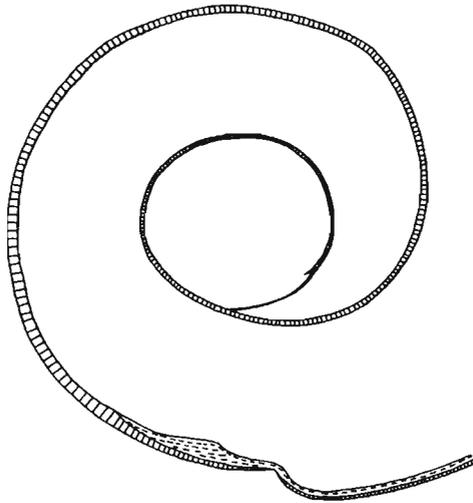


Fig. 6. A schematic drawing showing a violent increase in spiral radius behind the nepionic constriction in *Quenstedtoceras henrici* R. Douv. juv., Z. PAL. No. Am. I/14.

the nepionic constriction (Text-fig. 6) are a frequent phenomenon in *Quenstedtoceras*. The irregularities of this type are not observed, however, on the first whorl before the constriction.

Discussion

Characters, on the basis of which the authors mentioned at the beginning separate the larval (in the case of distinguishing three stages) or embryonal (in the case of two stages only) stage from the juvenile

stage of cephalopod, are proper, on the one hand, of the wall of shell and, on the other, of the products of the posterior part of an individual's body, that is, of siphonal elements and septa.

Changes in the structure of the wall of shell, occurring at the nepionic constriction, do not arouse most authors' reservations that they might result from the transition between two different stages of the ontogenetic development. What may, however, cause some controversies is the question if the swelling of shell was formed as a result of the metamorphosis of larva (Erben *et al.*, 1969) or after hatching from egg capsule following a direct development (Druzcic & Khiami, 1970). Considerable doubts are aroused by the boundary of the two stages, determined on the basis of the structure of septa.

Believing in the existence of a free-floating larva of the *veliger* type, Erben, Flajs & Siehl (1968, 1969), correlate the structural changes at the nepionic constriction with those occurring between proseptum and the second septum and consider them as simultaneously formed as a result of the larval metamorphosis. These authors are, however, unable to answer the question why not only the first, but also the second septum are composed of the prismatic layer, while the rest of them — of the nacreous layer. According to Druzcic & Khiami (1970), the second septum may also belong to this same ontogenetic stage as the first and a different shape of proseptum may be connected correlatively with the formation of caecum, while the anterior bend of the posterior part of the ammonite body (the dorsal and ventral saddles on proseptum) might serve as a space for caecum. There is also the third possibility, so far never taken into account, that the bend of the posterior part of the ammonite body was of an adaptative importance to the functioning of the primary hydrostatic apparatus of the juvenile form.

The problem of a different relation of proseptum to the outer wall of shell has not so far been elucidated. The observations of Erben, Flajs & Siehl (1968, 1969), showing the continuity of the structure of proseptum and the inner prismatic layer of the initial chamber, were conducted only on medial sections, while those of Palframian (1967), showing the discontinuity of proseptum and the inner wall of shell, were conducted on sections parallel to the medial one, but running through lobe 1. It is likely, therefore, that proseptum is a product of the posterior part of the ammonite body, which only at first was formed in some places parallel to the wall of shell.

In Recent cephalopods such as the *Sepia* and *Nautilus*, whose shell plays the role of a hydrostatic organ, the hatching from egg capsule is marked by changes in distances between septa. In *Sepia officinalis* and *S. esculenta*, the eighth septum, situated at the most reduced distance from the preceding one, is the first postembryonal septum (Denton & Gilpin-Brown, 1966). Studying the capacity of phragmoconal chambers

in *Nautilus macromphalus*, Denton & Gilpin-Brown (*l. c.*) found, between the fourth and fifth chamber counting from the apical part of shell, a reduction in capacity which they compared with the reduction in distance between the seventh and eighth septum in the *Sepia*. Concerning the number of septa in the embryonal shell of *Nautilus pompilius*, these are the following two views: (1) that the embryonal shell had, prior to hatching, about seven septa, and that the next, postembryonal septum was situated at a reduced distance from the preceding one (Willey, 1896; Naef, 1928; Stenzel, 1964) and (2) that the embryonal shell had only two or three septa (Eichler & Ristedt, 1966). Furthermore, according to the latter view, a difference in spaces was supposed to be marked between the embryonal and postembryonal septa (see Eichler & Ristedt, 1966, Fig. 4).

A reduction or change in spaces between septa in *Quenstedtoceras*, which falls between septa 3 and 4, 4 and 5 and 5 and 6, may be compared with similar differences between the last embryonal and first post-embryonal septum in *Sepia* and *Nautilus*.

The constancy of the length of living chamber in *Quenstedtoceras* confirms the correctness of correlating the anterior margin of the nepionic constriction with the nacroseptum (which precedes the reduced chamber of the initial sector of phragmocone) as extreme elements of the embryonal shell.

In Recent cephalopods, the process of hatching from egg capsules is related with effects of enzymes on these capsules, but it is to a considerable extent also the mechanical action of the embryo itself leads to the perforation of capsule and to its rejection (Zuev & Nesis, 1971). When the outer (ventral) wall of shell closely adheres to the egg capsule, which was the most likely case in ammonites, the mechanical action of embryo is directed both at the egg capsule and the margin of shell. The thinning margin of shell, composed only of the prismatic

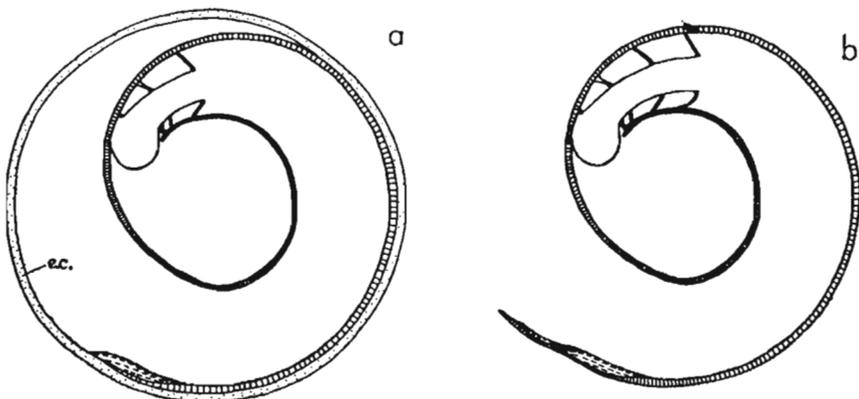


Fig. 7. A diagram showing the last stage of the embryonal development (a) and the early stage of the postembryonal development (b) egg envelope (e.c.) taken into account.

layer, whose crystals are relatively thin and oriented with their longer axis perpendicularly to the surface of shell, might be broken to pieces. The observed withdrawal of the pallial margin served to form the swelling of shell at the end of the embryonal stage (it directly preceded the hatching from egg capsule) and the swelling itself was of an adaptative importance and served to reinforce the primarily thinning margin of shell composed of the prismatic layer only. Erben, Flajs & Siehl (1968) also assumed the withdrawal of the pallial margin in the process of the formation of shell swelling at the nepionic constriction, but they related it with far-reaching changes in the arrangement of mantle during the metamorphosis of larva. Loading the anterior margin of shell so that the young animal could take an advantageous position after hatching was probably another adaptative function of shell swelling at the nepionic constriction.

The egg capsules in all Recent Decapoda are composed of a jellied substance varying in consistence. In the process of embryogeny, the dimensions of egg capsules in some genera may increase, much the same as in some marine gastropods (Roginskaja, 1962). In the final stage of growth, the embryos of ammonites already having a primitive hydrostatic apparatus developed, were marked by a considerable 'volume as compared with the rest of body. It was larger than that of Recent cephalopods and, therefore, it is very likely that, in the ammonites, the process of the growth of egg capsules also took place. Spherical forms, described by Lehmann (1966) as "Eihülen von *Eleganticerias*?" are nearly equal in size to the initial chamber in *Eleganticerias*, but no embryo remains were found inside them.

The following facts may be explained under the assumption that the effects of egg capsules on the growth of embryonal shell were limited: (1) The embryonal shell in ammonites lacks as a rule an ornamentation characteristic of a postembryonal shell, that is, spines or ribs, for the formation of which an unconstrained position of pallial margin is necessary. (2) The transitory occurrence of growth lines on the embryonal shell may be explained as above (*item* 1) and partly also by a higher degree of stability of physico-chemical and feeding conditions inside the egg capsule. (3) The presence of a rather long terminal sector of the embryonal shell which does not display an increase in the radius of spiral and width of whorl and which displays an only slight increase in the area of transverse section.

The first irregularities in the increase in the parameters mentioned above occur behind the nepionic constriction. The drop in an increase in the radius of outer spiral over the last sector of embryonal shell in the Recent *Nautilus pompilius* was revealed by Eichler & Ristedt (1966).

The following statements may sum up the discussion: (1) Changes in ornamentation trace of growth lines and coloration of shell, interpreted

by Erben (1962), Erben, Flajs & Siehl (1969) and Makowski (1971) as a result of larval metamorphosis, also occur on the boundary between the embryonal and postembryonal shell in the Recent *Nautilus* (Stenzel, 1964; Eichler & Ristedt, 1966).

(2) Changes in shell structure which occurred in ammonites at the nepionic constriction probably were not synchronous with those occurring between the first and second septum. This brings in question the importance of these changes as resulting from larval metamorphosis.

(3) Several morphological characters of the sector of ammonite shell reaching the nepionic constriction may be explained by limiting effects of egg capsules on the growth of embryonal shell.

(4) There is no justification for separating the initial chamber as an independent development stage only on the basis of morphology and structural differences. As follows from Denton's & Gilpin-Brown's (1961, 1966) studies, the spherical initial chamber in ammonites should be treated rather as an element of a particularly well-developed hydrostatic organ, which represents an adaptation to the planktonic mode of life of the early postembryonal stages. This problem is similarly presented by Druzzic, Doguzhajeva & Mikhajlova (1973) and Zakharov (1972).

(5) The problem of homology of the embryonal structures of ammonites with the larval structures of other molluscs (Makowski, 1971, p. 331) requires more studies within paleozoic groups and a more extensive discussion.

THE POSTEMBRYONAL DEVELOPMENT OF THE AMMONITES OF THE GENUS *QUENSTEDTOCERAS* HYATT

The diagrams of a relative density of septa, drawn for many male and female representatives of the genus *Quenstedtoceras*, display certain regularities, which may be explained by comparing them with the Recent Decapoda (Text-fig. 2a—j).

Beginning with the second septum (the situation of proseptum is incomparable with that of further septa with the use of the method of measuring angles), we may distinguish in these diagrams, in both male and female forms, depressions corresponding to concentration of septa, and elevation corresponding to their wider spacing. The situation of some depressions displays a considerable constancy in relation to the number of whorls.

The minimum of the first depression occurs behind the first, second or third nacroseptum in all the specimens examined. In all of them, regardless of sex and species, a fairly steep elevation, terminating with the second depression and occurring at the beginning of the second whorl, is situated behind the first depression. A sector of diagram with a fairly varied trace in particular specimens is situated behind the second de-

pression. This sector is marked by considerable amplitudes of fluctuations. Several smaller depressions and elevations, occurring on this sector, are variously situated in various specimens. In males, this sector terminates in a distinct depression, that may be called the third depression, whose minimum occurs at the beginning on or halfway the fifth whorl (Text-fig. 2d—e). The last sector of diagram of males makes up an elevation, more or less prominent in relation to the third depression and terminating in the fourth depression usually situated lower than the third. The situation of the fourth depression is constant and falls at five and one-third to five and two-third whorls (Text-fig. 2d—f).

In females, the depression marked as the third takes more or less constant position and is situated in the second half of the fifth whorl or in the first half of the sixth (Text-fig. 2a—c). The width of this depression is variable. The terminal section of the diagram of relative density of septa in the *Quenstedtoceras* females is formed by one or two elevations (Text-fig. 2a—c). The first of them terminates in the fourth

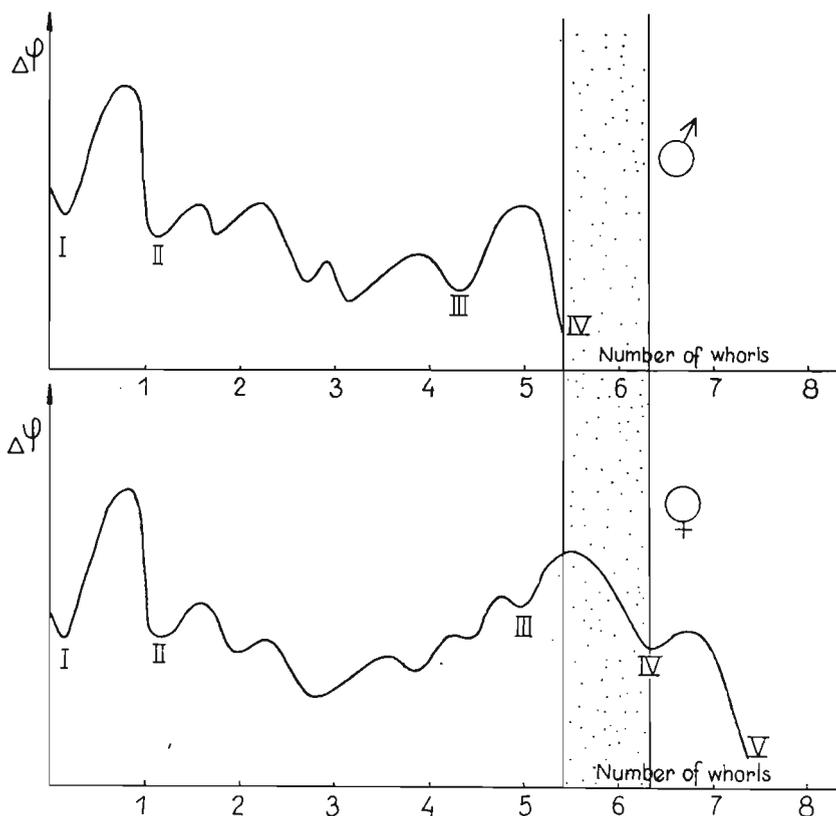


Fig. 8. An idealized sketch presenting curves of relative density of septa in the genus *Quenstedtoceras*. Depressions marked by Roman numerals. The dotted area corresponds to a morphological hiatus of one whorl, for the products of the posterior part of body of the type of dimorphism "A".

and the second with the fifth depression. The situation of the fourth depression is constant, about halfway the sixth whorl, the same as that of the fifth depression, halfway the eighth whorl. In some females, the fourth depression is a final one which results from the morphology of living chamber (Text-fig. 2c; Pl. VI, Fig. 1a, b).

The considerable individual variability is observed in the trace of the curves of relative density of septa, but the elements of curves mentioned above are characteristic, have a fairly constant position in the representatives of the genus and may be distinguished in each diagram. Idealized curves of relative density of septa in the genus *Quenstedtoceras* are shown in Text-fig. 8.

COMPARISONS AND INTERPRETATIONS

Certain regularities in the ontogenetic development of the genus *Quenstedtoceras* may be explained comparing them with Recent squids, in particular those of the suborder Miopsida.

The dependence of the growth of molluscs on environmental conditions is generally known. In squids, winter periods are marked by an arrested increase in body mass (Zuev & Nesis, 1971). In pelecypods, both winter and spawning periods are marked on shells in similar manner (Rhoads & Panella, 1970). Thus, we may suppose that the growth parameter characteristics of shells are affected, on the one hand, by external environmental factors, that is, temperature, salinity, etc. and, on the other, by factors closely connected with the life-cycles, such as the sexual cycle or by environmental changes related with hatching or a change in the mode of life in a definite stage of ontogenetic development. A close correlation between the annual and sexual cycle (Akimushkin, 1963; Zuev, 1971; Zuev & Nesis, 1971) is observed in Recent Decapoda, the same as in most of the remaining molluscs.

The biological importance of the first depression, discussed above, may be related with hatching from egg capsule. The steep elevation, which occurs between the first and second depression may be referred to the larval stage as understood by teuthologists, who give the name of larva to the earliest postembryonal stage, marked by a pelagic mode of life. The life period of the larval stage is varying and may amount from a few days in *Sepia officinalis* to three months in *Loligo vulgaris*. Afterwards, larvae sink to the bottom (Zuev & Nesis, 1971). Considering the fact that hatching from egg capsules takes place in the same environment in which eggs were laid, that is, under the conditions of a relatively high temperature, one can suppose that the increased distances between septa (elevations of the curve) correspond to a relatively rapid increase in shell margin, produced by pallial margin. The place in which Recent Decapoda lay their eggs has to assure a strictly determined water

temperature during the incubative period. As a consequence of exceeding, both upwards and downwards, the limit of temperature proper to a given species in its incubative time, the young individuals may not be hatched at all (Akimushkin, 1963; Zuev & Nesis, 1971). The places of spawning and laying eggs are also definite areas, so that some of species frequently cover long distances to reach their spawning-grounds. The Miopsida, or what is known, as neritic squids, enter shallow, well-insolated bays, sometimes only several scores of centimeters deep and there they lay their eggs (Akimushkin, 1963; Zuev, 1971; Zuev & Nesis, 1971). The Oegopsida, or oceanic squids, frequently migrate to remote warmer zones of oceans (Zuev & Nesis, 1971).

A particularly well-developed hydrostatic organ, most likely a spherical, initial chamber and several other phragmoconal chambers, represented an adaptation to the pelagic (planktonic) mode of life of ammonite larvae.

The larvae of Recent squids have the specific gravity of their body always slightly larger than that of sea water, but they keep in superficial layers of the water due to their fins and a particularly well-developed funnel. For this purpose, they also may profit of the turbulence of marine currents (Zuev & Nesis, 1971). In the ammonites, the fins probably did not occur (their bodies were sheathed in shells) and the funnel, even if well-developed, would have to overcome a considerable resistance offered by the water to a relatively large shell. The main role in the "larval" stage of ammonites was probably played by vertical movements. Most curves do not display considerable deviations from a mean trace between the first and second depression, which may be indicative of the stability of environmental conditions in the larval stage. The second depression might determine the end of larval stage and the transition to deeper waters.

The sector of curve between the second and third depression, marked by a considerable variability of its trace and high amplitudes of fluctuations, concerns the existence of individuals in an environment proper to this period. It is most likely that the ammonites stayed in this stage in the bottom zone of a not very deep sea and could wander horizontally in search of food. It follows from an analysis and comparison of the jaws of the Mesozoic ammonites with those of Recent cephalopods, conducted by Kaiser & Lehmann (1971) and Lehmann (1967), that the Mesozoic ammonites fed on a not very mobile food, most likely found on the bottom, which was confirmed by the finds of specimens with the contents of crops preserved (Lehmann & Waitschat, 1973).

The third depression was marked by the beginning of the sexual cycle, consisting of the maturing of gonads, possible migrations to the spawning-grounds and the stay on these grounds with a simultaneous evacuation of sexual products.

The males would display only one sexual cycle, terminating in the

fourth depression. In the females, the fourth depression would end the first sexual cycle, while the fifth might be indicative of passing through the second sexual period. Thus, the females might have one or two sexual cycles (Pls VI—IX).

The males and females of the genus *Quenstedtoceras* displaying gerontic characters, have a shortened living chamber (Pl. VIII, Figs 3a, b) which was also noted by Makowski (1962). The shortening of the gerontic living chamber may be ascribed to the atrophy of sexual organs after the termination of sexual cycle.

In the males of the maturing of gonads usually falls in winter, autumn or spring (Zuev & Nesis, 1971). Some species of Recent squids, have only one spawning-season in their lives, other have more, but usually the last spawning-season terminates in the reduction of gonads and in death. The cases were described in which near the eggs laid the bottom was covered with dead bodies of squids (Akimushkin, 1963). The mature gonads make up a considerable percentage of body weight, e.g., in the *Ommastrephidae* females the ovary, oviduct and the nidamental gland represent together 30 to 35 per-cent of body weight (Zuev & Nesis, 1971). The male sexual organs make up a slightly smaller percentage of the total body weight. The degeneration of such large organs has to result in considerable changes in body weight and proportions.

The difference between the termination of the sexual cycle in males and the first sexual cycle in females of *Quenstedtoceras* was expressed in about one whorl. This difference is probably caused by a later sexual maturing of females and their faster growth during this period.

Squids reach sexual maturity halfway or at the end of their lives. Males always mature earlier than females and this applies both to the species in which they are larger and in which they are smaller than females e.e., in *Sepioteuthis lessoniana*, males become sexually mature within 6 months and females 12 to 14 (Zuev & Nesis, 1971).

The facts discussed above explain a one-whorl morphological hiatus, observed by Makowski (1962a, b) between male and female forms in the genus *Quenstedtoceras*.

The curves of relative density of septa may serve as a basis for determining the length of the lifetime of ammonites. The phenomenon of the correlation between the sexual and the annual cycle is common in the invertebrates. We can thus assume in all probability that the ammonites, like the Recent squids, had their sexual cycle correlated with their annual cycle and, therefore, the fourth depression in males and the fifth or fourth (if it is the last one) in females, indicating the termination of the last sexual cycle, should be referred to the autumn or winter periods. In females, the fourth depression, separating two curve elevations, is probably connected with an interval in or a minimum intensity of the sexual cycle usually falling in the winter. In Recent squids, the

spawning-season varies in length and depends to a considerable extent on the latitude. The species of squids which live at higher degrees of latitude have a relatively short spawning-season late in the summer or in the autumn. In the species which have in the tropical zone, the spawning-season extend to include the early springtime and the late autumn (Akimushkin, 1963; Zuev, 1971; Zuev & Nesis, 1971). In the tropical and subtropical zones, there live species of squids in which the spawning-season lasts the whole year, but it is possible to distinguish a peak period usually falling in the warmest-season (Zuev & Nesis, 1971).

The determination of the length of a period which precedes the termination of the first sexual cycle is less certain. The fact should be taken into account that, in Recent Decapoda the rate of the growth of juvenile forms is faster than in later stages of the ontogenetic development (Zuev & Nesis, 1971). In ammonites, this phenomenon would be manifested by a larger number of juvenile whorls in an annual cycle than in the forms in a later stage of the ontogenetic development. It is most likely that only one winter period is marked in the stage of the ontogenetic development indicated by a curve sector between the second and third depression. Its situation is variable and depending on the season of the year in which eggs were laid and hatched.

The males of *Quenstedtoceras* would reach an age of two years and females with two sexual cycles up to three years.

Conclusions, reached by Stahl & Jordan (1969) on the basis of their paleotemperature studies on the Jurassic ammonites and according to which an annual growth in *Quenstedtoceras* supposedly amounts to a quarter to one-third of a whorl and to two-fifth of a whorl in *Stauphenia*, are rather improbable. In both cases, only fragmentary whorls were examined by these authors. In regard to *Quenstedtoceras* from Łuków, the present writer could find, on the basis of photographs, that in all likelihood this is a female specimen of *Q. vertumnum* about 8 cm in diameter and, therefore, a depression shown on the curve of paleotemperatures (Stahl & Jordan, 1969, Fig. 2) may correspond to the fourth depression of females distinguished on the curves of a relative density of septa.

Four to six annual cycles, cited by Westermann (1971) on the basis of, among other things, distances between septa determined by Oechsle (1958) and Rieber (1963), represent a more reliable result, but Westermann, did not take into account the fact that not all concentrations of septa, in particular in the initial development stage, correspond to seasonal changes in conditions.

Among the many female specimens of *Quenstedtoceras* from Łuków found with excellently preserved shells, those without numerous lifetime injuries of shell are rare. These injuries occur on a smooth part of shell corresponding to sexually mature individuals (Pl. VI, Figs 3, 4). In ear-

lier stages of the ontogenetic development of males and females, the lifetime injuries are very rare. It is likely, that most of them occurred during the spawning season or when eggs were laid on the bottom of shallow, coastal areas of the sea. The eggs of all Recent Miopsida (Akimushkin, 1963; Zuev, 1971; Zuev & Nesis, 1971) are laid under similar conditions.

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CYPRIAN KULICKI

UWAGI O EMBRIOGENEZIE I ROZWOJU POSTEMBRIONALNYM AMONITÓW

Streszczenie

Poddano dyskusji dotychczasowe poglądy dotyczące typu embriogenezy u amonitów, oraz wskazano na pewne nowe cechy morfologii komory początkowej wraz z pierwszym skretem przemawiające za nielarwalnym typem embriogenezy. Przed-

stawiono szczegółową analizę zgrubienia muszli na przewężeniu nepionicznym, wyjaśniono sposób tworzenia się zgrubienia, oraz wysunięto hipotezę przystosowawczego znaczenia zgrubienia.

Przeprowadzono analizę wykresów względnej gęstości septów w rodzaju *Quenstedtoceras* i na ich podstawie wykazano pewne podobieństwa rozwoju postembryonalnego amonitów z rozwojem współczesnych Decapoda. Lukę morfologiczną — brak jednego skrętu — charakterystyczną dla dymorfizmu płciowego „A” objaśniono na podstawie *Quenstedtoceras* różnicą jednego skrętu w zakończeniu jedynego cyklu płciowego samców i pierwszego cyklu płciowego samic.

СЫРІАН КУЛІСЬКІ

ПРИМЕЧАНИЯ НА ТЕМУ ЭМБРИОГЕНЕЗА И ПОСТЭМБРИОНАЛЬНОЙ
ЭВОЛЮЦИИ АММОНИТОВ

Резюме

Критически анализируются взгляды на характер эмбриогенеза аммонитов и отмечаются некоторые новые морфологические признаки начальной камеры и первого оборота, указывающие на безличиночный тип эмбриогенеза. Детально анализируется утолщение раковины на непсионическом пережиге, объясняется способ образования утолщения и высказывается предположение о приспособленческом значении утолщения.

Выполнен анализ графиков относительной густоты септ у рода *Quenstedtoceras* и на основании этого анализа констатировано некоторое сходство в постэмбриональном развитии аммонитов с развитием современных Decapoda. Наличие морфологического пробела — недостающий один оборот — характерного для полового диморфизма типа „А” объясняется на основании *Quenstedtoceras* разницей на один оборот в окончании единственного полового цикла мужских и первого полового цикла женских особей.

EXPLANATION OF PLATES

Plate IV

- Fig. 1. *Quenstedtoceras* sp. b, juv., Łuków, Calovian, Z. PAL. No. Am. I/19, negative plate No. Sc. 9.254. A comparison of the surface of a postembryonal shell with that of an embryonal shell in the place distinguished by Erben as the first change in growth, $\times 1000$.
- Fig. 2. *Quenstedtoceras* sp. a, juv., Łuków, Calovian, Z. PAL. No. Am. I/20, negative plate No. Sc. 9.252. The surface of the first whorl of a postembryonal shell with growth lines visible, $\times 1000$.

Plate V

- Fig. 1a, b. *Quenstedtoceras henrici* R. Douv. juv., Łuków, Callovian, Z. PAL. No. Am. I/21, negative plate No. Sc. 9. 242-9. 247. A longitudinal section of the ventral wall of shell at the nepionic constriction, $\times 1.200$.

Plate VI

- Fig. 1. *Quenstedtoceras henrici* R. Douv. ♀, Łuków, Callovian, Z. PAL. No. Am I/17. a lateral view; b medial section of female with the first sexual cycle completed; the concentration of the last septa corresponds to the fourth depression, $\times 0.61$.
- Fig. 2. *Quenstedtoceras mariae* (d'Orb.) ♀, Łuków, Callovian, Z. PAL. No. Am. I/7. a lateral view; b medial section of a female with two sexual cycles, $\times 0.44$.
- Fig. 3. *Quenstedtoceras vertumnium* (Leck.) ♀ Łuków, Callovian, Z. PAL. No. Am. I/22. A view of the ventral side with distinct traces of a lifetime injury of a considerable sector of the margin of shell. These lifetime injuries might occur in the zone of waring, near the bottom, $\times 0.70$.
- Fig. 4. *Quenstedtoceras henrici* R. Douv. ♀, Łuków, Callovian, Z. PAL. No. Am. I/23. A part of the lateral side covered with growth lines, with two irregularities marked in their trace and indicative of a lifetime injury of a small sector of pallial margin, $\times 0.84$.

Plate VII

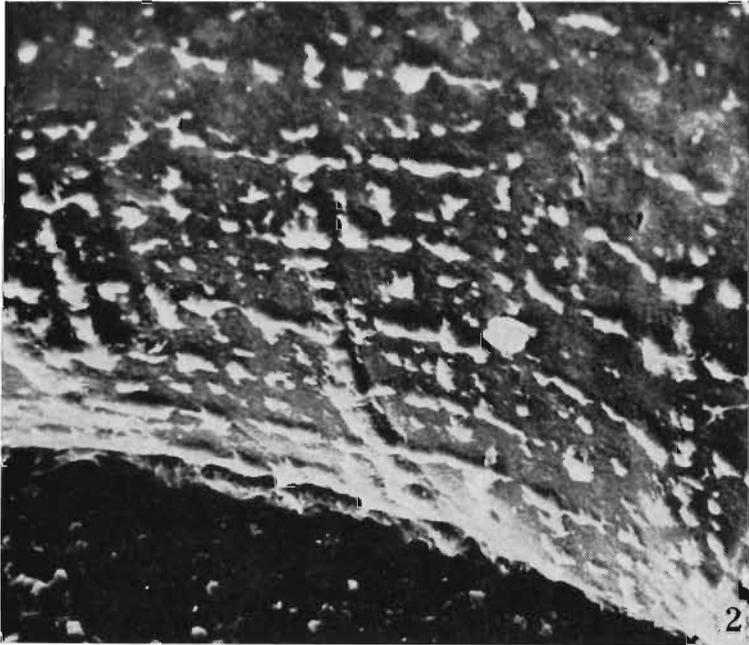
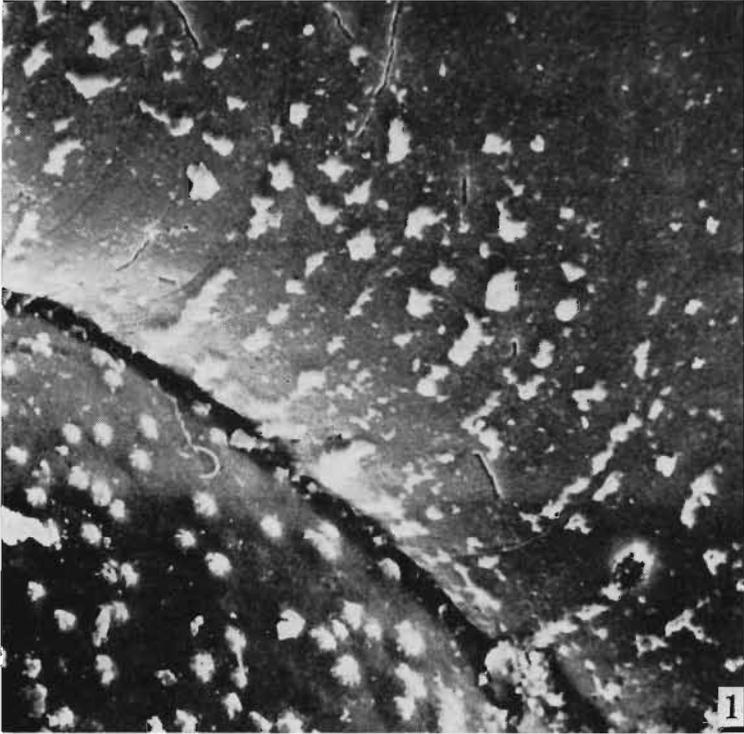
- Fig. 1. *Quenstedtoceras vertumnium* (Leck.) ♀, Łuków, Callovian, Z. PAL. No. Am. I/9. a lateral view; b medial section of a female with two sexual cycles. Terminal concentration of septa corresponding to the fifth depression, $\times 0.36$.
- Fig. 2. *Quenstedtoceras vertumnium* (Leck.) ♀, Łuków, Callovian, Z. PAL. No. Am. I/16. a lateral view; b medial section of a female with a single sexual cycle. Terminal concentration of septa corresponding to the fourth depression, $\times 0.73$.
- Fig. 3. *Quenstedtoceras mariae* (d'Orb.) ♀, Łuków, Callovian, Z. PAL. No. Am. I/8. a lateral view; b medial section of a female with two sexual cycles. Terminal concentration of septa corresponding to the fifth depression, $\times 0.39$.

Plate VIII

Quenstedtoceras henrici R. Douv. ♂, Łuków, Callovian, Z. PAL. Nos Am I/104, 106, 107. Terminal concentrations of septa 1b, 2b and 3b corresponding to the fourth depression. 3a, b — specimen displaying gerontic characters, including a smooth apertural part and considerably shortened living chamber. Nat. size.

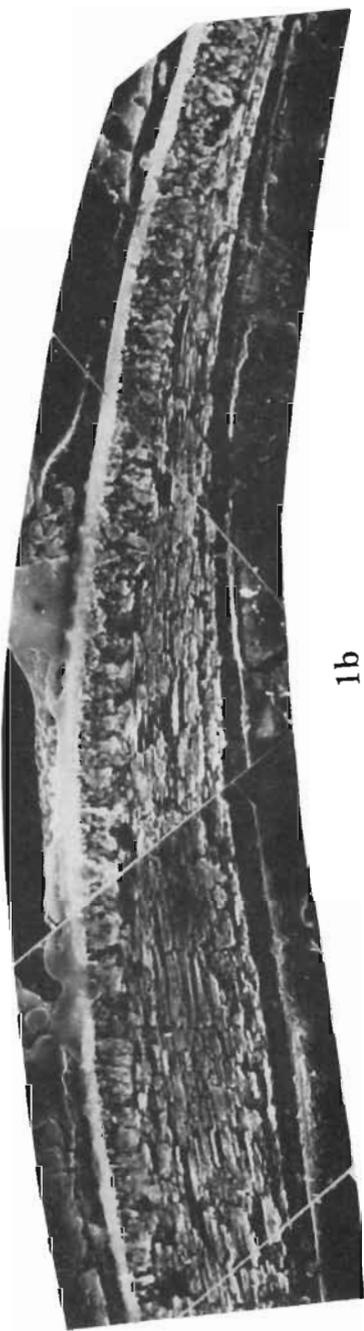
Plate IX

- Fig. 1. *Quenstedtoceras mariae* (d'Orb.) ♀, Łuków, Callovian, Z. PAL. No. Am. I/501. a lateral view; b medial section of an immature female. The last septa within limits of the third depression. Nat. size.
- Fig. 2. *Quenstedtoceras mariae* (d'Orb.) ♂, Łuków, Callovian, Z. PAL. No. Am. I/12. a lateral view; b medial section of a male at the end of its sexual cycle. The last, slightly concentrated septa, are within limits of the fourth depression. Nat. size.
- Fig. 3. *Quenstedtoceras henrici* R. Douv. ♂, Łuków, Callovian, Z. PAL. No. Am. I/335. a lateral view; b medial section of a male at the end of its sexual cycle. The last septa within limits of the fourth depression. Nat. size.





1a



1b

