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ACCELERATION OF DEVELOPMENT IN FOSSIL CEPHALOPODA

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WITH FIFTEEN PLATES

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Acceleration of Development in Fossil Cephalopoda

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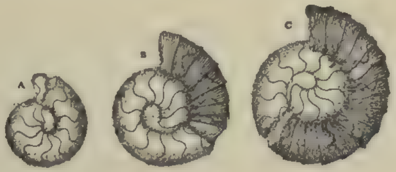
Ideal Recapitulation in Progressive Forms.

IN THE development of organisms there are two theoretical extremes, the one with simple persistence without modification, the other with complete modification. The former is almost realized in the Protozoa, the latter is approached by the higher vertebrates. All other organisms, in their development, fall somewhere between the two extremes, coming into being in simpler form, and becoming more complex in the course of life. Each starts out on somewhat the same plane of development as its distant ancestors, inheriting potentially all the characters of all its ancestors, tending to take on some characters that its ancestors never had, and to transmit the old and the new to its own posterity.

Theoretically, each organism ought to recapitulate all its race history, each stage of growth corresponding in character and in size to successive ancestral forms. This is true, in a general way, in some groups, for most later members of genetic series have increased in size with increased complexity of development.

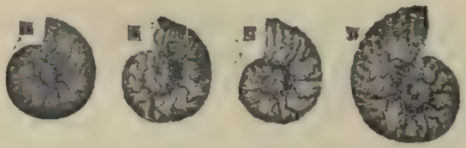
FIG. 1.



This is partly true even of the highly specialized Cephalopods, for there is a constant tendency to increase in size from the simple Goniatites of the Devonian to the complex Ammonites of the Jurassic. The increase in size accompanying the addition of ontogenic stages is especially striking in a primitive genetic series of genera near each other in time, and relatively near the beginning of the race, as in the lineage of *Goniatites–Gastrioceras–Columbites.*

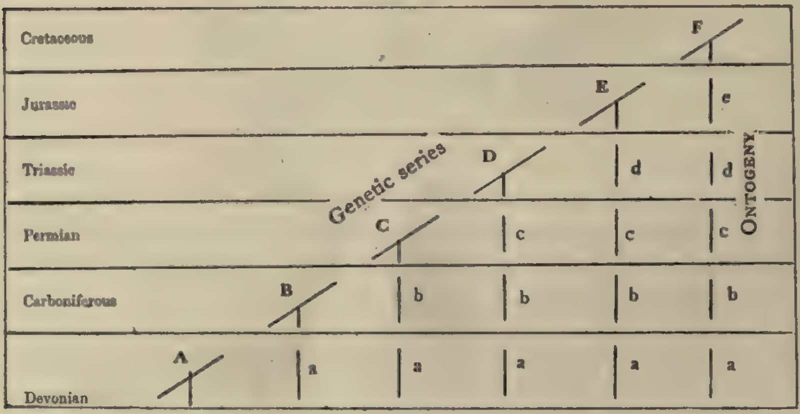
But even in these, while there is in general a constant increase in size of the successive mature forms, there is a much more rapid decrease in size of the corresponding growth stages. This fact is illustrated by the accompanying diagram, showing a constantly lengthening ontogeny as more stages must be passed through before maturity is reached.

FIG. 2.



The contrast between the size of mature Goniatites of the Paleozoic and that of the goniatite stages of later Mesozoic Ammonites is even greater; see for example the development of *Goniatites* of the Carboniferous (Pl. I, figs. 1-9), and of *Placenticeras,* (Pl. XIII, figs. 22-28), a Cretaceous genus. The same thing is seen in the development of the genetic series leading up to *Columbites* of the Lower Triassic. Its immediate ancestor, *Gastrioceras,* of the Carboniferous, when mature might reach a diameter of several inches, as shown on Pl. I, figs. 10-14; but the adolescent *Columbites,* (Pl. IV, figs. 1-10), ceased to resemble *Gastrioceras* at a diameter of about ten millimetres. And *Tropites,* a still later descendant of the same stock, in the Upper Triassic, ceased to show the gastrioceran characters at a diameter of three millimetres, (Pl. IV, figs. 11-21).

FIG. 3.



In a genetic series of progressive forms all individuals in their development should start out, theoretically, from the same stage, since all must develop from an egg. Each individual would have to pass through in its growth from the egg to maturity all the stages that the successive generations of mature forms passed through during the long history of the race. Characters that were present at maturity in the ancestors should appear by palingenesis in the development history of the descendants, and the cœnogenetic, or later characters, should gradually be pushed back into the ontogeny.

In a general way, too, this is true. As, for instance, in the Ammonoid stock the primitive simple shell, with its calcareous protoconch and siphuncle, when once introduced as a cœnogenetic or secondary character, persists throughout the history of the race, becoming a primary character, and finally appearing only as a palingenetic character in some of the modern cephalopods. All this is seen in the history of the race from the primitive *Orthoceras* of the early Paleozoic, with its chambered shell and siphuncle, but without the calcareous protoconch or embryonic shell. Some members of the *Orthoceras* group finally acquired a calcareous protoconch, and this soon introduced with it another cœnogenetic character, the marginal position of the siphuncle, forming the group of *Bactrites* (Pl. XIV, fig. 7), which was to become the starting point for the Ammonoids and the Belemnoids. Some *Bactrites* began to become coiled, and developed into the primitive Goniatites, (*Mimoceras,* Pl. XIV, fig. 8). Others remained straight, but began to cover up the slender shell with the mantle, and finally to secrete a secondary covering of lime to protect it, growing into the race of Belemnites. But even in the Belemnites the chambered shell, inherited from the parent *Orthoceras* is still retained as a youthful character, once cœnogenetic, but now so long present in the race history that it is pushed back into the larval stages, and finally appears as a mere reminiscence only in the embryology of some sepioids.

The cœnogenetic lime secretion that covered the chambered shell of the Belemnites has had a similar history, disappearing in most modern forms, but retained as a vestigial character in the cuttlefish "bone."

All characters were once secondary or cœnogenetic, and all may become primary, and finally vestigial.

Lost Stages.

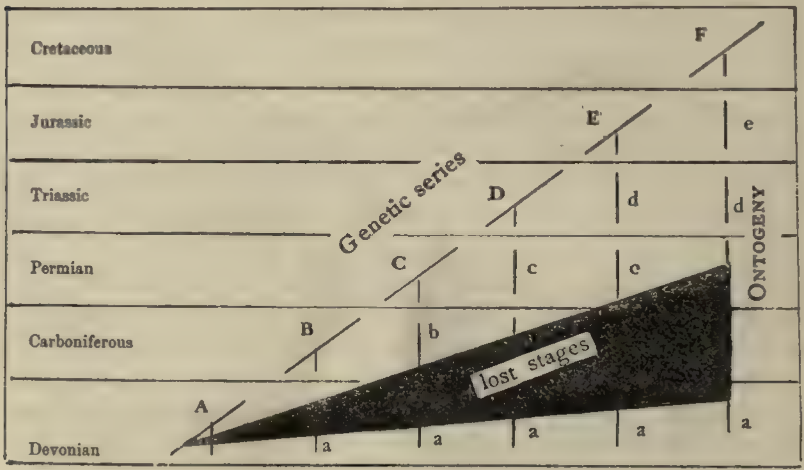
But recapitulation in later forms is by no means so simple as suggested by the diagram given above; the ontogeny is abbreviated, and the successive forms do not repeat their full history. There is a constant loss of stages or characters all along the race history, they being pushed back and crowded out of the ontogeny, as Hyatt expressed it.

All Goniatities must have sprung from a *Bactrites* radicle, but only one, *Agoniatites,* shows a *Bactrites* stage. No later genera have even a reminiscence of it, so completely is it lost from the ontogeny. Probably all later Goniatites had for their ancestor the group of *Anarcestes,* and yet the *Anarcestes* stage persists only in Devonian and a few Carboniferous genera, being lost, or buried, in the development of later groups.

The first stage of growth in the shell of all Ammonoids is the protoconch; this is an adapted form, suitable to life in the egg, not corresponding to any ancestral form, yet remaining the same in all genera. It even keeps its minute size, about a half millimetre in diameter, whether the mature form is a pygmy of half an inch or a giant of six feet. The earliest stages of growth of several genera of Ammonites are shown on Pl. XIII.

Much of the ancient history is gone through while the animal is in the egg, and thus obscured or even obliterated, even in living forms. In fossil forms it is wholly lost to us. And after the embryonic stage is passed, it is advantageous to the young animal to shorten, or at least, not to prolong, the larval development, during which it is helpless and at the

FIG. 4.



mercy of enemies. Thus, even after the egg-stage, characters will be eliminated, or, at any rate, so obscured that they can not be recognized. So the diagram should show a constant shortening or eliminating of stages at the lower end of each ontogeny, corresponding to the egg development. It should also show a constantly increasing length of ontogeny, probably not in time, but in the number of stages gone through, and hence, by inference, an ever increasing rapidity of development. From this idea came Hyatt's name "tachygenesis." Thus, for example, the development becomes successively more complex in *Bactrites, Anarcestes, Goniatites, Gastrioceras, Columbites, Tropites,* all steps in the same series, even with the complete elimination of the earlier stages; while the actual length of the larval stage was probably not greater in *Tropites* than in *Bactrites.* Mesozoic genera, as a rule, show scarcely any reminiscences of ancestors older than the Carboniferous, except in the case of fixed or left-over types, such as *Lecanites,* which has persisted into the Middle Triassic with characters little in advance of its Devonian ancestor.

Paleozoic and early Mesozoic genera repeat, in their ontogeny, their ancestral history with a fair degree of exactness, for they are not yet greatly affected by unequal acceleration of development, and scarcely at all by retardation or arrest of development. Their ontogeny is beautifully simple and direct, and in them it is easy to find genetic series of adult genera with which to compare the ontogenic series of stages in any species. Such simple development and positive recapitulation is shown in *Goniatites* of the Carboniferous, (Pl. I, figs. 1-9) ; *Cordillerites,* (Pl. XII, figs. 1-8), and *Ussuria,* (Pl. XI, figs. 1-14), of the Lower Triassic. Distinct recapitulation with considerable acceleration is shown in the ontogeny of *Columbites* of the Lower Triassic, (Pl. IV, figs. 1-10) ; in the same genetic series, *Tropites,* (Pl. IV, figs. 11-21), of the Upper Triassic, shows a recapitulation of nearly all the ancestral characters, but much obscured by unequal acceleration, or "telescoping" of characters and stages of development.

In later Mesozoic genera the recapitulation of phylogeny in ontogeny is not so distinct, since all the disturbing factors have combined to obscure the record. All have still a goniatite stage at the beginning of their larval development, but in Cretaceous genera it is no longer possible to point out with certainty the particular ancestral goniatite genus. The young of all that have been examined resemble the Carboniferous family Glyphioceratidæ, which may mean that all Cretaceous ammonoid genera came from that stock, or else, more probably, that the round form was the safest for the larva. This would make the larval stages of these later forms almost wholly adaptive and cœnogenetic. This is illustrated by the development of *Schloenbachia,* (Pl. XIII, figs. 16-21), *Placenticeras,* (Pl. XIII, figs. 22-28), and *Lytoceras,* (Pl. XIII, figs. 10-15), all of the Upper Cretaceous, in which the larval stages are very much alike, although the phylogeny of the three genera is very different. *Lytoceras* goes back in an unbroken genetic series to the Lower Triassic, and probably sprang from some Carboniferous member of the Prolecanitidæ. *Placenticeras* is a phylogerontic form of the Stephanoceratidæ, most likely an offshoot of the Tropitoidea of the Triassic, and hence of the Glyphioceratidæ. If this is true it has every right to resemble the Carboniferous genus *Goniatites.* The case of *Schloenbachia* is not so clear, but it is probable that this genus is an offshoot from the Triassic Ceratitoidea, and hence from still a third Paleozoic phylum, the Gephyroceratidæ.

Sharply contrasted with this uncertain and garbled recapitulation of their ancient history is their positive testimony as to their immediate ancestry. And what is true of these three genera chosen for illustration is true of all Cretaceous Ammonites. This is reflected in the lack of agreement in their classification by various authors, and the utter failure to construct a satisfactory family tree for them. *Lytoceras* and *Phylloceras* are the only Cretaceous genera of which we know positively the genealogy; in fact they are almost the only Jurassic genera of which this is true.

UNEQUAL ACCELERATION.

Useful characters tend to be inherited by the succeeding generations at constantly earlier stages, and finally may appear, in the ontogeny of later groups, simultaneously with characters that belonged to other genera in the genetic series. In other words, the growing young shell is not strictly in sequence *Anarcestes, Goniatites, Gastrioceras, Columbites, Tropites,* the family line, stretching from Devonian to Upper Triassic, but has in the successive stages some resemblance to each of them, with few characters lost, rather obscured by association with other characters that were not synchronous with them. The characters of later genera do, indeed, appear successively in ontogeny, but some appear at earlier and still earlier periods of growth, until they may even get back into the larval stages. Thus the keel, which is a late character of the Tropitidæ, having been developed only towards the end of the Middle Triassic, is pushed back in the ontogeny of *Tropites,* until it appears in the larval stage, associated with septa like those of the Devonian *Anarcestes,* and form and sculpture like that of the Carboniferous *Gastrioceras.* The ontogeny of *Tropites* is shown on Pl. IV, figs. 11-21, where it may be compared with the simpler development of *Columbites.* The ontogeny of the ancestral *Goniatites* is shown on Pl. I, figs. 1-9.

In a like manner, in the development of *Clionites,* (Pl. XV, figs. 1-12), the ventral furrow, which is a late or cœnogenetic character of the group *Trachyceras,* is accelerated in inheritance until it appears in association with characters belonging to genera far below *Trachyceras* in the series. The term, "telescoping," which has been applied by Grabau to this phenomenon is graphic, but hardly accurate enough for use in strictly scientific nomenclature.

Fixed Types.

The first step towards degeneration is cessation of progress, seen in the case of all persistent types. Such types may become finally "left overs," fixed in the ancestral characters, anachronisms, or "contemporary ancestors." They usually become dwarfed, or at least seem so, for they retain the small size of the ancient forms, of which they are the unmodified, or little modified descendants. Such types among Ammonites are *Lecanites* and *Nannites,* which persist until the Middle Triassic with the characters of Devonian and Carboniferous genera. (See Pl. III, figs. 1-3, Pl. III, figs. 4-8, for the characters of these genera). These dwarf genera are represented by few species at any time in their later history, showing by their very fewness the lack of that virility which is characteristic of progressive forms. Their ancestors, the Goniatites, and their contemporary kinsfolk, the highly specialized Ammonites, are both characterized by abundance of individuals, species, and genera. *Nannites* and *Lecanites* are "poor-relations," few, small, and unimportant, though wonderfully interesting, for they give us an insight into the beginning of the phenomenon of degeneration.

Stretching the Ontogeny.

The next step towards degeneration consists in prolonging the ontogeny, as when a specialized group remains longer in the larval and adolescent stages than did its ancestors, while finally reaching to the full perfection that they had attained. The best example of this is seen in the development of *Ceratites* in the Germanic basin in the Middle Triassic.* Here we have a group descended from *Meekoceras* of the Lower Triassic, and in general as far removed from that genus in specialization as in time, but delaying in the *Meekoceras* stage, retaining until almost mature many of the characters of that genus, and scarcely progressing beyond it at maturity.

Pavlow** has observed a similar phenomenon in the Ammonites of the Lower Cretaceous of Russia. In both cases we have a beginning of degeneration caused by unfavorable conditions of life in basins partly shut off from the sea. A beginning of this stretching of the ontogeny is seen in *Trachyceras* of the Upper Triassic (Pl. XV, figs. 13-16), where stages that had long been obsolete in the group persist almost until maturity, probably brought out by atavism.

ARREST OF DEVELOPMENT.

The next step in degeneration is arrest of development, where the youthful stages are prolonged, and the form on reaching maturity finally fails to reach the complete development of that species, and does not attain to the complexity of its immediate ancestors. Such cases are known in the Brachiopods, where in a living species sexual maturity may be reached in stages much lower in specialization than the normal mature form, so much so that these stages have even been described as independent genera. Such arrested forms may even give rise to a stock that never reaches the full generic evolution of its ancestors.*

Dr. C. E. Beecher** has aptly described this same phenomenon: "In each line of progression in the Terebratellidæ the acceleration of the period of reproduction, by influence of environment, threw off genera which did not go through the complete series of metamorphoses, but are otherwise fully adult, and even may show reversional tendencies due to old age; so that nearly every stage passed through by the higher genera has a fixed representative in a lower genus. Moreover, the lower genera are not merely equivalent to, or in exact parallelism with, the early stages

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*See E. R. Philippi, Die Ceratiten des oberen deutschen Muschelkalkes. Pal. Abhandlungen von Dames und Kayser, Bd. VIII, Heft 4, 1901, p. 359.

**Le Crétacé inférieur de la Russie et sa Faune. Nouv. Mém. de la Soc. Impér. Nat. Moscou. Tome XVI, 1901, Part I, p. 62.

*Fischer and Oehlert, Brachiopodes, Mission Scientifique du Cap Horn, p. 50-60.

**Amer. Nat., vol. XXVII, 1893, p. 603.

of the higher, but they express a permanent type of structure, so far as these genera are concerned, and after reaching maturity do not show a tendency to attain higher phases of development, but thicken the shell and cardinal process, absorb the deltidial plates and exhibit all the evidences of senility."

E. D. Cope,* too, has expressed himself clearly on this question: "The acceleration in the assumption of a character, progressing more rapidly than the same in another character, must soon produce, in a type whose stages were once the exact parallel of a permanent lower form, the condition of inexact parallelism. As all the more comprehensive groups present this relation to each other, we are compelled to believe that *acceleration* has been the principle of their successive evolution during the long ages of geologic time. Each type has, however, its day of supremacy and perfection of organism, and a retrogression in these respects has succeeded. This has, no doubt, followed a law the reverse of acceleration, which has been called *retardation.* By the increasing slowness of the growth of the individuals of a genus, and later assumption of the characters of the latter, they would be successively lost." This statement of Cope might apply equally well to unequal acceleration or "telescoping" of characters, but in another part of the same work he gives a clearer statement:* "Where characters which appear latest in embryonic history are lost, we have simple retardation, that is, the animal in successive generations fails to grow up to the highest point of completion, falling further and further back, thus presenting an increasingly slower growth in the special direction in question."

Examples of arrest of development are very common among the Ammonites, especially towards the end of the history of stocks. These, naturally, are more common and better known in the Jurassic and Cretaceous, where the family history is not so well understood, and where it is not possible to correlate the arrested stages with ancestral genera.

Lecanites and *Nannites,* of the Triassic, are regarded by some authors as cases of reversion by arrest of development, but the writer regards them as fixed persistent types. Much better illustrations are found in the great families, Tropitidæ and Ceratitidæ, of which the genealogy is well known, and where the arrested stages may be compared with antecedent genera in the same line. Among the Tropitidæ the development

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*Origin of the Fittest, p. 142.

*Op. cit., p. 13.

of *Metasibirites, Homerites* and *Leconteia,* illustrates clearly arrest of development, with accompanying retardation of characters, and partial reversion to ancestral types.

Metasibirites is a dwarf, degenerate genus, confined to the Upper Triassic, in India, California, and the Alps. The ontogeny of only the American species has been published, but the statements made here are based on the development of several American species, of which only two have been described, *Metasibirites* (*Tardeceras*) *parvus* H. and S., and *M.* (*Tropiceltites*) *Frechi* H. and S. (Pl. VII, figs. 1-10). In early youth *Metasibirites Frechi* is a typical *Gastrioceras,* with broad low trapezoidal whorls, strong umbilical knots, frequent constrictions, and simple goniatitic septa. Towards maturity the whorls become higher, the sculpture begins to run up the sides, and ribs begin to develop from the knots, which themselves become weaker and often obsolete. These ribs run up to and finally across the venter. But before this is complete a weak keel appears, bounded in some cases by weak furrows. The keel speedily becomes obsolete, often disappearing entirely at maturity. When nearly mature the shell in nearly all its characters is a minature of *Acrochordiceras* of the Middle Triassic, but the septa remain goniatitic, or at least only very weakly serrated.

This is not a persistence of *Sibirites* from the Lower Triassic, but an arrest of progress so that some of the characters fail to get beyond the complexity that they had in that genus. In other characters the genus has gone beyond *Sibirites,* in some respects even fallen short of it. The genetic series of adult forms is as follows: *Pericylus* of the Subcarboniferous developed into *Gastrioceras,* which in turn changed over into *Sibirites* of the Lower Triassic; this by gradually increasing strength of sculpture and increasing complexity of septa developed into *Acrochordiceras.* There the stock became partly degenerate and development was arrested: The forms affected failed to grow up to the size and complexity of the immediate ancestor, *Acrochordiceras,* but stopped nearly in the *Sibirites* stage of development, and in some characters even reverted to the more remote ancestor, *Pericyclus.*

The tendency to form a keel was strong in nearly all the groups of the Tropitoidea, and crops out weakly here in the temporary development of the vestigial keel. No member of *Sibirites* or *Acrochordiceras* ever possessed a keel, so its development in *Metasibirites* can hardly be charged to palingenesis of this character by heredity from some long dead Lower or Middle Triassic form. It is rather a manifestation of a latent tendency in all the Tropitoidea to form keels late in the history of the stock. All true Tropitoidea show this character well developed, and among the Haloritidæ *Homerites* shows the same tendency, and develops a vestigial keel just before maturity, losing it entirely at maturity, as shown on Pl. VI, figs. 16-21. *Leconteia* H. and S. has a somewhat similar history, with the same retardation of the septa, and the same reversion to the *Pericylus* ornamentation, but without the formation of a keel at any stage. This form is also illustrated on Pl. VI, figs. 11-15, for comparison with *Metasibirites* and *Homerites.* This parallel development in rather closely related genera may be called orthogenesis. The reappearance of the *Pericyclus* and *Sibirites* characters is undoubtedly atavism, but the parallel development of the keel in *Metasibirites* and *Homerites* can only be ascribed to the bringing out of a tendency always present, though previously latent. The immediate cause, in both cases, is the disturbance of heredity consequent upon arrest of development and incipient degeneration.

Another clear case of arrest of development is seen in *Clionites,* of the Upper Triassic. This genus, when fully developed, has the sculpture of *Trachyceras,* and a form something like it, but the septa are ceratitic; and even when nearly mature *Clionites* is evolute and square shouldered, with prominent shoulder knots, like *Tirolites,* of the Lower Triassic. This genus, then, has a mixture of characters that ought not to occur together. In the ceratitic septa it shows a stoppage of development in the stage characteristic of Middle Triassic forms, and in the square-shouldered whorl and shoulder knots it has been arrested in a stage corresponding to a Lower Triassic genus. But in its sculpture and in the median furrow it is as far along as its immediate ancestor. This is shown on Pl. XV, figs. 1-8, in the development of *Clionites* (*Traskites*) *robustus,* where the youthful stages are very like *Tirolites,* differing from it in the possession of the median furrow, inherited from an ancestor later than *Tirolites.* The mature stage of *Clionites* takes on the sculpture of *Trachyceras* and approaches it in form, but fails to reach the complexity of septation of that genus. Ordinarily *Trachyceras* does not show any trace of the *Tirolites* stage, but in the lower part of the Upper Triassic there are several species which have prolonged their ontogeny, and do show a distinct *Tirolites* stage. Such a species, *Trachyceras duplex,* is figured on Pl. XV, figs. 13-16. This species shows the beginning of retardation, which is more complete in *Clionites.* Still more complete arrest of development is seen in *Clionites* (*Californites*) *Merriami,* Pl. XV, figs. 9-12, which has remained in the *Tirolites* form, and septa, and developed little beyond it in sculpture, but has inherited the trachyceran furrow. It is then a lower form than the subgenus *Traskites,* but lower in the sense of being more retrograde, that is more thoroughly retarded. Both are partial reversions towards *Tirolites* by loss of characters, but both have retained the furrow, which *Tirolites* never had, and which they have inherited from the progressive ancestor *Trachyceras.* The genetic series is: *Tirolites,* Lower Triassic; *Trachyceras,* Middle and Upper Triassic; and *Clionites,* Upper Triassic. It should be stated here that *Trachyceras* is a polyphyletic genus, not all of its species coming from the line of *Tirolites,* but some from the stock of *Meekoceras;* and it is not yet known to which branch the type of the genus, *Trachyceras Aon,* belongs.

Another case of arrest of development is seen in *Paraganides,* of the Upper Triassic, Pl. VI, figs. 22-26, where a member of the*Nannites* group has lagged behind its fellows until it is scarcely beyond *Aganides* of the Devonian and Lower Carboniferous, but shows its inheritance from more complex intermediate genera in the internal lobes. This is the last member of a genetic series that began in *Aganides,* (Pl. I, fig. 15), continued in the fixed type *Nannites* (Pl. III, figs. 4-8), and finally perished in the retarded and reversionary *Paraganides.*

Reversion.

When a form develops normally and then strikes back to its ancestral type we have real reversion. It is not known positively that we have any examples of this, but the development of *Lituites,* of the Silurian, Pl. XIV, fig. 6, and of *Baculites,* of the Cretaceous, Pl. XIII, figs. 1-9, is probably to be explained in this way. The ancestral stock was *Orthoceras,* Pl. XIV, fig. 1; then came *Cyrtoceras,* Pl. XIV, figs. 2 and 3; then *Gyroceras,* Pl. XIV, fig. 4; then coiled nautilian shells, Pl. XIV, fig. 5, and finally *Lituites,* after becoming coiled, strikes back at maturity to the straight orthoceran type. Most degenerate types are reversionary, at least in some characters, though none are probably completely so.

Baculites among the ammonoids has a similar history. Its remote ancestor was *Orthoceras;* then came *Bactrites* of the middle Paleozoic; then the coiled Goniatites; then the Ammonite stock of *Lytoceras;* and finally, after being coiled normally, it strikes back to the straight form of its progenitor. The reversion is only partial in either case. Such a partial reversion is seen also in *Crioceras,* of the Cretaceous, Pl. XIV, fig. 11, where the shell becomes uncoiled, and reverts partly to the primitive type that came between *Bactrites* and the coiled Goniatites, a type that is unknown as a fossil, but one whose former existence is indicated by the young stage of *Mimoceras*, Pl. XIV, fig. 8, itself one of the earliest and most primitive of Goniatites.

Partial reversion is probably a common phenomenon among the Ammonites, but outside of such striking cases as those mentioned above it can be recognized only in the reappearance of the same character or characters in later forms. This is possible only when the genetic series is well known, which is but seldom the case.

Beyrichites, in the Middle Triassic, Pl. VIII, figs. 14-23, after becoming rough shelled and ornamented, reverts to the flattened shape and nearly smooth shell of its ancestor, *Meekoceras*, so much so that it has several times been described as *Meekoceras*. Some species of *Trachyceras* in the Upper Triassic, after going through the rough shelled stage characteristic of that genus, become flattened and nearly smooth, and thus show a partial reversion to the far removed parent *Meekoceras*, although they are still progressive in the complex septation.

Reversion by arrest of development is far more common than the sort just described, but in this case, too, the reversion is only partial. *Metasibirites* has already been mentioned as an example of this, where there is a reappearance of the sculpture of *Acrochordiceras*, and of the form and septa of *Pericyclus* or *Gastrioceras*, an apparent palingenesis of the long extinct genus *Sibirites*, but with some later characters that *Sibirites* never had.

The so-called ''Ceratites'' of the Cretaceous give us the classic example of reversion by arrest of development. Although there were no Goniatites after the Paleozoic, nor Ceratites after the Triassic, there are in the Upper Cretaceous several genera with form and septa so like those Paleozoic and Triassic groups that they were once called ''Ceratites.'' We now know that they are not cases of generic persistence through this long time, but are retarded and arrested forms, reverting to goniatitic or ceratitic stages of growth after long obsolescence of those characters, but with such a commingling of characters from various steps in the family history that it is impossible to determine what was the particular ancestor. One of these, *Neolobites* (Pl. X, fig. 1), although a Cretaceous genus, is arrested in the Goniatite stage. No adult Goniatites are known in the immense interval between the Permian and the Cretaceous. But also no genus is known in the Paleozoic that is comparable to *Neolobites,* and probably none like it ever existed. Its characters are a combination handed down from various members of its long family line.

Other genera of the Cretaceous have ceratitic septa, and here again we have a reversion by arrest of development to an older type of structure. It is not likely that these "Pseudoceratites" are really reversions to the genus *Ceratites,* for they appear to belong to several different phyla, in which the stage of development with serrated lobes was present in either Permian or Lower Triassic time. The resemblance is so marked that Steinmann* regards *Heterotissotia* (Pl. X, figs. 2-4) of the Cretaceous as a direct descendant of *Ceratites* of the Middle Triassic, and does not even regard it as a case of atavism, or arrest of development, but simply a persistence of the genus, intermittent because of our lack of knowledge of the intervening forms. No doubt there are numerous gaps in our existing records of extinct faunas, and it is premature for us to be too positive in our denial of the possibility of this being the correct explanation. But that it is extremely improbable nearly all paleontologists will agree. Steinmann compares *Heterotissotia* with *Ceratites semipartitus,* which according to Philippi* is a somewhat degenerate type, already reversionary, and probably not an ancestor of later forms. It is, then, more probable, if in the "Pseudoceratites" we have a case of atavism, the reversion is to some still older member of the Ceratitoidea, the *Meekoceras* group, for instance *Aspidites* or *Koninckites,* of the Lower Triassic.

In any case, whether it is due to atavism, or to independent development of the same characters in different stocks and in widely separated times, this is a remarkable case of parallelism. Another of the "Pseudoceratites," *Sphenodiscus,* of the Upper Cretaceous (Pl. X, fig. 11), approaches closely to the septation of the primitive Arcestoidea of the Permian, especially *Waagenoceras* (Pl. X, fig. 12) and *Cyclolobus.* Also here there is no probability of atavism, for the phylum of the Arcestidae seems to have died out at the end of the Triassic, and the affinities of *Sphenodiscus* seem to point to a relationship with the Jurassic Stephanoceratidae, which certainly did not come from the Arcestidae.

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*Sitzungsber. Niederrhein. Gesell. für Natur- und Heilkunde zu Bonn. Naturwiss. Abtheil. 1909. Probleme der Ammoniten-Phylogenie (Gattung Heterotissotia), pp. 1-16.

*Die Ceratiten des oberen deutschen Muschelkalkes, Pal. Abhandl. Bd. VIII, 1901, Heft 4, p. 357.

But in all speculations on the phylogeny of Cretaceous genera we must not forget that there still exists a great gap in our knowledge of the connections between Triassic and later groups, and that some of the stocks may possibly have lived on in unknown regions, to reappear in later ages so greatly modified that their ancestral history comes out only in their reversion to the parent type, when senescence has awakened the latent tendencies of their far distant youth. A case that may illustrate this is the parallelism of *Paratissotia* of the Cretaceous, Pl. X, figs. 8-10, with *Otoceras* of the Lower Triassic, Pl. X, figs. 6 and 7. *Otoceras* belongs to the family Hungaritidae, the most ancient line of the Ceratitoidea, and *Paratissotia* belongs to the Amaltheidae, which are thought by some to have come from the Ceratitidae. In this case the parallelism may be due to atavism.

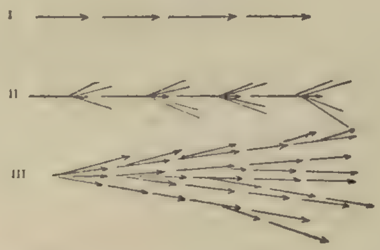
In the cases discussed above, generic persistence from the Permian until the Upper Cretaceous is out of the question, and even the families referred to have not outlived the Triassic in most cases. But the Cretaceous forms must have had Paleozoic and early Mesozoic ancestors which were in the transition between the goniatitic, ceratitic and ammonitic stages of development. And being all somewhat retarded, and in most cases affected by arrest of development, it is highly probable that they would revert to some of the characters of those remote progenitors.

GENETIC SERIES.

Ever since the acceptance of the theory of evolution, genetic series have been sought by geologists with more or less success. Waagen's studies in the *Formenreihe* of *Oppelia*, and Hyatt's ''Genesis of the Arietidae'' have become classic. But some more conservative paleontologists have always cherished secret doubts of the demonstration, while admitting the truth of the principle. It is extremely doubtful if we can establish any genetic lines of species, or that we can ever tell from which particular species a certain genus originated. Did it, indeed, come from only one? What the paleontologist sees is rather a group of species tending in somewhat the same direction; and those species most alike he classes, for convenience, under one genus. Further, the conservative paleontologist can not always point to the individual genus from which another genus sprang; and if he does he is probably mistaken. Every virile progressive stock is characterized by its wealth in variation, its genera and species as we grade them, any one of which, or all of which, might have been ancestors of later forms.

There are three sorts, or rather ideas, of genetic series, as shown by the accompanying diagrams. No. I, on the diagram, where we have a narrow straight line of connected genera or species, would show straight natural selection, if this were in harmony with the evidence of paleontology, but it is not.

FIG. 5.



No. II in the diagram gives the commonly accepted idea of a genetic series. Hyatt's genesis of the Jurassic Ammonites proposes such a genetic line, and derives all the later forms from *Psiloceras,* which is itself a degenerate. I have always agreed with Steinmann in thinking that this idea was improbable, to say the least. We find early in the Lower Jurassic the Arietidae distributed in Europe, Asia, North and South America, and the Indian Ocean; hence it is unlikely, leaving morphology out of the question, that the rare dwarf *Psiloceras* of the Mediterranean Region was the parent of this varied progeny. The theory expressed in No. II in the diagram has always reminded the writer very forcibly of the Noachian fable in the history of the human race.

No. III in the diagram shows the conditions as the paleontologist finds them, regardless of any theory. He sees a number of species in a genus, and a number of genera, in a family, all tending in somewhat the same direction, as he traces them upwards through the geologic ages. He finds no complete unbroken series, but a series of steps.

Is this orthogenesis? In a general way it is, although giving a name to a phenomenon is not giving an explanation. There are only certain lines of variation possible, and when the organism starts out with certain characters it can vary only in more or less definite directions, some of which will coincide in different species, genera, and families. There need not be any mysterious force directing the evolution; it may be merely the limitations of the characters of the organisms.

The best genetic series of Ammonoids are found in the Paleozoic and early Mesozoic. There we get a nearly unbroken series of adult forms that show by their sequence and intergradation that they are genetically connected. In most of these genera we have also their individual development repeating the ancestral history, not the whole history distinctly, but that part nearest to them most positively. Such a series leads from the Glyphioceratidae through *Gastrioceras* of the Carboniferous, to *Columbites* of the Lower Triassic, and up to the Tropitidae of the Upper Triassic. The writer is strongly of the opinion that this phylum will yet be traced still higher, into the Arietidae and Stephanoceratidae of the Jurassic.

Such a series is seen also in the Ceratitoidea. The parent, or radicle, of this group, *Lecanites,* as we know it in the Triassic, is still virtually a Goniatite, with simple unbranched septa, and repeats the race history of the Devonian Gephyroceratidae. The more primitive members of the Meekoceratidae of the Permian and Lower Triassic repeat this part of the history, and all show a distinct *Lecanites* stage. The earlier members of the *Ceratites* are still nearly smooth, and intergrade with the later members of the Meekoceratidae, still showing in their youth a decided reminiscence of *Lecanites.* From the earlier and simpler smooth *Ceratites* there branched out two groups of rough shelled forms, one leading towards the keeled *Ceratites,* group of *C. trinodosus,* the other leading through the group of *C. bosnensis* to the Trachyceratea, all connected by series of mature forms, but not showing their phylogeny in their ontogeny, except in cases of arrest of development and retardation.

The division between Permian and Triassic was a deadline for most Paleozoic groups; on the one side we have rugose corals and tabulates, on the other the modern Hexacoralla; on the one side *Productus* and *Orthis,* on the other a predominance of Terebratulacea and Rhynchonellacea; on the one side Palæocrinoidea, on the other Neocrinoidea. It is not so with the Ammonoids, for in them there is a nearly perfect transition, not with any species, but with a number of genera surviving from Permian into the Lower Triassic, and with many getting across the line so little modified that, while we call them by different generic titles, they are still virtually the same as their Paleozoic forebears.

The following genera survive from Permian into the Triassic: *Otoceras, Hungarites, Xenodiscus, Xenaspis, Pronorites, Medlicottia*

(Episageceras), Lecanites (Paralecanites), Dalmatites, Popanoceras, Celtites (Paraceltites).

The following Permian genera had reached a stage of development as high as that of Triassic forms, but are not yet known in Triassic faunas: *Cyclolobus, Waagenoceras, Thalassoceras, Stacheoceras.* The following genera appear at the very bottom of the Triassic, already fully developed, and must have existed somewhere during Permian time, although they are not yet known in any Permian faunas: *Ussuria, Columbites, Monophyllites, Nannites, Meekoceras, Flemingites, Hedenstroemia, Pseudosageceras, Ophiceras, Aspenites, Lanceolites, Cordillerites. Kymatites* and *Ambites* of Waagen may not be goniatitic survivors from the Permian faunas, but merely Meekoceratidae in which the lobes have not been well preserved on account of weathering. The later groups, such as *Proavites, Metasibirites, Paraganides, Tornquistites, Dieneria, Leconteia, Tropiceltites, Styrites, Polycyclus* and *Lobites,* all of which are as simple as Permian forms, are merely cases of arrested development and reversion.

Karpinsky's* work in tracing the Ammonoids of the Carboniferous into the Permian, and comparison of ontogeny with phylogeny, has given us our most convincing example of real genetic series. The work of J. P. Smith** has carried our knowledge of the Ammonites further back into the Carboniferous, and later he has traced many of the Carboniferous genera and families into the Triassic,* combining the study of ontogeny and phylogeny.

The monographs of Diener, von Krafft, and Waagen, on the Lower Triassic Cephalopoda of India, of Kittl and von Arthaber on those of the Mediterranean Region, have added greatly to our knowledge of the transitional faunas at the border-line between Paleozoic and Mesozoic, and out of them have come some real genetic series. The combined result of all this work is given here in the form of a table showing the relationship of the early Mesozoic Ammonoids to those of the Paleozoic.

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*Ueber die Ammoneen der Artinsk-Stufe, Mém. Acad. Impér. Sci. St. Pétersbourg, 7th Ser. Vol. XXXVII, No. 2, 1889.

**The Carboniferous Ammonoids of America, Mon. XLII, U. S. Geological Survey, 1903.

*The Triassic Cephalopod Genera of America, Prof. Papers No. XL, U. S. Geol. Survey, 1905.

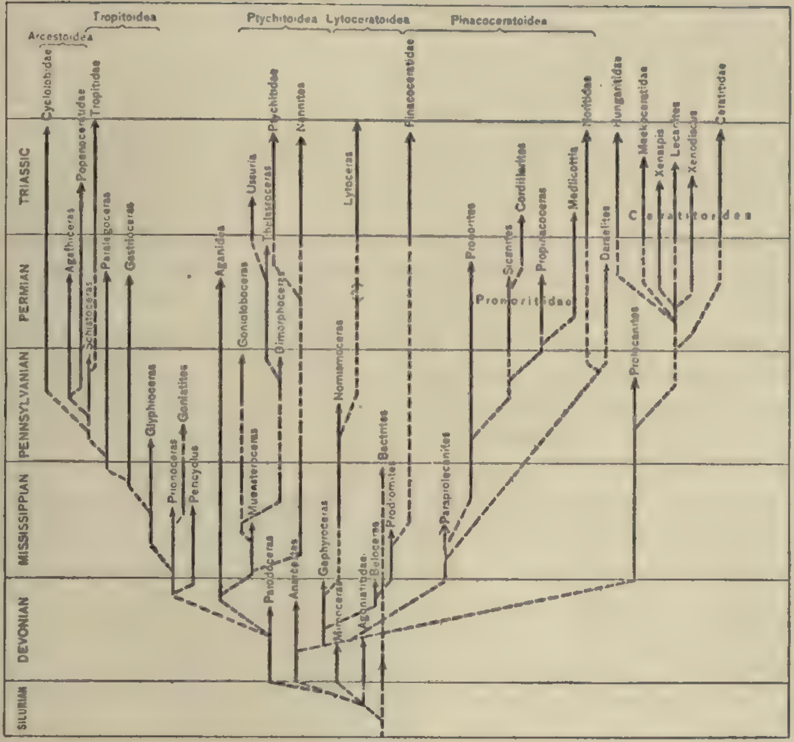

FIG. 6.

It is not complete, and is, of course, subject to constant revision, but it does show probable genetic series, in the light of our present knowledge of the subject.

In his studies of the genealogy of Jurassic and Cretaceous genera Steinmann* has gone to great lengths in finding genetic connections with Triassic genera, where connecting links are absolutely unknown, and extremely improbable. In some instances he does make a strong case for relationship, but none for generic persistence. The doubtful relation-

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*Rassenpersistenz bei Ammoniten. Eine Erwiderung. Centralblatt für Geol. Min. und Pal. 1909, No. 8, pp. 199-203, and 225-232; and in Probleme der Ammoniten-Phylogenie (Gattung Heterotissotia), Niederrhein. Gesell. für Natur. etc. 1909, pp. 1-16; also in Die Abstammung der "Gattung Oppelia" Waagen. Centralblatt für Geol. etc. 1909, No. 21, pp. 641-646.

ships he brings out may be explained much better on the basis of reversion by arrest of development, as has already been shown under the head of reversion.

Convergence.

It is impossible to conceive of the same species or genus as originating in different times, or in different places. But natural selection sorts out certain characters, or environment calls them out, and so we often get very similar results from diverse materials. Similarity of habit produces external, but not fundamental, similarity of characters. In the case of forms living together in time and place, convergence may well be due to mimicry, and thus explained by natural selection. But where the forms are separated by geologic ages, mimicry can not be appealed to.

In the case of reversion by arrest of development we have a virtual reappearance of generic types in widely separated epochs. Only, when we know their history, we do not call the aggregation of characters by the same generic names, especially since the reversionary forms are usually easily to be distinguished from the older types. Thus *Arpadites,* Pl. VIII, figs. 1-10, and *Beyrichites,* Pl. VIII, figs. 14-23, both show a partial reversion towards their ancestor *Meekoceras,* yet neither genus need be confused with the ancient progenitor.

Convergence is sometimes seen in widely separated stocks and in widely separated times. *Eutomoceras* of the Middle Triassic, Pl. IX, figs. 5-7, the end genus of the *Dalmatites-Hungarites* stock, has been confused with the Upper Triassic *Discotropites* (Pl. V, figs. 1-13), a late member of the genetic series leading up from *Gastrioceras-Columbites* to the Tropitidæ. Ontogeny shows the heredity of the two genera to be different back to the Devonian. Their resemblance can hardly be due to atavism, for their development is not parallel, as both genetic series of adults and ontogeny of each generic step show. It can also hardly be due to natural selection, for along with these keeled members of each stock there are numerous others without keel, as the geologic record shows, equally prosperous and prolific. It is also not due to the inheritance of this character from a common ancestor, for the remote ancestors were not common, and did not possess the keel, anyway.

Again, we may have parallel development of very similar characters in nearly related stocks. As an example of this may be cited the development of the ventral keel in the *Dalmatites-Hungarites-Eutomoceras* phylum, and the same thing in the *Meekoceras-Ceratites* line. *Eutomoceras* has a keeled lineage extending back to the Devonian, while the keeled *Ceratites* extend no further back than Middle Triassic. But the tendency to form a keel sometimes crops out even in the ancestry of *Ceratites,* since at least one species of *Lecanites* has shown this character. And both stocks appear to have come from the same Devonian genus, *Gephyroceras, Ceratites* from the main group, and *Eutomoceras* from the keeled subgenus *Timanites,* as shown in this series:

Gephyroceras-Lecanites-Meekoceras-Ceratites;
Timanites-Dalmatites-Hungarites-Eutomoceras;
Timanites-Aspenites-Hedenstroemia-Pinacoceratidae.

It would seem that there may have been in the descendants of the Gephyroceratidæ a strong tendency to form keels. This was already present in *Timanites,* a subgenus and contemporary of *Gephyroceras,* and is continuous in the Hungaritidæ and Hedenstrœminæ, which branched out from *Timanites,* as shown in *Longobardites,* Pl. IX, figs. 14-16. The same character appears belated in the keeled *Ceratites,* certainly not inherited from the collateral *Timanites* branch, and not known to have been present in the ancestor of the two stocks.

Equally difficult to explain is the apparent genesis of the polyphyletic genus *Trachyceras* from the two lines, one from *Meekoceras-Ceratites,* the other from *Tirolites.* To state that both lines had a strong tendency to develop rough shells, a median furrow, and complex septa does not explain the phenomenon. Nor yet does it explain the strong resemblance of mature *Sagenites* of the Tropitidæ to *Trachyceras,* so strong, in fact, that careful paleontologists have confused them, although their ontogeny separates them at once.

The term *orthogenesis* is a statement of a fact, rather than an explanation. Ammonites have developed constantly in certain directions, in form and ornamentation of the shell, and increasing complexity of septation, in parallel series coming from the same or nearly related ancestors, as well as in series coming from different ancestors. In neither case are the characters hereditary, though in both cases the tendency to develop those characters seems to have been hereditary. Genera derived from nearly related ancestors have frequently become more alike with the lapse of time, and this has also occurred often with genera whose ancestry was wholly different. This has made the study of Ammonite-phylogeny exceedingly difficult; in it fact and fancy have been so mixed that it has sometimes been called the "happy hunting ground" of theorists. But it has also been the happy hunting ground of observers of fact. Along with speculations concerning the phylogeny of the Ammonites there has been a much greater mass of painstaking accurate systematic work, by which species have been carefully recorded, variation and morphology studied most minutely, and a wealth of material amassed for the use of the philosophic student of evolution.

Conclusion.

It may be that, when this paper is read by ardent members of the ''Hyatt school'' of paleontologists and adherents of the biogenetic law, they will be inclined to call the writer a deserter from the camp, and to suggest that the paper ought to have been entitled, ''Why recapitulation does not recapitulate.'' The writer is still a firm believer in the biogenetic law, but that law is not such a simple thing as it was once thought to be. In the youth of every theory everything is beautifully clear, and ideally simple. As time goes on we are compelled to drop one idea after another, until it almost seems that the whole will be lost. When sceptics concerning the recapitulation theory throw up to us that ontogeny does not *always* recapitulate phylogeny, we are prepared to admit this, even to go further and admit that it does not *often* recapitulate. In fact, the writer would be prepared to go still further, and to state that, in the sense in which the term has been used by most adherents of the theory, it *never* recapitulates. Our over-zealous friends have claimed too much, and have done more to prevent general acceptance of the theory than a host of enemies.

ILLUSTRATIONS.

Lituites, Pl. XIV, fig. 6, a reversionary Nautiloid, striking back towards *Orthoceras.*

Timanites, Pl. III, figs. 12-14, the Paleozoic goniatite ancestral stock of the Hungaritidae, transitional from *Gephyroceras.*

Goniatites, Pl. I, figs. 1-9, a group transitional from the Goniatites to the Ammonites; the distant ancestral stock of Tropitidae and Arcestidae.

Gastrioceras, Pl. I, figs. 10-14, a progressive development from the Goniatites; the family radicle of Tropitidae and Arcestidae; a form with the septation of a Goniatite, but with the sculpture and inner structure already advanced to the stage of Ammonites.

Paralegoceras, Pl. II, figs. 1-5, a more advanced member of the gastrioceran stock, showing the advance towards becoming an Ammonite.

Schistoceras, Pl. II, figs. 6-13, a direct transition from the Glyphioceratidae towards the Tropitidae.

Waagenoceras, Pl. X, fig. 12, a late Paleozoic member of the Arcestidae, showing an advance to Mesozoic characters.

Ussuria, Pl. XI, figs. 1-14, transitional Ammonite, showing distinct recapitulation of race history in ontogeny.

Cordillerites, Pl. XII, figs. 1-8, transitional from Goniatite to Ammonite, showing simple and direct recapitulation in ontogeny.

Pronorites, Pl. XII, figs. 9-12, ancestral stock of *Cordillerites.*

Aspenites, Pl. IX, figs. 1-4, transitional from Gephyroceratidae to Pinacoceratidae, showing strong reminiscences of the Devonian radicle, *Timanites.*

Meekoceras, Pl. VII, figs. 1-12, the primitive stock of Ceratitidae, connecting this group with *Lecanites,* the family radicle.

Inyoites, Pl. IX, figs. 8-13, an accelerated member of the Hungaritidae, showing convergence with the stock of Tropitidae.

Paranannites, Pl. XI, figs. 15-20, a primitive progressive link between *Nannites* and the Ptychitidae.

Columbites, Pl. IV, figs. 1-10, a primitive Ammonite, transitional from *Gastrioceras* to Tropitidæ, showing simple recapitulation; this is the probable radicle of *Tropites* and its near kindred, and connects them with the Glyphioceratidæ.

Lecanites, Pl. III, figs. 1-3, an unprogressive or persistent form, an Ammonite retarded in the Goniatite stage of development, probably representing the radicle of the Ceratitoidea, and connecting them with the Gephyroceratidæ.

Nannites, Pl. III, figs. 4-8, a persistent, unprogressive type, a Mesozoic Ammonite retarded in the Paleozoic Geniatite stage of development; probably representing the radicle of the Ptychitidae.

Tropites, Pl. IV, figs. 11-21, a progressive Ammonite, showing distinct recapitulation, but with very unequal acceleration, or ''telescoping'' of characters and stages of development.

Lytoceras, Pl. XIV, fig. 10, a persistent group of Ammonites, lasting with little change throughout the Mesozoic.

Longobardites, Pl. IX, figs. 14-16, family Pinacoceratidae. *Eutomoceras,* Pl. IX, figs. 5-7, family Hungaritidae. *Discotropites,* Pl. V, figs. 1-13, family Tropitidae. *Paratropites,* Pl. V, figs. 14-19, family Tropitidae. *Ceratites,* Pl. V, figs. 20-26, family Ceratitidae. *Gymnotropites,* Pl. VIII, figs. 11-13, family Tropitidae.	Illustrating convergence in different stocks, in the development of the keel and sculpture. A good example of orthogenetic evolution.

Paraganides, Pl. VI, figs. 22-26, family Ptychitidae, retarded and reversionary to the primitive Glyphioceran stock.

Leconteia, Pl. VI, figs. 11-15, family Tropitidae. *Metasibirites,* Pl. VI, figs. 1-10, family Tropitidae. *Homerites,* Pl. VI, figs. 16-21, family Tropitidae.	Reversionary, by arrest of development; showing vestigial characters, and probable orthogenesis in closely allied stocks.
Arpadites, Pl. VIII, figs. 1-10. *Beyrichites,* Pl. VIII, figs. 14-23.	Showing reversion to the ancestral *Meekoceras,* in some characters.

Schloenbachia, Pl. XIII, figs. 16-21.	Showing similarity of young stages, due to adaptation in stocks that are wholly distinct. The young stages are probably cœnogenetic.
Lytoceras, Pl. XIII, figs. 10-15.	
Placenticeras, Pl. XIII, figs. 22-28.	

Baculites, Pl. XIII, figs. 1-9, a reversionary form from *Lytoceras.*

Trachyceras, Pl. XV, figs. 13-16, one of the most highly specialized of the Ceratitidae; showing the beginning of arrest of development in the prolongation of the entogeny, and persistence of the ancestral *Tirolites* stage throughout adolescence.

Clionites, Pl. XV, figs. 1-8, a retarded descendant of *Trachyceras,* reversionary by arrest of development toward *Tirolites.*

Clionites (Californites), Pl. XV, figs. 9-12, a form still more strongly reversionary than the preceding species, with almost complete palingenesis of *Tirolites* characters, but with inheritance of the trachyceran furrow and sculpture from its immediate ancestor; these are characters that *Tirolites* never had.

Otoceras, Pl. X, figs. 6 and 7, a transitional Permian genus.

Paratissotia, Pl. X, figs. 8-10, a Cretaceous genus, arrested in development, and showing atavistic reversion to characters very like those of *Otoceras.*

Waagenoceras, Pl. X, fig. 12, a Permian genus, primitive and progressive.

Sphenodiscus, Pl. X, fig. 11, a Cretaceous genus, arrested in development, and showing a close approach to the septation of *Waagenoceras.* These two genera do not belong to the same line of descent, hence the convergence is not due to atavism.

Heterotissotia, Pl. X, figs. 2-4, a Cretaceous genus, showing arrest of development, and reversion to some form like *Ceratites,* but probably not to any member of the Ceratitidae.

Ceratites, Pl. X, fig. 15, a Triassic genus, like the reversionary forms of later Cretaceous groups, the "Pseudoceratites."

Neolobites, Pl. X, fig. 1, a Cretaceous genus, showing arrest of development and reversion to the Goniatite stage, though probably not to any known Paleozoic genus.

EXPLANATION OF PLATES.

PLATE I.

Goniatites crenistria Phillips, Lower Carboniferous, Arkansas.

Fig. 1, a-j, development, shown in septa, from protoconch to maturity.

Fig. 2, early larval stage, diam. 0.47 mm.

Figs. 3 and 4, larval stage, diam. 0.92 mm.

Figs. 5 and 6, adolescent stage, diam. 1.29 mm.

Figs. 7-9, adult shell and septa.

A highly specialized Goniatite, and a representative of the group radicle of the Tropitidae and Arcestidae among the Mesozoic Ammonites.

Gastrioceras Listeri Martin, Coal Measures, Arkansas.

Figs. 10-11, adult shell.

A still more highly specialized Goniatite, showing further progress toward the Tropitidae.

Gastrioceras Branneri Smith, Coal Measures, Arkansas.

Figs. 12-14, adult shell and septa.

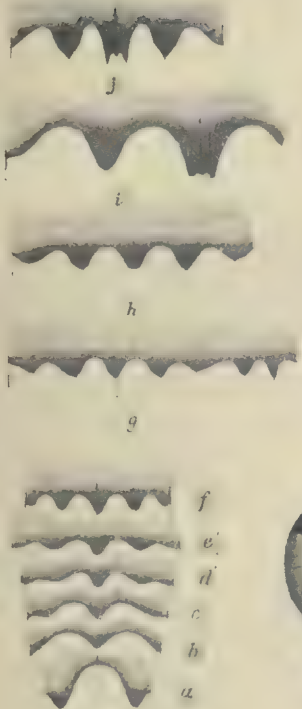
Aganides rotatorius de Koninck, Lower Carboniferous, Indiana.

Figs. 15 and 16, adult shell.

The genera illustrated on this plate show the stage of evolution of the common Carboniferous groups, and the early ancestral types of the Arcestidae and the Tropitidae.

All figures on this plate are from J. P. Smith, Carboniferous Ammonoids of America, Mon. XLII, U. S. Geological Survey, 1903.

PLATE I.



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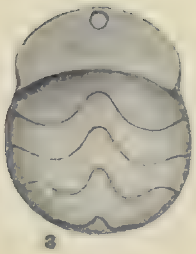

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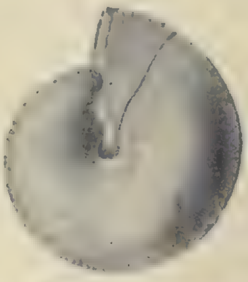

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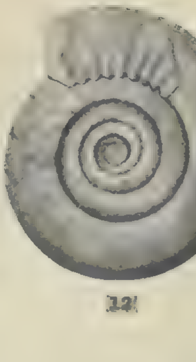

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PLATE II.

Paralegoceras iowense Meek and Worthen, Coal Measures, Iowa.

Fig. 1, adult specimen.

The two species of *Paralegoceras* figured on this plate show a transition from *Gastrioceras* to *Schistoceras.*

Paralegoceras Newsomi Smith, Coal Measures, Arkansas.

Figs. 2-4, adult shell and septa.

Fig. 5, adolescent stage.

Schistoceras Hildrethi Morton, Coal Measures, Ohio.

Figs. 6 and 7.

The three species of *Schistoceras* figured on this plate show a distinct step toward the Arcestidae, although it is not probable that any one of them was the family radicle.

Schistoceras fultonense Miller and Gurley, Coal Measures, Illinois.

Figs. 8-10.

Schistoceras Hyatti Smith, Coal Measures, Texas.

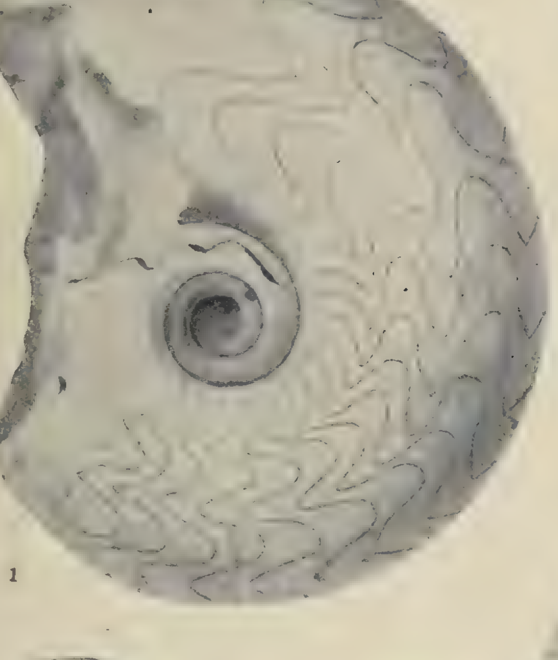
Figs. 11 and 12, adult shell and septa.

Fig. 13, adolescent stage.

The genera illustrated on this plate show an advance of the Glyphioceratidae towards the Arcestidae and the Tropitidae.

All figures on this plate are from J. P. Smith, Carboniferous Ammonoids of America, Mon. XLII, U. S. Geological Survey, 1903.

PLATE II.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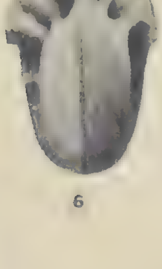
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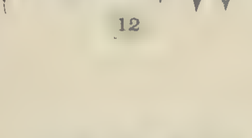
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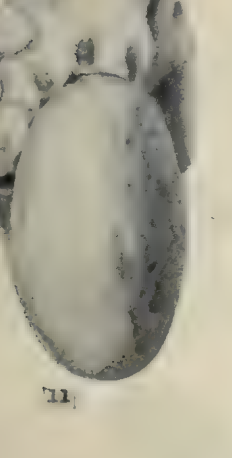
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PLATE III.

Lecanites Vogdesi Hyatt and Smith, Middle Triassic, Nevada.

Figs. 1-3, adult stage, showing persistence in the Goniatite stage, a beginning of arrest of development. This species retains many of the characters of *Gephyroceras* of the Devonian.

Nannites Dieneri Hyatt and Smith, Lower Triassic, California.

Figs. 4-8, adult stage, showing persistence in the Goniatite stage, a beginning of arrest of development, but without reversion. This species retains many of the characters of the group of *Gastrioceras globulosum* of the Carboniferous.

Gephyroceras uchtense Keyserling, Upper Devonian, Russia.

Figs. 9-11, adult stage. A primitive radicle, like the ancestor of the Meekoceratidae and Ceratitidae.

Timanites acutus Keyserling, Upper Devonian, Russia.

Figs. 12-14. A primitive Coniatite, a lateral branch of *Gephyroceras*, and the probable ancestor of the Hungaritidae and of the Sageceratidae.

Figs. 1-8, from Hyatt and Smith, Triassic Cephalopod Genera of America.

Figs. 9-12, from E. Holzapfel, Die Cephalopoden des Domanik im südlichen Timan. Mém. Com. Géol. (St. Petersbourg), Vol. XII, No. 3. 1899.

PLATE III.

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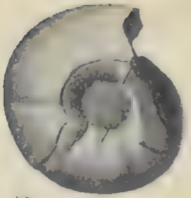

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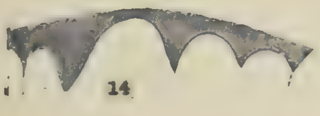

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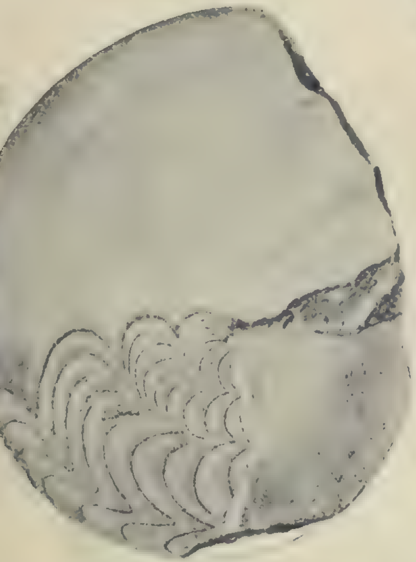

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PLATE IV.

Columbites parisianus Hyatt and Smith, Lower Triassic, Idaho.

Figs. 1-3, adult stage.

Figs. 4 and 5, adolescent stage, diam. 10 mm., corresponding to *Gastrioceras*.

Figs. 6 and 7, easily adolescent stage, diam. 1.75 mm.

Figs. 8-10, embryonic and early larval stages.

Columbites shows a transition from the group of *Gastrioceras* towards the Tropitidae.

Tropites subbullatus Hauer, Upper Triassic, California.

Figs. 11-13, adult stage.

Figs. 14-15, adolescent stage.

Figs. 16-21, larval stages, showing development from the Goniatite to the Ammonite stage, with very unequal acceleration, ''telescoping'' of characters and stages.

Columbites is the Lower Triassic ancestor of the Tropitidae, and connects that family with the Paleozoic ancestors, Glyphioceratidae.

All figures on this plate are from Hyatt and Smith, Triassic Cephalopod Genera of America, Prof. Paper No. XL, U. S. Geological Survey, 1905.

PLATE IV.


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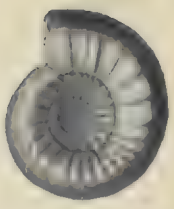
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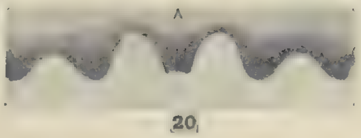
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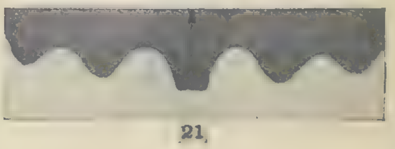
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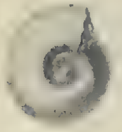
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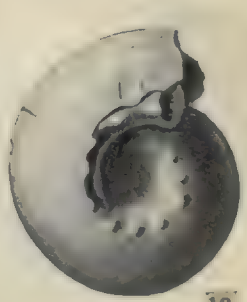
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PLATE V.

Discotropites sandlingensis Hauer, Upper Triassic, California.

Figs. 1-4, adult stage, showing ornamentation and septa.

Figs. 5-7, larval stage, diam. 5.5 mm., showing beginning of keel.

Figs. 8-10, larval stage, diam. 4.25 mm., showing beginning of serration of lobes, and transition from Goniatite to Ammonite stage.

Figs. 11-13, early larval stage, diam. 2.68 mm., Goniatite stage, corresponding to *Gastrioceras.*

Paratropites Sellai Mojsisovics, Upper Triassic, California.

Figs. 14-16, adult stage.

Figs. 17-19, larval stage, diam. 5 mm., showing transition from Goniatite to Ammonite stage.

Ceratites humboldtensis Hyatt and Smith, Middle Triassic, Nevada.

Figs. 20-21, adult stage.

Figs. 22-24, adolescent stage.

Figs. 25-26, larval stage, diam. 8 mm.

The three genera figured on this plate show convergence in different stocks.

All figures on this plate are from Hyatt and Smith, Triassic Cephalopod Genera of America.

PLATE V.


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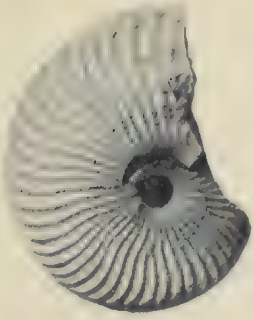
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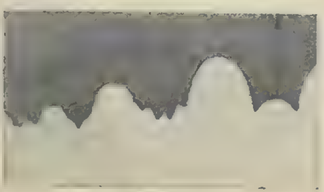
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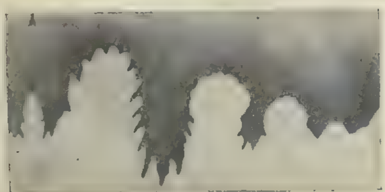
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PLATE VI.

Metasibirites Frechi Hyatt and Smith, Upper Triassic, California.

Figs. 1-10, adult stage, showing arrest of development, reversion to the Goniatite stage, and many characters of genera that came between the primitive Goniatites and the more specialized Ammonites in the history of this stock.

Leconteia californica Hyatt and Smith, Upper Triassic, California.

Figs. 11-13, adult stage, showing arrest of development, and reversion to the primitive ancestral type.

Figs. 14-15, larval stage, diam. 2.5 mm.

Homerites semiglobosus Hauer, Upper Triassic, California.

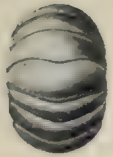
Figs. 16-21, adult stage, showing arrest of development, and reversion toward the ancestral stock. Both *Homerites* and *Metasibirites* show a tendency to develop a rudimentary keel, probably as a convergence phenomenon.

Paraganides californicus Hyatt and Smith, Upper Triassic, California.

Figs. 22-26, adult stage, showing arrest of development, and reversion to the Goniatite characters.

All figures on this plate are from Hyatt and Smith, Triassic Cephalopod Genera of America.

PLATE VI.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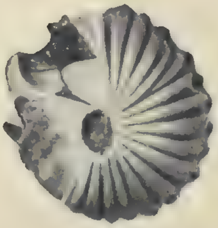
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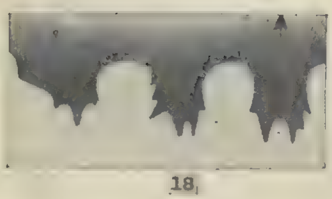
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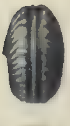
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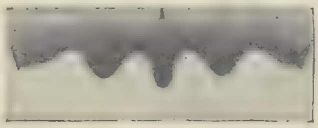
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PLATE VII.

Meekoceras mushbachanum White, Lower Triassic, Idaho.

Figs. 1-5, adult stages, showing development towards *Ceratites.*

Meekoceras gracilitatis White, Lower Triassic, Idaho.

Figs. 6-12, showing development from early stage to maturity.

Both species are primitive forms, intermediate between the Goniatite ancestry and the Ceratitic posterity. Both are intermediate in characters between the Paleozoic and the Mesozoic types.

All figures are from Hyatt and Smith, Triassic Cephalopod Genera of America.

PLATE VII.


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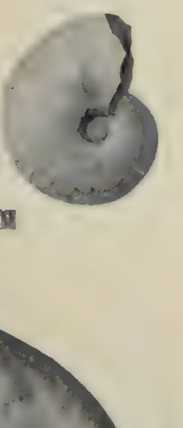
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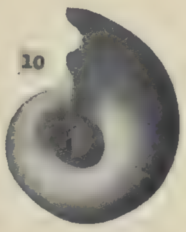
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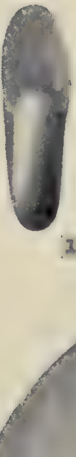
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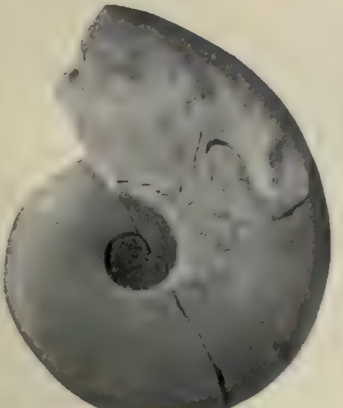
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PLATE VIII.

Arpadites Gabbi Hyatt and Smith, Upper Triassic, California.

Figs. 1-10, showing development from late larval stage to maturity, and reversion at maturity to some of the ancestral *Meekoceras* characters.

Gymnotropites californicus Hyatt and Smith, Upper Triassic, California.

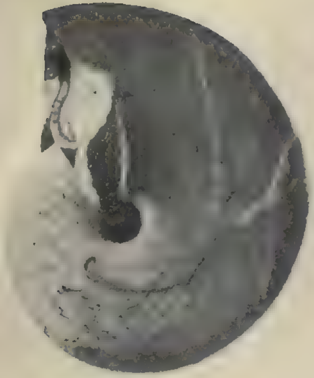
Figs. 11-13, showing convergence with *Discotropites* and *Eutomoceras.*

Beyrichites rotelliformis Meek, Middle Triassic, Nevada.

Figs. 14-23, showing development from late larval stage, and partial reversion at maturity to the ancestral *Meekoceras* characters. This species also shows convergence with *Ptychites,* an entirely different stock.

All figures from Hyatt and Smith, Triassic Cephalopod Genera of America.

Plate VIII.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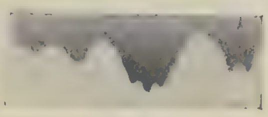
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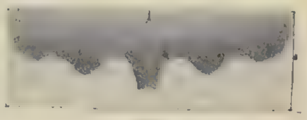
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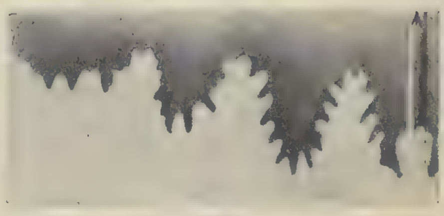
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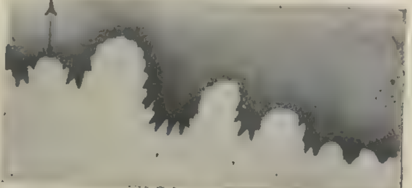
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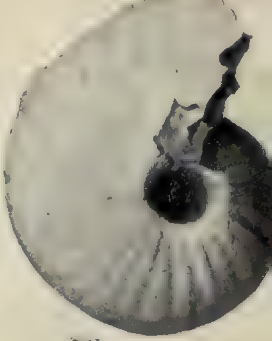
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PLATE IX.

Aspenites acutus Hyatt and Smith, Lower Triassic, Idaho.

Figs. 1-4, adult stage, showing resemblance to the Devonian *Timanites.*

Eutomoceras Laubei Meek, Middle Triassic, Nevada.

Figs. 5-7, showing convergence of Hungaritidae with Tropitidae.

Inyoites Oweni Hyatt and Smith, Lower Triassic, California.

Figs. 8-13, showing convergence of Hungaritidae and Tropitidae.

Longobardites nevadanus Hyatt and Smith, Middle Triassic, Nevada.

Figs. 14-16, showing convergence of Pinacoceratoidea with Hungaritidae, through partial reversion towards the same ancestral *Timanites.*

All figures from Hyatt and Smith, Triassic Cephalopod Genera of America.

PLATE IX.


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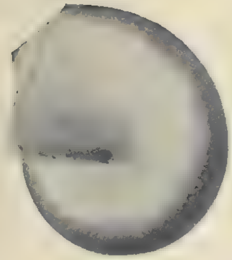
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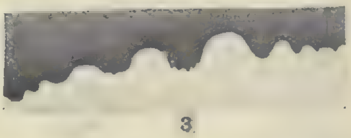
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PLATE X.

Neolobites Choffati Hyatt.

Fig. 1, showing arrest of development and reversion of a Cretaceous genus to the Paleozoic Goniatite stage.

Heterotissotia neoceratites Peron, Upper Cretaceous, Peru.

Figs. 2-4, convergence with the Triassic *Ceratites,* by reversion to some ceratitic ancestor, though probably not *Ceratites.*

Ceratites semipartitus v. Buch, Middle Triassic, Germany.

Fig. 5, septa for comparison with the ''Pseudoceratites'' of the Cretaceous.

Otoceras Woodwardi Diener, Lower Triassic, India.

Fig. 6 and 7, a transitional Permian and Lower Triassic genus, to show heterochronous convergence with some of the ''Pseudoceratites'' of the Cretaceous.

Paratissotia serrata Hyatt, Upper Cretaceous, Peru.

Figs. 8-10, a Cretaceous genus, arrested in development, and showing atavistic reversion to characters very like those of *Otoceras* of the Permian and Lower Triassic.

Sphenodiscus Hilli Hyatt, Upper Cretaceous, Texas.

Fig. 11, septa, showing resemblance to Arcestidae of the Triassic, though probably not indicating relationship.

Waagenoceras Hilli Smith, Permian, Texas.

Fig. 12, septa, showing resemblance to those of *Spenodiscus* of the Cretaceous—a case of heterochronous convergence.

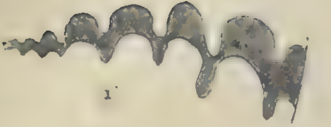
Figs. 1, 8, 9, 10, 11, from Hyatt, Pseudoceratites of the Cretaceous.

Figs. 6 and 7, from Diener, Cephalopoda of the Lower Trias. Mem. Geol. Survey, India, 1897.

Figs. 2-5, from Steinmann, Probleme der Ammoniten-Phylogenie. Sitz. Niederrhein. Gesell. Bonn, 1909.

Fig. 12, from J. P. Smith, Carboniferous Ammonoids of America.

PLATE X.



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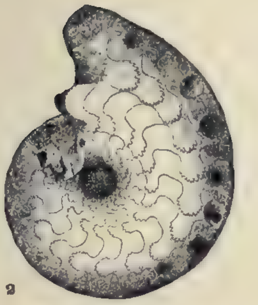

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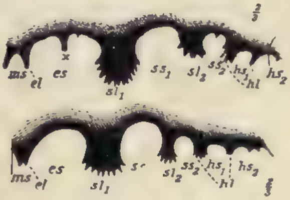

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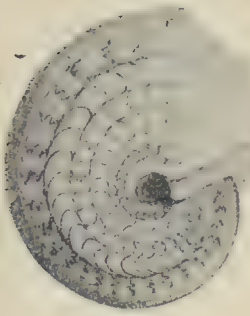

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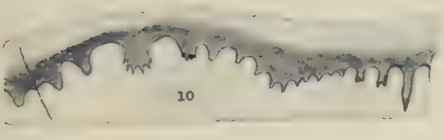

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PLATE XI.

Ussuria Waageni Hyatt and Smith, Lower Triassic, Idaho.

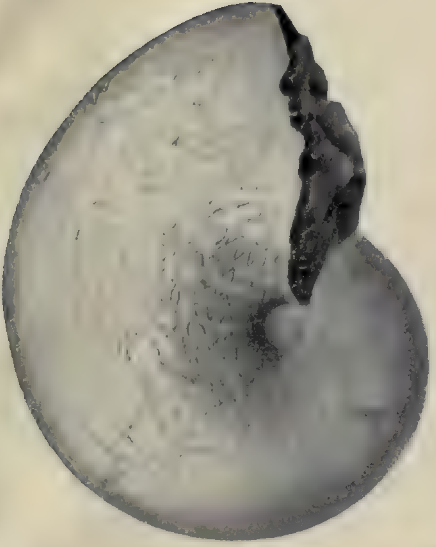
Figs. 1-14, showing development from larval stage to maturity. A primitive progressive form, showing simple recapitulation of its ancestral history.

Parananmites aspenensis Hyatt and Smith, Lower Triassic, Idaho.

Figs. 15-20. Primitive Ammonite, transitional from the Paleozoic Glyphioceratidae to the Mesozoic Ptychitidae, an example of a radicle of a group.

All figures from Hyatt and Smith, Triassic Cephalopod Genera of America.

PLATE XI.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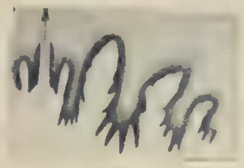
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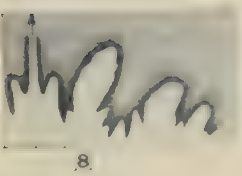
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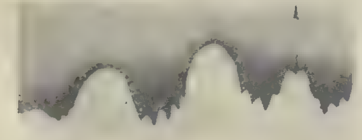
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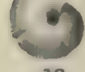
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PLATE XII.

Cordillerites angulatus Hyatt and Smith, Lower Triassic, Idaho.

Figs. 1-8, development from larval stage to maturity. A primitive Ammonite, showing simple recapitulation; a very perfect repetition of phylogeny in ontogeny.

Pronorites cyclolobus Phillips, Lower Carboniferous, England.

Fig. 9, showing development of the septa. The three species of *Pronorites* illustrated are examples of the ancestral stock of *Cordillerites* and *Medlicottia.*

Pronorites mixolobus, Carboniferous, England.

Fig. 10, septa, for comparison with *P. cyclolobus.*

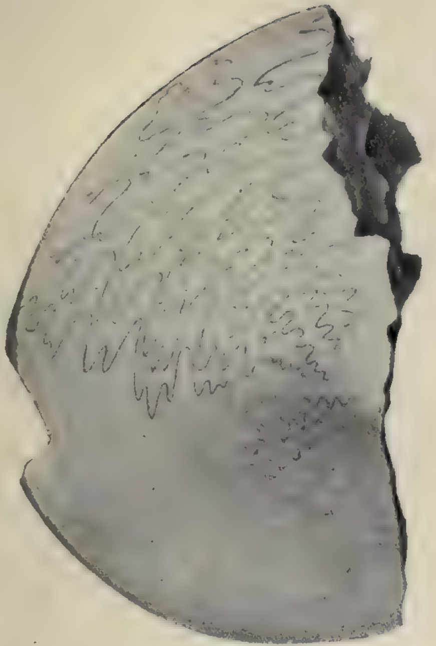
Pronorites cyclolobus, var. arkansasensis Smith, Lower Carboniferous, Arkansas.

Figs. 11 and 12, shell and septa.

Figs. 1-8, from Hyatt and Smith, Triassic Cephalopod Genera of America.

Figs. 9-12, from J. P. Smith, Carboniferous Ammonoids of America.

PLATE XII.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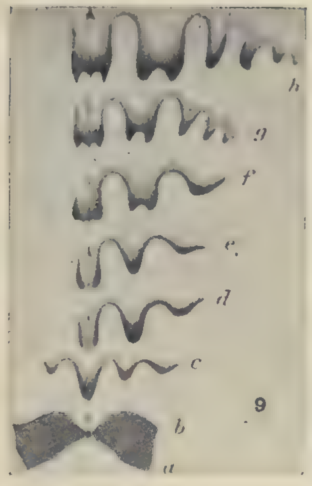

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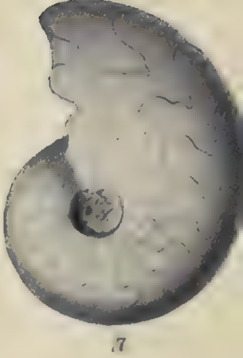
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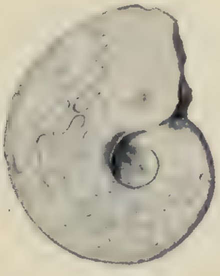
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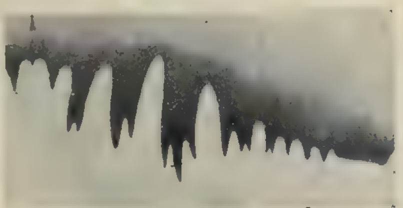
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PLATE XIII.

Baculites chicoensis Trask, Upper Cretaceous, California.

Figs. 1-9, larval stages, showing coiled young, and derivation from the normal genus, *Lytoceras.*

Lytoceras alamedense Smith, Upper Cretaceous, California.

Figs. 10-15. Larval and adolescent stages, showing resemblance to young of *Baculites.*

Schloenbachia oregonensis Anderson, Upper Cretaceous, Oregon.

Figs. 16-21, larval and adolescent stages.

Placenticeras pacificum Smith, Upper Cretaceous, California.

Figs. 22-28. Larval and adolescent stages, showing recapitulation of phylogeny in ontogeny.

Lytoceras, Schloenbachia, and *Placenticeras* belong to wholly different stocks, with different ancestry; and yet their young stages are very much alike, due to adaptation and not atavism.

All figures are from J. P. Smith, figs. 1-9, Larval Coil of Baculites, American Naturalist, 1901; figs. 10-15, The Development of Lytoceras and Phylloceras, Proc. Calif. Acad. Sci., 1898; figs. 16-21, Larval Stages of Schloenbachia, Journal of Morphology, 1899; figs. 22-28, The Development and Phylogeny of Placenticeras, Proc. Calif. Acad. Sci., 1900.

PLATE XIII.

PLATE XIV.

Fig. 1. *Orthoceras timidum.*
Fig. 2. *Cyrtoceras corbulatum.*
Fig. 3. *Cyrtoceras Murchisoni.*
Fig. 4. *Gyroceras alatum.*
Fig. 5. *Nautilus planotergatus.*
Fig. 6. *Lituites lituus.*
Fig. 7. *Bactrites (protoconch).*
Fig. 8. *Mimoceras compressum.*
Fig. 9. *Tropites phoebus.*
Fig. 10. *Lytoceras Liebigi.*
Fig. 11. *Crioceras Emerici.*
Fig. 12. *Turrilites catenatus.*
Fig. 13. *Baculites compressus.*
Fig. 14. *Macroscaphites Ivanii.*

All figures are from J. P. Smith, Evolution of Fossil Cephalopoda, Chapter IX, in D. S. Jordan's Footnotes to Evolution, 1898. They illustrate various stages in the evolution of Cephalopoda mentioned in the text.

PLATE XIV.


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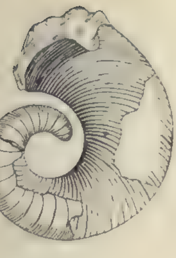
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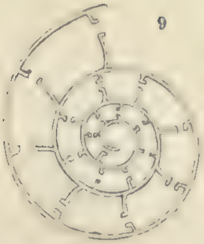
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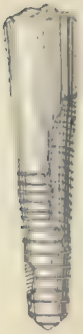
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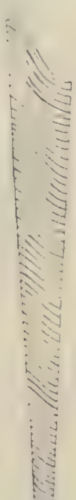
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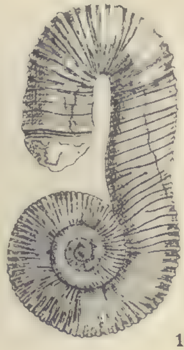
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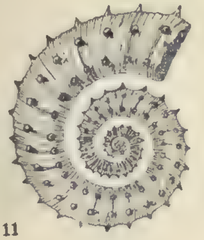
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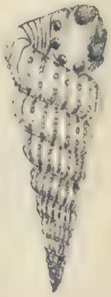
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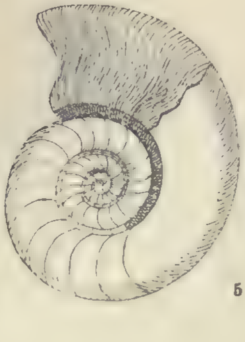
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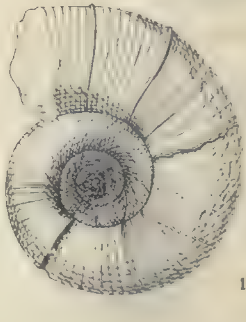
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PLATE XV.

Clionites (Traskites) robustus Hyatt and Smith, Upper Triassic, California.

Figs. 1-8. A form arrested in development, and partly reversionary to *Trachyceras.*

Clionites (Californites) Merriami Hyatt and Smith, Upper Triassic, California.

Figs. 9-12. A form more retarded than *C. robustus,* and showing more of the ancestral characters. Reversionary, by arrest of development, to *Tirolites,* in everything but the retention of the trachyceran furrow.

Trachyceras duplex Mojsisovics, Upper Triassic, Alps.

Figs. 13-16. A progressive form, but showing the beginning of arrest of development in the prolongation of the ontogeny, and persistence of the *Tirolites* stage in adolescence.

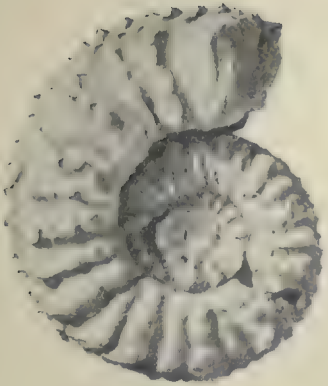
Clionites (Neanites) californicus Hyatt and Smith, Upper Triassic, California.

Figs. 17-20. Reversionary by arrest of development to the ancestral type, *Tyrolites,* but still showing the trachyceran furrow inherited from its intermediate ancestor *Trachyceras.*

Figs. 1-12, and 17-20, from Hyatt and Smith, Triassic Cephalopod Genera of America.

Figs. 13-16, from E. von Mojsisovics, Das Gebirge um Hallstatt, II, 1893.

PLATE XV.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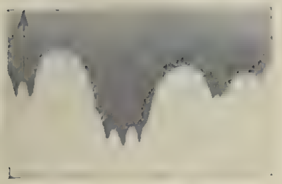
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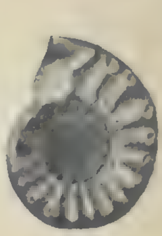
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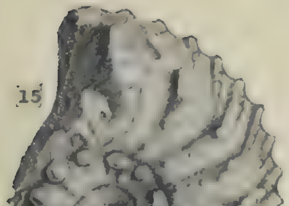
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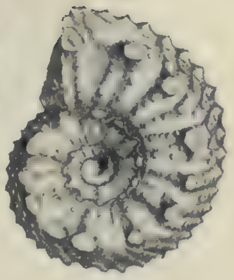
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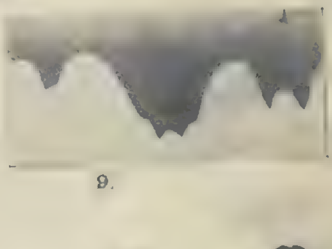
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