

## ON THE BASES OF THE CLASSIFICATION OF AMMONITES.

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*Being the Presidential Address delivered 3rd February, 1893.*

AMMONITES, at present, form the happy hunting ground of theorists. Their varieties are almost infinite, and the resemblances between them are many-sided; what then can be simpler or more attractive than to pick out a series of forms which seem to be connected in one way or another, and give the series a name? Assuming the principle that all the forms are in some way genetically connected,—either as direct descendants, or as having a common ancestor more or less remote in time—it follows that there is a high probability that some of the series so selected represent the facts of nature. But how are we to distinguish the true from the false? What principles are to be our guide? Some of the more general, as the similarity of ontogeny to phylogeny,<sup>1</sup> and the law of acceleration of development, have been already laid down, and scarcely admit of controversy; but these are not sufficient. For the detailed work that has to be done, we want some more special principles which shall apply to the Cephalopoda as a class. I do not think that in thus limiting our view, for a time, to one particular group, we are warning off the student of evolution as a whole: for if we can place the history of any one group on solid grounds, we show at least that it is possible to discover such a history with the materials at our command. The principles we thus seek, must not be laid down on *a priori* grounds, but must be obtained by induction from as wide a review of acknowledged facts as possible. I hoped at one time that I should have been able to deal with the whole class; but now I have sorrowfully to confess, that, even after restricting myself to the Ammonites alone, I am not in a position to lay down any definite conclusions, but in view of the overwhelming mass of material to be dealt with, can only make some desultory observations which may, I hope, tend to elucidate the matter.

In the absence of any recognised representative of the Ammonites amongst living animals we have only the shell to deal with. The elements of the shell in which one Ammonite differs from another are as follows:—the *form*, the *size*, the *body-chamber*, the *aperture*, the *aptychus*, the *first chamber*, the *ornaments*, and the *sutures*.

As it is impossible to deal with all these fully in the course of

<sup>1</sup> This principle has, however, been recently controverted.  
MAY, 1893.]

an Address, some of them must be dismissed with few words. The length of the body-chamber was placed in the first rank by Suess when he began to divide the Ammonites<sup>2</sup>, because it was specially distinctive amongst Triassic Ammonites, and its use as a generic character was extended by Waagen<sup>3</sup>; but little use has been made of it by other authors, partly no doubt because it cannot often be observed, and partly because it is not a very definite character. Its extreme length becomes a special character in *Arcestes*, and its extreme shortness in *Lytoceras*, but these genera are otherwise characterized. The length would also seem to be correlated with the amount of involution. If the interior part of the whorl is occupied by the previous whorl, the loss of space is apt to be made up for by the length of the last chamber; but no general rule can be laid down. The form of the aperture is another of the characters that cannot often be observed, and little use has been made of it except in special cases. Still rarer is the discovery of an aptychus: so that the assertion of its absence in any group, or its universal presence in another, is extremely hazardous; and in any case this character has to do with the larger groups, which are not at present attracting much attention. The form of the first chamber is one of the elements to which, as pointed out last year, Branco<sup>4</sup> attaches some importance; but this is rather in comparing Goniatites with Triassic and later Ammonites, and does not enter into the question of the classification of Ammonites as we have them in this country. There are left then—1, the form; 2, the size; 3, the ornaments; and 4, the sutures, on which I propose to say something in order.

1. THE FORM. Of this there are four elements:—(A) the amount of curvature; (B) the involution; (C) the thickness of the whorl; (D) the shape of its transverse section.

(A). *The amount of curvature.* Some years ago I wrote a Mathematical Paper "On the curves formed by Cephalopoda and other Molluscs"<sup>5</sup>, in which I showed that the curvature can be determined, independently of all other elements, by drawing a straight line through the centre across the Ammonite, and determining the ratio of the intercept on the outer half-whorl (AB, Plate i, figs. 1, 2) to the intercept on the penultimate half-whorl (CD). This method assumes that the rate of curvature of the inner edge is the same as that of the outer. If this is not the case, the curvature can be represented, either by the ratio of the larger to the smaller of the two parts into which any diameter is divided by the centre, or by the square of the ratio of two diameters at right angles to each other.

<sup>2</sup> Sitz. k.-k. Akad. Wiss. Wien, lii. 1865.

<sup>3</sup> Benecke's Palæont. Beitr., Bd. ii. Heft. 2, 1869.

<sup>4</sup> Palæontographica, Vol. xxvii. No. 12, 1880.

<sup>5</sup> Phil. Mag., S. 5, vol. 6, 1878.

Now the greater this ratio, the less is the curvature<sup>6</sup> of the shell. From this a curious result is obtained, when we compare, for example, the figure of *Crioceras Duvalii* as given by D'Orbigny (Pl. i, fig. 2), with that of *Ammonites Largilliertianus* (Pl. i, fig. 1); we find that the ratio in the former is 1.56, while that of the latter is 1.86. In other words, there is more curvature in the open-whorled *Crioceras* than in a perfectly involute Ammonite. Indeed, as a general rule, we find the least curvature amongst the most involute shells, as though the overlapping of the whorls made up in part for the want of curvature. We must, therefore, be very cautious in saying, as Hyatt does, that Ammonites "uncoil" when we refer to their whorls being separate. They do not necessarily do so.

This may be very well shown by drawing the figure of an imaginary Ammonite with the whorls just in contact. (Pl. i, fig. 4.) Now, if without touching the outside, and without, therefore, interfering in any way with the curvature, we fix on the centre the apparent inward continuation of the whorls, we get a form resembling that of *Phylloceras* (Pl. i, fig. 3); if, on the other hand, we fix on the centre a pattern which cuts off the inner part of the whorls, we get a form resembling that of *Crioceras* (Pl. i, fig. 5): so that such an Ammonite is a veritable "transmogrificabilis." It demonstrates that the difference between the form of *Phylloceras*, *Arietites*, and *Crioceras* has nothing whatever to do with their curvature.

There are certain forms, such as *Ancyloceras* and *Scaphites*, in which the rate of curvature suddenly changes at one part of the shell; so that they may become straight, or even slightly reversed. Are we to look upon these as senile types, and their uncoiling a mark of degeneracy? It seems to me that such a shell as *Ancyloceras Renauxianus*, D'Orb. (Terr. crét., pl. cxxiii), negatives such a view; for all the vigour which produces knobs is found on the uncoiled part, and the sudden turn in all these forms is produced by a rapid increase of curvature. I have not been able to discover any observations which might throw light upon the question whether an *Ancyloceras* has at all periods of its life its peculiar shape, or whether its prolongation is an adult feature. If the former is the case, the hinder part of the body-chamber must be constantly absorbed, to enable the coiled part to increase after the formation of the straighter portion. Such an absorption is supposed by Hyatt to take place in a similar case, but it is to be noticed as against this view, that there are sutures in this straighter portion.

Before leaving these abnormal forms, attention may be called to the extraordinary parallelism there is between the *Cochloceras* and *Lobites* of the Trias, and the *Turrilites* and *Scaphites* of the

<sup>6</sup> Some authors speak of a shell which attains a large diameter with few coils as a "quick-coiling" shell; such shells have less curvature than the "slow-coiling" ones.

Upper Cretaceous, and in a lesser degree between *Choristoceras* and the uncoiled *Toxoceras*, &c.; while the development of *Ancyloceras* characterizes two distinct epochs—the Callovian and the Neocomian. The significance of this will be discussed further on.

Turning now to the earlier whorls of the shell: if the curvature be estimated in a series of sections through the centre of the Ammonite, such as those given by Vacek in his "Fauna der Oolithe von Cap S. Vigilio", by a comparison of the consecutive radii, it will be found by no means constant. There are invariably irregularities in the earlier whorls, and comparative constancy only sets in after a certain size is attained: the curvature of the last whorl being in some greater, and in some less than the average. So far as I have been able to trace them, there is always a period, while the shell is still small, at which there is an unusual increase in size, *i.e.*, a diminution of curvature; and it is immediately after this stage that greater regularity sets in. If a wider research should confirm this rule, we might consider it as connected with the life-history of the animal. For the curvature of the shell is brought about by the more rapid growth of the outside: hence a diminution of curvature means a more rapid relative growth of the inside (*i.e.*, the part nearer to the centre). It is still, I think, a moot point whether the outside of an Ammonite is dorsal or ventral, *i.e.*, whether it be curved in the opposite or in the same sense to a Nautilus. It may perhaps be suggested that the more rapid growth of the inside at a certain period of life is due to the development of the generative organs, and in this case they must be on the opposite side to those of the Nautilus, and the outside of the Ammonite may be dorsal.

(B). *The amount of involution.* This is one of the most important of the characters of the shell. When all is regular, the inner edge of the whorl represents a part of the same curve as the outer, but a part further back towards its origin, and one, therefore, of less rapid growth. The involution depends upon how much the inner edge is retarded, *i.e.*, on how far back in an ever more slowly growing series of points it stands. It follows, therefore, that unless some special irregularity supervenes, Ammonites are necessarily more evolute in their youth than in later life, for there is less possibility of lagging when the outer edge has not advanced so far. Thus there is nothing in the evolute character of the young to show that the radical of the race was evolute in any case. Those who, like Hyatt and Buckman, seek an evolute ancestor for every form, should show how any form can have an involute embryo, when there is an "ovisac" (so-called) in the centre of the whorl. That a shell may become more evolute in age than in middle life is certain, but this is because the inner edge changes its rate of coiling relatively to

that of the outer edge. It is said by Hyatt that involution is characteristic of the acme of groups, and, when combined with compression, of their degeneration; while elsewhere he says that uncoiling is a geratologic character, which, as I have shown, depends for the most part, not on the lack of curvature, but on the lack of involution. So far as I can make out, this theory is first laid down, and then the species are placed in their proper position to suit it, without any proof that they actually occur in that order. All we seem justified in saying is that in any true genetic series we may expect that the involution will either remain constant, or constantly either increase or decrease, as we pass along the line of descendants.

(C). *The thickness, i.e., the diameter of the whorl from side to side.* Whilst we have been dealing with the breadth of the whorl, we could not say much as regards its absolute rate of increase as the necessary measures involve the curvature as well; but as the Ammonites are coiled in one plane, we can measure the relative rate of growth by the increase of the breadth. We thus see that Ammonites might be divided into two groups which are parallel to the *longicones* and *brevicones* amongst *Orthocerata*, and distinguished as *compressed* and *depressed* forms respectively. There is, however, some difficulty even in this, as the true rate depends on the length of the spiral, *i.e.*, on the rate of coiling. Nevertheless, in allied forms the thickness divided by the radius from the centre of the Ammonite may give us an approximate measure. There is, however, an important remark to be made in this connection. We know that in all *Orthocerata* the rate of increase is not constant, but the sides of the shell make a curve, concave towards the middle line, in the neighbourhood of the apex. The corresponding phenomenon to this is that the whorls of an Ammonite become naturally more compressed with growth. There is nothing, therefore, in the fact that the earlier whorls are more depressed, that should warrant the assumption that any particular species is derived from a more depressed ancestor, unless we are prepared also to admit the proposition that longicone *Orthocerata* are derived from brevicones, of which there is no indication in the order of their occurrence, some of the oldest being longicones.

(D). The last element of the shape is the particular pattern of the transverse section. This, of course, is largely dependent on the ornaments, and almost belongs to that class of character, so that it will be best to leave its discussion till later.

2. THE SIZE. We are so much in the habit of handling cabinet specimens that we fancy such must be ordinarily adult, and compare the characters of a series at about the same size. Yet there must be races of giants such as that culminating in the 4 ft. *Am. ganesa*, and races of dwarfs as *Am. trivialis* of the Lias, and it does not appear to me that either of these extremes is likely to be the progenitor of a new race of forms. Giants require for

their production a long continuance of favourable circumstances, with comparatively few competitors, and thus they gradually lose their elasticity, and are exterminated on the occurrence of new conditions. Dwarfs, on the other hand, may be either the representatives of a diminutive race, or the final terms of a degraded series, subject to harder and harder conditions. It is the average-sized species that are most likely to break out into new forms and to start a new series. I mention this with particular reference to *Ammonites planorbis* now known as *Psiloceras*, which is considered by Hyatt to be the ancestor of the whole family of the *Arietida*, and which he figures as of small size. The fry are abundant, but the race was really gigantic, as may be seen by the specimen over 3 ft. in diameter in the British Museum. Another point with regard to size has relation to the extinction of types. Hyatt looks for extinction only in the supervention of senile characters, and tells us to look in each case for a retrogressive series; but, to judge by examples from all parts of the animal kingdom, a gigantic size is of itself a cause of extinction from the increasing difficulty of sustenance, and it is often accompanied by specialization rather than by degeneration. We cannot call the elephant or the iguanodon degraded types. Thus types may perish at their acme, as I believe has been the case with some of the *Orthocerata* of the Carboniferous, with the *Arcestes* of the Trias, the *Ancyloceras* of the Neocomian, and the giant Ammonites of the *Lewesiensis* type in the Chalk.

How are we to tell whether an Ammonite has attained its full size? In some, it is indicated by its becoming senile, as shown by the loss of ornaments; in others, by the development of new, and usually somewhat irregular, forms of whorl, as in the Neocomian *Ancyloceras*, or in the *Phylloceras* of the Lias, and *Arcestes* of the Trias. Again, without saying that every full grown Cephalopod has the same number of septa, when they are far apart we may look upon the growth as still vigorous, and the animal destined to attain a larger size (and certainly the giant *Orthocerata* seldom have approximate septa), while an abnormal approximation indicates usually that the last septum has been reached.

We now have left for our main consideration the two great groups of characters, which have divided between them the affections of systematists—the ornaments and the sutures. To show the different estimates of the importance of distinctive characters that are held by different writers, and the confusion that thence arises in the mind of the student, it will be well to compare the figures given by Buckman (Pal. Soc., Mon. Ammonites Inf. Ool.) of *Grammoceras aalense* (Pl. xxxi, 15, xxxii. 6) and *Dumortieria striatulo-costata* (Pl. xl, 10, 11, 12), which shells are placed in different genera, with those given by Futtlerer of *Cycloceras binotatum* and *C. Flandrini* (Tab. xi, 34, and xii, 6, 7), which are placed in the same genus—the two species in both cases coming

from the same beds. It seems to me that most observers would place the former two not only in the same genus, but almost in the same species, and the latter two not only in distinct genera, but in distinct families. Perhaps they might be wrong, but it is difficult from these examples to discover any "accepted" principles of Ammonite classification.

3. THE ORNAMENTS. One of the most remarkable points about the ornaments is their habit of undergoing change during the growth of the shell—those of the earlier whorls being different from those of the later. This change is taken, as explained last year, as a guide to the course the development has followed. We may conceive that at any one of the stages special peculiarities may be developed, which do not succeed in so deeply fixing themselves in the organization of the animal as to be carried on to the next member of the series; and in the necessary abbreviation of development in the later members, it is possible to speculate as to which of the stages will be crowded out. These possibilities open out a wide field for arbitrary assumption. When to this we add that Ammonites are supposed (without much reason that I can see) to progress and retrograde alternately and irregularly, it will be seen that there is very little limit to the number of genealogies an Ammonite may possess which happens to attract the attention of various writers. An example will illustrate this. According to Buckman, *Levesquei* is derived from *polymorphus* and leads on to *radians*, but according to Haug it is derived from *binotatum*; while *binotatum* according to Futtlerer leads to *insigne*, which has a separate origin according to Haug. Whatever, however, may be the later changes, it is obvious that the primitive form must be more simple than the later ones, and, unless the latter have some strongly marked feature, the young shell will naturally commence with being smooth and evolute. It seems, therefore, to be an entirely gratuitous assumption to suppose, with Hyatt, a constant line of simple radicals from which new stocks arise from time to time. It is like supposing a toothless progenitor for man, or a blind one for dogs.

This mistaking of mere negative embryonic characters, for indications of origin has far-spreading and, to my mind, disastrous results. It leads to the drawing out of long parallel lines of forms showing a theoretical development in one direction, totally regardless of any stratigraphical evidence, the corresponding series being connected only by being descendants from the same wretched little characterless form, incapable of contradicting any theory that may be made about it. Even the very evidence which has led to the acceptance of the doctrine of evolution we are thus bidden to ignore—the similarity between the various forms, which has convinced us that they cannot be disconnected genetically, we are told is mere "homoplasy," the exhibition of "morphological equivalence," and they have no genetic connection except by way

of some *Ammonites miserabilis*, as one of these supposed ancestors is appropriately called.<sup>8</sup>

It must be admitted, of course, that very fundamental principles are involved in the way of looking at this matter, which are very well put by Haug in his monograph on the *Harpocerata*. As he points out, we cannot restrict this doctrine of morphological equivalence to Ammonites, and he calls to mind how some have traced the various groups of Gasteropods to corresponding groups of worms; how others have considered the subdivisions of birds as derived from different divisions of reptiles, and others again the horses of the old and new world as polyphyletic in origin. Nor can we stop there: if this be the case, we can no longer have any confidence in calling the negro our black brother: he may only be our millionth cousin through some arboreal ape, or possibly through some common ancestor still more remote among the worms. If this principle be accepted we must also give up all conclusions on the changes of physical geography indicated by the similarity of faunas and floras unless the similar forms are in the direct genetic line.

Of course the term "homoplasy" as used by Hyatt, is a misnomer: that word amongst biologists signifies the superficial resemblance of non-homologous organs, whereas the ornaments of Ammonites are strictly homologous; and the admitted occurrence of the true homoplasy in no way aids the acceptance of the doctrine of the polyphyletic origin of homologous organs.

If, however, we should ever come to admit such a polyphylogeny as a law of nature, it would immediately become a question whether morphological equivalence was not of much greater importance than genetic connection; whether, in fact, the bond of community of structure was not far closer than descent from an unlike ancestor. Are we justified in taking Ammonites as a group at all, if they be descended from different species of Goniatites.

It appears to me however, that the facts admit of a much more rational explanation by the monophylogeny of types, their rapid dispersal and migration, and their interaction whether by breeding or otherwise when brought into the same region. In some cases where a polyphyletic origin has been asserted, it is possible to account for the facts in a more simple way. To take the example that has been most fully worked out: Hyatt derives *Arietites* and *Schlotheimia* from different varieties of *Psiloceras*, and places *Oxynoticer* as a senile modification of the former. Thus the whole of this group is supposed to arise along different lines from the simple form in the lowest beds, and the different branches are not in any way connected beyond the second stage. If, however, we examine the Triassic types of *Trachyostraca*, we find that these forms are already differentiated, and we have only

<sup>8</sup> See Hyatt, "Evolution of *Arietidae*," Smithsonian Cont. to Knowledge, 1889.



to suppose their arrival at different epochs into the Liassic seas to account for their order of appearance. To show this we have only to compare the following:—*Celtites epolensis*, Mojs. (Pl. ii, fig. 10) with *Psiloceras tortile* (D'Orbigny, Paléontologie Française, Terrain jurassique, Pl. xlix); *Sibirites Eichwaldi*, Mojs. (Pl. ii, fig. 11) with *Ammonites angulatus thalassicus* (Quenst. Ammoniten, Tab. ii, fig. 9), *Balatonites prezzanus*, Mojs. (Pl. ii, fig. 12) with *Am. Kridion*, Hehl, or *Am. Bodleyi* (Hyatt, Arietidæ, Pl. ii, fig. 24) or *Meekoceras cadoricum*, Mojs. (Ceph. Med. Triasp., Tab. xii, fig. 9) with *Am. oxynotus* (Quenstedt, Ammoniten, Tab. xxii, fig. 29), the last being a somewhat doubtful comparison. All the earlier forms have their sutures less developed, but the general outline of them is such that a little more complication would produce those of the later.

Again there are cases in which a new type has arisen, not from a simple uncharacterized form, but from a previously existing type of another character. A good example of this appears in the description by M. Vacek, of the Ammonites of the Oolite at Cap S. Vigilio, (*op. cit.*) By comparing the figures taken from this work we seem to see how the *Stephanocerata* (Pl. i, fig. 11) may have arisen from *Hammatoceras* (Pl. i, fig. 10); and by comparing this with Pl. ix, fig. 1, of Vacek's work, almost from *Harpoceras*. In another direction we can pass towards *Perisphindes* (Pl. i, fig. 13) and in a third towards *Aspidoceras* (Pl. i, fig. 12), and there is little to distinguish them in the outlines. It is not suggested that one of these gave rise directly to the others, but that some more elastic type originated a whole series having this apparent range of forms. Seeing that we thus pass from family to family Vacek remarks that these families do not seem to have any genealogical basis, as usually supposed.

I would now draw attention to a remarkable phenomenon, the bearing of which I will afterwards discuss, *viz.*, the recurrence of similar types (the sutures alone excepted) at different epochs. The most remarkable of these is the parallelism of Triassic and Cretaceous forms, particularly in Southern Europe. This will be best seen by putting the corresponding species side by side (see Pl. ii, figs. 1-9). Thus *Am. varians* of the Chalk (fig. 1) is well matched by *Ceratites felsö-örsensis* (figs. 2, 3) of the Trias; *Am. polyopsis* (fig. 4) by *Carnites floridus* (fig. 5); *Am. navicularis* (fig. 6) by *Acrochordiceras Fischeri* (fig. 7); and *Am. coesfeldensis* (fig. 8) by *Trachyceras Reitzii* (fig. 9). So, too, it will be found that *Am. gosauicus* of the Cretaceous (Hauer, Cephalopoden der Gosauschichten,<sup>9</sup> Tab. ii) corresponds to *Balatonicus gemmatus* (Mojs. *l.c.* Tab. vi, fig. 3); *Am. latilavivus* (Sharpe, Chalk Ceph.<sup>10</sup> Pl. xiv, fig. 1) to *Trachyceras Curionii* (Mojs. *l.c.* Tab. xiv, fig. 4), as well as many others in which the resemblance is

<sup>9</sup> Beiträge zur Paläontographie von Österreich. Bd. 1, Vienna and Olmutz, 1858.

<sup>10</sup> Palæontographical Society, 1853.

less close, but in the bulk extremely remarkable. So, too, if we examine the plates of a comprehensive work like that of Quenstedt on Ammonites, we find remarkable repetitions. There is very little to choose between the figures of *pettos* and *coronatus* (see Pl. i, figs. 6, 8), though these are placed in different families by Hyatt, nor between these and *crenatus* as given by Quenstedt (see Pl. i, fig. 9) and *fonticulus* (Pl. i, fig. 7)—all derived from widely separated horizons. A similar example is that of *Am. concavus*, which has been identified by different authors, sometimes with a shell from the base of the Upper Lias, sometimes with one from a central zone of the Inferior Oolite, as the two species which occur in those horizons can scarcely be distinguished. These forms are so connected in time that throughout the entire Jura, one of the group with flexuous ribs is followed by one of the coronate group.

There are other curious facts of the same description. Thus the Arietic form dies out in the Lower Lias, till it is revived in the Upper Chalk in *A. tricarinatus*, *A. tridorsatus* and *A. marge*.<sup>11</sup> The depressed exterior between two rows of knobs, as in *Trachyceras*, &c., disappears with *Schlotheimia* at the bottom of the Lias till it is renewed in a modified form in the Oxfordian in *bimammatus*, and becomes characteristic again in the Cretaceous *Hoplites*. At the same time the planulate and coronate types come to their maximum in the Jura, so that in the Upper Jura scarcely a keel of any sort is to be found.

How are we to account for these phenomena? The recurrence of Triassic types in the Cretaceous might be called an example of senile reversion. In that case, however, we must remember that the latter are stouter and have more complex sutures. Moreover the forms are not feeble characterless ones, but full of youthful vigour. The main question, however, is how we are to connect the two: are we to draw a line across the ages as though their representatives had been living somewhere on the quiet all the time, which is something like what Steinman does when he connects *Schloenbachia* with *Amaltheus*, with only a small branch—*Cardioceras*—as a connecting link between them; or are we to suppose a line of primitive radicals, without any characters of their own, but capable of starting either new or old types of form according to their surroundings, as Hyatt would appear to do; or are we to conceive of one type changing into another directly, and doing so again and again? It is because I cannot as yet give any definite answer to this question that I have said my remarks can only be desultory.

4. THE SUTURES. What relation the pattern of the sutures may have to the organization of the animal it is not easy to say. As I have many years ago pointed out, the fact of the septa being convex forwards, both in the centre and in the lobes of the

<sup>11</sup> Schlüter, Beitrag zur Kenntniss der jüngsten Ammonen Norddeutschlands, Tab. v.  
MAY, 1893.]

saddles, proves that there was a *vis a tergo* in the form of gas, pushing the animal forwards; and the apices of the lobes and their branches are the points of attachment of the mantle surface to the shell, by which it was held there till it was time to move. Hence the branching of the lobes are the real organic peculiarities, the shape of the saddles depending on the greater or less separation of these. In most cases the shell of the Ammonite was so thin that the pattern of the outside was reproduced on the inside, only in cases of very sharp keels or spines was the process cut off by a special shell deposit. Hence the disposition of these lobes is affected by the ornaments of the shell, and their general build has inevitably to be related to the shape.

Their ultimate form may therefore depend on two causes—first, the internal organization of the animal resulting from its law of progress independent of the immediate surroundings, but dependent on its history; and secondly their adaption to the shape and ornaments, which may change according to different laws—and it is easy to see by an examination of specimens that both these causes operate: on the one hand we can point to many instances in which the form of the sutures follows the shape of the shell, and on the other we can find numerous examples of shells with practically identical shapes which have very distinct sutures. It is only in the latter case that they can be taken as *independent* guides to affinity. And not only for this reason does their use in classification require the greatest care. It is well known that, as the animal grows, the sutures increase in complexity, so that if we compare the adult of one with a younger specimen of another they may seem much more distinct than they really are. It will thus be seen that the sutures present so many points of comparison that it is easy to discover resemblances and overlook differences or *vice versâ*, in accordance with one's theories.

If it is difficult to come to any general conclusions with regard to the ornaments, it is still more so with regard to the sutures. I do not refer to the minute differences in sutures of similar form, which are taken to distinguish the supposed series of genetically-connected mutations within the limits of a small family, but to the wider differences which *may* characterize larger groups. In the first place the broad distinction between ceratitic and ammonitic sutures has been shown to be of comparatively little significance: the non-crenated saddles are not universal even among Ceratites themselves, though from other points of view the type is constant in the genus; nor are such sutures confined to that genus, but are even better shown in some of the Dinarites. Branco has also shown (*l.c.*) that in the development of the sutures it is by no means universal that a ceratitic stage is passed through, as the digitations sometimes commence first on the saddles. This form of suture is, therefore, no more than a special variety. This is confirmed by the occurrence of such forms as

*Buchiceras* in Cretaceous times. Amongst Triassic Ammonites it is possible to separate out three distinct types which may be called respectively the *serial*, the *centro-serial* and the *normal* (fig. 1). The last (fig. 1, D), being almost universal amongst Jurassic and Cretaceous Ammonites, has imposed its nomenclature on the others; and all besides the "siphonal" and "superior" and "inferior lateral" lobes are denominated "adventitious" and "auxiliary" lobes. Hence it has been necessary for Mojsisovics, in studying the Triassic forms, to resort to an arbitrary definition of lateral lobes as those beyond the projection of the previous whorl—a definition obviously inapplicable when we have to deal with evolute forms.

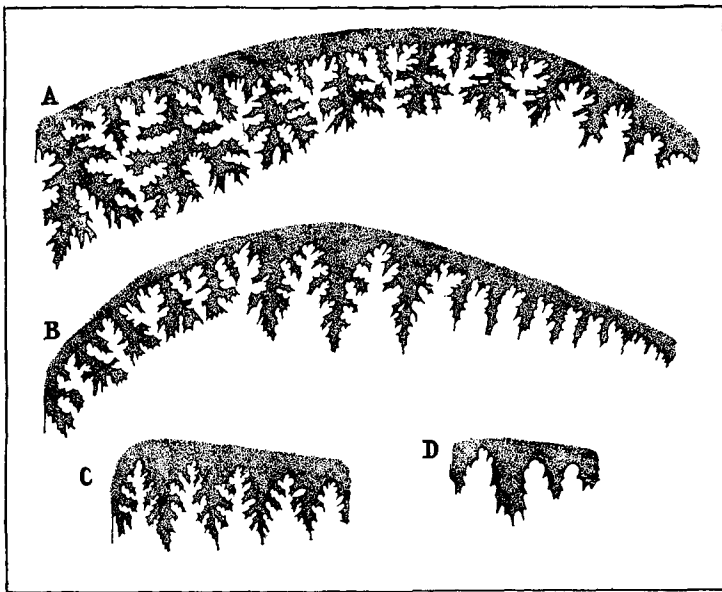


FIG. 1.—A. Serial suture of *Arcestes cymbiformis*.  
 B. Centro-serial suture of *Pinacoceras subparma*.  
 C. Serial suture of *Arcestes pseudogaleatus*.  
 D. Normal suture of *Trachyceras archelaus*.

The size of the lobes and saddles must necessarily be related to that of the shell, and as the outside of the whorl is larger than the inside (measured along the radius) the exterior lobes are naturally larger than the interior, and any deviation from their gradual decrease towards the inside is a specialization. The type of sutures which I call *serial* (fig. 1, A, C.) shows little or no specialization in this sense. It is best seen in *Arcestes* and its allies, called *Leiostraca* by Mojsisovics. *Arcestes* itself dies out with the Trias,

but *Phylloceras* is continued through the Jura and Cretaceous, and always shows more uniform lobes than other genera. In this case of serial sutures, there seems to be a definite relation to groups of forms, all of which are more or less involute, inflated in cross section, and liable to have constrictions crossing the shell. In the last case the sutures have a definite relation to the constrictions, the summits of the saddles running parallel to them.

The *centro-serial* type of sutures (fig. 1, B.) is a very remarkable one. The series is always a long one, and two or three of the central members are of larger size and special character. These are best seen in the Triassic *Pinacoceras* (fig. 1, B), some species of which show the greatest complication of a particular kind that Ammonites ever attain to at any period of their existence. We can trace this kind of suture from the Devonian amongst the Goniatites, the last of which in the Trias is *Sageceras*. In later periods it is never seen to perfection, but some approach to it is sometimes made. This type is also characteristic of broad involute whorls, but depressed in cross section; but is not merely a result of this form, as there are numerous examples of similar shapes with quite distinct forms of suture; nor in this case is there any evidence that this form of whorl is a senile modification. But these types of suture belong to shells with little or no ornament, and are best developed in involute forms. The more evolute members of the same smooth group and even some of the involute, show an approach to the normal type, by the special enlargement of one or both of the two outer lobes. These may be called *serio-normal*, as in *Gymnites*. The importance, however, of the other lobes in these, and their general complexity, show their relation to the former, and certainly their distinctness from all members of the rough-shelled group or *Trachyostraca*. The later Ammonites of the Lias, on the contrary, have sutures which can easily be developed from the simpler forms of suture among the Trachyostraca. For this reason it is impossible to agree with Hyatt in deriving Lias Ammonites from *Gymnites incultus*, whose sutures are serio-normal and highly developed.

It would seem, in fact, that in Triassic times the course of Ammonite development parted into two directions. In the one direction the shell remained simple, and though the involution varied greatly, the curvature remained small, and the development was concentrated in the sutures. In the other direction the sutures remained simple, while the curvature increased, and the development took place in the narrowing of the whorls, and in the ornamentation of their surfaces. The latter branch has proved to have the greater vitality, and is the source of the remarkable Ammonites of later times. I thus agree with Mojsisovics (*l.c.*), on the ground of the sutures, in tracing Liassic Ammonites to the Trachyostraca, as I have already done on the ground of their

ornaments and general build. If this be their true source the theory of a line of simple radicals falls to the ground.

In speaking of the complexity of the sutures amongst the Leiostraca, it is important to call attention to the particular kind of complexity. Complexity of sutures may mean either the complex branching of comparatively few lobes, or the multiplication of lobes with comparatively simple digitations of the sides. Amongst the Leiostraca, it is the latter form of complexity that occurs: the sutures may be many-lobed, and even deeply incised, but only very occasionally do they become compound, by the bifurcation of their saddles. Amongst the successors of the Trachyostraca the complexity of individual lobes is greatest, but in the Triassic forms the lobes are both simple and few, and their arrangement is of the "normal" type.

Amongst the almost infinite variety of form of normal sutures it is extremely difficult, and in our present state of knowledge probably impossible, to lay down any general laws. The pattern appears to be in many cases strictly dependent on the form of the shell, so that given the sutures one can sometimes predicate the shape and ornaments of the shell, but the cases in which we cannot are much more numerous, and it is still harder to predict the sutures from the shell. Examples in which the sutures appear to be directly dependent upon the external features may be noted.

In general, if the exterior is keeled or marked in any way by a central line, the siphonal lobes tend to be parallel; if the exterior is broad, they tend to diverge.

A peculiar form appears to accompany the straight ribbed *Arietites*: the outer saddle is divided by a lobe so that the *outer* half is the largest, and the inner saddle is either larger or longer than the outer (*cf.* D'Orb. Terr. Jur. Pl. xlv.). A contrary form accompanies falcate ribs, *i.e.* is characteristic of the *Harpoceratidæ*: the outer saddle is divided into two parts, so that the *inner* half is the larger, and the outer half tends to become almost separate, so as to look like an additional saddle in the siphonal lobe, which might be called a parasiphonal saddle (*cf.* D'Orb. Terr. Jur. Pl. lv.). This form of suture is seen even in the falciferous Ammonites of the Cretaceous, which can scarcely perhaps, be genetically connected with *Harpoceras*, and are certainly placed in a distinct genus.

What may be called the broad "palmate" type of lobes, particularly the outer, is markedly shown in *Lytoceras*, which thus seems to me not very closely allied to *Phylloceras*, as it is usually considered, but to be rather a descendant of the Trachyostraca. The same type, however, is less well seen in Ammonites with two spines, such as *Birchii* and *Henleyi*. Whether this is any indication of genetic connection appears to be quite an open question.

Another peculiar form of saddle which may be called

"protense," is found in forms which have bands across the whorls, either as constrictions or elevations. The saddle seems pulled out and is Y shaped (*cf.* D'Orb. Terr. Jur. Pl. cxcvii.). These, however, approach the "serial" type, and may belong to the Leiostracan group (*cf.* D'Orb. Terr. Jur. Pl. clxxxix.).

As an example of the non-dependence of sutures upon form, when the species are widely separate in time, may be cited those of *Am. achilles* (D'Orb. Terr. Jur. Pl. ccvi.)<sup>12</sup>, which are the most complex of all, and have in a high degree the sloping position on the inner side which is called "dependent"; yet, the form which most nearly approaches it in the Lias, *Am. communis*, has simple and non-dependent sutures. It is easy to say that they belong to different genetic stocks: the question is, why has the external form come back again to its old characters?

On the other hand, there is a great similarity in the general form of the sutures between *Am. raricostatus* (D'Orb. Terr. Jur. Pl. liv.) and *Am. lamellosus* (D'Orb. Terr. Jur. Pl. lxxxiv.) which belong to two different groups.

Similar observations might be multiplied; and they serve on the one hand to show the difficulty of obtaining any general laws, and on the other to hold out hope that such may some day be discovered. As to the modern genera of Ammonites that are supposed to have a bond of union in the sutures, they go but little way towards the solution of the problem in hand, for they do not range much beyond the ancient idea of species. Hence having found the sutures of any given example of such a "genus-species," we can expect the same in the other members of the same "species-genus." But when we leave the period, and except in the case of the wider-spread species, even the locality of these minor groups, the threads which serve as a clue become so numerous and tangled together that we easily get lost.

In concluding this address I am more than ever conscious how little of a conclusion it really presents. In the study of Ammonites, as in the climbing of a mountain, each step in the ascent only reveals further heights to be surmounted; and though the sweet plains of genealogical speculation stand invitingly before us with their numerous interlacing paths, and shady labyrinths, if we want to know the history of Ammonites as a whole, we must be cautious of their allurements, lest they lead us up and down in no particular direction, and leave us pretty much where they found us.

It is my conviction that in spite of the large quantity of material that has been collected, we still want much more information about the fossils, and their range in space and time, before we are in a position to lay the outlines of their true history, and this information will come, not altogether by

<sup>12</sup> D'Orbigny's *Paléontologie Française* is quoted throughout as being most easily accessible.

discovering more so-called new species, but by comparing the material already in hand, guided by the principles of evolution, but guarded against the trammels of any one particular theory.

## EXPLANATION OF THE PLATES.

## PLATE I.

FIG. 1. *Am. Largillierianus*, from D'Orbigny, Terrain crétacé, Tab. xcv.

" 2. *Crioceras Duvalii*, from D'Orbigny, *l.c.*, Tab. cxiii.

These two figures illustrate the method of measuring the curvature in Ammonites by the inverse ratio of AB: CD. The latter of the above species has more curvature than the former.

FIGS. 3-5. An imaginary Ammonite ("*Am. transmogrificabilis*"), to illustrate the effect of involution alone. All three have the same external curve, *i.e.*, the same curvature, and differ merely in the breadth of the whorl.

FIG. 6. *Am. pettos*, Middle Lias, from Quenstedt, *Die Ammoniten*, vol. i, Tab. xxxiv, fig. 23.

FIG. 7. *Am. fonticulus*, Upper Lias. Original.

" 8. *Am. coronatus*, Lower Oolite, from Quenstedt, *l.c.*, vol. ii, Tab. lxvii, fig. 8.

FIG. 9. *Am. "crenatus"*, Middle Oolite, from Quenstedt, *l.c.*, vol. iii, Tab. xciv, fig. 26.

These figures illustrate the recurrence of similar forms of Ammonites at different periods.

FIG. 10. *Hammatoceras tenuisigne*, from Vacek, *Fauna der Oolithe von Cap S. Vigilio*, Tab. xii, fig. 7. (Abh. k.-k. geol. Reichs, Bd. xii, Wien, 1886.)

FIG. 11. *H. sagax*, from Vacek, *l.c.*, Tab. xv, fig. 15.

" 12. *H. pugnax*, from Vacek, *l.c.*, Tab. xvi, fig. 1.

" 13. *H. gonionotum*, from Vacek, *l.c.*, Tab. xvi, fig. 9.

These illustrate the connection of genera. The first is keeled and has the general build of the Harpocerata. The others only show signs of connection with this by the line down the centre of the siphonal side, and they show respectively the general characters of *Stephanoceras*, *Aspidoceras*, and *Perisphinctes*.

## PLATE II.

FIG. 1. *Ammonites varians* from Sharpe, *Chalk Cephalopoda* (Pal. Soc.), Plate viii, fig. 4, to compare with

FIGS. 2 and 3. *Ceratites felsö-brsensis*, from Mojsisovics, *Cephalopoden der Mediterranen Triasprovinz*, Tab. xiii, fig. 1.

FIG. 4. *Ammonites polyopsis*, from Schlüter, *Beitrag zur kenntniss der jüngsten Ammonen Norddeutschlands*, Tab. iv, fig. 1, to compare with

FIG. 5. *Carnites floridus*, from Hauer, *Cephalopoden des Muschelarmors von Bleiberg in Kärnthen*, Tab. i, fig. 12.

FIG. 6. *Ammonites navicularis*, from Sharpe, *Chalk Ceph.*, Pl. xviii, fig. 3, to compare with

FIG. 7. *Acrochordiceras Fischeri*, from Mojs., *l.c.*, Tab. xxxiii, fig. 8.

" 8. *Am. caesfeldensis*, from Schlüter, *l.c.*, Tab. i, fig. 5, to compare with

" 9. *Trachyceras Reitzii*, from Mojs., *l.c.*, Tab. vii, fig. 3.

The above illustrate the parallelism between many Cretaceous and Triassic Ammonites.

FIG. 10. *Celtites epolensis*, Mojs., *l.c.*, Tab. xxxviii, fig. 13, a supposed forerunner of *Psiloceras*.

FIG. 11. *Sibirites Eichwaldi*, Mojs., *Arktische Triasfaunen*, St. Petersburg, 1886, Tab. x, fig. 1-9, a supposed forerunner of *Schlotheimia*.

FIG. 12. *Balatonites prezzanus*, Mojs., *Med. Triasp.*, Tab. xxxviii, fig. 4, a supposed forerunner of *Arietites*.