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THE INFLUENCE OF THEORETICAL IDEAS ON AMMONITE CLASSIFICATION FROM HYATT TO TRUEMAN

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ABSTRACT

The origins of the theory of recapitulation as applied to the evolution of fossil groups are examined. The theory is shown to have originated independently at least three times, with L. Agassiz and Hyatt, Müller and Haeckel, and S. S. Buckman, respectively. Hyatt further introduced the idea of cycles of evolution whereby many independent lineages underwent similar changes.

Buckman, like Hyatt before him, applied recapitulation and cyclic evolution to problems of the systematics of Jurassic ammonites. He recognized, however, that recapitulation was imperfect and that some stages of phylogeny were often omitted from ontogeny, especially when a more direct development was thereby produced. Buckman's application of recapitulation was accompanied by extreme taxonomic splitting.

Trueman applied the theory of recapitulation to the Lower Jurassic family Liparoceratidae and reconstructed nine lineages each evolving from capricorn to sphaerocone form. This interpretation was later challenged by Spath. Trueman and Williams later attempted to use the theory to elucidate the family Echioceratidae but were unable to trace any lineages.

Pavlov and Spath opposed the universal application by certain paleontologists of recapitulation theory and drew attention to sequences of fossils which did not support it. Their views were supported by biological critics of the theory. The theory was abandoned by English ammonite workers by the end of the 1920's.

INTRODUCTION

This paper is intended as an introduction to the accompanying systematic revision of genera in the Lower Jurassic ammonite family Echioceratidae by T. A. Getty. This was probably the last family to the study of which the theory of recapitulation was applied, about 45 years ago by Trueman. The origins of this theory and its application to some Jurassic ammonites are briefly described.

This treatment is in no sense a complete account of the ideas of Hyatt and his school or of their effect on ammonite systematics, which was extensive and often disastrous. Such a study would be lengthy and probably tedious, and it is doubtful whether the labor necessary to compile it would be worthwhile. I have naturally followed the chain of influence which led up to Trueman's papers, but many other threads could be followed.

The relationship between ontogeny and phylogeny aroused much interest during the nineteenth century. Von Baer (1828) had pointed out that animals resemble one another more closely in their young than in their adult stages. Ontogeny proceeds by progressive differentiation and complication of structure and as differentiation increases in the "higher" animals, the earlier stages passed through show characteristics of "lower groups." The gill slits shown by embryonic mammals are a well-known example. The embryonic mammal in no way resembles any known adult fish; it shows resemblances to embryonic fishes.

With increasing interest in evolution and the publication of the *Origin of species* in 1859 these phenomena came to be viewed in an evolutionary light. The embryonic gill slits of the mammal could be seen as evidence of mammalian derivation from fishes, or at least from animals in which gill slits were functional at some stage of the life history. Recapitulation in the later nineteenth century, however, came to mean more than this. The seeds were sown by Fritz Müller in his book *Für Darwin* (1864) where he recognized two kinds of evolutionary modification: 1) in which descendants deviate from their parents by modification of the ontogeny at an earlier or later stage, and 2) in which the descendants, in ontogeny, attain the form of their parents and then advance further.

In evolution of Müller's type 1, clearly, the structure of the descendants would give no precise clues as to their ancestry, but in type 2, the ontogeny should present a series of stages corresponding to ancestral adult stages. Müller illustrated his views from the Crustacea which he believed to have ontogenies largely of the second type.

Müller's ideas were taken up enthusiastically by Ernst Haeckel who in 1866 gave the first statement of his famous Biogenetic Law declaring "ontogeny is the short and rapid recapitulation of phylogeny," although he did at the same time point out that this ideal relationship between phylogeny and ontogeny was obscured by secondary adaptations, e.g., for larval life. Later (1874) he used the terms *palingenetic* for characters which obeyed the Biogenetic Law and *kenogenetic* for ones which resulted from fetal or larval adaptations.

The essential point of the Biogenetic Law is that ontogeny recapitulates a series of *adult* ancestors. It is this feature which, if true, would permit the reconstruction of detailed phylogenies from their end members. It is this assumption which has given rise to so much controversy; the persistence of embryonic stages is not in doubt.

ACKNOWLEDGMENT

I am grateful to Dr. Mary Whitear for advice on nineteenth-century biological literature.

ALPHEUS HYATT

In the same year that Haeckel published his Biogenetic Law, Alpheus Hyatt (1838-1902) read a brief communication, on 21 February 1866, to the Boston Society of Natural History (Hyatt, 1866):

> Mr. A. Hyatt made a communication upon the agreement between the different periods in the life of the individual shell, and the collective life of the Tetrabranchiate Cephalopods. He showed that the aberrant genera beginning the life of the Nautiloids in the Palaeozoic age, and the aberrant genera terminating the existence of the Ammonoids in the Cretaceous Period, are morphologically similar to the youngest period and the period of decay of the individual; the intermediate normal forms agreeing in a similar manner with the adult period of the individual. He also pointed out the departure of the whorl among the aberrant Ammonoids from its complete development among the normal forms, its final appearance as a straight tube in the Baculite, and the close connection between this morphological degradation of the whorl and the production of the degradational features in the declining period of the individual, demonstrating that both consisted in the return of embryonic or prototypical characteristics of the form, and partly of the structure.

The supposed "agreement" is stated in the most general terms, and is based on a wild simplification of cephalopod history. The earliest cephalopods had rather simple shells, whereas some later ones acquired ornamented shells or complicated septa or both. But all cephalopod shells are simple in their earliest growth stages, and hence the earliest stages of more elaborate forms appear to recapitulate the adults of primitive forms, in which there is little change during growth. The evidence does not contradict von Baer's Law or the later critics of Recapitulation who pointed out that early stages of ontogeny recapitulate early stages of ancestors, not their adults. However, because the primitive genera do not change much during ontogeny it was possible to interpret the evolution as Müller's type 2, whereas it can equally well be regarded as being of type 1.

The end of this very brief report referred to the "constant tendency . . . in the young of the higher species, to adopt the adult, and finally the old age peculiarities of species which were lower than themselves." No detailed examples were given to support any of these ideas.

This resumé, given less than four years after Hyatt graduated at Harvard and in the year following his release from armed service (he had enlisted immediately after graduation), already contained the germs of most of his later views. Its origins lay in the thinking of his teacher, Louis Agassiz.

Agassiz, unlike Hyatt and the later workers considered in this paper, was not an evolutionist. He had worked in Cuvier's laboratory and held Cuvier's belief that successive creations accounted for the sequence of fossil faunas. As a result of about 10 years' work on fossil fishes Agassiz had come to the conclusion that "the successive creations have followed phases of development analogous to those followed by the embryo during its growth" (*"les créations successives ont parcouru des phases de développement analogues à celles que parcourt l'embryon pendant son accroissement"*) (Agassiz, 1844, p. xxvi). Agassiz apparently held that the Creator had improved the design with each successive model, rather like a motor car, and it is somewhat surprising to find him in opposition to Darwin after 1859. Clearly it would have been easy to transfer his ideas to an evolutionary context.

In the work quoted above, Agassiz (1844, p. xvii) also wrote of the proliferation of "tortured" forms of ammonites prior to the extinction of the group at the end of the Cretaceous, and implied a causal relationship between the two phenomena.

These ideas must have been expressed in lectures by Agassiz, who had also expounded with enthusiasm the ideas of von Baer (Brooks, 1909). Hyatt is very unlikely to have known in early 1866 of Müller's work, published in Germany while he was on active service. His theory of recapitulation applied to evolution arose from that of Agassiz worked out on a nonevolutionary basis. So long as the Creator was involved, there could be no objection to it, and indeed it had a certain plausibility. The defects in the theory as applied to evolution had their origin in its nonevolutionary source.

Hyatt's original views were not precisely identical with Haeckel's. Hyatt believed that an evolutionary series of species had a "life cycle" like that of an individual, and he was particularly insistent on the importance of old-age characters, i.e., that the senile forms of today become the normal adults of tomorrow, and so the species or lineage itself passes into old age. Hyatt himself spoke of his "old-age theory" as the guiding motive in all his work.

Hyatt must have been the first to extend the ideas of von Baer and Agassiz to form a hypothesis which could be used to relate evolutionary sequences of forms in time. This was presumably the reason for his great influence among paleontologists, who could now seize upon a theory of development to complement the work of Darwin and explain the evolution of fossil lineages.

Hyatt later (e.g., 1883, p. 349) expounded a more strictly Haeckelian form of recapitulation: "an exact correspondence between the life of an individual Cephalopod and the group to which it belonged: namely the young and adolescent stages having direct correspondence with and repeating the past history of its own group to a greater or less extent, the adult corresponding to the present . . . and the metamorphoses of old age to the pathological modifications and changes found in the types which arose in unfavourable localities, or which were found as a rule to terminate the history of the group in time." Hyatt extended the Biogenetic Law to cover the incorporation of old-age ("geratologous") or pathological features into racial history. As the history of earlier cephalopods appeared to him to be a case of progression from straight to tightly-coiled so the Mesozoic "uncoiled" heteromorphs were seen as a genetic fixation of the tendency, seen in some coiled cephalopod shells, toward more open coiling and weaker ornament on the latest whorls. Increased coiling was regarded as "progressive" and uncoiling as "retrogressive." Hyatt, with no good reason, constantly applied adjectives such as "pathological," "degraded," and "distorted" to the heteromorphs. By doing so he started the practice of referring to "racial old age" and similar rubbish which haunted paleontological textbooks for so long. The origin of the idea lay in one of Louis Agassiz's lectures in which he had "compared the twisted forms found in the Cretaceous just before the extinction of the group, to the writhing contortions of a death struggle" (Mayer, 1911, p. 131).

One of Hyatt's major contributions was to realize that the history of the Cephalopoda involved a number of separate lineages, and that the old generic names based on the shape of the shell were merely form genera. In 1883 Hyatt wrote (p. 330): ". . . the genera, Orthoceras, Cyrtoceras, Gyroceras and Nautilus, as those terms are now applied, are in reality generalized descriptive terms for representative forms of different series, which resemble each other in form, but are distinct structurally. Each series can be distinguished . . . but each one springs from some straight or arcuate form, and passes through a parallel series of transformations. . . ." The modern student of fossil cephalopods would agree as to the extent of homeomorphy, but would probably regard the "parallel series" as altogether too rigid in their supposed sequence of forms. Hyatt was right when he distinguished a number of evolutionary series on structural criteria, but wrong when, turning to ontogenies, and finding "everywhere a similar repetition of arcuate, gyroceratan and nautilian forms" (*ibid.*, p. 330), he saw in this evidence for a closely similar evolutionary sequence in each lineage. Many Paleozoic coiled cephalopods are not tightly coiled to begin with, they have an "umbilical perforation," and the shell comes into contact with its earlier-formed part only after one complete whorl. In Hyatt's view such genera were descended independently from less tightly coiled ancestors. While the theoretical basis for this assumption was unsound, and probably the detailed phylogenies were at fault, it led Hyatt to realize that there had been much parallel evolution and that some shell forms had been evolved, not once, but many times.

Hyatt's ideas of recapitulation and the evolution of parallel, homeomorphous lineages were first worked out with regard to the major features of cephalopod evolution. He later came to apply them to much smaller taxonomic units, for example, the Lower Liassic family "Arietidae" (*recte* Arietitidae) in 1889. Evolutionary changes within a much smaller range were repeated in parallel lineages, within a family and even a genus, in a brief span of geological time (Fig. 1).

This was the stage that Hyatt's work had reached when it came to the notice of Buckman and through him influenced other English workers on ammonites. These workers were not concerned with the grand picture of cephalopod evolution but with the minutiae of individual groups, mainly in the Jurassic. Hyatt expounded his views on many occasions.[1] They were formulated in great detail with little attempt at conciseness of expression, and more than one of his biographers (Brooks, 1909, p. 319; Mayer, 1911, p. 144) remarked on the difficulty of following his reasoning. The following salient points are quoted from the memoir of 1889, one of the works well known to Buckman:

A. *Law of morphogenesis* (p. viii, item 1): ". . . a natural classification may be made by . . . a system of analysis in which the individual is the unit of comparison, because its life in all its phases . . . (ontogeny), correlates with the morphological and physiological history of the group . . . (phylogeny)."

B. *Morphological equivalence* (p. viii, item 4): "In the different genetic series . . . derived from one ancestral stock there is a perpetual recurrence of similar forms in similar succession . . . often falsely classified together, though they really belong to divergent, genetic series." (p. ix, item 10): ". . . morphological equivalents can be predicted with the same certainty as the recurrence of cycles in physical phenomena. Thus we can say of any new series of Nautiloids or Ammonoids, that, the habitat remaining similar, they will, whenever or wherever found, tend to develop arcuate, coiled, close-coiled, or discoidal and finally involute forms in progressive series, and reverse this process in retrogressive series."

C. *Acceleration in development* (later called tachygenesis) (p. ix, item 11): "All modifications and variations in progressive series tend to appear first in the adolescent or adult stages of growth, and then to be inherited in successive descendants at earlier and earlier stages according to the law of acceleration, until they either become em-

[1] A bibliography of Hyatt's writings, which, however, is not complete, was given by Brooks (1909).

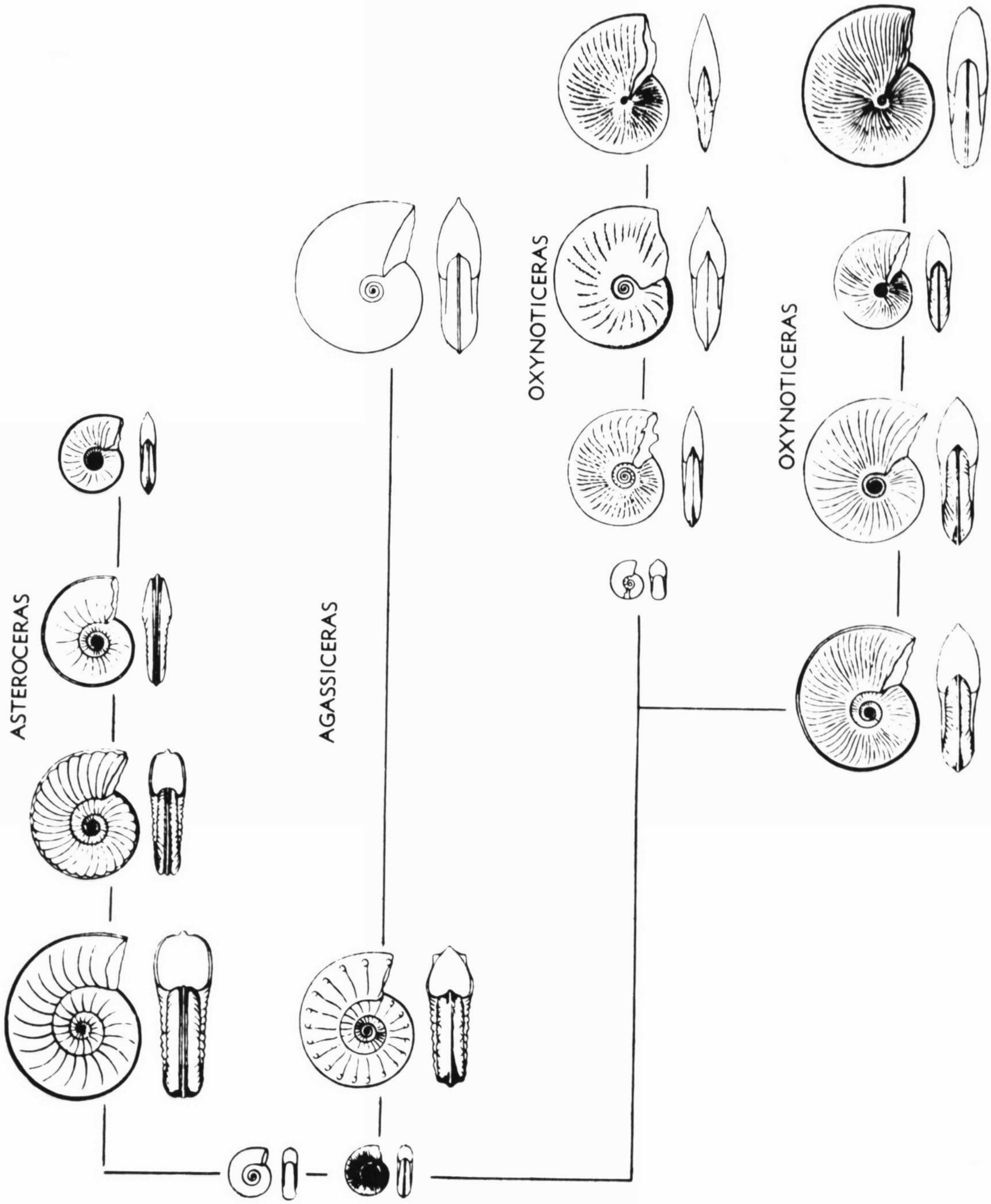


FIG. 1. Parallel evolutionary lines leading to oxycone shells in Arietitidae. Reproduced from Hyatt (1889, summary plate XIII), with the addition of generic names from the plate explanation.

bryonic, or are crowded out of the organization, and replaced in the development by characteristics of later origin." (p. x, item 14): "the law of acceleration in development seems, therefore, to express an invariable mode of action of heredity."

D. *The three phases of development* (p. x, item 15): "In following up series, it has been found that the development of ancestral forms is simple and direct (Epacme); that of their more specialised descendants becomes gradually indirect (Acme), acquiring complicated intermediate or larval stages; and that of the terminal retrogressive or geratologous and pathological forms becomes again more or less direct (Paracme)." (p. x, item 17): "Agreement between ontogeny and phylogeny is completed by the correlation between the mode of development of the individual and its phylogenetic position. Using Haeckel's nomenclature, the three periods of ontogenesis, Anaplasis, Metaplasis and Cataplasis, correlate with the three periods of phylogenesis, Epacme, Acme and Paracme."

A brief nontechnical summary was given by Mayer (1911).

Hyatt's views did not find much favor with contemporary zoologists, but his influence on paleontologists was considerable. The "Hyatt school" included F. A. Bather, C. E. Beecher, S. S. Buckman, J. M. Clarke, E. R. Cumings, A. W. Grabau, R. T. Jackson, R. Ruedemann, T. W. Stanton, J. Perrin Smith, Burnet Smith, Charles Schuchert, and Van Ingen, according to Mayer (1911). They worked on many groups of fossils, but the ammonites, with the whole ontogeny clearly displayed in the more evolute forms, were among the most suitable for the application of Hyatt's theories and they came in for their full share of attention.

S. S. BUCKMAN

In Britain the law of recapitulation was once more stated independently by S. S. Buckman (1860-1929), whose first major work was *A Monograph of the Ammonites of the "Inferior Oolite Series" of England* (1887-1907). In part 3 (March, 1889) he formulated (*ibid.*, part 3, p. 134) three laws governing the evolution of the Jurassic ammonites he had been studying. One of these (III) is virtually identical with the principle of Acceleration of Development expounded by Hyatt. The others concerned (I) the tendency towards greater involution of the shell[1] and (II) a tendency towards sigmoidally-curved ribs. Buckman was at that time unaware of Hyatt's work, but a year later (part 4, p. 159, footnote 3; published March, 1890), he noted the close agreement between Hyatt's and his own views. In the same part (*ibid.*, p. 159, footnote 1) Buckman stated that "the omission of a stage of development may be formulated as a general rule," a phenomenon to which the term *Lipopalingenesis* was later applied. This had also been noted by Hyatt.

In 1892 (Buckman, 1887-1907, part 6, p. 288), Buckman noted that it had hitherto been supposed that ontogeny exactly repeated phylogeny, but that this was not in fact the case—the earliest whorls did not show all the characters of the stage they represent; "earlier inheritance acts partially, in that it allows certain characters to be retained and not others. Presumably only those characters adapted to the requirements of the animal at that stage of life are retained, while others disappear." He further stated (*ibid.*, p. 289, footnote 1):

> Developmental variations may be classed as progressive (*anagenesis*, Hyatt) and retrogressive (*catagenesis*, Hyatt). . . . Among Ammonites proper (excluding Lytoceratinae Hyatt) ontogenetical investigations have shown me that the progressive . . . variations may be referred to the following stages, which follow each other in regular order as here set down:—Globose; smooth evolute; striate; costate; unispinous; bispinous; multispinous.

Thus Buckman, while accepting the principle of Acceleration (or Law of Earlier Inheritance as he often called it), had found from his own work on ammonite lineages that the recapitulation was imperfect, and on p. 290 he expounded three reasons why this was to be expected. But he also followed a Hyattian idea of predetermined cycles of evolution. Hyatt had recognized them in coil-

[1] A similar tendency had been discerned by Hyatt (e.g., 1883, p. 343).

ing. Buckman applied them to small-scale evolution of ornament.

In part 9 of the *Monograph* (1894, p. 382) Buckman explained that although each character (shell form, ornament, etc.) passed, in phylogeny, through a series of stages (progressive and retrogressive, as noted above), the relative rates of change of different characters might be different in different lineages. Since the phylogenetic changes were repeated in the individual, individuals which had acquired more or less the same adult form could (in Buckman's view) be distinguished and attributed to different stocks according to the relative times of appearance of different characters in ontogeny. He used formulae to express the different rates of evolution in different stocks, foreshadowing his later numerical treatment (in *Type Ammonites*, 1909) of developmental stages.

These views were applied in practice to the Bajocian ammonite genus *Sonninia*, and resulted in Buckman's recognizing a large number (ca. 25) of parallel lines of descent, from a few ancestral species (Fig. 2). From the nomenclatural point of view he retained all these forms in the one genus, in which he recognized 70 species, each lineage containing from one to five species. All but one of the 70 species had been collected from a single bed about one foot thick within a very small area in southern England. To the modern view it is difficult to understand how so many separate lineages could have differentiated and persisted within the same area. At the other extreme Westermann (1966), after studying the original material, reduced the number of species to two.

Although the coverage of the subject was still far from complete, part 9 was the last normal part to be published and Buckman embarked on a series of five supplements (1898-1907) in which the earlier parts of the *Monograph* (parts 1-6) were revised in great detail, and many new generic and specific names were introduced. Most of the new species were described very briefly and an elaborate set of terms was used in order to condense the morphological descriptions. In 1907 the Council of the Palaeontographical Society terminated publication of the *Monograph* in an unfinished state. Two years later Buckman embarked on his second major undertaking, *Type Ammonites*.

This is not an appropriate place to consider in detail the further development of Buckman's work as embodied in *Type Ammonites* (1909-30) which in any case consists mainly of plates (1,052 of them figuring 797 species, most of these new; Davies, 1930) with little text. The text included sporadic references to ammonite development and evolution and Buckman at one time employed a method of allotting numerals (from 1 to 5) to denote stage of development of each character of a specimen. These numbers could be added and averaged to give a representative number for the specimen as a whole. If this was done for several specimens they could then be placed in "biological order" according to the totals obtained. While this may today appear as a crude predecessor to numerical taxonomy, it was coupled with extreme splitting (see Donovan, 1954, p. 4) and with a readiness to set up assumed stratigraphical successions based on the supposed phylogenetic order of specimens. Much of Buckman's work has thus fallen into disrepute.

A. E. TRUEMAN

A. E. Trueman (1894-1956) was born in 1894 and after a notable academic career became chairman of the University Grants Committee of Britain in 1949. A full account of his life and work is given by Pugh (1958). He studied geology at Nottingham from 1912 to 1917 with H. H. Swinnerton who was at the time assembling material for his book *Outlines of palaeontology*. This book takes a strongly biological view of fossils and also gives Hyattian ideas a prominent place. It was not published until 1923 but Swinnerton's lectures must have developed along the same lines.

While still a schoolboy, Trueman began to study variation in the banded snail *Helix* [now *Cepaea*] *nemoralis* Linné and eventually collected about 20,000 examples. He published a paper on the subject in 1919. He found that some of the variation, especially in shell thickness, showed partial correlation with the substrate, but on the

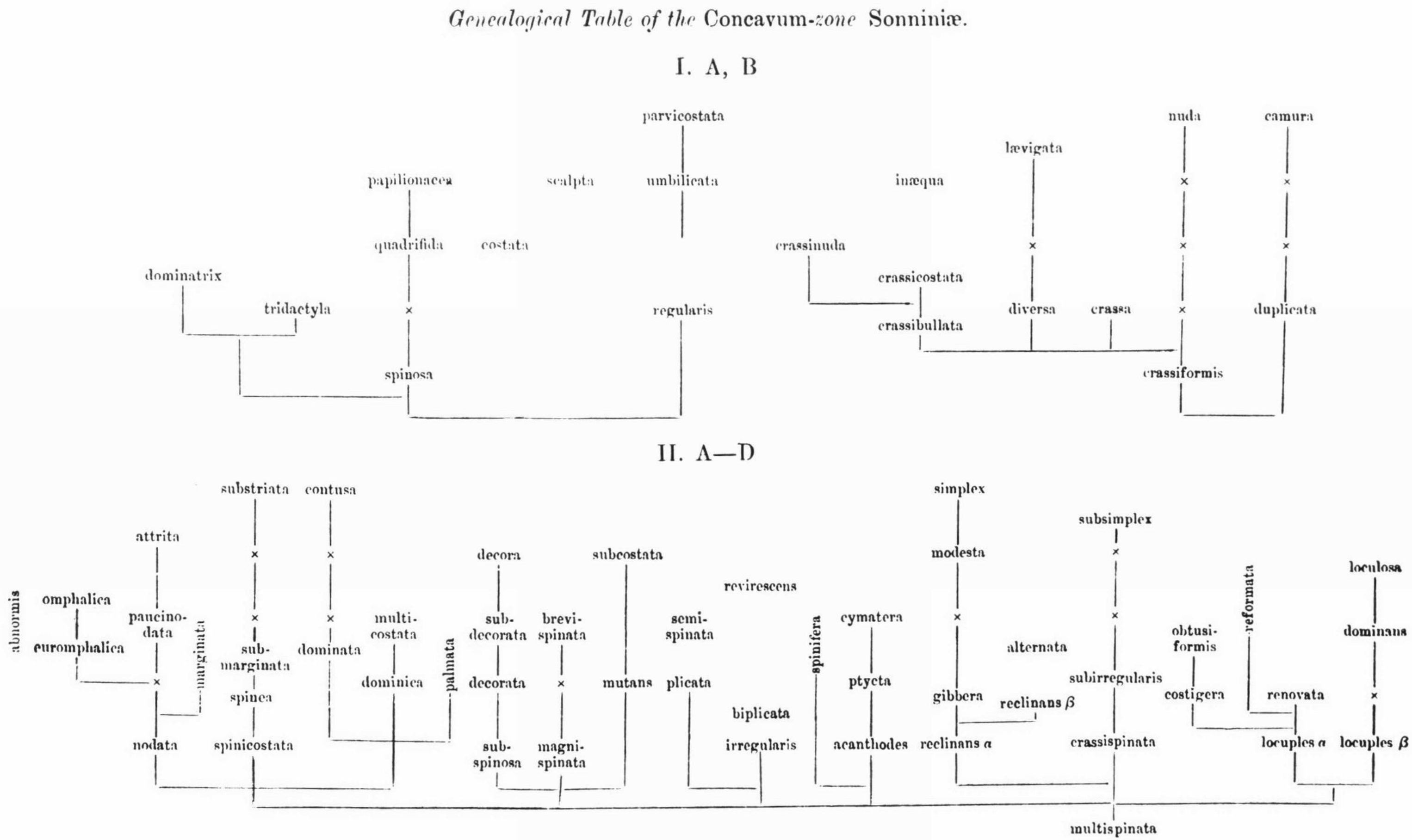


FIG. 2. Evolutionary relationships of southern English species of *Sonninia* according to Buckman (1894, p. 445). "Morphic equivalents" in the different lineages are placed on the same horizontal line. The *concavum* Zone of Buckman included beds now placed in the *concavum* and *discites* Zones.

whole he was inclined to minimize environmental influences on the composition of local populations. Studying the order of appearance of the five color bands in ontogeny, he found this to be different for populations in different parts of Britain. He concluded that "if the order of appearance of the bands in ontogeny in any way reproduces the order of their appearance in phylogeny," the ancestral shells were unbanded, and that banding had been evolved independently in each group. The "if" in the sentence quoted appears to be rhetorical and the context shows that Trueman was inclined to accept the view that "ontogeny recapitulates phylogeny" and its application to the snails. He did remark on the difficulty of explaining the normal presence of five similar bands in each group. We see here the conclusion that what is to some naturalists a single (though highly variable) species in fact consists of groups which are homeomorphous (except for ontogenetic details) and have evolved independently. The model of a series of parallel, homeomorphous lineages, worked out on the basis of recapitulation, is similar to that previously inferred by Hyatt for cephalopod evolution and by Buckman for *Sonninia*. The references to this paper show that Trueman had read standard works of the time such as Bateson on variation and on genetics, and numerous papers on variation in molluscs.

Trueman had already written his first paper on ammonites (1916), stimulated by Spath's detailed account in 1914 of the ontogeny and inferred ancestry of the English Lower Liassic ammonite *Tragophylloceras loscombi*. Spath in this paper was a thorough-going recapitulationist, tracing the ancestry of the genus back to Triassic forms on the basis of ontogenetic details, although he was shortly to turn strongly against Hyatt's ideas. Trueman studied a series of specimens from Old Dalby (Leicestershire) railway tunnel spoil heaps, their relative stratigraphical positions being unknown, and inferred an evolutionary sequence on the basis of recapitulation. His next ammonite paper in 1917 described further Old Dalby material of the genus *Polymorphites*. The ontogeny of *P.* sp. cf. *P. jupiter* (d'Orbigny) was described, and because this smooth form has ribbed inner whorls it was inferred to have descended from ancestors ribbed in the adult. Furthermore, differences between the ribbed inner whorls of different individuals suggested to Trueman that *P.* sp. cf. *P. jupiter* might be polyphyletic, being "catagenetic descendants of several different more highly ornamented forms." This paper also shows that Trueman accepted the "ornament cycle" adopted for ammonites by Buckman (YTA, i, p. xiii).

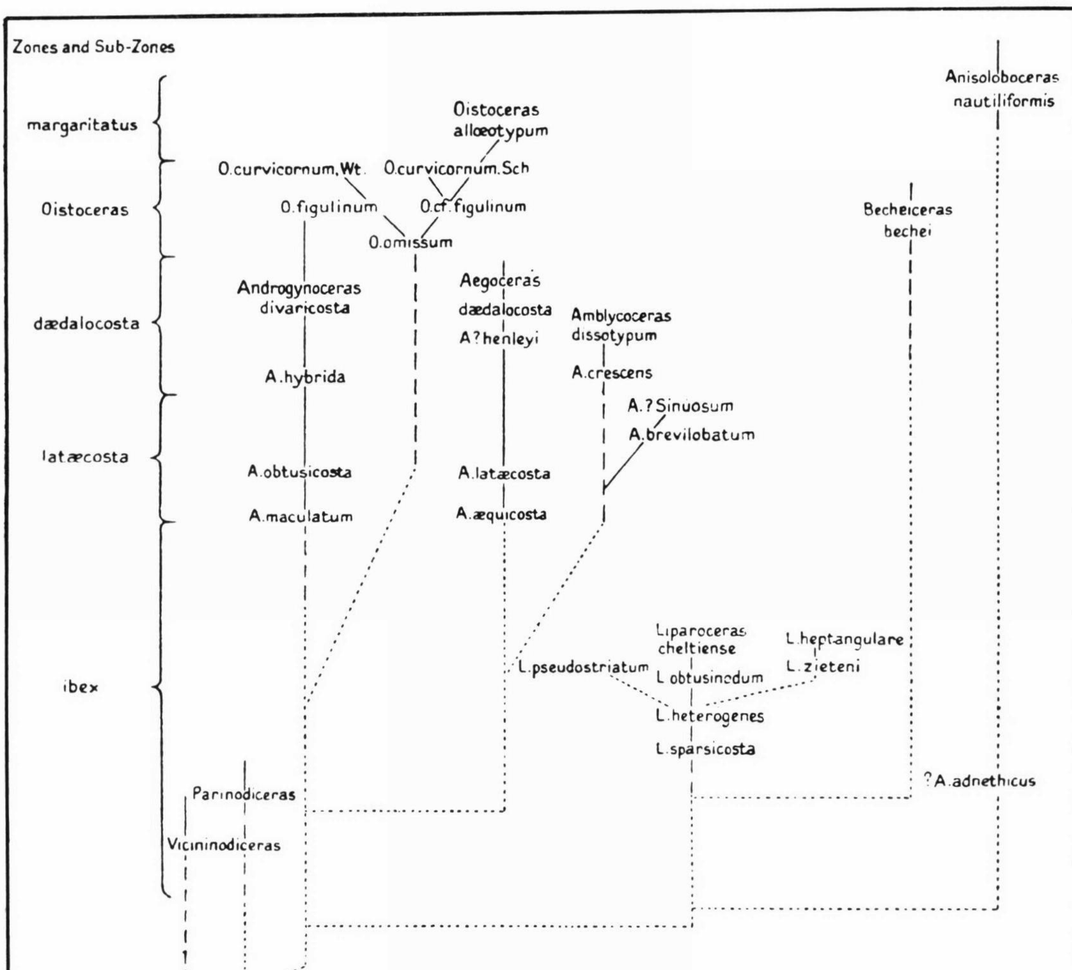
Trueman's first major work was a study of the "Evolution of the Liparoceratidae," a family of Lower Jurassic ammonites. The paper was read to the Geological Society of London in April, 1918, and published in 1919. These ammonites fall into three main groups: 1) capricorns, or serpenticones, which are wholly evolute; 2) sphaerocones, wholly involute forms with inflated whorls; and 3) intermediate types with capricorn inner whorls and inflated outer whorls ("dimorphs" or "hybrids" of some authors). In 1867 Hyatt had proposed the three generic names *Microceras*,[1] *Liparoceras*, and *Androgynoceras*, for these three groups, respectively. This was originally a purely morphological classification. For adherents of the law of acceleration of development, however, it was clear that ammonites of type 3 were descended from type 1 by addition of an inflated outer whorl, and it was but a small step to suppose that the sphaerocones of type 2 were descended from ammonites of type 3, the evolute stage now having been completely suppressed in the ontogeny. This step was taken by Buckman (1891, p. 289, footnote), who later, evidently believing that a genus should comprise a single evolutionary line of descent, used Hyatt's three genera for presumed separate lineages, each of which evolved from capricorn to sphaerocone (Buckman, 1909). Thus, the simple gross morphological definitions of the genera were lost, and the names were applied to supposedly homeomorphous forms where distinction rested on subtle points of morphology, and on stratigraphical age.

Trueman carried Buckman's interpretation further, recognizing nine genera each constituting a separate line of descent (Trueman, 1919, p. 206, table III) (Fig. 3, herewith). Some of these included a complete series from capricorns to sphaerocones, while others comprised only partial series which had to be separated for theoretical reasons. For example, the earliest known Liparoceratidae are in fact sphaerocones, but,

[1] Later replaced on account of homonymy by *Aegoceras* Waagen, 1869.

since according to the recapitulatory interpretation these must be end forms of lineages, they were placed in two distinct genera (i.e., *Parinodiceras* and *Vicininodiceras*, differing in whorl section) with unknown capricorn ancestors. These early genera also differ from later sphaerocones by having paired tubercles. The remaining seven genera were distinguished on sutural details, except for *Amblycoceras* and *Oistoceras*, which were said to be characterized by respectively slightly and sharply curved ribs on the venter. A sequence of evolution of ornament was discerned as well as a sequence of shell forms. Stages (a) to (e) (Trueman, 1919, p. 256), of

TABLE — *showing the probable relationships of the species of the Liparoceratidæ.*



[**Continuous vertical lines = proved range of the genus ; broken lines = probable range ; dotted lines indicate affinity ; for *dædalocosta* read *dædalicosta*.**]

FIG. 3. Probable evolutionary relationships within the family Liparoceratidae (after Trueman, 1919, p. 286).

generally increasing elaboration, were said to be anagenetic, while stage (f) (returned to paired tubercles) was catagenetic.

The paper was well received by Buckman, A. M. Davies, and Swinnerton, although G. W. Lamplugh, President of the Geological Society, in opening the discussion complained of the difficulties of the field geologist confronted with such a complex classification. Trueman, like Buckman, used generic names for lineages, and the practical result was (as he noted, 1919, p. 257) that there is much greater similarity between the corresponding evolutionary stages of different series (genera) than between different stages of the same series. Simple morphological definitions of genera are not possible.

As a result of his work on Liparoceratidae Trueman wrote a paper (1922) entitled *"Aspects of ontogeny in the study of ammonite evolution"* which had the object, more limited than the title suggests, of drawing attention to the skipping of stages in recapitulation or lipopalingenesis.[1] The phenomenon was divided into chapters "The omission of earlier characters" and "The omission of comparatively late characters" and for the latter phenomenon the example of the liparoceratid sphaerocones was used—although supposedly descended from comparatively near (in time) capricorn ancestors, there was no trace of the capricorn stage in their ontogeny. This was explained on the grounds that the earliest whorls in all members of the group are stout, and the omission of the slender capricorn stage enabled ontogeny to proceed in the most expeditious way, from stout direct to stout.

Buckman, in discussion of Trueman's 1919 paper, quoted the Liparoceratidae as illustrating the principle of faunal repetition, "successive waves of capricorns developing into bituberculate sphaerocones." This principle had emerged from a study of the upper Sinemurian on the island of Raasay, Scotland, where a thick section shows alternating fossil horizons with echioceratid and with eoderoceratid ammonites (Buckman in Lee, 1920, p. 69-71). Presenting these results to the Geological Society of London about a year before Trueman's paper was read, Buckman (1918, p. 268) said that the Scottish ammonites had not yet been critically studied—"a very long task"—, but that "as the product of development at intervals during a very long period of time, they are much more understandable than as the product of one date; and, as the outcome of repetitive series evolving on parallel lines, the frequent similarity but not identity in the Echiocerata is explicable." Buckman regarded the Echioceratidae as showing an evolutionary pattern like that postulated by Trueman for the Liparoceratidae. Trueman's paper on Liparoceratidae may thus be useful in understanding his less explicit paper on echioceratids.

The work on the Echioceratidae was Trueman's second and last major study in ammonite systematics (Trueman & Williams, 1925). It was undertaken in collaboration with Miss D. M. Williams, a research student at University College Swansea. Trueman had been at Swansea as Head of the Geology Department since 1920, but took an active interest in the geology of north Somerset. An important stratigraphical paper on the Lias of the Radstock area (Somerset) had resulted from collaboration with the well-known Bristol amateur J. W. Tutcher (1858-1951) (Tutcher & Trueman, 1925). Trueman was thus familiar with the abundant and well-preserved echioceratid material in the "Armatus Bed" of the Radstock quarries, a condensed deposit containing in its basal few inches fossils from several subzones. Out of 36 new species set up in the paper, 19 were founded on holotypes from the Armatus Bed. Material was also studied from measured sections on the Dorset coast, where the late W. D. Lang was engaged on his meticulous study of the Lias succession (Lang, 1926), from the Yorkshire coast, from the Inner Hebrides of Scotland, and from inland exposures in the English Midlands.

In reviewing this work the question of species may be mentioned first. Trueman and Williams recognized 79 species in their paper, which was almost wholly restricted to the British fauna. They remarked (Trueman & Williams, 1925, p. 704) that "Unquestionably there are great numbers of other Echiocerates which have been examined which might legitimately be admitted to specific rank, and the immensity of the Echioceratid fauna is yet scarcely indicated by the numbers of figured species." It is clear that if

[1] A complex nomenclature grew up to describe different aspects of recapitulation. Some of the terms are still useful and others forgotten. For the purpose of this review it does not appear necessary to explain this nomenclature.

they had carried out a full monographic treatment a very large number of species would have been recognized. This is in contrast with the approach of more recent British workers, such as M. K. Howarth, who recognized 24 British species in the Middle Liassic ammonite family Amaltheidae, placing about 20 further species into synonymy, and T. A. Getty, who reduces Trueman and Williams' 79 species of Echioceratidae, plus about 30 more unknown to them, to about half this total in a current unpublished study. Howarth and Donovan in a study of the genus *Tragophylloceras* (1964) reduced 14 nominal species to four. Trueman's approach is explained in a paper on *The Species-concept in Palaeontology* (1924), in which many of the difficulties resulting from the time-dimension and from incomplete preservation were cogently discussed. Trueman thought that the Linnean system of binomial nomenclature was inadequate for the needs of paleontology, although he thought it premature to propose an alternative. At the end of this paper Trueman declared himself to be in favor of "restricting the use of the specific name to specimens identical with the holotype." He was under no illusion that a species used in this way was any kind of biological entity,[1] and he realized that doing this "must lead to enormous increases in the numbers specific names." Notwithstanding the many studies of variation in assemblages of fossils which had been published, he evidently did not consider that fossil species in any real sense, i.e., natural communities, could be recognized by paying attention to the ranges of variation shown by different characters.

The present writer has rejected this approach because it leads to a "species for every specimen" situation and because he believes there is a need to try to recognize natural assemblages which are bound to show variation. It was, however, common in Trueman's day, not only with Buckman (who was a notorious splitter) but with avowedly more progressive specialists such as Spath and Arkell. It is interesting, however, that it was consciously accepted by Trueman as a logical consequence of using binomial nomenclature.

The multiplication of genera which was indulged in by Trueman and Williams was unrelated to the multiplication of species. They had no objection in principle to genera containing a large number of species, and those used ranged from monotypic ones to *Echioceras* with 29 British species. But separate lineages should be given generic status, as in the Liparoceratidae (Fig. 3). No phylogenetic diagram was given for the echioceratids, but the authors wrote "In making these genera . . . attention has naturally been paid as far as possible to the presumed phylogeny of the family. It must be noted, however, that this family is a very large one, with apparently numerous stocks evolving along more or less parallel lines. It is not unlikely that in several cases members of different stocks have been placed on one genus . . . the genera are in most cases much more than mere lineages, the species referred to each genus probably represent related and parallel lineages" (Trueman & Williams, 1925, p. 706). The different lineages were worked out on the basis of differences between inner whorls, supposed to indicate different ancestry according to the Recapitulation Theory. The differences were slight, however (e.g., "*Paltechioceras* represents a parallel development from a stouter stock with stronger ribbing," *op. cit.*, p. 707). One wonders whether such fine generic distinctions would have been maintained in any other group of fossils! In the case of the Liparocaratidae, several homeomorphous lineages required by Recapitulation were of different ages, so there was some reason for separating them generically. With the Echioceratidae, the supposedly homeomorphous groups were of the same age, and their separation at generic rather than specific level must have been the result of a belief that a genus should correspond with a lineage. There is no agreement on this point among ammonite paleontologists, others (e.g., Arkell, 1940, p. 399) using the genus (or subgenus) for grades of evolution.

There is an important difference in taxonomic treatment of these lineages between Liparoceratidae by Trueman (1919) and Echioceratidae by Trueman and Williams. In the former case, as already remarked, each lineage included a range of morphological forms from capricorn to sphaerocone. In the echioceratids each genus has a much smaller morphological range and corre-

[1] Compare the revealing statement made later by Spath (1938, p. 25) that "the examination of numbers of individuals of *Beaniceras* leads to the conviction that, with the numerous passage-forms to *Androgynoceras* and *Liparoceras*, all the species of *Beaniceras* formed one interbreeding population."

sponds to only one evolutionary stage of a supposed lineage. The authors remarked that several sulcate genera "are probably derived from several different stocks of pre-sulcate forms," but they were in fact unable to identify these ancestors. The taxonomic treatment was therefore unavoidable. Notwithstanding its introductory apologia for recapitulation, the paper represents a failure of the theory to separate the multiple lineages which were assumed to exist.

Trueman and Williams' paper was the last in the English-language literature on Jurassic ammonites to give prominence to the theory of recapitulation. Trueman himself transferred his attention to the correlation of the Coal Measures and the systematics of their nonmarine lamellibranchs. He became much concerned with variation and with problems of naming and defining fossil species. In a paper published in 1930, he seemed to have been more ready to admit exceptions to recapitulation, although he wrote that "evidence of recapitulation have been observed in most groups of animals, and . . . some degree of recapitulation is to be expected in any organisms which have arisen from ancestors different from themselves" (1930, p. 137). This is rather different from the thorough-going recapitulation implied by his earliest systematic work. In the same paper (1930, p. 133) Trueman dismissed as unlikely, with regard to the *Ostrea-Gryphaea* faunas of the early Jurassic, the possibility that a "lineage" really consisted of a great number of parallel lines of evolution, such as he had inferred for *Cepaea.*

DECLINE OF THE BIOGENETIC LAW

The Biogenetic Law probably had more followers among paleontologists than neontologists (Mayer, 1911). However, it had enough adherents among biologists to provoke repeated refutation, for example, by Sedgwick (1894), Garstang (1922, 1929) and again by De Beer (1940). Biological critics argued largely from the obvious fact that developmental stages do not usually resemble adult types, though they may resemble development stages of other animals in accordance with the generalization of von Baer. Paleontological critics, at least among workers writing in English, were surprisingly slow in coming forward. Hyatt, for example, had (1889) constructed detailed phylogenies for Liassic ammonites, largely on the basis of museum specimens. But because the general succession of forms was known, and because evolutionary changes in groups largely affected the outer whorls, his results were not too different from what would be accepted today. However, it needed only one exception to be demonstrated by careful stratigraphical collecting for the "Law" as applied by Hyatt and by Buckman to be invalidated. Such an exception was supplied in 1901 by the Russian paleontologist A. P. Pavlov who pointed out that in *Kepplerites* and other genera new characters first appear in young stages and spread to the adult only in fossils from later strata. He cited other instances of the same thing in belemnites, gastropods, and vertebrates, and wrote "it is to be hoped that, under the influence of the facts, the limitations of the recapitulation hypotheses will soon be realised and that outside those limits the field will be left free for other interpretations" (quoted by Arkell, 1949, p. 405).

Hyatt, who died in 1902, is unlikely to have known of Pavlov's criticisms, and they seem to have been unknown to Buckman and to Trueman, perhaps because they were Jurassic specialists while the title of Pavlov's paper referred to the Cretaceous. Pavlov's work was certainly known to Spath (1882-1957), whose knowledge of ammonite literature was legendary, and it was Spath who (after a first paper [Spath, 1914] in which recapitulation was enthusiastically embraced) was the first among English ammonite workers to rebel, recanting his earlier beliefs. Unfortunately Spath habitually assumed that his readers' knowledge and intelligence matched his own, and merely referred in passing to the "discredited laws of recapitulation" (1924, p. 198). This did not seriously worry Trueman and Williams who complained (1925, p. 700) that Spath had adduced no good evidence in support of his heterodox views. It is more surprising that Trueman was not aware of, or ignored, Garstang's criticism of the theory which was read before the Linnean Society on 2nd June 1921 (Garstang, 1922). It is true that Garstang was diffident about attacking the ammonoid "evidence," being apparently baffled by the barrier of names and complex terminology which had been introduced by ammonite systematists. He was on surer ground with echinoderms, however, and presented a detailed and scathing attack on the recapitulatory interpretation of echinoderm evolution favored by the paleontologist F. A. Bather and the embryologist E. W. MacBride.

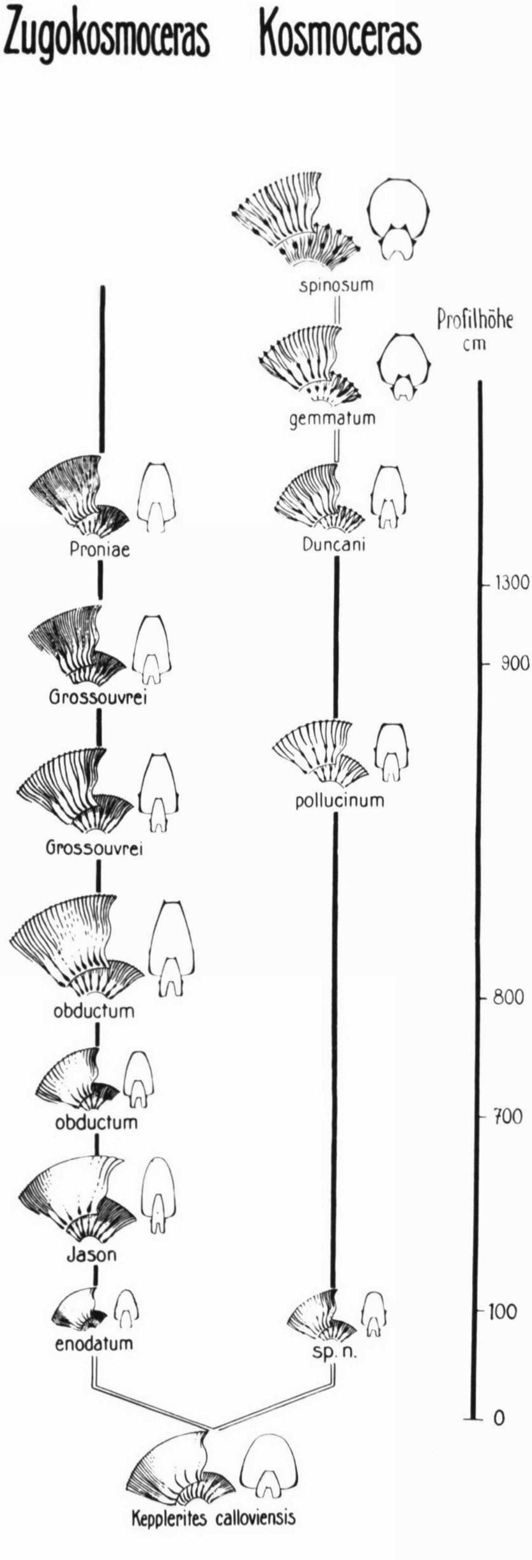
The 1920's, then, saw the end of the theory of recapitulation among English paleontologists. About this time Roland Brinkmann studied kosmoceratid ammonites from the Upper Jurassic Oxford Clay of England, and published, in 1929, a now classic paper on their detailed evolution.[1] One of his lineages (*Gulielmites-Zugokosmoceras*) showed that a tabulate venter, present on the inner whorls only of earlier specimens, persists throughout growth on later examples; the reverse of recapitulation (Fig. 4). Spath published a detailed refutation of the theory as applied to fossil cephalopods in 1933, and an interpretation of the Liparoceratidae, in which the evolutionary sequence accepted by Buckman and by Trueman was reversed, in 1938. Although W. D. Lang in a preface to this work drew attention to Spath's "challenge," it was not taken up; Trueman published no more ammonite systematics after 1925, Buckman had died in 1929, and Bather in 1934.

How could the theory of recapitulation dominate ammonite studies for so long, and come to be accepted uncritically by able men such as Bather and Trueman? There is probably no simple or satisfactory answer. The influence of able and enthusiastic teachers: of Agassiz on Hyatt, Swinnerton on Trueman, was doubtless both real and important. The most brilliant minds often begin by emulating their teachers, and instant rebellion is rare. Buckman, however, was virtually self-taught as a paleontologist, and so was Spath. Deeper reasons must be found in the personalities of the people involved and the general background of biological thinking of their time. Hyatt seems to have become obsessed with recapitulation and his "old-age theory," but paleontologists must always depend on the opinions of biologists as to what may be genetically possible, and Hyatt had the famous Haeckel, whose works ran into many editions, to encourage him. He also had Lamarck, and in days before our modern knowledge of genetics made a Lamarckian position untenable he could believe, as he did, that "pathological" aberrations of shell form, induced by unfavorable circumstance (Hyatt, 1883, p. 349), could be inherited. In those days of uncertainty he could also largely reject Darwinian ideas of variation and natural selection (*ibid.*, p. 340, 347). Recapitulation *per se* is not incompatible with natural selection, although palingenetic stages of ontogeny must have escaped the action of selection, or they would not have survived unmodified. All exponents of recapitulation conceded cenogenetic modifications of ontogeny, due to adaptation for larval or miniature life, and these would have resulted from natural selection. Hyatt's ideas of evolutionary cycles and racial old age were, however, incompatible with natural selection, implying predestined evolutionary programs and irreversible progress toward extinction. Before the rediscovery of Mendel's work on genetics such views, although anti-Darwinian, were not controverted by clear biological evidence.

Similarly, the views of Buckman and Bather, Swinnerton and Trueman may to some extent, perhaps, be explained by the climate of biological thought of their time, however indirectly it may have affected them. Julian Huxley (1942, p. 22) has noted the "eclipse of Darwinism" in the earlier years of this century—the universal application of Mendelian inheritance was far from being understood, and natural selection was less widely accepted than it is today. An authority such as Bateson gave it little emphasis, and his views, propounded to the British Association in 1914, that all mutation is loss from an ancestral complex containing all hereditary factors (Huxley, 1942, p. 24), could be squared with Hyatt's predestined cycles of evolution. In the absence of a clear lead from biologists the theories of paleontologists could achieve wide acceptance and respectability. Even J. B. S. Haldane in 1932, stumbling over the ammonite evidence like Garstang before him, was "not competent to judge between them [Spath and Hyatt], but wish [ed] to state the anti-Darwinian position as fairly as possible" (quoted by Huxley, 1942, p. 508).

More difficult to understand is paleontologists'

[1] This paper is difficult to obtain; I owe my copy to the kindness of Professor Hans Grüneberg. It has been summarized by Woodford (1963).



failure to test the theory of recapitulation by careful stratigraphical collecting. It was not really tested at all. Hyatt was a museum specialist who did no field work. Buckman was a careful collector but the Inferior Oolite whose ammonites he monographed is a thin, condensed deposit not suited for working out detailed phylogenies. Trueman's liparoceratids occur in beds averaging several hundred feet thick, but exposed at a number of localities, correlation between them not being adequate in Trueman's day. It is hardly surprising that clear geological evidence of evolutionary sequence did not emerge from their work.

Most surprising of all, perhaps, is the fact that both Buckman and Trueman acknowledged that evolution could be either cenogenetic or palingenetic, yet they seem to have assumed that palingenesis had occurred. They did not state how, in practice, the two modes of evolution were to be distinguished. Clearly one is involved in a circular argument; one cannot safely assume that palingenesis has occurred unless the course of evolution is already known. Once one exception is admitted, and there are now many, it becomes useless as a general rule. It is a pity that it dominated English and American work on ammonites for so long.

Fig. 4. Evolution of *Kosmoceras* and *Zugokosmoceras* in the Oxford Clay of Peterborough, England (part of pl. 5 of Brinkmann, 1929, mod.). [*Profilhöhe*=vertical distance.]

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