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The Study of Ammonites in Thin, Median Sections

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ABSTRACT

During the preparation of the second part of the Catalogue of Ammonoidea of the Trias, several hundred thin median sections of ammonites were prepared and examined. Structural features of such sections are shown to have helped in the interpretation of *Didymites*, *Lobites*, and *Paraganides*, and some reference is made to characters of other genera, mainly Trachyceratida.

POLISHED sections of ammonites have always been popular. They were figured by the early iconographers as well as by more recent authors and they are still sought by the visitor to famous fossil localities like Lyme Regis. They are useful for showing in a general way the internal structure of the ammonite shell as, for example, the magnificent " longitudinal section of *Ammonites obtusus* " figured by Buckland over a hundred years ago. Few of the sections, however, were truly median, and the inner whorls were often badly or wrongly restored and generally considered too small to be of any importance.

Hyatt, in his *Embryology* (1872), was the first to extend the principle of examining the internal characters of ammonites and to prepare median sections for study under the microscope. He made mistakes in interpretation and put forward startling theories which discredited his work in Europe. Moreover, Hyatt did not follow up his investigation of the internal features of the Ammonoidea ; and in his renowned *Genesis of the Arietidae* (1889) he stated that the characteristics of the embryos and of the earliest stages did not yet seem sufficiently well known to be used for the classification of the Ammonoidea. These, according to him, were not divisible into two " grand divisions " but into six sub-orders ; and in the recognition of these emphasis was laid on the external characters, mainly the suture-line.

Meanwhile Branco (1879–1880) published his famous researches on the internal features of ammonites and goniatites and these held the field for many years and influenced the work of all students of cephalopods. Branco had many followers in his purely ontogenetic work and the development of a number of individual ammonites became known ; but with the exception of the brilliant researches of F. Grandjean (1910) few observations were made on the less obvious features of the inner whorls of ammonites and goniatites in general. It is not only that the preparation of median sections requires patience and technical skill, apart from almost unlimited material, in view of the many failures, due to a variety of factors. These range from the vagaries of mineralization to the wandering siphuncle which rarely lies in one

[1] Published by permission of the Trustees of the British Museum.

plane ; moreover, the original of a finished thin section cannot be redeemed for examination by ordinary methods and the attendant risk precludes from sectioning all type-specimens and most of the rarer forms—in fact, all examples too precious to be sacrificed. One investigator (Böhmers, 1936) found that in his collection of about a hundred preparations of Permian ammonites there were only four that showed a small portion of the siphuncular sheaths, while none of the sections retained the coecum (the bulb-like beginning of the siphuncle) or its supporting membrane.

Steady advance, nevertheless, is being made in this line of research and we now know the internal structure of a large number of goniatites, Permian and Triassic ammonites, while comparatively little has been done on Jurassic and Cretaceous forms since I discussed some of them in 1933. During the preparation of the second part of the Catalogue of the Ammonoidea of the Trias (about to be published by the Trustees of the British Museum), however, the writer had occasion to prepare and examine thin sections of most of the commoner forms of that period. For while some (Miller and Unklesbay, 1943) hold that the siphuncular structures (the most obvious features in median sections) are not so valuable, in taxonomy, as the (external) suture-lines, others (v. Voorthuysen, 1940) maintain that the internal characters are of the highest importance for determining the inter-relations of the different ammonite families. The evidence of the median sections, therefore, had to be taken into account, even though I myself had previously (1933, 1936) pointed out the vagaries of the siphuncle in the early stages and doubted its value for phylogenetic purposes.

It is not now intended to give more than a brief summary of some of the results of examining several hundred sections of Triassic ammonites. But before doing so I may direct the attention of the reader to some Liassic ammonites, described and figured by v. Voorthuysen, because they seemed to offer an excellent opportunity of testing the usefulness of median sections for purposes of identification of genera or families. It may occur to some that my former doubts as to the systematic value of the characters of the innermost whorls of ammonites were not unfounded.

The Liassic ammonites in question were stated to be "*Aegoceras* sp.", and they were said to come from a black limestone from Gloucestershire, scarcely auspicious representatives of the host of Jurassic ammonites. Van Voorthuysen, however, considered his own four sections to agree with a section of *Ammonites planicosta* (Sowerby) figured by Branco, and comparison was therefore made first of all with about a dozen sections of *Promicroceras* (*planicosta*-group) in the collection. It became clear that of all the characters tabulated by v. Voorthuysen (size of the protoconch, increase in whorl-height, position of the initial constriction, spacing of the septa, thickness of the siphuncle, its position, direction of the siphonal funnels) only the first two were against identification of the doubtful "*Aegoceras*" with *Promicroceras*, the protoconch being only about ·35 mm. in the latter, instead of about ·5 mm., and the whorls increasing in the proportion of about ·30 : ·50 : ·75 in *Promicroceras*, instead of about ·35 : ·75 : 1·30.

Now the size of the protoconch may be a useful generic character in some Triassic forms, as mentioned below; unfortunately, it requires a perfect, median section, with the innermost whorl intact. In the Jurassic, too few observations have so far been made; and as regards the "*Aegoceras*" in question, it suffices to mention that not only in *Androgynoceras* (of which "*Aegoceras*" is a synonym) but in many other genera formerly included in "*Aegoceras*" (from *Schlotheimia* below to *Oistoceras* at the top of the Lower Lias) the size of the protoconch does not differ materially from that of *Promicroceras*. So this first character is of little use in our attempt to identify the doubtful "*Aegoceras*". The second character, namely the increase in the rate of growth (of the spiral or whorl-height) agrees with that of *Androgynoceras*. But in the adult there is often scarcely specific value attached to this increase in coiling; and in *Androgynoceras* both slowly increasing (evolute) and more quickly coiled (involute) types occur, with many intermediate forms in between. Nevertheless, in the very young of Triassic ammonites the increase in whorl-height has been found to be a useful character; and the same applies to the spacing of the septa in some groups, although on the whole this is probably the most unstable of all the characters.

Van Voorthuysen's "*Aegoceras*" has 16 and 18 septa in the first two whorls, which compares well with the numbers (14 and 15) in a typical section of *Promicroceras* before me, or with 16 and 20 in Branco's section, already referred to, and 14 and 17 in a section figured by Hyatt (1872).[1] In another excellent *Promicroceras* section, however, there are only 7 and 8 septa in the first two whorls, whereas in a typical section of *Androgynoceras* the numbers are 11 and 7. Not to overload this account with negative evidence from still more sections, I may say that the number of septa will not enable us to identify the "*Aegoceras*", any more than the position of the initial constriction which in any case is always near the end of the first whorl and which is at a different angle in each of the four sections examined by v. Voorthuysen.

The siphuncle in *Androgynoceras* may become external after only 1½ whorls, instead of at the end of the second whorl, as in *Promicroceras* or the doubtful "*Aegoceras*", but there is variability also in this character, for in one *Promicroceras*-section the siphuncle remains

[1] The locality "Wiltshire" may be in error for Somerset (Marston).

away from the periphery for 2¾ whorls. The width of the siphuncle is more or less constant in all the genera mentioned, but the character of the siphonal funnels of the first whorl could not be observed in any which leaves the "*Aegoceras*" as doubtful as ever. A glance by an expert at the actual specimens, before sectioning, might have settled their identity.

In the case of the far less well-preserved Triassic material it would be surprising if results were entirely satisfactory, but it will be advisable to let the evidence speak for itself. In any case, all the observations made (such as on structure and position of the siphuncle, the protoconch, the septation, the coiling, etc.) have been recorded in the Catalogue, in case future investigators with access to the many genera necessarily omitted from the present account are in a better position to evaluate the seemingly contradictory evidence. Thus, a first difficulty was encountered in a sharp-edged genus (one of the Middle Triassic family Hungaritidae) in which, as expected, the siphuncle was external from the start but only in six sections, and not in one. In this isolated section the siphuncle was still away from the venter (i.e. the periphery) at the end of the septate stage. Now the possibility of an error in the identification of that particular specimen cannot be ruled out ; but it could only have been an example of a closely allied genus which happens to occur in the same rock. An examination of five specimens of that form again showed the siphuncle to be external from the protoconch onwards though, of course, in the average imperfect section the siphonal funnels (which are much more frequently preserved than the siphuncular tube) are never seen along the entire spiral even when there are no complications through secondary mineralization.

The isolated section just mentioned may represent an individual aberration or a pathological specimen. If so, it need cause no misgiving, for an anomalous case can always be checked by additional sections. At the same time, however, it could be held to indicate an inherent instability of the position of the siphuncle, not only found in goniatites but liable to reappear in any later stock. In another sharp-backed genus, the Lower Triassic *Owenites*, Hyatt and Smith, a certain Timor species was found by Böhmers to have at first a central and then a permanently centro-ventran siphuncle ; but on examination of an example of the original Californian type-species in the Collection, it was discovered to have an exactly similar, non-external siphuncle to the end. The position of the siphuncle in *Owenites*, therefore, is obviously a generic character. Protection of the siphuncle has been claimed to be a function of the keel or sharpened periphery. In one genus (the Upper Cretaceous *Hoplitoides*) the original asymmetry of the siphuncle is lost when the venter becomes acute. On the other hand, in another oxynote, i.e. acute-ventered Cretaceous genus (*Platylenticeras*) the siphuncle is known to have been permanently displaced to one side and this has been explained as an adaptation to a benthonic mode of life (like flatfish). The position of the siphuncle in the sharp-backed forms above mentioned cannot have been due to such asymmetry because it was too far below the venter.

Moreover, in round-backed genera also, e.g. in *Didymites, Lobites, Paraganides*, etc., the siphuncle is not yet external at the end of the chambered stage and the same applies to certain Trachyceratids in which the periphery has a median groove, like the Californian *Traskites*. The genus *Didymites* is of late Triassic age and though it has also been grouped with Arcestids of somewhat similar appearance it is almost certainly a member of the Tropitida. It is connected with them not only by external characters and transitions like *Indonesites* Welter, but it has the same thick siphuncle, septal funnels, and other internal characters of that family. The Tropitidae, however, appear in great numbers in the Carnian, at the base of the Upper Triassic, and their siphuncle is internal or central for only a short stage and becomes external after only about 2½ to 3 whorls, i.e. at a diameter of some 5 or 6 mm. *Didymites* may then be looked upon as a group in which the position of the siphuncle away from the venter is retained much longer than in the ancestral Tropitidae.

In *Lobites* the internal evidence had to be pieced together from ten sections because the inner whorls were partly or entirely replaced by crystalline calcite. Nevertheless the wide siphuncle could be seen to be subventral ; and in the largest section, the last septum, at 21 mm. diameter, well shows the siphonal funnel which is definitely away from the periphery, though less so than in *Didymites, Paraganides*, or *Traskites*. In spite of its wide siphuncle and small protoconch I am not including *Lobites* in the Tropitida ; for it not only occurred already in the Ladinian (Middle Triassic) but it specialized in its own way in its external characters, even in the suture-line. Hyatt therefore quite rightly created for *Lobites* a separate super-family, and it can well be kept distinct from other stocks, including the Arcestida with which *Lobites* had been grouped by most authors. These have a large protoconch and a slender, thin siphuncle, at least on the outer whorls and in the later, Upper Triassic species. In the early, Middle Triassic *Proarcestes* the siphuncle also is thicker and external already at the end of the first whorl ; in the later true *Arcestes* it becomes external only at the end of the second whorl. But they are both characterized by their polygyral coiling and close septation, so that at 18 mm. diameter a section of *Arcestes* shows 23 septa to the whorl, one of *Lobites* at same diameter only 9.

Paraganides, Hyatt and Smith, is another genus whose interpretation was facilitated by median sections. The degenerate suture-line completely baffled its authors who grouped *Paraganides* with the Nannitinae. Although I consider that this genus can be recognized as a Tropitid (of the family Haloritidae) by its general resemblance to *Anatomites*, yet its thick, centro-ventran siphuncle is conspicuous and was in fact described (Spath, 1933) as a *Tropites*-siphuncle. As Böhmers (1936) stated, it is internal at first, then central and it becomes centro-ventran (a third of the whorl-height away from the venter) in the fifth whorl. This is the end of the septate stage, at 6 mm. diameter, so that, like *Didymites*, it retained throughout its ontogeny the internal (i.e. non-ventral) siphuncle of the inner whorls of *Tropites*. The equally degenerate and related *Tardeceras* of the same family also has the small protoconch and thick siphuncle of the Tropitida but the position of the latter is subventral, as in *Lobites*, rather than centro-ventran, as in *Paraganides*. *Tardeceras*, which is not the same as *Metasibirites*, as J. P. Smith (1927) thought, is characterized in all six sections by its unusually thick test.

Thickness of the test as well as of the septa may eventually prove of generic importance ; so far the writer has not found this character helpful except in isolated cases like that of *Tardeceras*, just mentioned, or of *Norites* which seems to have unusually thick septa. It should be recorded, however, that the peculiar structure of the test in thin sections revealed an unexpected affinity between *Hannaoceras* (formerly " *Polycyclus* ") and *Leconteiceras* (*olim* " *Leconteia* "). A resemblance had been admitted, but J. P. Smith (1927) pointed out that the young of *Leconteiceras* were not like those of the Ceratitidae but subglobose like those of *Sagenites*. There is no resemblance in thin sections, for *Sagenites* is quickly coiled, having about $3\frac{1}{2}$ whorls at 12 mm. diameter, whereas *Leconteiceras* is polygyral, with $5\frac{1}{2}$ whorls at the same diameter. Nevertheless the latter genus was assigned to the family Haloritidae of the Tropitoidea. In median sections both exhibit a siphuncle that is not quite external at the end of the septate stage and a small protoconch, so that they could equally well be Tropitida or Trachyceratida. *Hannaoceras*, however, is of almost world-wide distribution whereas *Leconteiceras* is confined to California and is possibly merely an extreme development of *Hannaoceras*. If the latter is correctly included in the Trachyceratida (family Choristoceratidae) then *Leconteiceras* may have to be removed from the Haloritidae. It should be added that the peculiar folding of the middle layer of the test which was first noticed in a Californian form of *Hannaoceras henseli* (Oppel) and revealed its close affinity with *Leconteiceras*, is equally developed in a Hallstatt example of Oppel's species. Unfortunately it is uncertain whether the siphuncle in the latter is subventral as in the Californian specimen.

Traskites, already mentioned as one of the genera with internal (centro-ventran) siphuncle to the end is one of the Clionitidae or evolute Trachyceratida; but even in these the sections show the more rapid increase in coiling which all Trachyceratida inherited from their Ceratitid ancestors with external siphuncle. The tendency to delay its passage to the exterior was found also in species of *Trachyceras*, *Nevadites*, *Klipsteinia*, and *Drepanites*, in all of which the siphuncle was not external at the end of the septate stage.

In some Trachyceratids it may be difficult to decide whether the siphuncle is quite external or not, especially as truly median sections are rare ; and as the examples sectioned were comparatively small, I had cut and polished a large specimen of *Trachyceras aonoides* (diameter = 90 mm.) to compare with that figured by Mojsisovics (1893). The siphonal funnels do seem to become external after about 15 mm., but the outer half of the funnel remains conspicuous to the end of the septate stage, at just over 50 mm. diameter, and the siphuncle does not touch the shell-wall as it does in Ceratitids. There is no doubt, however, of the position of the siphuncle in the case of *Traskites*, because the siphonal funnels can be seen to the last septum in two sections, at 8 and 13 mm. diameter respectively, and they are well away from the venter. The protoconch (·3 mm.) is smaller than in some other Trachyceratids, but in *Drepanites* it is not much larger and in the Ceratitids (e.g. *Gymnotoceras*) it is the same (·35 mm.)

In *Arcestes*, on the other hand, the protoconch is ·5 mm. in diameter and in *Joannites* even ·6 mm. In case, however, too much importance be attached to these differences, I hasten to add that in *Cladiscites* (of the same super-family Arcestida) the protoconch is only ·42 mm. in diameter, as it is, at the same size, in an entirely unrelated species of *Discophyllites*, whereas in a form of *Diphyllites* it may be as small as ·29 mm. Since these two forms belong to the only ammonite family that transgressed the fatal Triassic-Liassic border, it would be particularly interesting to have more information on the Jurassic and Cretaceous members of the Phylloceratida, the most stable of all ammonite stocks.

Without going into detail concerning the remaining Triassic families, I may mention that useful evidence has been obtained for example in Ptychitidae and Gymnitidae, as recorded in the Catalogue. The investigation of Pinacoceratidae, however, was less successful, partly on account of the extreme slenderness of the shells, partly because of lack of duplicate material. In this connection I should like to acknowledge with gratitude the expert assistance I received from the technical staff of the Geological Department of the British Museum, especially from Miss P. Hammond.

Enough has been said to show how the evidence of the internal characters is now being utilized in the interpretation of ammonites. There is as yet plenty of scope for the study of ammonites in thin sections, and in time, no doubt, this will be extended to ever more features so far neglected. It may be for future generations to evaluate all the evidence, but in view of the essential uniformity of the Ammonoidea as a whole and the difficulties of classifying a group in such a state of flux, it seems to me that every additional source of information is to be welcomed.

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