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Buoyancy regulation and macroevolution in nautiloid cephalopods.

With 18 text figures.

Rex E. Crick.

Abstract.

This paper discusses buoyancy regulation within nautiloid cephalopods, how the various groups solved the problem of buoyancy regulation, and how such solutions were a basic factor in the macroevolution of nautiloid cephalopods where evolutionary success is measured as generic diversity and length of stratigraphic record. The evolutionary record of nautiloid cephalopods can be viewed as a series of experiments in an attempt to "find" the most energy efficient compromise between buoyancy regulation, stability, orientation, locomotor design, and environment. Buoyancy regulation was a major factor in cephalopod evolution, because all ectocochleate cephalopods had to regulate buoyancy to some degree as a consequence of the design of the camerate shell, and because other factors (stability, orientation, locomotion, etc.) were dependent on equilibrium between buoyancy and mass. Solutions to buoyancy control were five: 1) short orthoconic and cyrtoconic longicones with water ballast, 2) large orthoconic and cyrtoconic longicones with mineral ballast, 3) orthoconic and cyrtoconic brevicones with water ballast, 4) coiling, and 5) truncated shells. Comparing these solutions to the stratigraphic record of nautiloid cephalopods reveals a complex relationship between buoyancy solution, habit, and competitive stresses. Divergence and success of the Nautilida strongly suggests that evolute coiling required a minimum expense of energy for buoyancy regulation and therefore was superior to the metabolically expensive ballasted systems of their cyrtoconic and orthoconic ancestors.

Kurzfassung.

[Auftriebs-Regulierung und Makroevolution bei nautiloiden Cephalopoden.]

Alle ectocochleaten Cephalopoden hatten, in Abhängigkeit vom Bauplan ihres gekammerten Gehäuses, das für die Stabilität, Orientierung, Lokomotion und Lebensweise grundlegende Gleichgewicht zwischen Auftrieb und Körpermasse herbeizuführen. Dadurch stellt sich die Auftriebs-Regulierung als ein wesentlicher Faktor der Makroevolution dar, und die

The author's address: Dr. Rex E. Crick, Department of Geology, University of Texas at Arlington, Arlington, TX 76019, USA.

paläontologischen Dokumente belegen einen auf den energiemäßig günstigsten Kompromiß zwischen den verschiedenen Faktoren gerichteten Großversuch. — Fünf Wege der Auftriebs-Regulierung lassen sich feststellen: (1) durch Wasserballast, bei kurz orthoconischen und cyrtoconischen Longiconen, (2) durch Mineralballast (Aragonit), bei großen orthoconischen und cyrtoconischen Longiconen, (3) durch Wasserballast, bei orthoconischen und cyrtoconischen Breviconen, (4) durch Gehäuse-Einrollung sowie (5) durch Abstoßen destabilisierender (älterer) Gehäuse-Abschnitte. Der Erfolg dieser Lösungswege läßt sich aus der jeweiligen Vielfalt an Gattungen sowie aus der Länge der stratigraphischen Nachweise ableiten. Dabei wird offenkundig, wie komplex die Beziehungen zwischen Problemlösungen, Lebensweise und Konkurrenzdruck gewesen sein müssen. Der stammesgeschichtlich besondere Erfolg der Nautilida läßt vermuten, daß die Auftriebs-Regulierung auf dem Wege der evoluten Einrollung der Gehäuse den geringsten Energiebedarf erforderte und infolgedessen den stoffwechsel-mäßig aufwendigen, mit Wasser- oder Mineralballast arbeitenden Systemen der cyrtoconischen und orthoconischen Vorfahren überlegen war.

Introduction.

While the subject of buoyancy regulation often surfaces in discussions of cephalopod evolution, either directly (TEICHERT 1967; YOCHELSON & al. 1973; HOLLAND 1987) or indirectly (cf. DZIK 1981), it is seldom considered a major factor of sufficient influence to shape the macroevolution of the group. From the origin of the Cephalopoda during the late Franconian (CHEN & TEICHERT 1983a, 1983b; LI 1984) to modern *Nautilus* LINNÉ 1758 buoyancy regulation, more than any other factor, presented cephalopods with major obstacles to mobility, stability, orientation and habit.

Buoyancy regulation attained this importance because the general mechanics of growth of ectocochleate cephalopods dictated that the visceral mass grew in length at a slower rate than the chambered portion of the shell or phragmocone. This caused a continuing conflict between the need to maintain a preferred orientation in the water column for feeding, mobility and defense and the ever increasing buoyancy of the phragmocone. The constraints of the design of the camerate shell limited the methods available to solve the problem of buoyancy regulation. Because of the density of shell carbonate, the shell of cephalopods would have accounted from approximately 90% of the total weight in water (CHAMBERLAIN 1988).

CHAMBERLAIN (1988) has made a convincing case that not only was the buoyancy device inordinately large and consumed space which could have better used for other purposes, but that the majority of the buoyant force was expended on the apparatus (shell) and not the soft parts.
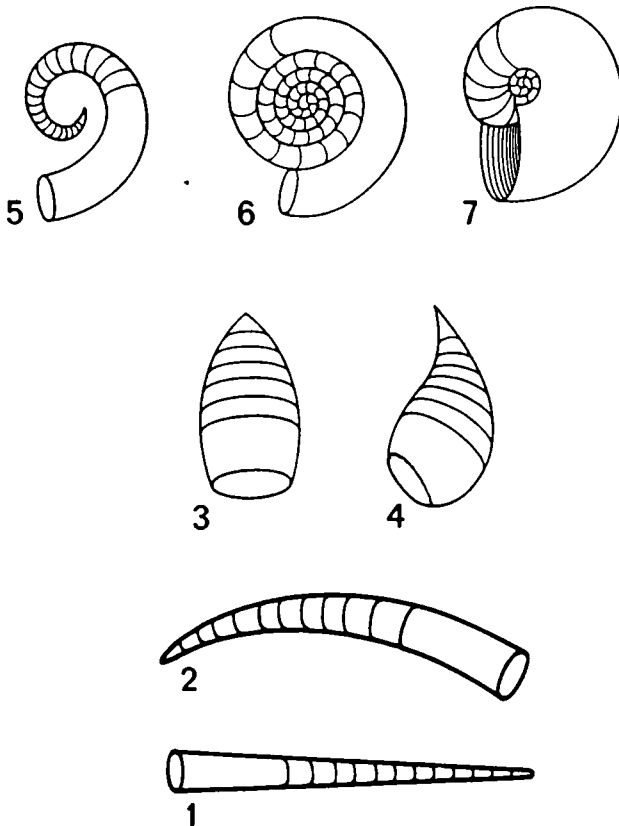
The stratigraphic record of nautiloid cephalopod families reveals several interesting patterns between the decline or disappearance of orders and the rise and expansion of others. It is convenient to view these patterns in the context of competitive pressures at some level, with the understanding that it is much easier to identify possible competitive relationships than to prove them. Such relationships are offered here as possible explanations for certain patterns.

Advances in biochemistry, biomineralization, and biomechanics since the publication of seminal works on buoyancy regulation in nautiloid cephalopods (TEICHERT 1933, 1935; FLOWER 1955; FISCHER & TEICHERT 1969) allow a more comprehensive description and synthesis of buoyancy regulation than has been previously possible.

Aspects of buoyancy regulation.

Hydrostatics and buoyancy.

The phrase b u o y a n c y   r e g u l a t i o n has been used in cephalopod literature variously in reference to conditions of b u o y a n c y, the upward pressure of fluid on an immersed or floating body, or conditions of h y d r o s t a t i c s, the pressure and equilibrium of fluids. It should also encompass e q u i l i b r i u m   c o n t r o l or stability of the shell (CHAMBERLAIN 1988). For the purposes of this paper, b u o y - a n c y   r e g u l a t i o n refers to the physiological characteristics of ectocochleate cephalopods which allow adjustments to be made to the body or shell to compen- sate for the upward pressure of sea water and thereby maintain a preferred and stable orientation in the water column.

Text fig. 1-7. General modes of coiling within nautiloid cephalopods. — 1 = orthoconic longicone; 2 = cyrtoconic longicone; 3 = orthoconic brevicone; 4 = cyrtoconic brevicone; 5 = gyrocone; 6 = serpenticone (evolute coil); 7 = nautilicone (involute coil).

The rôle of hydrostatics in buoyancy regulation will be limited to the movement of water or body fluid into or out of camerae to trim buoyancy by adding or subtracting ballast. The other hydrostatic functions are the use of fluids in the construction of septa and the removal of these fluids from camerae following septum formation. The mechanics of camera formation is a basic feature of all ectocochleate cephalopods (WARD & al. 1981) and thus the physiology applied to hydrostatics is similar among all groups, with important differences in the few preserved elements of that process, namely connecting rings and certain siphuncular structures. Hydrostatics overlap with buoyancy regulation because the presence of cameral fluid in camerae produces a negative component of buoyancy and contributes to the overall buoyancy configuration.

Therefore, in groups with coiled shells, buoyancy regulation became largely a passive exercise since the solution of buoyancy regulation was the coiling of the shell and hydrostatic adjustments to buoyancy (removal of water from chambers, etc.) were largely the same among groups, coiled or otherwise. For purposes of this discussion, I will restrict buoyancy regulation and its affects to: mineralized structures, including cameral deposits and endosiphuncular deposits or other adaptations, such as coiling, developed specifically to counter the effects of buoyancy, especially on orthoconic and cyrtoconic longicones and brevicones (text figs. 1-7).

Mineralogy.

The shell and septa of cephalopods from at least Devonian time were aragonite (CRICK 1985, 1988), and there is no evidence, either structural or chemical, which suggest that cephalopods have used anything but aragonite as the major building material from their origin (RUNNEGAR 1988). Nautiloids used aragonite in the formation of cameral deposits from at least the Carboniferous (CRICK 1982; CRICK & OTTENSMAN 1983) and, again, there is no reason to suspect that another mineral was used prior to this time.

On the basis of simple efficiency in buoyancy regulation, aragonite of density 2·94 should have been the choice over calcite of density 2·71. The choice of aragonite for shell material was on the basis of the better structural properties of aragonite which allowed the development of a much thinner and stronger shell than was possible with calcite (RUNNEGAR, 1988). The greater density of aragonite in the shell was apparently offset by the decrease in volume of shell material over what would have been required had the shell been constructed of calcite.

Although structures deposited in the siphuncle may have been in contract and under the control of cells within the epithelium of the siphuncular cord, cameral deposits were precipitated extracellularly in camerae out of contact with the siphuncular cord. There was no provision nor need for cameral deposits to be formed from membranes (TEICHERT 1933, 1935) or the cameral mantle (FLOWER 1939, 1955) on structural or physiochemical grounds (CRICK 1982, 1988). Each cameral deposit can be viewed mechanically as a void-filling inorganic cement precipitated from a thin layer of cameral fluid, and not unlike the growth of druse cements. Differences are that cephalopods controlled the timing and duration of precipitation by adjusting the supply and composition of fluid delivered to each camera.

Organics synthesized from cameral fluid were used as templates for beginning the growth of acicular aragonite and as media for stopping crystal growth (for a review of the biochemistry see DEGENS 1979). The growth of cameral aragonite began either on the mural portion of the camera, that is the interior surface of the outer shell wall, or the concave and convex surfaces of septa, but never adjacent to the connecting ring. As layers of cameral aragonite accumulated, each deposit grew toward the connecting ring which served as the pathway for fluid. When the deposit covered the connecting ring, precipitation ceased in that camera. The precipitation of cameral aragonite was not confined to one camera, but proceeded in several camerae simultaneously. In many groups, especially the orthocerids, the growth of endosiphuncular deposits developed under similar controls (CRICK 1982).

Prior to fossilization, the connecting rings, but excluding the septal necks, were not the mineralized structures often portrayed in descriptive literature. Their mode of formation corresponds to the "scaffold" type of RUNNEGAR 1988) where needles of aragonite are set into an organic mesh. The connecting ring grades into the septal neck by virtue of an increase in the percentage of aragonite in the organic mesh; that is, the difference between the septum or septal neck and the connecting rings is the concentration of aragonite (MUTVEI 1964, 1972a, 1972b; GRÉGOIRE 1984). The organic matrix or mesh of the two is essentially the same. Arguments for mineralized connecting rings do not satisfy hydrostatic requirements. Connecting rings had to be permeable to serve two purposes: (1) to allow for the removal of cameral fluid following formation of septa; and (2) to allow for fluid to be reintroduced to selected camerae for trimming buoyancy and for the precipitation of cameral aragonite.
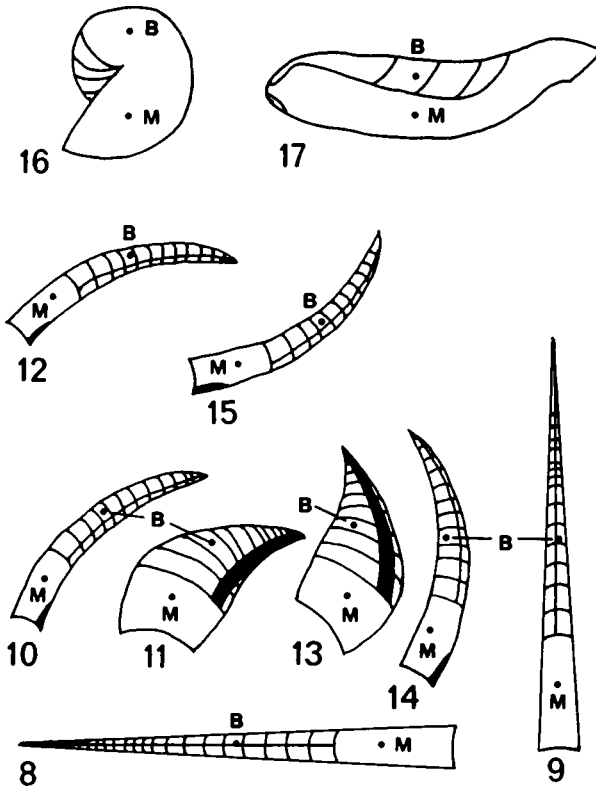
Shell Design.

By the very nature of the design of the camerate shell, all ectocochleate cephalopods had to deal with buoyancy regulation as does living *Nautilus* LINNÉ 1758. But distinctions must be made between the general effects of buoyancy on coiled shells and its effects on orthoconic and cyrtoconic longicones and brevicones. The centers of buoyancy and mass of orthocones and cyrtocones (text figs. 8-12) were positioned along or near the central axis of the shell. If the force of buoyancy was unchecked, the increased buoyancy as a consequence of growth would have resulted in first, the center of buoyancy being positioned directly above the center of mass with the apex of shell being up and the living chamber down (text fig. 9), and, second, a net positive buoyancy causing the animal to rise to the surface. The accepted view of cephalopod ecology is that neither of these events would have been particularly advantageous to cephalopods believed to have been nektonic predators or nekto-benthic scavengers.

"Normal" Longicones.

Although size and allometry varied, the vast majority of Paleozoic nautiloid cephalopods shared two basic shell designs, orthoconic or cyrtoconic longicones (text figs. 1-4). Groups with these shell designs were forever confronted with expending energy to counter the effects of buoyancy, but also to position the ballast in such a way as to provide for stability and proper orientation of the shell. They devised ways of regulating the positions of centers of buoyancy and mass along the

central axis of the shell which were not fixed by shell design, but were subject to constant change in response to growth.

Within the various orders, nautiloid cephalopods with these shell designs generally conform to Cope's Rule, the long-term phylogenetic trend toward increased body size, and the fossil record of cephalopods supports the view that increased size was advantageous. Unfortunately for most cephalopods, the rate of increase in the volume of the phragmocone was greater than the rate of increase in the volume of viseral mass, thereby resulting in positive buoyancy. Ectocochleate cephalopods were then left with the options of either designing the shell to compensate for buoyancy or designing the shell to maximize for other factors such as locomotion, and secondarily modifying buoyancy with some form of ballast. The choice between these two options appears to have been made along the lines of environment.

Text figs. 8-17. Relationships between orientation and centers of buoyancy and mass. — 8 = ballasted orthocone; 9 = unballasted orthocone; 10-12 = possible orientations of endogastrically coiled cyrtocones; 13-15 = possible orientations of exogastrically coiled cyrtocones; 16 = typical coiled nautiloid; 17 = mature ascocerid. — Symbols: B, approximate position of center of buoyancy; M, approximate position of center of mass.

Coiling.

Coiling of the cone in one plane, either evolutely or involutely (text figs. 5-7), effectively fixed the positions of centers of buoyancy and mass in a relatively compact shell design (text fig. 16). Once the shell design was chosen, including the degree of involuteness or evoluteness, the position of centers of buoyancy and mass were fixed within narrow limits and selective pressures relative to buoyancy regulation would have been diminished. Cephalopods belonging to this group were left to deal with hydrostatic adjustments to the shell to provide a slight negative buoyancy. Tarphycerids and barrandeocerids began experimenting with coiling during the early Ordovician by using slowly expanding gyrocones and serpenticones (text figs. 5-6), the latter with many whorls. One tarphycerid family, the lituitids, used a combination of gyrocone and orthocone within individual shells. The widely separated centers of buoyancy and mass in these shell designs would have resulted in fairly unstable configurations (RAUP 1967; CHAMBERLAIN 1988). The nautilids originally used an evolute shell having rapid expansion and few whorls. Later nautilids used a progressively more involute shell until the strongly involute nautilicone was developed, as in *Nautilus* LINNÉ 1758.

"Short" Cyrtocones.

An alternate and perhaps effective form of buoyancy regulation was the short, cyrtoconic shell where the shell is curved but never completes one volution of coiling (text figs. 10-15). For groups which carried the shell above and forward of the body, this style of shell geometry had the same effect on positioning of centers of buoyancy and mass as coiling (CHAMBERLAIN 1988), but without the added advantages of compactness and streamlining afforded by a coiled shell. Some reconstructions of nautiloid ecology reverse this orientation of the cyrtoconic shell, and direct the apex away from the head (e.g., YOCHELSON & al. 1973). Cyrtoconic forms are said to be either endogastrically or exogastrically coiled for purposes of orienting the shell in life position. The definition of endo- or exogastrically coiled has long been determined by whether the venter of the shell is considered to be on the concave side (former) (text figs. 10-12) or on the convex side (latter) (text figs. 13-15). This condition of the shell is meant to be determined objectively on position of the hyponomic sinus which is generally considered to be on the venter, but preservation of the sinus is not common. In the absence of the sinus, the convention has been to use the position of the siphuncle to determine the endo- or exogastric character of the shell.

This reasoning may be flawed in many cases because of the lack of a demonstrated anatomical relationship between the position of the siphuncle and the position of the hyponomic sinus. There are many orthoconic groups with central siphuncles. A number of tarphycerid genera have serpenticonic shells in which the siphuncle is close to the dorsal wall; in absence of a hyponomic sinus their orientation would be reversed. Other tarphycerid genera (lituitids) have a short portion of the early phragmocone coiled, but the majority of the phragmocone is orthoconic in which the have siphuncle is subdorsal and a well developed hyponomic sinus is on the venter. Interestingly, there are discosorid genera with very short cyrtoconic brevicones which are clearly endogastrically coiled, but orientation is not a problem because the buoyancy of the phragmocones is offset by

body and shell mass. When a hyponomic sinus is not present, great care should be taken in defining forms without hyponomic sinuses as being endo- or exogastrically coiled. The effects of mistaking an exogastrically coiled form for one with endogastric coiling, or the reverse, are significant in terms of interpreting solutions to buoyancy regulation, ecology, biology, and evolution.

Connecting Rings.

Specifics of connecting ring morphology are commonly used in a taxonomic sense but may provide information about general depth limits of habits as a function of hydrostatics and shell mechanics (WESTERMANN 1973, 1975; CHAMBERLAIN 1978; CHAMBERLAIN & al. 1981; WARD 1982). The rate at which fluid can be removed or introduced into camerae is dependent on the surface area of the siphuncular epithelium in contact with the connecting ring. The greater the surface area of siphuncular epithelium, the higher the pumping rate. While increasing the diameter of the siphuncle increases its pumping efficiency by increase in surface area, it also decreases its resistance to explosion as a result of the pressure differential between the ambient pressure of liquid in the siphuncle and pressure within camerae. Thus, cephalopods had to choose a hydrostatic compromise between pumping efficiency and rupture of the connecting ring. The choice of compromise presumably had some influence on cephalopod ecology by limiting the depths to which they could descend without rupturing the connecting ring or siphuncle (WESTERMANN 1973, 1975).

Cephalopods adopted a wide variety of connecting ring styles, some with taxonomic importance, but many were homeomorphic and presumably reflect ecologic rather than taxonomic importance. The choice of a large diameter siphuncle is usually associated with short camerae, which would have made the connecting ring less susceptible to explosion but would have reduced pumping efficiency. WESTERMANN (1973, 1975) inferred that this group would have lived in water shallower than 50 m. Medium diameter siphuncles are generally associated with thickened or layered connecting rings expanded between septa of moderate spacing. The layered or thickened connecting ring may have been an attempt to increase the resistance to explosion, and expansion of connecting rings between septa would have offset the loss in pumping efficiency caused by thicker connecting rings. A depth limit of 150 m is proposed for this group (WESTERMANN 1973, 1975). Small diameter siphuncles connecting widely spaced camerae would have offered the optimum resistance to explosion and the optimum in pumping efficiency (e. g., *Nautilus* LINNÉ 1758). WARD (1982) offers this as evidence for the success of the ammonoids, and the same reasoning can be extended to nautiloid cephalopods. WESTERMANN (1973, 1975) assigned this group a maximum depth of 400 m. Even though depth estimates can be argued, the relationship among connecting ring style, shell design, and ecology appears sound.

Ballast.

Ectocochleate cephalopods having orthoconic and cyrtoconic longicones employed two methods of compensating for the positive buoyancy of the phragmocone. One was precipitation of calcium carbonate in camerae or in siphuncular

tubes, and a second was filling camerae wholly or partially with fluid. Fluid may have fulfilled a major role in some groups, but, because of the lower density of cameral fluid relative to calcium carbonate, it is more likely that cameral fluid was used as a means of trimming buoyancy while the major ballast was calcium carbonate. Ballast was precipitated: (1) in the siphuncle posterior of the siphuncular strand (endosiphuncular deposits); (2) within camerae (cameral deposits); or less commonly (3) adjacent to the siphuncular strand (actinosiphonate and annulosiphonate deposits). Thus, all cephalopods with orthoconic and cyrtoconic longicones used either one or a combination of these deposits to compensate for buoyancy. Endosiphuncular deposits comprised a relatively large volume of the phragmocones of several early groups having large-diameter siphuncles (especially endocerids); cameral deposits are essentially limited to two major groups (orthocerids and actinocerids). Actinosiphonate and annulosiphonate deposits (TEICHERT 1964a) are found in groups with other methods of buoyancy regulation, commonly shell design as in the discosorids, and were not a major form of ballast. Cameral deposits and endosiphuncular deposits were deposited in a series of thin layers (see section on mineralogy), and for cameral deposits this serial development was spread over several camerae simultaneously in such a way as to maintain the maximum stability of the shell (CRICK 1982). The volume of many endosiphuncular deposits and all cameral deposits greatly exceeded the volume of shell material. The production of such quantities of calcium carbonate would have required a considerable expenditure of energy to extract metals from sea water in the required proportions to produce aragonite. Many nautiloid cephalopods chose to do so regardless of the energy cost, and their success must be taken into consideration when discussing the evolution and ecology of ectocochleate cephalopods.

The conditions outlined above for the development of ballast systems of calcium carbonate reflect the current knowledge of biomineralization. There are, however, many discrepancies between the taxonomic distribution of cameral and endosiphuncular deposits supported by personal observations, museum collecitons, and plates accompanying published literature v e r s u s certain dogma in cephalopod literature. Many published studies report the p r e s e n c e of cameral deposits in orthoconic and cyrtoconic brevicones and serpenticones or the a b s e n c e of cameral deposits in post-Cambrian orthoconic and cyrtoconic longicones. The former did not need cameral deposits whereas cameral deposits or endosiphuncular deposits were mandatory for the latter group. Why these discrepancies? They are most likely the result of historic precedent and the failure to view "deposits" in the context of biomineralization and diagenesis. Cameral deposits and endosiphuncular deposits have been reported from the Tarphycerida, but true cameral deposits are restricted to members of the Lituitidae, all of which have a coiled early portion of the phragmocone with the majority of the phragmocone being an orthoconic longicone. Other reports of cameral deposits and endosiphuncular deposits in serpenticones are based on single occurrences of these deposits in four genera from three different tarphycerid families (ULRICH & al. 1942). In each case, the features reported as cameral deposits or endosiphuncular deposits do not have the distribution patterns nor the developmental characteristics of these deposits, but exhibit all of the characteristics of druse calcite cement. Review of museum collections and published literature indicates that reports of cameral deposits in groups with other than orthoconic and cyrtoconic longicones result from misinterpretations of druse calcite

cement lining the interior of camerae as cameral deposits. This is not surprising since the majority of such misinterpretations occurred in the first half of this century.

The other aspect of the problem is the reported a b s e n c e of cameral deposits in groups with orthoconic and cyrtoconic longicones. The same review of museum collections and published literature indicates that the seemingly anomalous absence of cameral deposits in groups whose shell morphologies required ballast, for the most part, is based on descriptions of ontogenetically young camerae in which cameral deposits had not been deposited at the time of death. In a great many cases, descriptions of longiconic specimens without cameral deposits were based on camerae attached to living chambers and were therefore the youngest camerae (last formed). While the number of the newest formed camerae which remained empty of cameral deposits certainly varied among groups, at least 7 to 14 of the youngest camerae remained empty of cameral deposits (CRICK 1982). The preservational potential of camerae wholly or partially filled with cameral deposits was greater than camerae without cameral deposits, and it is not uncommon for phragmocones with cameral deposits to be found separated from living chambers with attached camerae — a situation which further complicates cephalopod systematics. The presence of spar calcite in early camerae of orthoconic phragmocones was viewed by many workers as evidence of the lack of cameral deposits. Petrographic examination of such deposits reveals either the presence of relics of cameral aragonite or that neomorphic calcite has faithfully preserved portions of the cameral deposit morphology.

For camerae containing cameral deposits, the aragonitic shell and cameral deposits most often convert to neomorphic calcite showing preservation of at least gross details of structure and morphology. Though the acicular habit of cameral deposit aragonite and the degradation of the organics in cameral deposits made them more susceptible to dissolution than shell aragonite, it is uncommon to find camerae containing spar calcite without preservation of cameral deposit structures, while at the same time preserving all or a portion of connecting rings. Camerae of longiconic forms, where the shell is now neomorphic calcite may or may not show destruction of connecting rings whereas camerae which contain spar calcite without evidence of cameral deposits show destruction of connecting rings and shattered septa. The indication is that specimens containing cameral deposits commonly experienced neomorphism of shell and cameral aragonite to calcite which left connecting rings and other structures more or less undeformed.

Camerae of specimens without cameral deposits or portions of phragmocones without cameral deposits may contain: (1) sparry calcite of large equant grains if the integrity of the phragmocones is lost early and circulation of pore water is relatively free; (2) calcite formed as fine grained (equant to blade shaped crystals) druse cement on camera walls if the integrity of the phragmocones is such that the movement of fluids is kept to a minimum; or most commonly (3) two sequences in the development of diagenetic calcite. F i r s t , a layer of fine grained druse calcite was deposited during the period when phragmocones integrity was maintained, and s e c o n d , when phragmocone integrity was lost (due to borings, fractures, etc.) and the remainder of the void space was filled with more corasely grained spar calcite (PAPENGUTH 1983). It is this last sequence which gives the appearance of cameral deposits which were partially developed (druse cement stage) and then the remainder or the camera was filled with spar calcite following death. This two-stage

development of druse calcite and void-filling spar calcite is a commonly preserved feature in the camerae of nautilids and ammonoids which, for obvious reasons, is never referred to as cameral deposits.

The misinterpretation of inorganically formed druse calcite as cameral deposits in groups which did not form cameral deposits, and the misinterpretation of camerae void of cameral deposits as evidence that certain orthoconic and cyrtoconic longiocones did not form cameral deposits both bear heavily on the proper interpretation and understanding of ectocochleate cephalopod ecology and evolution.

Evolutionary aspects of buoyancy regulation.

Solutions.

Solutions to the problem of buoyancy regulation are not many and some, such as coiled and shortened phragmocones with short camerae, were used several times throughout the evolution of cephalopods. These are introduced here in general terms.

Solution I: small cyrtocones and orthocones.

The earliest solution, and perhaps the most primitive, was to develop slender, short cyrtoconic or orthoeonic longicones (2-6 cm) consisting of phragmocones with extremely short camerae, moderately long living chambers, and simple siphuncles of a diameter one-fifth or less of shell diameter (text figs. 10, 12, 14, 15). The density of the body and aragonite of the short shell was sufficient to create a mass to buoyancy ratio with negative buoyancy or perhaps a slightly positive buoyancy. Cameral fluid may have been either retained in camerae following septum formation or introduced at a later stage to trim buoyancy, but no evidence exists of other forms of buoyancy regulation, such as deposits. Although this design solved buoyancy regulation, it had the disadvantages of limiting size, stability and mobility. Groups with this shell design are limited to the Cambrian.

Solution II: calcium carbonate as ballast.

Calcium carbonate, in the form of aragonite, was precipitated in camerae or within the siphuncle proper of orthoconic and cyrtoconic, longicones to offset the buoyancy of the phragmocone and to control the attitude of the shell. The exclusive use of endosiphuncular deposits for buoyancy regulation required a large diameter siphuncle, which placed severe restrictions on depth limits and consequently groups of this type typically have closely spaced septa. Groups that used cameral deposits as the major ballast typically have siphuncles of much smaller diameter; i. e., one tenth or less of shell diameter. Groups having cameral deposits may or may not have developed endosiphuncular deposits.

Controlling the attitude or orientation of the orthocone or cyrtocone was a major part of buoyancy regulation in these groups. This was accomplished by beginning the precipitation of cameral deposits or endosiphuncular deposits in the oldest portion of the phragmocone and, as growth continued, deposition occurred in progressively younger portions of the phragmocone. The formation of cameral

deposits occurred simultaneously in several successive camerae, thereby having the effect of producing a smaller conical shaped buoyancy chamber resembling a shortened phragmocone. This staggered development of cameral deposits would have allowed greater control over centers of buoyancy and mass and provided greater stability. Large marginal to submarginal siphuncles with endosiphuncular deposits would have contributed to the rotational stability by lowering the center of mass.

Solution III: orthoconic and cyrtoconic brevicones.

In some cephalopods the phragmocone was short but expanded rapidly with camerae that rapidly increased proportionately in volume, followed by a living chamber of large volume relative to the phragmocone. Siphuncles are typically one-tenth shell diameter where they pass through the septum and expand to one-fifth to one-third shell diameter between septa. Centers of buoyancy and mass would have been reasonably close (text figs. 11, 12). The large volume of visceral mass and shell material relative to the small volume of the phragmocone were the major means of buoyancy regulation. Cameral fluids may have been used to trim buoyancy.

Solution IV: coiling.

Coiling of the cone in a planispiral placed the center of buoyancy directly over the center of mass and fixed their relative positions within the coil (text fig. 16). The close proximity and fixed positions of these centers resulted in hydrostatics being the primary mechanism of buoyancy regulation, and coiling appears to have been the optimum shell design available to ectocochleate cephalopods. The differences in shell design among groups are basically in the position of the siphuncle and the degree of evoluteness of the shell. The latter is considered more important because of its contribution to both the positions of the center of buoyancy and the center of mass.

Solution V: ascocerid conch.

Ascocerids evolved a very highly specialized shell where the mature conch consisted of an enlarged portion of the phragmocone lying directly above the majority of the living chamber (text fig. 17). Early portions of a typical orthoconic phragmocone were apparently truncated, although the mechanism of truncation is not understood. This form was yet another means of placing the center of buoyancy above the center of mass, and in design is analogous to the cuttlebone of modern *Sepia*.

Macroevolution and buoyancy control.

Text fig. 18 presents the stratigraphic of 131 families of nautiloid cephalopods grouped into their respective orders. The stratigraphic data are based on MOORE (1964), but the ranges of Paleozoic families have been modified considerably using the works of BALASHOV (1960, 1968), BARSKOV (1972), CHEN & TEICHERT (1983a), CRICK (1978, 1980, 1981), RUZHENTSEV & al. (1962), TEICHERT & al. (1979), ZHURAVLEVA (1972, 1974), and stratigraphic information contained in systematic work since 1960. Ranges of Cambrian, Ordovician, Silurian, and Devonian families

are based on review of all available published work since RUEDEMANN (1906). The width of text fig. 18 is scaled to the duration of the Phanerozoic. The durations of periods and epochs or ages are scaled as described in HARLAND & al. (1982). Families are arranged within orders on the basis of first appearance, and no evolutionary significance is implied by this arrangement.

Plectronoceratida, Ellesmerocerida, Protactinocerida, and Yanhecerida (Solution I).

These Cambrian orders can be grouped together on the basis of their choice of Solution I for buoyancy regulation. CHEN & TEICHERT (1983a) reported that spaces between diaphragms within siphuncles of protactinocerids, yanhecerids, and some ellesmerocerids were filled with either matrix or calcite deposits. They left open the question of the organic or inorganic origin of these deposits, but discussion of their systematics (especially CHEN & TEICHERT 1983b) implied that the calcite was neomorphic after existing organically produced calcareous deposits. If so, these deposits represent the oldest record of deposits designed to counter positive buoyancy.

Members of these orders were not without means of buoyancy regulation. CHEN & TEICHERT (1983a) considered the principal mechanism of buoyancy regulation to be crowding of septa (= increasing the density of the phragmocones by increasing the volume of aragonite). However, two additional aspects of buoyancy regulation deserve mention, first, retention of water or body fluids in camerae, and, second, the mass of the siphuncular cord. It is very probable that Cambrian cephalopods relied on hydrostatics to trim to the desired equilibrium configuration (CHAMBER-LAIN 1988). Members of these orders possessed moderate to large diameter siphuncles, the length of which may have been filled with siphuncular cord during life, particularly if hydrostatic adjustments were necessary. This would have had the effect of placing a portion of the mass directly beneath the region of flotation. A review of the literature produces an approximate siphuncle to shell diameter ratio of 1:5 for these groups, which agrees with ratios reported by CHEN & TEICHERT (1983a).

The plectronocerids, protactinocerids, yanhecerids, and Chambrian members of the ellesmerocerids have been described as being endogastrically coiled (CHEN & TEICHERT 1983a; FURNISH & GLENISTER 1964b) (text figs. 10, 12). The brief stratigraphic record of the plectronocerids, protactinocerids, and yanhecerids may point to problems associated with this style of buoyancy regulation. The elles-merocerids appear to be an exception with a stratigraphic record from Late Cambrian to the end of the Ordovician. Of the four Cambrian families, however, only the Ellesmeroceratidae (text fig. 18, Fam. 3) survived to the Middle Ordovi-cian. The composition of this large family consists of a majority of orthoconic longicones and a mixture of cyrtoconic longicones with reportedly endo- and exogastric coiling, and it is the orthoconic and exogastrically coiled forms which extend the family to the Middle Ordovician. What then about the 6 families which originated and went extinct in the Ordovician? They consist of generally larger forms having a greater variety of shell morphologies and modifications to connect-ing rings. Two (text fig. 18, Fam. 7, 8) are exogastric, three are orthoconic longico-

nes (text fig. 18, Fam. 9, 10, 12) and one is endogastrically coiled. This suggests that the design of the orthoconic longicone and the exogastrically coiled cyrtoconic longicone were more advantageous to longevity of these early cephalopods than was the endogastrically coiled cyrtoconic longicone. For the successful groups having orthoconic longicones, the implication is that camerae contained fluid to assist in buoyancy regulation.

Endocerida and Intejocerida (Solution II).

Endocerids and intejocerids used a modified form of Solution II to solve buoyancy regulation. Endocerids have a varied shell morphology, ranging from orthoconic and cyrtoconic longicones to orthoconic and cyrtoconic brevicones, with orthoconic longicones being the most common. Shell morphology of intejocerids is essentially restricted to orthoconic longicones, although rare cyrtoconic longicones occur. Shared characteristics of these two orders are large to moderately large phragmocones consisting of short camerae penetrated by large marginal or submarginal siphuncles, filled in part with either endocones or lamellae and in part with the siphuncular strand or tube. Communication between a camera and siphuncle was not possible once endocones covered the inner surface of the connecting ring. Distribution of endocones within the siphuncle of endocerids shows that a length of siphuncle extending posteriorly from the living chamber and corresponding to the distance of the youngest 10 to 14 camerae was always free of endocones and that communication was possible between these camerae and the siphuncle (CRICK & TEICHERT 1983). In many groups the diameter of the siphuncle is one-half that of the phragmocone. The combined mass of both structures and the siphuncular cord presumably served to counter the effects of positive buoyancy and provided an orientation generally agreed to have been horizontal or nearly so. The marginal to submarginal position of the siphuncle had the additional advantage of providing rotational stability by lowering the center of gravity of the organism (phragmocone + visceral mass).

Endocerids and intejocerids were essentially Early to Middle Ordovician taxa (text fig. 18). The two families reported from the Silurian (text fig. 18, Fam. 25, 27) are monotypic and known only from fragments of siphuncles. The stratigraphic ranges are accurate, however, and only the systematics need to be re-evaluated. The use of endocones and siphuncular tissue for ballast appears to have been a reasonable solution to buoyancy regulation for a short period of time, but one which did not survive the shake-out of various evolutionary trends in buoyancy regulation begun during the Ordovician (text fig. 18). Other groups which originated during the Ordovician and had apparently more sophisticated methods of buoyancy regulation survived at least through the Silurian, and most survived to the Carboniferous (text fig. 18). It is tempting to suggest that endocerids may have succumbed to selective pressure from the then rapidly rising orthocerids which soon became the dominant nektonic group.

Orthocerida (Solution II).

The order is known for its long, slender, orthoconic to slightly cyrtoconic longicones showing very little ornamentation. Shell length is generally less than that of coeval endocerids and actinocerids, and shell diameter is considerably less. Living

chambers are short, relative to length of the phragmocone. Shell walls are thin and camerae are typically long, with one to two camerae occupying a length of phragmocone corresponding to the shell diameter. Siphuncles are small in diameter and positioned in the central to subcentral portion of the shell. Connecting rings are simple. The light-weight shell with long camerae provided an extremely buoyant phragmocone. Cameral deposits of calcium carbonate were used for ballast, and were the most sophisticated of all nautiloids (CRICK 1982). Endosiphuncular deposits may or may not be present, but because of the small diameter of siphuncle they would not have been a major part of buoyancy regulation. Within the Orthoceratidae and Pseudorthoceratidae (text fig. 18, Fam. 29, 31), differences in the design and morphology of cameral deposits occur among genera and provide a valuable taxonomic tool (McFARLAND 1986; CRICK 1988).

The Orthocerida are believed to have originated from an ellesmerocerid ancestor during the Early Ordovician (SWEET 1964a). They dominated the nektonic cephalopod faunas from the Late Ordovician through the Carboniferous and survived to the Late Triassic. The Orthoceratidae (text fig. 18, Fam. 29) were numerically superior from the Ashgillian through Emsian and the Pseudorthoceratidae (text fig. 18, Fam. 31) from Eifelian through Stephanian. The Geisonoceratidae and Proteoceratidae (text fig. 18, Fam. 32, 33) were important at various times during the Silurian and Devonian. The remaining families consist of six or less genera, and, with exception of the Lamellorthoceratidae and Brachycycloceratidae (text fig. 18, Fam. 41, 42), are not important to this discussion.

A comparison of the characteristics of the longer-lived families (text fig. 18, Fam. 29, 31-33) with shorter-lived families does not reveal any clear differences which might suggest a causal relationship between longevity and physiology; that is, all have cameral deposits and orthoconic longicones. There are, however, a few differences which, taken together, may have provided a selective advantage. The most successful genera within the Orthoceratidae and Pseudorthoceratidae and those responsible for the trends in text fig. 3 have the longest camera length to shell diameter ratios (e. g., *Michelinoceras* FOERSTE 1932 and *Pseudorthoceras* GIRTY 1911), the lowest expansion rates, no ornamentation, and apparently the most precise control over formation of cameral deposits (CRICK 1982, 1988). The long camerae connected by straight or slightly expanded siphuncles of small diameter, together with a long, slightly tapered shell — one with a low expansion rate — having little or nor ornamentation, implies a nektonic habit capable of extending down to approximately 400 m (WESTERMANN 1973, 1975). This combination may have been sufficient to protect these groups of orthocerids from competitive pressures and predation from other cephalopods and from chondrichthian fish (PACKARD 1972; CHAMBERLAIN 1988).

Tarphycerida (Solution IV).

As outlined by FURNISH & GLENISTER (1964c), the tarphycerids appear as an unnatural biological group. Three characters are responsible for defining the group: (1) all members have some aspect of coiling associated with their shell morphology, (2) mature portions of the shell are slightly to strongly divergent from the coiled portion, and (3) siphuncles may appear in any location between the ventral shell margin and the dorsal shell margin. It is not the purpose of this paper to dissect

classification schemes, but the lack of a solid biological base for the tarphycerids poses obstacles to the discussion of their solution to the problem of buoyancy regulation. Living chambers are long, extending from one-half whorl to one complete whorl. Connecting rings are relatively simple and some are layered. Cameral deposits have been reported for the group, but recent work reveals that only the Lituitidae deposited calcium carbonate in camerae. The earliest portion of the lituitid phragmocone was loosely coiled in two to three whorls and the remainder was orthoconic. The straight portion of the phragmocone functioned in the same manner as an orthoconic phragmocone and the lituitids secreted cameral deposits to counter excess positive buoyancy (Solution II).

Reports that four serpenticone genera had cameral deposits (ULRICH & al. 1942) (two from the Tarphyceridae and one each from the Trocholitidae and Estonioceratidae) are based on post-mortem druse calcite cement (CRICK 1988), as mentioned under the discussion of "ballast". The use of the gyrocone and the serpenticone (text figs. 5-6) was in early attempt to produce a compact, stable design without the metabolic expense of producing calcium carbonate for ballast. In the Raupian analysis scheme of shell design (RAUP 1967), gyroconic and serpenticonic shells would have been stable, providing living chambers were reasonably short (< one-half whorl). However, the long tarphycerid living chamber moved the centers of mass and buoyancy close together, and the shell would have been subject to rotation about this common center. Tarphycerids apparently countered this condition by allowing divergence of the final one-quarter to one-half whorl of the living chamber. Thus, the energy saving and stability advantage of gyroconic and serpenticonic coiling were probably offset by the disadvantage of long living chambers.

The order is typically Ordovician, with only one family and a few genera of another occurring in the Silurian (FLOWER 1975). The longest stratigraphic records belong to the Lituitidae and Trocholitidae (text fig. 18, Fam. 51, 52), which also have the highest generic diversity. Lituitids are unique by having a combination of early coiled and late straight portions of the phragmocone. More work is necessary to determine the advantages of this shell design. Trocholitids are similar to the remainder of the Tarphycerida with only three exceptions: trocholitid living chambers are the shortest in the order; their expansion rate is the highest; and they have the only dorsal siphuncles in the order. How these characteristics combined to make the trocholitids more successful has not yet been determined.

Barrandeocerida (Solution IV).

Barrandeocerids are a numerally small group which are superficially like tarphycerids in shape but with thinner connecting rings of reportedly one layer (SWEET 1964c). Living chambers are as long as in tarphycerids, and the siphuncle generally lies in the ventral region away from the shell margin. Cameral deposits are absent, as might be anticipated; and gyroconic and serpenticonic coiling was the solution to buoyancy regulation. Interestingly, there is greater "morphological distance" between tarphycerid families than among tarphycerids and barrandeocerids.

Most barrandeocerids are confined to the Ordovician and Silurian. The Devonian outlier of the Barrandeoceratidae (text fig. 18, Fam. 104) belongs to the monospecific genus *Haydenoceras* FLOWER 1949 (text fig. 18, Fam. 105), though

there is little evidence for it being assigned to the Barrandeoceratidae. The Ne-phriticeratidae (text fig. 18, Fam. 107) are a valid group without a pre-Emsian record. The next oldest barrandeocerid is of Ludlow age. Family differences are generally attributable to ornamentation and coiling design. Barrandeocerids were subject to the same advantages and disadvantages brought by gyroconic and serpenticonic coiling and long living chambers. The group never attained the generic diversity of their nearest competitors, the tarphycerids.

Actinocerida (Solution II).

The group consists mainly of medium to large, slender orthocones, with a few being slightly cyrtoconic. The most distinctive characteristic of actinocerids is the siphuncle. The diameter is commonly one-third to one-half the shell diameter, and segments are greatly expanded between septa. The siphuncle of most mature actinocerids is filled with endosiphuncular deposits which form in and around a pre-existing endosiphuncular canal system (TEICHERT 1933, 1935, 1964c) consisting of a central tube with radial tubes branching off to connecting rings. The endosiphuncu-lar canal system surely functioned hydrostatically, to remove cameral fluids follow-ing septum formation or for moving fluids into camerae for the formation of cameral deposits. Its function would have ceased with the precipitation of endosiphuncular deposits in the siphuncle.

Actinocerids do not form a major segment of cephalopod evolution and reached their maximum diversity during the Ordovician and Silurian (text fig. 18). The Ormoceratidae have the longest history (text fig. 18, Fam. 56), Early Ordovician (Arenigian) to Middle Carboniferous (Viséan). There is nothing pertaining to shell morphology or buoyancy regulation system which provides a clue as to why this family has a longer evolutionary history than the two other major families, the Actinoceratidae and Armenoceratidae (text fig. 18, Fam. 55, 61). The Carboniferous outlier is based on the Carbactinoceratidae (text fig. 18, Fam. 63) which has ties to the Ormoceratidae (TEICHERT 1964c) and contains the common North American genus *Rayonnoceras* CRONEIS 1926. The small number of genera (38) in the order, most of which are short-lived, spread over 9 families (text fig. 3) may reflect the disadvantages of what must have been an energy expensive system of buoyancy regulation.

Ascocerida (Solution V).

Ascocerids are without doubt the most unusual group of nautiloid cephalopods. Their ultimate solution to buoyancy regulation was to develop an exoskeleton equivalent of the endoskeleton "cuttlebone" of *Sepia* where the gas filled camerae were placed above the visceral mass of the animal (text fig. 17). This effectively placed the center of buoyancy above the center of mass and, if proportions were correct, would have created a relatively stable configuration. What is more unusual is that each member is believed to have passed through an initial stage consisting of a short, orthocone or cyrtocone without cameral deposits, to an intermediate stage in which the phragmocone was truncated and the living chamber enlarged, to the final ascoceroid stage described above where all of the typical phragmocone is truncated and the ascoceroid phragmocone lies above the visceral mass (FURNISH & GLENIS-TER 1964b).

Although the ascocerid solution to buoyancy regulation may appear to have been a successful design, the stratigraphic record of the group shows that they never achieved even marginal diversity in genera or families (text fig. 18, Fam. 64-66). The design of the mature ascocerid phragmocone, while it presumably solved buoyancy regulation, was probably unstable with only low mobility.

Oncocerids (Solution III).

Superficially like discocerids in shell morphology and habit, oncocerids contain the bulk of the longiconic and cyrtoconic brevicones, although a few groups extend shell morphology to torticones, gyrocones, and nautilicones. Oncocerids used Solution III for buoyancy regulation, but water ballast was a definite possibility (CHAMBERLAIN 1988). The group is predominantly exogastrically coiled, and it is likely that all forms were coiled in this manner. Siphuncles are marginal and moderately large in diameter having thin connecting rings expanded between closely spaced septa. Actinosiphonate structures within the siphuncle have been termed endosiphuncular deposits (SWEET 1964b), but are actually extensions or growths from connecting rings which extend into the siphuncular space (CRICK & TEICHERT 1979). These features have been regarded commonly as deposits in their own right, but it is probably more correct to consider them as structures developed in the mode of RUNNEGAR's (1988) "scaffolds" and formed as extensions to mature connecting rings. Most common are blade-like extensions from the connecting ring which form longitudinal lamellae (TEICHERT 1964a; CRICK & TEICHERT 1979).

A hydrostatic function for actinosiphonate structures was suggested by CRICK & TEICHERT (1979) where a ratio of the number of lamellae to camera volume and diameter of siphuncle was shown to hold for certain oncocerids. Presumably the tissue of the siphuncular cord was invaginated around lamellae, thereby increasing the exchange surface for removing cameral water from newly formed camerae. True endosiphuncular deposits have not been reported, and there is no evidence that oncocerids formed cameral deposits. Because these deposits are absent from the siphuncular canal, it is possible that the siphuncular strand and hydrostatic system remained active over the length of the phragmocone. This implies a very sophisticated system of buoyancy regulation by water ballast.

The group has been described in general as having a benthic (FURNISH & GLENISTER 1964a) or nektonic habit with a depth limit of 150 m (WESTERMANN 1973, 1975). However, WESTERMANN (1973, 1975) did not consider the rôle of cameral fluid in maintaining negative buoyancy configuration. This, in addition to the large volume of living chamber to phragmocone, strongly suggests that most oncocerids operated with a slight negative to slight positive buoyancy and would have been most likely to occupy a benthic habit. Buoyancy regulation was essentially negated by shell design, and the remaining buoyancy was ballasted by the adjustment of fluid volume in camerae.

Oncocerids first appeared during the Middle Ordovician (Llanvirnian) and rapidly expanded to become the dominant nautiloid group during the Silurian. The rapid rise of oncocerids during the Ordovician and Silurian suggests that Solution III, together with exogastric coiling, had competitive or survival advantages over the more slowly evolving discosorids of similar habit. Family diversity exceeded that of discosorids during the Devonian (text fig. 18) even through the

generic diversity of discosorids was greater (see discussion of Discosorida below). As noted in the discussion of discosorid evolution, this apparent turn around in oncocerid fortunes may be more apparent than real. The greater standing generic diversity of oncocerids during the Ordovician and Silurian, and perhaps the Devonian, would seem to indicate that the oncocerid version of Solution III provided a competitive edge relative to the discosorids. Further evidence for this view comes from the fact that the Nautilida originated from an oncocerid ancestor (text fig. 18, Fam. 108). It is tempting to consider that the rise of nautilids resulted from selective pressures being less on the few oncocerid groups whose solution to buoyancy regulation was coiling.

CHAMBERLAIN (1988) offered an interesting alternative explanation for the rapid decline of cephalopods with characteristics like those of Solution III. He notes that chondrichthian fish became dominant in the late Devonian, and suggests that cephalopods having less stable orthoconic and cyrtoconic brevicones, that is, discosorids and oncocerids, were preyed upon by chondrichthians. In CHAMBER-LAIN's analysis, cephalopods that developed coiled shells were able to avoid this predatory pressure by being more compact and mobile. It is also possible that selective pressure resulted from competition between discosorids and oncocerids and marine placoderm and osteichthyan fish.

Discosorida (Solution III).

The discosorids had little need for a sophisticated mechanisms of buoyancy regulation. The order is polymorphic including various groups of relatively short, rapidly expanding orthoconic and cyrtoconic brevicones having in common closely spaced septa and large volume living chambers. Siphuncles are expanded within camerae. The ratio of mass of shell material and viseral mass to buoyancy of the phragmocone apparently created a slight positive buoyancy.

The group is noted for complex connecting rings, which suggest a sophisticated hydrostatic system using cameral fluids as a major part of buoyancy regulation. Even trough the diameter of siphuncles in discosorids is not particulary large with respect to diameter of the shell, most siphuncles consist of segments expanded within camerae so that the actual surface area of the siphuncle is considerable. The ratio of the siphuncle surface area to the volume of the camera is remarkably consistent for both discocerids and oncocerids (CRICK & TEICHERT 1979) and implies a hydrostatic dependent relationship. Siphuncles with or without extensions of parietal deposits as endosiphuncular deposits would have contrributed mass towards reducing the positive buoyancy. Most workers consider discosorids to have been nekto-benthic, and in this regard would have had little need of a sophisticated buoyancy regulation system. WESTERMANN's analysis of septal strength and connecting ring structure suggests that discosorids had a maximum depth limit of 100 m.

Discosorids are reported as being either predominantly exogastrically or predominantly endogastrically coiled (FLOWER & TEICHERT 1957; TEICHERT 1964b). In an exogastric orientation, the phragmocone would have contributed to a stable orientation of apex carried up or up and over the mass of the animal (text figs. 13-15). However, there are several genera with clearly endogastrically coiled shells. These

genera are contained within the Phragmoceratidae and Mandaloceratidae (text fig. 18, Fam. 90, 93), noted for contracted and modified apertures where the hyponomic sinus is commonly preserved. The shell design for these families consists of very short brevicones and the volume of phragmocone is approximately equal to the volume of living chamber. Cameral deposits have been reported from two genera, *Westonoceras* FOERSTE 1924 and *Ruedemannoceras* FLOWER 1940 (FLOWER & TEICHERT 1957). Examination of specimens of these two genera shows no evidence of cameral deposits, but druse calcite cement is common in the camerae (CRICK 1988).

Features of the connecting ring and siphuncle, such as bullets and parietal deposits, may be mistaken for ballast, but acquired their present crystalline nature through diagenesis. Connecting rings in most groups were clearly differentiated, as eloquently described by FLOWER & TEICHERT (1957), and where present were formed of aragonite crystals set in a mesh-like organic matrix (the "scaffolding" of RUNNEGAR 1988). Consequently, much of the structure of connecting rings was lost through diagenisis; the structures described by FLOWER & TEICHERT (1957), TEICHERT (1964b) and many others were neomorphosed as diagenesis proceeded at different rates, depending on the amount of organics remaining in various layers.

Discosorids first appeared during the Middle Ordovician (Llanvirnian) and disappeared from the stratigraphic record during the latest Devonian (Famennian). The ranges of pre-middle Silurian forms are relatively short with the exception of the Discosoridae (text fig. 18, Fam. 92). Late Silurian and Devonian families tend to be longer lived, but much of this longevity is restricted to genera reported by ZHURAVLEVA (1972, 1974), geographically restricted to the western U.S.S.R. ZHURAVLEVA's taxonomic and biostratigraphic data are included in text fig. 18, but with some reservations regarding the taxonomic criteria used by ZHURAVLEVA for distinction of oncocerids and discosorids. As discussed by TEICHERT & al. (1979), these criteria need re-evaluation. In any case, the remains of cephalopods do exist and the biostratigraphic data, when cross-checked with associated faunas, appear reasonable. ZHURAVLEVA's work either extends the ranges of established discosorids or oncocerids, or adds genera to the Discosorida, or the Oncocerida, or both.

Taken as illustrated in text fig. 18, the generic diversity of Devonian discosorids gives the appearance of rapid evolution and dominance of nautiloid cephalopod faunas. This dominance and radiation is at variance with macroevolutionary trends of cephalopods already established during the Ordovician and Silurian and with that of the oncocerids, the other benthic cephalopod group. A late radiation of such explosive proportions is without precedent in the evolutionary history of ectocochleate cephalopods. The generic diversity of discosorids rose slowly during the Ordovician and stabilized at approximately 25 genera during the late Ordovician and the Silurian. The generic diversity of the oncocerids rose rapidly to stabilize at approximately 50 genera during the Ordovician, Silurian and Devonian. If this generic increase is either spread across the Discosorida and Oncocerids or used to extend existing genera, the picture of discosorid evolution fits with ongoing trends. Although the variety of shell types within discosorid families, and often genera, makes it difficult to assess the impact of style of buoyancy regulation on the evolutionary history of the group, the low diversity of discosorids may indicate that endogastric coiling, together with peculiarities of shell design and hydrostatic system, made the group less competitive than their oncocerid rivals.

The only major crisis in discosorid evolution occurred during the Famennian when the order became extinct. The cause for this extinction has never been seriously considered, but within the Cephalopoda one has to consider both the long-term effects of competition with the oncocerids and the additional competition from the Nautilida as they rapidly evolved from an oncocerid ancestor (KUMMEL 1964). The shell design and buoyancy regulation of early nautilids were oncocerid-like and it is likely that habits overlapped with discosorids. Predation by chondrichthian fish or possible competition with marine placoderms and osteichthygians would have affected discosorids, as well as oncocerids.

Nautilida (Solution IV).

Simply stated, the Nautilida contain all coiled nautiloids from the Devonian to the Recent, with exception of a few barrandeocerids (KUMMEL 1964). The majority of nautilid shell designs consist of closely coiled, widely umbilicate to convolute and involute conchs. A few members of early families exhibit shell designs which are nearly orthoconic or gyroconic. Siphuncles are subcentral, narrow and cylindrical with thin connecting rings; rarely, the siphuncle may be ventral or dorsal. Sutures are sinuous, as opposed to the straight sutures of earlier groups, and the type and range of ornamentation and modifications of shell architecture is greater than previous groups. In general, the nautilid version of Solution IV differs from those of the tarphycerids and barrandeocerids by being more involute, having a higher rate of expansion, longer camerae, smaller diameter siphuncles, and, by virtue of rate of expansion, shorter living chambers. All of these combine to create a shell design with an efficient hydrostatic system, high stability and good locomotor design (CHAMBERLAIN 1988).

From a proposed origin in the Oncocerida (FLOWER 1952; KUMMEL 1964), nautilids rose to become the dominant nautiloid group during the Carboniferous and Permian. Nautilids suffered a major crisis event in the Late Triassic (TEICHERT 1986) and emerged as the only remaining nautiloid group. They suffered another crisis event in the late Tertiary from which *Nautilus* LINNÉ 1758 is considered the only survivor. In general, the evolution of the order can be viewed as Devonian to Triassic, Jurassic to late Tertiary, and Recent.

Early nautilids were not significantly different in shell design and style of buoyancy regulation from late oncocerids, all being cyrtocones and gyrocones and all being exogastrically coiled (text fig. 18, Fam. 108, 110). The Liroceratidae (text fig. 18, Fam. 111) were the first to develop the involute coiled shell without ornamentation and a central siphuncle connecting widely spaced septa — the optimum design, as explained by CHAMBERLAIN (1988). The Tainoceratidae, Koninchioceratidae, Trigonoceratidae, and Grypoceratidae (text fig. 18, Fam. 112-115) continued this trend, while increasing the rate of expansion (greater involuteness) modified by experiments in ornamentation and cross-section shape. The extent of their stratigraphic ranges and numbers of genera attest to the success of this design. Families with short ranges and a low number of genera are generally characterized by being extremely compressed, and having unusual ornamentation, or modified apertures, but exceptions do occur.

At the level of detail used in this paper, there is little to differentiate families of post-Triassic nautilids. All are involute to occluded, that is with the last whorl

34

FRANCONIAN TREMPEALEAUAN

CAMB	ORD	SIL	DEV	CARB	PERM	TRI	JURA	CRET	TERT

PLECTRONOCERIDA
1 [12]
2 [2]

ELLESMEROCERIDA
3 [51]
4 [2]
5 [3]
6 [1]
7 [9]
8 [13]
9 [17]
10 [2]
11 [1]
12 [1]

13 [7] PROTACTINOCERIDA

14 [4] YANHECERIDA

ENDOCERIDA
15 [4]
16 [24]
17 [38]
18 [2]
19 [5]
20 [3]
21 [2]
22 [10]
23 [1]
24 [3]
25 [4]
26 [1]
27 [1]

ORTHOCERIDA
28 [6]
29 [34]
30 [3]
31 [46]
32 [14]
33 [10]
34 [3]
35 [1]
36 [2]
37 [1]
38 [1]
39 [1]
40 [5]
41 [5]
42 [1]
43 [1]
44 [1]

INTEJOCERIDA
45 [1]
46 [1]
47 [2]
48 [2]

TARPHYCERIDA
49 [10]
50 [9]
51 [9]
52 [13]
53 [1]

ACTINOCERIDA
54 [2]
55 [8]
56 [8]
57 [3]
58 [2]
59 [2]
60 [1]
61 [7]
62 [1]
63 [1]

FRANCONIAN TREMPEALEAUAN

CAMB	ORD	SIL	DEV	CARB	PERM	TRI	JURA	CRET	TERT

64 [9] **ASCOCERIDA**
65 [3]
66 [1]

67 [25] **ONCOCERIDA**
68 [10]
69 [4]
70 [5]
71 [5]
72 [22]
73 [13]
74 [14]
75 [6]
76 [5]
77 [20]
78 [5]
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82 [8]
83 [2]
84 [3]
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86 [4] **DISCOSORIDA**
87 [7]
88 [13]
89 [2]
90 [7]
91 [1]
92 [5]
93 [7]
94 [1]
95 [3]
96 [16]
97 [12]
98 [16]
99 [12]
100 [3]
101 [16]

102 [1]
103 [7]
104 ? [10] **BARRANDEOCERIDA**
105 [4]
106 [9]
107 [9]

108 [36] **NAUTILIDA**
109 [3]
110 [8]
111 [12]
112 [23]
113 [11]
114 [20]
115 [15]
116 [5]
117 [2]
118 [2]
119 [4]
120 [1]
121 [4]
122 [1]
123 [1]
124 [1]
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126 7
127 [3]
128 [4]
129 [10]
130 [4]
[1]

encompassing the previous whorl, and differ in details of ornamentation, cross-section shape and suture design. These similarities presumably reflect the origin of post-Triassic nautilids (text fig. 18, Fam. 126-131) from a surviving member of the Syringonautilidae, *Cenoceras* HYATT 1884 (text fig. 18, Fam. 122) (KUMMEL 1964). The shell design and style of buoyancy regulation of post-Triassic nautilids is a compromise between the efficient management of buoyancy by simple hydrostatic adjustments and stability a n d locomotor design, and the extension of habit depth.

Nautilus LINNÉ 1758 first appears in late Eocene or early Oligocene strata in the region of the Caspian and Aral Seas (SHIMANSKIY 1957) but has not been reliably reported from late Oligocene through Pleistocene rocks, appearing again in Holocene strata. TEICHERT (1985, 1986) and TEICHERT & MATSUMOTO (1986) make the interesting observation that *Nautilus* LINNÉ 1758 should be viewed not as a "living fossil", but as the genus in the position of a starting a new radiation of nautiloid cephalopods, just as *Cenoceras* HYATT (1884) was to the post-Triassic nautilids.

Conclusions.

The influence of buoyancy regulation on the macroevolution of nautiloid cephalopods can be summarized by comparing the five solutions outlined above with the total stratigraphic record of the groups (text fig. 18). The success of Solution I as used by the Cambrian orders and Ellesmerocerida, and exemplified by the Ellesmeroceratidae (Fam. 3), may have been more of a success in the absence of direct competition than the success of a mechanism of buoyancy regulation. That is, they may have been afforded the luxury of a fairly inefficient system. The fact that this method of buoyancy regulation did not occur again in the evolutionary history of nautiloid cephalopods suggests that the system was not without flaws.

The Endocerida, Intejocerida, and Orthocerida were the first to add mineral ballast to the phragmocone (Solution II). The Endocerida and Intejocerida added ballast within large siphuncles, whereas the Orthocerida added ballast to camerae and occasionally to small diameter siphuncles. The extremely short evolutionary history of the Intejocerida presumably reflects the expense of energy required to fill a very large diameter siphuncle (up to one-half diameter of the shell) with longitudinal, radially arranged lamellae. In terms of biomineralization, the intejocerid buoyancy system is much more complex and energy expensive than that of coeval endocerids. Even though they were successful relative to intejocerids, the Endocerida were clearly less successful than the coeval Orthocerida (text fig. 18). The most successful orthocerid families (text fig. 18, Fam. 29, 31, 32) optimized design of the orthocone into a long, slowly expanding shell, maximized hydrostatics by the use of long siphuncle segments of small diameter, and developed sophisticated buoyancy control and placement of ballast. The Actinocerida employed a combination of endocerid and orthocerid styles with limited success.

The Oncocerida and Discosorida were both successful in developing the system of buoyancy regulation categorized as Solution III. This success must be viewed in the context of a benthic habit, as opposed to the nektonic or nekto-benthic habit of most other nautiloid cephalopods. By reducing the buoyancy of the phragmocone through shell design, they eliminated the need to precipitate mineral ballast; instead, they developed efficient hydrostatic systems for managing water ballast.

The trade-off was a decrease in mobility. Their abrupt disappearance may reflext their inability to outmaneuver the then rapidly evolving chondrichthian fish (CHAMBERLAIN 1988), or competitive pressures from early nautilids with similar habits and greater mobility.

Too little is known about the Ascocerida and the biomechanical advantages and disadvantages of shell truncation and the cuttlebone-like exoskeleton (S o l u t i o n

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Text fig. 18. Stratigraphic record of nautiloid cephalopod families. Scale of periods, epochs, or ages is that of HARLAND & al. (1982). Range control is by age where possible and by epoch when not. Families are arranged within orders on the basis of first appearance and may not reflect evolutionary significance. The number in brackets is the generic diversity of a family. Sources for the data are listed in the text. Families by orders are: P l e c t r o n o c e r i d a : 1 = Plectronoceratidae, 2 = Balkoceratidae. — E l l e s m e r o c e r i d a : 3 = Ellesmeroceratidae, 4 = Acaroceratidae, 5 = Huaiheceratidae, 6 = Xiashanoceratidae, 7 = Bassleroceratidae, 8 = Protocycloceratidae, 9 = Baltoceratidae, 10 = Bathmoceratidae, 11 = Cyrtocerinidae, 12 = Shideleroceratidae. — P r o t a c t i n o c e r i d a : 13 = Protactinoceratidae. — Y a n h e c e r i d a : 14 = Yanheceratidae. — E n d o c e r i d a : 15 = Cyrtendoceratidae, 16 = Proterocameroceratidae, 17 = Endoceratidae, 18 = Emmonsoceratidae, 19 = Allotrioceratidae, 20 = Manchuroceratidae, 21 = Thylacoceratidae, 22 = Piloceratidae, 23 = Chihlioceratidae, 24 = Yorkoceratidae, 25 = Narthecoceratidae, 26 = Botryceratidae, 27 = Humeoceratidae. — O r t h o c e r i d a : 28 = Troedssonellidae, 29 = Orthoceratidae, 30 = Sactorthoceratidae, 31 = Pseudorthoceratidae, 32 = Geisonoceratidae, 33 = Proteoceratidae, 34 = Clinoceratidae, 35 = Stereoplasmoceratidae, 36 = Dawsonoceratidae, 37 = Mysterioceratidae, 38 = Sphooceratidae, 39 = Offleyoceratidae, 40 = Paraphragmitidae, 41 = Lamellorthoceratidae, 42 = Brachycycloceratidae, 43 = Folioceratidae. — I n t e j o c e r i d a : 44 = Engorthoceratidae, 45 = Majoceratidae, 46 = Bajkaloceratidae, 47 = Padunoceratidae, 48 = Intejoceratidae. — T a r p h y c e r i d a : 49 = Tarphyceratidae, 50 = Estonioceratidae, 51 = Lituitidae, 52 = Trocholitidae, 53 = Ophidioceratidae = A c t i n o c e r i d a : 54 = Polydesmiidae, 55 = Actinoceratidae, 56 = Ormoceratidae, 57 = Wutinoceratidae, 58 = Gonioceratidae, 59 = Georginidae, 60 = Meitanoceratidae, 61 = Armenoceratidae, 62 = Huroniidae, 63 = Carbactinoceratidae. — A s c o c e r i d a : 64 = Ascoceratidae, 65 = Hebetoceratidae, 66 = Choanoceratidae. — O n c o c e r i d a : 67 = Oncoceratidae, 68 = Valcouroceratidae, 69 = Graciloceratidae, 70 = Tripteroceratidae, 71 = Diestoceratidae, 72 = Acleistoceratidae, 73 = Polyelasmoceratidae, 74 = Nothoceratidae, 75 = Karoceratidae, 76 = Cyrtoceratidae, 77 = Jovellaniidae, 78 = Hemiphragmoceratidae, 79 = Trimeroceratidae, 80 = Tripleuroceratidae, 81 = Poterioceratidae, 82 = Ptenoceratidae, 83 = Archiacoceratidae, 84 = Bolloceratidae, 85 = Aktjubocheilidae. — D i s c o s o r i d a : 86 = Ruedemannoceratidae, 87 = Cyrtogomphoceras, 88 = Westonoceratidae, 89 = Lowoceratidae, 90 = Phragmoceratidae, 91 = Greenlandoceratidae, 92 = Discosoridae, 93 = Mandaloceratidae, 94 = Mesoceratidae, 95 = Entimoceratidae, 96 = Naedyceratidae, 97 = Ukhtoceratidae, 98 = Taxyceratidae, 99 = Devonocheilidae, 100 = Mecynoceratidae, 101 = Brevicoceratidae. — B a r r a n d e o c e r i d a : 102 = Plectoceratidae, 103 = Lechritrochoceratidae, 104 = Barrandeoceratidae, 105 = Uranoceratidae, 106 = Apsidoceratidae, 107 = Nephriticeratidae. — N a u t i l i d a : 108 = Rutoceratidae, 109 = Tetragonoceratidae, 110 = Centroceratidae, 111 = Liroceratidae, 112 = Tainoceratidae, 113 = Koninckioceratidae, 114 = Trigonoceratidae, 115 = Grypoceratidae, 116 = Aipoceratidae, 117 = Ephippioceratidae, 118 = Solenochilidae, 119 = Rhiphaeoceratidae, 120 = Permoceratidae, 121 = Scyphoceratidae, 122 = Syringonautilidae, 123 = Clydonautilidae, 124 = Gonionautilidae, 125 = Siberionautilidae, 126 = Nautilidae, 127 = Pseudonautilidae, 128 = Paracenoceratidae, 129 = Cymatoceratidae, 130 = Hercoglossidae, 131 = Aturiidae.

V) to provide any real insights into their evolution, although they were as successful as several other groups.

In terms of longevity and number of genera within orders, coiling (Solution IV), as exemplified by the Nautilida, was the optimum solution for an energy efficient method of establishing equilibrium between buoyancy and mass. Not only did coiling eliminate the need for mineral ballast, but also most of the need for water ballast. Thus the hydrostatic system could be simplified, while shell design was gradually modified to produce a "best" compromise between stability, buoyancy equilibrium, and mobility. Such was not always the case. Both the Tarphycerida and Barrandeocerida used the coiled shell in attempts to reach the same optimum solution. Their failure can be traced to their not being able to achieve an involute shell design. The gyroconic to evolute coiling and long living chambers resulted in a mechanically unstable shell design and must certainly reflect the typical slow rate of shell expansion which is typical of early Ordovician nautiloid cephalopods.

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