ON MECHANISM OF SOFT BODY MOVEMENT WITHIN BODY CHAMBER IN AMMONITES

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ABSTRACT

In separate phragmocone chambers of Paleozoic and Mesozoic ammonoids, different imprints have been discovered, such as crumples, folds, scars and lines. Calcite linear longitudinal and concentric structures are most important among them. The formers are observed only on cores of phylloceratids and lytoceratids and are called "lines of longitudinal contacts", whereas the latters, observed almost in all the studied ammonites, are called "pseudosutures". They all are secreted by mural parts of the body rear end while displacement in the shell. The mantle displacement was carried out by pressure of chamber liquid on the rear part of ammonite body : most likely, started from the near-ventral part, whereas near-sutural element of the soft body shifted at the end. The displacement process was long, complex and arhythmical. Three stages are distinguished in it - initial, intermediate (main) and final. Displacement proceeded slowly on the first and final stages, while on intermediate stage its rate was comparatively fast.

KEY-WORDS : AMMONITIDA, PSEUDOSUTURE MANTLE, CAUCASUS, CALLOVIAN, APTIAN.

RÉSUMÉ

Différentes traces en forme de rides, plis, traits, lignes ont été découvertes dans certaines loges du phragmocône des ammonoïdes mésozoïque et paléozoïques. Les plus importantes sont les structures calcaires longitudinales et concentriques. Les premières sont marquées seulement sur les moules internes des Phyllocératidés et Lytocératidés, que nous appelons "les lignes de contacts longitudinaux" et les secondes, observées presque chez toutes les ammonites étudiées - dites "pseudosutures". Tous ces éléments sont sécrétés par les parties arrières du corps pendant son déplacement dans la coquille. Le déplacement du manteau se réaliserait grâce à la pression hydrostatique du liquide caméral sur l'extrémité du corps de l'ammonite. Le déplacement commençerait par la partie préventrale et se terminerait par les éléments préombilicaux du corps. Le processus du déplacement était long, compliqué et arythmique. On distingue 3 étapes : initiale, intermédiaire (principale) et terminale. La vitesse de déplacement était faible pour les étapes initiale et terminale, relativement forte pour l'étape intermédiaire.

MOTS-CLÉS : AMMONITIDA, PSEUDOSUTURE, CAUCASE, CALLOVIEN, APTIEN.

T. ..lv. the .r.b..m u..der discussi n, paleontological material was purposely selected from collection gathered during several years when compiling geological sections of the Callovian (Northern Caucasus, r. Cherek Balkarski ; Russian Platform, r. Oka) and Aptian (Northern Caucasus, r.r. Ardon, Pshekha, Khokodz) sediments. Collection of the Paleozoic Ammonoids from G.D. Kharatishvili Museum at Department of Paleonlogy and Geology in the Georgian Technical University have been used, as well. Several tens of fairly preserved samples including representatives of almost all main groups of ammonites, except Clymenia and Ceratites have been studied. The Aptian ammonites deserve greatest interest by amount and diversity.

The material described, is kept in the G.D. Kha..tishvi.i Mus.um at D.p.rtm.nt of Geology and Paleontology in the Georglan Technical University (collection N 8).

Various imprints occuring as bands, striae and longitudinal as well as concentric lines are observed on casts of Ammonites under discussion. They are registered within the limits of phragmocone between lobe lines. The imprints occasionally occur in the rear of body chamber, as well. They are mostly represented by calcitized thin bonds, that are attached to the inner prismatic layer of the shell. They are well pronounced by white colouring against the background of yellowish transparent calcite, that infills intrachamber space. The imprints are not visible all over the whorl. They mostly occur locally on the ventral and lateral sides. The imprints do not exceed h bound f ndiv al h m r n i y differing from each other merely in grade of preservation. It must be noted, that they are practically connected with lobe lines repeating roughly the latters configuration. It is the case particularly of concentric linear imprints (Fig. 1-6). It should be noted, that in Agoniatitida of the *Neopronorites* 40-50 mentioned structures occur between adjacent lobe lines, while in *Timanites* 5-6 elements are observed. It is notewortly, that the former concentric lines are very thin being equalidistant. In *Timanites* distance between the lines is also equal, though considereably greater. The phenomenon is of certain value for interpretation mechanism of chamber formation. In Phylloceratida and Lytoceratida concentric lines are mostly connected with secondary elements of lobe line. Near the latter the structures are closely spaced, distance increasing moving away from the elements. In Ammonitida the lines nearly always are connected with lobes repeating their configuration. They are characterized by regular disposi-

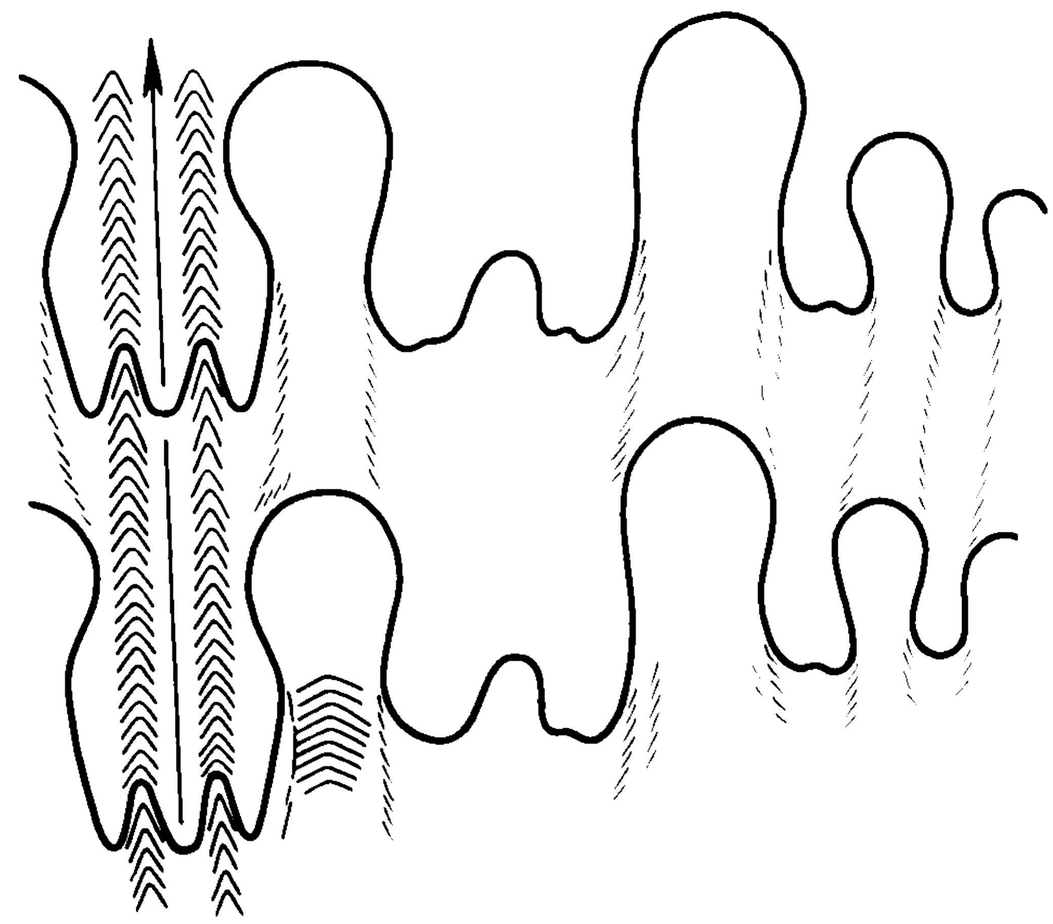

Figure 1 - ***Neopronorites permicus*** TSCHERNOV, sample N134 ; D = 13,00 mm (x 12). Actubinsk, Lower Permian. *Permien inférieur.*

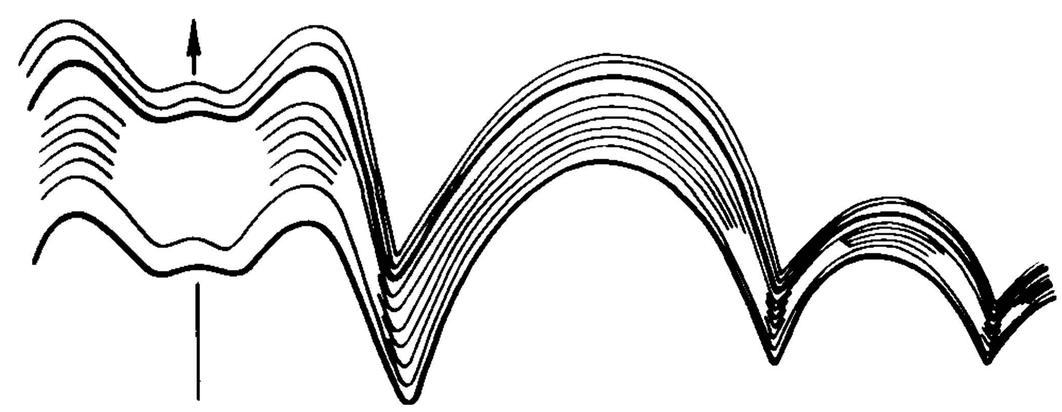

Figure 2 - ***Timanites acutus*** KEYSERLING ; sample N175 ; D = 58,00 mm (x 2) ; Southern Timan, r. Chut, Upper Devonian. *Sud du Timan, riv. Chut, Dévonien supérieur.*

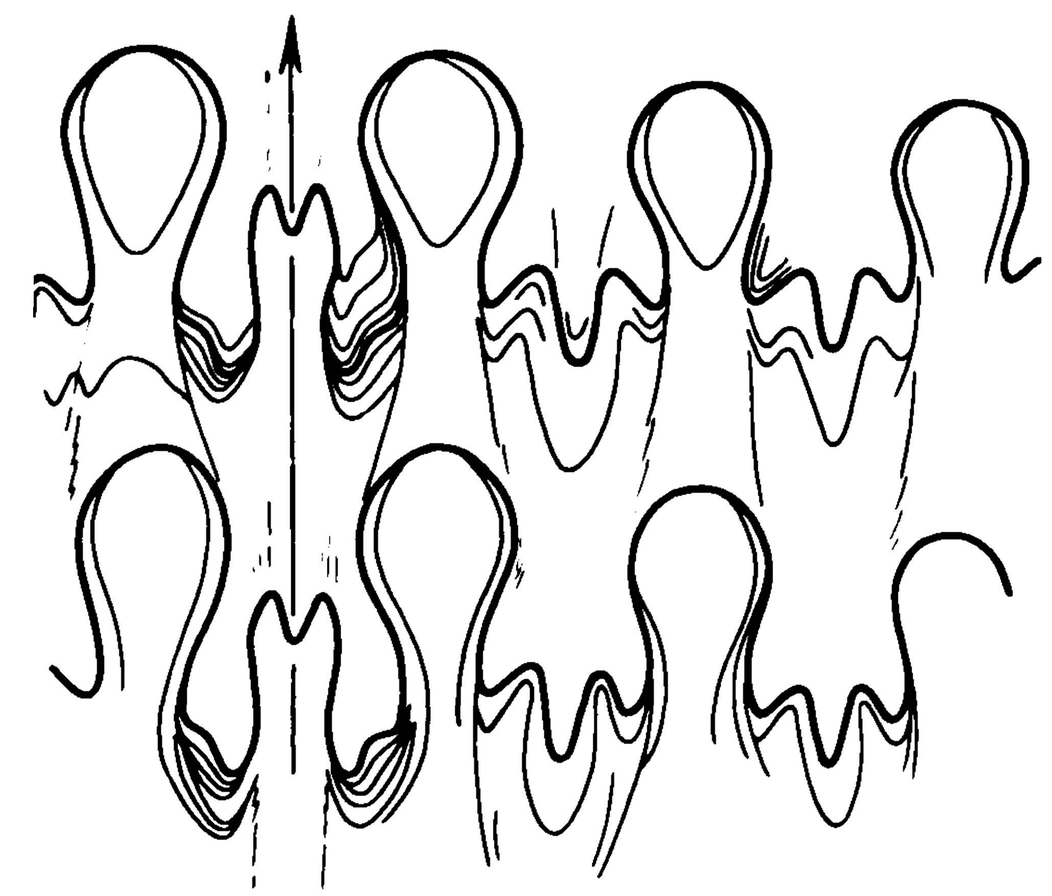

Figure 3 - ***Kargalites typicus*** PUSHENTZEV ; sample N1252 ; D = 19,00 mm (x 7). Actubinsk, Lower Permian. *Permien inférieur.*

tion. Goniatitida (e.g., *Kargalites*, Fig. 3) essentually does not differ from Mesozoic Ammonoids in disposition of concentric lines. We terme the lines pseudosutures.

On shells casts longitudinal lines, trails, small folds, grooves and dark bands are also observed. The latter are mostly visible under inclined illumination in binocular. In adult specimen of Phylloceratida and Lytoceratida longitudinal lines paint complicated picture of treelike ramification. They are always located in central part of main and secondary saddles (Fig. 4, 5). The lines, as well as pseudosutures represent thin lime elements, that are fastened to the inner prismatic layer of the shell. We term them the lines of longitudinal contact.

In Ammonitida pseudosutures seem to vary in amount at various stages of growth. In adult specimen of Phylloceratida and Lytoceratida they number 30-40, while in Ammonitida - much less - 10-20 within limits of a chamber. As to regularities, it generally may by concluded, that the more complex the lobe line the more pseudosutures occur. The same is also true of the lines of longitudinal contacts - they are developed only in Ammonitida with multiple - dissected lobe lines.

John (1909) was the first author, who noticed such structures. Afterwards imprints in the form of longitudinal furrows, wrinkles, linear and concentric structures have been described on siphon side of the shell by Grandjean (1910), Neaverson (1927), Hölder (1954), Vogel (1959), Birkelund (1965), Bayer (1977), Henderson (1984), Zaborski

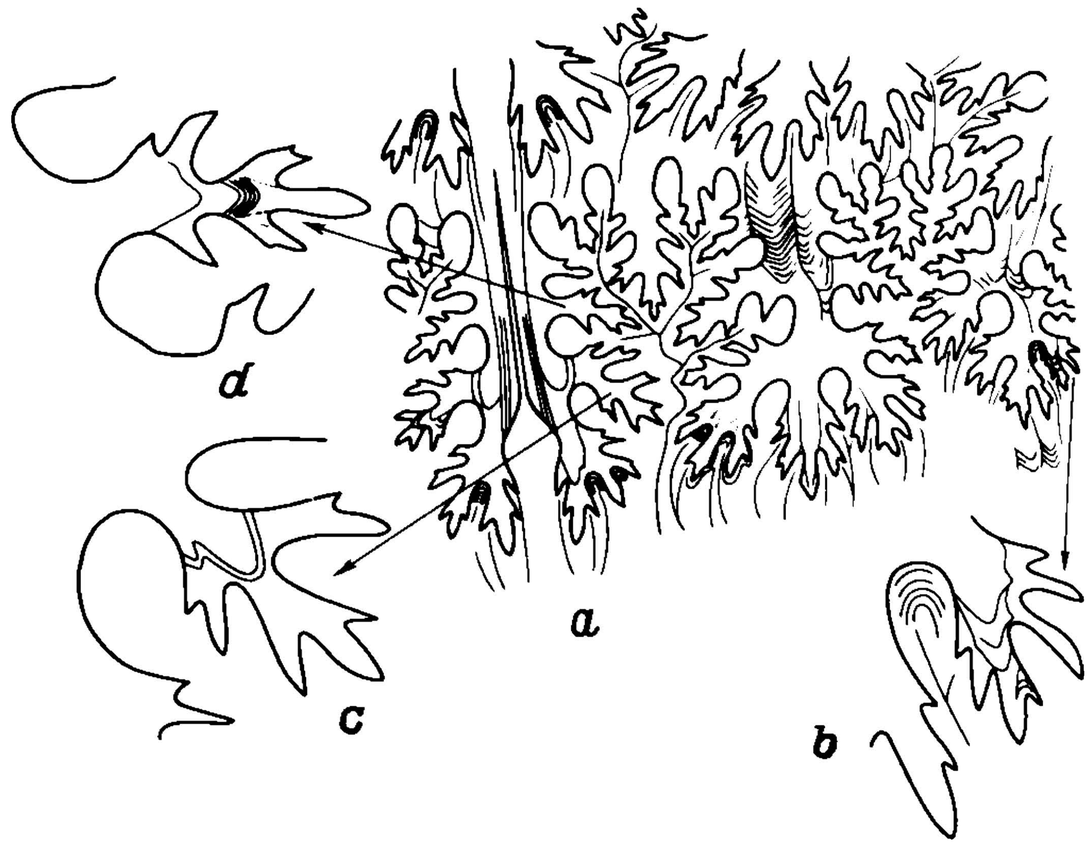

Figure 4 - ***Phyllopachyceras bahorense*** COQUAND : sample N8 (403/108) ; D = 22,50 mm ; a x 4, b-c (details), x 12. North Western Caucasus, r. Pshekha, Upper Aptian. *Aptien supérieur.*

(1986). John considered concentric furrows as "drag striae" of lobe lines in Triassic Ceratitida-*Roninckites* and *Clypeoceras*. According to this author various types of the imprints were related to the growth and movement of the mantle especially to late growths of musches, that are concentrated on lobes. Hölder (1954) terms imprints in the form of dark longitudinal furrows and folds ("Haftstreifen"), while concentric grooves, that reflect saddles of lobe lines - "drag striae"

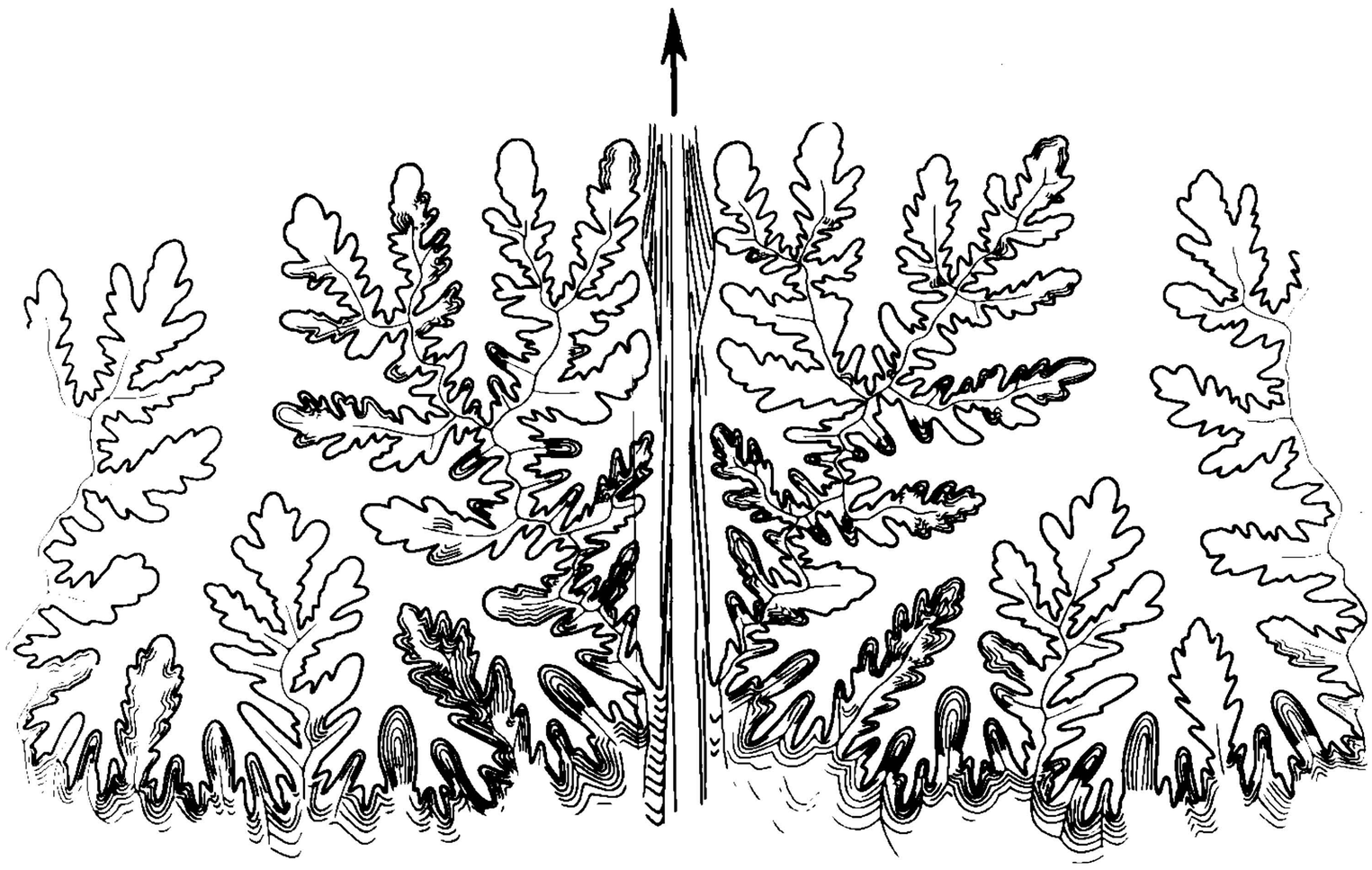

Figure 5 - ***Hemitetragonites*** sp. ; sample N8 (403/117) ; D = 62,00 mm (x 3). North-Western Caucasus r. Pshekha, Upper Aptian. *Aptien supérieur.*

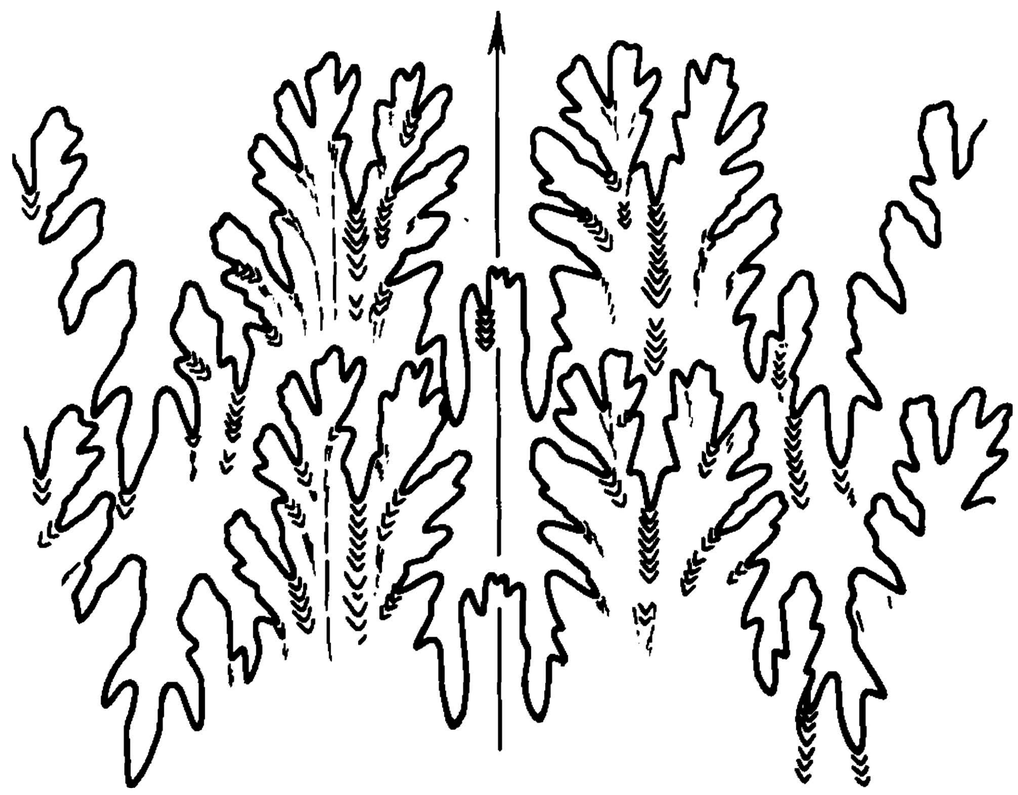

Figure 6 - ***Acanthohoplites nolani*** SEUNES ; samples N8 (403/119) ; D = 34,00 mm (x 3). North-Western Caucasus, r. Pshekha, Upper Aptian.

("Schleppstreifen"), subsequently, Hölder and Vogel suggested that drag stria were formed during movement of the pallium in chamber. According to Bayer the imprints ("Pseudolobenline") were related to small folds on ventral side of shell. He regarded them as a result of secretion of underdeveloped septum after incomplete fastening of septal mantle to the shell wall.

In Late Cretaceous *Sciponoceras glaessneri* WRIGHT, Henderson (1984) found out a band consisting of prismatic material so-called "preseptal prismatic zone". The band is wider on saddles being traceable at considerable distance.

Zaborski has described linear and concentric imprints on casts of the Late Cretaceous *Paravascoceras*. He suggests close relation of them to the saddles of lobe lines. It should be noted, that in reality they are mostly connected with secondary lobes on saddles. In the mentioned author's opinion the lines reflect processes occuring on upper surface of preseptal prismatic zones of shell substance, secreted by parts of mantle, that corresponded to the saddles in the process of the mantle displacement.

As it was shown above, structures, described, are confined to separate chambers being closely connected with lobe lines and in general repeating their configuration. This enable to suggest that they are left by peripheral (mural) parts of soft body, that are secreting septum. Imprints, under discussion and most of all pseudo- sutures enable to judge mechanism and dynamics of soft body movement in body chamber. Since the imprints [illegible] groups of [illegible]nite it may be supposed that apical part of the body moved in body chamber not quite equally.

Let us first discuss in brief the results of investigation of modern Cephalopoda - *Nautilus* and *Spirula*. In particular such problems, as movement of soft part of body, formation of new chambers, regulation of buoyancy and so on were recently discussed in the works of quite a number of authors (Denton & Gilpin-Brown 1966, 1973 ; Mutvei 1973 ; Denton 1974 ; Ward & Martin 1978 ; Ward 1979 ; Ward & Chamberlain 1979 ; Collins, Ward & Westermann 1980 ; Chamberlain 1981, 1982 ; Ward & Greenwald 1981 ; Ward, Greenwald & Magnier 1981 and others). It turned out, that chamber formation takes 70-120 days in *N. macromphalus* while in *N. pompilius* it takes 85-132 days (Ward & Chamberlain 1979 ; Collins, Ward & Westermann 1980 ; Ward, Greenwald & Magnier 1981). Last chambers of phragmocone contain liquid that seems to be secreted by organism. Liquid performs two functions : 1) it supports newly formed septum until sufficient degree of calcitization is achie- ved ; 2) it provides reserve of ballast by throwing the liquid out. According to Ward and others (Ward & Greenwald 1981 ; Ward, Greenwald & Magnier 1981, becomes completely free of the liquid on the 135-th day. In *Nautilus* vertical migration through the funnel takes place. According to Chamberlain's (1981) calculations, if mechanism of buoyancy variation had operated in *Nautilus*, the latter would have spent 3 hours to overcome water column 100 m thick while through the funnel the same process requires only 7 min. Chamber liquid is of considerable importance only during the growth of animal. In specimen, that completes growing, last chambers of the fragmocone are actually free of liquid (Ward 1979 ; Collins, Ward & Westermann 1980). In *Nautilus* when growing, apical part of the body moves slowly, though faster in comparison with aperture growth. In *N. macromphalus* movement takes 6 days at most (Ward & Greenwald 1981 ; Ward, Greenwald & Magnier 1981 ; Henderson 1984), while in *N. pompilius* - 10-20 (Ward & Chamberlain 1979).

According to Denton (1974), Denton & Gilpin-Brown (1973) in *Spirula* chamber is formed slowly. Newly formed chamber is filled by liquid, that is secreted by tissue of the body. In order to support neutral buoyancy, liquid with drawn from previous chambers fills newly formed chambers.

Linear imprints-pseudosutures, described most likely indicate temporary ceasation in movement of apical part of the animal's body. As it was

shown above in Ammonitida pseudosutures reach quite large quantity. Hence the process of the body movement seems to be prolonged in Ammonites than in *Nautilus*, as the secretion of structures require certain time. If these suggestions are right then the process of body movement in body chamber must have been longest in Phylloceratids and Lytoceratids, that are characterized by great number of body chambers.

Discussing the problem in imitation of *Paravascoceras*, Zaborski (1986) notes that mantle movement was not so "impetuous" there as in *Nautilus*. According to Henderson (1984) functioning of longitudinal muscles seems to have been ceased during mantle movement. Proceeding from the aforesaid the mentioned author concludes, that mantle move intensely, probably, during only a few hours.

At least two circumstances contradict this suggestion. Firstly, conditions favourable for fast displacement imply high velocity of chamber liquid redistribution to support neutral buoyancy. Such a speed is not registered in present-day Cephalopods. It seems to be hardly probable in Ammonitida. Secondly, it must be taken into account that in Ammonitida (except Phylloceratida and probably, Lytoceratida) siphon is formed beyond the body chamber and hinder side of the body was "attached" to the septum by siphon. Fast movement of hinder part of the body require formation of new "piece" of connecting ring in a few hours, that looks hardly probable.

Amount of pseudosutures indicate intensity of movement, the greater the amount of pseudosutures the slower is the process. Existence of longitudinal contact lines also speaks in favour of such consideration. Hence, the mantle seems to have moved much slower in Phylloceratida and Lytoceratida than in other groups of Ammonitida. Soft body movement has been carried out lonely with liquid, that entered a new chamber. The liquid seems to have performed the following main functions : 1) it favoured separation hinder part of the body from septum at the initial stage of displacement ; 2) it played a part of buffer to support hinder part of the body during secretion of new septum ; 3) it served as ballast to maintain neutral buoyancy ; 4) it acted as a secker ; entering the new chamber the liquid exerted pressure upon the hinder part of body favouring it's gradual displacement. Speed of movement seems to be dependent upon intensity of water inflow in a new chamber. Volume of liquid, entered and accordingly a length of newly formed chamber seem to be controled by supporting neutral buoyancy.

Movement of hinder part of the body, more likely, may be broken up into three stages : 1) initial - slow stage ; 2) intermediate (main) - relatively fast one ; 3) final - slow one. Phasic movement is especially well pronounced in cephalopods and Lytoceratida, in which within the limits of a chamber at the beginning pseudosutures are closely-spaced, at the intermediate stage they get widely spaced, while to the end, as they approach site of new septum fastening pseudosutures become again close-pecked (Fig. 4, 5). For example proceeding from disposition and amount of pseudosutures, in *Neopronorites* (Fig. 1), regular and slow movement may be suggested ; in *Timanites* movement runs fast at initial stage, when it gets slower though regular, while to the end it becomes rapid again. Phasic movement of mantle is more or less pronounced in other groups of Ammonitida, as well (Fig. 6).

At first stage chamber liquid seems to be secreted by animal body (Zaborski 1986). At the initial stage of movement the liquid does not seem to be pumped from fragmocone into a new chamber over, siphuncle.

According to Mutvei & Reyment (1973) the process can't take place until septal tube and connecting ring, partly adjoining the latter, attain their full thickness to withstand hydrostatic pressure of the water. In this case (at final phase of the first stage) liquid seems to be transported through siphuncle in Phylloceratida and some Lytoceratida, connecting ring of which is considered to be formed in body chamber prior to the mantle displacement. Arrival of the liquid between septum and adjacent septal epithelium causes deflation and deformation of hinder part of the body, the latter is separated from the septum and moves slowly forward as fast as hydrostatic pressure increases. Secondary elements of lobes and saddles intensely decrease in size losing their configuration. The more complicated lobe line the more intense is deformation of hinder part of the body (Fig. 4, 5). For example, judging by outline of pseudosuture deformation does not take place in *Timanites* (Fig. 2). Obviously, the more serrated lobe lines in Ammonitida the more durable and complicated is the process of soft body displacement.

At initial plase of the second stage soft parts of body go out of narrow necks of septum in Ammonitida with multiple-dissected lines. Then, peripheral parts of hinder end of the body, that correspond mainly, to primary and secondary lobes, widen (Fig. 4, 5). In consequence adjacent lobes come into-contact, with the exception of seconda-

ry saddles in Phylloceratida and Lytoceratida (Fig. 4, 5). At contacts thin linear calcite elements begin to secrete. The latter are termed "lines of longitudinal contacts" by the present authors.

At given stage of movement general mass of liquid seems to be pumped from previous chambers into a new one siphuncle. According to Mutvei & Reyment (1973) such a process can be expected only in the Phyllo- ceratida and partly in Lytoceratida. Liquid supply in new-chamber increased causing acceleration in movement of the body compared with initial and final stages. Zaborski (1986) assumes liquid transport from phragmocone into a new chamber through siphuncle in *Paravascoceras*. In such a case, speed of body movement seems to have been dependent upon a size of connecting rings of siphon. The longer and wider the latter, the process of liquid pumping into chamber and accordingly the mantle movement appear to have been the more intense. This seems to have caused relatively low displacement of the body in body chamber in Phylloceratida and Lytoceratida, that are characterized by small connecting rings. The latter closely adjoin the wall of shell.

At the third, final stage of movement when hinder part of the body approaches a new site of attachment the body begins to differentiate. At contacts of separate parts of body, that are secreting lobes, secretion of longitudinal calcite elements conus to an end. The hinder part of the body aquire initial form as a result of liquid pressure increase in the chamber. At that very moment separate parts of septal epithelium begin to fasten at sites of future septum secretion. The liquid penetrates along contacts of individual parts of the body gradually separating the latter. As a consequence, peripheral parts of hinder end of the body assume again an usual "normal" configuration (Fig. 4, 5). At that stage liquid inflow from previous chambers through connecting ring gradually decreases or comes to the end as fast as the interchamber pressure increases. The interchamber pressure increase favoured liquid supply from the body in chamber. At final phase of the stage liquid pressure in chamber, siphon and body equilibrates liquid removal being terminated. A new important period begins in the life of Ammonitida - body starts to fasten to the wall of shell a new septum being secreting. It is noteworthy, that the model of the body movement in body chamber, under discussion, seems to be more acceptable to Phylloceratida and Lytoceratida.

Above data enable to maintain discrete movement of soft body. Each stage, under consideration, may be divided into the shorter phases judging by amount of pseudosutures. Short-term stoppages of hinder part of the body accompanied by secreting of pseudosutures were needed to secure move of the body over a new short intercept, as a result of inflow of a new portion of liquid as well as of pressure increase.

Interchamber organic membranes, that are common in siphon area, may be considered as elements secreting during momentary stoppages of hinder part of the body.

According to Zaborski (1986) mantle movement and aperture growth have been proceeded at the sometime in *Paravascoceras*. While in our opinion aperture growth yielded to mantle movement in speed growth lines of shell are almost equidistant but much closer spaced than pseudosutures, i.e. shell growth and body movement in body chamber considerably differ in speed, that confirms our suggestion. Even allowing for arrest of aperture growth at a time of septum secreting it does not give ground to assume synchronety of the processes (Doguzheva 1982).

Summarizing the aforesaid we can arrive at the following conclusions.

In separate chambers of phragmocone various imprints occuring as wrinkles, folds, striae and lines are observed in Paleozoic and Mesozoic Ammonoids, Calcite linear longitudinal and concentric structures are most important of them. The former are registered only on casts in Phylloceratida and Lytoceratida, being termed by us "lines of longitudinal contacts", while the latter are found almost in all Ammonitida, under investigation. These are called "pseudosutures". All of them have been secreted by hinder end of the body when moving in the shell.

Pseudosutures, that are secreted by mural parts of septal epithelium mark short-term stoppages of the body during its movement in body chamber. They reflect duration and dynamics of the process. Lines of longitudinal contacts secreting at joint of peripheral parts of hinder end of the body indicate degree of body deformation when moving. Both structures enable to reconstruct configuration of hinder end of the body in the process of movement in body chamber.

The movement seems to have begun most likely from near ventral part, while to the end nearsuture elements of soft body appear to have made a

start. The process was durable, complicated and unrhytmical. Three stages can be distinguished there, these are : initial stage, intermediate (main) stage and final stage. At initial and final stages movement proceeded slowly, while at interme- diate stage the process runs fast. In Ammonitida with multiple-dissected lines (Phylloceratida and Lytoceratida) the process of movement was more durable and complicated than in ammonites with simple lines (Agoniatitida). By character of soft body movement Goniatites bear closer resemblance to Ammonoids than to Agoniatitida. In all Ammonites aperture growth yields to mantle epithelium movement in speed.

Mantle movement has been conducted by hydrostatic pressure affecting the hinder part. Besides, liquid performed the following functions : it secured deflation in hinder part of the body at initial stage of movement ; it served as buffer to support apical part of the body during secretion of a new septum ; it was ballast to maintain neutral buoyancy.

In Phylloceratida (possibly in Lytocetatida, as well) in which siphuncle was formed in body chamber main liquid mass has been supplied from previous chambers of phagmacone through siphuncle. This seems to be the main function of siphon formation in body chamber. While in other groups of Ammonoidea considerable portion of chamber liquid appears to have been secreted by body.

Speed of movement has been in direct relation to the rate of liquid pumping. The latter, in its turn, has been conditioned by size and position of connecting ring in siphon. All this as well as great amount of pseudo-sutures most likely indicate low speed of soft body movement in body chamber in Phylloceratida and Lytoceratida. Intensity of liquid inflow and accordingly the length of newly formed chamber appear to control neutral buoyancy.

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