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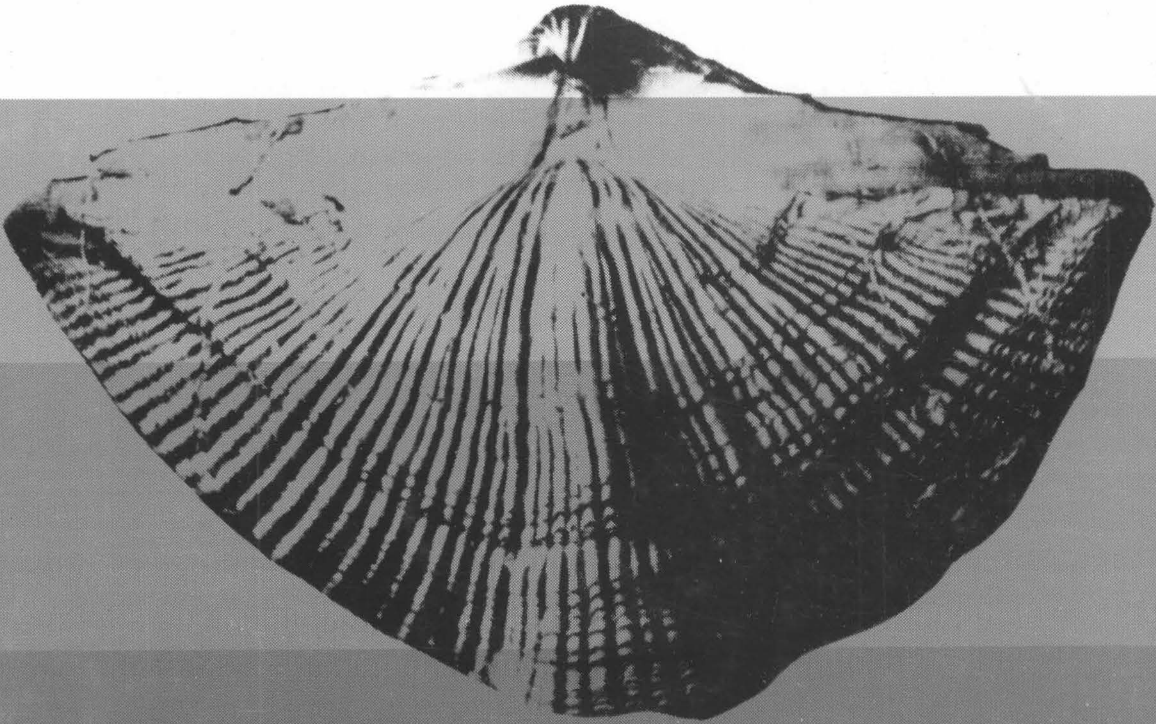

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HIGHER TAXA OF JURASSIC AND CRETACEOUS AMMONITIDA

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Abstract: The division of the order Ammonitida into the four suborders Ammonitina Hyatt, 1889, Haploceratina Besnosov et Michailova, 1983, Perisphinctina Besnosov et Michailova, 1983 and Ancyloceratina Wiedmann, 1966 is substantiated, and the phylogenetic relationships among the suborders and superfamilies are considered.

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This article completes the systematics of taxa of ordinal, subordinal and superfamilial ranks of the Jurassic and Cretaceous ammonoids that we began in previous publications [3-5]. These set forth the history of the problem and the current ideas on the system of the Jurassic and Cretaceous ammonoids, and consider the orders Phylloceratida and Lytoceratida, within the latter of which the independence of the suborder Turrilitina is documented.

We believe that the Jurassic and Cretaceous ammonoids should be regarded as belonging to three orders: the Phylloceratida, Lytoceratida and Ammonitida. The first of these orders is small in volume and includes only one superfamily; the second is divided into two suborders and four superfamilies; and the third and largest order, the Ammonitida, combines four suborders and 15 superfamilies (fig. 1).

The present system of the higher taxa of the Jurassic and Cretaceous ammonoids was described in the *Treatise on Invertebrate Paleontology* [25] and the Soviet *Principles of Paleontology* [12, 13]. Substantial changes were later subsequently introduced into it by Schindewolf [23] and Wiedmann [26, 27], and also by Donovan, Callomon and Howarth [15]. The revision of the taxa of ordinal and familial rank proposed here is based primarily on phylogenetic research both in and outside the Soviet Union during the last three decades [4]. The data on the internal structure of the ammonoid shell [6-8] have become extremely important.

ORDER AMMONITIDA HYATT, 1889

Diagnosis. Jurassic and Cretaceous ammonoids with primary five-lobed primasuture (VUU^{1}ID); unstable five-lobed primasuture established in some Cretaceous forms [10]. New

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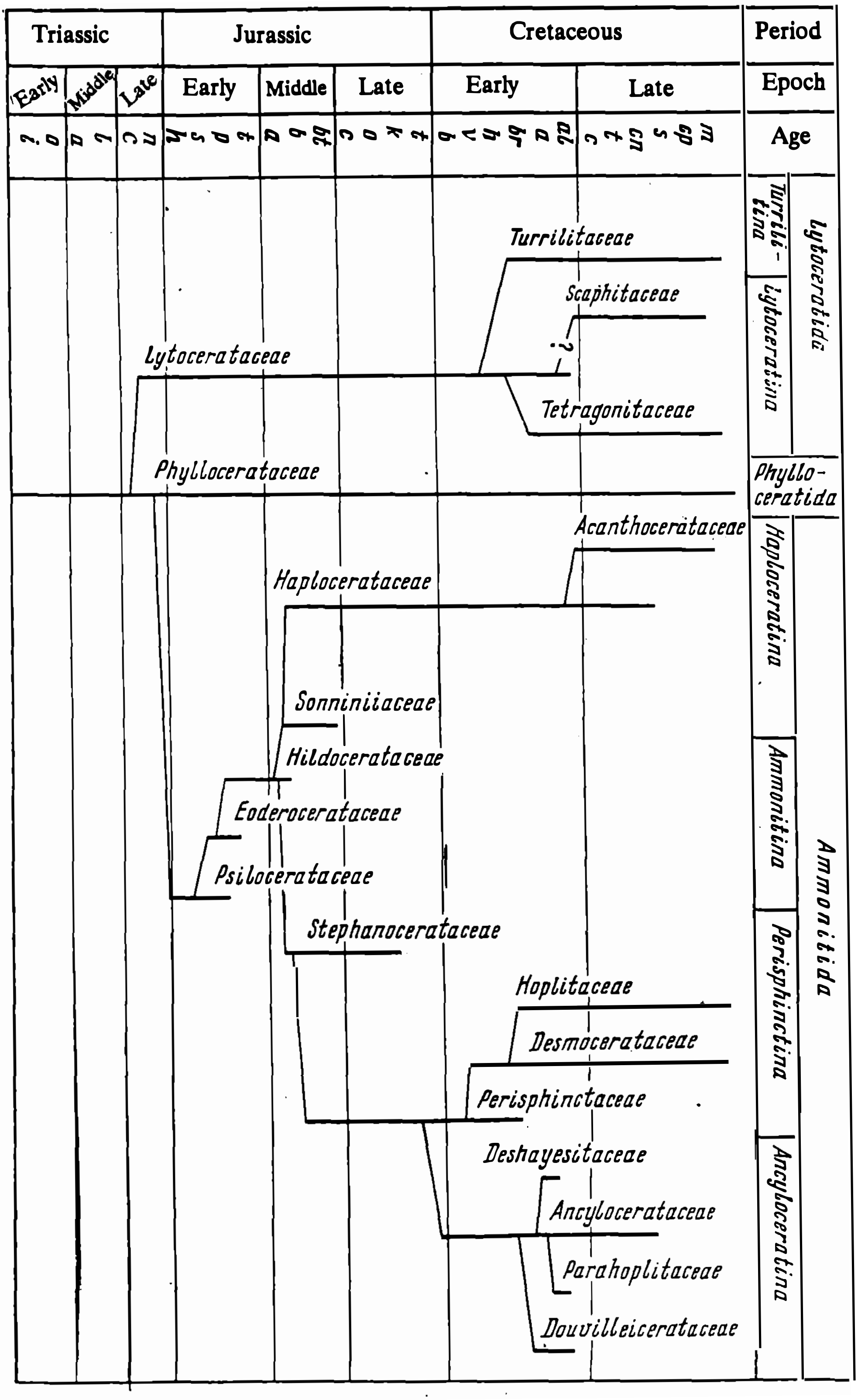

Fig. 1. Phylogenetic diagram of Jurassic and Cretaceous ammonoids [3].

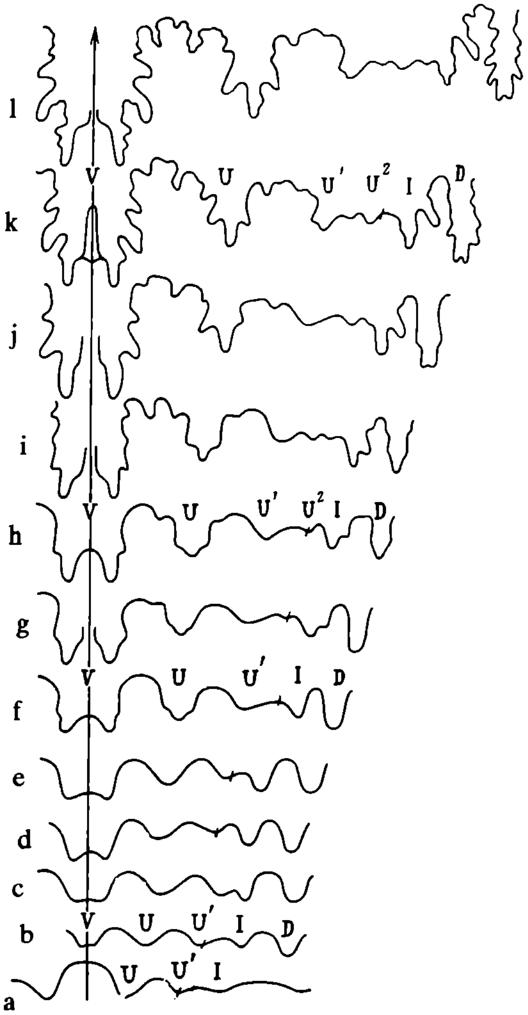

Fig. 2. Changes in suture line during ontogenesis of *Zugodactylites braunianus* d'Orb.; Spec. No. 10370: *a, b* - 1st and 2nd line (×26), *c* - 7th line, 0.5 whorl (×25.5), *d* - 9th line, 0.8 whorl (×25.5), *e* - 13th line, 1.2 whorls (×25.5), *f* - 22nd line, 1.8 whorls (×25), *g* - 32nd line, 2.3 whorls (×17), *h* - 36th line, 2.5 whorls (×11), *i* - 47th line, 3.2 whorls (×10.5), *j* - 54th line, 3.6 whorls (×10.5), *k* - 53rd line, 4.2 whorls (×8), *l* - 69th line, 4.6 whorls (×6); Omolon massif, Tonkur-Yuryakh River; Middle Toarcian.

elements formed in various ways: by division of saddle U^1/I and appearance of new umbilical lobes (U^1, U^2 ...), occasionally by division of saddle I/D and appearance of inner lateral lobes (I^1, I^2 ...) or as a result of subdivision of inner lateral lobe; combination of these modes sometimes seen, more rarely umbilical lobe dividing, and in extreme cases lateral lobe arising. Umbilical lobe predominantly tripartite. Dorsal lobe in last stages initially bipartite, then becoming tripartite; again becoming bipartite extremely rarely in Cretaceous forms. In course of ontogenesis saddles dividing somewhat later than lobes or at same time.

Composition. Four suborders: Ammonitina, Haploceratina, Perisphinctina and Ancyloceratina.

Comparison. Differs from Phylloceratida and Lytoceratida in variety of shells and in modes of formation of lobes. Additionally differs from Phylloceratida in division of saddle by direct formation of denticles, and from Lytoceratida in development of new lobes from saddles U^1/I and I/D and more rarely as a result of division of lobe I, and also in tripartite umbilical lobe.

SUBORDER AMMONITINA HYATT, 1889 (EMEND. BESNOSOV ET MICHAILOVA, 1983)

Diagnosis. Early-Middle Jurassic monomorphnic, intensely divergent descendants of phylloceratids with primary five-lobed primasuture (VUU^1ID), possibly grading into four-lobed suture (VUID). Formation of new lobes in ontogenesis and occurring both as a result of appearance of new umbilical lobes and by full division of inner lateral lobe (I), and also by division of lobe U^2 (fig. 2). Modes of formation of new lobes may be combined. Dorsal lobe bipartite, and in later representatives of suborder may be tripartite, owing either to asymmetry of primary bipartite lobe or to formation of paired lateral denticles in its lower part. Aptychi and diaptychi developed. Dimorphism possibly manifested.

Suture line formula:

$$
\begin{gathered}
(V_1V_1)\,UU^1U^2 \ldots I_1I_2(D_1D_1); \\
(V_1V_1)\,UU^1U^2 \ldots I_1I_1(D_1D_1); \qquad (V_1V_1)\,UU^1U^2 \ldots I_2I_1(D_1D_1); \\
(V_1V_1)\,UU^1U^2 \ldots I(D_1D_1); \qquad (V_1V_1)\,UU^1U_1^2 \ldots U_1^2ID; \\
(V_1V_1)\,UU^1I_1 \ldots I_1(D_1D_1); \qquad (V_1V_1)\,UU^1I_2 \ldots I_1(D_1D_1); \\
(V_1V_1)\,UU^1U^2 \ldots I_2I_1I_2(D_1D_1); \qquad (V_1V_1)\,UU^1U^2 \ldots I_2I_1I_3(D_1D_1); \\
(V_1V_1)\,UU^1U^2I_1I_2I_3(D_1D_1); \qquad (V_1V_1)\,UU^1U^2 \ldots I_1I_2I_3(D_2D_1D_2).
\end{gathered}
$$

Composition. Three superfamilies and 13 families (fig. 3): Psilocerataceae Hyatt, 1867 (fam. Psiloceratidae Hyatt, 1867; Schlotheimiidae Spath, 1923; Arietitidae Hyatt, 1874; Oxynoticeratidae Hyatt, 1875; Cymbitidae Buckman, 1919; Echioceratidae Buckman, 1913); Eoderocerataceae Spath, 1929[1] (fam. Eoderoceratidae Spath, 1929; Polymorphitidae Haug, 1887; Liparoceratidae Hyatt, 1867; Amaltheidae Hyatt, 1867; Dactylioceratidae Hyatt, 1867); Hildocerataceae Hyatt, 1867 (fam. Hildoceratidae Hyatt, 1867 and Hammatoceratidae Buckman, 1887).

Comparison. Differs from suborders Haploceratina and Perisphinctina in unstable formation of new lobes in ontogenesis and in predominantly bipartite dorsal lobe.

Remarks. The oldest Ammonitina are characterized by instability of their distinctive

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[1] After revision of familial composition, according to rules of priority superfamily Eoderocerataceae may be called Liparocerataceae or Amaltheaceae or Dactyliocerataceae (Russian Editor's note).

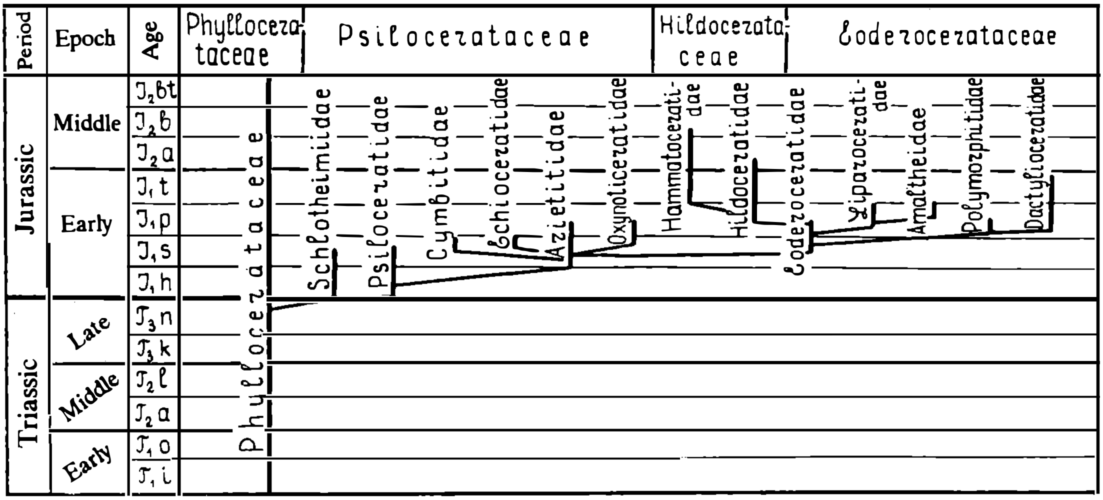

Fig. 3. Phylogenetic diagram of suborder Ammonitina.

features and by their short duration. For example, within the Psilocerataceae and Eoderocerataceae, the duration of the individual families does not exceed two geologic ages. In the superfamilies Psilocerataceae and Eoderocerataceae the shell is predominantly evolute, with a very wide, shallow umbilicus; much more rarely it is semi-involute and in extremely rare cases involute. The sculpture is represented by straight solitary, more rarely branching, curved costae; tubercles and spines are present fairly often, and from one to three carinae on the ventral side; sometimes the sculpture is fairly indistinct. In the superfamily Hildeocerataceae the shells range from semi-involute to semi-evolute, and only occasionally are evolute. Their sculpture on the whole is less prominent than in the preceding superfamilies. The costae are predominantly curved and fairly often branching; carinae are present, and tubercles can be seen in extreme cases.

SUBORDER HAPLOCERATINA BESNOSOV ET MICHAILOVA, 1983

Diagnosis. Middle Jurassic to Cretaceous monomorphic ammonoids with five-lobed primasuture (VUU^1ID) and formation of new lobes by appearance of umbilical lobes and sometimes by complete division of inner lateral lobe into two branches. Dorsal lobe bidenticulate in older and tridenticulate in most younger forms. Oxycones and platycones with apertures bearing lateral crests and ventral crest or rostrum predominate. Diaptychi developed. Dimorphism may occur.

Suture line formula:

$$(V_1V_1)UU^1U^2U^4 \ldots U^3I(D_1D_1);$$
$$(V_1V_1)UU^1U^2U^4 \ldots U^3ID; \qquad (V_1V_1)UU^1U^2U^4 \ldots U^3I_1I_2(D_1D_1);$$
$$(V_1V_1)UU^1U^2U^5 \ldots U^3U^4ID; \qquad (V_1V_1)UU^1U^2U^3U^5 \ldots U^4I_1I_1(D_1D_1);$$
$$(V_1V_1)UU^1U^2U^3U^5 \ldots U^6U^4I_1I_1D; \qquad (V_1V_1)UU^1U^2U^3U^4 \ldots U^5I_1I_1D;$$
$$(V_1V_1)UU^1U^2U^3 \ldots U^4I_2I_1D; \qquad (V_1V_1)UU^1U^2U^3U^4 \ldots U^5I_2I_1D;$$
$$(V_1V_1)UU^1U^2U^3 \ldots U^4I_1I_1D; \qquad (V_1V_1)UU^1U^2U^3 \ldots I_1I_2D.$$

Composition. Three superfamilies and 18 families: Sonniniiaceae Buckman, 1892 (fam. Graphoceratidae Buckman, 1905; Sonniniidae Buckman, 1892; Thamboceratidae Arkell, 1952;

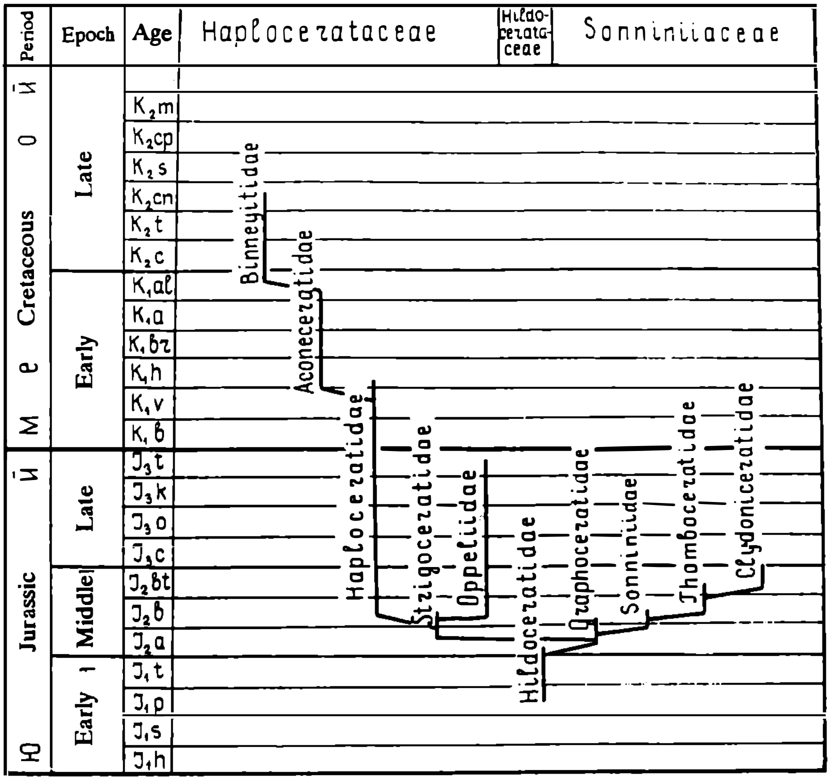

Fig. 4. Phylogenetic diagram of suborder Haploceratina (superfamilies Haplocerataceae and Sonniniiaceae).

Clydoniceratidae Buckman, 1924); Haplocerataceae Zittel, 1884 (fam. Strigoceratidae Buckman, 1924; Haploceratidae Zittel, 1884; Aconeceratidae Spath, 1923; Binneyitidae Reeside, 1927; Oppeliidae Bonarelli, 1894); Acanthocerataceae Hyatt, 1900 (fam. Brancoceratidae Spath, 1933; Flickiidae Adkins, 1928; Lyelliceratidae Spath, 1921; Acanthoceratidae Hyatt, 1900; Vascoceratidae Spath, 1925; Tissotiidae Hyatt, 1900; Coilopoceratidae Hyatt, 1903; Collignoniceratidae Wright et Wright, 1951; Sphenodiscidae Hyatt, 1900).

Comparison. Differs from suborder Perisphinctina in complication of suture line by formation of umbilical lobes.

Remarks. The suborder Haploceratina is based on the long-existing superfamily Haplocerataceae, which was preceded by the family Sonniniiaceae (fig. 4). The superfamily Haplocerataceae gave rise to the large Late Cretaceous superfamily Acanthocerataceae, whose first representatives arose in the Albian (fig. 5). The segregation of this superfamily took the path of a sharp intensification of the sculpture accompanied by synchronous dissection of the suture line, while maintaining the type of its transformation in phylogenesis through the development of new umbilical lobes and a tripartite dorsal lobe (fig. 6). The character of the morphogenesis of the suture line in the Acanthocerataceae, which we have studied in *Hysteroceras* and *Mantelliceras* [11], does not permit the conclusion that the Acanthocerataceae are related to the Desmocerataceae [30].

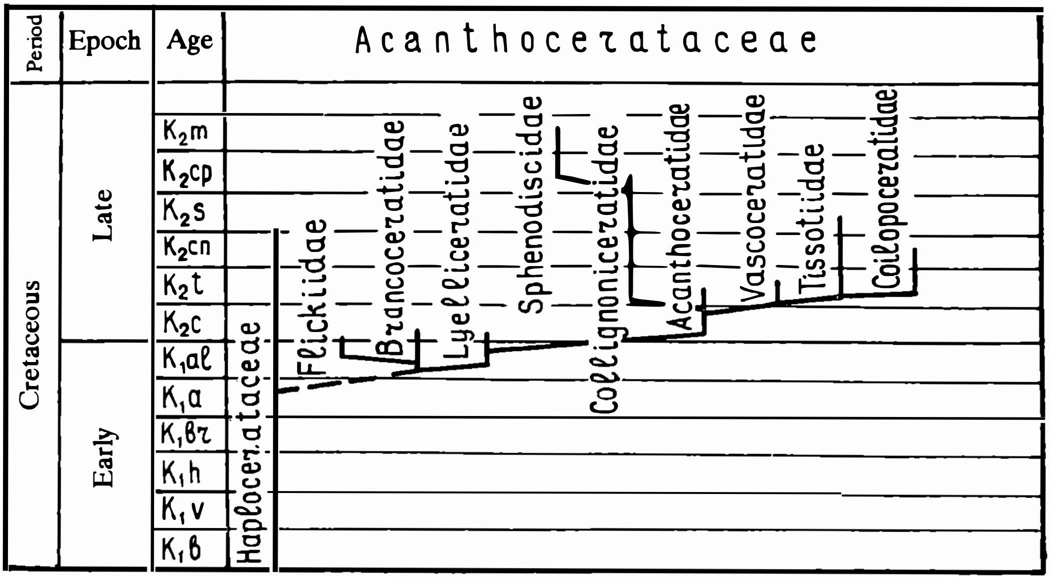

Fig. 5. Phylogenetic diagram of superfamily Acanthocerataceae (suborder Haploceratina).

SUBORDER PERISPHINCTINA BESNOSOV ET MICHAILOVA, 1983

Diagnosis. Middle Jurassic to Cretaceous monomorphic, more rarely heteromorphic, ammonoids with five-lobed primasuture (VUU^{1}ID). New lobes usually formed by full division of inner lateral lobe (I) into three or two parts (fig. 7). Occasionally division of saddle between outer and middle parts of inner lateral lobe; lobes thus formed during ontogenesis possibly shifted to vertices of adjoining saddles, occupying positions analogous to those of lobes U^2 and I^1. Division of inner lateral lobe possibly changing in character (fig. 8). In some cases additional inner lateral lobe I^1 formed on saddle I/D. Dorsal lobe always tripartite. Diaptychi developed. Dimorphism widely manifested.

Suture line formula:

$$(V_1V_1)UU^1I_2\ldots I_1I_3D;\quad (V_1V_1)UU^1I_2\ldots$$
$$\ldots I_1I_3I^1D;\quad (V_1V_1)UU^1I_2\ldots I_1I_2D;\quad (V_1V_1)UU^1I_3\ldots I_1I_2D;\quad (V_1V_1)UU^1I_{1\cdot 1}\ldots$$
$$\ldots I_{1\cdot 1}I_1D;\quad (V_1V_1)UU^1I_{2\cdot 1}\ldots I_{2\cdot 1}I_1D;\quad (V_1V_1)UU^1\ldots I_1I_2I_3D;$$
$$(V_1V_1)UU^1I_2\ldots I_1D;\quad (V_1V_1)UU^1I_1\ldots I_1D;\quad (V_1V_1)UU^1I_2\ldots I_1I_3I_4D.$$

Composition. Four superfamilies and 33 families: Stephanocerataceae Neumayr, 1875 (fam. Erycitidae Spath, 1928; Otoitidae Mascke, 1907; Stephanoceratidae Neumayr, 1875; Sphaeroceratidae Buckman, 1920; Tulitidae Buckman, 1921; Macrocephalitidae Buckman, 1922; Pachyceratidae Buckman, 1918; Kosmoceratidae Haug, 1887; Cardioceratidae Siemiradzki, 1891; Mayaitidae Spath, 1928; Oecoptychiidae Arkell, 1937); Perisphinctaceae Steinmann, 1890 (fam. Perisphinctidae, Steinmann, 1890; Parkinsoniidae Buckman, 1920; Morphoceratidae Hyatt, 1900; Parapatoceratidae Buckman, 1926; Spiroceratidae Hyatt, 1900; Reineckeiidae Hyatt, 1900; Berriasellidae Spath, 1922; Aspidoceratidae Zittel, 1895; Craspeditidae Spath, 1924; Olcostephanidae Haug, 1910); Desmocerataceae Zittel, 1895 (fam. Desmoceratidae Zittel, 1895;

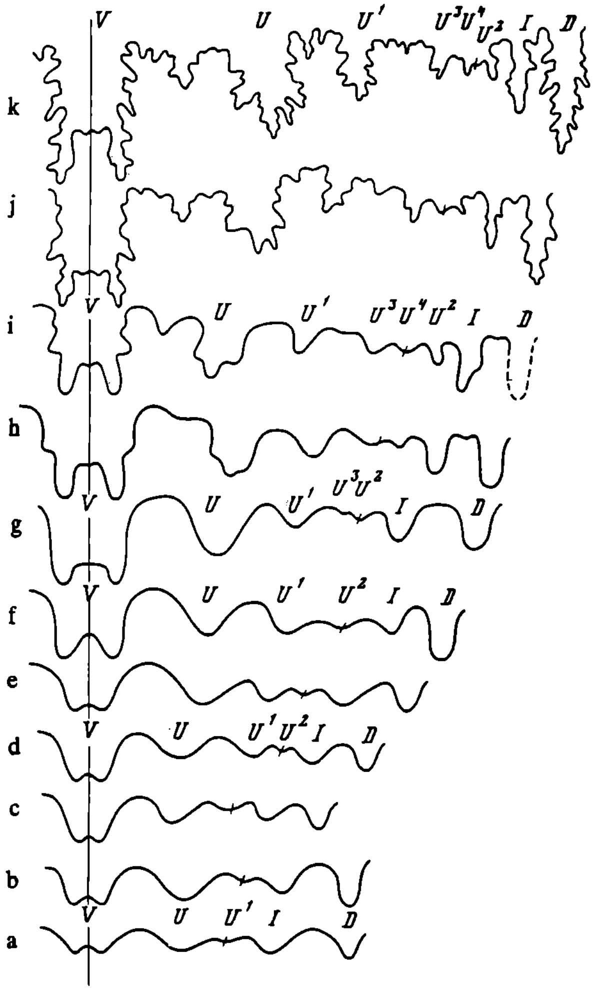

Fig. 6. Changes in suture line during ontogenesis of *Mantelliceras mantelli* Sow.; Spec. No. 135/13450: *a-c* - 2nd, 7th and 9th suture lines (×42), *d* - 14th line, beginning of 2nd whorl (×34), *e* - 17th line, 1.2 whorls (×33), *f* - 26th line, 2.2 whorls (×25.5), *g* - 29th line, 2.5 whorls (×25), *h* - 34th line, 3 whorls (×15), *i* - 3.6 whorls (×11), *j* - 4.2 whorls (×5), *k* - 5 whorls (×4); Mangyshlak region, Besokty; Cenomanian [11].

Holcodiscidae Spath, 1924; Silesitidae Hyatt, 1900; Kossmaticeratidae Spath, 1922; Pachydiscidae Spath, 1922; Muniericeratidae Wright, 1952); Hoplitaceae H. Douville, 1890 (fam. Pulchelliidae Hyatt, 1903; Leymeriellidae Breistroffer, 1951; Hoplitidae H. Douville, 1890; Schloenbachiidae Parona et Bonarelli, 1897; Placenticeratidae Hyatt, 1900; Engonoceratidae Hyatt, 1900).

Comparison. Differs from suborder Haploceratina in absence of newly formed umbilical lobes.

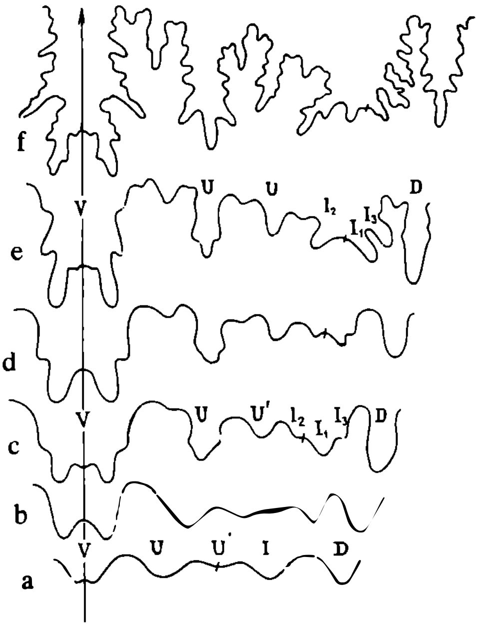

Fig. 7. Changes in suture line during ontogenesis of *Planisphinctes* ex. gr. *tenuissimus* (Siemiradzki); Spec. No. 1268: *a* - 2nd line (×50), *b* - 2.2 whorls (×33.5), *c* - 2.8 whorls (×22.5), *d* - 3.2 whorls (×20), *e* - 4.5 whorls (×10), *f* - 6.2 whorls (×4); Dagestan, Dantuna settlement; Bajocian-Bathonian boundary beds.

Remarks. The shell of the perisphinctina is monomorphic, but the superfamily Perisphinctaceae includes a few Middle and Late Jurassic heteromorphs (the family Spiroceratidae). An indistinct sculpture is characteristic of most Desmocerataceae (in the presence of constrictions) and the youngest Hoplitaceae (the family Placenticeratidae). In the remaining representatives the sculpture is distinct and often coarse (costae with various types of branching, quite often in combination with tubercles). The youngest family of this suborder, the Placenticeratidae, shows a weakening of its sculpture and considerable changes in its suture line during phylogenesis (the umbilical lobe usually divides into two new lobes, so that it ceases to be tripartite; and a lateral lobe L, which is atypical of the Mesozoic ammonoids, is superimposed on the saddle V/U).

The oldest superfamily of this suborder is the Stephanocerataceae (fig. 9). Despite its undoubted similarity in the character of its sculpture to the Perisphinctaceae, it differs in the appearance of new elements by division of the inner lateral saddle—that is, by the formation of additional inner lateral lobes. Schindewolf has called such a development of lobes heterochronous. It is also known in the Aptian Deshayesitaceae (of the suborder Ancyloceratina). The heteromorphic Perisphinctinae were studied by Schindewolf, who observed in them the simplification of the suture line characteristic of all heteromorphs.

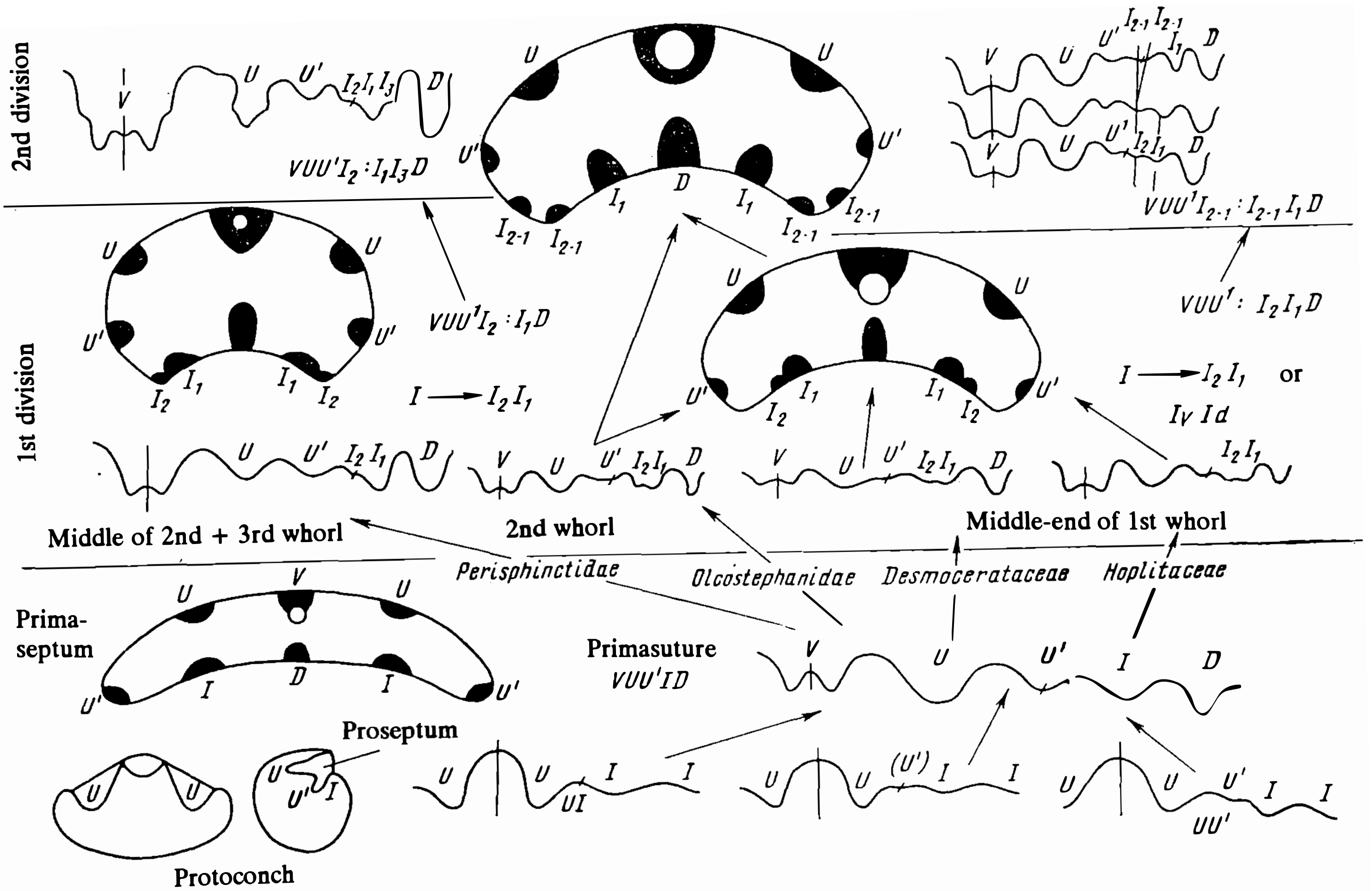

Fig. 8. Early ontogenesis of Perisphinctaceae, Desmocerataceae and Hoplitaceae [11].

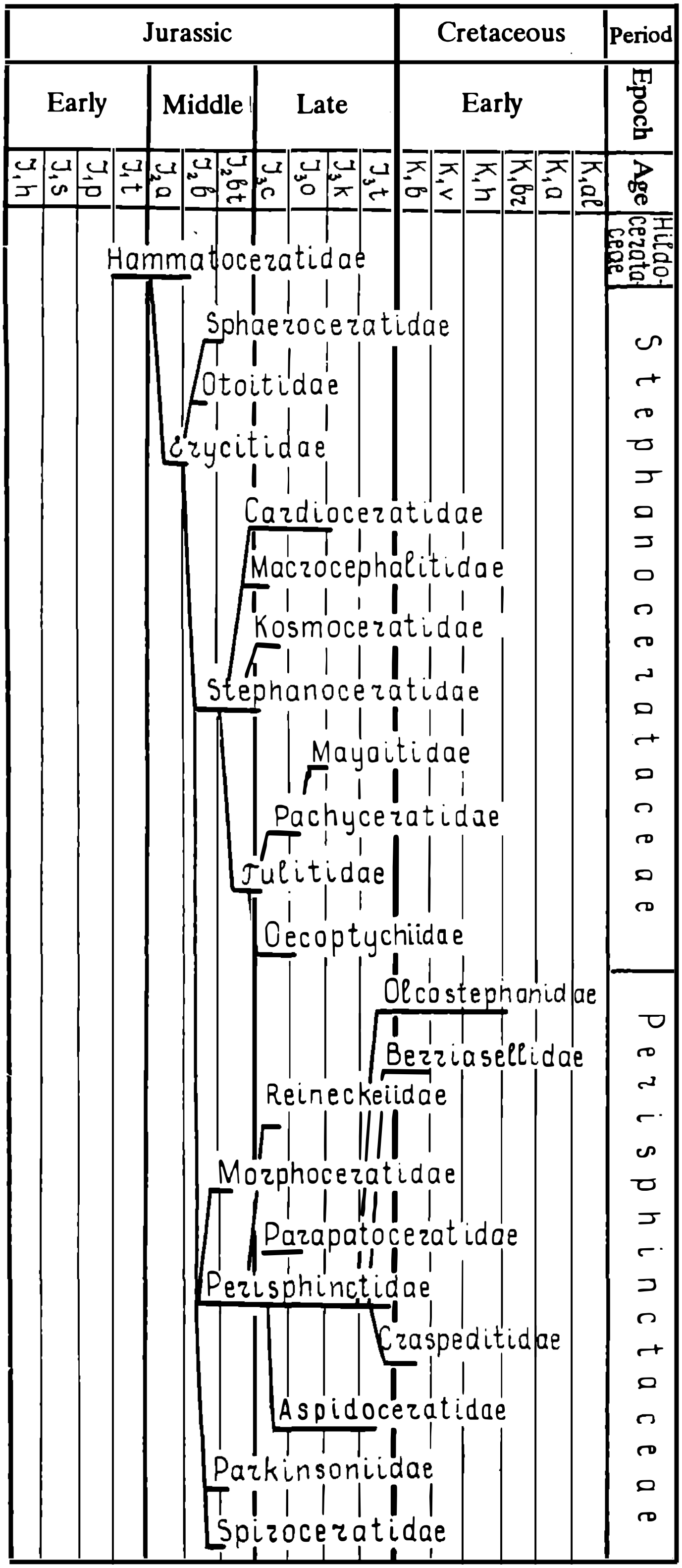

Fig. 9. Phylogenetic diagram of suborder Perisphinctina (superfamilies Stephanocerataceae and Perisphinctaceae).

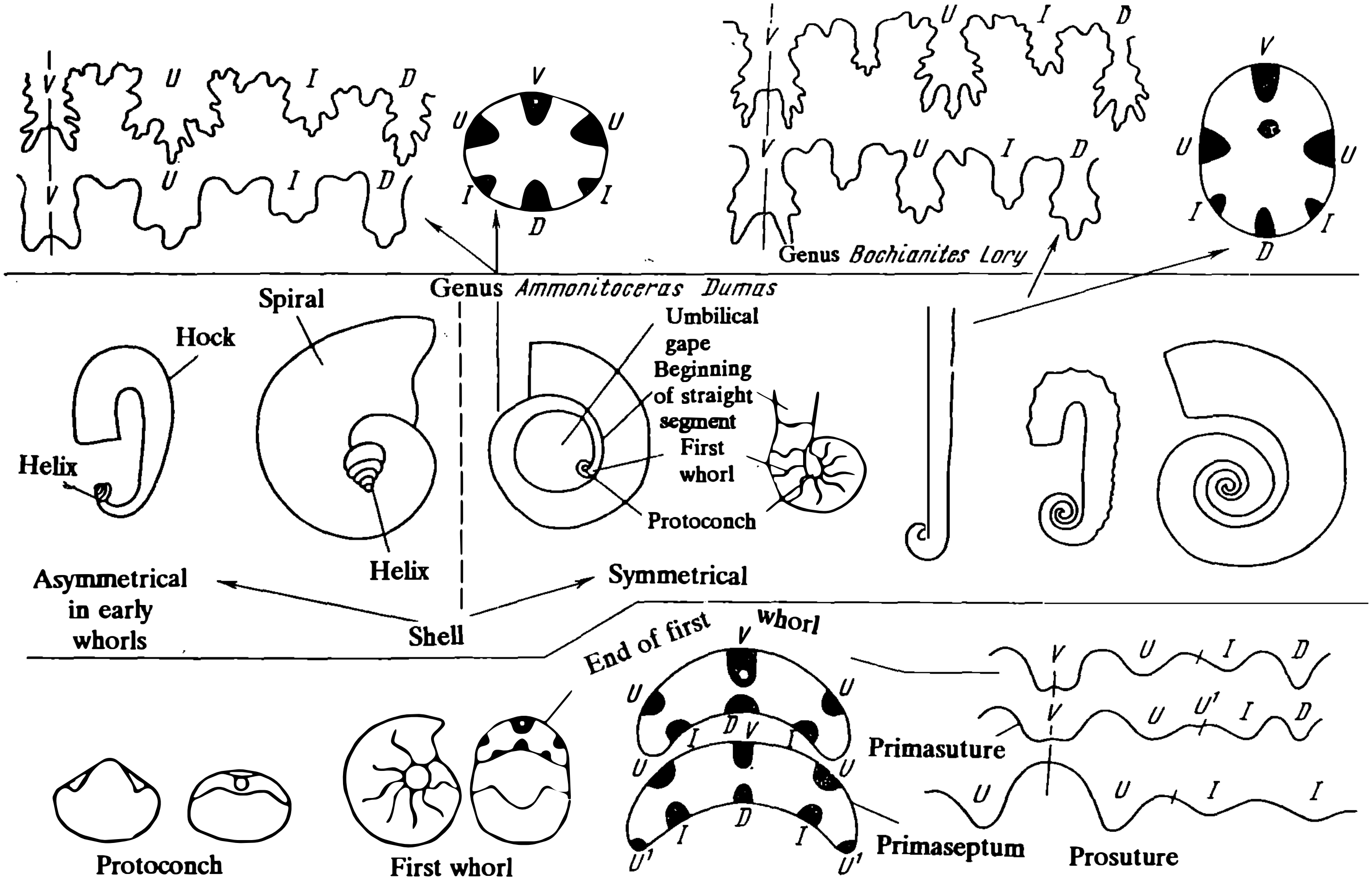

Fig. 10. Early ontogenesis of superfamily Ancyloceratаceae [11].

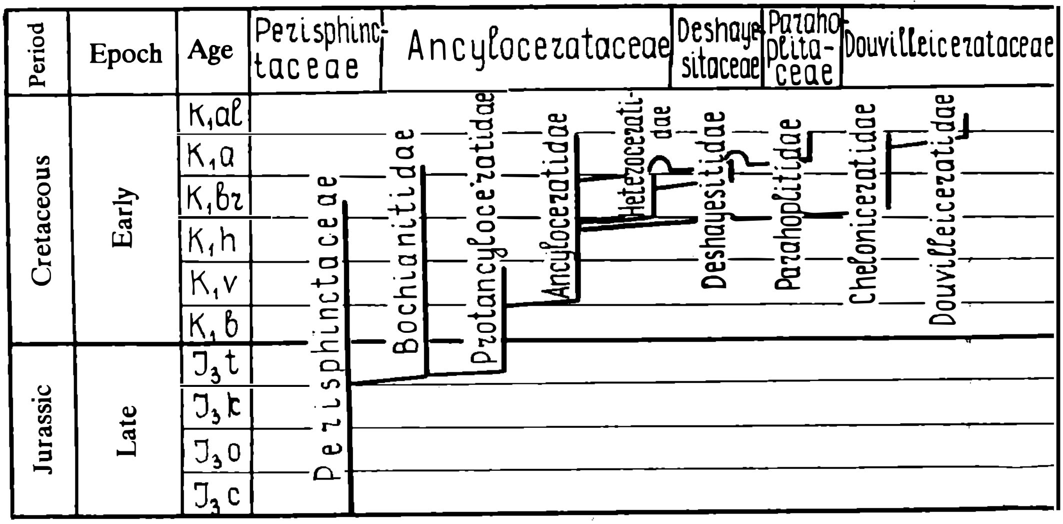

Fig. 11. Phylogenetic diagram of suborder Ancyloceratina.

SUBORDER ANCYLOCERATINA WIEDMANN, 1966 (EMEND. BESNOSOV ET MICHAILOVA, 1983)

Diagnosis. Predominantly Early Cretaceous heteromorphic ammonitids and monomorphic ammonitids with unstable five-lobed primasuture diverging from them (at beginning of first whorl, lobe U^1 is reduced). New lobes usually not formed in ontogenesis of heteromorphs (of superfamily Ancyloceratacea) (fig. 10), and total number of lobes limited to four (VUID). In monomorphic descendants three variant modes of development of new elements: by division of lobes ($U \rightarrow U_1U_2$ and $I \rightarrow I_2I_1$), in superfamily Douvilleicerataceae; by division saddle U/I (appearance of lobes U^1 and U^2) in superfamily Parahoplitaceae; and by division of saddle I/D (appearance of lobes I^1, I^2 ...) in superfamily Deshayesitaceae. Dorsal lobe tripartite or bipartite (in certain monomorphs). Umbilical lobe predominantly tripartite.

Suture line formula:

$$(V_1V_1)UI(D_2D_1D_2);\quad (V_1V_1)UU^1I(D_2D_1D_2);$$
$$(V_1V_1)UU^1U^2I(D_2D_1D_2);\quad (V_1V_1)UU^1U^2I(D_1D_1);\quad (V_1V_1)UII^1(D_2D_1D_2);$$
$$(V_1V_1)UII^2I^1(D_2D_1D_2);\quad (V_1V_1)U_1U_2I_2I_1(D_2D_1D_2).$$

Composition. Four superfamilies and eight families (fig. 11): Ancylocerataceae Meek, 1876 (fam. Bochianitidae Spath, 1922; Protancyloceratidae Breistroffer, 1947; Ancyloceratidae Meek, 1876; Heteroceratidae Hyatt, 1900); Deshayesitaceae Stoyanow, 1949 (fam. Deshayesitidae Stoyanow, 1949); Parahoplitaceae Spath, 1922 (fam. Parahoplitidae Spath 1922); Douvilleicerataceae Parona et Bonarelli, 1897 (fam. Cheloniceratidae Spath, 1923; Doubillleiceratidae Parona et Bonarelli, 1897).

Comparison. Differs from suborders described above in unstable five-lobed primasuture and in formation of adult suture line on basis of four lobes (VUID).

Remarks. The heteromorphic Turrilitaceae and Ancylocerataceae are regarded by most non-Soviet researchers as belonging to the lytoceratids. We cannot agree with this view. In the transition from the monomorphic ammonites to the heteromorphic (for example, from the Heteroceratidae to the Deshayesitidae), the outer side maintains its form, but the inner side undergoes a complete reorganization. The structure of the suture line in the outer part of the shell is, therefore, of secondary importance. The sharp difference in the outer parts of the suture lines between the Ancyloceratacea and the Turrilitaceae is indisputable. The first of these superfamilies is characterized by a tripartite umbilical lobe and the lack of a gap in the ventral lobe (a slow shifting of the siphon toward the ventral side), and the second by a bipartite umbilical lobe and a gap in the ventral lobe (a rapid shifting and full attachment of the siphon to the ventral side). This feature is a criterion of very high (ordinal) rank. We, therefore, assign the Ancytlocerataceaeto the order Ammonitidae, and the Turrilitaceaeto the order Lytoceratida.

* * *

The earliest ammonitids—the Hettangian-Sinemurian Psiloceratidae (suborder Ammonitina)—have much in common in their shell structure and the development of the suture line with the phylloceratids and the early lytoceratids. They differ from the phylloceratids in the full dissection of the inner lateral lobe, and from the lytoceratids in the appearance of the lobe U^2 during ontogenesis, but not always of U^3 or subsequent lobes. Since the lytoceratids diverged from the phylloceratids at the beginning of the Jurassic, the fact that the ammonites continue to form new umbilical lobes testifies unambiguously to their descent from the Ussuritidae. The similarity between the early ammonitids and the lytoceratids is that between descendants of the same ancestor.

The ammonitinids show a variety of adaptations and, unlike the phylloceratids and monomorphic lytoceratids, extensively occupied the continental shelves, anticipating the majority of ecological types of shells and later ammonitids. It is clear that no heteromorphs arose among the Ammonitina. The only find of the Pliensbachian *Arcuceras* Potonié, 1929, is, obviously, part of a sea lily stem.

The Ammonitina diverged intensively during the Early Jurassic. The groupings of genera and families and the relationships among families are variously proposed. The most appropriate seems to be that in the *Treatise on Invertebrate Paleontology* [25]. Less appropriate, in our view, is the phylogeny of the Ammonitina worked out by Schindewolf [21-23]. Although the first of these theoretically does permit the polyphyletic origin of the Ammonitina, it is actually based on tracing the changes in shell form and sculpture over time. Schindewolf's classification is based mainly on the study of one feature—the manner of formation of new lobes in ontogenesis—and in some instances errs in breaking the chronological succession, and especially in appraising the measure of similarity between the Ammonitina and the Lytoceratina.

Previously one of us [1] followed Salfeld [19] in taking the paired termination of the dorsal lobe as one of the most important criteria. Later Schindewolf [21, 22] and Kazakova [9] showed that in the very same genera of the Hammatoceratidae and Graphoceratidae, the dorsal lobe may end in either two or three denticles. If the false tripartite termination of the dorsal lobe resulting from asymmetry of a bidenticulate lobe is not confused with the true tripartite lobe that is due to the formation of paired lateral denticles, it turns out that of the approximately 180 genera assigned to the suborders Ammonitina and Haploceratina (the superfamily Sonniniiaceae and family Graphoceratidae), only five to seven have a proper tripartite dorsal lobe, and they are all Late Toarcian and Aalenian—that is, this criterion is violated only in extremely rare cases.

The suborder Haploceratina was derived from Ammonitina of the family Hildoceratidae, some of whose genera (*Pleydellia* and *Dumortieria*) take on tripartite termination of the dorsal lobe and are characterized by the formation of numerous new umbilical lobes. Three main lines can be discerned in the evolution of this suborder. The first includes the families Graphoceratidae, Sonniniidae, Thamboceratidae and Clydoniceratidae, for which the superfamily Sonniniiaceae is proposed. They are characterized by the existence of genera with bi- and tripartite terminations of their dorsal lobe and a change in this feature during ontogenesis (for example, *Clydoniceras, Delecticeras* and *Dorsetensia*) [22, figs. 201-203], and also by unstable dissection of the inner lateral lobe. The superfamily Sonniniiaceae combines the most archaic groups of the suborder. Its geographic range (despite the prolonged existence of the superfamily) decreased from the beginning of the Late Bajocian, becoming limited to the tropical belt, with individual genera migrating in epochs of maximal transgressions (for example, *Clydoniceras* in the Late Bathonian).

The second line—the superfamily Haplocerataceae—is derived from the Graphoceratidae and includes the families Strigoceratidae and Haploceratidae, in which the inner lateral lobe does not undergo full division. The Aconeceratidae, with a similar type of division of the inner lateral lobe, are assigned to the Haplocerataceae on the basis of the chronological relationships. We follow Schindewolf [22] in including the Oppeliidae, whose ontogeny has not been studied, in the latter superfamily.

The family Oppeliidae is descended from the Strigoceratidae and is characterized by complete division of the inner lateral lobe into two parts.

The third line of the suborder Haploceratina—the superfamily Acanthocerataceae—most likely arose from the superfamily Haplocerataceae. The interrelationships of the families within it are consistent with the ideas of Wright [25].

The suborder Haploceratina had platyconic and oxyconic shells adapted to active swimming. Judging by their occurrence in the deposits of various kinds of basins, including some deep-water basins, most haploceratinids led a pelagic way of life. This adaptation to a relative stable environment promoted the long duration of the suborder.

The phylogeny of the haploceratinids proposed here is close to Schindewolf's classification of the "Hammatocerataceae" and "Haplocerataceae" [22]. But his exclusion of the oppeliids from the "Haplocerataceae" on the basis of the full division of the inner lateral lobe is inconsistent with their closeness to the Strigoceratidae.

The suborder Perisphinctina is derived from the Hammatoceratidae. Its earliest representatives, the Erycitidae (the genus *Erycites* Gemmellaro and *Abbasites* Buckman), are often combined with this family. An original feature of the suborder is the loss of its capacity to form the new umbilical lobes U^2 and subsequent ones during ontogenesis. New lobes are formed in phylo- and ontogenesis by complete division of the inner lateral lobe and the appearance of new lobes on the saddle between its outer and inner branches, and in certain cases by the formation of a second inner lateral lobe I^1 (the heterochronous mode, according to Schindewolf). The parts of lobe I in onto- and phylogenesis may occupy positions analogous to those of the lobes U^2 and I^1; moreover, such a shift takes place repeatedly in different branches of the Stephanocerataceae and Perisphinctaceae. The formal indexation of these lobes by their position in the adult shell, first of all, loses the characteristic feature of the suborder and, second, makes possible the most artificial phylogenetic constructions, for example, the division of the single family Perisphinctidae into two "sections": the "Perisphinctida" and "Pseudoperisphinctida" [20], the latter of which is artificially placed close to the Stephanocerataceae, or the combination of the latter with the parkinsoniids, whose descent from the early perisphinctids (Leptosphinctinae Arkell) has been traced almost without interruption [2].

Unlike the Haploceratina, the Perisphinctina radiated intensively. Their basic type of shell—a costate serpenticone—was adapted to a bottom-dwelling way of life in a hydrodynamically active environment. The Perisphinctina dispersed widely in the epicontinental seas of the Jurassic and Cretaceous, losing and again regaining their relationships. This led to the formation of many parallel lines with similar adaptations and accordingly to similar features of development. Different phylogenetic branches repeatedly became adapted to other environments, and changed to an active pelagic and, perhaps, planktonic way of life. All this led to an extensive development of homeomorphism. In addition, the Perisphinctina were characterized by very widespread dimorphism, which was so strong that the series of dimorphous pairs can be grouped not only into independent subgenera and genera, but also included in different subfamilies and, in the case of the formation of heteromorphic shells, in different families, superfamilies and even orders (for example, the microconchs of *Pseudogarantiana* and *Strenoceras* and the respective corresponding macroconchs of *Apsorroceras* and *Spiroceras*). All this, of course, rather complicates decipherment of the phylogenetic system of the Perisphinctina.

The accepted classification of the Stephanocerataceae and Perisphinctaceae we have adopted differs little at the level of families from that of Arkell [14, 25]. What remains undetermined is the position of the Tulitidae, which may be descendants of the Morphoceratidae and, if so, should be included in the Perisphinctaceae. Part of the heteromorphs should be assigned to the Perisphinctaceae. Besides the Spiroceratidae (the genera *Apsorroceras* and *Spiroceras*), which are regarded as macroconchs of the planispiral *Pseudogarantiana* and *Strenoceras* [2], an analogous pair is formed by *Epistrenoceras* and *Sulcohamites* among the morphoceratids. To the Perisphinctaceae, evidently, should also be assigned *Parapatoceras* Spath. The Tithonian-Berriasian representatives of the Bochianitidae were probably closely related to the Berriasellidae.

In contrast to their Jurassic predecessors and in comparison to their hoplitid direct descendants, the superfamily Desmocerataceae lasted for a very long time (about 60-65 mln yrs) with only small deviations from the basic morphotype. The interrelationship of the combination of features (the form, sculpture and septum) turned out to be optimal. Although they were a constant component of the Cretaceous ammonite communities, the Desmocerataceae nevertheless rarely played a leading role in them.

The superfamily Desmocerataceae is divided into six families, only one of which (the Desmoceratidae proper) existed through practically the entire Cretaceous; the families Silesitidae and Holcodiscidae were confined to the Early Cretaceous; and the Kossmaticeratidae, Pachydiscidae and Muniericeratidae existed predominantly in the Late Cretaceous. It is widely believed that the Desmocerataceae originated from the phylloceratids [16-18, 25, 29]. Less common is the opposite view—that the desmoceratids arose from lytoceratid ancestors. Fairly recently Wright [30] considered it possible to relate the Desmocerataceae to the Haplocerataceae. There are also adherents of the view that the Desmocerataceae are of polyphyletic origin [24].

Such sharp differences of opinion were indisputably due to insufficient study of the initial stages of ontogenesis. The earlier division of the inner lateral lobe in combination with other features is a reliable indication that the ancestors of the Desmocerataceae must be sought among the Jurassic superfamilies that had a divided inner lateral lobe, a tripartite umbilical lobe, a similar structure of the dorsal lobe and a tendency to form a sutural lobe. Such a superfamily is the Perisphinctaceae, the most likely ancestors of the Desmocerataceae. The latter in turn gave rise to the Hoplitaceae, which inherited the division of the inner lateral lobe and the mode of forming a sutural lobe. The earlier division of the inner lateral lobe and subsequent repeated division of its outer branch, with the separation and sideward shift of first the ventral and then the dorsal element, are features that have been established in all the taxa studied.

The youngest suborder—the Ancyloceratina—first appeared at the end of the Jurassic. The derivation of the heteromorphic Ancylocerataceae from the Perisphinctaceae is not strictly proven. Heteromorphic shells have appeared repeatedly in the history of the ammonoids. The Late Triassic Choristoceratidae, the Jurassic Spiroceratidae, and the Cretaceous Ancylocerataceae, Turrilitaceae and Scaphitaceae are all separate, independently developing groups. The presence among the Jurassic Perisphinctaceae of the heteromorphic *Spiroceras, Parapatoceras* and other closely similar genera is interpreted by Wiedmann [28] as the result of a monophyletic development (*Spiroceras* → *Metapatoceras* → *Parapatoceras* → *Infrapatoceras* → *Paracuariceras* → *Acuariceras*), although no less likely is the independent repeated development of heteromorphic Perisphinctaceae in both the Middle and the Late Jurassic. In view of what has been said above, therefore, it seems to us fully possible that the family Bochianitidae could have arisen repeatedly at the end of the Jurassic.

In comparison to the Turrilitaceae, the Ancylocerataceae are less varied, but in the latter the planospiral type of shell with whorls not in mutual contact achieved its maximal development (in the family Ancyloceratidae). The dissection of the suture line can attain considerable complexity, while retaining the same four elements (VUID).

The Ancylocerataceae are a progressive branch line which gave rise to groups of monomorphic ammonites that are small in number but very representative. For example, the monomorphic Deshayesitaceae were derived from the family Heteroceratidae, and the Ancyloceratidae were ancestral to the Douvilleicerataceae and Parahoplitaceae. All three of these superfamilies have an unstable five-lobed primasuture with a subsequent reduction of the first umbilical lobe. The almost synchronous return to monomorphy was manifested in the reorganization of the inner part of the suture line and led to the rise, from the two separate heteromorphic families Heteroceratidae and Ancyloceratidae, of the two monomorphic superfamilies Deshayesitaceae and Douvilleicerataceae. Each of them is typified by its own special type of morphogenesis of the suture line (Deshayesitaceae: $VUU^1ID \rightarrow VUID \rightarrow VUII^1D$; Douvilleicerataceae: $VUU^1ID \rightarrow VUID \rightarrow VU_1U_2I_2I_1D$), which reflects their parallel development.

REFERENCES

1. Besnosov, N. V., 1960, On the systematics of the Jurassic Ammonitida. Paleont. zhur., No. 1, pp. 29-44.
2. Besnosov, N. V. and V. V. Kutuzova, 1982, The systematics of the parkinsoniids (Ammonitida). Paleont. zhur., No. 3, pp. 41-52.

3. Besnosov, N. V. and I. A. Michailova, 1983, The evolution of the Jurassic-Cretaceous ammonoids. Dokl. Akad. Nauk SSSR, Vol. 269, No. 3, pp. 733-737.
4. Besnosov, N. V. and I. A. Michailova, 1984, The higher taxa of Jurassic and Cretaceous Phylloceratida. Byul. Mosk. o-va ispytat. prirody, Otd. geol., Vol. 59, No. 3, pp. 82-91.
5. Besnosov, N. V. and I. A. Michailova, 1985, The higher taxa of Jurassic and Cretaceous Lytoceratida. Byul. Mosk. o-va ispytat. prirody, Otd. geol., Vol. 60, No. 3, pp. 100-113.
6. Doguzhayeva, L. A. and I. A. Michailova, 1982, The siphon of the Cretaceous heteromorphic ammonoids. Dokl. Akad. Nauk SSSR, Vol. 264, No. 4, pp. 965-968.
7. Doguzhayeva, L. A. and I. A. Michailova, 1982, The early ontogenesis of the Cretaceous heteromorphic ammnoids. Dokl. Akad. Nauk SSSR, Vol. 263, No. 5, pp. 1233-1237.
8. Drushchits, V. V. and L. A. Doguzhayeva, 1981, Ammonity pod elektronnym mikroskopom (Ammonites Under the Electron Microscope). Moscow Univ. Press, 238 pp.
9. Kazakova, V. P., 1971, Rezul'taty izucheniya nekotorykh toarskikh, aalenskikh i nizhnebayosskikh ammonitov iz nadsemeystva Hildocerataceae Hyatt (Results of a Study of Some Toarcian, Aalenian and Lower Bajocian Ammonites of the Superfamily Hildocerataceae Hyatt). Moscow Univ. Press, 108 pp.
10. Michailova, I. A., 1978, Types of prosuture and primasuture in the Cretaceous ammonites. Paleont. zhur., No. 1, pp. 78-93.
11. Michailova, I. A., 1983, Sistema i filogeniya melovykh ammonoidey (The System and Phylogeny of the Cretaceous Ammonoids). Moscow, Nauka, 280 pp.
12. 1958, Osnovy paleontologii. Mollyuski-golovonogiye (Principles of Paleontology. Mollusca—Cephalopoda). Vol. 2. Gosgeoltekhizdat, 339 pp.
13. 1962, Osnovy paleontologii. Mollyuski-golovonogiye (Principles of Paleontology. Mollusca—Cephalopoda). Vol. 1. Moscow, AN SSSR Press, 424 pp.
14. Arkell, W. J., 1950, A classification of the Jurassic ammonites. J. Paleontol., Vol. 24, No. 3, pp. 354-365.
15. Donovan, D. T., J. H. Callomon and M. K. Howarth, 1981, Classification of the Jurassic Ammonitina. In: Ammonoidea, London-New York, Acad. Press, pp. 101-155.
16. Douville, H., 1916, Une famille d'ammonites, les Desmoceratides: Essai d'une classification rationelle, valeur et subordination des charactères. C. R. Acad. Sci., Vol. 162, pp. 369-373.
17. Grossouvre, A., 1893, Recherches sur la Craie supérieur. 2. Paléontologie. Les ammonites de la Craie supérieur. Mem. Carte Géol. det. France, p. 264.
18. Roman, F., 1938, Les Ammonites Jurassiques et Crétacées: Essai de Genera. Paris, 554 pp.
19. Salfeld, H., 1920, Über die Ausgestaltung der Lobenlinie bei Jura — und Kreide — Ammonoideen. Nachr. Ges. Wiss. Gottingen. Math.-Phys. Kl., No. 3, pp. 449-467.
20. Schindewolf, O. H., 1923, Über die Ausgestaltung der Lobenlinie bei den Neoammonoidea Wdkd. Centralbl. Mineral. Geol. und Paläontol., Vol. 24, pp. 337-350.
21. Schindewolf, O. H., 1962, Studien zur Stammesgeschichte der Ammoniten. Abh. Akad. Wiss. und Lit. Math.-Nat. Kl., No. 8, pp. 111-257.
22. Schindewolf, O. H., 1963, Studien zur Stammesgeschichte der Ammoniten. Abh. Akad. Wiss. und Lit. Math.-Nat. Kl., No. 3, pp. 261-407.
23. Schindewolf, O. H., 1968, Studien zur Stammesgeschichte der Ammoniten. Abh. Akad. Wiss. und Lit. Math.-Nat. Kl., No. 3, pp. 731-901.
24. Spath, L. F., 1923, A monograph of the Ammonoidea of the Gault. Palaeontogr. Soc. London, Pt. 1, pp. 1-72.
25. 1957, Treatise on Invertebrate Paleontology. Pt. L. Mollusca. 4. Cephalopoda.

Ammonoidea. New York, Lawrence, Geol. Soc. America-University of Kansas Press, 490 pp.

26. Wiedmann, J., 1962, Ammoniten aus der Vascogotischen Kreide (Nordspanien). 1. Phylloceratina, Lytoceratina. Palaeontographnica. A, Vol. 118, pp. 119-237.
27. Wiedmann, J., 1966, Stammesgeschichte und System der posttriadischen Ammonoiden: Ein Überblick. Neues Jahrb. Geol. und Paläontol. Abhandl., Vol. 127, No. 1, pp. 13-81.
28. Wiedmann, J., 1969, The heteromorphs and ammonoid extinction. Biol. Rev., Vol. 44, No. 4, pp. 563-602.
29. Wright, C. W., 1955, Notes on Cretaceous ammonites. 2. The phylogeny of the Desmocerataceaeand Hoplitaceae. Ann. Mag. Natur. Hist., Ser. 12, No. 92, pp. 363-375.
30. Wright, C. W., 1981, Cretaceous Ammonoidea. In: The Ammonoidea. London-New York, Acad. Press, pp. 157-174.