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CEPHALOPOD ADAPTATIONS—THE RECORD AND ITS INTERPRETATION

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IT SHOULD be recognized at the outset that the present paper is highly speculative in character. Not that the author has much faith in such a method of attacking a problem, but, as will appear in the sequel, because this is the only method of approach in any consideration of the probable structure of the soft parts or habits of life of the extinct representatives of this very important class of the Mollusca.

The abundance of fossils of this class in the English midlands, where William Smith first developed the idea of stratigraphic succession, their similar abundance in the historic eastern Alps and elsewhere in Europe near centers of scientific population, early stimulated speculation regarding the characters of the inhabitants of these fossil shells, and so much has been written upon this subject that it is doubtful whether any of the ideas advanced here have not already been proposed in one form or another. I have tried to acquaint myself with the literature, but will not attempt citation in most cases, contenting myself with the foregoing disclaimer of originality.

The Cephalopoda, whose ancient line extends over at least a hundred million years from the oldest known forms of the Cambrian period to the present, and which easily comprises upward of 10,000 known extinct species of great variety of form and presumably of habits, is represented

in existing seas by a single restricted (Willey, 1902, recognizes four species) genus with an external shell—the familiar pearly Nautilus; by the less known monotypic genus *Spirula*, with an internal shell; by the variety of active squids and cuttles, with an internal highly modified vestige of a shell; and by the less active octopus tribe, without any trace of a shell.

Throughout the greater part of the geological record their representation in the rocks will naturally be the shelled forms, which alone furnish the requisite hard parts for normal preservation as fossils. Among these the great group of ammonites, with their highly specialized septa, have been entirely extinct since Cretaceous time. (I do not think that I need waste space in refuting Steinmann's idea that the existing dibranchiates are their direct descendants.) The racial history of the ammonite order extended from the late Silurian to the close of the Upper Cretaceous—an inconceivably long period, during which they developed a multitude of forms, and they were easily the dominant cephalopods throughout much of the Mesozoic era.

Since the existing shell-less forms are geologically modern and show every indication of post-Paleozoic evolution culminating in modern times, they afford but slight basis for comparison with the multitude of shelled forms that go back to the oldest fossiliferous rocks. The

existing *Spirula*, which is itself related to the ancestral squids, is quite unlike the remote shelled ancient stock; so that the existing *Nautilus* alone can serve as a point of departure from which to envisage the structure and habits of the majority of fossil forms.

This lack of existing comparable forms has led to serious misinterpretations of extinct forms, stratigraphic and taxonomic paleontologists usually not having seen the forest because of the trees, and has opened the way for a multitude of diverse speculations and generalizations, more often dogmatic than probable. It is proposed in the following pages to pass in review what may be logically inferred regarding the structure and habits of these long vanished races, and it is freely admitted that a single fact of observation may upset a sheaf of deductive philosophy.

CEPHALOPOD CLASSIFICATION

Richard Owen, who gave us an admirable account of the anatomy of the pearly *Nautilus* in 1832, divided the existing cephalopods into two sub-classes—the two-gilled, shell-less Dibranchiata, and the four-gilled *Nautilus* or Tetrabranchiata. Paleontologists have rather generally assumed that the extinct nautiloids and ammonoids had four gills as in the single surviving genus *Nautilus*, although the two-gilled forms were obviously derived from the same stock. This assumption is highly illogical and equally improbable. It is not a matter of great moment whether the extinct forms had two, four, or some other number of gills—there is a great amount of diversity in this feature throughout the molluscan phylum; but it is important, it seems to me, not to base their segregation into major groups upon the number of gills when we can never hope to know what the number was in 99 per cent of the cases. The sub-classes

of Owen are therefore meaningless throughout all time but the present. The alternative terms Ectocochlia and Endocochlia for the two classic sub-classes are not particularly euphonious, fail to recognize the threefold diversity of the cephalopods, and are most inappropriate, since a considerable number of the Endocochlia lack all traces of a shell, and others—the extinct belemnoids and the existing *Spirula*—are ectocochlia in their youth and become endocochlia during their ontogeny.

Three subclasses should be recognized, namely: the Nautiloidea, Ammonoidea, and Coleoidea or Dibranchiata—the last largely living, and the fossil forms furnishing enough indications of their soft anatomy in the fine grained muds of the Jurassic to give a fairly clear idea of their structure.

A second rather general misconception of another morphological feature of the extinct animal has been the assumption that since the pearly *Nautilus* has numerous tentacles, all fossil nautiloids and ammonoids were similarly equipped. We know that in *Spirula*, the existing squids and Octopoda, and the extinct belemnoids, quite a different and more restricted number of more specialized tentacles was universally present, and since these groups were derived from the more primitive shelled stock, the question of whether fossil nautiloids and ammonoids had many tentacles or a few so-called arms is to be determined, if at all, by evidence drawn from the geological record and not from their supposed position in the taxonomic scheme of the systematists.

The keynote of evolution of the hosts of extinct cephalopods, as it appears to me, is adaptation—a thought already ably voiced by Diener. The founders of the more modern study of fossil cephalopods—men like Alpheus Hyatt—were entirely

dominated by a sort of theological philosophy, and particularly by one of the outstanding tenets of the American school of Neo-Lamarckianism, namely: that of racial senescence as expressed in seemingly bizarre appendages or ornamentation, and supposed atavistic simplification of the shell architecture. What could seemingly be more conclusive evidence of senescence than *Baculites*, appearing near the close of the geological record of the ammonites, with its tiny coiled baby shell like that of its ancestors, early forsaking the ancestral plan of rectitude and straightening out into a large orthocone? It would even have an immoral quality in the mind of the late John M. Clarke.

However, since racial senescence, in the sense that the protoplasm, vital force, nucleic control, or whatever you choose to call it, had suffered an old-age devitalization which was responsible for the observed changes in form, is non-existent, some other explanation must be sought, and my answer would be that this was adaptation to new environments or habits. Racial senescence is only permissible as a descriptive phrase for a race, not necessarily old, which is not overly successful in competition with its contemporaries and is therefore dwindling. Such a one, and there are many throughout the history of all fossil groups, is more appropriately compared with a backward human race than with a senile individual. In any case the use of the phrase is not the explanation of the observed changes of form or ornamentation that the fossil record discloses.

THE EVOLUTION OF THE CEPHALOPODS

In the following pages I shall endeavor to give a very much abridged account of the evolution and adaptation of the group, and then discuss a few selected examples in somewhat more detail. To attempt

a complete survey of a group containing as many described species as all the known mammals—both recent and fossil—would be to write a book, and probably to obscure the subject. The general phylogenetic relations of the different groups and a simplified epitome of their geological history are shown on Plate 1.

Malacologists are rather generally agreed that the archetypal stock of all of the Mollusca could not have differed greatly from the synthetic form which E. Ray Lankester constructed many years ago, and such a form is shown in longitudinal section in Plate 2, figure 1, in which the shell, visceral cone, course of the alimentary canal, and crawling foot are differentiated. Such a form might readily give origin to gastropod, scaphopod, lamellibranch, or amphineuron. To become an incipient cephalopod it would have merely to narrow the aperture of the shell, heighten the cone, and cut off its apex by septa. How this came about I shall consider presently.

At this point it is necessary to correct another misconception of the soft parts. When the short body of the pearly *Nautilus* is compared with that of a more active squid the proportions are in striking contrast, and it has been tacitly assumed that the extinct shelled species had bodily proportions comparable to those of the *Nautilus*. Many had, or were even shorter; others had not, and were quite as elongated as a squid or even longer. Examples can be cited at almost any time during geological history. For instance, the cigar-shaped body of the immature *Proterocameroceras brainerdi* (Whitfield) of the Ordovician was eight or nine times as long as it was wide.

Other early nautiloids with elongated bodies were the genera *Ophidioceras* (fig. 13), *Schroederoceras* (fig. 12), *Deltoceras*, *Piloceras*, *Vaginoceras*, *Lituites*, etc. Among the later ammonoids the genus *Macro-*

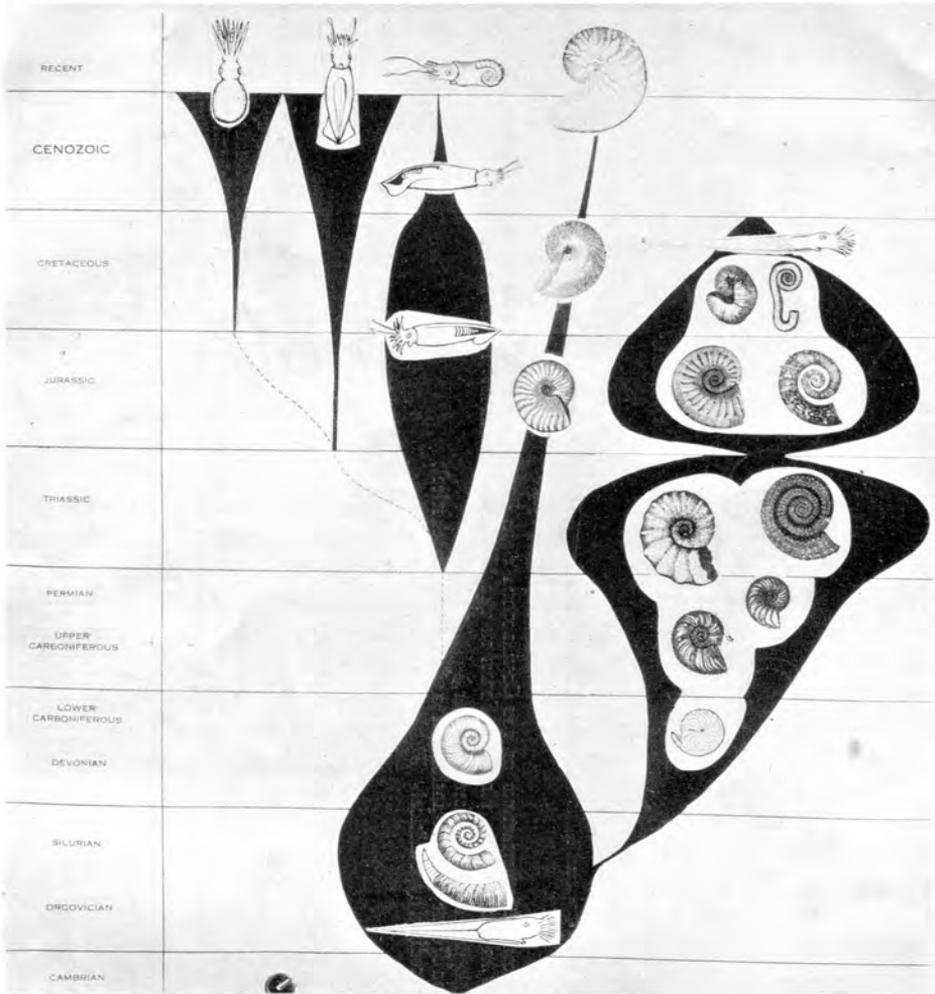


DIAGRAM ILLUSTRATING THE PHYLOGENETIC RELATIONSHIPS OF THE VARIOUS CEPHALOPOD TYPES, THEIR RANGE IN TIME, AND RELATIVE REPRESENTATION IN THE PAST

At the left is the life-line of the relatively modern Octopoda; the next life-line is that of the somewhat more ancient and less specialized Decapoda; the next is that of the Belemnitoidea, which reached their maximum during the Mesozoic and are represented in existing seas by *Spirula*; the next is that of the Nautiloidea, which reached their maximum in the earlier Paleozoic. The right hand life-line is that of the Ammonoidea, which appeared in the record in the late Silurian, reached an early maximum of differentiation in the Triassic, became nearly extinct in the late Triassic, rapidly attained a second maximum in the Jurassic and became extinct with the Upper Cretaceous.

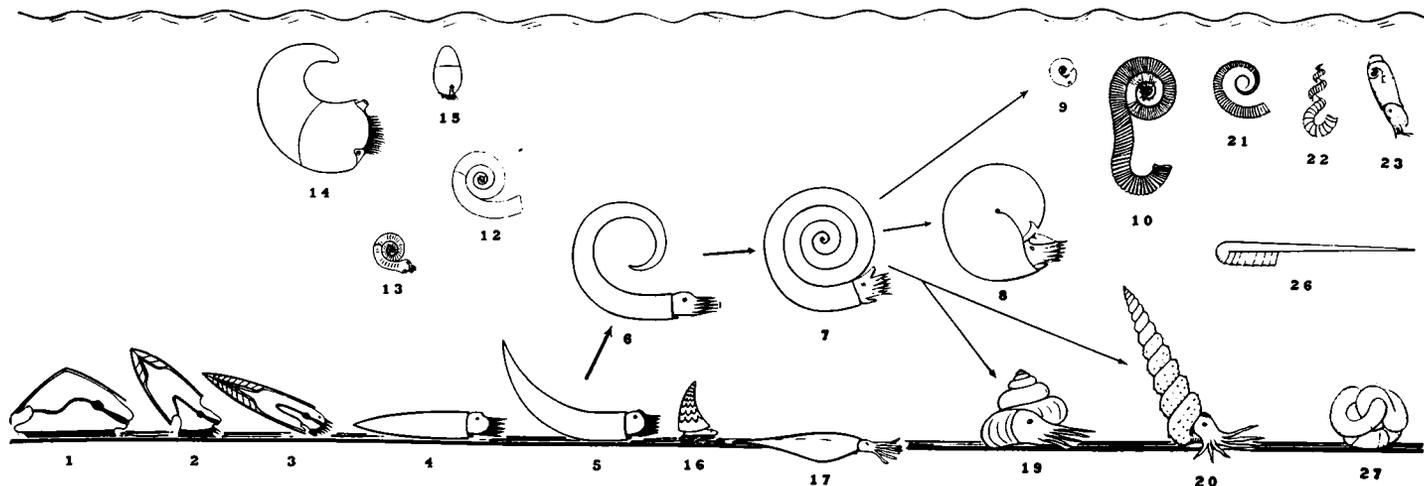


DIAGRAM ILLUSTRATING THE ADAPTATIONAL MODIFICATIONS OF THE CEPHALOPODA WITH EXTERNAL SHELLS, TO BE READ FROM LEFT TO RIGHT. BENTHONIC FORMS AT THE BOTTOM, NEKTONIC FORMS IN THE MIDDLE, AND PELAGIC FORMS AT THE TOP

- FIG. 1. The Molluscan archetype, hypothetical. (After Lankester.)
 FIG. 2. Elongation and contraction of cone, partial transformation of the foot, hypothetical.
 FIG. 3. More advanced stage of preceding, hypothetical.
 FIG. 4. Horizontal Orthoceras stage.
 FIG. 5. Cyrtoceras stage.
 FIG. 6. Gyroceras stage.
 FIG. 7. Fully coiled stage.
 FIG. 8. Involutely coiled stage.
 FIG. 9. *Morphoceras pseudoanceps* Douvillé, a pelagic Jurassic ammonite with partially closed aperture. (Bajocian of France, after Douvillé.)
 FIG. 10. *Macroscaphites ivani* (d'Orbigny), a Lower Cretaceous non-swimming ammonite. (Barremian of France, after d'Orbigny.)
 FIG. 12. *Schroedoceras eatoni* Whitfield, an Ordovician partially floating nautiloid. (Fort Cassin beds of New York, after Ruedemann.)
 FIG. 13. *Ophioceras simplex* Barrande, a Silurian partially floating nautiloid with constricted aperture. (Étage E of Bohemia, after Barrande.)
 FIG. 14. *Pbragnoceras inflexum* Hedström, an endogastric prevalingly floating Silurian nautiloid with constricted aperture. (Silurian of Gotland, after Hedström.)
 FIG. 15. *Mandaloceras bohemicum* (Barrande), a pelagic Silurian nautiloid with constricted aperture. (Étage E of Bohemia, after Barrande.)
 FIG. 16. *Cyrtoceras parvulum* Barrande, a representative of the breviconic small forms which retained the primitive crawling foot as late as Silurian time. (Étage E of Bohemia, after Barrande.)
 FIG. 17. *Goniceras*, representing a group of greatly depressed benthonic crawlers. (After Ruedemann.)
 FIG. 19. *Turrilites robertianus* d'Orbigny, a Lower Cretaceous benthonic crawler. (Albian of France, after d'Orbigny.)
 FIG. 20. *Turrilites tuberculatus* Bosc. Another late Lower Cretaceous benthonic crawler. (Albian of France, after d'Orbigny.)
 FIG. 21. *Spiroceras bifurcatum* (Quensted), a Jurassic feebly swimming and floating ammonite (Callovian of Würtemberg, after Quenstedt.)
 FIG. 22. *Heteroceras reussianum* d'Orbigny, an Upper Cretaceous pelagic ammonite. (Emscherian of Germany, after E. Fraas.)
 FIG. 23. *Spirula australis* Lamarck, floating position. (After Chun.)
 FIG. 26. *Ptyhoceras puzosianus* d'Orb., a Lower Cretaceous swimmer. (Neocomian of France, after d'Orbigny.)
 FIG. 27. *Nipponites mirabilis* Yabe, a sessile Upper Cretaceous form from Japan. (After Yabe.)

scaphites (fig. 10), the family *Lytoceratidae*, and numerous others, show a similar elongation of the body chamber.

Without attempting a detailed explanation, it may be noted that in either swimming or passively floating forms there seems to be a direct correlation between the weight of the body and the buoyancy of the empty chambers of the shell, calculated to maintain the animal in a normally functional position according to its habits. This may seem like reasoning in a circle, but I shall try to show in a few selected cases that it is not.

Plate 2, figure 2 shows a hypothetical stage in which the shell had become partially elongated and contracted, the visceral cone was correspondingly narrowed, and a few partial septa, lined internally with horny endocones, had developed, much as in the family *Endoceratidae* of the Ordovician and Silurian periods, though not in such an advanced manner as in that family. The shell had not yet developed enough air chambers to be appreciably buoyant, and the foot had shortened progressively, although still possessing a partially functional crawling surface; its anterior portion had commenced to encircle the mouth, and to assume tactile and prehensile functions.

Plate 2, figure 3 shows a second, more advanced hypothetical stage, with a still narrower and more elongated shell and visceral cone, and more numerous septa. The foot is almost entirely transformed into tentacular segments, which completely encircle the mouth; its hinder portion has the two reduced lateral halves appressed, much as in the taxodont genus *Nucula*, and this part becomes the incipient swimming siphon or hyponomic funnel.

In Plate 2, figure 4 we pass from the hypothetical to the actually observed *Orthoceras* form with which it is customary to start cephalopod phylogeny. The

most obvious feature, giving its name to this type, is that the shell is an orthocone, or straight cone. However, a more searching study of the orthocones that are so abundant in the older Paleozoic rocks shows the greatest amount of variety in the details of structure, and is clearly indicative of a like variety of habits of life. When we recall that orthocones swarmed in the older Paleozoic seas, and largely filled the rôle of the fishes of later times, we are bound to admit the probability of their having become adapted for every possible environmental niche. Some were sluggish, others active; some were benthonic, crawling on the sea bottom; others nectonic or swimming forms; and still others may have been planktonic, floating on the surface. They ranged in size from that of a lead-pencil to giant forms a dozen feet or more in length. (Certain species of *Endoceras* are said to have attained a length of 15 feet.) Their siphuncles were tiny to excessively large, and variously modified; their early chambers were empty or filled to various degrees with organic deposits; some fashioned accessory chambers far forward on top of the adult living chamber, whose buoyancy enabled them to maintain an even keel (See Plate 3). I shall return to some of these modifications of the orthocones and their probable interpretation after following the general course of evolution of the whole group on through to the attainment of the enrolled shells so typical of the late Paleozoic and succeeding Mesozoic era.

PROGRESSIVE COILING OF THE SHELL

If one single feature may be said to characterize the phylogeny of the shelled cephalopods as a whole, it is that of progressive coiling. The older naturalists found a supposed reason for this in the phrase "natural selection favored the

compactly coiled shell," but as Dunbar has pointed out, this explanation, like so many of the natural selection sort of explanations, fails to explain why, or to take into account the intermediate curved (cyrticone) and incipiently coiled (gyrocone) stages, and this same author, adopting Buckman's idea (1919), has elaborated the true reason, namely: that progressive coiling is an adjustment to the buoyancy of the empty chambers of the shell which induced it.

The older naturalists, commencing I believe with Buckland in 1835, believed that the early chambers of the shell served for hydrostatic purposes, a belief due in the first instance to one of the few mistakes in the account of the anatomy of *Nautilus* given by Owen, who described the axial canal of the siphon as forming a communicating conduit between the empty chambers and the mantle cavity. When the animal wished to descend, these chambers were filled with water; when it wished to rise they were emptied—exactly on the operative principle of a submarine. This idea is perpetuated in the last edition of Eastman's Zittel (1913, p. 589), although Dean's (1901) observations on the identical buoyancy in the living and dead *Nautilus* and Willey's (1902) demonstration that the siphon does not communicate with the mantle cavity in *Nautilus* should set at rest the hydrostatic myth. The empty chambers in *Nautilus* are buoyant once for all, and what is true in this respect for *Nautilus* should apply to all of the extinct camerated forms that did not fill the early chambers with organic deposits.

This buoyancy of the unfilled earlier chambers is the keynote to the observed changes in shell form, in both phylogeny and ontogeny, and the merit of first applying it in any detail belongs to Dunbar (1924).

With the formation of complete septa shutting off the apical chambers in the developing orthocones, their buoyancy in those forms that did not weight this end by organic deposits filling the chambers or elaborate deposits about the enlarged siphuncle would tend to tilt the shell forward. Such a tilting would be a handicap in either a nectonic or benthonic animal. Whether the resulting tension on the ventral side would cause a more rapid growth of the ventral shell margin, or whether normal secretion of the animal in so orienting its body as to keep its mouth out of the mud of the bottom or to remain horizontal in the water would be the predominant factor cannot be decided. In any event, the more rapid growth on the ventral side would result in an arcuate shell—the cyrticone (Plate 2, fig. 5), and the more the curvature, the more the forward migration of the center of gravity would be retarded.

This finally resulted in the gyrocone type of shell (Plate 2, fig. 6). The progressive coiling would not stop with this type since, as the shell is an expanding cone, the newest chambers immediately behind the living chamber, with their exterior position and much increased volume, would throughout adolescence tend to tilt the animal forward, and this would eventually result in the coiled type of shell known as an ophiocone (Plate 2, fig. 7). Complete equilibrium with the animal in a horizontal position most effective for swimming is only attained when the later chambers entirely invest the earlier whorls as in the existing *Nautilus pompilius*, a completely involute form. Or an ophiocone may attain the same stability if there are many volutions to the shell, which serves to explain the persistency of the latter type.

The foregoing simplified series of stages, illustrated by figures 1-8 of Plate 2, is

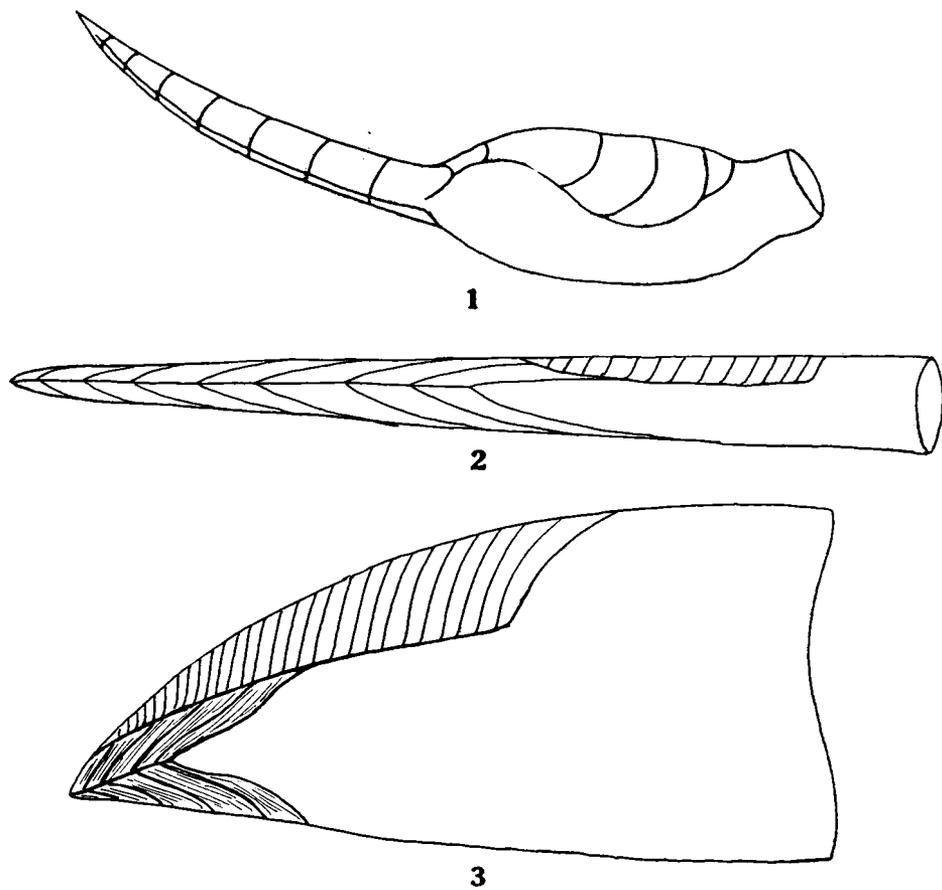
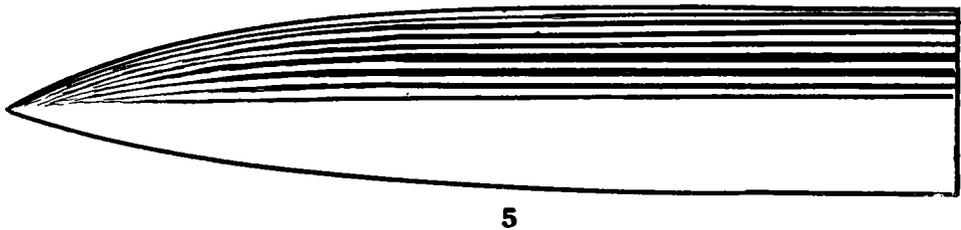
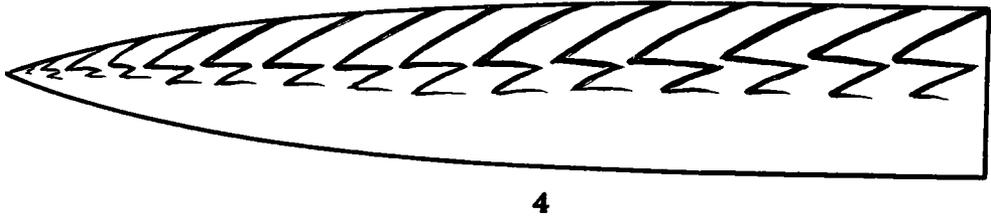
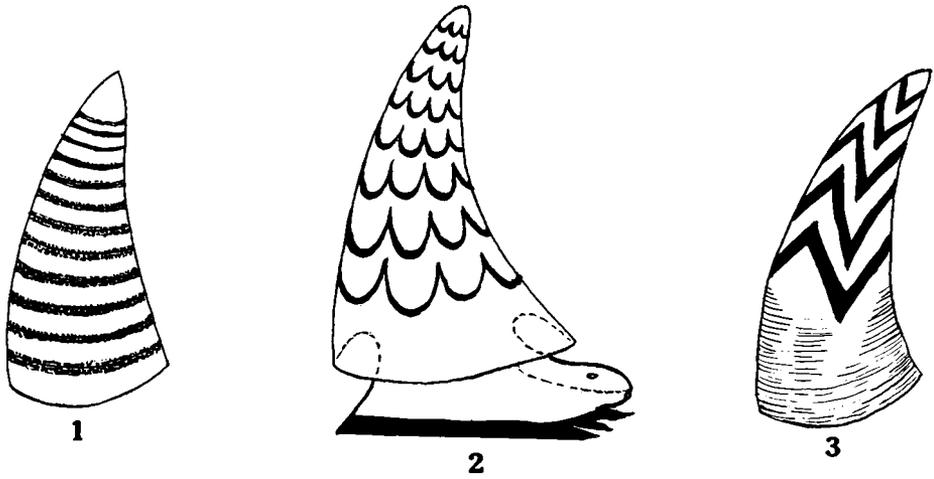


FIG. 1. *Ascoceras*, based upon *Ascoceras bohemicum* Barrande, from the Silurian of Bohemia.
FIG. 2. *Proterocameroceras brainerdi* (Whitfield). Ordovician of New York. (After Ruedemann.)
FIG. 3. *Piloceras*. (After restoration by Ruedemann.) An Ordovician type.
All in median longitudinal section.



COLOR PATTERN AND ATTITUDE AMONG THE EARLY NAUTILOIDS

- FIG. 1. *Cyrtoceras fallax* Barrande. Silurian of Bohemia.
- FIG. 2. *Cyrtoceras parvulum* Barrande, showing color pattern and restoration of soft parts. Silurian of Bohemia.
- FIG. 3. *Cyrtoceras decurio* Barrande. Silurian of Bohemia.
- FIG. 4. *Orthoceras anguliferum*. Middle Devonian of Germany. (After Dunbar.)
- FIG. 5. *Geisonoceras tenuitextum* (Hall). Middle Ordovician of New York. (After Ruedemann.)

an epitome of the general and normal trend of evolution in the shelled cephalopods. The end product would be a nectonic animal with greater or less locomotive powers—as were the majority of shelled forms. But there are a host of exceptions to this general trend, as there necessarily must have been if these animals were to adapt themselves fully to the varying environments of the seas—as they undoubtedly did.

LIFE HABITS OF THE ORTHOCONES

In considering these modifications we may first consider the variations shown in the early orthocones. Fully half of the known Ordovician cephalopods had shells which were orthocones. Speculations as to their habits of life have been more fantastic and mutually exclusive than is the case in any of the later cephalopods. They have been pictured as swimming in both vertical and horizontal attitudes, as having dragged their horizontal shells over the bottom, as having lived obliquely buried in the bottom, or as having been attached vertically by the apical end.

Ruedemann (1921) has shown conclusively that some of them were horizontal in their normal attitude. This is proved in the case of *Geisonoceras tenuitextum* of the Ordovician of New York by the preservation of a well marked longitudinal color pattern (Plate 4, fig. 5) on one side of the shell, which must have been the dorsal, since all marine organisms with a color pattern have the side toward the light contrasted with the opposite side. Not only so, but this author cites shells of this species with incrusting bryozoa in which the zoarium begins near the apex and extends forward on one side of the shell only, *pari passu* with its growth, which would be a most unlikely occur-

rence if the bryozoan had started on a dead shell.

If this dorso-ventral color pattern were an isolated case it might possibly be open to doubt, but it has been observed in specimens of orthocones of very different ages and widely separated geographically. Naturally the preservation of the color pattern of life in fossils of great antiquity is unusual, so that many such instances are not to be expected. Nevertheless I may cite such features in *Orthoceras trusitum* of the Silurian of New York, *Orthoceras anguliferum* of the Devonian of Germany (Plate 4, fig. 4), *Orthoceras* sp., of the Upper Carboniferous of Oklahoma, and I have no doubt that a protracted search through the systematic literature would disclose other instances. Those cited extend pretty well through the Paleozoic and over two continents, and I think that we may legitimately conclude that the horizontal attitude was the normal one for the majority of the orthocones.

Ruedemann considers such forms to have been benthonic and to have dragged their shells over the Paleozoic sea-bottoms. The objections to this interpretation are that their apertures are not oblique, the shells do not show wear incident to such a mode of life, and many show a hyponomic sinus which is usually correlated with a functional hyponomic funnel.

This last is not an especially weighty objection, since all cephalopods must have preserved the funnel for respiratory purposes even when it ceased to be functional as a locomotive organ; at least in the modern *Nautilus* its regular pulsation causes incurrent and excurrent streams, and the mantle does not take part in causing these movements, as it does in the dibranchiates.

I believe such forms to have been swimmers. Some doubtless hovered near the bottom or spent most of their time resting upon it, but others surely must have been more active. The idea that locomotion

backward was awkward is wholly anthropomorphic—it is to us, but is decidedly not for a cephalopod. The other idea that they would run the risk of fracturing the apex of the shell is altogether fanciful—they did not find their optimum conditions of life on a stern and rock-bound coast, and in any event nature usually provides against accidents in its tendency to overpopulation. (Pathological rostra of the Mesozoic belemnites are found fossil.)

Many students can not dismiss the idea from their minds that the cephalopod shells were too heavy and too unwieldy to have been propelled by the relatively simple method in vogue among these animals. This rests almost entirely upon the handling of museum specimens in which the chambers are filled with sediments, lithified, or calcified, or impregnated, or replaced with marcasite, etc. In the vast majority of forms throughout their whole geologic history, the shells were thin and in life were relatively light and easily propelled, and the specific gravity of the whole animal was close to that of the medium—so close, I imagine, that when the animal was expanded to its maximum extent it would float or rise in the water, and when withdrawn within its living chamber it would sink.

A belief in the swimming habits of the majority of orthoconic forms is also a reason for regarding them as having had "arms" like a squid rather than tentacles like a *Nautilus*, since when swimming these would trail behind, as do the extended tentacles in the *Nautilus*, and would furnish the necessary rudder to guide their passage through the water more effectively than tentacles. Obviously not all orthoconic forms were swimmers. I would expect such swimming forms to show some compression in the cross profile of the shell, and this is

perhaps true in a majority of cases. Crawling or grovelling forms should show some depression in the cross profile of the shell, and this can be seen in a number of forms.

The extreme example of depressed shell form, undoubtedly indicating a sedentary bottom-dwelling animal, which had probably lost the swimming habit and could move only by dragging its shell by the use of its arms, is the genus *Gonioceras* (Hall, 1847). This includes five or six Ordovician species found in Ontario, New York, Illinois, Wisconsin, Minnesota, and northern China. The shell is several times as wide as it is high, with lateral flanges; the septa are closely spaced and sinuous; and the siphuncle is large and nummuloidal. At maturity the aperture is greatly constricted. Since the muscular attachment of the animal to its shell is not especially firm throughout the Cephalopoda, this constriction of the aperture in *Gonioceras* would serve to prevent the rupture of the muscular attachment when the shell was pulled along over the bottom, and the angularity of the septa would also serve to give the animal a firmer hold on its shell. Hyatt (1884 and 1900) made some wild guesses regarding the affinity of this curious form; we are not, however, at present concerned with its taxonomic position, but only with its obvious adaptation to a benthonic existence; from this point of view it is completely adapted, and ceases to be curious—the large nummuloidal siphuncle may be regarded as ballast, helpful in maintaining an even keel (Plate 2, fig. 17).

I have already mentioned the habit of some of the earlier orthocones of using the siphuncle in this way, or of filling the earlier chambers to a greater or less degree with organic deposits to counteract their buoyancy. Large and often elaborately ornamented siphuncles occur in a number of families of nautiloids, as for example in the families Endoceratidae, Pilo-

ceratidae, and Cyrtendoceratidae; and every degree of internal filling of the earlier chambers may be seen in the families Actinoceratidae, Jovellanidae, and Poterioceratidae—collectively covering the time from Ordovician to Devonian.

An equally effective method of maintaining horizontality is illustrated by the families Ascoceratidae and Mesoceratidae—constituting the sub-order Mixochoanites of Hyatt—Ordovician and Silurian nautiloids. In these the shells have advanced slightly beyond the orthoconic form in most of the genera and are more or less cyrtocoenic. The living chamber of the adult is long and inflated, often contracted at the aperture, which is sometimes crested. The manner in which the center of gravity is kept back is by the formation of a linear series of air chambers (saddles) along the dorsal wall of the living chamber. Two examples of this are shown in the accompanying figures (Plate 3): *Proterocameroceras*—an orthoconic form, and *Ascoceras*—a cyrtocoenic form. A somewhat similar arrangement is exhibited in the allied family Piloceratidae of the Ordovician. In *Piloceras* the shell is relatively short and wide; the animal was stout, its visceral cone extending backward over six-sevenths of the distance to the apex of the shell; the living chamber is restricted dorsally and the animal thus rendered buoyant by the development of numerous dorsal saddles (air chambers), and the apex of the shell is ballasted by pseudosepta and conchyolin endocones.

According to Geikie, (I have not taken the pains to verify his count) the Silurian of the Bohemian basin furnished Barrande with 1127 species of Cephalopoda. Of these 554 were orthocones, and other statistically minded students have estimated the number of orthocones in the Ordovician as approximately fifty per cent of the total number of species of Cephalopoda known from that period. The

percentage is somewhat less for the Silurian as a whole, about 25 per cent for the Devonian, and about 20 per cent for the Carboniferous as a whole, although some very large sized forms do survive as late as Carboniferous times. In post Triassic times there are no orthoconic nautiloids. This proves that the general course of evolution in this sub-class was as I have indicated, and effectually combats the seemingly eccentric view of Owen—in which strangely enough he is followed by Willey and Spath—that the orthoconic are uncoiled from whorled ancestors.

THE CYRTOCONES

The number of species of cyrtocoenes in the Silurian of the Bohemian basin was 330. Both orthocones and cyrtocoenes were all originally referred to the two comprehensive genera *Orthoceras* and *Cyrtoceras*, but later systematists have partially segregated them into more natural generic groups. I have already indicated a probable variety of habits among the orthocones, and this is quite as clearly indicated among the cyrtocoenes. There can be slight doubt that what might be called the normal cyrtocoene was derived from orthoconic ancestors in the manner already outlined, or that such a one as is shown in Plate 2, figure 5 was a horizontal swimmer.

Among the cyrtocoenes, however, there are a considerable number of so-called breviconic forms, all from the Silurian (Étage E), which it seems to me throw an important light on their structure and habits. They are all of about the same size, i.e. 4 to 5 centimeters long and 2 to 3.5 centimeters in maximum diameter, and hence justly called small forms, and are conspicuously marked by mostly transverse color patterns that entirely encircle the shell and prove conclusively

that these shells were held erect in life and equally illuminated on all sides. By the same token the animals were benthonic crawlers and not swimmers. Not only were they crawlers, but I believe that they crawled by means of a soled foot like that of a gastropod and not by means of their tentacles as does the existing octopus. In fact, were it not for their camerated shells and siphuncles one would be disposed to doubt their cephalopod character and consider them gastropods.

My restoration of *Cyrtoceras parvulum* Barrande will indicate sufficiently my conception of the animal (Plate 4). The extent to which the soled foot has assumed a tentacular form in front is, of course, entirely problematic. If these forms were organized as I have assumed, they would represent a survival, as late as the Silurian, through a continuous ancestry, of the primitive nautiloid organization of the early Cambrian or pre-Cambrian, and would be otherwise unrelated to their contemporary cyrtoceran associates.

Among these cyrtocoines with color patterns on all sides of the shell are *Cyrtoceras fallax* Barrande, with straight transverse bands; *Cyrtoceras zebra* Barrande, with closely spaced fine subparallel wavy bands; *Cyrtoceras intricans* Barrande, with somewhat more angular and less regular bands, more pointed backward than forward and perhaps pre-nuncial to chevrons; *Cyrtoceras veteranum* Barrande, with closely spaced chevrons; and *Cyrtoceras decurio* Barrande with large angular chevrons. A sixth species is ornamented with spots all around.

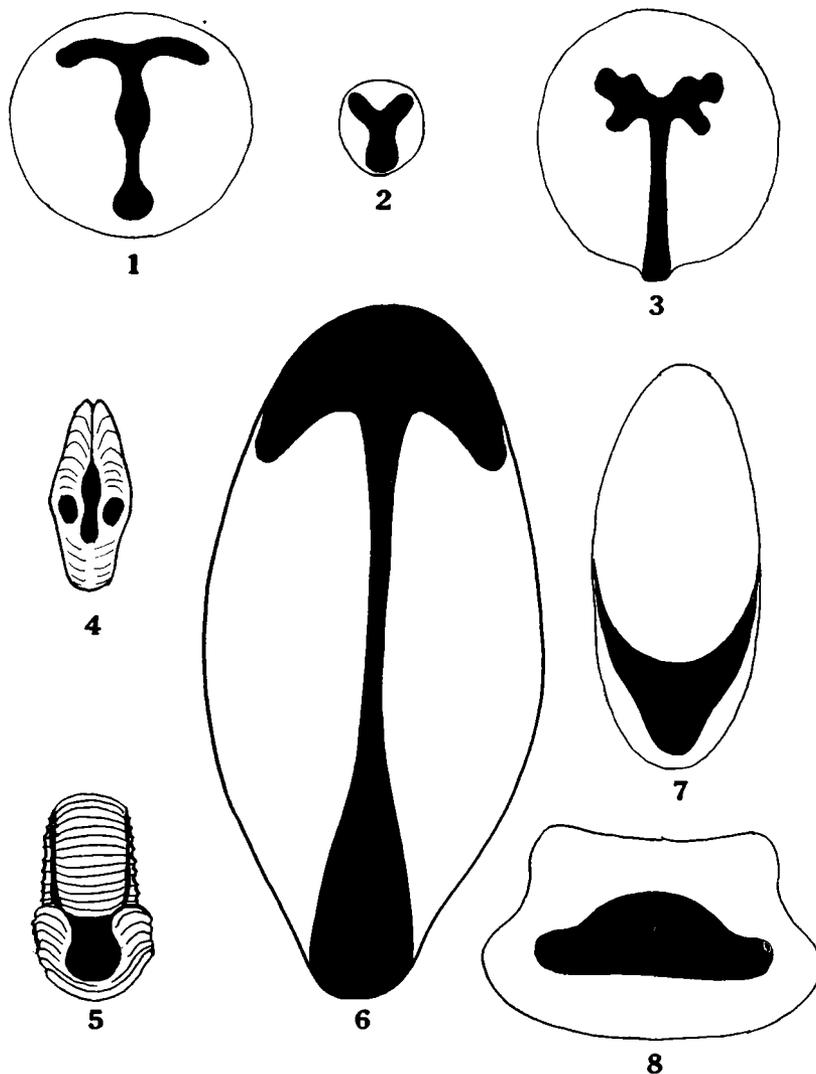
ADAPTATIONS FOR A MORE OR LESS PASSIVELY FLOATING MODE OF LIFE

Adaptations by means of which the animal spent most of its existence in passively floating are various and are attained in unrelated stocks throughout the geological history of the class. Whether they floated near the surface, in

intermediate depths, or hanging over the bottom—the feeding ground of the existing Nautilus—is immaterial; certainly those forms which retained locomotive powers could readily maintain their position at any desired depth. In the adaptation diagram (Plate 2) all floating forms have been placed near the surface, but this is solely a matter of composition on a crowded diagram. The recurved aperture in such an ammonite as *Macroscaphites*, or in some species of *Heteroceras* or *Nostoceras* leads to the conclusion that they drifted over the bottom while feeding, but in other genera there is no definite evidence on this point.

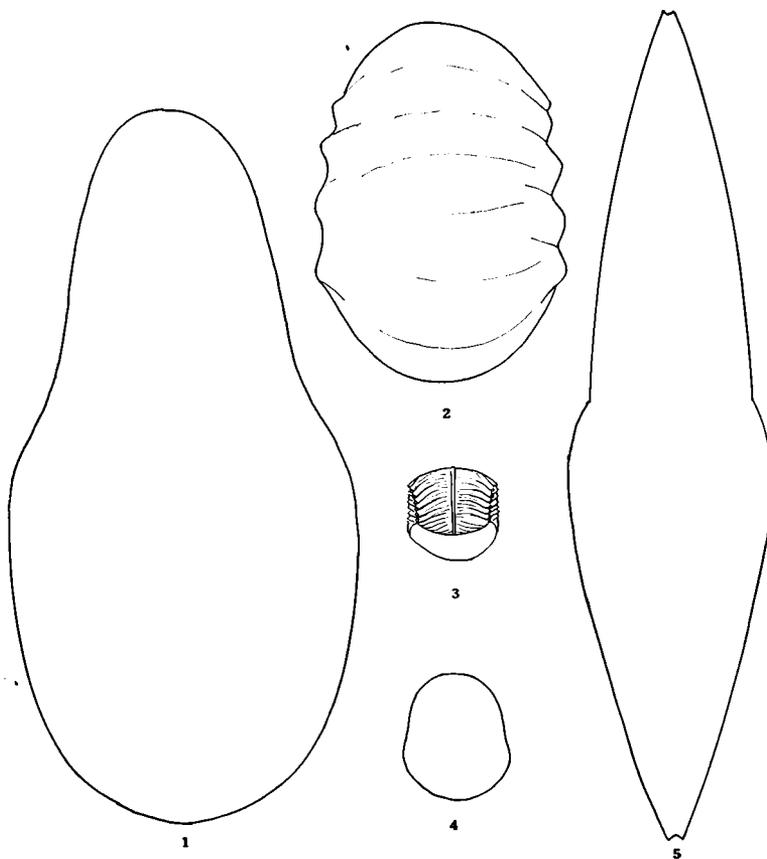
There are a considerable number of orthoconic Nautiloidea, prevailingly small and breviconic, found from the Ordovician to the Carboniferous, and principally in the families Rizoceratidae, Oncoceratidae, Poterioceratidae, and Trimeroceratidae, represented by a variety of genera, and exhibiting numerous differences in their structural details, which floated head downward by reason of the gas filled chambers of the apex of the cone. This type is illustrated in the diagram by *Mandaloceras* (Plate 2, fig. 15), a Silurian genus.

In *Mandaloceras* this position must have been maintained from infancy onward. At maturity the aperture of the living chamber was greatly contracted, but the hyponomic funnel probably retained its propulsive powers, since the space in front of it was not roofed over by the inflected margins of the aperture. The expulsion of water from the mantle cavity through the funnel would cause the animal to rise vertically. Many other of these forms had variously contracted apertures leaving only restricted openings for the eyes, tentacles, mouth, and funnel. Many students have thought that this was to be interpreted as indicating that their food



VIEWS OF VARIOUSLY CONSTRICTED APERTURES, ALL NATURAL SIZE

- FIG. 1. *Mandaloceras bohemicum* (Barrande). Silurian of Bohemia.
 FIG. 2. *Ophioceras simplex* Barrande. Silurian of Bohemia.
 FIG. 3. *Tetrameroceras panderi* (Barrande). Silurian of Bohemia.
 FIG. 4. *Morphoceras pseudoanceps* Douvillé. Bajocian of France.
 FIG. 5. *Normannites braikenridgei* (Sowerby). Middle Jurassic of France.
 FIG. 6. *Phragmoceras inflexum* Hedström. Silurian of Gotland.
 FIG. 7. *Arcestes intuslabiatus* Mojs. Upper Triassic of Austria.
 FIG. 8. *Hercoceras mirum* Barrande. Devonian of Bohemia.



END PROFILES OF VARIOUS CEPHALOPOD SHELLS, REDUCED ONE-HALF

- FIG. 1. *Nautilus pompilius* Linné, the best known existing species of *Nautilus*.
 FIG. 2. *Polyprychites laticosta* von Koenen. Neocomian of Germany. (After von Koenen.)
 FIG. 3. *Tropites subbullatus* (Hauer). Upper Triassic of Austria. (After Hauer.)
 FIG. 4. *Cyclolobus stachei* Gemmellaro. Late Paleozoic of Sicily. (After Gemmellaro.)
 FIG. 5. *Platoniceras meeki* Boehm. Upper Cretaceous of South Dakota.

was microscopic, and Abel has dubbed such forms microphagous. I see no reason for limiting the size of their food except by the size of the opening through which it had to pass (Plate 5).

The existing *Nautilus* is a voracious carnivore, very catholic in its taste. Doubtless the size of the aperture in such a fossil form as *Mandaloceras* imposed somewhat narrow limits with respect to size of the food particles, since it could not exert its jaws and tentacles through so narrow an opening and tear large sized prey to pieces. The contracted aperture was not, however, an adaptation due to feeding habits, but exactly the opposite, the contracted aperture having originated as a protective device which also served to keep the animal from becoming dislodged from its living chamber, exactly comparable with the apertures in such land snails as *Polygyra*, *Anastomia*, and *Pyrbia*. Such a form as *Mandaloceras*, if its aperture had been an open one, would have been a juicy morsel for its larger and more actively swimming contemporaries, and to call such apertures gerontic features is about as absurd as Schmidt's suggestion that the young may have been protected within the living chamber of the mother by them.

Many of these early floaters had shells which were cyrtocoines, often endogastric, as in the Silurian nautiloid *Phragmoceras*, shown in the diagram (Plate 2, fig. 14). These were in general somewhat larger forms than the breviconic orthocoines like *Mandaloceras*, but like them they retained the functional hyponomic funnel, and had greatly constricted apertures during their adult life. What was said of *Mandaloceras* applies also to forms like *Phragmoceras*, except that the latter could probably propel themselves horizontally. To rise or sink they would have to depend on the extension or contraction of the arms to

induce changes in their specific gravity, unless, like the existing *Spirula*, they could point their funnel in different directions.

Another series of evolutionary changes in the direction of adaptations for floating is exhibited by those nautiloids whose ancestors had completely coiled shells (ophiocones). These may have open apertures, as in *Schroederoceras* (Plate 2, fig. 12), an Ordovician genus; or contracted apertures, as in *Ophioceras* (Plate 5, fig. 2), a Silurian genus. They are contrasted with such adaptations as *Mandaloceras* or *Phragmoceras* in that they were normal swimmers with normally coiled shells during adolescence. At maturity the living chamber became partially free (uncoiled), the margins being built outward to accommodate the growth of the animal, which was then strikingly elongated as compared with the short bodied *Mandaloceras* or *Phragmoceras*, and must have passed the remainder of its life suspended obliquely in the water—the weight of the body causing the shell to tilt forward.

The end product of such an evolutionary adaptation as *Ophioceras*, in which it is pre-nuncial, is exhibited by the nautiloid genus *Lituities* Breyn., which in early Paleozoic time (Ordovician) set an example of modification that was repeated in substantially the same way by ammonoid genera like *Macroscaphites*, cons later. *Lituities* was a fairly large form in which the first three whorls form an ophiocone, indicative of its ophioconic ancestry, as well as its normal swimming attitude during adolescence. After this stage of its ontogeny the diameter of the shell increases rapidly and it is nearly straight in its growth for a distance about 14 times the diameter of the coiled early portion. The aperture has a shallow hyponomic sinus, narrow ventro-lateral crests, broad

lateral sinuses, and fairly well developed dorso-lateral crests. The living chamber was extraordinarily long, and the consequent weight of the animal must have caused the shell to assume an almost vertical attitude in the water. The adult *Lituites* must have drifted, head down, picking up its food on or near the bottom. If the hyponomic funnel remained functional, as the presence of a hyponomic sinus would seem to indicate, it would serve to propel the animal upward, which would then sink slowly. A very slight action of the funnel would serve to keep the animal at any favorable horizon where food happened to be abundant.

Among the ammonoids floating adaptations are expressed in various ways. Least modified are various genera of the family Stephanoceratidae, such as *Normanites* Munier-Chalmas of the middle Jurassic, in which the aperture is so contracted (Plate 5, fig. 5) that it is difficult to visualize a functional hyponomic funnel, although this is not impossible. Another involutely coiled small form which seems to have been pelagic is the genus *Morphoceras* Douvillé (Plate 2, fig. 9) of the Jurassic and Cretaceous, in which the adult aperture was almost entirely closed and swimming would seem to have been precluded (Plate 5, fig. 4). I have pictured it as planktonic.

Modified in a different way are those forms which were tightly coiled in their youth, but which have the very long adult living chamber suspended, and frequently recurved near the aperture. A good example of this adaptation is furnished by the Lower Cretaceous genus *Macroscaphites* Meek (Plate 2, fig. 10), which, like the Ordovician nautiloid *Lituites*, must have been a swimmer in its youth. At maturity the body chamber hangs down for a distance about equal to

the diameter of the coiled disk and finally curves upward at its lower end. I consider *Macroscaphites* to have normally drifted, foraging over the bottom, the position of the aperture raising the head above the bottom in an advantageous manner. Possibly the specific gravity was so adjusted that the shell would sink when the animal was withdrawn within the living chamber, and rise when it was extended; or when extended and foraging the funnel, by its action, might either reinforce the induced buoyancy or tilt the hook-shaped distal end of the shell so that the animal had no difficulty in seizing its prey on the bottom.

The genus *Hamites* Parkinson, of the Cretaceous, functioned exactly as did *Macroscaphites*, only in the former genus the early shell was not tightly coiled but was a gyrocone. All of the members of the sub-family Scaphitinae, as exemplified by the genus *Scaphites* Parkinson, a world-wide Cretaceous type, were more or less floaters. Indeed it is difficult to see how the adult of such a species as the Cenomanian *Scaphites aequalis* Sowerby could have swum at all. On the other hand it is readily conceivable that a form with the aperture oriented as in *Scaphites spiniger* Schluter—a German Upper Cretaceous species—might well have been able to swim.

Still another type is illustrated by such genera as *Spiroceras* Quenstedt of the Jurassic (Plate 2, fig. 21), or *Crioceras* Leveillé and *Ancyloceras* d'Orbigny, of the Cretaceous. In these the shell is a gyrocone, and such a type might well be a form leading in the direction of *Hamites* (supra). Another form that appears to me to indicate a floating existence is such a species of *Heteroceras* as *Heteroceras reussianum* d'Orbigny (Plate 2, fig. 22) from the Upper Cretaceous of Germany. This was relatively a small form with a

shell coiled in an open ascending spiral, its apertural end recurved as in *Macroscaphites*, and, I believe, had from infancy the habits described above for the mature *Macroscaphites*. The genus *Heteroceras* of d'Orbigny is confined to the Cretaceous period, and all of its species have trochoid spiral shells, but many tend to irregularity, and some appear to have been benthonic crawlers rather than pelagic. Such a form as *Heteroceras stevensoni* appears to me to have had a crawling rather than a swimming or floating habit.

Such genera as *Hamulina* d'Orbigny and *Ptychoceras* d'Orbigny of the older Cretaceous appear to include highly anomalous forms. During growth their shells are relatively slender chambered orthocones, and if the earlier chambers contained gas, as there are no reasons for doubting, it is impossible to see how they could have been oriented except head downward. At maturity the shell, now much enlarged, bends through an arc of 180 degrees and continues its growth in the opposite direction, the animal now facing the apex of the shell. This adult enlargement of the body, faced about as it was, would thus shift the center of gravity backward, so that the animal would now be able to swim in a horizontal position, as I have indicated (Plate 2, fig. 26). In some species of *Ptychoceras* the living chamber extends further backward than in the species that I have figured. For example, in the much smaller Neocomian species, *Ptychoceras emericianus* d'Orbigny, it extends three-fourths of the distance toward the apex of the shell.

In the genus *Ptychoceras* the flexed portion is in contact with the earlier part of the shell. *Hamulina* differs merely in that the two parts do not come into juxtaposition. Hyatt and other authors speak of such forms as these partially uncoiled

or secondarily straightened ammonites as "degenerate," but they are obviously not degenerate in any way unless one adopts a creed, and considers the closely coiled form of shell the ideal of perfection. Doubtless the last was an ideal for a swimming habit, and that is why such forms predominate in the geological record of the Mesozoic era, but from the point of view of adaptation a *Macroscaphites* was more specialized, and in its adult form would have avoided a certain amount of competition which it suffered in its youth. If cephalopods, or other organisms, can have imputed to them any purposes other than to live and reproduce their kind, then, and then only, is it permissible to speak of modifications such as these as degenerate.

ADAPTATIONS FOR A CRAWLING BENTHONIC LIFE

In considering the mode of life of the swarming ammonites of the Mesozoic and in endeavoring to find some sort of seemingly rational explanation for their remarkably complicated septa, the older naturalists, noting that the growth lines across the venter and the margin of the aperture, when this was preserved, usually showed no trace of a hyponomic sinus such as is present in the majority of the nautiloids, reasoned that there was no hyponomic funnel, and hence that the ammonites as a group were not swimmers, but crawlers on the bottom by means of their tentacles; and that this habit had induced the development of the lobes and saddles in the septa, since this would enable the animal to hold and balance its shell more effectively while crawling.

This view has been widely accepted, although it is open to insuperable objections. It entirely ignores the meaning of their prevailing high and often greatly compressed, bilaterally symmetrical, planospiral shells; it ignores the fact that

a hyponomic funnel is essential for respiration; it ignores the universal principle of organisms, namely: that a dominant group tends to utilize all available habitats more or less completely; and it disregards the meaning of the wide geographic range that a number of species show.

Narrow planospiral shells fulfil what might be called the stream-line form for disks. Many, such for example as a large *Sphenodiscus*, have lines that obviously indicate a movement through the water, and how such high and narrow shells could have been manipulated by a crawling animal is incomprehensible. It is true that there are a number of genera of benthonic gastropods scattered through many families and sub-orders that have planospiral shells. In the planospiral gastropods the shells are generally small and their apertures wide—usually wider than high. None approach the cephalopod shell-form, unless it is the tiny early stage of the genus *Caecum*, so that I think it may be conceded that the normally lenticular form of the coiled Cephalopoda—whether nautiloids or ammonoids—is indicative of a swimming habit.

There are, however, great differences in the transverse profiles of their shells, which doubtless indicate different degrees of resistance to slipping through the water, and in a general way ammonites as a whole are more compressed than nautiloids, the most compressed ammonites, with "cut water" keels or venters, being, in general, among the later forms.

Among the coiled shells of both nautiloids and ammonoids the swimming ability was not only conditioned by the form of the shell and the resistance it offered to passage through the water, but also by the power of the hyponomic funnel, and there is no means of obtaining information on this second factor, since I

do not regard the presence or absence of a hyponomic sinus as a reliable indication. This last may perhaps be used with caution, but there are forms—*Placenticerias*, for example—that I regard as active swimmers, but that show no hyponomic sinus.

Transverse profiles of various forms from all horizons show variations from wide ellipticity to extreme compression. The existing *Nautilus*, which has almost as blunt prowed a shell as can be imagined (Plate 6, fig. 1), a shell certainly wider than in the majority of fossil forms, is known by observation to swim moderately well, which shows how cautiously shell form must be used in predicating locomotive ability. I have shown three more depressed and wider forms in the accompanying illustrations—a *Polyptychites* (Plate 6, fig. 2) from the Lower Cretaceous, a *Tropites* (Plate 6, fig. 3) from the Triassic, and a *Cyclolobus* (Plate 6, fig. 4) from the late Paleozoic, all of which would seem to have been exceedingly poor swimmers. For comparison with these a profile of *Placenticerias*, with what I regard as fast lines, is shown. I believe that all highly compressed forms, and the ammonites show them at all later horizons—*Sageceras* and *Pinacoceras* (*layeri* Hauer) from the Triassic, *Oxynticerias* from the Jurassic, *Placenticerias* and *Sphenodiscus* from the Upper Cretaceous, etc.—were rapid swimmers. Otherwise their shell form is meaningless, and it is impossible to imagine the animal as having been able to handle such high and narrow shells in any other way.

There are shell forms, however, both among Nautiloids and more commonly among the Ammonoids, appearing sporadically throughout all cephalopod history from the Devonian to the Upper Cretaceous, that became secondarily adapted for a benthonic mode of life. All trochoid

shells, unless they can be referred to habits of life such as I inferred for *Heteroceras reussianum* (supra), may be considered to have led a benthonic existence, and their shells, although much less diversified, may legitimately be compared with those exceedingly numerous gastropods whose shell plan is an ascending spiral. Instances of a greater degree of reversed adaptation are furnished by the marine limpet-like pulmonates *Siphonaria* and *Gadinia*, whose ancestors became terrestrial, their descendants of these two genera reentering the sea and becoming benthonic.

That such modifications of the cephalopod shell are not confined to the closing days of ammonite history, but occur also in the Paleozoic nautiloids, is proof that they are adaptations, and not degenerations or phylogerontic features. As I have stated, trochoid shells are far more numerous among ammonoids than among nautiloids; and among the latter are unknown from horizons earlier than the Devonian. This is just what might be expected if cephalopod evolution was anything like I have outlined. Not only did they take their origin from a benthonic stock, but it required long ages to acquire the coiled shell. Even as late as the Devonian 25 per cent of the cephalopods were orthocones and, as has been shown, some of these were benthonic, as were also the breviconic cyrtocoines, so that there was no especially untilled field on the sea bottom to tempt the adoption of this mode of life among the nautiloids.

We may also infer from the transverse profiles of the shells, although this is highly problematic, that the nautiloid swimmers as a class were less effective swimmers than the later ammonoids, and fed for the most part near the bottom, as does the existing *Nautilus*. We may also infer that competition for food was

keener among the Mesozoic ammonoids than it was among the Paleozoic nautiloids, or that the food of the latter was more exclusively nectonic, so that there would have been a greater stimulus for the adoption of a benthonic habit in the Mesozoic than in the Paleozoic, although this is very hypothetical. Nor can the influence of the great abundance of mostly benthonic arthropods in the older Paleozoic (trilobites and meristomes), or of the arthrodiran, ostracoderm, and true fishes, be ignored in seeking an evaluation; but the influence of these factors, important as they are, is so obscure that I will not attempt to discuss them.

A secondarily benthonic nautiloid, descended from a coiled swimming ancestor is the Devonian genus *Trochoceras* Barrande. Among the ammonoids the small Cochloceratinae, as exemplified by such genera as *Cochloceras* Hauer, or *Paracochloceras* Mojs., of the marine Triassic, may be mentioned as among the earliest. In the later Mesozoic there are a number of such genera, for example: *Turrilites* Lamarck, *Emperoceras* Hyatt, *Helicoceras* d'Orbigny, and probably some species of *Heteroceras* d'Orbigny—all from rocks of Cretaceous age. The first especially often reaches a large size. Two of these secondarily benthonic ammonoids are shown in the adaptation diagram (Plate 2, figs. 19 and 20). Doubtless the empty early chambers in these forms so reduced their specific gravity that the energy of handling them was reduced to a minimum.

The extreme of benthonic adaptation is that of the apparently sessile, or at least static, genus *Nipponites*, described by Yabe recently from the Upper Cretaceous of Japan, but much fuller information is desirable before attempting to visualize its habits. *Nipponites* was irregularly coiled like some species of *Vermetus* or *Serpula*—a tendency which may be said to

be shown to a very slight degree in species of *Heteroceras* or *Nostoceras*, but which in its extreme development in *Nipponites* is, for the present, highly anomalous. As in the Gastropod genus *Vermetus*, *Nipponites* was undoubtedly derived from a trochoid coiled ancestor.

THE PROBLEM OF SEPTA AND SUTURES

The familiar septal and resulting sutural progression from nautiloid (smooth curves), through goniatic (angular) and ceratitic (frilled lobes), to ammonitic (frilled or digitate lobes and saddles), is well known, and in a general way is an epitome of the evolution of these parts. It is not, however, a simple linear series. Early forms often show unusual specialization, and later forms simplification, but it is well to avoid the philosophic implications of the terms acceleration and retardation, so much a part of the vocabulary of the cephalopod students of the penultimate generation.

A comparable change from septal simplicity to septal complexity may be observed in the ontogeny of the more evolved types, and this is the basis for the enormous literature on the biogenetic law as exemplified by the shelled cephalopods. It is commonly assumed that the sutural are the most constant features, and that however much the body-form or ornamentation may vary, the court of last resort in determining genetic relationships is the suture, which is said to be constant in species when individuals of the same degree of maturity are compared. This has now become a tradition among students of ammonites, but like all similar traditions, it is unsound, and the only way to establish it would be for systematists to consider every slight variation indicative of distinct species. In an account, shortly to be published, of the ammonite faunas

of Peru, a student of mine, M. M. Knechtel, has shown considerable variation of single sutures on the two sides of the shell, and similar features have occasionally been recorded by earlier workers. In such a case the dogmatist must either admit sutural variation or contend that the two halves of the same shell belong to different species.

It is not my purpose in this essay to go deeply into this vexed question, with all its implications, but it may be stated as a general principle that the taxonomic value of such features as sutural pattern, shell form, ornamentation, etc., will vary greatly from genus to genus. In some cases one and in other cases another feature will be entitled to the greatest weight, but there will be no single magical criterion.

The factors that led to the increasing complexity of septa in the ammonoids have been a favorite field for speculation since von Buch first emphasized its existence by proposing the so-called genera *Goniatites*, *Ceratites*, and *Ammonites*. The subject remains obscure to the present, and none of the suggestions that I have encountered seem satisfactory. That it is related in some way to habit would seem probable by the essentially goniatic form of the sutures in such a nautiloid as *Aturia*, which every beginner thinks is an ammonite; but that benthonic forms can be distinguished from planktonic or nec-tonic by the characters of the sutures, as Schmidt implies in a recent paper, or that Keferstein's wholly hypothetical "pre-septal gas" shows that animals with highly complicated sutures were divers, is wholly without foundation.

In a way progressive sutural complexity is to be correlated with increase in bodily size in excess of increase in shell capacity. This is also a factor in the corresponding sutural modification during ontogeny, for

I do not believe that all of the blame can be fastened upon the hereditary genes. Also, and more clearly, it is to be correlated with a more secure connection between the animal and its shell. This is to be rather conclusively inferred from the complementary relationship between the degree of development of adjacent lobes and saddles, where highly modified laterals tend to bring about underdevelopment in their fellows.

We are now fairly familiar with the formation of the septa in the existing *Nautilus*, which have their inception in the epidermis of the hind part of the visceral sac; this first becomes a membrane, is then conchyolinized, and finally calcified from the periphery inward on its anterior side next the animal. Hence the horny nidus is left behind the calcified septum. That septa are formed periodically, and alternately with periods of active metabolism, is inferred from their general regularity of spacing and from the correlation between growth lines of the shell and the spacing of the septa, as is shown, for instance, in Ruedemann's description of the shell of an Ordovician species of *Geisonoceras*.

It was long supposed that the flaccidity following the expulsion of the sexual products marked the time of septal formation, but as Willey has shown in *Nautilus*—and I think that his observation may be used for generalization—the last septum is formed before puberty. Perhaps

septal formation may be correlated with seasonal climatic change, either as a direct factor or through the influence of climatic change upon food supply, although it must be admitted that seasonal climatic variations are minimized in the seas.

If snakes had shells, the annually shed skins would be accumulated in such a shell exactly (homologously) as are the endocones of the early Endoceratidae, and we may visualize in this periodic shedding of the hardened skin of the apical cone in the earliest nautiloids the beginnings of septal formation. If the extinct cephalopods had some muscular connection between the hinder part of the body and the shell in the region where the septum joins the shell wall, such a connection would supplement the comparatively feeble attachment of the lateral and annular muscles, and would influence the crumpling of the apex of the visceral cone; or, if there was such a connection directly between the body and the septum, any increase in the area of the latter by folding would increase the effectiveness of such a union; or, not to go beyond the well ascertained facts of observation, such a folding of the septum around its periphery—whether of a goniatic or ammonitic character—into which the periphery of the hinder mantle penetrated, would enormously strengthen the bond between the animal and its shell, even though they merely remained in juxtaposition and were not directly united.

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