

PHYLOGENY AND SYSTEMATICS OF PERISPHINCTIDS AS INTERPRETED FROM SUTURE ONTOGENIES

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ABSTRACT

Mode of early differentiation of the inner part of the suture line is most important for taxonomy of Perisphinctids. Six types of suture lines can be distinguished, each characteristic of corresponding superfamily : a) the perisphinctoidal type is characterized by asymmetric division of the internilateral lobe (I_1I_2) , in adult specimens the two branches are non-isolated and aslant; b) the stephanoceratoidal type is characterized by the formation of a new lobe near the peak of the saddle I/D, on the inner slope of the lobe I and by the following sinking; c) the olcostephanoidal type is defined by symmetric (I_1I_1) or asymmetric (I_2I_1) division of the lobe I; d) the desmoceratoidal type by symmetric division of the lobe I, and by the formation of sagging suture lobe; e) the hoplitoidal type by early symmetric division of an independent lobe in the saddle I/D.

KEYS-WORDS : PERISPHINCTINA, EVOLUTION, SUTURE LINE, PHYLOGENESIS.

Résumé

Le mode de différenciation précoce de la partie interne de la ligne de suture s'est révélé d'une importance capitale pour la taxinomie des Perisphinctides. Ainsi, on peut distinguer six types de lignes de suture, chacun étant caractéristique d'une superfamille : a) le type périsphinctoïde montre une division asymétrique du lobe latéro-interne (I_1I_2) , les deux branches obliques n'étant pas isolées sur les exemplaires adultes ; b) le type stéphanoceratoïde est caractérisé par la formation d'un nouveau lobe près du sommet de la selle I/D, sur la pente interne du lobe I et sur les pentes suivantes ; c) le type olcostéphanoïde est défini par la division symétrique (I_1I_1) ou asymétrique (I_2I_1) du lobe I ; d) le type desmoceratoïde montre la division symétrique du lobe latéral interne (I_1I_1) et la formation d'un lobe arqué ; e) le type hoplitoïde se singularise par une division symétrique précoce du lobe I et par la formation d'un lobe sutural généralement linéaire ; enfin f) le type cardiocératoïde présente la formation d'un lobe indépendant dans la selle I/D.

MOTS-CLÉS : PERISPHINCTINA, ÉVOLUTION, LIGNE DE SUTURE, PHYLOGENÈSE.

INTRODUCTION

Perisphinctina represent one of the most significant and widespread group of ammonites. They are of great importance for the Jurassic and Cretaceous biostratigraphy as well as for the solution of many questions of ammonites biology. We have thoroughly investigated the ontogeny of hundreds of suture lines in Perisphinctina. The data attained enable us to establish various trends in their evolution.

When considering the problems of suture line evolution in onto-phylogeny, the mode of formation of new elements, [indexation of suture (1989) to a certain degree differs from the terminology suggested in this paper], their location and pattern as well as the discrimination of homologous and analogous lobes deserve special attention. The processes of formation and evolution of new elements of suture lines were discussed in historical aspect.

Besidesour own observations, data of other authors have been analyzed (Westermann 1956; Schindewolf 1963, 1965, 1966; Mikhailova 1983; Kullmann & Wiedmann 1970; Wiedmann & Kullmann 1981; Thierry 1975, 1978; Shevirev 1960; Beznosov 1960; Alekseev 1982; Shulgina 1985, and others).

Comparison of some ammonoid suture-symbol terminologies is given below (Table 1).

Wedekind- Schindewolf	Ruzhentsev	Terminology accepted by us
E, external lobe	V, ventral lobe	V, ventral lobe
I, internal lobe	D, dorsal lobe	D, dorsal lobe
L, lateral lobe	U, umbilical lobe	L, lateral lobe
U ₁ , first umbilical	I, internilateral	I, internilateral
lobe	lobe	lobe
U ₂ , second umbilical	U1,first umbilical	U, umbilical
lobe	lobe	lobe

Table 1

In most Perisphinctina the primary suture and initial lobe lines consist of five lobes. These are : ventral lobe (V), lateral lobe (L), umbilical lobe (U), internilateral (I) and dorsal lobe (D). The ventral lobe is always bifid, while the other lobes are undivided. It is noteworthy that in Macrocephalites the primary suture is sixlobate (Fig. 1). The sixth element occurs as a result of division of the umbilical lobe. At the base of the latter a small secon- dary saddle becomes reduced and the suture line becomes fivelobate. It should be noted that a similar pattern is observed in Tetragonitidae (Schindewolf 1968 ; Mikhailova 1977, 1979 ; Krivoshapkina 1978 ; Sharikadze 1984). In Tetragonitidae, the secondary saddle, which was also formed at the base of umbilical lobe, becomes reduced at the end of the first whorl and the line becomes fivelobate too (Schindewolf & Krivoshapkina negated this reduction in Tetragonitidae). There is no doubt, that these data cannot be considered as evidence for direct genetic relations between Tetragonitidae and Macrocephalitidae. Firstly, the bifidity of the umbilical lobe is not always well pronounced in these two groups, and secondly, the secondary saddle vanishes without any trace. It has no influence upon subequent evolution of the lobe. The early formation of the umbilical lobe and the subsequent reduc-



Figure 1 - Ontogenetic development of suture line in *Macrocephalites* sp. juv. ; sample N301/1, Northern Caucasus, r. Ardon, Lower Callovian. 1,2 - first and second lines ; W_1, W_2 ...-first, second and etc. whorls.

tion of the secondary saddle may be considered as a result of their location on the umbilical seam, where new elements usually are formed and on the other hand of the whorl narrowing in the area of primary constriction. The existence of a sixlobate primary suture in the above mentioned ammonites may also be the result of relatively high chamber pressure at this early stage of evolution - compared with the period of reduction of the secondary saddle.

It must be noted, that in Desmoceratoidea and Hoplitoidea the formation of new lobes is well accelereted, and new elements appear in more and more earlier stages of evolution. For example, the division of the lobe I in the Early Aptian *Pseudohaploceras* takes place at the beginning of the second whorl, in the Late Aptian *Pseudosilesites* in the middle of the first whorl, in the middle Albian *Parasilesites* (MIKHAILOVA, 1983, fig.79) on the third line, and in the Early Turonian *Beschtubeites beschtubensis* ILYIN (Hoplitoidea, Placenticeratidae) - as soon as in the primary suture (Mikhailova 1983, fig. 106). Thus, also in some Placenticeratidae the primary suture is sixlobate, but in difference from the above cases the



Figure 2 - Ontogenetic development of suture line in *Epivir-gatites nikitini* MICHAILOV ; sample N11/4n Russian Platform, r. Volga, v. Kadhpir, Middle Volgian.

secondary saddle is not reduced. It should be noted, that in all cases under discussion, the existence of a six-lobate primary suture has no taxonomic significance.

It is worth mentioning that in some *Macrocephalites* and *Cadoceras* the primary suture sometimes "sits astride" of the prosuture. At the same time the primary suture looks rudimentary - it is weakly divided. It consists of four lobes that strictly differ in size and configuration from each other as well as from other initial suture lines. It must be noted that the ventral lobe remains undivided.

There is a regular size variation of elements of the initial suture lines in ontogeny and in phylogeny. In particular, older elements are greater (protolobes : V,L,D) in comparison with younger ones (metalobes : I and U). Lateral and inner saddles dominate over the saddles of the primary suture. Equality between separate elements of suture line is preserved to a considerable extent at later stages of evolution.



Figure 3 - *Dorsoplanites gracilis* SPATH ; sample N2145/26, Eastern slope of nearpolar Ural, r. Jatria, Volgian.

The general outline of the ventral lobe remains almost invariable in ontogeny and phylogeny. Only a limited complication by secondary elements can be observed. The lateral lobe is almost always asymmetrically trifid with exception of some hoplitidae ; in adult Late Cretaceous Placenticeratidae in particular, this lobe is asymmetrically bifid (Mikhailova 1983). The umbilical lobe which occurs last in Mezozoic ammonites is usually the smallest of all initial lobes, it occurs always of the primary suture in a strictly definite site, i.e. on the lobe and divides it into two equal parts. In the area of initial squeeze, as a result of narrowing of the whorl, the lobe is reduced and looks often like a small hollow. Later on the umbilical lobe gradually shifts to the margin of the shell. In most cases lobe U becomes trifid and asymmetrical, though in some Olcostephanoidea it is asymmetrically bifid (Figs. 2,3).

No essential changes are observed in the evolution of the dorsal lobe ; the process of complication of the dorsal lobe follows the common scheme of various groups. At the beginning a pair of marginal appendices occur and then other small



Figure 4 - Ontogenetic development of suture line in *Kosmoceras jason* (REINECKE) ; sample N1001/1, Russian Platform, r. Oka, v. Elatma, Middle Callovian.

subsidiary elements are formed. At the same time, the lobe gradually narrows while being elongated. With rare exceptions the base of the dorsal lobe is always undivided. The internilateral lobe, however, as well as the adjacent areas undergo essential changes in ontogeny and phylogeny.

In contrast the saddles have been disregarded in ontophylogenetic studies due to their conservatism ; but they evolved in different ways in different groups of Perisphinctina. In Perisphinctoidea and Olcostephanoidea as well as partly in Stephanoceratoidea, saddles are mainly asymmetrical, bifid and low. In Desmoceratoidea, L/U is the highest saddle ; the mode of dissection of the saddle I/D in representatives of Otoitidae, Sphaedroceratidae, Macrocephalitidae, Kosmoceratidae an Cardioceratidae deserves attention. It becomes bifid already at early stages of ontogeny. At later stages of growth two independent saddles are formed instead of the initial saddle as a result of deepening and widening of a secondary lobe (Figs. 1,4). Almost the same is true for the ontogeny of the saddle V/L in some Hoplitoidea. The



Figure 5 - *Parkinsonia densicosta* (QUENSTEDT) ; sample ND-14/1, Daghestan, v. Golotl, Lower Bathonian.

secondary lobe, that occurs on the top of the saddle gets divided into two parts as a result of gradual deepening and differentiation of the lobes. This phenomenon is better visible in the Late Cretaceous Placenticeratidae (Smith 1900 ; Matsumoto 1953 ; Schindewolf 1966 ; Mirzoev 1967 ; Mikhailova 1967, 1978, 1983 ; Ilyin, Mikhailova & Khakimov 1982).

The most essential changes in phylogeny of suture line, however, take place within the lobe I and adjacent areas, as it was mentioned above. Judging by the ontogeny of *Erycites fallifax* ARK. (after Schindewolf 1963, fig. 245), the complication of the suture line - in this most probably ancestral group of Perisphinctina - Hammatoceratidae goes on in the following way. First, the lobe U^1 occurs ventrally of the lobe I near the saddle U/I. Later, a new lobe I₂ is generated at the base of the lobe I on the latter's dorsal side. Later on, new elements of suture lobe appear as a result of dissection of the saddle U^1/I_1 . It must be noted, that in most of the Mezozoic Ammonoidea, including Perisphinctina, lobes are formed in the area



Figure 6 - **Pseudohaploceras douvillei** (FALLOT); sample N8(107/32) Daghestan, v. Tsudakhar, Lower Aptian.

of umbilical seam. Lobes I_1 and I_2 , divided by a secondary narrow saddle elongate and grow narrower. They become oblique without being isolated. In Perisphinctina heterotopy is observed in the formation of U^1 : its site is often displaced not only within the limits of our family, but also within the limits of one and the same genus. For example, in Parkinsonia (Fig. 5; see also Schindewolf 1963 ; fig. 282-286) it is generated on the saddle U/I. However, the limits for site displacement are not wide - from the top of the saddle U/I to the lower part of the ventral side of the lobe I. The place of generation of the lobe depends upon the degree of involution of the shell, i.e. which part of the lobe is located at the umbilical seam. It is noteworthy, that heterotopy of the lobe U¹ sometimes seems to be the result of the authors subjectivity, since various authors differently interpret the place of generation of definite element on one of the same taxonomic group. For instance, according to Schindewolf (1966, fig. 370-378 et al.) the lobe U^1 is generated on the top of the saddle U/I in Desmoceratoidea,



Figure 7 - *Pseudosilesites seranoniformis* EGOIAN ; sample N8(404/9) Western Caucasus, r. Vulan, Upper Aptian.

while following Mikhailova (1983, fig. 77-80), Grabovskaja (1984, fig. 1-3) and our own data (Figs. 6-8) they are generated on the ventral side of the lobe I1, or at the latter's base. With regard to the time of occurrence of the lobe U^1 in phylogeny, a certain displacement towards earlier stages of evolution is observed. In particular, if in old representatives of the suborder Perisphinctina U^{1} appears to the end of the second lobe, or at the beginning of the third whorl, in younger samples U^1 is generated approximately in the middle of the second whorl. It must be noted also, that the lobe U^1 is often originated on the suture or behind the umbilical seam, during ontogeny it shifts to the lateral side and from this side it becomes part of the sutural lobe. No matter where the lobe has been formed in ontogeny on the side or at the base of the lobe I - it always must be designated by symbol U¹. Since in older representatives of Perisphinctina and in the supposed ancestral group the Hammatoceratidae, it occurs within the saddle U/I.



Figure 8 - Leymeriella terna SAVELIEV ; sample N1309/1. Western Kopet-Dag, Lower Albian.

It may be concluded, that despite the variety in ways of formation of the lobe U^{I} , the latter is still conservative in the sense of morphological structure and further differentiation, therefore being of no essential taxonomic significance.

ATTEMPT OF SUTURE CLASSIFICA-TION IN PERISPHINCTIDS

Alterations, observed within the internilateral lobe and the adjacent saddle I/D are however, of the most taxonomic value for Perisphinctoidea. According to Schindewolf (1963), asymmetrical division of lobes I-I1I2 takes place in Hammatoceratidae. Later on both branches remain uncomplicated. They are located on the ventral side of the saddle I/D, being oriented obliquely. Almost the same is true of the early Perisphinctina which are Bigotites, Zigzagiceras, "Pseudoperisphinctes" (SCHINDEWOLF, 1966, fig. 302, 303, 305), Bajosisphinctes (Obsoletosphinctes), B. (Siemiradzkia), Leptosphinctes (Leptosphinctes) (BEZNOSOV & MIKHAILOVA, 1981, fig. 1,3,4) as well as Reineckia (SCHINDEWOLF, 1966, fig. 338), Collotia (SCHINDEWOLF, 1966, fig. 340), Choffatia



Figure 9 - Choffatia kontkiewiczi SPATH ; sample N2144/1, Russian platform, r. Oka, v. Elatma, Middle Callovian.

(Fig. 9), Volgaites (Fig. 10), Erymnoceras (Fig. 11) and others. The same is also true of the family Himalayitidae, i.e. the genera Corongoceras, Aulacosphinctes, Micracanthoceras? (SCHINDEWOLF, 1966, fig. 327-330) with the difference that in the latter the inner branch of the lobe I-I2 and the secondary saddle I_1/I_2 are more developed, but at the same time they are less oblique. From the Oxfordian on, the trend of "slipping" of the site of I₂ to the base of the internilateral lobe is observed during evolution of the lobe I in some perisphinctids, i.e. Properisphinctes, "Prososphinctes", Perisphinctes (SCHINDEWOLF, 1966, fig. 311,313-315); this leads finally to the almost asymmetric division of the lobe. At the same time the inner branch of the internilateral lobe, I1, and a newly formed secondary saddle evolved rather intensely and in the adult, these elements acquire complete independence. However, the lobes I_1 and I_2 are slightly oblique in most cases. This trend is well pronounced in the ancestors, as it was mentioned above. The symmetric division of the internilateral lobe in the onto- and phylogeny becomes a stable characteristic for the descendants. In Olcostephanoidea the lobe I is sometimes divided somewhat asymmetrically (Olcostephanidae, Dorsoplanitidae, Ataxioceratidae), while in other cases it is divided symmetrically (Berriasellidae, Craspeditidae). Symmetrical division becomes more typical of Desmoceratoidea and Hoplitoidea. It must be noted also, that in



Figure 10 - Volgaites elatmaensis SASONOV ; sample N2144/4, Russian Platform, v. Elatma, Middle Callovian.

older perisphinctid U^{I} is often generated before I₂, while in younger representatives this is not the case, and the division of the lobe I precedes the occurence of U^{1} .

Subsequently, in spite of the early division, the dorsal branch evolves more intensely in comparison with the ventral one. The former replaces the internilateral lobe becoming completely isolated. All elements of the suture line are placed on a straight line. A sutural lobe is formed as a result of dissection of the saddle U^1/I_1 .

Representatives of Desmoceratoidea and Hoplitoidea are practically undistinguishable from Olcostephanoidea in mode of the early differentiation of the suture line. The lobe I is almost symmetrically divided, while, later on, the lobe U^{I} is generated. Subsequently, the branches of the internilateral lobe become isolated, the dorsal one is connected with the lobe D, while the ventral one shifts to the umbilical seam. A sutural lobe is generated as a result of dissection of the ventral side of the ventral branch (Figs. 6,7).

A different way of suture development is represented in Stephanoceratidae, Morphoceratidae as well as in Parkinsoniidae. In particular, in Stephanoceratidae new elements are generated



Figure 11 - Erymnoceras doliforme (ROMAN) ; sample N20/56-1, Northern Caucasus, r. Cherek Balkarski, Middle Callovian.

asymmetrically on both sides of the lobe I either simultaneously or at different times. On the ventral side of the lobe I and near its base, the lobe U^1 occurs; while on the dorsal side and near the top of the saddle, I₂ is generated (Fig. 12). Almost the same is true of Parkinsoniidae (Fig. 5) and Morphoceratidae (Schindewolf 1965, fig. 297-299). Here, new elements are first generated on the ventral side of the lobe I. Later on, the lobe I₂ develops at the top of the saddle I/D, and abruptly descends deepening. It becomes larger than the lobe I_1 . Both branches (I_1I_2) are directed obliquely. It must be noted, that in one of relatively young representatives of Stephanoceratidae (i.e. Polyplectites) a new element originates closer to the top of the saddle I/D (Schindewolf 1965, fig. 258, 259). Later I2 on it deepens, becomes isolated and straightens. If trace the way of evolution of the given lobe in phylogeny it may be noted that unlike Hammatoceratidae and early Perisphinctoidea, here the place of its generation shifts up to the inner side of the lobe I manifesting tendency to isolation and straightening. The same is observed in other, genetically quite remote groups of ammonites (Aptian Chelonicerati-



Figure 12 - Stephanoceras sp., sample N589, localities unknown, Upper Bajocian.



Figure 13 - Suture lines of *Macrocephalites* cf. *canizarroi* (GEMMELLARO) ; sample N420/58-2, Northern Caucasus, pass Gerchoch, Lower Callovian.

dae and Acanthohoplitidae) as well. In Acanthohoplitidae, the new element occurs on the ventral side of the internilateral lobe and near the top of the saddle U/I, while in the probably ancestral Cheloniceratidae the element is generated slightly lower, in the middle of the ventral side or near the base of the lobe I. Heterotopy of new elements is observed within the lateral lobe, as well. Thus in older Cheloniceratidae the lateral lobe is divided almost symmetrically, while in younger ones the place of generation of the new Hammatoceratidae, early representatives of Perisphinctoidea and the families mentioned above, do not differ essentially in the general scheme of development of the suture line. We consider the lobe developing on the dorsal side of the lobe I as homologue of the lobe U^1 , while the lobe originating in the top of the saddle I/D as homologue of the lobe I₂. Consequently, they must be designated by corresponding symbols.

The whole group of ammonites comprising Sphaeroceratidae, Macrocephalitidae, Cardioceratidae, Otoitidae and Kosmoceratidae is considerably different in the evolution of the dorsal part of suture line. In ancestral representatives such as Otoitidae and Sphaeroceratidae, a new lobe is originated on the side of dorsal lobe. During ontoand phylogeny it gradually shifts to the top of the saddle I/D. At the same time the lobe deepens. It becomes independent and then replaces the lobe I. According to Schindewolf (1965) as well as proceeding from our data this phenomenon is well pronounced in the phylogenetic sequence; Otoitidae \rightarrow Sphaeroceratidae \rightarrow Macrocephalitidae \rightarrow Kosmoceratidae \rightarrow Cardioceratidae. An interesting pattern is observed in representatives of the family Macrocephalitidae having an intermediate position in this sequence. At an early stage of ontogeny of some species (Fig. 1), the lobe I^1 is generated symmetrically on the top of the saddle I/D; in other ones, the same lobe asymmetrically is dividing this saddle (Fig. 13). According to Thierry (1975, 1978), a similar pattern is observed in other *Macrocephalites*, as well. In our opinion, the heterotopy of the lobe I^1 may, thus serve for evidence of generic relations between Macrocephalitidae and Sphaeroceratidae as well as between Macrocephalitidae and Cardioceratidae.

The lobe U¹ often develops on the ventral side of the lobe I, closer to its base. Two cases of deviation from the above described normal evolution of suture line are observed. In the first case, in some representatives of Otoitidae, particularly in Otoites and Emileia (Schindewolf 1965, figs. 246, 250) an asymmetric division of the internilateral lobe I_1I_2 takes place after formation of U¹ and I¹ like in Hammatoceratidae and Perisphinctidae. We consider this a base for suggesting phyletic relations between Hammatoceratidae and Otoitidae. Heterotopy in the formation of lobe U^{\perp} is also oberved in representatives of Kosmoceratidea. Sometimes U^{f} is generated on the ventral side of the internilateral lobe, near its base (Fig. 4), or higher up the side, near the top of the sad-



Figure 14 - Different types of suture line ontogeny in Perisphinctina, a, Hammatoceratidal (Erycites fallifax ARKELLI (after Schindewolf 1965, fig. 245); b, Stephanoceratoidal (Stephanoceras sp.); c, Perisphinctoidal (Insphinctes nikitinoensis SASONOV) ; d, Car-(Macrodiocetoidal cephalites nikitini Michailov) ; f. Desmoceratoidal (Melchiorites emerici (RASP.); g, Hoplitoidal (Cleoniras dubium MICHAILO & TERECHOVA (after Michailova 1983, fig. 89).

dle U/I (Schindewolf 1965, figs. 271-273). In certain cases it is generated at the base of the lobe I, thus resulting in an almost symmetrical division of the latter. However, in our opinion, wherever the U¹ lobe is generated - either at the base of the lobe I or at the top of the saddle U/I, it is always located at the umbilical seam and most likely it is a homologue of the lobe U¹ in Hammatoceratidae, as it was mentioned above.

It must be noted, that adult suture line of the considered ammonite groups bear a certain resemblance with some representatives of Olcostephanoidea, Desmoceratoidea and Hoplitoidea. This similarity is manifested primarily by the similar position of the new lobe. This similar positioning is, however, since these lobes are not homologues, as was mentioned above.

A few words about some other regularities of suture line development in Perisphinctina : most of the representatives of the suborder perisphinctina are characterized by a suture line with a medium degree of differentiation. At the same time a progressive evolution of the suture line is observed in phylogeny. This particularly manifested by the early occurence of new elements in the onto- and phylogeny of young representatives of Perisphinctina, by the increase in number of elements as well as the rise of differentiation degree. In general, it may be concluded that the more complex the suture line is, the better pronounced is the symmetry of it's individual elements. In this respect Perisphinctidae (Figs. 9, 10), or Parkinsoniidae (Fig. 5) may be compared with Desmoceratidae (Figs. 6,7). On the other hand, in some phylogenetic branches a reverse picture is observed : the suture line becomes simplified possibly related to specialization, when sculpture coarsens, degree of involution decreases and whorls width become in comparison with the ancestors. This may be exemplified by representatives of the family Leymeriellidae (Fig. 8) in wich suture line is markedly simplified as compared with ancestral forms (e.g. *Pseudosilesites*, Fig. 7). The same is true of same representatives for Himalayitidae, Kosmoceratidae and Polyptychitidae, which suture line is weakly differenciated in comparison with their ancestors.

CONCLUSIONS

In Perisphinctids the prosuture is threelobate, while the primary suture is four-, five-or sixlobate. A fourlobate primary suture is rarely observed when it "sits astride" of the prosuture. Fivelobate primary sutures occur in most Perisphinctina. Sixlobate primary sutures are observed in some Placenticeratidae (VLU1111D) and Macrocephalitidae (VLU101ID). In the latter however, the line soon becomes fivelobate as result of reduction of the secondary saddle U_1/U_1 , while in the Placenticeratidae I111 evolve subsequently in ontogeny. Existence of fouror sixlobate primary sutures has no taxonomic value.

In the differentiation process of the internilateral lobe and adjacent saddles an acceleration effect is noticeable, when new elements progressively occur in early stages of ontogenetic evolution. The occurence of the sixth element in the primary suture of some Late Cretaceous Placenticeratidae may be considered as a result of such an acceleration.

Heterotopy is pronounced in the formation of lobes U^1 , I₂ and I^1 in onto- and phylogeny.

Based in the morphology of the dorsal parts of the suture line two general types of differentiation may be distinguished. In one group (Perisphinctoidea, Stephanoceratoidea an analogue of the true internilateral lobe is absent. The branches of the initial lobe I are relatively undeveloped. They are not isolated, being arranged obliquely. In the other group of ammonites (Car-



Figure 15 - Perisphinctid phylogeny assuming a hammatoceratid origin.

dioceratoidea, Olcostephanoidea, Desmoceratoidea and Hoplitoidea), next to the dorsal lobe occurs an isolated, straight-forward and rather well differenciated lobe and replaces the internilateral lobe. The formation of various morphogical types of suture lines seems to correlate to intercameral hydrostatic pressure as well as to the absolute size of the involute part of the shell.

In ontogeny a series of new small elements occurs in the area of the umbilical seam often forming a sutural lobe. The latter is built as a result of dissection of the initial outer side of the lobe I.

Evolution of the ventral part of the suture line follows the common scheme nearly in all representatives of Perisphinctina. In this respect the mode of early differentiation of the inner part of the suture line acquires special taxonomic significance for this suborder. Most attention should be paid to the dissection of the lobe I and saddle I/D. The following types of suture lines may be distinguished with in Perisphinctina (Fig. 14): - Perisphinctoidal type (Fig. 14c), with asymmetric division of internilateral lobe (I_1I_2) these branches are not isolated being oriented obliquely in the adult stage;

- Stephanoceratoidal type (Fig. 14b), with occurence of a new lobe I₂ near the top of the saddle I/D on dorsal side of the lobe I and with it's subsequent descending;

- Olcostephanoidal type (Fig. 14e), with symmetric (I_1I_1) or asymmetric (I_2I_1) division of the lobe I;

- Desmoceratoidal type (Fig. 14f), with symmetric division of the internilateral lobe (I_1I_1) and with formation of a sagging sutural lobe;

- Hoplitoidal type (Fig. 14g), with early symmetric division of the lobe I, in most cases with formation of a linear sutural lobe as well as of an adventive lobe ;

- Cardioceratoidal type (Fig. 14d), with the formation of an individual lobe on top the saddle I/D.

The desmoceratoidal type is the most conservative. This type of suture line turns out to be the most viable and lasting. It was functioning during the whole Cretaceous period.

Proceeding from data on the morphogeny of the shell, three phylogenetic lines may be draw in Perisphinctina. These are : I. Hammatoceratidea \rightarrow Perisphinctoidea Olcostephanoidea \rightarrow Desmoceratoidea \rightarrow Hoplitoidea ; II. Hammatoceratidae \rightarrow Stephanoceratoidea ; III. Hammatoceratidea \rightarrow Cardioceratoidea (Fig. 15).

The suborder Perisphinctina includes the following superfamilies a) Superfamily Stephanoceratoidea Neumayr 1875 [Families Stephanoceratidae Neumayr 1875 ; Morphoceratidae Hyatt 1900; Parkinsoniidae Buckman 1920; ? Tulididae Buckman 1921; ? Oecoptychiidae Arkell 1957]; Superfamily Cardioceratoidea Siemiradzki b) 1891 [Families Otoitidae Mascke 1907; Sphaeroceratidae Buckman 1920 ; Cardioceratidae Siemiradzri 1891 ; macrocephalitidae Buckman 1922 ; Mayaitidae Spath 1928; ? Kosmoceratidae Haug 1887]; c) Superfamily Desmoceratoidea Zittel 1895 [Families Desmoceratidae Zittel 1895; Holcodiscidae Spath 1924 ; Silesitidae Hyat 1900 ; Kosmoceratidae Spath 1922; Pachiscidae Spath 1922 ; Muniericeratidae Wright 1952 ; Leymeriellidae Breistroffer 1951]; d) Superfamily Hoplitoidea H. Douvillé 1890 [Families Hoplitidae H. Douvillé 1890 ; Placenticeratidae Hyatt 1900 ; (Schloenbachiidae Parona & Bonarelli 1897;? Trochleiceratidae Beistroffer 1953; ? Engonoceratidae Hyatt 1900]; e) Superfamily Perisphinctidoidea Steinmann 1890 [Families Perisphinctidae Steinmann 1890 ; Reineckiidae Hyatt 1900 ; Pachyceratidae Buckman 1918; ? Himalayitidae Spath 1925]; f) Superfamily Olcostephanoidea Pavlow 1892 [Families Olcostephanidae Pavlow 1892; Craspeditidae Spath 1924; Berrisellidae Spath 1922; Ataxioceratidae Buckman 1921; Dorsoplanitidae Arkell, 1950; Polyptychitidae Spath 1924; Aulacostephanidae Spath 1924; Aspidoceratidae Zittel 1895; ? Oosterellidae Breistroffer 1940; ? Simoceratidae Spath 1924].

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REFERENCES

- ALEKSEEV S.N. 1982 Razvitie lopastnikh linii v ontogeneze nekotorikh pozdnejurskikh i rannemelovikh Craspeditidae i polyptychitidae. Stratigraphie triasovikh i jurskikh otlozhenii neftegazonosnikh basseinov SSSR : 115-128.
- BEZNOSOV N.V. 1960 K systematike jurskikh Ammonoidea. Paleont. Zhurnal, 1:47-60.
- BEZNOSOV N.V. & MIKHAILOVA I.A. 1981 Systematika srednejurskikh Leptosfinctin i Zigzagiceratin. *Paleont. Zhurnal*, **3**: 47-60.
- GRABOVSKAJA V.S. 1984 Ontogenez lopastnoi linii pozdnemelovikh desmoceratacei Sakhalina. Systetika i evolucia bespozvonochnikh Dalnego Vostoka : 94-99.
- ILYIN V.D., MIKHAILOVA I.A. & KHAKIMOV F.Fh. 1982 -Morfogenez senomanskikh Placenticeratid. - Doklady AN SSSR, 266, 2: 474-477.
- KRIVOSCHAPKINA V.S. 1978 Ontogenez lopastnoi linii pozdnemelovikh tetragonitid Sakhalina. *Paleont. Zhurnal*, 1: 69-77.
- KULLMANN J. & WIEDMANN J. 1970 Significance of sutures in phylogeny of Ammonoidea. Paleontol. Contrib. Univ. Kansas, 47: 1-32.
- KVANTALIANI I.V. 1989 Early cretaceous ammonites of the Crimea and Caucasus and their biostratigraphic significance. *Mezniereba* : 228 p.
- MATSUMOTO T. 1953 On the ontogeny Metapla- centiceras subtilistriatum (JIMNO). Jap. J. Geol. Geogr., 23: 139-150.
- MIRZOEV G.G. 1967 O vzaimootnoshenii semeistv Hoplitidae i placenticeratidae. *Paleontol. Zhurnal*, 4:56-70.
- MIKHAILOVA I.A. 1974 Sviazi rannemelovikh i pozdnemelovikh goplitacii. Spisanie na Bolgarskogo geol. druzhestvo., 35, 2: 117-132.
- MIKHAILOVA I.A. 1977 O schestilopastnoi primasuture melovikh ammonitov. *Doklady. AN SSSR*, 234, 5:213-216.
- MIKHAILOVA I.A. 1978 Osobennosti morfogeneza semeistva Placenticeratidae Hyatt. Doklady AN SSSR, 242, 1: 207-210.
- MIKHAILOVA I.A. 1979 ontogeneticheskoe razvitie nekotorikh pozdnemeovikh tetragonitid. Vestnik MGU, 4, geologia, 1: 23-34.
- MIKHAILOVA I.A. 1983 Systema i filogenia melovikh ammonoidei. Nauka : 280 p.

- SHARIKADZE M.Z. 1984 O schestilopastonoi primasuture rannemelovikh tetragonitid (Ammonoidea). Doklady ANN SSSR, 275, 5 : 1182-1184.
- SCHINDEWOLF O.H. 1963 Studien zur Stammesgeschichte der Ammoniten. Lief. 3. Abhandl. Akad. Wiss. und Lit. Mainz, math.-natur. Kl., 6: 261-406.
- SCHINDEWOLF O.H. 1965 Studien zur Stammesgeschichte der Ammoniten. Lief. 4. Abhandl. Akad. Wiss. und Lit. Mainz, math.-natur. Kl., 3: 411-508.
- SCHINDEWOLF O.H. 1966 Studien zur Stammesgeschichte der Ammoniten. Lief. 5. Abhandl. Akad. Wiss. und Lit. Mainz, math.-natur. Kl., 3: 511-640.
- SCHINDEWOLF O.H. 1968 Studien zur Stammesgeschichte der Ammoniten. Lief. 7. Abhandl. Akad. Wiss. und Lit. Mainz, math.-natur. Kl., 3: 731-901.
- SHEVIREV A.A. 1960 Ontogeneticheskoe razvitie nekotorikh verkhnejurskikh ammonitov. Bjull. MOIP, otd. geologicheski, 35: 69-78.
- SHULGINA N.I. 1985 Borealnie basseini na rubezhe juri i mela. Nauka : 162 p.

- SMITH J.P. 1900 The development and phylogeny of Placenticeras. Proc. Cal. Acad. Sci., 3, 1, 7 : 181-240.
- THIERRY J. 1975 Ontogeneze de la ligne de suture et origine des Mayaitidae Spath, 1928 (Ammonitina, Stephanocerataceae) de l'Oxfordien moyen de la province Indo-Malgache. C. R. Acad. Sci. Paris (D), 280 : 1543-1546.
- THIERRY J. 1978 Le genre Macrocephalites du Callovien inférieur (Ammonites, Jurassique moyen). Mém. Géol. Univ. Dijon, 4 : 490 p.
- WESTERMANN G. 1956 Phylogenie der Stephanocerataceae und Perisphinctaceae des Doffer. Neues Jb. Geol. Paläontol., 103, 1/2 : 233-270.
- WIEDMANN J & KULLMANN J. 1981 Ammonoid sutures in ontogeny and Phylogeny. In M.R. HOUSE & J.R. SENIOR (eds.) : The Ammonoidea. N.Y.. Acad. Press, Systematics Assoc., Spec. Vol. 18 : 215-255.