

The origin of ammonoid locomotion

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Evolution of the coiled ammonoid conch from the uncoiled bactritid conch was probably coupled with changes in manoeuvrability and swimming velocity. The gradual transformation of uncoiled to coiled ammonoid conchs has essential functional consequences. The radical change in conch geometry during phylogeny but also in ontogeny of early ammonoids implies a shift of the aperture from an original roughly downward, via a downward oblique and an upward oblique to an upward orientation, presuming a neutrally buoyant condition of the ammonoid animal. Similar trends were reconstructed for the three main ammonoid lineages in the Middle Devonian, the agoniatitid, the anarcestid, and the tornoceratid lineages. This allowed an increase in manoeuvrability and in the maximum horizontal swimming speed.

Key words: Bactritida, Ammonoidea, ontogeny, phylogeny, locomotion, coiling, Devonian.

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Introduction

Although ammonoids are among the most famous and the most common fossil invertebrates in the Palaeozoic and Mesozoic, little is known about the animals' ecology. Their conchs consisted of a body chamber and a gas-filled chambered phragmocone to maintain neutral buoyancy. It is largely accepted that they possessed a hyponome for propulsion (Jacobs and Chamberlain 1996). Backward movements can be achieved in Recent *Nautilus* by two actions; (1) by oscillation of the wings of the hyponome and thus generating a continuous weak stream of water over the gills and out of the hyponome, inducing a gentle motion, and (2) by contracting the mantle cavity, they produce a strong jet of water and move backward at a higher velocity (Packard et al. 1980). It appears likely, that ammonoids were able to propel themselves by the same means. Their conch geometry allows calculation of flow resistance and swimming velocities (Jacobs 1992; Jacobs and Chamberlain 1996; Seki et al. 2000), septal strength and maximal diving depths (Westermann 1973, 1975, 1982; Daniel et al. 1997), the positions of the centres of gravity and buoyancy, and the orientation of the shell in the water column (Trueman 1941; Raup and Chamberlain 1967; Saunders and Shapiro 1986; Swan and Saunders 1987; Saunders and Work 1996; Westermann and Tsujita 1999).

Several times in their evolutionary history, ectocochleate cephalopods developed conchs with horizontally aligned centres of gravity and aperture (and by implication the position of the hyponome, as in modern *Nautilus*). The most common strategy leading to a rotation of the aperture was the evolution of planispiral (i.e., coiled) shells. More than ten clades of the Nautiloidea (Dzik 1984), the early Ammonoi-

dea, and several additional clades of Mesozoic ammonoids embarked on this strategy.

It is generally accepted that the coiled ammonoids originated from a group of uncoiled cephalopods—Bactritida (Erben 1960; Dzik 1984; Doguzhaeva 1999; Korn 2001), as documented by numerous transitional Early Devonian ammonoid species (Schindewolf 1932; Erben 1960, 1964, 1965; Korn 2001). This process was accompanied by significant morphological transformations such as the shapes of apertures and growth parameters (e.g., whorl expansion, umbilical width), as well as consequent changes in body chamber length and orientation of the ammonoid conch within the water column (Klug 2001; Korn and Klug 2001, 2003). All of these morphological transformations both during phylogeny and during ontogeny allow interpretations with regard to ammonoid manoeuvrability.

The energy cost for achieving a position of the conch suitable for rapid and directed horizontal movements was lower in planispiral than in orthoconic conchs. In passive moments, the orthocones were simply “hanging” in the water column with the aperture facing downwards (Westermann 1977). During horizontal swimming manoeuvres in order to reduce drag, their conchs had to rotate into an inclined or possibly horizontal position. In contrast, most cephalopods with planispiral conchs could maintain the same orientation or slightly rotate the conch until the hyponome reached the same level as the centre of gravity. In many ammonoids, this must have resulted in a rocking movement, as has been observed in Recent *Nautilus* (Chamberlain 1987). In the subsequent paragraphs, we discuss the constraints of these morphological transformations of conchs in phylogeny and ontogeny of the earliest ammonoids regarding manoeuvrability and swimming speed.

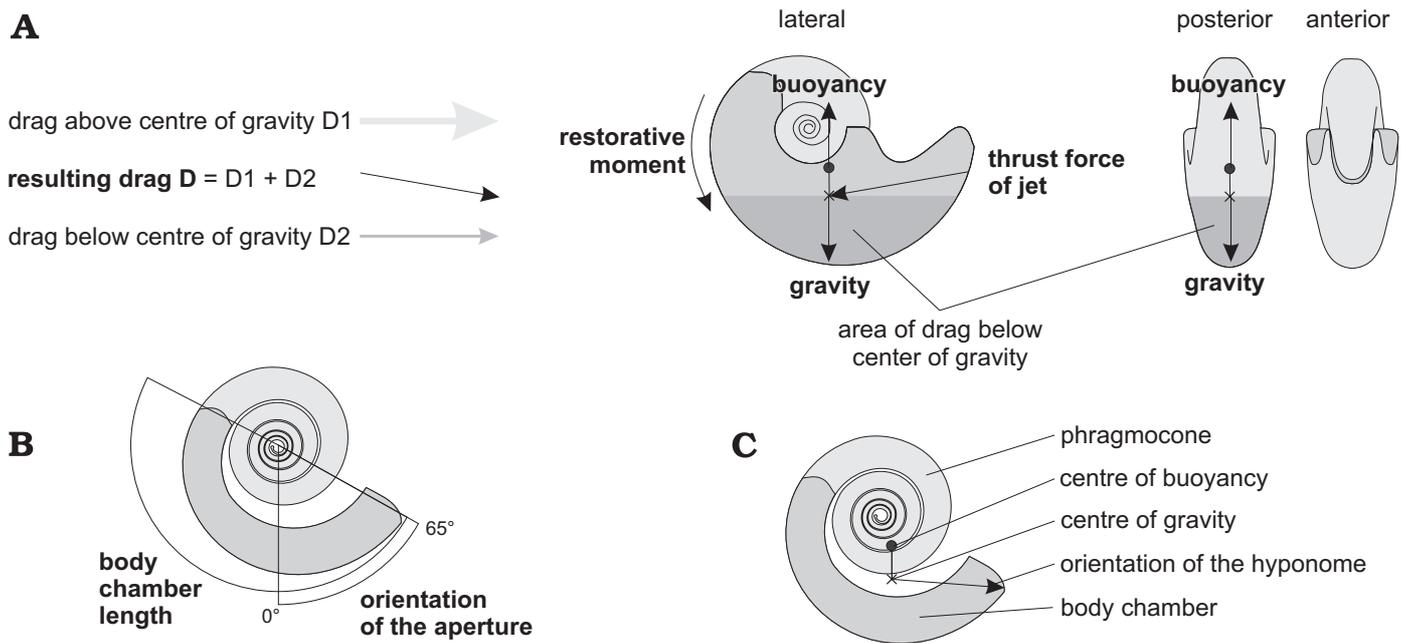


Fig. 1. Forces operating on ammonoids during swimming, parameters, and terminology. **A.** Forces operating on ammonoids during swimming (modified from Jacobs and Chamberlain 1996). The thrust force produced by the jet which is expelled by the hyponome acts on the centre of gravity. This causes an oblique downward momentum which is opposed by the restorative moment (resulting from buoyancy and gravity) and the drag. At relatively high velocities, this might result in a fairly stable horizontal movement in some derived ammonoids. **B.** Angles of the body chamber length and of the orientation of the aperture. **C.** Terminology.

Materials and methods

This entire study is based on the premise that the bacitrids and the early ammonoids were neutrally buoyant. We investigated the phylogenetic change in the orientation of the conch from bacitrids to early ammonoids. For this purpose, we sculptured simple 3D models out of plastics of the conchs of a bacitrid and a variety of curved and coiled early ammonoids to experimentally identify the centres of gravity and buoyancy of the entire conch and the separate body chamber (Figs. 1, 2). These models are based on actual specimens, measurements of which were taken both from material at Tübingen and from the literature. Since some of the taxa (*Cyrtobacitrites* and *Kokenia*) are only incompletely known, they were reconstructed. The models of *Erbenoceras* and *Mimagoniatis* were produced at a smaller scale. The ornament and the siphuncle were not sculptured in these models.

According to Raup and Chamberlain (1967: 572), “the center of buoyancy is equivalent to the center of gravity of the volume displaced by the whole shell and the center of mass may be estimated as the centre of gravity of the body chamber”. Consequently, both the complete model and the isolated body chamber of the model were mounted on a thin foil. Then they were balanced on a needle, to identify the centres of masses of the isolated body chamber of the model and of the complete model.

The result of our experiment for *Agoniatites* (the most derived genus among the studied taxa) confirmed the results of

the theoretical approach of Raup (1967). Raup’s equations (Raup and Chamberlain 1967; Raup 1966, 1967; Raup and Michelson 1966), however, cannot be applied to the more loosely coiled Early Devonian forms because these equations presumed isometric growth whereas many of these primitive ammonoids grew allometrically (Kant 1973; Kant and Kullmann 1980; Klug 2001).

Like all numerical models for the reconstruction of the orientation of ammonoid conchs, our physical models are simplified, neglecting all subtle details of the distribution of mass in the septa and in parts of the ornament. In contrast to the mathematical models, all aspects of allometric changes are included. It was our intention to test our hypothesis that a significant change in life position happened in the course of the phylogeny of the earliest ammonoids. This was confirmed by the results on the one hand. On the other hand, the numerical details certainly lack precision and have to be understood as approximations.

Results

Within the phylogenetic lineage from the orthoconic *Lobobacitrites* (straight conch) to *Agoniatites* (planispiral with embracing whorls), several morphological changes took place. Regarding morphologies in this morphocline, an increase in whorl expansion rate and a decrease of umbilical width can be observed (Fig. 2). We hypothesise that the ap-

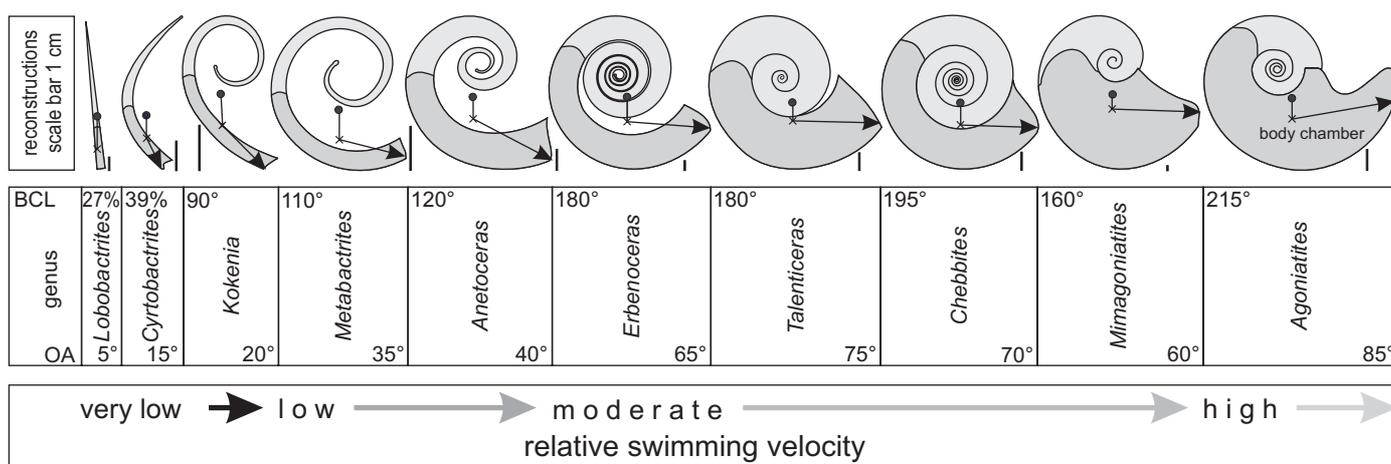


Fig. 2. Phylogenetic change in orientation of the conchs and swimming velocity of Bactritida and primitive Ammonoidea. Outlines of the conchs of one bactritid and nine ammonoids from the Early and Middle Devonian with body chamber lengths (BCL), orientation of the aperture (OA), and relative swimming speed. Centre of gravity is indicated by a cross and the centre of buoyancy by a circle (for further explanations see Fig. 1).

erture began to move first from a slightly oblique downward (*Lobobactrites*) to a downward more strongly oblique position (*Cyrtobactrites*, *Kokenia*), then to an upward oblique position (*Metabactrites*, *Anetoceras*, *Talenticeras*, *Chebbites*, *Mimagoniatites*), and finally to a more or less upward horizontal position in several Middle Devonian ammonoid lineages including the Agoniatitina (Figs. 2, 3). The arrangement of the centres of gravity and buoyancy of these cephalopods, which were identified experimentally, supports the above hypothesis (Figs. 2, 3). Considering *Lobobactrites*, the ventral siphuncle and the oblique aperture are indications for the slightly oblique orientation of the living animal.

Based on these experiments, the ventral side of the aperture (and thus the hyponome) was probably already more or less aligned in one horizontal plain with the centre of gravity in *Erbenoceras* (Fig. 2). This provided stability during horizontal motion at moderate velocities. Accordingly, the genera *Talenticeras*, *Chebbites*, and *Mimagoniatites* had similar orientations of the aperture and positions of the centres of gravity. In some more derived ammonoids with moderate to high whorl expansion rates and embracing whorls such as *Agoniatites*, the position of the hyponome was higher than the centre of gravity. For moderately rapid movements, they had to tilt their aperture slightly downwards to avoid a rocking movement, as in *Nautilus*.

With regard to developmental transformations among the early ammonoids, two major trends can be documented (Fig. 4). In general, the curvature of the shell cone increased throughout phylogeny as well as ontogeny of many primal ammonoids. In the embryonic to preadult conch, this tendency is recorded in all forms included in this study except for *Lobobactrites* and the most derived genus, *Agoniatites*. In some of these ammonoids, however, this is reversed in late ontogeny towards a decrease in conch curvature which

caused the formation of loosely coiled adult whorls. This means that intermediate growth stages of some forms like *Erbenoceras* and *Talenticeras* display the most derived morphology in their conchs.

Similar reversals in conch growth and geometry throughout ontogeny of ammonoids also occur among geologically younger ammonoids; many involute (whorls strongly overlapping) ammonoids become more evolute (low whorl overlap) or even gyroconic (whorls not in contact) in late ontogeny (e.g., Triassic *Ceratites*, Jurassic *Morphoceras*, Cretaceous *Scaphites*) or advolute forms become gyroconic (e.g., Triassic *Choristoceras*, Cretaceous *Pictetia* and, in a broader sense, *Ancyloceras*), some evolute forms turn more involute with maturity (e.g., Devonian *Triainoceras*, Jurassic *Amaltheus*, and, in a broader sense, Cretaceous *Axonoceras*).

Discussion

The following discussion focuses predominantly on the relation between orientation of the cephalopod shell and locomotion. Influences of ornamentation and geometric aspects irrelevant for the orientation were not evaluated (for details on these aspects see Jacobs and Chamberlain 1996).

According to measurements from our plastic models, the aperture moved from a downward to an upward orientation during phylogeny of early ammonoids. Thus, we hypothesise that a high orientation of the aperture, and even more so that higher than the centre of mass, was advantageous for more rapid horizontal movements.

Jacobs and Chamberlain (1996) portrayed the physical constraints and advantages of an orientation where the hyponome and the centre of mass are more or less aligned. Nevertheless, it is difficult to explain the functional advantages of a

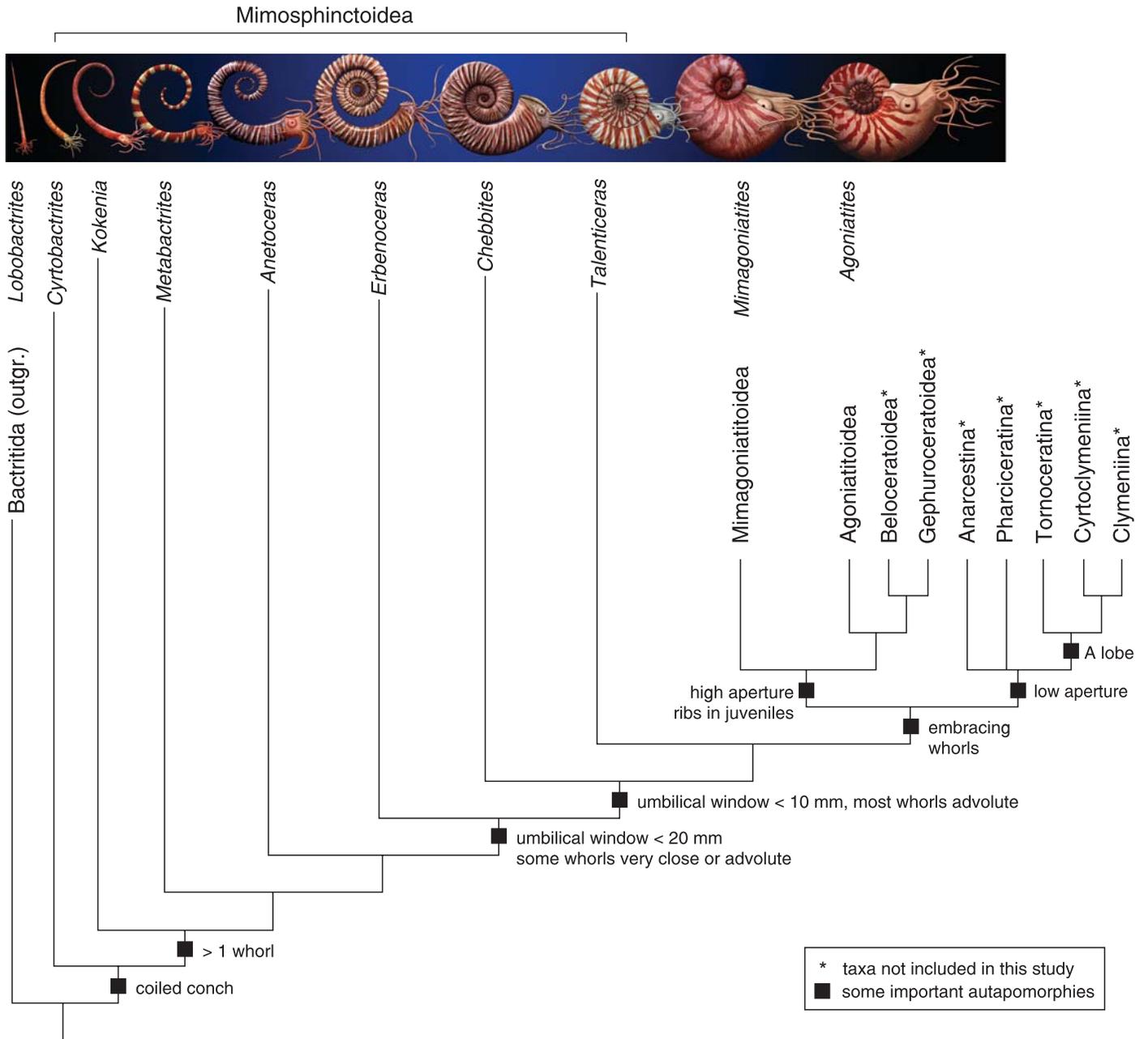


Fig. 3. Reconstructions and a simplified cladogram of one bactritid and nine primitive ammonoids from Early and Middle Devonian (from left to right: *Lobobactrites*, *Cyrtobactrites*, *Kokenia*, *Metabactrites*, *Anetoceras*, *Erbenoceras*, *Chebbites*, *Talenticeras*, *Mimagoniatites*, *Agoniatites*). Note the change in the orientation of the aperture and the increase of soft body volume in relation to the conch diameter. The morphology of the soft body is largely speculative. The number and proportion of arms, however, is here supposed to have been similar to coleoids, because of similarities in embryonic shell, radula and beak morphology between ammonoids and coleoids (Landman et al. 1997; Tanabe and Fukuda 1999). Additionally, the presence of a hood as in Recent *Nautilus* is presumed based on the absence of jaw apparatuses in early ammonoids which were suitable as a lid for the aperture. In the cladogram (modified after Korn 2001, see this article also for the character matrix) with the most important evolutionary steps among Devonian ammonoids, those taxa not discussed in detail are marked with an asterisk.

posture with the aperture above the horizontal plane that contains the centre of gravity. In the latter case, at higher velocities, drag played an increasingly important role. This might have been one functional advantage of the high position of the hyponome in *Agoniatites* because when the ammonoid animal exceeded a certain velocity, drag became higher above the centre of gravity and lower below it. This counter-

acted the restorative moment produced by the interaction of buoyancy and gravity (Fig. 1; see Jacobs and Chamberlain 1996 for further references). When the hyponome was horizontally aligned with the centre of gravity, it lost stability at high velocity because the restorative moment became smaller due to the higher drag above the centre of gravity. In *Agoniatites*, however, the level of the hyponome is above the

BCL genus OA ontogeny		morphologic states →	cyrtocoenic state	crioconic state	advolute state	evolute state
215°						
<i>Agoniatites</i>	85° D					
160°				•		
<i>Mimagoniatites</i>	60° BD					
195°				•		
<i>Chebbites</i>	70° BCDC					
180°				•		
<i>Talenticeras</i>	75° BCB					
180°				•		
<i>Erbenoceras</i>	65° BCB					
120°				•		
<i>Anetoceras</i>	40° BA					
110°				•		
<i>Metabactrites</i>	35° BA					
90°				•		
<i>Kokenia</i>	20° BA					

Fig. 4. Transformations in conch morphology of eight primitive ammonoids from the Early and Middle Devonian (from bottom to top: *Kokenia*, *Metabactrites*, *Anetoceras*, *Erbenoceras*, *Chebbites*, *Talenticeras*, *Mimagoniatites*, *Agoniatites*). Subdivision of the coiling modes is slightly arbitrary, especially the differentiation between the crioconic and the cyrtocoenic state. In that case, it was the intention to clarify the changes in coiling and not to quantify the curvature. Consequently, this imprecision appeared justifiable. In the left column, the body chamber length (BCL) is given at the top right, the angle of the orientation of the aperture (OA) at the bottom left and a code for the coiling mode (ontogeny) at the bottom right. The second column displays the complete conchs with the colour code for the coiling modes (white—cyrtocoenic, subtle curvature; light grey—crioconic, distinctly curved, but whorls not in contact; medium grey—advolute, whorls close or touching; dark grey—evolute, whorls slightly overlapping). Columns three to six show the isolated conch parts sorted according to the coiling mode.

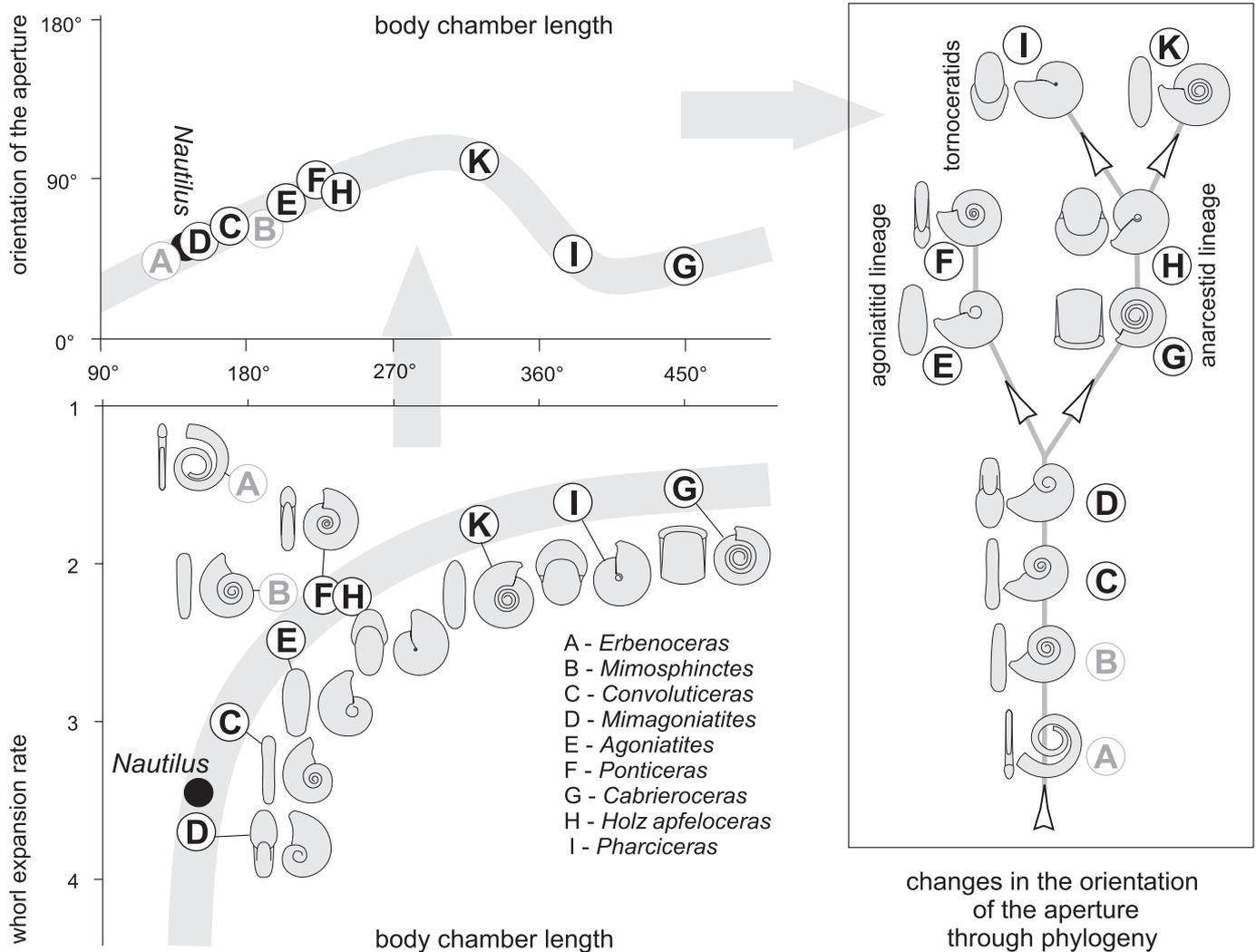


Fig. 5. Changes in the orientation of the aperture of the adult conchs of ten representative Early and Middle Devonian ammonoids and Recent *Nautilus* through phylogeny (*Erbenoceras*, *Mimosphinctes*, *Convoluticeras*, *Mimagoniatites*, *Agoniatites*, *Ponticeras*, *Cabrierocheras*, *Holzapfeloceras*, *Pharciceras*). The two graphs on the left are based on diagrams figured by Saunders and Shapiro (1985) and Okamoto (1996). Comments on the modifications of these graphs are given in Klug (2001) and Korn and Klug (2003). Shell thickness is impossible to determine in most Early and Middle Devonian ammonoids and thus the lines of correlation between WER, BCL, and OA are printed as broad lines in the graphs. Note the shift of the orientation of the aperture from oblique to more or less horizontal in the agoniatitid, anarcestid, and tornoceratid lineages. In the agoniatitid lineage (E, F), the horizontal position was achieved by an increase in whorl expansion rate (relatively short body chambers) compared to A and B. In the anarcestid lineage (G, I, K), the body chamber lengths first increased in the progress of evolution and subsequently decreased again, leading to moderate body chamber lengths (K, H) and consequently more or less horizontal apertures. The positions of *Erbenoceras* (A) and *Mimosphinctes* (B) are shown in grey because in their cases, the orientation of the aperture does not correlate with the body chamber length and thus whorl expansion rate, as it is the case for advolute, evolute, and involute species.

centre of gravity and compensates for the lesser restorative moment. Thus, horizontal apertures in ammonoids probably allowed higher swimming velocities.

Additionally, an approximately horizontal orientation of the aperture implies the largest possible horizontal distance from the aperture to the centre of gravity. This causes a decrease in stability during horizontal motions but an increase in manoeuvrability. When the hyponome was directed to either side, the effect on the motion direction was greater than in other taxa with apertures oriented at lower angles.

Most Nautiloidea (e.g., Devonian *Orthoceras*, Triassic

Germanonautilus, Recent *Nautilus*) had (and some still have) downward to oblique upward oriented apertures and therefore were possibly slower and less agile swimmers than some of the regularly coiled ammonoids (for a discussion of the locomotion of Recent *Nautilus* see Packard et al. 1980; Chamberlain 1987; Ward 1987).

The more or less horizontally upward oriented aperture evolved independently numerous times among ammonoids (Fig. 5; e.g., the Carboniferous *Anthracoeras*; Saunders and Shapiro 1986). The possible extremes of orientation of neutrally buoyant planispiral cephalopod conchs, i.e., 20° or over

90°, certainly both had advantages. A low angle implied that the arms could more easily reach down- and backwards and also, the hyponome could be directed backwards with less effort and thus, forward movements were a smaller problem. High angles and thus an upward orientation of the aperture means a higher manoeuvrability, possibly higher maximal swimming velocities but straight forward movements were difficult. Synchronous with changes of environmental parameters, the one or the other capability was favoured by natural selection, causing shifts in orientation.

Evaluation of changes in locomotion ability during the early ontogenetic stages of primitive ammonoids is difficult because it is influenced by several additional factors (Klug 2001). For instance, with increasing conch size the maximum sustainable swimming velocity rises (Jacobs 1992; Jacobs and Chamberlain 1996; Seki et al. 2000) and “As size increases, per-unit [energetic] costs decline, and optimal speeds occur at slightly higher velocities” (Jacobs and Chamberlain 1996: 209).

A scaling effect might also have played a role in the early ammonoids (Jacobs and Chamberlain 1996; Seki et al. 2000). Among the presented forms, several morphological trends could be recognised such as an overall increase in the whorl width / diameter ratio, the whorl expansion rate, the imprint zone rate, the conch volume / diameter ratio, the absolute conch volume and the conch diameter as well as a decrease of the umbilical width / diameter ratio and the size of the umbilical window (for actual values see Appendix 1 in Korn and Klug 2003).

Additional indications are sometimes yielded by muscle attachment structures which are, however, not yet known from these earliest ammonoids. Nevertheless, the morphological alterations during ontogeny of primal ammonoids appear to reflect changes in the mode of life because similar changes developed numerous times independently. Early growth stages, although comparatively cost-effective swimmers, certainly did not actively travel far. Long distances could only be covered by means of currents. Presuming a semelparous mode of reproduction for ammonoids (Stephen and Stanton 2002), the juveniles experienced more or less random selection, resulting in a low number of surviving individuals. Older premature specimens speculatively had a stronger influence on their fate; at these growth stages, conch geometry probably played a more important role and they could actively swim longer stretches and thus reach more or less distant aims with their motions. Finally, among mature specimens of many Devonian ammonoids, reproductive success remained as the key purpose and therefore, manoeuvrability and swimming velocity in combination with factors like the safety of the eggs and their spatial requirements within the body chamber became crucial in the search for suitable mating partners. Active motions were probably essential and it appears likely that this requirement also left its traces in the altered conch geometry of adult ammonoids.

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