

# The Phylogeny of the Cephalopoda.

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With Plate 9.

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## I. Introduction.

In a recent paper (1933c) I ventured to suggest that the problem of the evolution of the cephalopoda had to be restated. This may have seemed unnecessary to some, considering the "convincing evidence" of which SCHUCHERT (1934, p. 394) speaks. Perhaps unwisely I also tabulated my results in a form that I even then feared would only "invite categorical denials" (p. 420). If such things could be proved, there would have been no need for a restatement. TEICHERT (1935, p. 16), in fact, acknowledged that the problem of the evolution of the cephalopoda remained unsolved. Unfortunately, I also took rather too much for granted, especially an intimate acquaintance with the cephalopod literature. But I thought I had at least made it clear why I came to hold unorthodox views. I was so to speak brought up on HYATT. Twenty-five years ago there was not a paper by HYATT that I did not know, almost by heart, and, of course, implicitly accepted, even if I occasionally (1913, p. 167) and, I may add, unkindly, criticised the systematics of his ammonite families. I erroneously assumed that other workers on cephalopoda were equally familiar with HYATT's work. BUCKMAN also, working on Hyattian principles and popularising the "law of earlier inheritance" was

one of my masters and I was proud of his pronouncement that I was "evidently working on the right lines" (1913, p. 580). I have already given my reasons for trying to discover why these lines and practical experience did not agree; and I entered my protest irrespective of whether I had the great majority of "serious" investigators of cephalopoda on my side or not.

✓ Nor was I afraid of broadcasting our profound ignorance of the earliest types of ammonoids as well as nautiloids. This seemed to me particularly necessary and it is incidentally also about the only point on which I agree with another critic, SCHINDEWOLF (1934c), namely that in the Lower Devonian, that is (let it be well noted) during the most crucial "unstable phase of development" of the Ammonoidea (p. 269) the conditions for their preservation were deplorably unfavourable (p. 270) and that "at the moment" phylogenetic deductions concerning the early (Ozarkian) nautiloids are premature (p. 265).

On the other hand as soon as discussion turns on types that are comparatively well known, that is, the later ammonites, especially those of the Cretaceous period, it is admitted that there are various "difficulties" (p. 279). SCHINDEWOLF is confident that when he has opportunity for further research these "last" difficulties will be cleared out of the way; meanwhile he has no hesitation in asserting (1934a, p. 459), that "secondary uncoiling is only a rare and exceptional process" or in comparing the extraordinarily prolific and persisting hamitids, baculitids, and other heteromorphs of the Cretaceous with the almost insignificant aberrant offshoots in the Triassic. SCHUCHERT thought that SCHINDEWOLF's main work met many of my objections. In reality, even SCHINDEWOLF's most recent paper, with all its denials and assertions, not only avoids some of the most telling points, but re-echoes those recapitulatory views, put forward by HYATT many years ago, that I thought out of date.

I am under no illusions as to the difficulty of solving a problem like that of the evolution of the cephalopoda. These things are not done at one stroke, and instead of clearing away the last difficulties, the most one can hope to accomplish is to add some bricks to the common structure and perhaps knock down a few bad ones. I may have seemed too much occupied with the latter process of hacking other people's views to pieces, instead of expounding my own, as one critic put it; another coined the word cruciverbose for my paper but was probably not interested enough to read and re-read the whole in the only way in which it can be read, that is with a view to the general condemnation of recapitulatory "evidence". If it is admitted that many characters of the early stages

are not old but new, that is to say, that they have a prospective rather than retrospective significance, I may be excused for not being impressed by one-sided interpretation of ontogenetic evidence. If I can show how unstable and unreliable often are such internal features as the siphuncle or the suture-line, then I must be allowed to use them with discretion, however crude the emphasis on purely external, morphological characters may be made to appear by those theorists who have pinned their faith to one of these so-called internal features. If I can show the protoconch of cephalopods to have no more systematic or phylogenetic significance than the prodissoconch of pelecypods (embryonic development together with the size and characters of the original shell being probably similarly influenced by the amount of yolk in the egg)<sup>1</sup>, and if I also find the immediately post-embryonic stages of ammonoids too variable for phylogenetic purposes, then I am forced to rely on external resemblances in the adolescent and adult shells. In reality it is not so difficult to select the telling characters, whether they are internal or external, obvious or subtle, and to utilise as many of them as possible, even if they include differences in shape, amount of involution, intensity, proportion, arrangement, duration and small details of ornamentation. But the amount of time and labour spent in the unearthing of some obscure feature (that eventually turns out to be entirely unreliable) is no criterion of its greater value for systematic purposes as compared with some more obvious character.

To make my meaning clearer: if it could be shown that two families that produce homoeomorphs, like the Hildoceratidae (Graphoceratinae) and the Oppedidae (see SPATH: 1928, p. 74) are distinguishable by the position of the siphuncle on the earliest whorls, I should gladly avail myself of this feature, however laborious the investigation. Unfortunately it has no practical value since, for example, in *Ludwigella* the position may vary as much as in *Lissoceras*, though in *Ludwigella concava* (J. SOWERBY) or *L. cornu* (BUCKMAN) the siphuncle becomes ventral rather earlier. Like the hollow keel, occasionally constant, and the thickness of the siphuncle, also at one time considered to be a distinction between "*Harpoceras*" and "*Oppelia*", the position of the siphuncle in the young has proved to be useless for classificatory purposes, at least in these families, though it may conceivably help in others, e.g. Lytoceratids. Some day, perhaps, an investigator may find the clue to these homoeomorphs, and show that I was wrong concerning the origin of the

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<sup>1</sup> I am greatly indebted to Mr. H. WOODS, F. R. S., for drawing my attention to this line of research.

Oppelids; another brick will be added to the common structure, but we are as far now from finality as when HYATT wrote.

I do not propose to weary the reader with a re-affirmation of the views put forward in my first paper. Nor was it necessary for me to review my material or to make profound new investigations, for my opinions had been well considered. Since, however, there are several points on which I have not made myself quite clear I am glad of this opportunity to reply to my critics in detail; some illustrations published by SCHINDEWOLF greatly help in this discussion, though perhaps not in the way that he anticipated. With regard to the regrettable errors of which I am accused I am relieved to find that they are in reality nothing more than calling "microscopic" such objects as are always examined under the microscope, even if in one exceptional case the size is fully five-sixteenths of an inch, or referring to wrong figures in SANDBERGER and KARPINSKY when I pointed out that they did not agree with my own observations.

## II. The Supposed Cephalopod *Volborthella*.

There is little to add to what I previously wrote concerning this doubtful organism. The excellent figures published by SCHINDEWOLF (1934b, pls. 17—19) show clearly that it is just as uncertain now as before whether there really was septation, and I am content to let his change of opinion as to the spacing of the "septa" speak for itself. Again, there is no evidence that the irregular central column or whatever it was must have been a siphuncle. This is a mere assumption, scarcely less justified than the globular protoconch (pp. 193 and 187, text-fig. 1). Of course, microscopic examination of actual sections is necessary to realise the true nature of this "pteropod?", with twenty 'septa' to the millimetre (TEICHERT, 1935, p. 21); and on looking at SCHINDEWOLF's pl. xvii, it must not be forgotten that the ooze is enlarged three times, which makes as much difference to its appearance as the accidental rounding of the apical end of some of the cones (SCHINDEWOLF, 1934c, pl. xix, figs. 1—5) or the presence of a median stain (on some of the specimens) enhances the possibly entirely spurious resemblance to *Orthoceras*. That is to say, the preservation, as poor sandstone casts, may be claimed to have increased the resemblance to *Orthoceras* rather than obscured it. Yet SCHINDEWOLF has no hesitation in stating categorically (1934a, p. 458) that *Volborthella* is undoubtedly a primitive cephalopod.

While I stand by everything I said concerning the doubtful nature of *Volborthella*, I must confess that its connection with *Salterella* is

even more problematical. POULSEN's (1927, p. 150; 1932, p. 32) reconstruction of this equally doubtful genus (described as a cephalopod and referred to a new family Salterellidae) is possibly correct, yet it cannot be said to help in the interpretation. For neither the cone-in-cone structure of the branching septa, nor the nature of the central column make it probable that the minute shell was a hydrostatic apparatus. But I was not really concerned with *Salterella* which I thought, as interpreted by CLARK, was "possibly" identical with *Volborthella*. I stated it was necessary to keep an open mind regarding the nature of the latter genus and I merely wanted it left out of the discussion of the phylogeny of the nautiloids.

Regular septation and the possession of a siphuncle are tests good enough to define any true cephalopod; until they are shown to exist in *Volborthella* it cannot be called a cephalopod and it is useless to speculate whether the "septal" funnels were elliphoanitic or otherwise. There are various other groups of animals in the Lower Palaeozoic that are as yet incompletely known, some of them far bigger and more favourably preserved than *Volborthella*. And if it is contended that in a primitive form of cephalopod the shell was protective and did not yet serve as a hydrostatic apparatus (SCHINDEWOLF, 1934c, p. 264), why worry about septation and siphuncle at all? Would not any tube do? Twenty septa to the millimetre, indeed, and yet ULRICH and FOERSTE (1933) accept *Volborthella* as a cephalopod.

### III. Phylogeny of the Nautiloidea.

It is admitted that cyrtocoenes (*Plectronoceras*) appear in the Upper Cambrian and that in the oldest (Ozarkian) formations known to have truly representative cephalopod faunas the shells are still mostly cyrtocoenes, compressed and bilaterally symmetrical. Gyrocoenes, like orthocoenes, are rare at first and ophiocoenes are still later, as shown in my table I (1933, p. 455). I am not suggesting anywhere that a nautilicone is the ancestral type; but considering that highly specialised coiled shells existed already in the Tremadocian, and that the nautilids of the Carboniferous and the Triassic are connected with the earlier ophiocoenes by an unbroken series of coiled types, I concluded that both orthocoenes and nautilicoenes were developed independently from the primitive cyrticone.

The recognition of a distinct coiled stock (Nautilidae) as opposed to the various straight stocks, persisting side by side through the same beds and, apparently, connected with the first by so many transitional cyrtocoenes and gyrocoenes, may be viewed with alarm by the syste-

matist. It looks not only like a return to the old classification on the basis of the coiling, but it seems to forebode an artificial separation of closely allied forms merely because they differ a little in curvature. I have no fears on that score. KOBAYASHI (1933, p. 308) and TEICHERT (1935, p. 17) have shown how unreliable is a classification based on the septal funnels alone, and it is clear that a revised grouping will have to take into account all the available characters, as I suggested before. Nautiloids are just as homogeneous an order as the ammonoids and therefore their classification is equally difficult. But if I can show *Cyrtoceras* to be derived from a nautilian form like *Naedyceras* (p. 430) or a Carboniferous cyrtocone like "*Orthocera*" *paradoxa*, J. DE C. SOWERBY, to be a degenerate offshoot within the nautilian family Trigonoceratidae, then there is clearly nothing in their resemblance, in coiling, to cyrtocoines which, by their other characters are undoubted members of straight stocks, for example of Cycloceratids, Kionoceratids, or of some annulosiphonate group. There are many fusiform, gomphoceratid and other specialised offshoots in the straight groups, just as there are torticone developments among the nautilid families. Opinions also may differ for a long time to come as to what should be included in a family like the Lituitidae; and as regards the heterogeneous family Jovellanidae there is clearly as yet insufficient material to attempt the task of sorting out the primitive orthocoines from the secondarily uncoiled forms. There may be still more difficult groups, but generally only for those who are dependent on the literature. Thus, actual examples of such forms as *Aipoceras* ("*Gyroceras*") *gibbosum*, DE KONINCK sp., are readily classed with nautilids like *Asymptoceras* and *Solenocheilus*, and not with cyrtocoines like *Meloceras*. Again, "*Cyrtoceras*" *gesneri*, MARTIN sp., is too intimately connected with the other straight or slightly curved, fluted, species of the Carboniferous, resembling longitudinally ribbed Dentaliids, to be linked with the nautilid *Thrinco-ceras*. The genera *Bickmorites* and *Jolietoceras*, FOERSTE, are Trochoceratids, in the wider sense, whatever their coiling, while *Amphicyrtoceras* and *Monocyrtoceras*, FOERSTE, have nothing to do with *Uranoceras*, HYATT, in spite of a similarity in the siphuncular structure. Whorl-shape and modification of the body-chamber alone indicate that the former two genera belong to an entirely different stock. Considering, however, that only about 25% of the ancient cephalopod faunas are preserved to us as fossils, any classification proposed must in the first place be elastic (SPATH, 1935, p. 109).

SCHINDEWOLF cannot have read me correctly if he thinks that I suggested a reversal of the primary, progressive, "sequence" (from cyrtoc-

cone to nautilicone) which, however, is not a genetic series. The reader may compare the careful wording I used (on p. 430) with SCHINDEWOLF'S version (p. 266) of my views with regard to secondary uncoiling. What I most emphatically deny is that in numerous series within the Nautiloidea there may be observed again and again a production of nautilicones from originally straight types, i. e. that this is the "normal sequence for every nautiloid lineage". I hold that the Nautilidae existed side by side with the Endoceratidae and Orthoceratidae (in the widest sense, both including many actinosiphonate and other offshoots) throughout the Palaeozoic (see Table II, p. 457); and while I can show, for example by the peculiarities of ornamentation or the presence of dorsal furrows or of a hyponomic sinus, that Devonian and Carboniferous gyrocones (and some cyrtocoines and orthocoines) have been derived from coiled nautilids, no one can demonstrate a corresponding series going in the opposite direction.

SCHUCHERT (1934, p. 394) thinks that the chronological record does not bear out my statement that 'no series from straight to coiled are known but only such as go in the reverse direction, in *Nautiloidea* as in *Ammonoidea*'. I do not know what he can have in mind, although the earliest types (*Plectronoceras*) are as yet incompletely known. The fallacy that I am out to expose is that *Nautilus* can be traced back through gyrocones and cyrtocoines to *Orthoceras* or any similar straight ancestor in the Lower Palaeozoic. I would not even call the primary sequence from the ancestral capulicone or cyrtocone through *C. (Plectronoceras) cambria*, WALCOTT and *P. liaotungense*, KOBAYASHI to the Lower Canadian Tarphiceratids (see Table I, p. 455) a genetic series, because the members of that group of forms, with unstable or variable curvature, that produced the first coiled types could well have belonged to a single species. That is to say, the more distinctly coiled varieties probably were at first mere extremes in a homogeneous group of cyrtogyrocones and the result of a fortuitously increased curvature, not of a long continued tendency to closer and closer coiling. As an example of such an original nautilid stock or species group with variable coiling I may cite *Cyrtendoceras (?) priscum*, RUEDEMANN (1906, p. 430), without, however, claiming that it is the ancestor of the Nautilida. For not only is it a contemporary of the more typically nautilid family Tarphyceratidae, but its siphuncle may prove to be against such a connection, although this feature has been greatly over-rated by many. Again, the endoceratid siphuncle of the true *Cyrtendoceras* or the oncoceratid siphuncle of *Richardsonoceras* clearly indicate that reliance on coiling alone is likely to lead to wrong conclusions. To deny the possibility of a subsequent

'trend' in the Nautilida to increase the involution or to develop more advanced, later, types would be to deny the theory of descent; yet the only imperforate nautilids known are Lower Palaeozoic.

The early Ordovician species of *Orthoceras* are essentially the same as their Triassic descendents, and they are linked by an uninterrupted succession of *Orthoceras* faunas including types with unstable siphuncles; similarly the early stages of certain Tremadocian tarphyceratids and trocholitids are already much like the shell apex of the living *Nautilus*, truly an 'immortal' type. The coiled Nautilida and their offshoots, including the Lituitidae, can be shown to be distinct from the straight stocks and their modified derivatives, from the Cambrian onward, as inarticulate and articulate brachiopods existed side by side. The Articulata may be necessarily derived from the Inarticulata, yet no one has suggested that this evolution is the regular sequence for every brachiopod lineage. In my opinion no Silurian, Devonian, or Carboniferous cyrtocone ever gave rise again to a nautilid; and in case any reader should be influenced by the enlarged initial stages of a '*Barrandeoceras*' figured by SCHINDEWOLF (1934c, pl. xix, fig. 14), I may remind him that this is only one selected example out of an extraordinarily rich Silurian nautilid fauna and that there were ophiocones with an almost closed umbilicus as far back as the Tremadocian. Moreover, the nucleus of the perfectly involute Ordovician *Trocholites canadensis* (HYATT) WHITEAVES, at 1.66 mm diameter, with a thickness of 1.33 mm is an almost perfect miniature replica of a globose *Nautilus* or rather of the involute *Goniatites sphaericus* and the initial chamber is smaller than the protoconch of an *Anarcestes*. It would be as idle to claim that the nautilid forms at first were always more loosely coiled or had larger umbilical perforations than the later types, as it would be useless to adduce the supposed ammonoid sequence from '*Bactrites*' to *Agoniatites* (which HYATT attempted to prove) to substantiate the 'numerous' developmental series from straight to involute in the Nautiloidea. Even now, so many years after HYATT, it is impossible to point to a single such lineage. *Spirula*, not being an external shell, cannot here come into comparison. The significance of the internal phragmocone in this genus and its presumed ancestor *Spirulirostra* is very uncertain. They may not even be directly connected, and to trace this 'series' back to a belemnite with curved phragmocone is to me just another of those recapitulational generalisations that have been so overworked. There is really very little known about these fossil dibranchiates. For instance, the Aptian *Conoteuthis*, contrary to the customary reconstruction, has now turned out to be the phragmocone of a stout belemnite, and, in one form, the curved



apex of the phragmocone is first an exogastric and then an endogastric cyrtocone. I am describing these forms of *Conoteuthis* elsewhere, in case I am told again that such belemnites 'do not exist'.

While SCHINDEWOLF (1934 c, p. 265) quite rightly, urged a certain restraint in theorising about the earliest cephalopoda, TEICHERT (1935, p. 21) thought that even their 'unity and monophyletic descent' might be seriously doubted. He considered the types with narrow siphuncles (*Orthoceras*, *Nautilus*, etc.) to represent a line of development entirely different from the Endoceratids, Actinoceratids, etc., with wide siphuncles (Eurysiphonata). This, however, seems to me a mere transfer of the 'over-estimation' of one single character; instead of the form of the septal necks, on which HYATT's classification was based, TEICHERT favours the structure of the siphuncle itself, or, rather (since the siphuncle is a membranous organ), of the siphuncular tube. TEICHERT, moreover, admits that some forms of the first group (Nautiloidea in TEICHERT's sense) may be able to develop features of the siphuncle which resemble those known in Actinoceratids; only while intracameral deposits were merely 'common' among his Nautiloidea, they were 'more common' among the Actinoceratids. This seems to me to be more than a case of 'occasional convergences'; and on extending this classification to groups other than merely the Ordovician members of the Actinoceratids which TEICHERT chiefly had in mind, great difficulties are immediately encountered. Thus the Sactoceratidae, one of the families within the Actinoceratids, may be 'in need of further research'; but MILLER, DUNBAR and CONDRA (1933) have attributed to this family certain Carboniferous genera in which the siphuncle is almost cylindrical, though strongly contracted where it passes through the septa. Similar variations are found in the Silurian nautilid *Uranoceras* and in such unrelated poteriocones as *Amphicyrtoceras* and *Streptoceras*. But there are all kinds of transitions to the moniliform type of siphuncular tube found in such true nautili as *Germanonautilus* of the Triassic, *Paracenceras* and *Bisiphytes* of the Jurassic, or *Cimomia* of the Tertiary, and the width of the siphuncle is often greater than in certain Endoceratids. Again, the Ordovician Actinoceratids probably have nothing to do with the Carboniferous *Rayonoceras giganteum* (Sowerby) or the Devonian true *Cyrtoceras* and the Hercoceratidae, in the wider sense, including *Nothoceras*, BARRANDE, with lamellar siphuncle, which was even thought by MOJSISOVICS (1885, p. 161) to be a primitive ammonoid.

The calcification of the endosiphuncular tissue in Actinoceratids I take to be analogous to the hardening of the siphuncular sheath in ammonites to which TRUEMAN (1920), has directed attention and which,

in view of NEAVERSON'S (1924) doubts, I have verified in many Jurassic and later nautili. Loading of the siphuncular tube and other modifications were not confined to any one stock, and it seems to me that they varied even in members of one group, as they varied in the individual. I thus would confine the Actinoceratida to the typical Ordovician groups and certain specialised offshoots, like the Huroniidae, and I believe that, like the Orthoceratida, they are derived from the Endoceratida. But I doubt whether it could be maintained with TEICHERT (1935, p. 20) that in all lines of cephalopod development the marginal position of the siphuncle indicates a later and more specialised stage, since the marginal, and often wide, siphuncle is the most striking characteristic of the primitive forms, ignoring the doubtful *Volborthella*. If major divisions of the Nautiloidea are considered desirable at all, such elastic groups as the Endoceratida, Actinoceratida, Orthoceratida and Nautilida seem to me the most practicable and therefore the most natural and scientific. Such specialised subdivisions as the Diphragmoceratidae or the Pilooceratidae, the Oncoceratidae, Gomphoceratidae, Poterioceratidae, and Ascooceratidae, the Lituitidae, Trochoceratidae, and Hercoceratidae, to mention only some of the more commonly known families, can easily be accommodated within the larger divisions indicated; but sub-orders like the Orthochoanites (which unites such diverse elements as *Orthoceras*, *Trochoceras* and *Nautilus*) or the Stenosiphonata (which classifies a Cretaceous ammonite with an Ordovician *Orthoceras*, but separates the latter from *Endoceras*) are destined to pass eventually into the limbo that holds such groups as the Retrosiphonata and the Heterosiphonidae among the Nautiloidea and the Trachyostraca and the Mesoammonoidea among their descendants. However, as BATHER, himself the author of a number of theoretical groups, used to say, the other man's system is always "unnatural".

#### IV. On "Bactrites".

The marginal position of the siphuncle, even if it results in a ventral or dorsal lobe, does not change a nautiloid into an ammonoid, any more than an angular suture-line is enough to make it a goniatite. There are many nautili in which the siphuncle is marginal, or nearly marginal, internal or external, and nobody ever put them into the Ammonoidea. Then why should for example Ordovician or Permian forms of *Orthoceras*, but not the Silurian *Protobactrites*, be taken out of their natural groups, that is with the other Orthoceratids in the same beds, merely because the notoriously unstable siphuncle has wandered to the margin? In the case of perfectly smooth forms with no other

distinguishing feature, of course, it was natural to base "species" on the position of the siphuncle, but when a species like "*Orthoceras*" (*Brachycycloceras*) *koninckianum*, D'ORBIGNY, can be recognised by its external characters, the siphuncle is found to be variable. "*Eobactrites*" and "*Bactrites*" (= *Orthoceratites* BLUMENBACH<sup>2</sup> are typical Orthoceratids, except in the position of the siphuncle. It is idle to ignore the demonstrable instability of the various features of this organ when attempting a rational delimitation of the ammonoids as opposed to nautiloids. But there is generally no real difficulty in practice; and even the resemblance between the orthoceratid "*Bactrites*" and the presumed ammonoid *Lobobactrites* is probably superficial.

It is curious that the only "true" *Bactrites* known, that is the single species *Lobobactrites ellipticus*, FRECH sp. (= *Bactrites carinatus*, SANDBERGER) has always struck observers as peculiar, even before HYATT discussed it. SCHINDEWOLF also gave it a new generic name in 1933, although he now tries to minimise the differences, saying (p. 271) that the two genera are without the slightest doubt extremely closely allied and scarcely separable. In my first paper I had not been too dogmatic about *Lobobactrites*, speaking of it in one place (p. 446) as "presumably" an uncoiled goniatite, while elsewhere (p. 450) I particularly qualified the opinion that *Lobobactrites* represented a degenerate branch by adding that this would apply only "if there was any connection at all between it and *Gyroceratites*".

Among the not inconsiderable amount of material from Wissenbach etc. that I have examined there is nothing that could be considered transitional between the two genera "*Bactrites*" and *Lobobactrites*, but according to SCHINDEWOLF (1934c, p. 271) these transitions are manyfold. I was almost prepared to concede that *L. ellipticus* may, after all, be an Orthoceratid. After examining actual specimens again, however, I am very doubtful whether there are real transitions, or whether all those who thought that "*Bactrites carinatus*" was, or might be, an uncoiled goniatite, including HYATT himself, were wrong. Since the external position of the siphuncle in the stocks concerned is admitted by all, I offer no apology for again trusting to crude, morphological, considerations. The peculiar features of *Lobobactrites* are the presence

<sup>2</sup> LAMARCK's "*Orthoceratites*", 1799 (p. 81), was described as having the last chamber closed by an operculum and thus cannot have been a cephalopod. Since he used no specific name and in 1801 (p. 104) included *O.* as a synonym in *Hippurites*, the genus was no more defined than before LAMARCK; and BLUMENBACH (1803, p. 21) was the first to connect it with a species. Whether ARTHABER (1935, p. 89) likes the name or not is beside the point.

of a carina and of oblique ribbing. It is known that there are forms of *Orthoceras* with a "keel" and others with ornamentation. Considering that these are probably mere strengthening features, there is no reason why they should not be acquired by any stock. Yet nothing like the combination found in "*Bactrites carinatus*" was ever developed in any straight stock, orthoceratid, that is, with a tubular siphuncle, or otherwise. Neither the two-edged swordlike blades of a *Lambeoceras*, nor such keeled orthoceratids as *O. carinatum*, MÜNSTER, or *O. teres*, BARRANDE, are at all comparable to *Lobobactrites ellipticus*. For, as FOORD (1888, p. 31) already pointed out, the raised "keel" in these two forms of *Orthoceras* is only a so-called normal line; and in the many compressed species with more or less distinct lateral lobes there is no ornamentation at all. Those who had to rely on SANDBERGER's composite figure and description can hardly be blamed for not recognising the true "*Bactrites*"; and I may be wrong in my interpretation of those slender Upper Devonian forms like *B. clavus*, HALL, of which I have no actual specimens. But I may mention that at least the examples of the Uchta (Petchora Land) form that FOORD identified with "*Bactrites carinatus*" have nothing to do with this species, i. e. the genus *Lobobactrites*, and, to me, are merely *Orthoceratites*, with a marginal siphuncle. I do not want to be as dogmatic as SCHINDEWOLF (1933, p. 73) who renamed this form; and in view of the very long range of the admittedly uncoiled *Baculites*, I do not consider it impossible that *Lobobactrites* had Upper Devonian descendants. But, since no one claims these very long and slender Neo-Devonian forms as radicals of ammonoid lineages, the supposed long range of *Lobobactrites* is rather beside the point.

*Lobobactrites ellipticus*, the only species that can in any way be considered to be transitional between *Orthoceratites* and the goniatites, in fact has a very restricted range. When SCHINDEWOLF compares its range, vaguely confused with that of a spurious family "Bactritidae", with the "extremely short life" of other, secondarily uncoiled ammonoids, he is, in fact, on very unsafe ground. The Hamitids and Baculitids of the Cretaceous, that is to say, stocks that persisted through long periods and dominated cephalopod life in the end, cannot well be called either rare or exceptional. But *L. ellipticus* is not only short-lived; it occurs in the upper zone of the Wissenbach slate series while *Gyroceratites* (= *Mimoceras*) *gracilis*, with a less acute, i. e. less advanced dorsal saddle, is a characteristic fossil of the lower zone, at the very base of the Middle Devonian. Still earlier, that is, in the lower Devonian, there occur in addition to one doubtful *Gyroceratites* (*G. laevis*, EICHENBERG) those typical goniatites (*Mimagoniatites*) which have been sepa-

rated from *Agoniatites* merely on the basis of a slight umbilical perforation. Clearly this succession in time favours my view; and I cannot see how a "series" from the straight *Lobobactrites* through *Gyroceratites* to the more involute goniatites can be spoken of as perfect, incontrovertible and "observable step by step" when their order of appearance is the reverse. The late *Lobobactrites*, in any case, seems to me to be out of the running altogether.

SCHINDEWOLF also stated (1934c, p. 267) that *Lobobactrites* was an exact replica of a straightened-out *Gyroceratites*. Those who visualise the latter merely as a loose spiral and do not have access to adult specimens should consult the recent illustration in SCHINDEWOLF (1934c, pl. xix, fig. 10) and remember that even this is enlarged (x 2). Fully-grown examples, especially when the umbilicus is covered by matrix, show considerable resemblance to *Agoniatites*, but less so than the still earlier *Mimagoniatites*. It could be held that there is not really much resemblance between such a specialised goniatite, even when straightened out, and "*Bactrites*". In my opinion, moreover, the dorsal band or "keel" of *Lobobactrites* can only be interpreted as the analogue of the impressed dorsal zone or line of its coiled ancestors. It can be observed as a faint groove or band in *Gyroceratites gracilis*, at least on the body-chamber, and SCHINDEWOLF states that it was feebly developed already in the Lower Devonian *Mimagoniatites*. In a secondarily uncoiled form this dorsal line or double line would indeed appear as a band or "keel"; and the indistinct striation, strongly bent backward on each side of this carina also can be matched in *Gyroceratites* of the more ornamented type. There is no corresponding curve on the ventral side of *Lobobactrites ellipticus*, but the faint ribs, when seen at all, may be very slightly projected where they terminate on each side of a smooth, ventral zone, a suggestion of the original differentiation of the venter. Distinct bi-angularity, however, is found in *Pseudobactrites bicarinatus*, FERRONNIÈRE (1921, pl. 1, fig. 35, 2—3 only) which is a good reproduction of a straightened-out *Gyroceratites*, at least in a ventral view, showing the deep sinus in the striation. Unfortunately, the siphuncle in *Pseudobactrites* has not been observed and I am very doubtful whether the type species of this genus (*P. bicarinatus*) is related to the other species (*P. quadriangulatus* = "*quadriundulatus*" on the plate), tentatively included by FERRONNIÈRE in the same genus. The occurrence of a fragment with a central siphuncle which, in spite of its bi-angularity, may be an *Orthoceras*, makes it advisable not to be too dogmatic about these early Mesodevonian forms and especially about their fore-runners in the Eo-Devonian, the "period of unstable deve-

lopment" for the ammonoidea. But on account of the unusual interest of *Pseudobactrites*, associated at La Grange with a number of variable forms of *Gyroceratites* etc., I applied for the loan of the type material only to learn with regret that it cannot at present be found.

Considering that goniatites with overlapping whorls and specialised ornamentation existed already in the Lower Devonian, it is impossible to look upon the keel and angular periphery of *Lobobactrites* and especially the hyponomic sinus of *Pseudobactrites* as anagenetic features, leading up to an impressed dorsal area or band or bicarinate venter, instead of being catagenetic. It is known that in stocks that everybody considers uncoiled (*Spiroceras*, *Crioceras*) it is always the earliest whorls that are extremely unstable and only the later whorls or the body-chamber retain the family-characters of the ancestral stocks (Parkinsonidae or Hoplitidae). In an uncoiling nautiloid extreme like *Trigonoceras* ("Orthocera") *paradoxicum* there may be little left, except the hyponomic sinus and the dorsal carina, to suggest connection with the ancestral vestinautilid stock. Similarly *Lobobactrites* and perhaps *Pseudobactrites* can be assumed to have reduced the ornamentation of *Agoniatites* or *Mimagoniatites* which had reached some specialisation already in the Lower Devonian, especially in the ventral region. Such specialisation always ended in blind alleys, in Nautiloidea as in Ammonoidea, and it is only the smooth, simple stocks that provided the radicals.

This brings us back to some smooth, Silurian Orthoceratid with a marginal siphuncle as the supposed radical of the goniatites and I leave it to the reader to see whether "quantitatively" or "qualitatively" the resemblance is closer than in the case of my nautilicone ancestor with its hyponomic sinus. And, with *Lobobactrites* and *Gyroceratites* out of the sequence, the question arises at once as to where the transitions are. These are not essential in catagenetic series, as I have shown. There are no half-way forms between *Costidiscus* and *Macroscaphites*, between *Helicoceras* and *Turrilitoides*, between *Anisoceras* and *Pseudohelicoceras*. But in an anagenetic series from a smooth *Orthoceras* with a marginal siphuncle to a goniatite, transitions are absolutely necessary to make even the semblance of a case. No such passage-forms are known; and types like *Anetoceras*, SCHINDEWOLF, probably a nautiloid, or the late (Lower Mesodevonian) *Palaeogoniatites lituus* (BARRANDE), discussed below (p. 171), cannot come into consideration.

To expect a transversely ellipsoidal protoconch in *Lobobactrites* or *Gyroceratites*, to prove that they are uncoiled, seems to me to be entirely illogical. Mesozoic ammonoids only developed this barrel-shaped initial chamber after a long ancestry of closer and closer incoiling.

SCHINDEWOLF himself has shown that there were no imperforate goniatites in the Lower Devonian, so it would be impossible for their uncoiled derivatives to possess such a tightly coiled protoconch, whether we believe in the biogenetic law or not. But I have shown what can happen to the protoconch even in an uncoiled Jurassic type (*Spiroceras*); and in my condemnation of recapitulatory evidence I have all along relied more on the later ammonites that we know than on the early types that we do not know.

### V. The Earliest Goniatites.

As I mentioned that the earliest goniatites were essentially like the more or less imperforate nautilicones and that the inner whorls of *Tarphyceras seeleyi* in the Tremadocian already showed close agreement with those of early goniatites (p. 445), it seems unnecessary to discuss the breviconic Silurian "*Barrandeoceras*" *sacheri* (BARRANDE). I particularly pointed out that the Ordovician fore-runners of this nautiloid genus were occasionally much more like *Agoniatites* than the later, Silurian forms; and having many well-preserved examples before me, I was aware that the shell apex of these late so-called *Barrandeoceras*, especially *B. sacheri*, was totally unlike the beginning of the earliest agoniatitids. I have already mentioned that there is no need to assume the existence of completely imperforate goniatites in the Lower Devonian, that is, of forms more involute than those we know, agoniatitids or anarcestids. On the contrary, since few totally imperforate nautilicones were known, I said (p. 449) that the earliest goniatites are assumed to show more or less of an umbilical perforation. It is agreed that the goniatites became entirely involute only in the higher Devonian; and while I (p. 450) stated that all those goniatites that I had examined were closely coiled, I did not feel justified in doubting the existence of some apparent exceptions that had been figured by HOLZAPFEL and KARPINSKY. If these figures now turn out to be erroneous, it only strengthens what I myself said. Likewise some more "regrettable" errors for which SCHINDEWOLF now takes me to task, only clear the air; for a somewhat loose usage, on my part, of the terms coiling and incoiling, or of involution, as distinct from complete closing of the umbilicus, now makes SCHINDEWOLF ask which were those involute goniatites that gave rise to the uncoiled *Gyroceratites* and *Lobobactrites*. I can wish for nothing better than the Lower Devonian *Mimagoniatites* as the root-form of these two. It is the ideal agoniatitid to produce the uncoiled types just mentioned, and its inner whorls are sufficiently close to those of the nautiloid *Tarphyceras* I figured (fig. 4a, p. 427)

to show how little is necessary to effect the transformation of which I spoke (p. 443). Surely the differences are negligible, compared with the wide gap between "*Bactrites*" and the first goniatites. But *Mimagoniatites* which, like *Agoniatites*, has already a modified body-chamber or periphery, could itself be held to be in the catagenetic lineage to *Gyroceratites*, while forms like *Anarcestes* cf. *simulans* (BARRANDE) SCHINDEWOLF (1934c, pl. XX, fig. 3) represent the type of primitive goniatite that tended to closer and closer incoiling.

I must admit that the comparison of the early *Agoniatites fidelis* with the nautiloid "*Barrandeoceras*" *bohemicum* was rather crude, although I made it clear that, to me, resemblance in the adult often counts for more than similarity of the early stages. Thus the multitude of differences that SCHINDEWOLF (1934c, p. 272) now finds have all been discussed, from the well-authenticated instability of the siphuncle to the shape of the protoconch and the variable umbilical perforation. The striae of growth are admittedly different, but I showed how they became modified in nautiloids; and even in an ammonite like *Frechiella* we may get that sudden return to a recurved striation that caused it to be first described as a *Nautilus*. In any case, it may be agreed that ornamentation is only of secondary significance for purposes of systematics or phylogeny: but it has at least enabled us to recognise in the early goniatites a feature which in my opinion again clearly points to derivation from the nautilids, and that is the hyponomic sinus. In one of the forms of *Gyroceratites* figured by FERRONNIÈRE (1921, pl. 2, fig. 43d) this sinus is already well developed on the first whorl, where it comes into contact with the protoconch; and if we remember that the whorls are depressed and have concave dorsal areas at the same early stage, it will be seen that there is little recapitulation of a "*Bactrites*" ancestor. The difference in striation between the nautilids and the early goniatites is of no real significance, since there exist such perfect transitions as *Palaeogoniatites*<sup>3</sup> and the similar *Gyroceras?* sp. figured by FERRONNIÈRE (1921, pl. 2, fig. 42), with short ventral linguiform processes.

<sup>3</sup> HYATT (1900, p. 549) founded *Palaeogoniatites* on BARRANDE's *Goniatites lituus*, but this included two distinct forms of which the larger (figs. 1-5) is a nautilid, probably of the family Trochoceratidae. The genus must obviously be restricted to an ammonoid, i. e. the group of forms represented by BARRANDE's smaller example (figs. 6-7) which requires a new name (*Palaeogoniatites ferromierei*, nom. nov.). Judging by the specimens in the FERRONNIÈRE collection in the Geology Department of the University of Angers, kindly sent to me by Prof. PENÉAU, *Palaeogoniatites* is close to *Gyroceratites*, but has a far less sinuous radial line and a different, more circular whorl-section.



There is no need to count the characters in which an Upper Mesodevonian *Agoniatites* differs from the Silurian "*Barrandeoceras*" *sacheri*; I agree that they are entirely different. But I did not claim either this form or "*B.*" *bohemicum*, which may have a truncate venter, as the ancestor of the goniatites. These nautiloids belong to the breviconic type that still persists in the recent *Nautilus*, but there were many others in which the initial chamber is neither "voluminous" nor bluntly conical. Obviously a longiconic type of nautilid is indicated as the ancestor of the goniatites. As the genus *Tarphyceras*, already mentioned, includes forms with a conical beginning and others that are ophiocones and almost imperforate, so the Silurian genera comprise a variable series of types other than brevicones. It is true that protoconchs like that I figured for the early *Tarphyceras* or like those of the perfectly involute *Trocholites* are not easy to expose, and it must be remembered that the protoconchs of the Devonian *Orthoceras*, previously discussed, came out of a soft, washable limestone, an unusually favourable matrix, while the discovery of the impression of a globular initial chamber in a Triassic *Nautilus* was entirely unexpected. There is an extraordinarily varied series of nautiloids in the early Palaeozoic, compared with their post-Carboniferous descendants, but it seems preferable not to insist on, or single out, any particular genus like the so-called *Barrandeoceras* of the Silurian, leave alone a definite species, as the root-form of the goniatites. I am visualising the persisting Nautilida, with a hyponomic sinus, as a whole, that is, smooth forms of the evolute *Tarphyceras* or involute *Palaconutilus* type rather than the ornamented ophiocones ranging from *Antiplectoceras* and *Graftonoceras* to the somewhat isolated ophidioceratids.

The form described by SCHINDEWOLF as *Anetoceras arduennense* (STEININGER), and correctly referred to a new genus, was first recorded as *Cyrtoceratites* and then as *Gyroceras*; SCHINDEWOLF, however, now thinks that, if his interpretation be correct, this form is not only a goniatite but also an important piece of evidence for the derivation of the goniatites from a straight ancestor. The term "goniatite" seems as much out of place for a form like *Anetoceras*, as it is for the straight *Lobobactrites*; but in any case the extremely loose coiling of the former can only be matched by types that we can prove to be secondarily gyroceratid. Neither the coiling nor the ornamentation of *Anetoceras*, in fact, supports its ammonoid nature. It may be objected that these are features of minor importance, but we do rely on them in the case of other forms with external siphuncle. If *Anetoceras* is related to *Mimosphinctes*, as SCHINDEWOLF suggests (but as seems most improbable,

considering that the ornamentation of the latter genus resembles that of certain individuals of *Gyroceratites fecundus* before me), then the latter must be the original, not the derived, form.

I agree that the initial chamber of *Anetoceras* must have been egg-shaped or globular, but neither this nor the external position of the siphuncle or the suture-line would be sufficient to make it an ammonoid rather than a nautiloid. Taking all the characters into consideration and especially the slender beginning which is known only in uncoiling types, I do not deny that *Anetoceras* could be such an ammonoid. But it has yet to be shown that the numerous trochoceratid offshoots known from the Silurian, and immediately post-Silurian, deposits did not produce similar aberrant forms during the "unstable phase of development" for cephalopods generally, that is, the Lower Devonian. For, in such longicone nautiloids as "*Gyroceras*" *tenue* and "*G.*" *fritschi*, BARRANDE, or *Kokenia obliquecostata*, HOLZAPFEL, the initial chamber must also be assumed to have been globular, as much as in such early forms as the Silurian *Centrocyrtoceras duplicostatum* (WHITFIELD) or, perhaps, even the Ordovician *Apsidoceras magnificum* (BILLINGS) with crioceratid coiling, similar to that of *Anetoceras*. The mere shape of the slender whorls influences the shape of the protoconch, exactly as in longicone (as distinct from brevicone) species of *Orthoceras*.

Since the siphuncle of *Kokenia* is close to the venter it might be considered to be an ammonoid as much as "*Bactrites*" is called a "goniatite" by SCHINDEWOLF, especially in view of the presence of feeble ventral and dorsal saddles in the suture-line (the small ventral lobe in the saddle being dependent on actual contact of the shell with the siphuncle). The slightest move outward of the admittedly unstable siphuncle would make it absolutely ventral and it has yet to be proved that in some individuals of *Kokenia* the siphuncle is not actually at the margin, instead of being just inside it. But whether we leave these incompletely known early forms in the Nautiloidea or transfer them to the Ammonoidea, what has been said will show that the selection of the siphuncle as of the highest rank in systematics is not in keeping with the scanty knowledge we possess of its uses or functions or even the dictates of practical experience. In other words, it is stressing the importance of a character, the significance of which is extremely doubtful.

The value of coiling, by itself, of course is no less uncertain. I have already mentioned that no one could expect the earliest goniatites to have perfectly involute inner whorls and a barrel-shaped protoconch, when the persistent and conservative ancestral main stock of the Nautilidae included almost only imperforate forms; conversely, in an uncoiling

lineage like the Jurassic *Spiroceras* the protoconch soon changed back into a globular shape, but only in some individuals. In uncoiling Cretaceous forms of the general shape of the Devonian *Anetoceras*, the inner whorls also differ from individual to individual, as they really do in *Gyroceratites* and probably *Anetoceras*. But since coiling is admitted by SCHINDEWOLF (1934 c, p. 260) to be of only slight phylogenetic significance, the differences that may be found between the earliest goniatites and the ancestral nautilids with ophiocone coiling are not important. I myself do not find any real difference; comparing a Lower Devonian *Anarcestes* with a *Tarphyoceras* (with unstable siphuncle) of the Tremadocian, there is only a difference of size and an increase in the overlap of the whorls which, however, was common in the equally early and equally unstable Trocholitidae.

With the siphuncle so unstable and whorl-shape and coiling, like the ornamentation, of but slight importance, there remain only the suture-line and ontogenetic development to elucidate the true nature of a given form. I have already pointed out that for systematic purposes we may place the suture-line first in importance; unfortunately in the simple Devonian forms here discussed, it is anything but helpful. Ontogenetic evidence, which I am accused of neglecting altogether, in favour of purely external morphological characters, is important enough to be considered in a separate chapter (p. 177).

## VI. The Younger Ammonoidea.

As in the evaluation of the ontogenetic evidence just referred to, so in the choice of the character that is taken to have the greatest value for classificatory purposes, we may trust to every-day experience and judge by results. If the position of the siphuncle in young ammonites is as variable as I have shown it to be, it is in my opinion inadvisable to select this character for the division of the Ammonoidea into two great sub-orders: — Extrasiphonata and Variosiphonata, the latter division to include not only the Intrasiphonata of ZITTEL (or Clymenidae), but a host of unconnected later ammonoids in which the siphuncle is not ventral from the start. These two groups are widely separated in time; and for his first descendant of the Devonian *Clymenia*, SCHINDEWOLF has to jump to the Permian *Agathiceras*. Since even in this genus some species had the siphuncle ventral from the beginning, they were separated, not only generically, but transferred to the other sub-order. Perfect identity in all characters counts for nothing once the position of the siphuncle, even at a microscopic size, has been chosen,

in spite of its well-known instability, as the one and only feature that matters.

The categorical assertion is repeated that there are no goniatites with unstable siphuncle, notwithstanding all I had said to the contrary. In reply to my statement that in the Middle Carboniferous Glyphioceratidae and Gastrioceratidae, in any case, the siphuncle was known to be as unstable as in the Lower Triassic Ophiceratidae (pp. 434–35), SCHINDEWOLF merely mentions that nine sections of *Goniatites* s. s. showed external siphuncles, also some British Carboniferous forms of which he figures one poorly preserved *Reticuloceras*.

I did not cite *Goniatites* s. s. as an example; I could have told SCHINDEWOLF that its siphuncle was external from the start. But I mentioned that in the glyphioceratids from the Coal Measures the siphuncle, with the sheath continuous, was often of a rich, golden-brown colour, in a clear matrix, that is to say the preservation was often as perfect as in Lias ammonites, distinguished of course, by their siphonal funnels. I cited *Dimorphoceras*, *Homoceras* and *Reticuloceras*, but I could have added *Gastrioceras listeri* as a good example of a goniatite showing an unstable siphuncle, since I had a particularly large number of sections of this species. The fact that other forms of the genus *Gastrioceras* do not agree in this respect, and that even some examples of *G. listeri* have the siphuncle constantly more or less near the venter, only enhances the instability. For, in other sections, the siphuncle can be seen to be well away from the periphery, mostly on the second and third whorls, while the caecum, where it is preserved, is apparently always external. The same applies to *Reticuloceras* in which the ventral groove (note its appearance again in the young) may be held to have influenced the position of the siphuncle. This is occasionally external from the start, but in at least one example of *R. reticulatum* (PHILLIPS) the siphuncle can be seen to be well away from the venter still at 45 mm diameter and among fifteen or twenty sections of *R. davisii* (FOORD and CRICK), most of them showing the siphuncle but poorly (on the innermost whorls), those that are clear are not external, at least on the first whorl. Some young glyphioceratids, labelled *G. micronotum* in the HINDE-Collection, in excellent preservation, all have the siphuncle away from the venter from the (external) caecum onwards for about one and a quarter to one and a half whorls. In one of the best *Eumorphoceras* in the same collection (labelled "*bilingue*") the siphuncle is external in the first three chambers, then moves inwards for a whole whorl, is close to the venter again in the next three chambers (a quarter of a whorl), and moves away once more for half a whorl, to become more or less definitely external after that. In another, similar example it is still away from the venter at over two whorls.

One particularly good section of *Dimorphoceras gilbertsoni* (PHILLIPS) shows the siphuncle, with the caecum perfect, to be central even in the first chamber, to become almost external after the first whorl and a half, and after a renewed move inwards to be actually at the venter only at two and a half whorls. In two other examples of *Dimorphoceras* the siphuncle is central only in the second chamber and external already at the seventh; in a fourth it is central on the first whorl, from the caecum onwards, but then disappears altogether, but in a similar fifth specimen it is not external yet after two whorls. Several more specimens are intermediate, the siphuncle being away most towards the end of the first whorl, or immediately after; in some it remains external for the first three or four chambers and then moves away for a whorl or a whorl

and a half and in at least one the siphuncle is almost external from the second chamber onward, but not at the caecum. The position of this caecum itself, generally well-preserved in the English, but not the Belgian, specimens of *Dimorphoceras*, is thus unstable.

Of course, it would be easy to split the specimens of *Gastrioceras listeri* up into goniatite derivatives (those with an external siphuncle) and into descendants of *Clymenia* (those with a wandering siphuncle), as was done by SCHINDEWOLF in the case of *Agathiceras*. I leave it to the reader to appraise the value of such phylogenetic deductions and of such support for recapitulation. Even in *Agathiceras suessi* from Sosio, the siphuncle may be external already at under 6 mm diameter and may have moved to beyond the middle at just over 2 mm, surely a "minute size" for an ammonoid. It is impossible to find either law or order in the displacement of the siphuncle and HANIEL was probably right in suggesting that there was no regularity or constancy even in the characters of the funnels. It is only by absolutely denying the existence of an unstable siphuncle in goniatites and by arbitrarily selecting a few out of the thousands of motosiphonate ammonites that a progressive acceleration in the displacement of the siphuncle can be suggested.

It is not necessary to add to the overwhelming evidence from Triassic and later ammonites previously adduced; but a paper by SHIMIZU (1929) on the structure of the siphuncle in some Upper Cretaceous ammonites—which I have only recently seen—may profitably be consulted by those who still doubt the vagaries of the siphuncle and its insignificance for phyletic speculations. The preservation of the Japanese ammonites—as "restless a lot" and as liable to homoeomorphy as any other—is excellent; and it is interesting to compare the behaviour of the siphuncle, for example in different species of *Gaudryceras*, or to compare its position in late *Phylloceras* with that in the Triassic ancestors of this genus.

Let it be well noted that it is again on the inner whorls that the instability first appears, notably in such Carboniferous goniatites as *Gastrioceras* and especially *Dimorphoceras*, the former considered by many to be the ancestor of *Agathiceras*, the latter the most "ammonitid" of our goniatites. The phylogenetic speculations of those authors who studied the Permian ammonites, including *Agathiceras*, may have been "premature", and I am not surprised that they found everything to be in a state of flux; but SCHINDEWOLF's treatment of *Agathiceras* seems to me scarcely less justifiable than would be the linking of *Aturia* (with its internal siphuncle and long funnels) with the Devonian *Cyrtoclymenia* or of a late Cretaceous *Schloenbachia* with the clymenids on account of the triangular nepionic coiling of some.

## VII. On Recapitulation.

A brief discussion of some aspects of recapitulation is offered in this concluding chapter; but it is not so easy to state a positive creed as to criticise other people's views. One friend suggested that when (on p. 449) I spoke of the earlier volutions of *Frechiella* showing the *Hildoceras* characters, it looked as if I was very near to accepting the evidence of recapitulation. I may explain that *Frechiella* is a peculiar ammonite (see p. 171), a highly modified or degenerate *Hildoceras* which, however, still shows the suture-line pattern and three-keeled periphery that distinguish its contemporary, *H. bifrons* (BRUGUIÈRE), the commonest ammonite in these Upper Liassic beds. The degeneration in *Frechiella* affects the suture-line as well as the ornamentation, and the whorl-shape is different; but it has its own ontogeny which does not include a "*Hildoceras* stage". *Leukadiella*, RENZ, is a still more aberrant type of *Hildoceras* (again its associate) and it is totally unlike *Frechiella*. For, while its suture-line is far more degenerate, it has retained its arietoid periphery and shape. But the median keel, as in *Frechiella*, has become blunt and low, compared with the earlier whorls or the *Hildoceratid* ancestor. But this, to me, is not recapitulation; it is a phenomenon of growth, comparable to the loss of ornamentation, or the rounding of the venter, or other changes, in the final stages or in dwarf-or freak offshoots of hundreds of common ammonite genera that could not be satisfactorily classified without knowing the adolescent whorls. It is true that such modification is acquired in the adult or final stage (there being no "senile" stage in ammonites), and that it has not encroached from the earliest whorls. But such changes are probably connected with the overlap of the soft parts over the fully-formed shell or a change in the mode of life of the adolescent or adult, and they are without any phyletic significance.

Another friendly critic suggests that while I start by denying recapitulation, but admit some things, he starts by accepting it and cuts out a lot afterwards. He thinks that we really reach the same place in the end, so far as essentials are concerned, but that I am giving the impression that we differ more fundamentally than is really the case. There he is probably right; but my contention is that, shorn of all that is implied in the theory of descent, and what is heredity and normal growth, there is no meaning left in "recapitulation". An ammonite could not help being an ammonite, as I said before, and it is admitted to have been derived from a simpler goniatite. Like any other developing organism, its first necessity was that at every stage of its development

it must have been able to live. As another friend put it, this necessity alone makes perfect recapitulation utterly impossible; but where, he thinks, necessity does not dictate procedure, the organism falls back upon what its ancestors did, so that, provided that we try to get corroborative evidence before accepting ontogeny as a guide to phylogeny, the recapitulation principle is of real value. It is when I ask him "which ancestor" that my difficulty begins.

If we are not to expect to find more in ontogeny than traces of some undefined, generalised, Palaeozoic ancestor (SCHINDEWOLF, 1929, p. 57), and if ontogenetic evidence, this valuable aid in the construction of palaeontological theory, is to be applied so tentatively (GEORGE, 1933, p. 125), if it merely "suggests and implies, rather than fulfills", has the biogenetic law not become meaningless? Not one of the examples of ammonites cited by the latter author from among such "abundance", to support his palingenesis, in fact, is tenable. The capricorn stage in Liparoceratids is not ancestral (see SPATH, 1933a, p. 705); the Rhaetic ancestors of *Psiloceras* are known (SPATH, 1934, p. 313); close similarity in suture-line is not "unlikely" in independent series (Triassic *Beneckeia* and Cretaceous *Neolobites*); the trend to sharpening of the periphery in *Paracoronicerias* is not carried to a further stage in *Oxynoticerias*, a particularly dangerous group to select, as there are "too many of them". By its general resemblance to contemporary genera like *Eparietites*, *Slatterites* &c., *Oxynoticerias* s. s. has always been recognised to comprise certain specialised asteroceratid developments and it is therefore included in the family Ammonitidae (= Arietitidae). To speak of a skipped carinatisulcate stage in such an *Oxynoticerias*, just because we know it to be derived from the arietitids, seems to me as meaningless as to assume earlier, hypothetical *Caloceras*, *Psiloceras*, *Monophyllites* and goniatite stages, to suggest a complete phylogeny. This is indeed "straightforward recapitulation of phylogeny", but we have been putting into this lineage or series all that we want it to include. It was known to the older authors, long before the advent of the biogenetic law, that goniatites, ceratites, and ammonites were intimately allied, that all young ammonites were rounded and smooth, and that, for example, an oxynote form, during growth, must necessarily pass through intermediate stages.

It is sufficient again to look at the results of so much speculation. Since, moreover, it is admitted that caenogenetic characters mar the ontogenetic evidence, I may be forgiven for asking who is to be the judge of what is, and what is not, reasonable evaluation of such "evidence" for phylogenetic speculations? We may consider ourselves fortunate

that in the cephalopod shells there is preserved to us a record of growth-stages that can be useful for systematic purposes; and I used it thus myself (1914) in spite of a warning by BUCKMAN who had then lost faith in such evidence. J. P. SMITH (1914, p. 26) also had to admit that recapitulation "never recapitulates" in the sense of what he called the HYATT school. Now SCHINDEWOLF (1934c, p. 262) agrees that SMITH himself overstepped the bounds of reasonable evaluation in the recognition of distinct goniatite stages in the development of ammonites.

In view of what has been quoted, and bearing in mind the fact that we are comparatively well informed as to what happens in uncoiling stocks, which cannot by any stretch of imagination be called "rare", it seems to me far more crude to assume a straight ancestor for a goniatite or to postulate a clymenid fore-runner for an ammonite, than to trust to purely external characters. HYATT's deduction of his cycle of coiling from the individual development of a single example of *Gyroceratites fecundus* (BARRANDE) was indeed the masterpiece in overstepping the bounds of reasonable evaluation of ontogenetic evidence. I hope I have shown that our zoological friends need no longer dread the spectre of "HYATT's ammonites".

In conclusion it gives me pleasure to acknowledge the help I have received in this investigation from the many friends at home with whom I discussed the various problems, and correspondents abroad who noticed matters of detail or sent me encouraging letters.

### VIII. Summary.

This paper is both a sequel to my first review, necessitated by the rapid advance in this line of research, and a reply to the criticisms of SCHINDEWOLF, GEORGE, SCHUCHERT, TEICHERT, ULRICH and FOERSTE and others.

The principal conclusions previously arrived at with regard to the phylogeny of the Nautiloidea, the derivation of the goniatites, and the origin of the later ammonoids are not considered to have been shaken and additional evidence is offered. The errors of which I have been accused are also discussed.

The genus *Volborthella* remains as doubtful as before. The earliest true cephalopods known are cyrtocoines.

Various features that had not previously been mentioned are discussed, from the nucleus of the completely imperforate Lower Ordovician nautilid *Trocholites* to the hyponomic sinus of the early goniatites. The range in time of the latter is also taken to confirm my views.



Additional evidence is offered to show the instability of the siphuncle in the goniatites (Plate 9).

The advantages of an elastic classification are discussed, also some aspects of recapitulation.

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### Explanation of Plate 9.

Sections of two Carboniferous goniatites (a) *Dimorphoceras gilbertsoni* (PHILLIPS) from Halifax, Yorks (in plane of coiling) and (b) *Gastrioceras listeri* (MARTIN) from Littleborough, Lancs (transverse) to show position of siphuncle in young ( $\times 40$ ).

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## Über Bahnen von Hirnvenen bei Saurischiern und Ornithischiern, sowie einigen anderen fossilen und rezenten Reptilien.

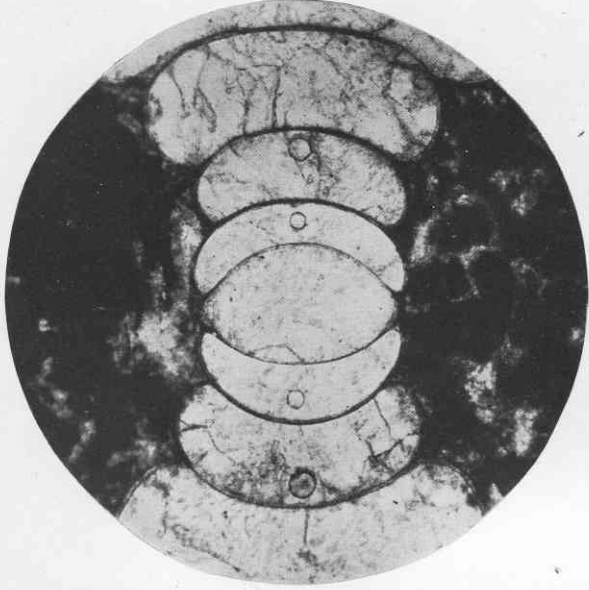
Von WERNER JANENSCH, Berlin.

Mit 5 Abbildungen.

Über Spuren von Venen an den Hirnkapseln fossiler Reptilien sind nicht allzu viel Beobachtungen in der Literatur zu finden. Das kann nicht auffallen, da am erwachsenen Schädel das intracranielle Venensystem nur in geringem Maße Äste durch die Schädelwand sendet. Wenn sich aber Foramina finden, für die die Deutung als Durchtrittsstellen von Venen in Frage kommt, dann müssen zu ihrer Deutung unsere Erfahrungen über die ontogenetische Entwicklung der intracraniellen Venen berücksichtigt werden. Wie wechsellvoll diese bei den verschiedenen Sauropsiden verläuft und wie weitgehend dabei wichtige Elemente rückgebildet werden, hat C. VAN GELDEREN (1924/25) in sehr klarer Weise dargelegt. Da derartige entwicklungsgeschichtliche Untersuchungen — verständlicherweise — wohl den Verlauf der Gefäße, aber nicht oder nur in geringem Maße die Frage behandeln, ob und welche Spuren sie der fertig entwickelten knöchernen Hirnkapsel aufprägen, so ist für den Paläontologen die Deutung fraglicher Venenlöcher schwierig

L. F. Spath, The Phylogeny of the Cephalopoda.

b



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