ON THE MODE OF LIFE OF HETEROMORPH AMMONITES (HETEROCONE, ANCYLOCONE, PTYCHOCONE)

M.V. KAKABADZÉ
Geological Institute Academy of Sciences of Georgian Republic, Z. Rukhadze str. 119, 380093 Tbilisi, Georgian Republic.
M.Z. SHARIKADZÉ
Georgian Technical University, Kostava str. 77, 380075 Tbilisi, Georgian Republic.

KAKABADZÉ M.V. & SHARIKADZÉ M.Z. 1993. On the mode of life of heteromorph ammonites (heterocone, ancylocone, ptychocone). [Du mode de vie des ammonites hétéromorphes (hétérocônes, ancylocones, ptychocônes)]. **GEOBIOS, M.S. n° 15 : 209-215.**

ABSTRACT

In the ammonitella stage the heteromorph ammonites have a planospiral shell and it seems they were free swimmers living near the sea floor. Among heterocones the helicoidal stage is regarded as benthonic, whereas ancylocones in the planospiral stage are considered to be comparatively active swimmers. With the beginning of the uncoiled stage heterocones, as well as ancylocones, could float passively near the bottom with the shaft in a subvertical position. But when obtaining food from the bottom, they would achieve a subhorizontal position. Ptychocones in the adult stage with compact and torpedo-like shells are regarded as necto-bentonic with a subhorizontal position of the shaft. Among *Ptychoceras* during growth a truncation of the first planospiral whorl and about 1/6-1/7 part of the first shaft is often observed. The character of the truncation, as well as an observed regeneration of the damaged shell (shell repair) shows that the shell of the ptychocone was not covered by the mantle.

KEY-WORDS : HETEROMORPHA, TRUNCATION, HETEROCONE, ANCYLOCONE, PTYCHOCONE.

RÉSUMÉ

Les ammonites hétéromorphes présentent, au cours de leur stade ammonitelle, une coquille planispiralée ; elles devaient être des formes nageuses vivant près du fond. Le stade hélicoïdal des hétérocônes est considéré comme benthique ; par comparaison, le stade planispiralé des ancylocônes correspond à une vie nageuse, active. Au début du stade non enroulé, les hétérocônes et les ancylocônes devaient flotter passivement près du fond avec la hampe en position verticale ; mais pendant leur nutrition sur le fond, elle devait être subhorizontale. Les ptychocônes à coquille adulte compacte et en forme de torpille sont considérés comme nectobenthiques à hampe subhorizontale. Chez *Ptychoceras* intervient une troncature du premier tour planispiralé et du 1er 1/6e ou 1/7e de la première hampe. Le caractère de la troncature et la régénération observée de la coquille endommagée montrent que la coquille des ptychocônes n'était pas recouverte par le manteau.

MOTS-CLÉS : HÉTÉROMORPHES, TRONCATURE, HÉTÉROCÔNES, ANCYLOCÔONES, PTYCHOCÔNES.

INTRODUCTION

Repeated ontogenic changes in shell morphology are characteristic of many representatives of heteromorphs and it is to be supposed that at each stage of individual development, on obtaining a different shell form, the animal also changed its mode of life (Kakabadzé 1981).

At the ammonitella stage heteromorphs, like monomorphs, have a planospirally coiled shell for one whorl up to the primary constriction. At this stage, in all probability, they were free swimmers living near the bottom.

It is thought that the ammonitella had a hyponome, although it should be supposed that the ammonitella could easily move in a suspended state with water flows. It is remarkable that the ecological differentiation of heteromorph ammonites took place directly after the ammonitella stage (Kakabadzé 1988).

HETEROCONES

Representatives of heterocones at the helicoidal stage are regarded as benthonic (Berry 1928, etc.), however, unlike gastropods, heterocones (as well as turricones or colchicones at a helicoidal stage) apparently could move actively on the bottom and sometimes swim near the sea floor (Fig. 1b). After the helicoidal stage the shaft is formed and we are inclined to think that animal at this stage become more mobile and it could swim, although we still regard them as mainly benthonic.

In the adult stage, with the development of a hook the animal could probably swim passively with the hook down (with a subvertical position of the shaft), supported by tbe buoyant chamber above. In relation of possible buoyancy control and orientation of the animal (both soft body and shell), it is interesting to note that the mathematical calculations do not give the desirable results (Westermann 1971, 1976) especially in heteromorph ammonites (Kakabadze 1981). When investigating this problem the ability of the animal to regulate the distribution of liquid in the last chambers should be taken into account. One should not forget either the great manouverability of the hyponome as well (Kakabadze 1971, 1981 ; Klinger 1980). Considering these factors, we are inclined to think that at the adult stage heterocones could swim passively with the hook down (with a subvertical position of the shaft). However it should be supposed that the animal could obtain a subhorizontal position thanks to ability for liquid regulation within the camerae and an actively functioning hyponome (Fig. 1 c,d). In such a position the animal could make direct contact with the substrate which would be quite impossible with a vertical position of the shaft.

ANCYLOCONES

After the ammonitella stage ancylocones are characterized by planospiral and uncoiled stages. In the planospiral stage ancylocones have loosely coiled whorls. Most representatives (*Ancyloceras, Proaustraliceras*, etc.) have rather wide whorls

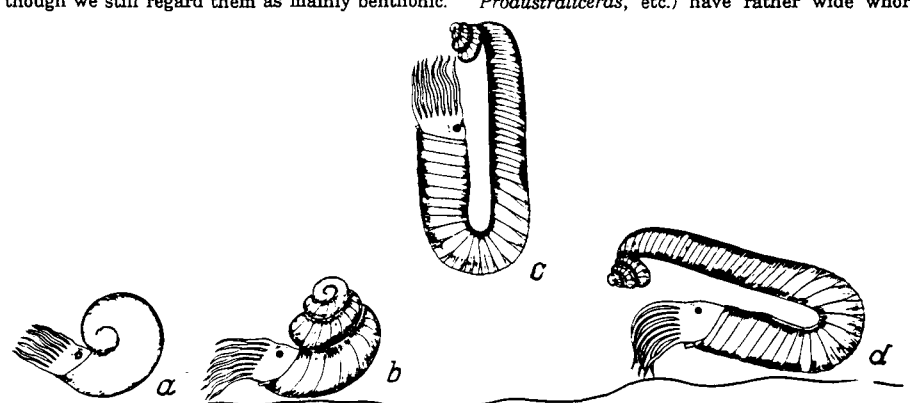

Figure 1 - Supposed living orientation of representatives of the heterocones : *a*, ammonitella stage ; **b**, helicoidal stage ; **c,d**, uncoiled stage. *Orientation de quelques hétérocônes en position de vie supposée. a, stade ammonitella ; b, stade hélicoïdal ; c,d, stade déroulé.*

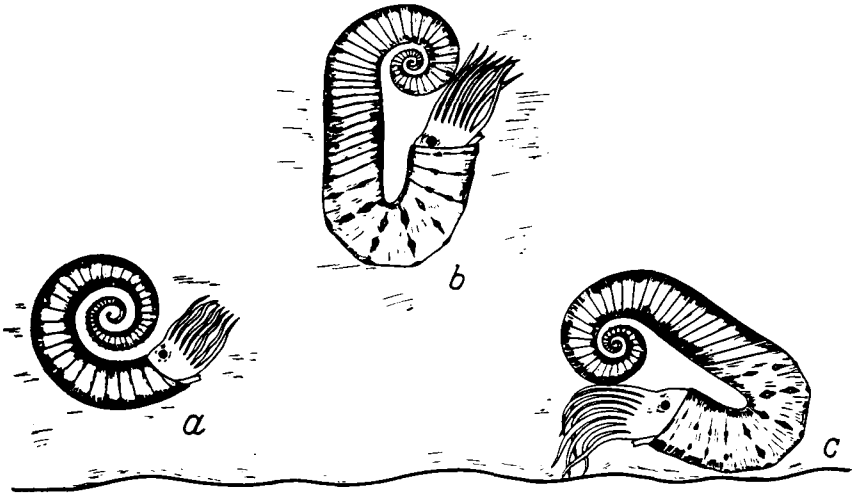

Figure 2 - Supposed life orientations of representatives of the ancylocones. *Orientation de quelques ancylocônes en position de vie supposée.*

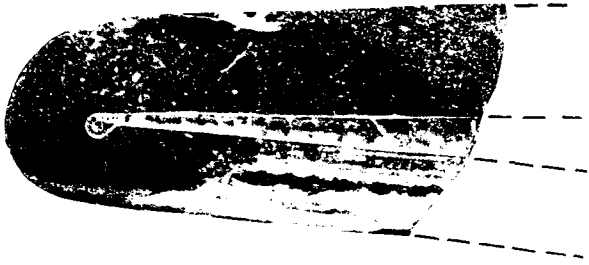

Figure 3 - Longitudinal median shell section of ***Ptychoceras*** sp. juv., specimen N 8 (403/121), North-Western Caucasus, River Pshekha, Upper Aptian (x 4). *Section médio longitudinale de* ***Ptychoceras*** *sp. juv. Aptien supérieur.*

with convex sides and highly developed sculpture. This is in contrast with representatives of monomorph ammonites with involute, plane and nonsculptured shells, that are rightly regarded by many authors as active swimmers. It is unlikely that ancylocones also were active swimmers in planospiral stage. Most probably they swam comparatively (here and elsewhere by the term "comparative" is meant the comparison with the floatability of modern *Nautilus*) slowly in the water and lived mainly near the bottom.

Among ancylocones there are forms (e.g. *Audouliceras*), which have the last flattened whorl of the plane spiral without tubercles. Perhaps such forms were relatively more active swimmers than the ancylocones mentioned above.

In the uncoiled stage the whorl first becomes stright and then it is hooked, i.e. they obtain a form similar to the uncoiled part of the heterocone shell. It is not excluded that the animal could passively float with a subvertical orienta-

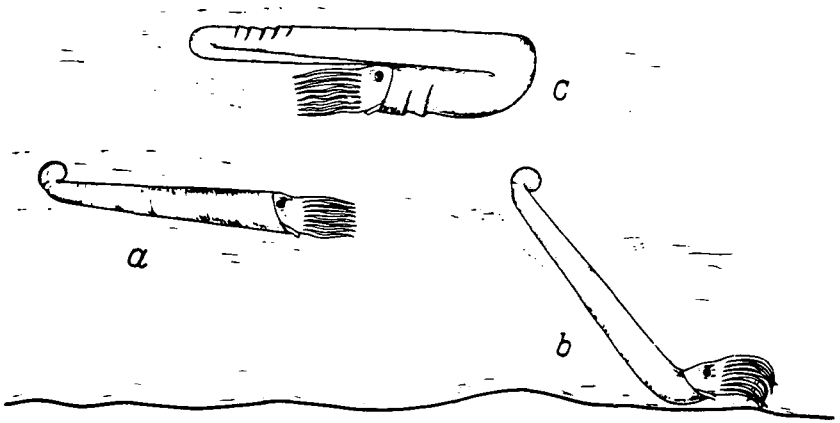

Figure 4 - Supposed life orientation of the ***Ptychoceras***. *Orientation de vie supposée.*

tion of the shaft, however we are taking into account that with such position of the hook the animal would lose direct contact with the substrate, and that is not conceivable. It is most likely, while getting food from the bottom, that the animal should reach, by liquid regulation within the camerae and activity of the hyponome, a subhorizontal position (Fig. 2).

PTYCHOCONES

Unlike the heterocones and ancylocones, the shell of ptychocones consists of three closely touching shafts and the first planospiral whorl is safely protected between the second and third sharts (Fig. 3). There are interesting points of view about the mode of life of representatives of *Ptychoceras* : the adult *Ptychoceras* is supposed to be a comparatively active swimmer with a horizontal position of the shafts (Berry 1928, Kakabadaze 1981), but during the formation of the first shaft, as well as at the adult stage, when necessary *Ptychoceras* could change its orientation from subhorizontal to subvertical (Drushchits, Dogudzhaeva 1981, Sharikadze 1986).

Deducing from the compact and torpedo-like shell, as well as from the smooth sculpture and apertural outline, we suppose that in the process or formation of the shafts and in the adult stage representatives of *Ptychoceras* were comparatively active swimmers (in the subhorizontal position), but during the formation of the kneebends of the shell they apparently lived near the bottom and in case of need could manouvre, obtaining subhorizontal or subvertical position (Fig. 4).

There are very important new data about the shell construction of *Ptychoceras* in a recent paper of Dogudzhaeva & Mutvei (1989). They show that in several cases fracturing of large parts of the shell took place often without removal of the shell fragments, followed by a large-scale repair of the shell. Besides, the outer prismatic layer at the level of the last septum (the middle of the second shaft) wedges out in the shell vertical wall; an additional nacreous layer appears on the inner surface of the living chamber in fully grown shells ; the nacreous layer makes up the entire shell wall of the apertural region in fully grown shells ; the outer shell surface, at least in the apertural region, is covered by a thin external nacreous-coating layer and all layers in the shell are traversed by numerous pore canals with a constant diameter of one millimicron. The authors suppose that the thin external nacreous layer was secreted from outside on the shell surface and suggest that the shell in *Ptychoceras* may have been covered, at least partially, by soft mantle during its lifetime.

We suppose that such an assuption is at variance with the following observations : a) of great interest are the specimens of *Ptychoceras* from our collection with damage during life. As is shown of Fig. 5a,b, the restoration of the lost broken part of the shell took place from the inner side of the shell wall, just as is mentioned in various representatives of monomorph ammonites (Drushchits,

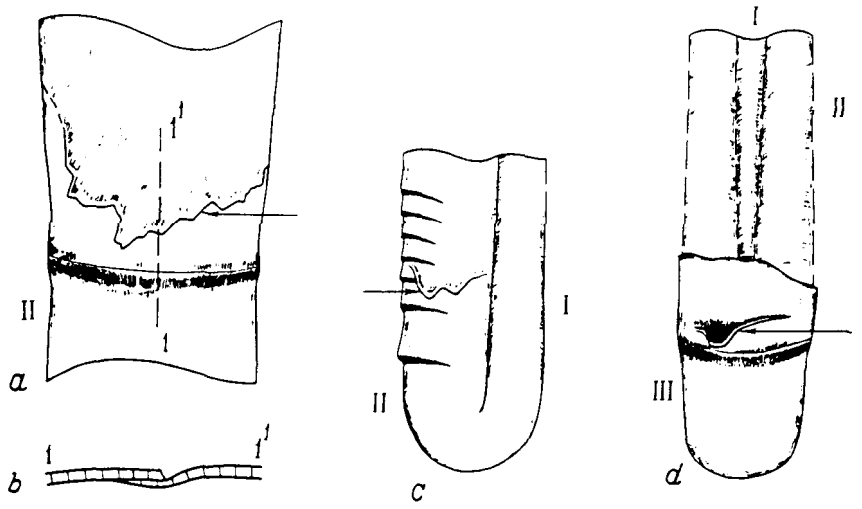

Figure 5 - Injuries during life of the shells of representatives of ***Ptychoceras***. **a**, ***Ptychoceras*** sp., specimen N8 (4018154) (x 7) ; b, regeneration of damaged parts of the shell (along the line 1-1[1]) ; **c**, ***Ptychoceras parvum*** Egoian, specimen N8 (4018152) (x 3) ; **d**, ***Ptychoceras*** cf. ***renngarteni*** Egoian, specimen N8 (4018151) (x 1,6). North-Western Caucasus, River Khokodz, Middle Aptian ; I, II, III, number of the shafts. The damaged parts of the shell are pointed out by arrows. *Blessures subies par les tests de quelques* ***Ptychoceras***. *b, régénération des parties endommagées de la coquille le long de la ligne 1-1[1]. I, II, III, numéros des hampes. Les parties endommagées sont indiquées par des flèches.*

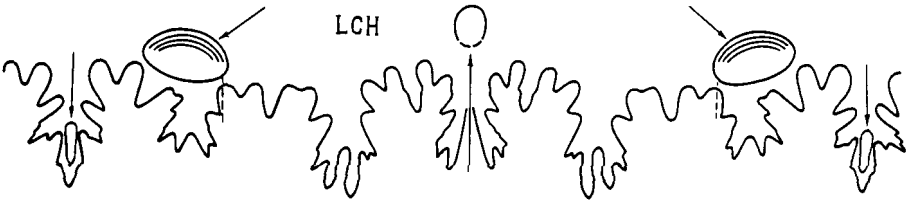

Figure 6 - Suture line and muscular scars of ***Ptychoceras*** sp., specimen N8 (4018141) (x 10) ; last part of the first shaft. North-Western Caucasus, River Khokodz, Middle Aptian. LCH - living chamber. *Ligne de suture et empreintes musculaires de* ***Ptychoceras*** *sp. Dernière partie de la première hampe. LCH = chambre d'habitation.*

Dogudzaeva & Lominadzé 1977) ; b) a similar type of injury and subsequent repair we investigated both on the second (often) and third (seldom) shafts of *Ptychoceras* ; c) there are scratches and other traumatic signs on the shell surface of some *Ptychoceras* specimens (Fig. 5c,d) that are similar to known injuries of other ammonites ; d) on the shell surface there are growth-lines that are parallel to the apertural outline and in some specimens the green-orange colour of the whole shell surface is preserved ; in both these ways they are totally similar to specimens of nonornamented monomorph ammonites (*Tetragonites, Zurcherella, Euphylloceras*), collected by us together with *Ptychoceras* (North Caucasus, section of River Uruch) ; e) it is remarkable also that by the form, quantity and location of muscle impressions on the inner surface of the shell (Fig. 6)

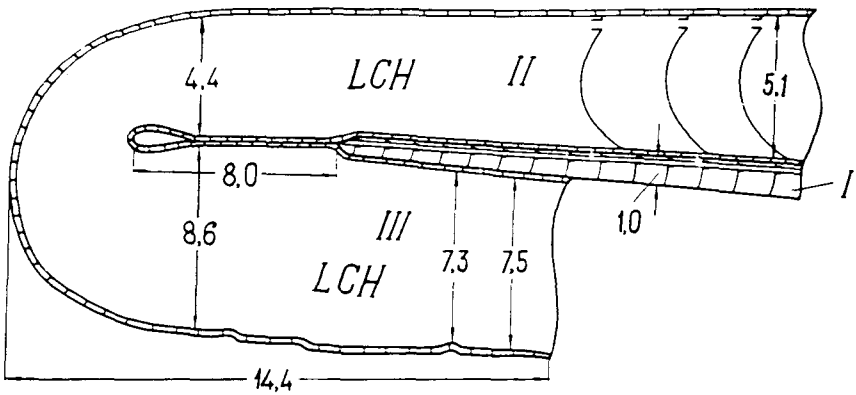

Figure 7 - Longitudinal median shell section of ***Ptychoceras parvum*** Egoian ; specimen N8 (4018153). North-Western Caucasus, River Khokodz, Middle Aptian. *Section médio-longitudinale d'une coquille de* ***Ptychoceras parvum*** *Eogian. Aptien moyen.*

representatives of *Ptychoceras* show a great resemblance to many representatives of monomorph ammonites.

These observations show that the smooth body of *Ptychoceras* would be closely connected to the inner side of the living chamber and in the extreme conditions of injuries noted the mantle secreted the lime matter for the cementation of the broken parts of the shell or for the whole restoration of the lost and broken parts. Thus, it can be concluded that during the building of the second and third shafts the representatives of *Ptychoceras*, like other ammonites, should to be regarded as typical ectocochliates.

There is also an interesting observation to add to the speculations on the mode of life of *Ptychoceras* during the early ontogenic stages. *Ptychoceras* is the sole representative among the various examples of heteromorph ammonites which has safely protected the early part of its phragmocone as a result of envelopment by the first and second shafts. However, it is remarkable that the truncation during life of the planospiral whorl and about 1/7-1/6 part of the first shaft (Fig. 7) is often observed (Sharikadze 1986, Dogozhaeva & Mutvei 1989). It is remarkable that such truncation during life is frequently observed in representatives of *Ptychoceras* with a large shell and, on the contrary, is very seldom seen in specimens with a small shell. This suggests the probability of such truncation in large forms was more common than in the little ones.

It is clear that the truncation is an accidental phenomenon and it is natural to assume that it could happen at various stages of the early ontogeny of *Ptychoceras*, namely during the formation of the first (of its last part) or second shafts. So, it is obvious that in these early ontogenic stages the shell also could not have been covered by mantle.

CONCLUSIONS

The heterocones, ancylcones, as well as ptychocones should be regarded as normally ectocochliate. In this paper some question of their mode of life were considered and particular attention was paid to the comparative morphology and functional analysis of the shell during the ontogeny, taking into account the peculiarities between each ontogenic stages.

Basing on data of shell truncation during life in *Ptychoceras* we conclude that the chambers of the phragmocone were well pressurized and the early parts of siphon in the following stages do not have some essential function because the truncation of the early parts of the shell (i.e. of the planospiral whorl and about 1/7-1/6 part of the first shaft) had no particular influence on the subsequent development of the animal.

No doubt similar processes of truncation might also happen in some other heteromorph ammonites whose early parts of the shell were not protected as in the ptychocones.

RÉFÉRENCES BIBLIOGRAPHIQUES

BERRY E.W. 1928 - Cephalopod adaptation, the record and its interpretation. *Quart. Rev.*, **3**, (1) : 92-108.

DOGUDZHAEVA L. & MUTVEI H. 1989 - *Ptychoceras*, a heteromorphic lytoceratid with truncated shell and modified ultrastructure (Mollusca : Ammonoidea). *Palaeontographica*, A, **208** : 91-121.

DRUSHCHITS V.V., DOGUDZHAEVA L.A. & LOMINADZÉ T.A. 1977 - Peculiarities of the shell inner constructions of the Middle Callovian ammonites. *Palaeont. J.*, 3 : 19-29.

DRUSHCHITS V.V. & DOGUDZHAEVA L.A. 1981 - The Ammonites under the electronic microscop. Moscow, MGU : 1-238 (in Russian).

KAKABADZÉ M.V. 1971 - The Colchidites and their stratigraphical significante. *Tr. Geol. Inst. AN GSSR*, **26**: 1-119 (in russian).

KAKABADZÉ M.V. 1981 - The Ancyloceratids of the south of the USSR and their stratigraphical significance. *Tr. Geol. Inst. AN GSSR*, **71** : 1-197 (in russian).

KAKABADZÉ M.V. 1988 - On the morphological classification of the Heteromorph Ammonites. *In* WIEDMANN J. & KULLMANN J. (eds) : Cephalopods. Present and Past, Stuttgart : 447-452.

KLINGER H.C. 1980 - Speculations on buoyancy control and ecology in some Heteromorph Ammonites. *In* HOUSE M.R. & SENIOR J.R. (eds.) : The Ammonoidea. *Systematics Association* special, **18** : 337-355.

SHARIKADZÉ M.Z. 1986 - Morphogenetic development of the genus *Ptychoceras* d'ORBIGNY (Lytoceratida, Ammonoidea). *Paleont. Sbornik Lvovski Gos. Univ.*, **23** : 12-17 (in russian).

WESTERMANN G.E.G. 1971 - Form, structure and function of shell and siphuncle in coild Mesozoic Ammonites. Royal Ontario Museum. *Life Sci. Centr.*, Toronto, **78** : 1-39.

WESTERMANN G.E.G. 1975 - Architecture and buoyancy of simple cephalopod phragmocones and remarks on Ammonites. *Paläont. Z.*, **49**, 3 : 221-234.