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Upon the Systematics of the Mesozoic Ammonitida

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ABSTRACT. Systematics of the ammonoids highest taxa is based on the septal line onto-phylogeny and the indexing of septal line elements is founded on the homology. Basing on the septal line development alongside with already known suborders (Ammonitina, Perisphinctina (emend.), Haploceratina, Ancyloceratina) we have stated two new suborders Olcostephanina and Cardioceratina.

Key words: systematics, homology, Ammonitida.

Systematics and phylogeny of the highest taxa of the Jurassic-Cretaceous Ammonitida are described in a number of works [1-9]. Analysis of the ontogenesis of septal lines (and some other signs) allowed N.Besnosov and I. Michailova [2,3] to establish four suborders within the order of Ammonitida - Ammonitina Hyatt, 1889; Haploceratina Besnosov et Michailova, 1983; Ancyloceratina Wiedmann, 1966 and Perisphinctina Besnosov et Michailova, 1983. A new suborder of Perisphinctina [3], identified by N. Besnosov and I. Michailova in 1983, and phylogenetically closely related to it systematics of taxa are of special interest. In turn, the suborder of Perisphinctina comprises four superfamilies (33 families): Stephanoceratoidea Neumayr, 1875; Perisphinctoidea Steinmann, 1890; Desmoceratoidea Zittel, 1895 and Hoplitioidea H. Douville, 1890 [3]. Within the superfamily of Perisphinctoidea s. lato the family of Olcostephanidae Pavlov, 1892, was previously mentioned. Earlier, on the basis of morphogenetic study of shells of some representatives of various families of Perisphinctidae [4-6], we recommended, that the family of Olcostephanidae should be regarded as an independent superfamily - Olcostephanoidea. The subdivision of the Perisphinctoidea s. lato superfamily into two ones was conditioned by considerable differences in phylogenesis of septal line morphology.

Here, we consider it necessary to dwell on some problems of principal significance concerning systematics of Mesozoic Ammonitida and indexation of septal line elements.

Systematics of the highest taxa of Ammonitida is based on the onto-phylogeny of septal line. In turn, indexation of septal line elements is based on the principle of homology - only elements of the same genesis are defined by the same index. At the same time, noteworthy are the following circumstances - where and when this or that element appears, how it develops in onto-phylogeny, what are its configuration, dimensions and location and, above all, how stable is a new septal line "model" historically. Ephemeral new-formations and deviations are not of essential importance. In this connection, in the septal line of perisphincts whose primasuture consists of five elements (VLUID), in the course of its genesis the sixth (or the seventh) element should be marked by U¹ no matter

where it originated as long as its ancestors (Hammatoceratoidea) had it on the U/I saddle. Besides, it should be noted that U^1 nearly always develops on or very close to the umbilical seam, i.e. heterotopia of this element is determined by a degree of shell's involution and, respectively, it is not of particular importance for systematics of the above-mentioned suborder. Of crucial importance are those elements that in this case are developed on the dorsal side, particular those changes that are observed within the limits of internilateral lobe [I] and on the saddle I/D. Lobe I_2 , according to our new data, developed on the middle stage of the third whorl (Fig. 1) at the expense of asymmetrical division of the internilateral lobe ($I_1 I_2$). After that, not a single branch of the lobe I reaches its independence and the latter are obliquely directed toward the dorsal lobe (see also [9]). As for

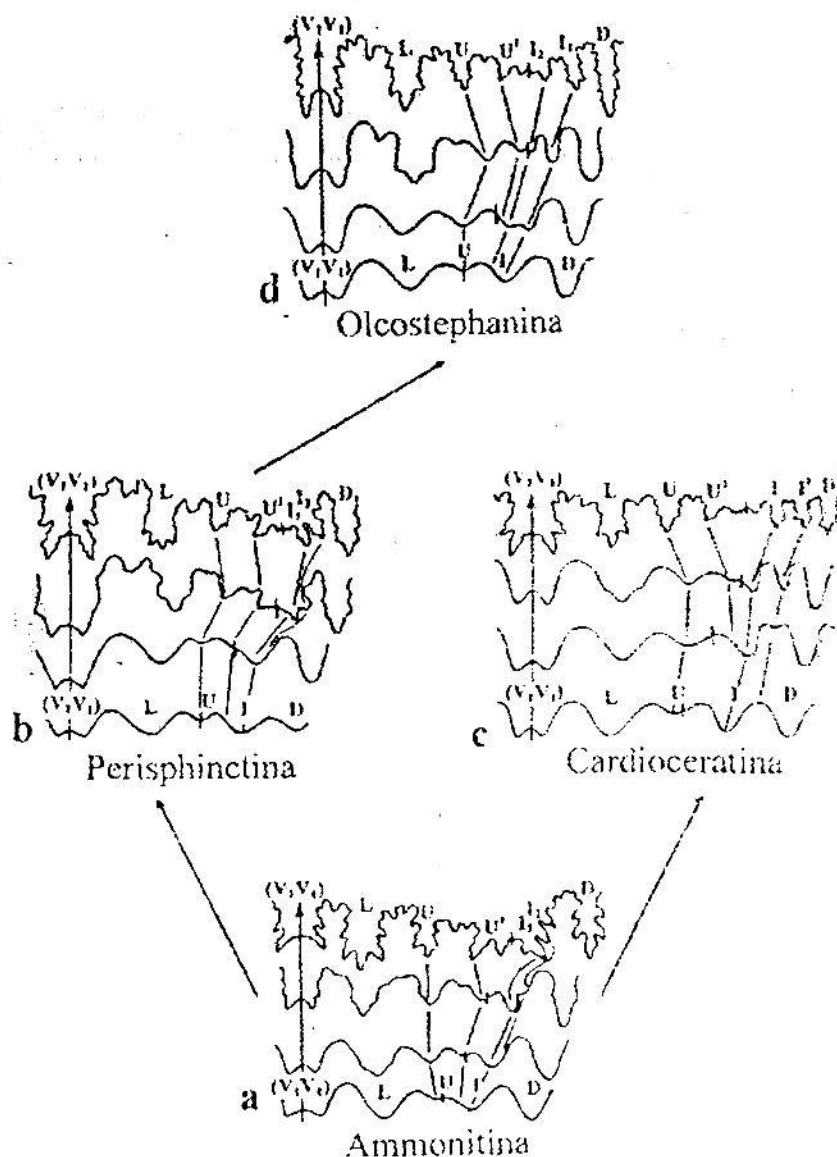


Fig. 1. Types of septal lines of Jurassic-Cretaceous Ammonitida: [parts] in their onto-phylogeny: a - Ammonitina (*Hammatoceras insigne* (Ziet.) [9, fig. 190]), b - Perisphinctina (*Indosphinctes nikitinoensis* Sas.), c - Cardioceratina (*Macrocephalites nikitini* Michailov, d - Olcostephanina (*Langeites borealis* Me.))

Perisphinctina proper the earlier development of its septal line has several modifications. Among them the principal families are those whose new element (I_2) develops on the inner slope of internilateral lobe close to their base (superfamily *Perisphinctoidea* Steinmann: *Perisphinctidae* Steinmann, *Reineckeidae* Hyatt, *Pachyceratidae* Buckman, *Himalayitidae* Spath) or near the I/D saddle (superfamily *Stephanoceratoidea* Neumayr: *Erycitidae* Spath, *Stephanoceratidae* Neumayr, *Morphoceratidae* Hyatt, *Parkinsoniidae* Buckman) and also, possibly, *Tulitidae* Buckman and *Oocoptychiidae* Arkell. At the same time, *Perisphinctoidea*'s septal line developed similar to that of *Hammatoceratoidea* with the difference that the earlier *Perisphinctoidea* (s. lato) I_2 forms closer to the base of lobe I whereas the younger representatives (*Himalayitidae*) have lobe I_2 and saddle I_1/I_2 more developed. As for *Stephanoceratoidea*, its lobe I_2 deepens rapidly and develops more strongly than lobe I_1 . At the same time, internilateral lobe branches of the adult individuals of the both superfamilies do not reach independence and are located obliquely relative to lobe D. The formula of septal line is $(V_1 V_1)LUU^1:I_1 I_2 D$.

The second type of septal line is characteristic of asymmetrical ($I_2 I_1$) or symmetrical ($I_1 I_1$) division of the internilateral lobe. Later on, these branches develop independently - the outer one bends toward the umbilical seam whereas the inner one takes the internilateral lobe's position. Almost all the elements of septal line are rectilineal and mutually parallel. Formula of septal line is $(V_1 V_1)LUU^1:I_2 I_1 D$ or $(V_1 V_1)LUU^1:I_1 I_1 D$. This type of septal line is characteristic of superfamilies of *Olcostephanoidea* Pavlov, *Desmoceratoidea* Zittel and *Hopliitoidea* H. Douville [2-8].

The third type of septal line differs strongly from the two others. It is characteristic of those groups of ammonitoids (*Otoitidae* Massee, *Sphaeroceratidae* Buckman, *Cardioceratidae* Siemiradzki, *Macrocephalitidae* Buckman, *Mayaitidae* Spath, *Kosmoceratidae* Haug) that form the superfamily of *Kosmoceratoidea* Haug [4-8]. Among them the oldest groups (*Otoitidae* and *Sphaeroceratidae*) have the sixth element (I') of septal line which forms on the slope of the dorsal lobe near the I/D saddle whereas in relatively young representatives it develops almost symmetrically at the top of the above-mentioned saddle. The only exception is *Kosmoceratidae* where I' develops on the opposite side (with respect to lobe I). Formula of septal line is $(V_1 V_1)LUU^1:I' D$. Later on, I' rapidly deepens, becomes independent and actually takes the internilateral lobe's place. It should be noted that the differentiation of the lobe I takes place after the formation of lobe U' (*Otoitidae*) as a result of which this group of Ammonitida becomes genetically related to *Hammatoceratoidea*. Further development of septal line takes place approximately in the same manner. The formation of new elements occurs at the expense of the differentiation of the saddles U'/I_2 or U'/I_1 .

Thus, on the basis of detail morphogenetic study and analysis of available published data on Mesozoic Ammonitida [1-9] we have come to the conclusion that their septal line experiences cardinal and essential changes, chiefly, within the limits of umbilical seam. This gives us a possibility to identify a number of congener ammonitid's groups regarded as suborders. Together with the already known suborders [*Ammonitina*, *Perisphinctina* (emend.), *Haploceratina*, *Ancyloceratina*] we have identified two new ones - *Olcostephantina* and *Cardioceratina*. Their brief diagnoses are presented below.

Order Ammonitida Hyatt, 1889**Suborder Perisphinctina Besnosov et I. Michailova, 1983**

(emend. Kvantaliani, Topchishvili, Lominadze, Sharikadze, 1999)

Diagnosis. Shells of various degree of involution are characterized by moderate round-sphere-shaped whorls. Sculpture is poorly or strongly expressed during the early stage of ontogenesis. Septal line formula - $(V_1 V_1)LUU^1: I_1 I_2 D$. During the later stage of evolution new elements evolve on the septal line of whorls where suture lobe of various degree of concavity appears.

Suborder's composition. Superfamilies: Perisphinctoidea Steinmann, 1890; Stephanoceratoidea Neumayr, 1875.

**Suborder Cardioceratina Kvantaliani, Topchishvili,
Lominadze, Sharikadze suborder nov.**

Diagnosis. Flattened shell is characterized by involuted or slightly involuted whorls. Cross section is of a spear-shaped or oval configuration. Umbilicus is narrow or moderately wide. Ribs are with or without tubercles, thin or coarse, sometimes sickle-shaped-nusous. Septal line formula at the earlier stage of evolution is $(V_1 V_1)LUU^1: II^1 D$. Its further development occurs at the expense of the lobe formed on the saddle U^1/D .

Suborder's composition. Superfamily: Mesomoceratoidea Haug, 1887., 1891.

**Suborder Olcostephanina Kvantaliani, Topchishvili,
Lominadze, Sharikadze suborder nov.**

Diagnosis. Shells are of a diskoidal configuration, flattened from the sides, or with highly-convex whorls. Ventral side can be flattened, convex, flattenedly-convex, with keel or groove. Shells are strongly or slightly sculptured. At the earlier stage of ontogenesis formula of septal line is $(V_1 V_1)LUU^1: I_2 I_1 D$ or $(V_1 V_1)LUU^1: I_1 I_1 D$. Its further complication occurs at the expense of the repeated division of lobes I_2 and I_1 within the limits of umbilical seam.

Suborder's composition. Superfamilies: Olcostephanoidea Pavlov, 1892; Mesomoceratoidea Zittel, 1895; Hoplitioidea H. Douville, 1890.

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