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THE JURASSIC JUVENILE AMMONITES OF THE JAGUA FORMATION, CUBA

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Early ontogenetic stages of some Ammonitina (mostly Perisphinctidae) are described from the Oxfordian Jagua Formation of western Cuba. Fourty six percent of the sample are specimens attaining the nepionic swelling with more than four septa developed. Juvenile jaw apparatus found for the first time in specimens with only 2,25 whorls, displays primitive elements corresponding to conchorhynch and rhyncholit of nautiloids, litoceratids and phylloceratids. The fauna and sediment features evidence a low water energy and low oxigenated conditions at the bottom during the sedimentation. The juvenile ammonites occur together with numerous adults which are represented by corresponding micro- and macroconchs; it indicates for the proximity of a breeding place.

K e y w o r d s: ammonites, juvenile shells, juvenile jaw apparatus, paleoecology, Jagua Fm., Oxfordian, Cuba.

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INTRODUCTION

In addition to adult ammonites, abundant early juvenile forms were observed among the Middle Oxfordian ammonites of the Jagua Fm., Pinar del Rio province, western Cuba (Wierzbowski 1976). In paleontological literature, only few localities are known with such an abundance of minute ammonites. Among them are: in the USSR, the Artinskian deposits of the Aktunbinsk Region and the Aptian of the environs of Ulyanovsk (Ruzhentsev 1962), only the last-named being studied in detail (Druzhits and Khiami 1970); several Lower Jurassic French and German localities (cf. Landman 1982); and in the USA and Jordan, the Upper Cretaceous ones (Bandel 1982; Landman 1982).

In regard to both their original accumulation in the deposits and the preservation of their fragile shells, the abundant occurrence of juvenile

ammonites was caused by ecological factors. An analysis of the structure of juvenile shells provided a basis for considering the ammonite embry-ogeny. Thus, at least, two approaches may be followed when studying such specimens of ammonites — the paleoecological and the paleobiological ones.

The description of structure of the shell and jaw apparatus of ammonites and conclusions on their ontogenetic development are by C. Kulicki; A. Wierzbowski is responsible for the paleoecological remarks.

Specimens are stored in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated as ZPAL).

MATERIAL AND METHODS

The material studied was obtained during the separation of ammonites from calcareous concretions of Jagua Fm., Sierra de los Organos, found in the following localities: La Jutia, El Hoyo de la Sierra, El Hoyo de San Antonio and Sierra de Guane (Wierzbowski 1976: fig. 1). A hundred and eleven thin sections were then made of dark bituminous limestones forming the concretions.

Of a large number of shell sections, 107 specimens were selected for measurements. Although efforts were taken to select sections as closely approximating the medial one as possible, considerable percentage of them all were paramedial and slightly oblique sections.

Simple histograms and biometric computations were prepared for the presentation of numerical data. The state of preservation of specimens is on the whole good, most of them having their body chambers preserved. The elements best visible in thin sections include the nepionic swelling, the nacreous layer of which is sometimes particularly well distinguishable from the prismatic layer, the wall of the first whorl and initial chamber, as well as proseptum. The body chamber is usually filled to three quarters of its length with sediment and in the remaining part with a light calcite. As a result of micritization, the thin wall of body chamber may be undistinguishable from the sediment, but it is usually visible when observed in polarized light. Proseptum is a relatively thick element easily perceptible in all specimens. In polarized light, thin and almost transparent second and further septa can be distinguished from the light calcite filling the phragmocone. Calcite infIling of the phragmocone and posterior part of body chamber makes difficult the location of the last septum. Consequently, determination of the length of body chamber may be subject to an error.

The distances beetwen the septa have not been measured, because of the random orientation of the thin sections planes.

The juvenile jaw apparatuses are preserved only in two specimens of the whole collection studied.

DESCRIPTION OF THE PALEONTOLOGICAL MATERIAL AND DISCUSSION

JUVENILE SHELLS

The diameters of specimens in the whole sample are between 0.42 and 3.68 mm, with $M = 0.87$ mm: $\delta = 0.415$. The distribution of diameters is distinctly asymmetric (fig. 1D) and its modal value occurs in class 0.6—0.8 mm.

Specimens in which the shell growth was stopped at the stage of distinct nepionic swelling with a nacreous layer, make up 46 per cent of the whole sample. Their diameters are 0.57 mm — 0.90 mm, with $M = 0.72$ mm and $\delta = 0.096$ (fig. 1E). The distribution discussed displays only a small degree of asymmetry, has a flat, wide apex and its modal value occurs in class 0.75—0.80 mm. The extension of the diagram and flattening of its apex are presumably caused by the fact that considerable part of the whole sample represents paramedial sections which display smaller diameters than the actual one. In this connection, it is possible that the mean value of diameter (M) occurs in the next class (0.75—0.80 mm) and is tantamount to the modal value, whereas the highest value of diameter, 0.90 mm, is certainly equivalent to the actual values.

The situation of the terminal part of nepionic swelling in relation to proseptum fluctuates within limits of 265° and 360°, on the average $M = 308.4°$ and $\delta = 23.49°$. The modal value is placed very near mean value, that is, in class 310°—320° (fig. 1F). The diagram curve of angular distance from proseptum to the termination of the nepionic swelling drops fairly abruptly on the side of lower values and very mildly on the side of higher values. It is due to: (1) in the sample measured, paramedial and variously oblique specimens occur together with medially sectioned ones, and (2) proseptum displays a characteristic strong anterior curve in its medial part and lateral parts withdrawn posteriorly. The aperture of shell, with the nepionic swelling, is exceptionally straight and, consequently, the sections, departing from the medial one, display a larger distance between the middle of proseptum and the margin of aperture than that observed in medial sections. Thus, one can presume that the extension of the diagram curve toward larger values results from the fact that the planes of a certain number of sections do not pass through the outer saddle of proseptum.

The length of body chamber of whole sample and in specimens reaching only terminal part of the nepionic swelling, as well as in larger specimens, is presented on diagrams (fig. 1A—C). The fact that their mean M's differ from each other only very slightly (maximum difference = 2.6°) and fluctuate around the value of 216° is a characteristic feature of all these sets. The distributions of the lengths of body chambers of the whole sample and of specimens only with nepionic swelling

are relatively symmetrical and their modal value is in the same class as their mean M. It is only the distribution of the lengths of body chambers of specimens larger than those reaching the nepionic swelling that is distinctly asymmetric and its modal value is contained in class 120°—160° (fig. 1C).
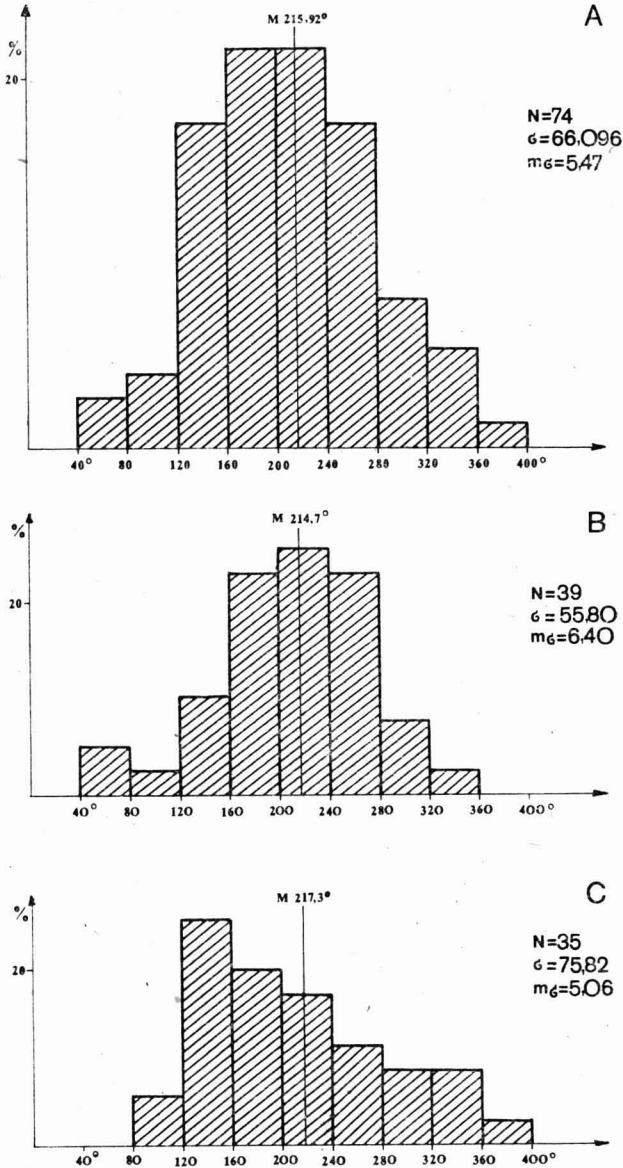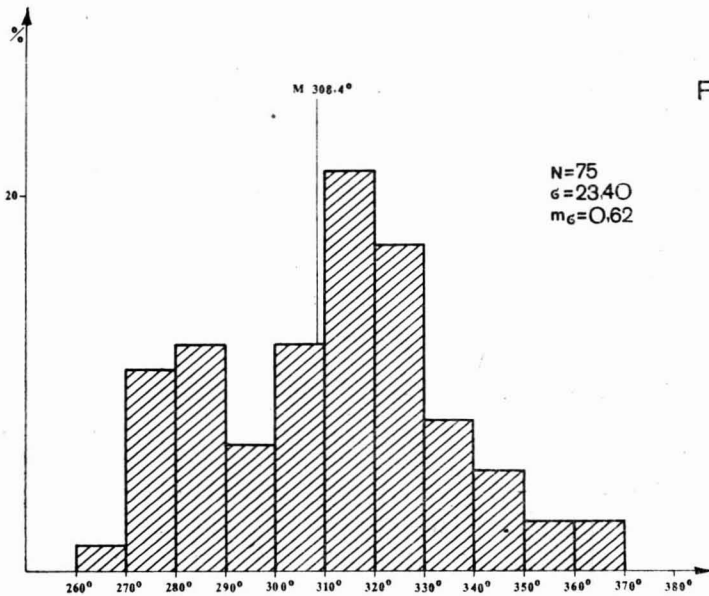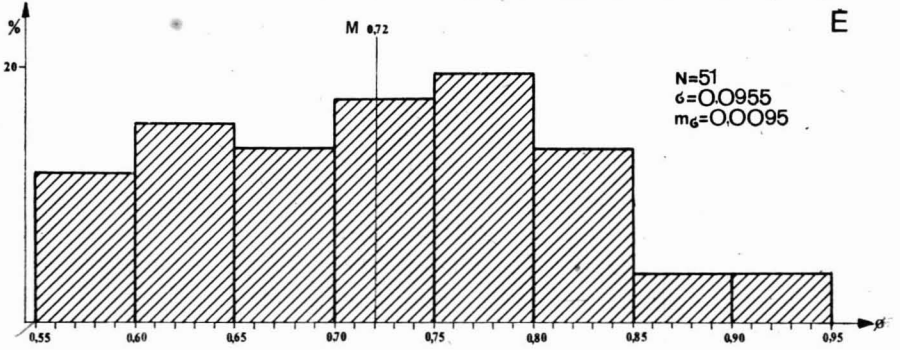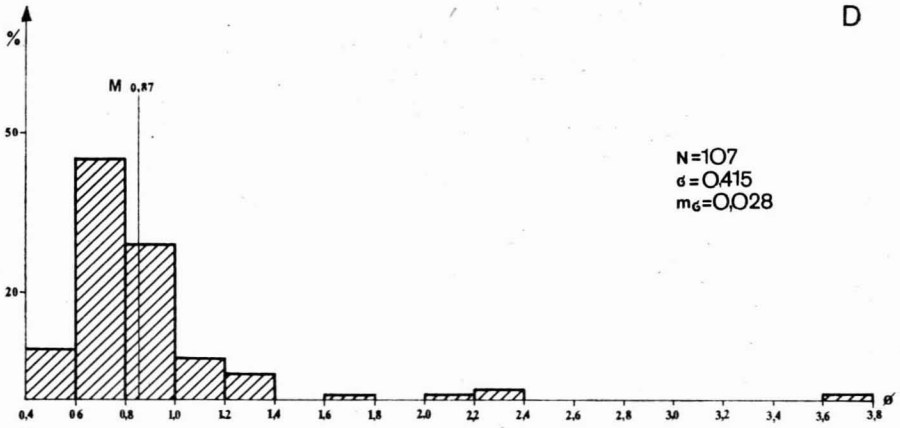

Fig. 1. A—F Histograms for the juvenile ammonites from the Jagua Fm. showing: A body chamber length of specimens in total sample; B body chamber length of specimens with nepionic swelling completed; C body chamber length of specimens after attaining the nepionic swelling; D diameters of specimens in total sample; E diameters of specimens with nepionic swelling completed; F angle distance from proseptum to the end of nepionic swelling.

The length of body chamber is considerably variable, but the real variability is much smaller. The extreme values of the lengths of body chambers are encumbered with an error resulting from an incorrect estimation of the presence or absence of septa (extremely long chambers) or shell walls (extremely short chambers). The values assembled around mean ones, or between the mean and modal values, should be assumed as the closest to the actual ones.

The number of septa in specimens with the complete nepionic swelling was the last of the elements measured. The distribution is asymmetric and ranges between one and eleven septa, on the average 4.75. Of importance is the fact that 90 per cent of all specimens have more than one septum. All remarks concerning the probable errors due to the preservation state refer in particular to the early juvenile stage up to the nepionic swelling, where all elements of shell are very fragile. The specimens having a distinct nepionic swelling, which makes up an excellent protection of shell margin against mechanical and chemical factors (including diagenesis), have only been made use of for measurements. Except for proseptum, the remaining septa are very thin, sometimes hardly recognizable and, in this connection, the number of septa may be lower than the one given here.

The shell in the stage with a complete nepionic swelling, which is most frequent in the material examined, may be characterized as follows. Initial chamber fusiform and about 0.5 mm wide in transverse section (pl. 7:1) and regularly circular in longitudinal medial or paramedial section, with a slightly flattened part situated opposite the nepionic swelling (fig. 2). In lateral parts of initial chamber, sections are usually circular and not displaying flattenings observed in medial and paramedial planes. The whole first whorl, up to the termination of the nepionic swelling, displays no increase in width (pl. 7:1), while the second half of the first whorl almost does not display any increase in height (pl. 7:2; fig. 2).

Siphon runs through proseptum closer to the ventral side and, further, through the second and subsequent septa, medially. It is only in the second half of the second whorl and at the beginning of the third that siphon takes a ventral position.

EARLY ONTOGENETIC STAGES

According to Druzhits and Khiami (1970), as well as Druzhits and Doguzhaeva (1981), the embryonal shell of an unhatched ammonite is composed of an initial chamber and the first whorl without the nacreous layer of nepionic swelling, prosiphon and coecum, as well as proseptum. The nacreous nepionic swelling is formed as a result of growth stagna-

tion after hatching. Nacrosepta are also formed after hatching. Likewise, the formation of the nepionic swelling and change in the shape of the posterior part of body, manifested by the inversion of the second suture in relation to the first, are related by Erben (1962), as well as Erben *et al.* (1968) with a deep metamorphosis of the larval veliger stage.

Kulicki found that, after the series of the first few septa, there occurs, on the diagram curves, the so-called first depression. It may be related to a physiological crisis occurring after hatching from egg or after the exhaustion of yolk and passing to feeding on external food; the nepionic swelling serves, among other purposes, for reinforcing the thin shell margin and is formed before hatching from the egg (cf. Kulicki, 1974; 1979: 129).

The specimens with complete nepionic swelling, a proseptum and some nacrosepta, characterized above, make up more than a half of the sample. They prove beyond a doubt that several nacrosepta occur in the stage of the completed growth of nepionic swelling and that this corresponds to a certain critical point in the life of the ammonite. In the present writers' opinion, this is a stage in which the embryos were released from their egg envelopes and passed to the planktic mode of life.

The problem of correlation between the moments of appearance of nacreous tissue in shell walls and in septa cannot yet be solved. According to Erben, Flajs and Siehl's conception (1969), the nacreous tissue
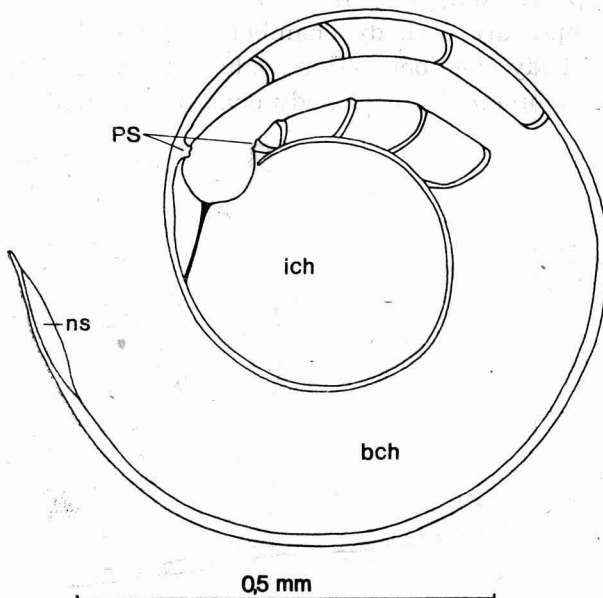

Fig. 2. Reconstruction of a juvenile ammonite shell representing the ontogentical stage dominant in thin sections examined; *bch* body chamber, *ich* initial chamber, *ns* nepionic swelling, *ps* proseptum.

appears in the shell wall during the metamorphosis and it is only afterwards that the epithelium of the posterior part of the body is capable to secrete the nacreous layer. Accepting this conception, one should also admit, on the basis of our data, that shortening of the body chamber by the deposition of consecutive few nacrosepta took place during the formation of the nepionic swelling (when the development of shell margin was stopped). According to Bayer (1972) the nepionic swelling of shell margin is related to the formation of the first septum, an idea based on the conception of Erben *et al.* (1969). Bayer evaluates the later length of the body chamber basing on the correlation between irregularity of radius of the coiled shell and approximation of the septa.

Embryonal shells of ammonites of the genus *Baculites* were described by Landman (1982) and Bandel (1982). Bandel's (*op. cit.*: fig. 38) observations, concerning the number of nacrosepta in an embryonic shell, are similar to those given in the present paper, whereas no nacroseptum was found by Landman (*op. cit.*) in similar shells. These differences, concerning juvenile shells of the same genus, are inexplicable and require more studies.

JUVENILE JAW APPARATUS

Jaw apparatuses were found in the body chambers of two specimens, but only one is sufficiently well preserved to be discussed in details.

Description. — Shell 1.60 mm in diameter, number of whorls 2.25 (counting from proseptum), number of septa 15, body chamber 355° in angular length, aperture of body chamber 0.48 mm high. As indicated by the length of body chamber and a gradual thinning of the shell wall, the specimen is complete. Wall of body chamber is slightly damaged on
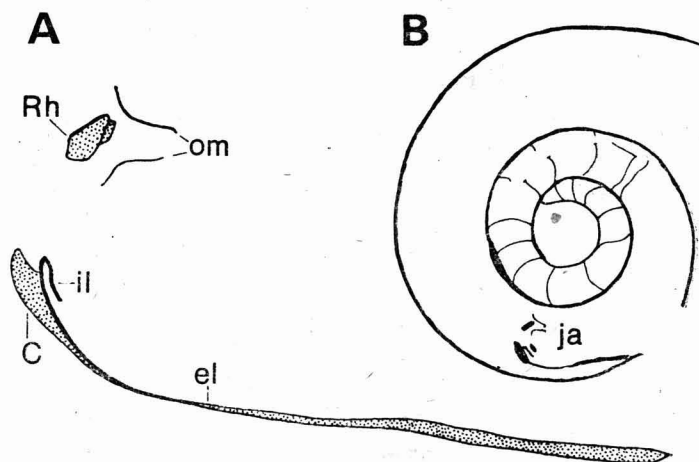

Fig. 3. A Sketch of a juvenile perisphinctid (?) jaw apparatus from the Jagua Fm., ZPAL Am.V/3; B location of jaw apparatus in body chamber; c conchorynch, el external lamella, il internal lamella, ja jaw apparatus, om organic membranes, rh rhyncholit.

the ventral side (pl. 7:3; fig. 3B). Both jaws are situated at one-third of the length of body chamber, measuring from the last septum.

Three distinct elements of lower jaw, an internal lamella, external lamella and calcitic covering are visible in median section. Internal lamella relatively narrow, composed of a thin organic membrane, the external lamella thin in its anterior part and, like the internal, dark and transparent. External lamella thickens posteriorly and becomes di-
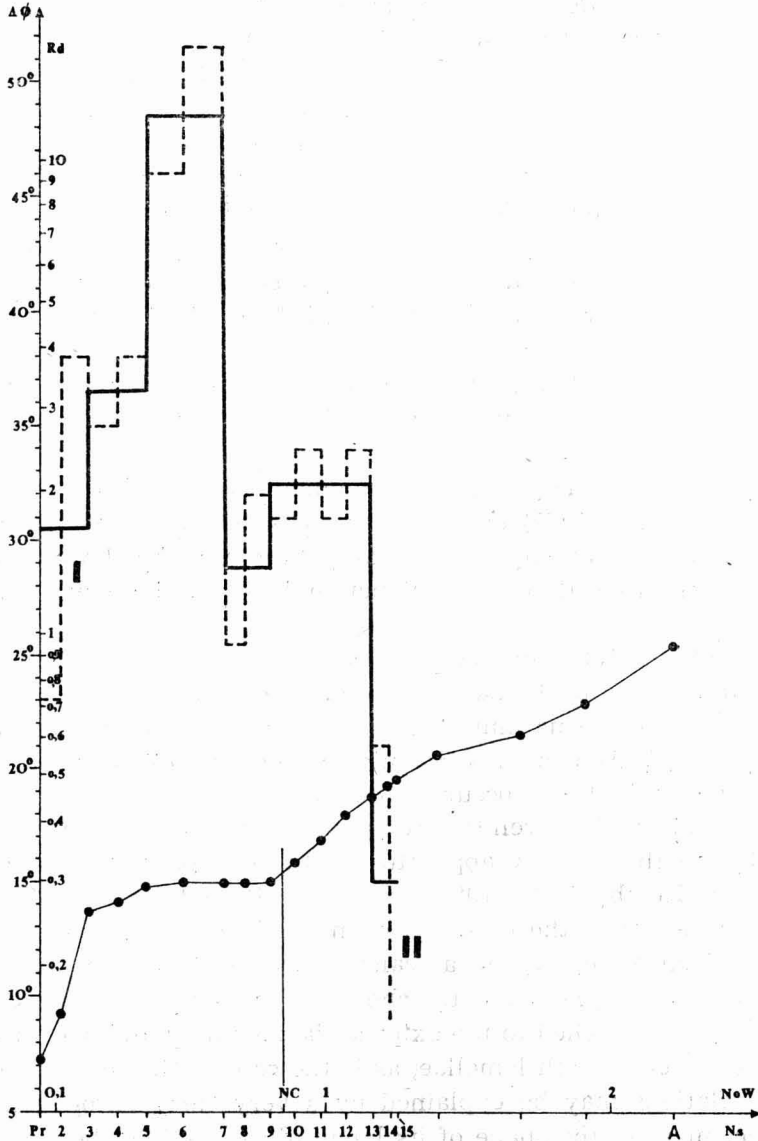

Fig. 4. Diagram showing the radius development (thin continuous line) and the relative density of septa (thick continuous line and broken line) of specimen with jaw apparatus preserved, ZPAL Am.V/3; $\Delta\Phi$ angle distance between the adjacent septa, Rd main radius of shell, NoW number of whorls, Ns number of septa, I—II first and second depression.

stinctly mineralized. A subterminally situated, characteristically shaped, calcareous covering (conchorhynch) occurs on the outer side of the anterior part of external lamella. Calcium carbonate of which the covering is composed looks indentically with that of the posterior part of external lamella. The longitudinal section of the external lamella in our specimen is similar in shape to that of the lower jaw of *Eleganticeras elegantulum* (Lehmann 1967: fig. 1). A complete length of the lower jaw in longitudinal section amounts to 0.47 mm. A calcareous structure of rhomboidal shape (pl. 7:4, fig. 3A) occurs in our specimen above the anterior margin of lower jaw. Its position is similar to that of the termination of the upper jaw in *E. elegantulum* illustrated by Lehmann (1967: fig. 1). In its situation and the shape of its longitudinal section, this structure corresponds to a calcareous covering of upper jaw (rhyncholite) observed in Recent nautiloids and Cretaceous ammonites (Tanabe *et al.* 1980: figs. 6C and 9D). The organic external and internal lamellae are not preserved. A shreds of organic film, occurring above and in the posterior part of our rhyncholite (pl. 7:4; fig. 3A), may correspond to their remains.

Radula indistinct. Some indeterminate structures occur in the place in which it should normally be located, but no radular teeth are visible (pl. 7:4).

Discussion. — Jaw apparatuses of ammonites were described for the first time by Closs (1967) and Lehmann (1967). Later, Lehmann (1970, 1972) proved that anaptychi and aptychi were the lower jaws of ammonites and that they could function both as the lower jaw and operculum.

Tanabe *et al.* (1980) proved that conchorhynch and rhyncholite, so far attributable only to the nautiloids and Recent nautili, are also present in the Upper Cretaceous ammonites of the suborders Litoceratina and Phylloceratina. This confirms Schmidt-Effing's (1972) supposition that these elements might also occur in the ceratites.

The section of the juvenile jaw apparatus we describe here is fully comparable to that of jaw apparatus of litoceratids and phylloceratids described by Tanabe *et al.* (1980) and of the Recent *Nautilus*. The similarity is expressed in the occurrence, in the lower jaw, of the external and internal lamellae, as well as calcitic coverings in both jaws corresponding to conchorhynch and rhyncholite in the nautili. In our specimen, conchorhynch is attached to the external lamella only and does not cover the edge connecting both lamellae, as is the case of the forms compared.

Such relations may be explained by a very early ontogenetic stage of our specimen. In the shape of its longitudinal section, the rhyncholite of our specimen is similar to those of *Gaudryceras* and *Nautilus pompilius* (Tanabe *et al.* 1980: fig. 9D). Comparing widths of external and internal lamellae of the lower jaw, we should state that *Nautilus* has both la-

mellae almost equal in width, while our specimen has a very wide external and very narrow internal lamella. In this respect, *Gaudryceras* takes a transitional place. The narrowest internal lamella occurs in an adult specimen of *Eleganticeras elegantulum*, illustrated by Lehmann (1967).

Due to the significance of the conclusions to be drawn, of importance is to determine at least an approximate systematic position of the specimen examined. The spherical shape of its initial chamber and relatively small increase in shell radius preclude the possibility of its representing the Nautilina. Our specimen undoubtedly belongs to the Ammonitina. Very short siphonal necks, without elongated posterior auxiliary deposits, visible at the end of the first whorl, preclude its belonging to the Litoceratina or Phylloceratina. As the perisphinctids predominate in the deposits under study (cf. Wierzbowski 1976: fig. 4), it is very likely that the specimen represents the Perisphinctidae. A common character of the specimen studied and aptychi-bearing ammonites is, that the width of the external lamella of lower jaw is approximately the same as the height of aperture.

The growth stage of our specimen may be determined as the end of the pseudo-larval stage: its phragmocone displays a deep second depression (fig. 4; cf. Kulicki 1974). Since our material includes fairly numerous isolated aptychi of the typical structure (pl. 8:1), the jaw apparatus of the juvenile form here described represents probably a developmental stage of aptychi. On the basis of our specimen, it is impossible to determine whether the lower jaw is an unpaired element or consists of two symmetric valves.

The following ontogenetic and phylogenetic conclusions can be drawn from the occurrence in the juvenile representative of Ammonitina of a jaw apparatus similar to those of the Cretaceous Litoceratina and Phylloceratina and of the Recent *Nautilus*:

(a) A stage of the *Nautilus*-type jaw apparatus occurs in the ontogeny of aptychi-bearing ammonites;

(b) The jaw apparatus of the *Nautilus*-type is a primary form of the jaw apparatus of the cephalopods and, consequently, Dzik's (1981) hypothesis, deriving the form of the lower jaw of Recent *Nautilus* from the operculum of marine gastropods through the apparatuses of the anaptychus-aptychus type, is doubtful.

The occurrence of jaw apparatus of the *Nautilus*-type in the representatives of the Litoceratina, Phylloceratina and Ceratitina, which are phylogenetically less advanced than the Ammonitina, confirms the thesis that the jaw apparatus of the *Nautilus*-type is primitive.

The modes of secretion of aptychi and the lower jaws of the *Nautilus*-type are in principle similar to each other (cf. Schindewolf 1958; Farinacci *et al.* 1976).

PALEOECOLOGICAL INTERPRETATION

The deposits of the Jagua Fm., containing the material under study, are developed in the form of bituminous marls and marly shales with calcareous concretions ("quesos") and marly limestone intercalations. They are rich in finely disseminated pyrite which occurs in the form of equant grains (up to 20 μm in diameter) and more rounded grains (? framboids) of the same size. The original voids within the calcareous fossils (e.g. chambers of ammonites) are often totally devoid of pyrite; however, some smaller shells can contain the single, equant pyrite grains attaining about 50 μm in diameter, and the fragmentary replacing of the calcitic shell can be observed. The uniform occurrence of fine-grained pyrite which is not limited only to protected micro-environments as fossil voids, indicates the presence of permanent anaerobic conditions within the sediment where the pore-water was charged with H_2S (Hudson 1982). Noteworthy is the fact that the deposits under study do not contain any grains giving evidence of a high water energy of the sedimentary environment, and certain micritic pelloids occurring locally and packed with calcitic (? biogenic) particles may be interpreted as faecal pellets.

The formation of carbonate concretions took place very early in the process of diagenesis and was connected with the decomposition of organic matter in the deposit which in turn caused a local precipitation of calcium carbonate from saturated pore fluids. This early cementation prevented a collapse of the ammonite shells and accounted for their good preservation in the undeformed state and without any traces of shell solution (cf. Seilacher *et al.* 1976).

The deposits under study contain an abundant fauna, particularly well preserved in calcareous concretions, primarily ammonites, with predominant Perisphinctidae (the genera *Vinalesphinctes, Perisphinctes* and *Discosphinctes*), less numerous Glochiceratidae (the genera *Ochetoceras, Cubaochetoceras* and *Glochiceras*) and Aspidoceratidae (the genus *Euaspidoceras*), as well as nautiloids, sepiids, small-sized gastropods, pelecypods (primarily oysters of the genus *Liostrea* encrusted on the ammonite shells), fishes and reptiles (Wierzbowski 1976 and earlier papers cited therein). In addition to abundant juvenile stages of ammonites and pelecypods, the thin sections also reveal planktic foraminifera. The decisive majority of the organisms mentioned above represent nectic and planktic forms. The only doubts may concern here the pelecypods and gastropods. However, some cemented pelecypods (*Liostrea*) may be also interpreted as being pseudoplanktic when attached to both sides of ammonite shell. The same is true about the pelecypods whose borings were found on a single specimen of drift wood. Small-sized gastropods could also live as a mobile epibenthos attached to floating objects. It

should be mentioned, however, that oysters occur sometimes encrusting only the upper side of ammonite shells and, sometimes, densely packed in the umbilicus. These pelecypods, which settled on ammonite shells lying on the sea floor, were the only unquestionable benthic forms. Striking is here the absence of burrowers. The good state of preservation of fossils which are often complete (e.g. skeletons of fish and reptiles), sometimes with imprints of the soft parts preserved and the aptychi found in the body-chambers of ammonites indicate a lack of scavenging organisms on the sea floor. Of flora, besides the drift wood, aciniform assemblages of *Globochaeta alpina* Lomb were found in thin-sections. This microfossil is probably related with present-day green algae of the family Chlorosphaeraceae the representatives of which may live free without any relation to the substrate (Skompski 1982).

The fossil assemblage here discussed gives evidence for anaerobic to low-oxygenated conditions which prevailed at the bottom during the sedimentation (Wierzbowski 1976). This is connected with a general lack of benthic organisms, except for oysters which settled, possibly only periodically, on the elevated parts of the dead ammonite shells which formed "benthic islands" comparable to those described by E. G. Kauffman (1978) from the Toarcian Posidonienschiefer of southwestern Germany (but cf. also Seilacher 1982) and by Aigner (1980) from the Lower Kimmeridge Clay of England.

The most striking feature of the ammonite fauna occurring here is the presence, in addition to juvenile forms, also of those with a differentiated dimorphism, very often fully grown, with the end-peristome preserved and representing the corresponding micro- and macroconchs (Wierzbowski 1976). It should also be mentioned here that the finds of corresponding micro- and macroconches of various groups of the Perisphinctidae and Glochiceratidae were numerically approaching each other at an approximate ratio of 1:1. These finds give evidence that the breeding place of the ammonites was situated not far from the area of the formation of the deposits under study. A considerable mortality in the juvenile stage may be related with a physiological crisis which arises after hatching from the egg, or with the exhaustion of the yolk resources. It is typical of most marine organisms and indicates the selection of the r-type (cf. Pianka 1981). However, it should be mentioned that, in the case under study, the high mortality may also be a net result of the regularity discussed above, as well as of the fact that the juvenile forms were floated into a poorly-oxygenated bottom water. The good state of preservation of the delicate calcareous shells of juvenile ammonites in the deposits under study is indicative of the lack of carbonate dissolution during the sedimentation and diagenesis. It may be attributed to the production of alkalinity from the anaerobic sulphate reduction of organic matter in the sediments (cf. Sholkovitz 1973).

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CYPRIAN KULICKI i ANDRZEJ WIERZBOWSKI

JURAJSKIE MŁODOCIANE AMONITY Z FORMACJI JAGUA, KUBA

Streszczenie

W ciemnych konkrecjach wapiennych z formacji Jagua zaliczanej do oksfordu środkowego, w prowincji Pinar del Rio w zachodniej Kubie, występują masowo mikroskopijne muszle amonitów obok dużych, często dorosłych form. Na podstawie wyraźnej dominacji przedstawicieli Perisphinctidae wśród dużych okazów można sądzić, że również wśród form młodocianych grupa ta jest licznie reprezentowana. Badania przeprowadzono na płytkach cienkich i opracowano statystycznie ponad sto młodocianych okazów (fig. 1—2). Okazało się, że 46% całej próby stanowią okazy, których muszle osiągnęły stadium definitywnie wykształconego zgrubienia nepionicznego. Okazy takie posiadają średnio ponad cztery septa (proseptum i nakrosepta). Większość współczesnych badaczy uważa, że stadium to jest charakterystyczne dla świeżo wyklutych osobników. Masowość występowania takich okazów potwierdza tezę, iż po wykluciu następował kryzys fizjologiczny eliminujący znaczną część osobników.

W dwóch młodocianych okazach znaleziono w komorze mieszkalnej szczątki aparatów szczękowych (fig. 3—4, pl. 7—8) stanowiące pierwsze znalezisko aparatów na tak wczesnym etapie rozwoju osobniczego. Szczęka dolna posiada organiczną blaszkę zewnętrzną o długości zbliżonej do wysokości ujścia komory mieszkalnej, podobnie jak w anaptychu i aptychu. Niestety, na podstawie przekrojów nie udało się stwierdzić, czy jest to twór parzysty czy nieparzysty. Obie szczęki posiadają wapienne elementy odpowiadające konchorynchowi w szczęce dolnej i ryncholitowi w szczęce górnej, dzięki czemu są podobne do aparatów szczękowych współczesnego łodzika oraz przedstawicieli górnokredowych Litoceratina i Phylloceratina. Występowanie aparatu szczękowego typu 'nautilusowego' u młodocianego

przedstawiciela Ammonitina świadczy z jednej strony o pierwotności aparatu typu 'nautilusowego', a z drugiej o rekapitulacji w rozwoju aparatu szczękowego typu anaptychowego i aptychowego. Obecność aparatu szczękowego typu 'nautilusowego' u górnokredowych Litoceratina i Phylloceratina jest zatem cechą pierwotną. W świetle powyższych danych mało prawdopodobna wydaje się koncepcja Dzika (1981), w której wywodzi on formę dolnej szczęki współczesnego łodzika od operkulum ślimaków morskich, poprzez formy typu anaptych-aptych.

Analiza paleoekologiczna zespołu skamieniałości występujących w osadach razem z amonitami wykazuje obfitość form nektonicznych i planktonicznych i ubóstwo form bentonicznych, ograniczonych do cementujących małży ostrygowatych, które zasiedlały leżące na dnie muszle amonitów. Ponadto, w osadzie uderza (1) brak składników ziarnistych, typowych dla wód o wysokiej energii, (2) obecność i równomierne rozmieszczenie drobnoziarnistego pirytu, (3) a także dobre zachowanie skamieniałości, które nie uległy niszczącemu działaniu czynników mechanicznych i biologicznych. Cechy te świadczą o niskiej energii środowiska sedymentacji i dominowaniu warunków redukcyjnych na powierzchni osadu. Warunki redukcyjne sprzyjały dobremu zachowaniu delikatnych muszli młodocianych amonitów, m.in. poprzez zwiększenie alkaliczności środowiska, co zapobiegało ich rozpuszczaniu w procesie sedymentacji i diagenezy.

Najbardziej typowym elementem omawianych osadów jest stowarzyszenie form młodocianych i dymorficznych form dorosłych amonitów, reprezentowanych przez odpowiadające sobie mikro- i makrokonchy (Wierzbowski 1976); w analizowanych rodzinach Perisphinctidae i Glochiceratidae proporcje ilościowe występowania mikro- i makrokonch mogą być określone 1:1. Znaleziska te mogą być interpretowane jako wskaźnik bliskości miejsca lęgowego amonitów.

EXPLANATION OF THE PLATES 7—8

All specimens are from the Middle Oxfordian, Jagua Fm., Cuba

Plate 7

1. Transverse section of the specimen with 1.5 whorls, × 60; ZPAL Am.V/1.
2. Slightly oblique section of specimen with nepionic swelling and about five septa, × 70; ZPAL Am.V/2.
3. Medial section of the specimen with the jaw apparatus preserved; general view, × 40; ZPAL Am.V/3.
4. Jaw apparatus of the same specimen, × 125.

Plate 8

1. Aptychus of the dominant type found in the sediment, × 92; ZPAL Am.V/5.
2. Section of the specimen with lower jaw preserved; general view, × 50; ZPAL Am.V/4.
3. The detail of the same specimen; lj lower jaw, ns nepionic swelling.