

## Functional morphology of Cretaceous helically-coiled ammonite shells

Peter Ward

**Abstract.**—Torticonic (helically-coiled) ammonoids have been most commonly interpreted as vagile, benthonic forms. Their mode of coiling, however, places the siphuncle in a functionally dorsolateral, rather than ventral position on the shell whorl due to: 1) their probable apex-upward shell orientation during life, and 2) size asymmetry of the lateral sutural saddles due to helical coiling, associated with upward siphuncle displacement. The resultant positioning of the siphuncle produces cameral liquid de-coupling soon after initiation of cameral liquid removal (emptying of liquid from a newly formed chamber within the phragmocone). Since in Recent chambered cephalopods cameral liquid de-coupling increases efficiency of vertical migration, a similar mode of life was indicated for the torticonic ammonites.

*Peter Ward. Geology Department, University of California, Davis, California 95616*

Accepted: June 14, 1979

### Introduction

Although the majority of chambered cephalopod shells were either orthoconic or planispirally coiled, a number of nautiloids and ammonoids departed from this form. One shell form developed in both ammonoids and nautiloids was the torticonic, (isotrophic) or helically coiled shell. This shell is similar in shape to many gastropod shells and can be described mathematically using the coiling parameters of whorl expansion ( $W$ ), distance between the axis and the generating curve ( $D$ ), shape of the generating curve ( $S$ ) and rate of translation ( $T$ ) (Raup 1966).

Torticonic shells were a brief experiment among oncocerid, discocerid, and barrandeocerid nautiloids during the Ordovician, Silurian, and Devonian. Their greatest diversity occurred during the Middle Silurian, when 8 genera accounted for 7% of all nautiloid genera. The last torticonic nautiloids were recorded from the Middle Devonian, with 2 genera.

Torticonic ammonoids evolved three times during the Mesozoic. In the Triassic, forms exemplified by *Cochloceras* and *Paracochloceras* were, like the torticonic nautiloids, evolutionary experiments of little success, judging by their short geologic range and low diversity compared to the planispiral stocks. In the Jurassic,

Dietl (1973) records one torticonic spirocerid which likewise may be considered a brief evolutionary experiment of short geologic range and probably negligible ecologic impact. During the Middle and Late Cretaceous, however, torticonic ammonites derived from lycoceratine ancestors flourished (Fig. 1) and in many horizons are among the most abundant fossils.

Previous investigators have speculated about the mode of life of these torticonic cephalopods, with the favored interpretation using the obvious convergence with gastropod shape as an indication of a vagile benthonic existence (Diner 1912; Beurlen 1928; Berry 1938; Trueman 1941; Wiedmann 1973; Ward 1976). All torticonic cephalopods, however, have maintained the necessary components of the buoyancy system in chambered cephalopods, and new information on buoyancy regulation in both Recent and extinct chambered cephalopods seems to warrant a re-examination of their functional morphology.

### Functional Analysis

The functional analysis of turreted ammonoids depends on assumptions about buoyancy control in extinct chambered cephalopods.

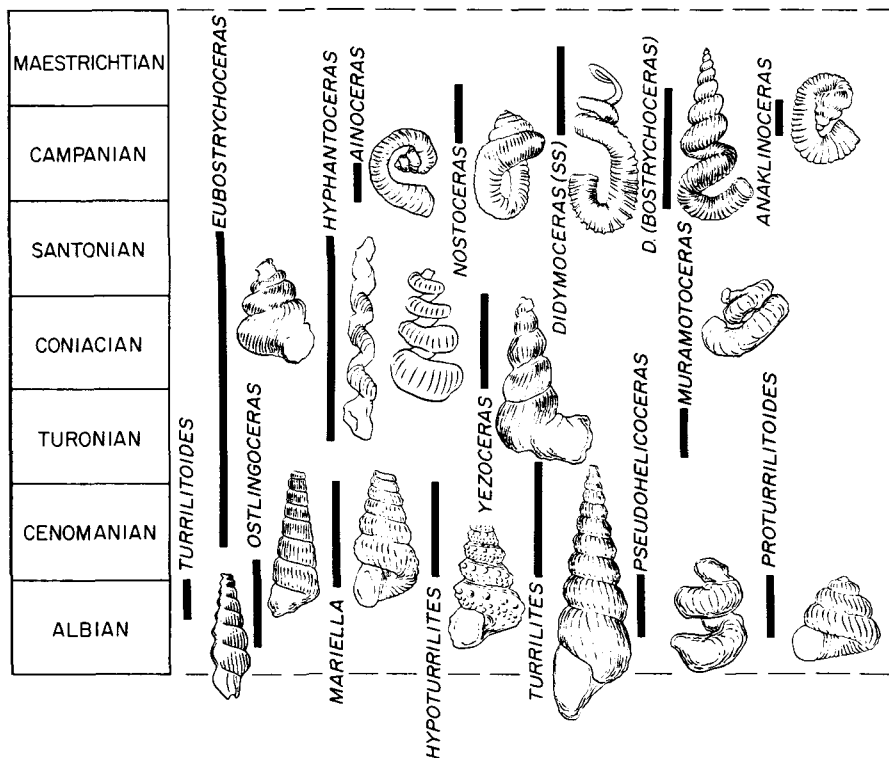


FIGURE 1. Approximate geologic ranges and life orientations of adult Cretaceous torticonic ammonites.

First, it must be assumed that chambers were formed and subsequently emptied by processes similar to those observed in Recent *Nautilus* and *Spirula*. Denton and Gilpin Brown (1966, 1973) have shown that these two genera secrete calcareous septa in front of a saline solution which completely fills the newest chamber. This cameral liquid is then removed through a two-step process involving the siphuncle. First,  $\text{Na}^+$  and  $\text{Cl}^-$  ions are actively transported from the cameral liquid by the siphuncular epithelial cells. The liquid thus becomes progressively hypotonic to liquid within the large central lumen of the siphuncle (blood), and thus passively flows into the siphuncle by simple diffusion. A similar succession of events likely took place in ammonites.

Secondly, it must be assumed that cameral

liquid could, in ammonites, be removed from a chamber when it was "de-coupled," i.e., not in direct contact with the siphuncle (Denton and Gilpin Brown 1966) and that de-coupling was more advantageous for the animal than immersion of the siphuncle in the cameral fluid. In *Nautilus* and *Spirula*, de-coupled cameral liquid migrates into the siphuncle due to wettable properties of an internal lining of septa and interior shell wall known as the pellicle, which is a permeable, wettable, acellular conchiolin membrane (Denton and Gilpin Brown 1966). This material has been only rarely identified in ammonites, since it was organic and therefore probably preserved only in rare instances, (Westermann 1971, fig. 5 & 6; Bayer 1975) but was probably present in all ammonoids.

Finally we might assume that ammonite

whorl shape and body chamber length are a clue to internal anatomy and that ammonites showing similar whorl shapes and body chamber lengths, even if from quite distinct families, may have been somewhat similar anatomically.

Based on these assumptions, it appears that the torticonic morphology 1) provided siphuncle position causing cameral liquid de-coupling in all chambers and 2) provided greater stability than planispiral coiling with similar whorl section and body chamber length (serpenticones such as *Dactylioceras*).

#### Liquid De-coupling in *Nautilus* and Ammonites

De-coupled cameral liquid may provide adaptive advantages to a chambered cephalopod. In *Nautilus* and *Spirula*, depth changes are apparently frequent in the course of foraging (Clarke 1966; Ward and Martin 1978). If the animal ascends, it enters areas of lower ambient pressure and tends to pump liquid out of the chambers at a more rapid rate until the salt gradient on either side of the siphuncle again matches the difference between ambient pressure at the new depth and the pressure within the animal's gas-filled chamber (always less than atmospheric pressure regardless of depth). The opposite is true if the animal descends, for liquid then tends to flow into the chamber. When the cameral liquid is in contact with the siphuncle, vertical migration requires that the osmolarity of the entire volume of cameral liquid be changed; in the case of an animal's ascent, the cameral liquid osmolarity would have to rise. In the de-coupled case, however, the same adjustment can be made by changing only the small amount of liquid within the porous "chalky" tube of the siphuncle and in tiny sacs within the siphuncular epithelium, since the main volume of liquid is no longer in contact with the siphuncle. This latter process obviously entails much less work for the animal.

The centralized position of the siphuncle within the chambers of *Nautilus* allows small amounts of cameral liquid to remain de-coupled no matter what the position of the chamber on the whorl. The ventro-marginal position of the siphuncle in ammonoids, however, resulted in a radically different situation. When a chamber

was in a dorsal position, or at the top of the whorl of an animal in living position, the cameral liquid would always have been de-coupled, except when the chamber was completely filled. However, when this chamber was at the bottom of the whorl, cameral liquid de-coupling would never have occurred, for even the smallest volume of cameral liquid would have rested in contact with the siphuncle which at this chamber position lay on the floor of the chamber (Fig. 2a).

In ammonoids, then, the position of the chamber on the whorl during the cameral liquid removal process may have had functional significance. Trueman (1941) calculated the approximate positions for center of gravity and buoyancy for a number of shell shapes, and arrived at estimates of probable floating orientations or attitudes for the living animal. Even if these estimates are only approximately correct, they indicate that the posterior of the body chamber lay at various positions around the whorl in living attitude, implying that chambers were formed at all whorl positions in ammonites. In Trueman's illustration of *Normannites* and *Promicroceras*, for example, chamber formation occurred at the top or dorsal part of the whorl, while the chambers in *Dactylioceras commune* were formed at a ventral position on the whorl. These two extremes would have had entirely different modes of cameral liquid removal. In the taxa with chamber formation occurring at the top of the whorl, cameral liquid would have become de-coupled as soon as the smallest volume was removed. In the opposite extreme, the siphuncle would have remained immersed until the chamber was completely emptied, or until continual growth and formation of new chambers rotated it upward. These two extremes are illustrated in Fig. 2b and 2c.

In Fig. 2b, *Dactylioceras* is illustrated in probable living attitude as suggested by Trueman. Chamber formation is occurring at a ventral position or the whorl, or at approximately the same relative position as shown by the chamber marked "1," shown in Fig. 2a. In this position, cameral liquid would always be in contact with the siphuncle, regardless of volume. In Fig. 2c, (*Promicroceras*), the opposite extreme is shown. Newly formed chambers are occurring at whorl positions equivalent to

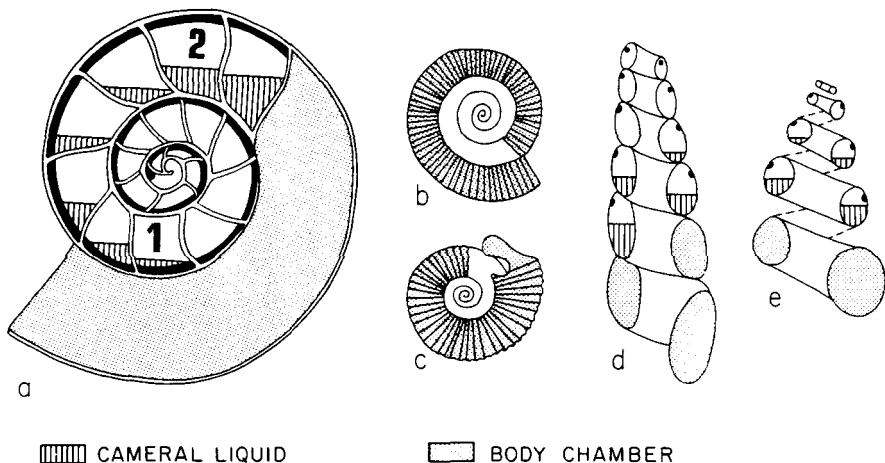


FIGURE 2. Relationship between siphuncle position and de-coupling in planispiral and torticonic ammonoids. a. Reconstructed planispiral ammonoid, demonstrating varying position of siphuncle to cameral liquid on various parts of the whorl. b. *Dactylioceras*, where new chambers were formed in ventral whorl position. c. *Promicroceras*, where new chambers were formed in dorsal whorl position. d, e. Tightly and loosely coiled torticonic ammonoids demonstrating constant position of siphuncle to cameral liquid at all whorl positions.

chamber "2," in Fig. 2a. De-coupling occurs soon after removal of any cameral liquid.

In contrast to the situation in planispiral ammonites, siphuncle position and de-coupling relationships in torticonic ammonites are less dependent of chamber position on the whorl. If it is assumed that torticones maintained a living orientation as illustrated by Trueman (1941), with apex upward, (which seems entirely reasonable since the airfilled chambers rested directly over the body and would cause the animal to float apex upward), then it is evident that the shell had rotated  $90^\circ$  with respect to a planispiral chambered cephalopod. The siphuncle in the torticonic shell was no longer either dorsal or ventral within a given chamber, depending on position of the whorl but was always at an outer marginal, or lateral position, and remained at a constant position within the chamber regardless of whorl position (Fig. 2d, 2e). In this type of shell, then, liquid de-coupling would have occurred when a constant proportion (10–50%?) of cameral liquid was removed, irrespective of whorl position. Due to the wettable properties of the pellicle, the cameral liquid would contin-

ue to be removed in normal fashion. The advantages of this system, however, would occur if changes of depth occurred over short periods of time.

#### Septal Shape and Whorl Position

In an orthoconic cephalopod shell with circular cross-section, the septa tend to be radially symmetrical. When the complication of planispiral coiling is added, however, the inner (dorsal) and outer (ventral) surfaces of the whorl are no longer of the same length or of the same radii of curvature; consequently, the septa become modified, so that lobes and saddles have greater amplitude on the outer (ventral) surface than on the inner. The advent of torticonic coiling adds still another axis of morphogenetic modification, translation, on the coiled cone and its enclosed septa, so that the septal face and sutures are again modified as illustrated by Seilacher (1973). This translation-produced asymmetry of suture and septum in the torticonic ammonoid has consequences for siphuncle position and thus influences buoyancy control. Unlike most

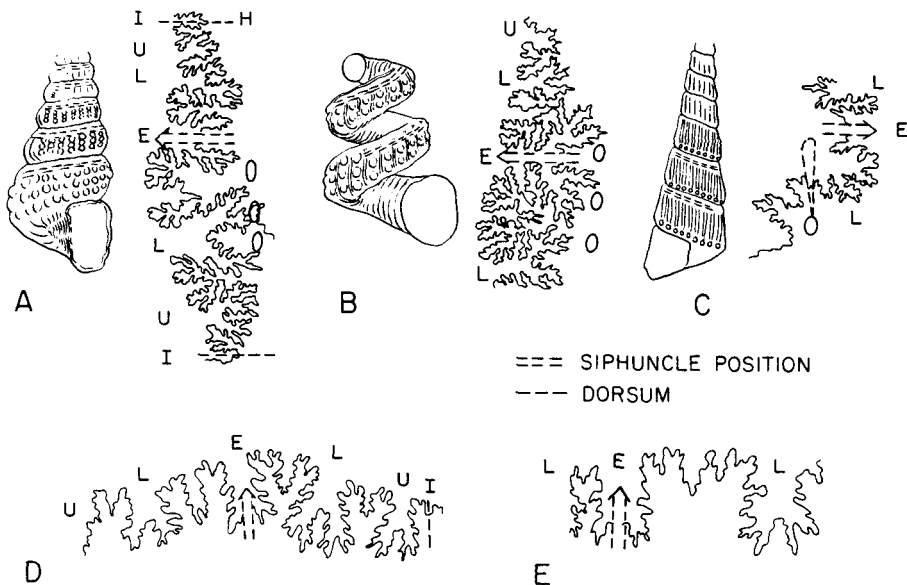


FIGURE 3. Septal suture patterns in torticonic ammonites, showing septal asymmetry and resultant siphuncle displacement. Sutural symbols: E: external lobe; L: lateral lobe; I: internal lobe; U: umbilical lobe. a. *Mariella bergeri* (Brongniart) b. *Pseudohelicoceras robertianum* (d'Orbigny) c. *Ostilingoceras puzosianum* (d'Orbigny) d. *Hyphantoceras orientale* (Yabe) e. *Turritiloides hugardianus* (d'Orbigny).

planispirally coiled forms, where the sutural elements decrease in size toward the umbilicus, but are bilaterally symmetrical on either side of the dorsum and venter, the septa and septal sutures of torticonic ammonites become asymmetrical, with lobes on the outer surface of the whorl being enlarged, while inner elements nearest the axis of coiling become reduced in size. This septal asymmetry is greatest on the lateral lobes and saddles in torticonic ammonites, with one lateral lobe (and saddle) becoming greatly enlarged, and the other reduced (Fig. 3). A consequence of this asymmetry is that the siphuncle carried by the external lobe is carried either upward or downward on the whorl, depending on which lateral lobe is reduced in size. In all but one genus of torticonic ammonite, the siphuncle is found on the upper shoulder of the whorl. This direction of migration favors increased efficiency of liquid decoupling, since the siphuncle in this position would be analogous to the planispiral case of a cham-

ber in topmost whorl position, where decoupling takes place as soon as chamber emptying commences. As discussed above, however, the chamber in the torticonic shell *always maintains the siphuncle in this position, even through 360° of whorl growth.*

The degree of siphuncle displacement is a function of sutural asymmetry, which itself is related to the degree of whorl translation. In high spired torticonic ammonites such as *Turritilites*, sutural deformation and resultant siphuncle displacement is greater than in forms such as *Nostoceras*, with greater apical angle and lower whorl translation.

Two factors suggest that of the two possible siphuncle positions, on the upper or lower whorl shoulder, the upper position was selected for. First, in turritilids and torticonic nostoceratids it was the ventralmost (torticonic shell in living position) of the lateral lobes which increased in size and therefore displaced the external lobe bearing the siphuncle upward on the whorl

shoulder, *regardless of coiling direction*. In both the turrilitids and torticonic nostoceratids it is becoming increasingly apparent that, within the same species, both dextral and sinistral coiling occurred and in approximately equal numbers (Clark 1965, p. 41; Ward 1976). This is very much unlike gastropods, where one coiling direction is either unique or preponderant. Since torticonic ammonites of the same species randomly became either dextral or sinistral, coiling direction probably had little adaptive value. However, if the same lateral lobe element enlarged in both a dextral and sinistrally coiled ammonite, the result would be upward displacement of the siphuncle in one and downward displacement in the other. Instead, we see uniform siphuncle position, regardless of coiling direction. During development, coiling was apparently randomly directed, but linked to that direction were commands to enlarge the correct lateral lobe.

A second piece of information which supports an adaptive function for upward migration of the siphuncle is that the siphuncle *did not necessarily have to be displaced upward*. Until recently, all known torticonic ammonites (but not all torticonic nautiloids) had upwardly displaced siphuncles, and it could be argued that this positioning was not in itself adaptive, but rather was a necessary consequence of shell coiling and septal formation of torticonic ammonoids; in other words, that the asymmetric expansion of the ventralmost of the two external lobes was the only possibility due to some constructional constraint. Recently, however, Matsumoto (1977) has monographed new, exceptionally preserved heteromorphous ammonites from the Upper Cretaceous of Japan. One of these, *Yezoceras* Matsumoto, is a high spired nostoceratid which has expanded the dorsalmost of the lateral lobes and consequently has a siphuncle displaced downward on the whorl. This genus has two species, represented by specimens all showing this unusual siphuncle placement. According to Matsumoto (p. 320) the siphuncle position in these species is constant at all growth stages. It seems likely that these species met with little evolutionary success, for according to Matsumoto they are rare and restricted to the Coniacian of Hokkaido,

Japan. In contrast, almost all other torticonic ammonites show longer geologic ranges and at the genus level world-wide distribution (Matsumoto 1973). Hence, upward displacement of the siphuncle seems to have been advantageous and to have been selected for in almost all lineages of torticonic ammonites. As an exception to this, *Yezoceras* is clearly worth further study.

### Shell Stability

In addition to possible adaptive advantages of lateral siphuncle position and upward siphuncle displacement, the torticonic form gave ammonite shells of low whorl expansion and circular whorl section higher stability than planispirally coiled shells of similar whorl expansion and cross-section. Trueman (1941) showed that shell stability was related to the distance between center of shell buoyancy and center of shell gravity, and that the wider the separation of these centers, the greater the stability. Stability, as shown by Raup (1966), is directly related to shell form, with evolute forms always having higher stability than involute forms; Trueman (1941) showed that most heteromorph shells had higher stability than any planispiral shell.

If the torticonic nostoceratids and turrilitids were recoiled in planispiral fashion, but with the same whorl expansion, cross-section, and body chamber lengths, they would probably have looked very much like their ancestors *Lytoceras*, or any of the diverse, evolute serpenticonic Ammonitina such as *Dactylioceras*. With their widely separated centers of gravity and buoyancy however, the torticonic cephalopods would have had much greater stability and much like the Recent *Nautilus* would probably have found it quite difficult to rotate the shell 360° through action of the hyponome.

Stability and its relative importance to an ammonite has been discussed by Raup (1967), who argued persuasively that it was probably of less importance as a selector for shell form than some other consideration, *in planispiral shells*. It is quite clear from the fossil record, however, that the development of Cretaceous lytoceratin heteromorphs of high stability and low streamlining clearly distinguishes the total spectrum of

Cretaceous ammonite shell shapes from those of the Jurassic. It is yet unclear why these non-planispiral shell shapes evolved during the Cretaceous and to what extent they differed in mode of life from planispiral forms. Shell stability may have been of importance, perhaps in feeding strategy, or in other ways still unclear.

Torticonic shell shape thus confers two properties to a chambered cephalopod. Liquid decoupling is accomplished easily and consistently throughout ontogeny, and perhaps in correlation with this, the shell has a very stable attitude in life position. The first property may have been adaptively advantageous. The second may also have been advantageous, or it may have simply been a consequence of these shell shapes and of no particular advantage or disadvantage to the organism. Presumably the disadvantage of torticonic shape is the lack of streamlining which is so well developed in many planispiral forms.

#### Speculations on Mode of Life of Torticonic Ammonites

In conclusion, a number of speculations concerning the mode of life of torticonic ammonites seem to follow from the preceding discussion. First it seems clear that the separation of the centers of buoyancy and gravity produced by the high (compared to planispiral forms) whorl translation of the torticonic shell produced very high stability and that the animal would thus be unsuited to a mode of life requiring a high degree of maneuverability. Secondly, the nature of the shell shape seems to preclude rapid, hyponeur-powered swimming. Two alternative hypotheses seem to follow. First, it is possible that the torticonic heteromorphs left their chambers largely flooded during life, and pursued a vagile, benthonic existence, much like an octopus carrying a torticonic shell over its viscera. The second possibility is that the animal spent much of its time in an environment that did not require rapid swimming ability, such as a benthic saltator, or midwater nektonic form.

The first hypothesis seems possible for the mid-Cretaceous turrilitids, for all of these genera had an aperture oriented in such a fashion that the animal could have faced the bottom

(radial aperture of Linsley 1977). The later Cretaceous nostoceratid torticones, however, would have had a much more difficult time in this mode of life, for the majority of these genera developed a "U"-shaped body chamber after an initial torticonic stage (Fig. 1). This adult morphology, coupled with the high-stability torticonic phragmocone, must have forced the body of the animal to be positioned upward or facing the surface of the sea. This seems to be a most awkward orientation for a saltating or crawling benthonic organism. As has been previously pointed out by this writer (Ward 1976; Ward and Westermann 1977), this particular "U"-shaped body chamber was not restricted to torticonic heteromorphs but was present in a wide variety of forms such as scaphitids, hamitids, and even aberrant forms such as *Nipponites*. The form seems most readily applicable to mesopelagic planktonic habitats, today occupied by the poorly streamlined but tremendously abundant and successful cranchid and spirulid squids.

Torticonic ammonites may have lived in a variety of habitats, some possibly benthonic, some in the mid-water regions as suggested by Packard (1972). In all except *Yezoceras*, however, there are adaptations for cameral liquid decoupling, indicative of a mode of life involving extensive vertical migration.

#### Acknowledgments

Richard Cowen provided the major stimulation for this paper. I would also like to thank G. Westermann and 3 anonymous reviewers for helpful criticisms.

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