12 | Speculations on Buoyancy Control and Ecology in some Heteromorph Ammonites

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Abstract: Possible buoyancy control in some heteromorph ammonite groups is investigated in terms of the position of the siphuncle. Groups investigated include some torticones, ancylocones and orthocones. In Turrilitinae the adapical position of the siphuncle causes rapid decoupling and may possibly permit the shell to retain significant amounts of cameral liquid, which may be favourable to a vagile benthonic mode of life. Ancylocones have a very stable floating position in the adult stage, but lateral movement appears restricted. Some forms with very large body chambers may be adapted to a mode of life close to the substrate. In orthocones a near-vertical floating position seems most likely. Apertural hoods may represent modifications for occasional resting on the substrate. To float horizontally underwater, very delicate buoyancy control is necessary, following a pattern quite unlike that of *Nautilus*, but comparable with *Sepia* and *Spirula*.

INTRODUCTION

If our analogies with extant *Nautilus* are valid, the ammonoid shell serves two basic functions – protection and buoyancy. Apart from structural modifications such as spines and ribs, the first function is self explanatory and needs no discussion. Buoyancy, however, largely determines the ecology of the ammonite. This includes, amongst others, the amount of energy necessary for carrying the shell, the

ability to undertake vertical migrations in search of food, escape reaction, the orientation of the shell plus animal and feeding posture.

Important data on the buoyancy control of *Nautilus* have become available over the last decade (Denton and Gilpin-Brown, 1973, provide a summary; see also Ward and Martin, 1978). Although details of the mechanism are not yet fully understood, we know that liquid is removed from newly formed chambers through the siphuncle. A chalky tube surrounding the siphuncle acts as a wick. Actual removal of the liquid is effected by the epithelial tissue of the siphuncular cord. As soon as the level of the liquid drops below the level of the siphuncle, i.e. if decoupling takes place, the thin hydrophylic membrane covering the walls of the chambers and septal surfaces assists in directing the remaining fluid towards the siphuncle. Slight rocking motions during swimming may further assist in bringing the remaining liquid into contact with the siphuncle for removal.

It is assumed that the same basic mechanism operated in ammonites, but uncertainty exists if a hydrophylic membrane lining the insides of the chambers and a chalky tube covering the siphuncle are present (see Kennedy and Cobban, 1976, pp. 30–31). Furthermore, Westermann (1975) suggests that ammonites may have been capable of transporting liquid in the chambers at will – a feature not observed in extant *Nautilus* (Ward and Martin, 1978), but seen in *Sepia*. Mutvei and Reyment (1973) have also shown that the buoyancy of the empty ammonite shell is significantly higher than that of extant *Nautilus*, and that in order to attain neutral buoyancy, a greater amount of liquid must have been retained in the shell. This statement, however, has been contested by Westermann who believes that "the actual liquid contained in ammonoid phragmocones rarely exceeded 10–15% of the total volume (i.e. equivalent to the one to three last camerae)" (Westermann, 1975, p. 230).

It seems logical to assume that a ventrally situated siphuncle would offer optimum buoyancy control (Westermann, 1971; Hepstonstal, 1973; Mutvei and Reyment, 1973; Kennedy and Cobban, 1976). A ventrally situated siphuncle would always be in contact with cameral liquid in ventrally situated chambers and would thus be able to operate through gravity alone. Cowen (see Kennedy and Cobban, 1976, p. 26; Westermann, 1975, p. 231), however, suggests that decoupling, and not immersion of the siphuncle

in cameral liquid, is functionally useful, preventing significant passive fluid transport as a result of pressure differentials during vertical movements by means of the hyponome.

HETEROMORPH AMMONITES

Speculation on the mode of life of heteromorph ammonites is diverse, ranging from sessile benthonic in *Nipponites* (Diener, 1912), through burrowing in soft sediments in *Scaphites* (Frech, 1915), to rapidly swimming in *Baculites* (Matsumoto and Obata, 1962, fig. 2). Bergquist and Cobban (1957) provide a good summary. In view of the diversity of coiling in heteromorph ammonites, a common mode of life seems unrealistic.

A mechanical, qualitative approach, taking the position of the siphuncle in the phragmocone, coiling of the shell and the relative position of the body chamber to the phragmocone into consideration, may give some indication as to the potential buoyancy control and floating position of some heteromorph ammonite groups.

For the present study, some examples of three morphotypes are examined: torticones (loose or tight spiral coiling), ancylocones (with U-shaped body chamber) and orthocones (straight or recurved shells).

1. Torticones

Loosely and tightly coiled forms occur in this group. Best documented here are the Turrilitinae, which, according to the latest count (Klinger and Kennedy, 1978) contains about 160–170 species. Due to similarities in external shell form, Turrilitinae have generally been compared with gastropods (Diener, 1912; Frech, 1915; Berry, 1928; Morton, 1958, etc.). In both, the shell serves to protect the animal, but in gastropods the shell serves mainly to accommodate the gastric organs, whereas in ammonites it is chambered and used for buoyancy. The spire is generally reconstructed almost vertically, implying that the shell is buoyant enough not to drag along the substrate (see Berry, 1928, pl. 2, fig. 20; Trueman, 1941, fig. 17). A horizontal orientation of the shell appears unlikely, unless the apex of the shell is weighted down to counteract the buoyancy of the early chambers, or if early chambers are completely filled with liquid.
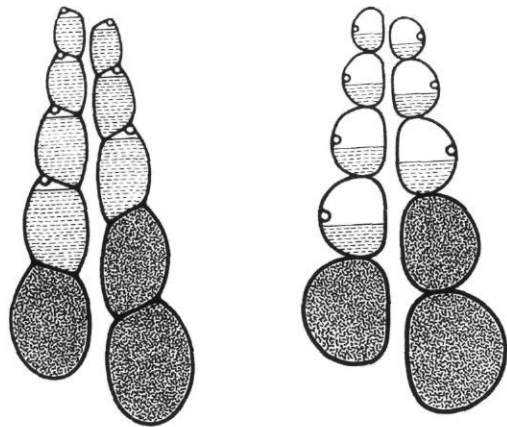
Fig. 1. Schematic cross-section of Cenomanian and Middle Albian Turrilitinae to show position of siphuncle and relative levels of cameral liquid after decoupling.

In the earliest Turrilitinae, which occur in the Middle Albian, the siphuncle is situated at mid-flank, or near the upper part of the flanks (i.e. the anatomical ventral position). Given this position, and a near vertical orientation, the level of the cameral liquid sooner or later drops to below the level of the siphuncle, and a substantial part of the liquid remains decoupled. Even though slight rocking motion may assist in removing some more of the liquid, it seems physically impossible to remove all the cameral liquid through gravity alone. Unlike the situation in normally coiled ammonites, where the position of the siphuncle varies according to growth and rotates about a horizontal axis, the siphuncle in torticones always remains near horizontal and rotates about a vertical axis during growth. In later forms in the Upper Albian and Cenomanian, the siphuncle in turrilitids has migrated to the upper adapical edge of the whorls and a greater amount of liquid should remain decoupled (Fig. 1).

This progressive adapical migration of the siphuncle could have been functional. By decoupling greater amounts of liquid in the camerae, the shell may have been weighted down sufficiently to attain neutral or perhaps even slight negative buoyancy, without any significant (osmotic) pumping involved. In addition, the adapical

position of the siphuncle may be interpreted as a braking mechanism in the sense of Cowen. Decoupling of the cameral fluid would prevent passive liquid exchange resulting from pressure differentials due to rapid vertical movement, as is postulated for some forms to be discussed below.

The turrilitid coiling may have possibly had further advantages which can be related to a mode of life close to the substrate. The animal could hover above or on the substrate in search of food by means of the buoyant shell. The buoyant shell could also prevent the animal from sinking into a soft substrate, as would be the case in gastropods. Due to the radial symmetry, the animal can turn rapidly about its vertical axis without expending much energy, as contrasted with the case in a planispiral shell which would encounter considerable drag.

The turrilitid shell, especially in forms with low apical angles such as *Turrilites costatus* Lamarck (Fig. 2), *T. scheuchzerianus* (Bosc), *Ostlingoceras* spp. and others, conforms to hydrodynamic requirements for rapid movement, and the animals were potentially capable of quick vertical escape manoeuvres, which may be advantageous against obligate benthonic predators. In this sense, the turrilitid shell may be compared with the orthoconic forms. Furthermore, the ornament in forms with low apical angle is generally not strongly developed, which fits in with the hypothesis of hydrodynamic streamlining. The presence of a well developed hyponomic sinus in *Turrilites costatus* and *T. scheuchzerianus* appears to indicate that these species were in possession of a hyponome potentially capable of rapid spurts of movement. The world-wide distribution of *T. costatus* (see Kennedy and Cobban 1976, p. 53, fig. 12) suggests that this was a very successful species.

From a hydrodynamic point of view, squat forms with wide apical angles appear ill-suited to rapid movement and are probably mainly restricted to vertical migrations. Several of these squat forms, e.g. *Hypoturrilites gravesianus* (d'Orbigny) (Fig. 3), *H. tuberculatus* (Bosc) and others are characterized by heavy ornament consisting of long, hollow spines. These spines must have been filled with liquid and were sealed off from the main body of liquid in the chambers by means of a basal septum. These liquid-filled spines may secondarily aid in further weighting the shell down as an adaptation to a vagile benthonic mode of life. Here the spines can also serve to deter
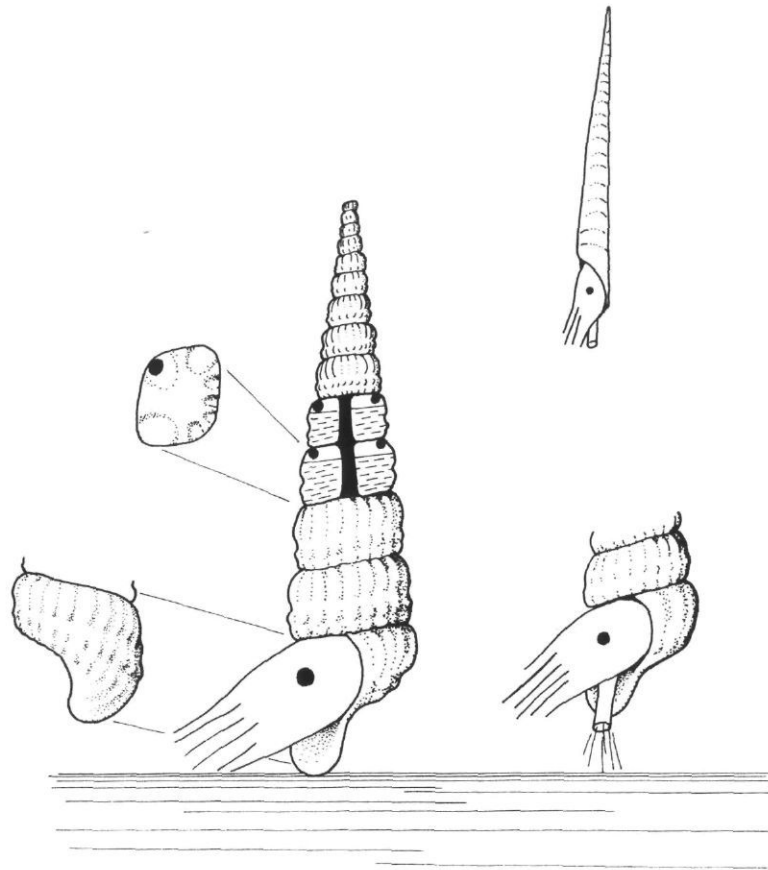
Fig. 2. *Turrilites costatus* Lamarck, an example of torticonic shell with low apical angle, potentially capable of rapid escape movement, showing details of aperture, septal face, position of siphuncle and analogy with baculitid shell.
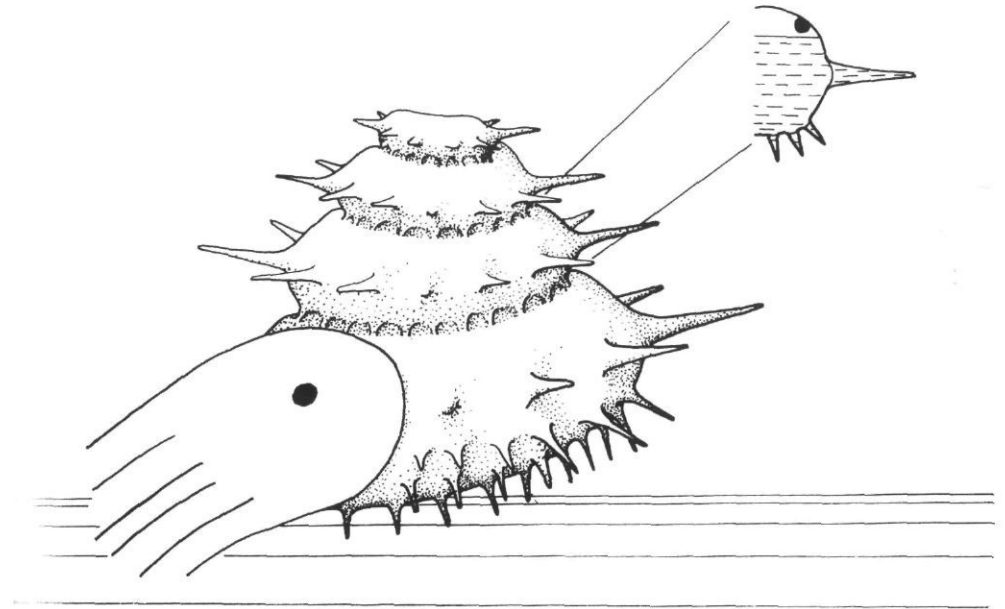

Fig. 3. *Hypoturrilites gravesianus* (d'Orbigny), an example of torticonic shell with low apical angle, probably adapted to vagile benthonic mode of life, showing details of liquid-filled hollow spines with basal septae.

encrustation by epizoans, although their primary function was probably protective.

Turrilitic coiling is bound to have some effect on the orientation and organization of the cephalopod inhabiting the shell. In normally coiled ammonites the position of certain organs in relation to fixed parts of the shell is assumed to be constant. The siphuncle is always situated ventrally (except in clymeniids), as are presumably the ctenidia and mantle cavity, and the head and eyes dorsally. If the animal were to retain a fixed orientation in relation to the siphuncle in Cenomanian Turrilitinae, the back of the head would face downwards and the mantle cavity, mouth and ctenidia upwards. This is a rather awkward orientation, and in order to become a successful bottom feeder, the animal would have to undergo a rotation of 180°. The ventral position of the hyponomic sinus in some forms, however, seems to indicate that the relative position of various organs in relation to the siphuncle may not have been as rigid as anticipated.

Body chambers of two to three whorls in length are common in the Turrilitinae, thus the animal was probably long and snake-like. The suture line in Turrilitinae is remarkably asymmetrical, as can be seen on the septal faces (Fig. 2). This raises the question of

whether this asymmetry also manifests itself in the animal by un-equal development of originally bilaterally symmetrical organs (as is the case in some gastropods, though for different reasons).

Juvenile and adult specimens of Turrilitinae are generally found together, thus suggesting that no age segregation took place.

Loose, helicoid coiling occurs in some turrilitids, e.g. *Pseudhelicoceras robertianum* (d'Orbigny), but is mainly found in representatives of the family Nostoceratidae, especially in the genus "*Bostrychoceras*". In these forms the shell is no longer hydrodynamically streamlined, and a larger surface area is exposed to predation and damage. One advantage of this type of coiling is that the animal may develop full symmetry. Another is the greater stability due to the separation of the centres of buoyancy and gravity. The siphuncle in all these forms is at mid flank, as in early turrilitids.

Yezoceras Matsumoto is another torticonic form that deserves mention. Here the whorls may be loosely coiled or touching. The ventral (abapical) position of the siphuncle, however, is unique amongst torticonic forms. Assuming a vertical or semi-vertical orientation for *Yezoceras*, decoupling cannot take place until the chambers are completely emptied of liquid. This would result in an extremely buoyant shell. In the type species, *Y. nodosum* Matsumoto, flared ribs with strong nodes develop on the body chamber, which could possible add extra weight to the very buoyant shell.

2. Ancylocones

A recurved, U-shaped body chamber in the adult stage occurs in a number of heteromorph groups with radically different coiling in the phragmoconic stage (Fig. 4). Virtually all types of coiling occur in the phragmoconic stage, including planispiral ammonitic, crioceratitid, torticonic loose and tight, polyptocheratoid, hamitid, or a combination of these, e.g. in *Colchidites*. An orthoconic stage followed by a recurved body chamber, however, is very rare.

It is obvious that the mode of life in the early phragmoconic stage must have been different from that of the adult stage. This explains why juvenile and adult stages are seldom found together (Casey, 1961; Westermann, 1971). In addition, the orientation of the animal must have changed a number of times, for example in *Nipponites*,
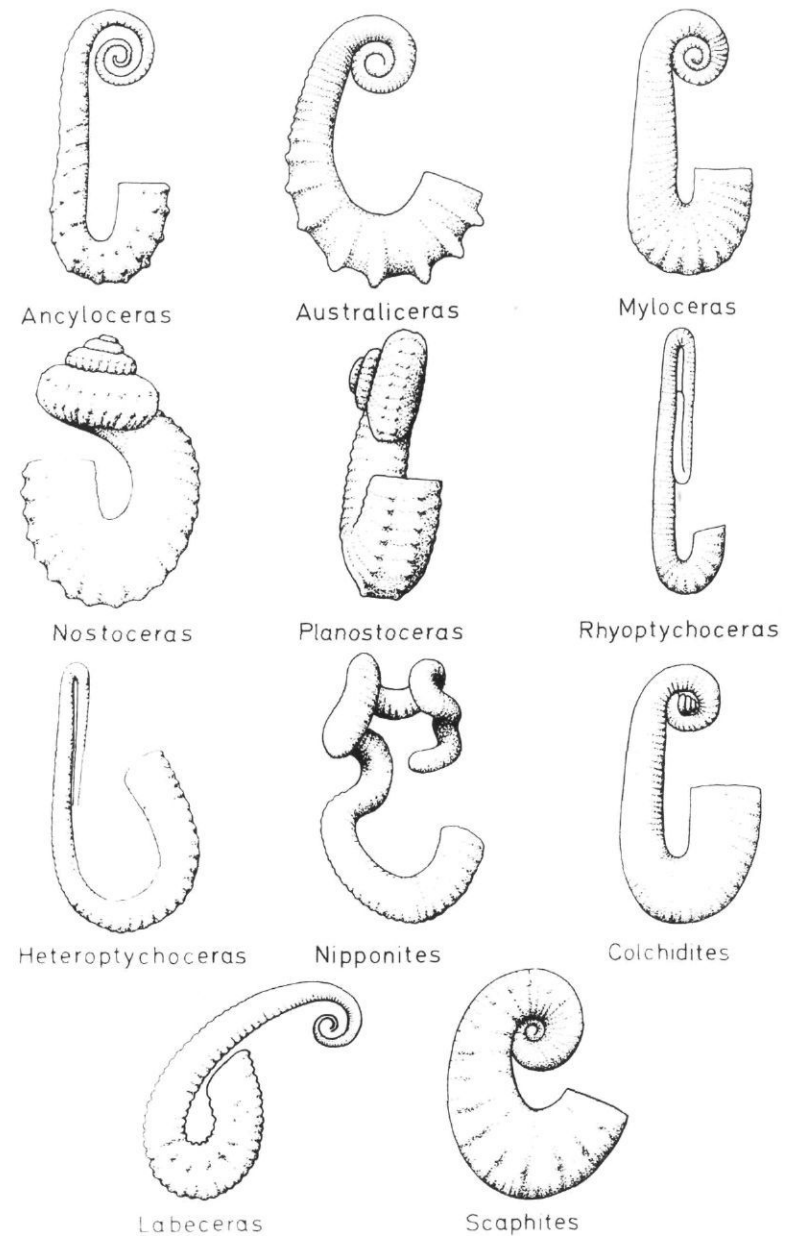

Ancyloceras   Australiceras   Myloceras

Nostoceras   Planostoceras   Rhyoptychoceras

Heteroptychoceras   Nipponites   Colchidites

Labeceras   Scaphites

Fig. 4. Examples of various heteromorph forms with ancyloconic recurved body chambers.

Colchidites and ptychoceratoid forms. Judging by the great number of forms which develop a recurved body chamber, this modification must have held some advantage to the adult organism. By separating the animal from the rest of the shell in a recurved body chamber, the distance between the centre of buoyancy and centre of gravity is increased. This results in a very stable orientation with the animal suspended below the phragmocone in a sort of pendulum effect.

From a hydrodynamic point of view, it is obvious that active swimming is restricted by this type of coiling, and movement is probably mainly vertical, although slight lateral movement is possible by means of the siphon.

Morphologies of the various groups with recurved body chambers differ considerably and are probably a reflection of the mode of life in the adult stage. From a purely functional point of view, a crawling or burrowing mode of life as suggested by Diener (1912) and Frech (1915) seems unlikely. The buoyant phragmocone and recurved body chamber keep the aperture well above the substrate and thus prevent direct contact between the animal and substrate (Fig. 5). A more likely mode of life is probably that of a planktonic floater (Berry, 1928; Donovan, 1964; Morton, 1958; Packard, 1972; Tanabe, 1975, *partim*; Ward and Westermann, 1977). Whether the animal was mainly restricted to a mode of life close to the substrate, or to diurnal migrations through the water column, may be largely dependent on the ratio of phragmocone to body chamber, but here the unknown quantity of liquid occluded in the phragmocone is decisive. Regulation of the buoyancy through expansion or contraction of the animal in the body chamber as suggested by Berry (1928) and Morton (1958) seems unlikely. Quantitative data here are scant and have to be limited to determining whether the shell plus animal was capable of floating, without taking the amount of possible occluded liquid in the phragmocone into consideration. Tanabe (1975) suggested that the older forms of *Otoscaphites puerculus* were benthonic, whereas Ward and Westermann (1977) found *Nipponites occidentalis* to be slightly positively buoyant. Forms in which the body chamber is very large in relation to the phragmocone could possibly be regarded as being largely restricted to the substrate. Morphology could then be interpreted as an adaptation to a soft substrate to keep the respiratory system clear from the sediment, for example *Myloceras* sp. (Fig. 5). Forms with delicate
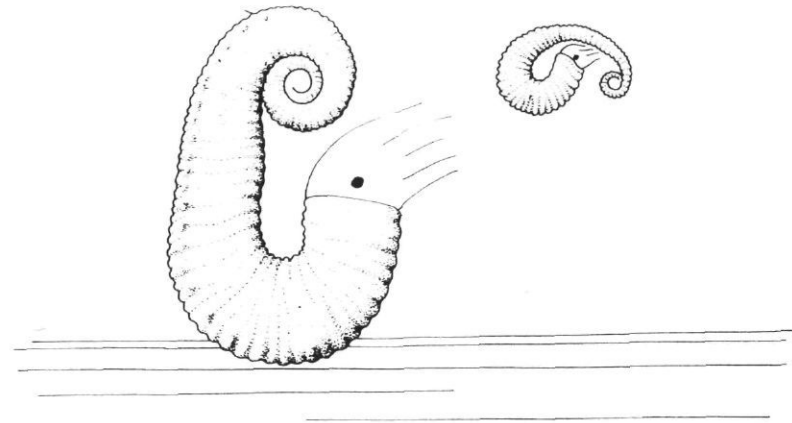

Fig. 5. *Myloceras* sp. and *Labeceras* sp. to illustrate position of aperture away from substrate and close proximity to phragmocone respectively.

ornament and slender whorls were probably adapted to passive floating, e.g. *Anisoceras raynaudi* (Fig. 6).

In some forms the aperture is very close to the base of the phragmocone, e.g. some *Nostoceras* or *Labeceras* (Fig. 5), suggesting that a macrophage feeding strategy in the adult stage seems unlikely.

3. Orthocones

Orthoconic shells have appeared iteratively throughout the history of the cochleate cephalopods. From a purely hydrodynamical point of view, the straight orthoconic shell seems to be the only form potentially capable of rapid movement (Donovan, 1964). (As discussed above, however, narrowly turreted turrilitids are also potentially capable of rapid movement.) The best documented forms here are the Cretaceous family Baculitidae. Size varies considerably from a few centimetres in *Bochianites* to well over a metre in some *Eubaculites*. Barring the very early ammonitic whorls, the shell is straight, or very slightly curved throughout. The whorl section varies from rounded in *Sciponoceras* to distinctly pyriform in *Eubaculites*. The aperture is forwardly directed in most *Eubaculites* and *Baculites*, but ventral hoods are known in *Sciponoceras*.

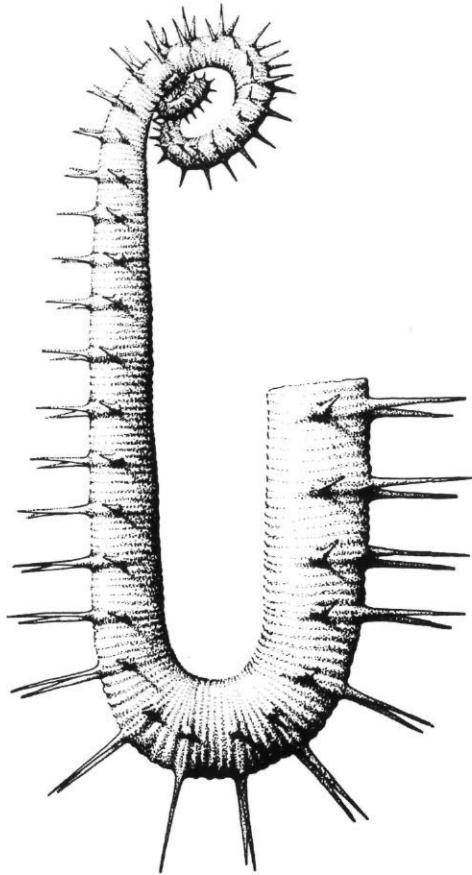As in the case of the torticonic forms, two orientations are possible:

Fig. 6. Reconstruction of *Anisoceras raynaudi* Boule, Lemoine and Thévenin. The delicate ornament and slender whorls possibly point to a passive floating mode of life.

Fig. 7. Optional floating positions of baculitid shell to illustrate position of siphuncle and cameral liquid.

horizontal or vertical (see Matsumoto and Obata, 1962, figs 1–3) (Fig. 7). In both orientations the siphuncle is in continuous contact with cameral liquid.

If the formation of new camerae and subsequent removal of liquid from the older camerae proceeds according to the pattern established in *Nautilus* and suggested for other ammonites, i.e. that the earliest formed chambers are devoid of liquid, and the newest formed chambers still contain liquid, it is difficult to suggest any other
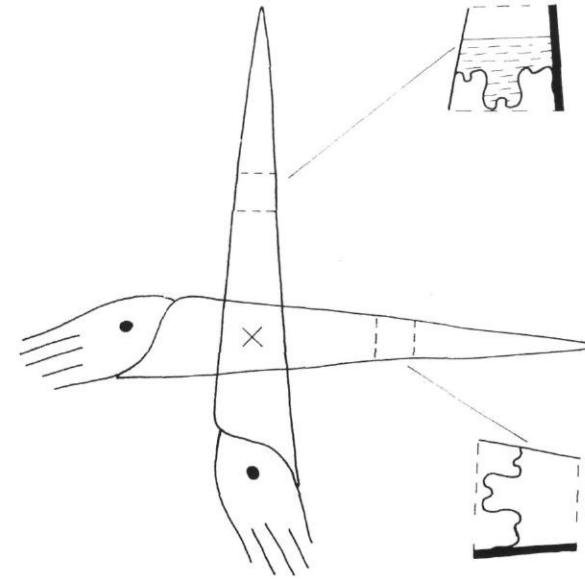
orientation than vertical or near vertical (see also Reyment, 1973). The earliest formed chambers are empty and provide lift, whereas the last formed chambers still contain considerable amounts of liquid and, together with the weight of the animal, produce the downward force. The centres of buoyancy and gravity are separated and the near vertical orientation is very stable. Thus, apart from the very early ammonitic stage which may have been adapted to a different mode of life (Spath, 1921), the greater part of its existence was spent in a near vertical orientation. Bilateral symmetry would be of little use in near vertical orientation, and a rounded whorl section would be optimal in offering least hydrodynamic resistence in rotating about the vertical axis. As in the case of ancylocones, the animal could either be a planktonic drifter, or be adapted to a mode of life close to the substrate, depending on the amount of liquid occluded in the chambers. The presence of an apertural hood in some forms of *Sciponoceras* seems to suggest that the animal could have rested on the substrate occasionally (Crick, 1986) (Fig. 8).
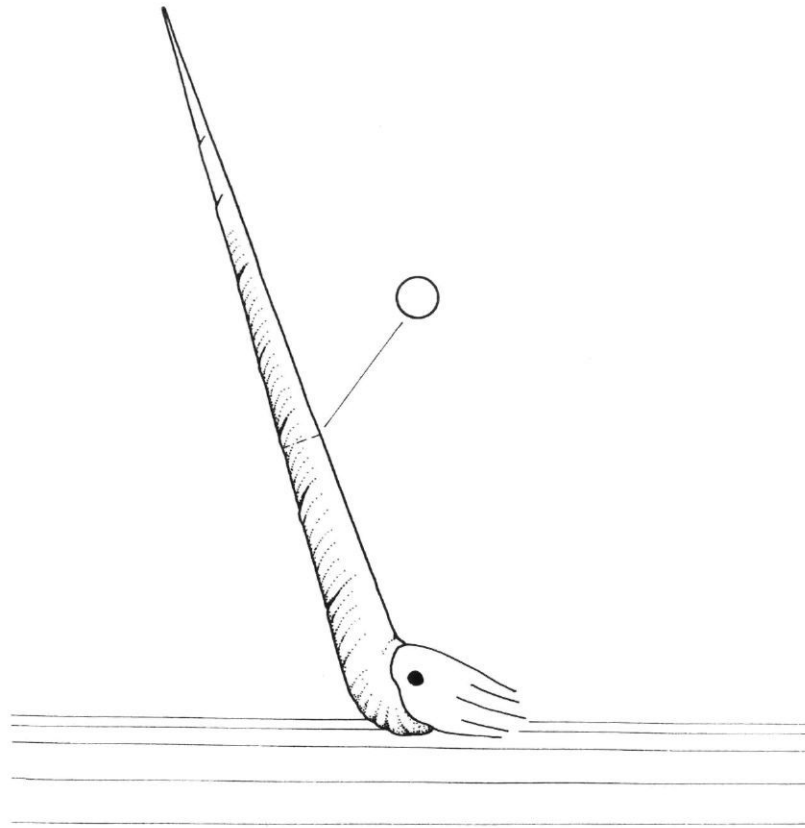
Fig. 8. *Sciponoceras* sp. illustrating specimen resting on substrate. (After Matsumoto and Obata, 1962).

A mode of life with the animal hovering above the substrate feeding on detritus seems possible. A mud-burrowing or boring mode of life has been suggested by Frech (1915) and Spath (1921) but this seems very unlikely.

Flower (1957) and Cowen *et al.* (1973) prefer a horizontal orientation for orthoconic nautiloids and the argument should also be valid for orthoconic ammonites. The protracted aperture and pyriform whorl section of some baculitids, especially the large species of *Eubaculites*, which may reach lengths in excess of one metre, are suggestive of a horizontal swimming position (Fig. 9). The possession
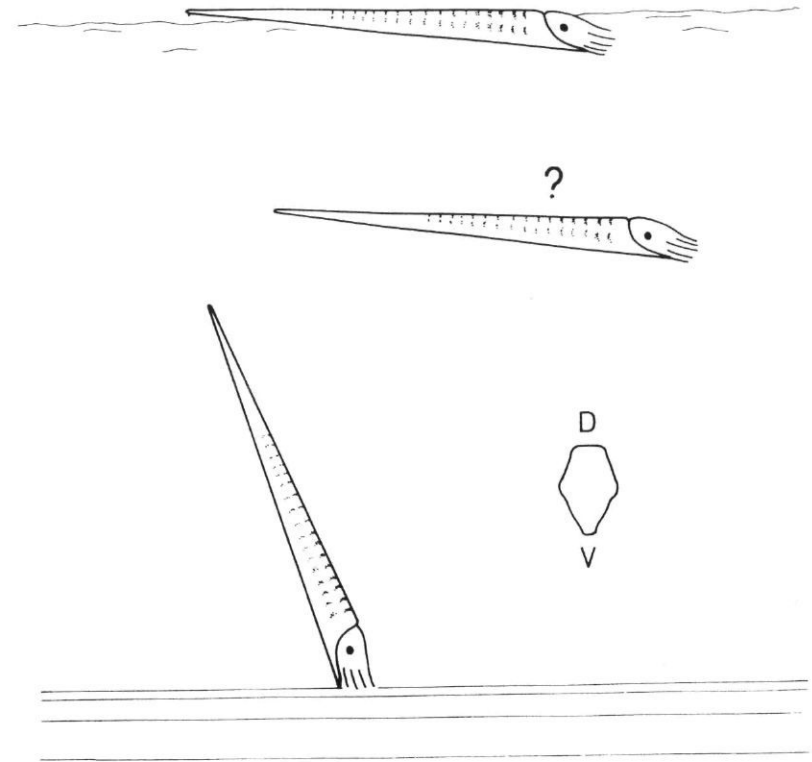
Fig. 9. *Eubaculites ootacodensis* (Kossmat) illustrating optional floating positions. (After Matsumoto and Obata, 1962).

of a ventral keel, combined with the close spacing of the septae in *Eubaculites* could be interpreted as methods to retain the liquid near the venter of the shell and thus aid in stabilizing the shell. Provided that sufficient liquid is removed from the chambers, large forms such as these can almost float horizontally at the water–air interface.

For orthocones to drift or swim horizontally beneath the surface, however, the apical end has to be weighted down sufficiently to counterbalance the weight of the animal in the body chamber and the last formed, liquid-filled chambers (Denton and Gilpin-Brown, 1973). In addition, sufficient buoyancy has to be retained to keep the shell adrift or at neutral buoyancy in a horizontal position.
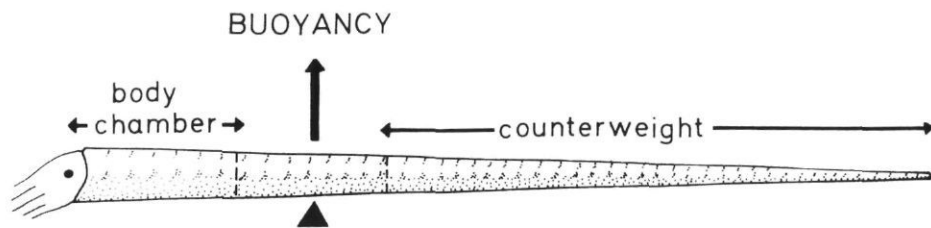
Fig. 10. Diagram to illustrate distribution of weight and buoyancy in baculitid shell to maintain horizontal floating position in water.

In Palaeozoic orthocones this problem was partially solved by the deposition of cameral and/or siphuncular deposits. As yet, however, no such cameral deposits have been reported in any Baculitidae nor, for that matter, in any ammonites nor any of the extant cochleate cephalopods. The only way possible in which to float the shell horizontally would be to flood the first-formed chambers to counterbalance the weight of the body and the liquid in the last chambers, and then to extract sufficient liquid from chambers near the centre of balance to provide sufficient lift (Fig. 10). A similar mechanism has been suggested for cyrtoconic nautiloids by Donovan (1964, p. 264, fig. 2D) and for orthoconic nautiloids by Denton and Gilpin-Brown (1973, p. 262). This, however, would deviate from the "traditional" concept of buoyancy control in ammonoids as based on observations on extant *Nautilus*. Furthermore, recent data on *Nautilus* (Ward and Martin, 1978) show that the animal is incapable of placing cameral liquid into empty chambers in shallow water. To provide a horizontal orientation, the baculitid buoyancy control must have been analogous to that of *Sepia* or *Spirula* (Denton and Gilpin-Brown, 1973, p. 262, fig. 14) and could in turn lend credibility to Westermann's (1975, p. 231) suggestion that in ammonites "the animal was able to transport this liquid at will and thus reorient its shell (and body)". The implications of this possibility on current concepts of floating position and buoyancy control in ammonites need not be stressed!

Ward (unpublished data) suggested that "the siphuncular epithelium 'degenerates' with time and that the apical chambers become refilled with liquid which has been forded across the siphuncular wall by ambient pressure in chambers in which the siphuncle can no

longer maintain an osmotic gradient". For the present, a horizontal swimming position for orthoconic ammonites must be viewed with extreme caution, unless buoyancy control here follows a pattern different from that suggested for other ammonites and observed in extant *Nautilus*.

SUMMARY

Theoretically possible buoyancy control was investigated in torti-conic, ancyloconic and orthoconic ammonites. In tightly coiled torticonic forms, best represented by the Turrilitinae, a progressive adapical migration of the siphuncle takes place, which may be interpreted as an adaptation to a mode of life close to the substrate. Slender forms are hydrodynamically streamlined and they were potentially capable of rapid escape movement. Squat forms were probably vagile benthonic. The asymmetry due to tight torticonic coiling could possibly have affected the anatomical symmetry of the animal. Loose helical coiling permits development of symmetry and a stable floating position.

Age segregation takes place in ancylocones. The U-shaped body chamber produces a very stable floating position. Movement was probably mainly vertical and these forms were probably mainly planktonic floaters, although forms with large body chambers could have been adapted to a mode of life close to the substrate in soft sediments.

Orthocones have appeared iteratively throughout the history of cochleate cephalopods, and are potentially capable of rapid movement. A near vertical floating position is possible if buoyancy control follows the same pattern as found in extant *Nautilus*. Large orthoconic forms with protracted apertures and laterally compressed whorl sections appear adapted to a horizontal mode of life. Floating at the surface presents no problems. For horizontal floating underneath the surface of the water, the apical end has to be weighted down. This involves buoyancy control analogous to that of *Spirula* or *Sepia* rather than *Nautilus*.

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