ISSN 0031-0301, Paleontological Journal, 2009, Vol. 43, No. 5, pp. 527–536. © Pleiades Publishing, Ltd., 2009.
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The Evolution of the Heteromorph and Monomorph Early Cretaceous Ammonites of the Suborder Ancyloceratina Wiedmann

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Received May 10, 2008

Abstract—The relationship between the appearances of heteromorph and monomorph ammonoids and changes in the abiotic environment was studied. The correlation of these processes was examined for different intervals in the Early Cretaceous. The phylogeny of the superfamily Ancyloceratoidea Gill from the time of appearance of early heteromorphs (due to changes in ecological specialization) and the reversal process of the return to monomorph shells is examined for four superfamilies. The origin of monomorph ammonites of the superfamilies Theodoritoidea Baraboshkin et I. Michailova, superfam. nov., Douvilleiceratoidea Parona et Bonarelli, Parahoplitoidea Spath et Deshayesitoidea Stoyanow from heteromorph ancestral families Crioceratitidae Gill, Ancyloceratidae Gill, Hemihoplitidae Spath, and Heteroceratidae Spath in the superfamily Ancyloceratoidea Gill is suggested.

DOI: 10.1134/S0031030109050086

Key words: ammonites, Early Cretaceous, phylogeny, Ancyloceratina.

PHYLOGENY AND COMPOSITION OF THE SUPERFAMILY ANCYLOCERATOIDEA GILL

In accordance with the system of higher taxa of Jurassic–Cretaceous ammonoids (Beznosov and Mikhailova, 1983, 1985, 1991; Bogoslovskaya et al., 1990), the suborder Ancyloceratina Wiedmann includes heteromorph ancestors and monomorph descendants (Fig. 1).

In the recent American *Treatise of Invertebrate Paleontology* (Wright et al., 1996), a revision of Cretaceous ammonoids included the suborder Ancyloceratina Wiedmann with three superfamilies: Turrilitoidea Gill, Scaphitoidea Gill, and Ancyloceratoidea Gill (Arkell et al., 1957) Fundamental differences between these superfamilies have been repeatedly stated in many publications. In addition to the nominal superfamily Ancyloceratoidea, the suborder Ancyloceratina includes two superfamilies of monomorph ammonoids: superfamily Douvilleiceratoidea Parona et Bonarelli, which at the final stage of its evolution possibly became heteromorph again (family Astiericeratidae Breistroffer) and the superfamily Deshayesitoidea Stoyanow with two families: Deshayesitidae Stoyanow and possibly Parahoplitidae Spath.

The generic diversity of the superfamilies of Cretaceous ammonites is shown in the histogram (Fig. 2). The superfamily Phylloceratoidea Zittel (order Phylloceratida Zittel) includes the minimal number of genera. The order Lytoceratida Hyatt is relatively representative due to the heteromorph superfamily Turrilitoidea Gill (suborder Turrilitina Gill) and the considerably less diverse superfamilies Scaphitoidea Gill and Lytoceratoidea Neumayr (suborder Lytoceratina Hyatt). Among Ammonitida Zittel, the Late Acanthoceratoidea Grossouvre (150 genera) are dominant. These are the descendants of the Jurassic–Cretaceous Haploceratoidea Zittel (suborder Haploceratina Zittel). In the first half of the Early Cretaceous Perisphinctoidea Steinmann were sufficiently representative (85 genera), and together with their descendants Desmoceratoidea Zittel and Hoplitoidea H. Douville constituted the suborder Perisphinctina Steinmann. The last suborder Ancyloceratina Wiedmann (Superfamily Ancyloceratoidea Gill) is slightly less diverse than Turrilitoidea Gill, whereas their monomorph descendants Douvilleiceratoidea Parona et Bonarelli, Deshayesitoidea Stoyanow, and Parahoplitoidea Spath are scarce.

In this paper, the superfamily Ancyloceratoidea is divided into eight families: Bochianitidae Spath, Ancyloceratidae Gill, Heteroceratidae Spath, Hemihoplitidae Spath, Hamulinidae Gill, Labeceratidae Spath, Ptychoceratidae Gill, and provisionally Macroscaphitidae Hyatt. The last two should be considered within the Turrilitoidea Gill because of their suture.

Our understanding of the relationships between the heteromorph and monomorph Ancyloceratina is shown in Fig. 3. Recently obtained data, in particular the establishment of a new genus *Theodorites* Baraboshkin et I. Michailova, 2006, allowed updating of the phylo-

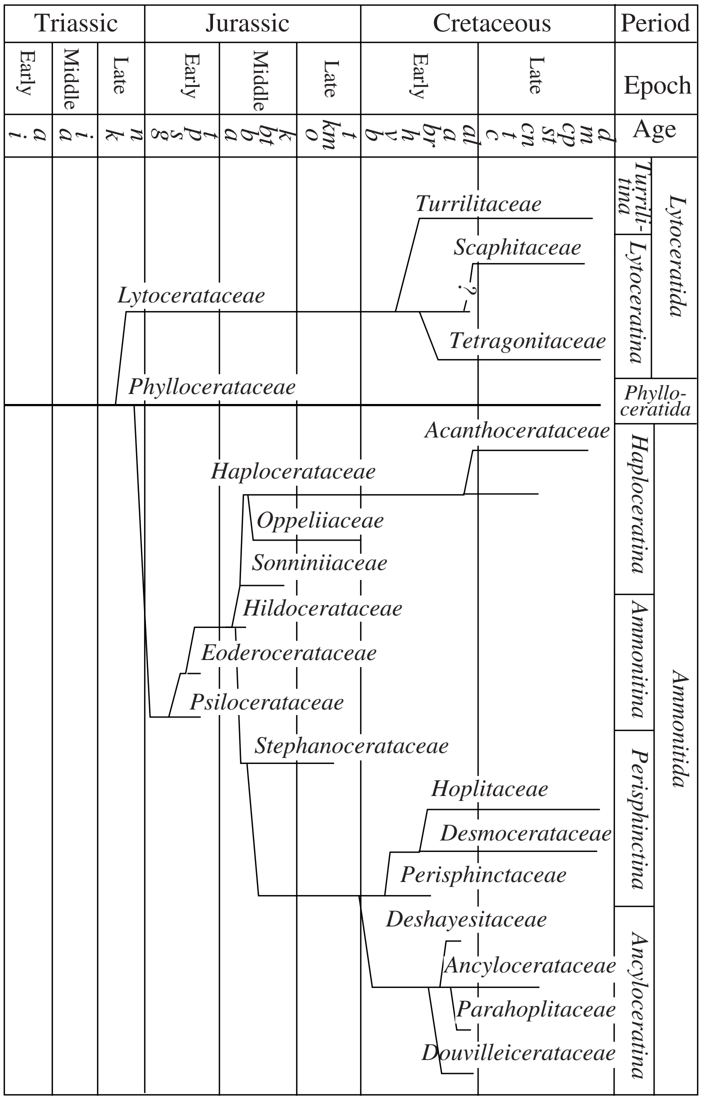

Fig. 1. Phylogeny of the Jurassic-Cretaceous ammonoids (Beznosov and Mikhailova, 1983).

genetic relationships of taxa of family and suprafamilial rank.

The origin of the superfamilies Ancyloceratoidea and Perisphinctoidea is not contested. The original family Bochianitidae was apparently ancestral to several families. Figure 3 shows four families, which were certainly ancestral to monomorph Douvilleiceratoidea, Parahoplitoidea, Deshayesitoidea, and Theodoritoidea Baraboshkin et I. Michailova, superfam. nov.

It was found that the evolutionary transformation of the shell of potential ancestral monomorphic ammonoids resulted in the development of an umbilical perforation. This perforation did not affect the embryonic shell. The first whorl always comes into contact with the protoconch. The second whorl, after the initial constriction, is a straight shaft, then becomes a flat arc, making a circle (Fig. 3, insert). The third whorl begins after the second perforated whorl with the first whorl. However, the umbilical perforation may not decrease and the transition from monomorphs to heteromorphs will be then incomplete.

Umbilical perforation is found in several genera in the suborder Ancyloceratina: *Leptoceras* Uhlig (Thieuloy, 1966), *Paraspiticeras* Kilian (Wiedmann, 1966; Doguzhaeva and Mikhailova, 1982), *Turkmeniceras* Tovbina (Bogdanova, 1971), *Theodorites* Baraboshkin et I. Michailova (Baraboshkin and Mikhailova, 2006), *Luppovia* Bogdanova, Kakabadze et I. Michailova (Kakabadse et al., 1978), *Caspianites* Casey (Bogdanova and Mikhailova, 1975), *Hemihoplites* Spath (Sharikadze et al., 1989), *Audouliceras* Thomel (Mikhailova and Baraboshkin, 2007), and *Leptoceratoides* Thompson. The above genera in some cases are assigned to the superfamily Ancyloceratoidea Gill, while others are assigned to their possible descendants.

The first whorl with a protoconch is rarely observed, but the presence of the umbilical perforation is certain in *Koeneniceras* I. Michailova et Baraboshkin (Baraboshkin and Mikhailova, 2002). However, a decrease of the umbilical perforation and completion of the whorl may not be present and the stage of monomorph shells is not reached.

The superfamily Ancyloceratoidea is generally less diverse than Turrilitoidea, although the planispiral loosely coiled shell became dominant (family Crioceratitidae Gill and Ancyloceratidae Gill). While the ammonitid features remained unchanged (trifid umbilical lobe (U))—the suture of adult ammonites can be very complicated although restricted to four basic elements: VUID.

The transition from the family Heteroceratidae Spath to the superfamily Deshayesitoidea Stoyanow (genera *Heteroceras, Colchidites* Djanelidze, *Turkmeniceras*) is the most thoroughly studied; the latter is included in the superfamily Deshayesitoidea based on the presence of a small perforation. The heteromorph origin of the monomorph Deshayesitoidea is supported by the reduction of the first umbilical lobe (U^1) and a return to a four-lobed suture. The explanation of this fact became possible after such a sutural change was described in *Caspianites wassiliewskyi* Renngarten (Bogdanova and Mikhailova, 1975).

A crescent-like cross-section of the first whorl is replaced in *C. wassiliewskyi* and similar forms by a rounded cross-section. Therefore, this five-lobed primary suture, inherited from Perisphinctoidea, became reduced and shifted to the initial stages, being preserved in the second- or third-line suture (Fig. 4). This type of primary suture—unstable five-lobed suture—is probably typical for most ancyloceratids. In the superfamily Deshayesitoidea, unlike in the other two superfamilies (Douvilleiceratoidea and Parahoplitoidea), new elements appear as the result of the subdivision of the saddle I/D and the appearance of the lobes I^1 and I^2. The suture in the adult forms is moderately strongly dissected. The family Ancyloceratidae gave rise to the superfamily Douvilleiceratoidea. The genus *Paraspiticeras* Kilian, that was included in the superfamily, had a bigger umbilical perforation than *Turkmeniceras*. Wiedmann (1969), followed by B. Kilian (Kilian, 1907–1913), proposed this genus because of the heloceratid appearance of the last whorls. The genus *Paraspiticeras* is included in the Douvilleiceratoidea (family Cheloniceratidae Spath) (see Wright et al., 1996). Wiedmann (1966) studied a young specimen of *Paraspiticeras schindewolfi* Wiedmann from the Barremian of Spain. Two specimens of *Paraspiticeras percevali* Uhlig from the Lower Barremian of the Southwestern Crimea are particularly interesting (Doguzhaeva and Mikhailova, 1982). The umbilical perforation in this species is slightly greater than that of *P. schindewolfi.* The genus *Leptoceras* (Thieuloy, 1966), which was considered by Wiedmann as ancestral to *Paraspiticeras*, shows a tendency to secondary coiling.

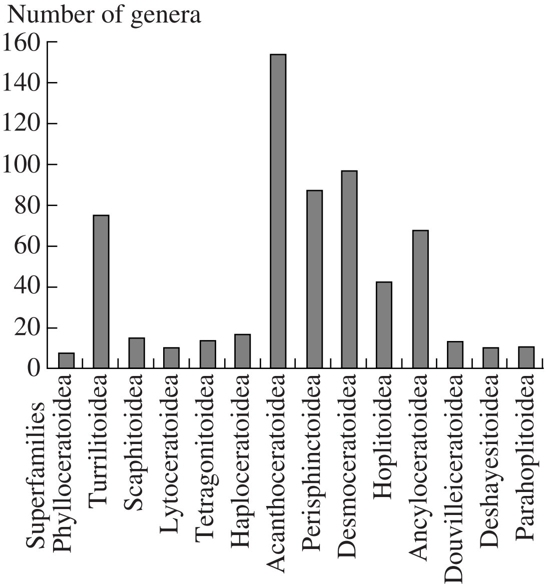

Fig. 2. A histogram showing the number of genera in superfamilies of Cretaceous ammonoids (after Wright et al., 1996, modified).

The morphogenesis of the suture in the superfamily Douvilleiceratoidea proceeds by the appearance of new elements by separating the umbilical (U) and inner lateral[1] (I) lobes to form the lobes U_1, U_2, I_1, and I_2. Schindewolf (1966) studied sutural morphogenesis in the ancestral genus *Paraspiticeras* (in *P. schindewolfi* Wiedmann). The separation of two umbilical lobes ($U \longrightarrow U_1U_2$,) in this species is not observed, but this lobe is bipartite.

At the same time an unstable five-lobed primary suture was found in Douvilleiceratoidea similar to that in Deshayesitoidea. Interestingly, the study of sutural morphogenesis in *Audouliceras* ex gr. *renauxianum* (d'Orbigny), one of the typical representatives of the family Ancyloceratidae showed the presence of an unstable five-lobed primary suture (Mikhailova and Baraboshkin, 2007).

The question of the origin of the superfamily Parahoplitoidea, consisting of two families: Parahoplitidae Spath and Acanthohoplitidae Stoyanow, is quite complex and controversial. Anticipating the discussion of controversial points, it is reasonable to identify the main morphogenetic features of the suture in the superfamily Parahoplitoidea. The primary suture is five-lobed and unstable like one of the two previously discussed superfamilies of monomorph ancyloceratins. The appearance of new elements occurs by subdivision

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[1] In the Russian original the term *innerlateral'naya lopast'* is used instead of *vnutrennyaya bokovaya lopast'* for harmonization of terms.

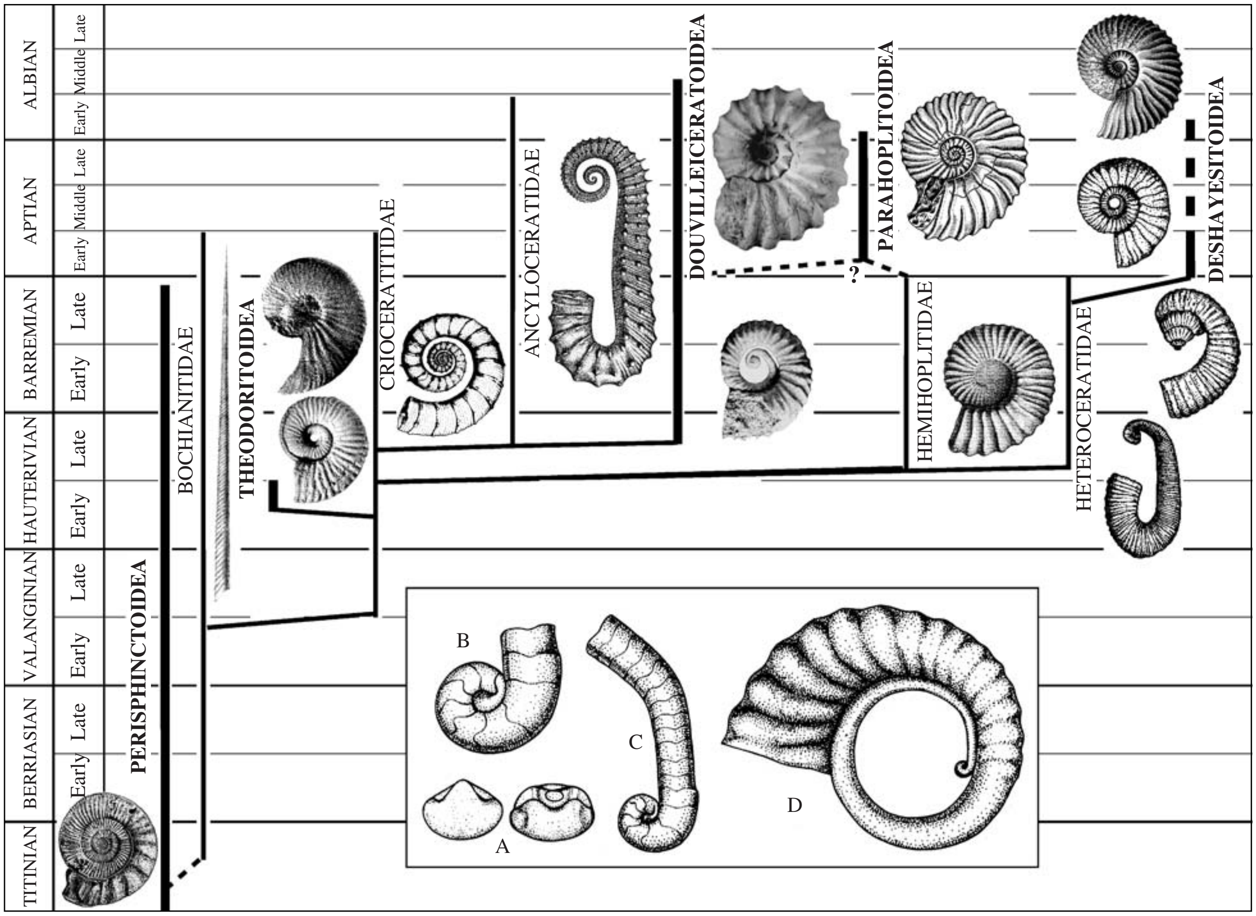

Fig. 3. Phylogeny of the superfamily Ancyloceratoidea Gill (without Labeceratidae Spath, 1925 and Hamulinidae Gill, 1871) and its monomorph descendants. In the box: (A) protoconch, (B) the first whorl and the beginning of the uncoiled part, (C) a shift from a straight to a bent shaft, (D) transition to the planospiral shell and appearance of the umbilical perforation in *Caspianites* (Bogdanova and Mikhailova, 1975).

of the saddle U/I, therefore, the new lobes are indexed as U^1, U^2, sometimes U^3, with the inner lateral lobe always located beyond the seam on the inner side of the whorl, whereas in Deshayesitoidea the saddle I/D is subdivided, and the inner lateral lobe (I) is shifted onto the external part of the whorl.

In accordance with the views of Casey (1965) that parahoplitids evolved from Deshayesitidae Stoyanow through the genus *Dufrenoyia* Kilian et Reboul, Wright et al. (1996) provisionally assigned them as a family to Deshayesitoidea Stoyanow. We cannot agree with this view, because the morphogenesis of the suture is a character of very high rank, while the differences between Deshayesitoidea and Parahoplitoidea are even more essential.

Some authors suggest that morphogenesis of the suture and ornamentation allows Douvilleiceratoidea to be considered as ancestral to Parahoplitoidea. Wiedmann (1966) and Tovbina (1979) interpret the appearance of new lobes in Parahoplitidae (the rank given in their work) as a result of division of the lobes. Schindewolf (1968), in contrast, emphasized the difference in the morphogenesis of the suture in the above groups, and the seventh part of his monograph, placed Douvilleiceratoidea Parona et Bonarelli and Parahoplitoidea Spath in Ancyloceratina Wiedmann separately. The uniqueness of the appearance of new elements in Douvilleiceratoidea was confirmed by Casey (1961) based on an example of the Early Aptian *Roloboceras hambrovi* (Forbes) and by Mirzoyev (1967) for Lower Albian *Douvilleiceras* Grossouvre from Gissar.

Kvantaliani and Sharikadze (1980, 1982, 1985) interpreted the evolution of these groups differently. They confirmed the presence of an unstable five-lobed primary suture in *Acanthohoplites* Sinzow and *Epicheloniceras* Casey and did not observe this suture in *Parahoplites* Anthula. Like Wiedmann and Tovbina, Georgian authors concluded that the umbilical lobe is subdivided in *Parahoplites*, as well as in *Epicheloniceras*, into two parts. Kvantaliani and Sharikadze proposed a new interpretation. They assigned *Parahoplites* to Douvilleiceratidae Parona et Bonarelli, and

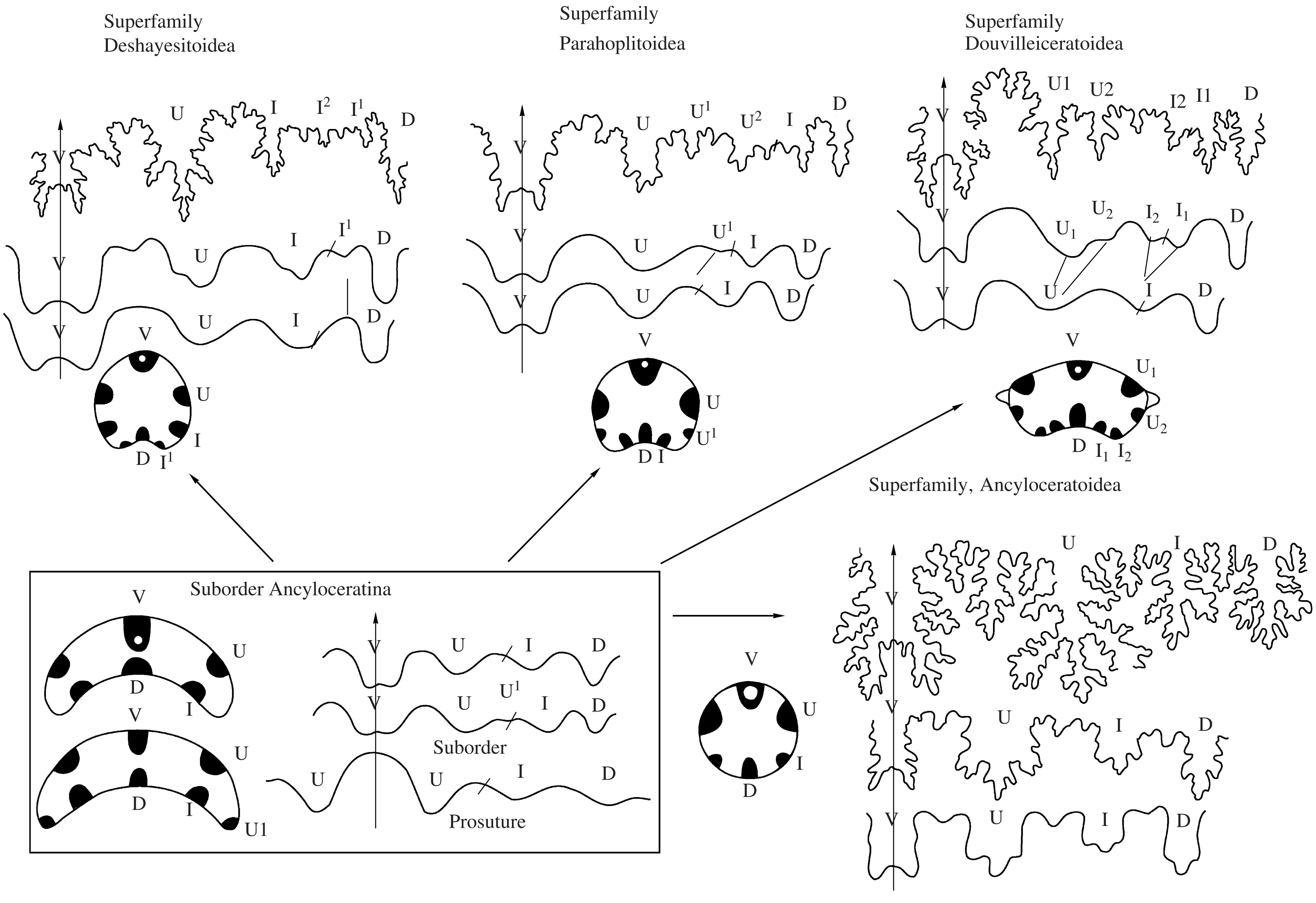

Fig. 4. Early morphogenesis of the suture and cross-section of the suborder Ancyloceratina Wiedmann (for Mikhailova, 1983 as amended).

raised the subfamily Acanthohoplitinae Stoyanow to the level of family. Recently, these taxa have been raised to the rank of superfamily (*Atlas* …, 2005).

Sharikadze and coauthors observed the existence of the umbilical perforation and studied sutural morphogenesis in *Hemihoplites ridzewskyi* (Karakasch). The authors noted that primary suture was observed only partially, whereas the third suture (Sharikadze et al., 1989, text-fig. 2) consists of four lobes (VUID). The appearance of new elements in *Hemihoplites* Spath, in which the whorls are weakly overlapped, is accompanied by a shift of the lobe I to the outer side of the shell, which is also typical of Deshayesitoidea Stoyanow.

We suggest that the superfamily of Parahoplitoidea Spath probably evolved from the family Hemihoplitidae Spath. This is based on the possibility of transition towards the morphology of the early acantohoplitids, similar to *Colombiceras*. Some increase in the degree of whorl overlap may result in the shift of the inner lateral lobe (I) onto the inner side of the whorl. Interestingly, Sharikadze and his colleagues have established the presence of the bipartite dorsal lobe (although not in all specimens) in some *Hemihoplites ridzewskyi* (Karakasch), which is not typical of Ancyloceratoidea Gill. At the same time, the bipartite dorsal lobe (D) distinguishes the family Acanthohoplitidae from the family Parahoplitidae, which appeared later and in which the dorsal lobe is almost always undivided. Therefore, two possible ancestors may be suggested for the superfamily Parahoplitoidea: (1) family Ancyloceratidae ⟶ Superfamily Douvilleiceratoidea ⟶ Superfamily Parahoplitoidea; (2) family Hemihoplitidae ⟶ Superfamily Parahoplitoidea (Fig. 3).

It has recently been established (Baraboshkin and Mikhailova, 2006), that the family Crioceratitidae Gill was also an initial family in the transition from heteromorph to monomorph shell. The Hauterivian of the Crimean Mountains was known to yield ammonites, sometimes identified as *Lyticoceras* Hyatt. After we established that these forms had an umbilical perforation, we proposed to assign them to the genus *Theodorites* Baraboshkin et Michailova (Baraboshkin and Mikhailova, 2006), which was the link between *Crioceratites loryi* (Sarkar) and *Lyticoceras nodosoplicatum* Kilian et Reboul: in the latter species the umbilical perforation is absent (pers. comm. by F. Reboulet, France). Two years ago, when establishing the genus *Theodorites*, we felt that *Theodorites* and its descendant *Lyticoceras* Hyatt should be assigned to the family Crioceratitidae, but the suggestion about the origin of monomorph neocomitids from heteromorph ones is highly debatable (Mikhailova and Baraboshkin, 2008), given that in one opinion *Crioceratites* itself descended from neocomitids (Cecca, 1997, 1998a, 1998b), and it would be more nomenclaturally correct to assign this group to Crioceratitidae in Theodoritoidea Baraboshkin et I. Michailova, superfamily nov.

Thus, four families of heteromorph Ancyloceratoidea Gill (Crioceratitidae, Ancyloceratidae Gill, Hemihoplitidae Spath, and Heteroceratidae Spath), with various degrees of certainty gave rise to four monomorph superfamilies: Theodoritoidea Baraboshkin et I. Michailova, superfam. nov., Douvilleiceratoidea, Parahoplitoidea, and Deshayesitoidea.

LIFESTYLE OF HETEROMORPH AMMONITES

The lifestyle of heteromorph ammonites has been interpreted by different researchers in different ways. Recently, most authors are inclined to regard most heteromorphs as "semiplanktonic"[2] or megaplanktonic, and to a lesser extent as benthic and nektonic. Note that throughout ontogeny the orientation of the shell, the method of feeding and environmental affinities could have changed (Ward, 1979; Nesis, 1985; Westermann, 1990, 1996; Kakabadze and Sharikadze, 1993; Cecca, 1997, 1998a, 1998b; Westermann and Tsujita, 1999; Lewy, 2002; Baraboshkin and Enson, 2003; Reboulet et al., 2005, etc.), although other opinions (Ebel, 1992, etc.) also exist.

Distribution of heteromorph ammonites in the Cretaceous: possible causes of fluctuations in diversity

Judging from the semi-planktonic lifestyle of heteromorph ammonites it is assumed that, as well as for modern meso- and megaplankton, their quantitative distribution is controlled by (1) depth, which allows development of plankton and, most importantly, (2) abundance of food (in this case plankton) resources (Vinogradov, 1968). The distribution and evolution of heteromorphs as a semi-planktonic group is also affected by such important factors of the environment, the characteristics of water masses (temperature, salinity, etc.), direction of currents and presence of cycles, determining the spread of populations (Beklemishev, 1969; Baraboshkin et al., 2007; Baraboshkin, 2008), etc. An important limitation was that these forms, while inhabiting the pelagic zone, could not exist at depths greater than 300–400 m (Westermann, 1990, 1996; Nesis, 1985), below which depth the siphuncle would have exploded and the weakest elements of the shell been destroyed, causing the mollusk's death.

Thus, it is quite clear that an increase in diversity of heteromorph ammonites coincided with an increase in the area of the pelagic regions, i.e., during transgressions and at time of the formation of huge epicontinental basins. The connection between the increase in heteromorph ammonite diversity and transgression has been previously proposed by Delanoy and Magnin

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[2] Organisms that most of their life are planktonic but exist as nekton and/or benthos at some developmental stages generally fit the definition of plankton (Aleev, 1976). Some authors use the term "quasiplanktonic" (Reboulet et al., 2005) or "planktonektonic" lifestyle (A.P. Kasatkina in Nesis, 1985).

(1994), but was challenged by those workers who consider trophic factors as the main driving force in the evolution of heteromorphs (Cecca, 1997, 1998b).

The fluctuations of the number of genera of heteromorph ammonites (Fig. 5), show the correlation of peaks of their evolutionary diversity with the largest "fast" transgressions: Hauterivian–Barremian (maximum diversity of Ancyloceratoidea), Albian–Cenomanian (maximum diversity of Turrilitoidea, appearance of Scaphitoidea), Campanian (maximum diversity of Turrilitoidea and Scaphitoidea), corresponding to second order fluctuations in sea level. This increase in diversity of heteromorph ammonites coincided with the beginning of transgression, i.e., when the new areas rich in food resources appear and have to be explored. Hence it is clear that there is no contradiction in interpretations linking the evolution of heteromorphs with either transgression or food resources.

The fall in overall diversity is most likely has a number of reasons. First, is the stabilization of sea level, when food resources are already being successfully exploited by ammonites, and new spaces do not appear in the marine basins. Secondly, is an actual large-scale drop in the sea level. Most clearly, this is observed in the diversity of heteromorphs in the early Aptian, mid-Albian, in the Middle Cenomanian, Late Turonian, Santonian and, naturally, at the end of the Maastrichtian. This minimum is observed less clearly in the mid-Campanian. Finally, the fall of diversity could have resulted from anoxic conditions, a phenomenon common in Cretaceous basins (Jenkyns, 1980; Bralower et al., 1994, etc.). These dysoxic conditions or partial anoxia, not affecting the entire water column, does not preclude the existence of plankton (Vinogradov, 1968), including ammonites (Reboulet et al., 2003, 2005). Only prolonged complete or nearly complete anoxia, which embraced all depths of heteromorph habitats, could be fatal for them. Such events can only occur at the peak of transgression, at the time of maximum sea level rise and extreme low water circulation in the oceans. One such event is known to have occurred at the Cenomanian–Turonian boundary, which is reflected in a significant drop of the diversity curve (Fig. 5).

Another, smaller, drop occurred at the Aptian–Albian boundary. At that time several different events could have played their role: (1) low level of water in the oceans, (2) extensive development of anoxic conditions, and (3) events in the evolution of heteromorphs, i.e., the extinction of Ancyloceratoidea and the beginning of the development of Turrilitoidea. General cooling of climate at this stage was unlikely to have affected the diversity of heteromorphs, as in other times of cooling (Barremian, Campanian), maximum development of these ammonites is observed.

The appearance of monomorph descendants of Ancyloceratoidea, in a few cases where the phylogenetic lineages are tracked, is connected with regression and sea level drop (third-order cycles, Fig. 5). This is observed, firstly, at the transition from the family Heteroceratidae Spath to the superfamily Deshayesitoidea Stoyanow (genus *Heteroceras* d'Orbigny ⟶ genus *Colchidites* Djanelidze ⟶ genus *Turkmeniceras* Tovbina, Fig. 6) (Bogdanova and Mikhailova, 1999). To a lesser extent, this has been proved for the lineage: *Crioceratites* Leveille ⟶ genus *Theodorites* Baraboshkin et I. Michailova ⟶ *Lyticoceras* Hyatt (Mikhailova and Baraboshkin, 2006), which is related to the establishment of a new superfamily, Theodoritoidea Baraboshkin et I. Michailova, superfamily nov. The question of the origin of the superfamily Douvilleiceratoidea and Parahoplitoidea remains open, but the times of these events, obviously, coincided with regressive epochs, from Late Hauterivian–beginning of the Aptian (Fig. 5).

During regression, the area of the basins decrease, as well as their depth (especially in the epicontinental basins), and plankton production is shifted to deeper sea zones. As a result, organisms that are trophically dependent on an abundance of plankton, migrate, become extinct or adapt. The semi-planktonic lifestyle excluded the possibility of active migration, so diversity decreased in times of regression, but at the same time the heteromorph shell became coiled and the transition to a nektonic and benthic way of life was observed, when rich food resources appeared in shallow water (Fig. 6).

This model, as it seems, can explain the transitions from monomorph ammonites to heteromorph, and vice versa.

SYSTEMATIC PALEONTOLOGY

Superfamily Theodoritoidea Baraboshkin et I. Michailova, superfam. nov.

Type genus. *Theodorites* Baraboshkin et I. Michailova, 2006.

Diagnosis. Shell evolute with umbilical perforation. Umbilical wall narrow and vertical. The cross section rounded-trapezoidal to rounded-hexagonal. Venter smooth, slightly keeled on the adult whorls. Ribs subradial, single, double and divided into four, intercalating, with two or three rows of small tubercles: umbilical, ventrolateral, rarely lateral. Ventrolateral tubercles flattened, subparallel to plane of symmetry of shell.

Suture strongly dissected. Ventral lobe, narrow with high median saddle and three lateral digits. More profound umbilical lobe trifid, nearly symmetrical, with a more developed branch facing the ventral lobe. The first lobe of the umbilical lobe much shorter, less strongly dissected and more asymmetrical.

Composition. Family Theodoritidae Baraboshkin et I. Michailova, fam. nov.

Comparison. From the superfamily Perisphinctoidea Steinmann, 1890 is distinguished by the umbilical perforation.

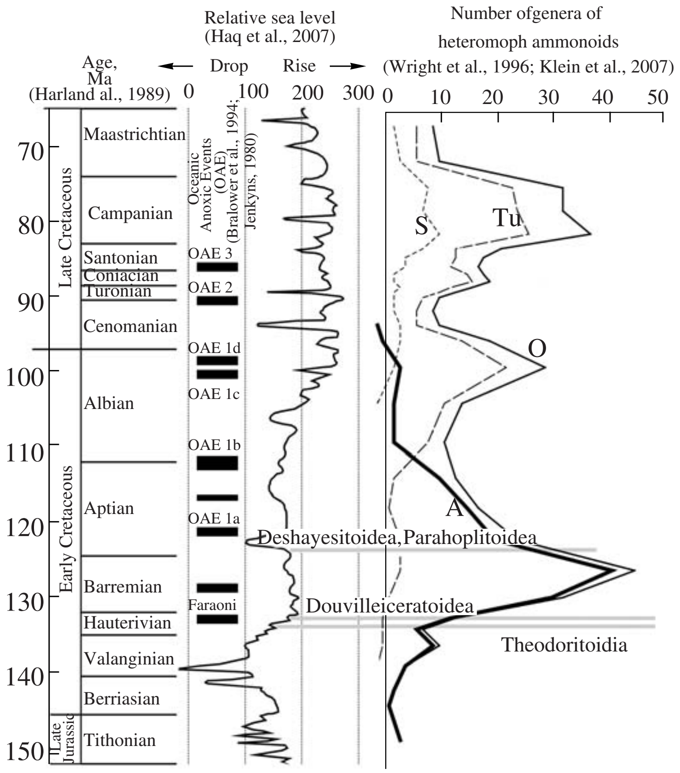

Fig. 5. Changes in diversity of genera of heteromorph ammonites, the levels of appearance of monomorph descendants of Ancyloceratoidea Gill, sea level fluctuations and global anoxic events. Superfamilies: (A) Ancyloceratoidea Gill, (Tu) Turrilitoidea Gill, (S) Scaphitoidea Gill, (O) the total diversity of the superfamily.

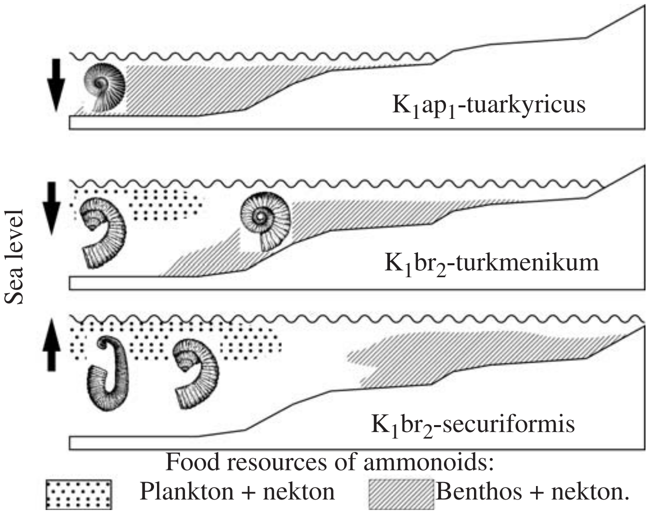

Fig. 6. A model of transition from heteromoph to monomorph planispiral shells (based on *Heteroceras* d'Orbigny ⟶ *Colchidites* Djanelidze ⟶ *Turkmeniceras* Tovbina).

Occurrence. Lower Hauterivian *Lyticoceras nodosoplicatum* of the Crimean Mountains.

Family Theodoritidae Baraboshkin et I. Michailova, fam. nov.

Type genus. *Theodorites* Baraboshkin et I. Michailova, 2006.

Diagnosis. As superfamily.

Composition. Type genus.

Distribution. As superfamily.

ACKNOWLEDGMENTS

This work was supported by the Russian Foundation for Basic Research (project no. 06-05-64167) and the program "Leading Scientific Schools" (grant НШ-841.2008.5).

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