Paleontology and the Recapitulation Theory.

By E. R. Cumings.

I.

In reply to a severe critique of the recapitulation theory, or biogenetic law, by Hurst (30), Bather remarks that "If the embryologists had not forestalled them, the paleontologists would have had to invent the theory of recapitulation." (1) This may be considered as a fair sample of the general attitude of paleontologists of the Hyatt school, to which Bather belongs, toward the recapitulation theory.

Even the more conservative paleontologists, while inclined to use the theory *cum grano salis*, recognize the weight of evidence that Hyatt and his coworkers in the realm of paleobiology, have brought together, as is evidenced by the following quotation from Zittel (65): "Nevertheless embyronic types are not entirely wanting among invertebrates. The Paleozoic Belinuridæ are bewilderingly like the larvae of the living Limulus. The pentacrinoid larva of *Autedon* is nearer many fossil crinoids than the full grown animal. . . . . Among pelecypods the stages of early youth of oysters and Pectinidæ may be compared with Paleozoic Aviculidæ. Among brachiopods, according to Beecher, the stages which living Terebratulidæ pass through in the development of their arm-skeleton correspond with a number of fossil genera. The beautiful researches of Hyatt, Würtenburger and Branco, have shown that all Ammonites and Ceratites pass through a goniatite stage, and that the inner whorls of an Ammonite constantly resemble, in form, ornament and suture line the adult condition of some previously existing genus or other."

In violent contrast with this full acceptance, or this guarded acceptance of the theory on the part of the paleontologists, is the position of a considerable school of embryologists and zoologists. Perhaps no one has put the case against the theory more baldly and forcibly than Montgomery in his recent book on "An Analysis of Racial Descent" (42). He says: "The method is wrong in principle, to compare an adult stage of one organism with an immature stage of another." And again: "Therefore we can only conclude that the embryogeny does not furnish any recapitulation of the phylogeny, not even a recapitulation marred at occa-

sional points by secondary changes. . . . An analysis of the stages during the life of one individual can in no way present a knowledge of its ancestry, and the method of comparing non-correspondent stages of two species is wrong in principle." Equally sweeping is the statement of Hurst (30) : "The ontogeny is not an epitome of the phylogeny, is not even a modified or 'falsified' epitome, is not a record, either perfect or imperfect of past history, is not a recapitulation of evolution."

It would seem as though two statements could not be more flatly contradictory than these of Hurst and Montgomery, and that of Bather quoted above. Nevertheless I venture to make the seemingly paradoxical assertion that both parties to the controversy may be right, for the simple reason that they are talking about quite different things. This has been nowhere better expressed than by Grabau (25). He says: "It has been the general custom to test the validity of the recapitulation theory by the embryological method; i. e., the comparableness of the changes which the individual undergoes during its embryonic period to the adults of more primitive types. Usually the comparison has been with the adults of existing types, since in most cases these alone were available for comparison. It is no wonder, then, that such comparisons have led to innumerable errors, if not absurdities, which have placed the recapitulation theory in an evil light and awakened in the minds of many serious investigators doubts as to the validity of the deductions based upon this doctrine. When, however, the *entire life history* of the individual is considered, instead of *only the embryonic period*, and when the successive stages of epembryonic development are compared with the adult characters of related types, in immediately preceding geologic periods, it will be found that the fundamental principle of recapitulation is sound, and that the individuals do repeat in their own *epembryonic* development the characters of their own immediate ancestors." (Italics mine.)

It is as a matter of fact true that the Hyatt school of paleontologists have based their phylogenies on epembryonic rather than embryonic stages —stages beginning with the nepionic or infantile—since in the nature of the case the true embryonic stages are scarcely ever accessible to the student of fossils. It is no less true that the severest critics of the theory of recapitulation have rested their case largely on the real or supposed lack of correspondence between the *embryonic* stages and the adult stages of assumed ancestors, or upon certain *a priori* considerations having to

do with the laws of development and inheritance. To the former class belong such critics as Von Baer, and to the latter class such as Hatschek, His, Hurst, Montgomery and others.

In making this statement I am aware that paleontologists sometimes compare true embryonic stages with adult stages of pre-existing types. As examples of this we might cite the comparison of the larval stage of *Antedon* with adult Paleozoic crinoids, as mentioned by Zittel; and the classic attempt of Beecher to reconstruct the ancestor of the Brachiopoda by a comparison of the phylembryonic stages of a representative series of genera of recent and fossil brachiopods. Nevertheless by far the greater number of comparisons that have been instituted by paleontologists have been between epembryonic stages of individuals and adult stages of older forms. Such comparisons are those of Hyatt, Branco, Karpinsky, Würtenburger, Buckman, Neumayr, Smith, Beecher, Clarke and others among the Cephalopoda; of Beecher and Schuchert, Raymond, Greene and Cumings among the Brachiopoda; of Jackson among the Pelecypoda; of Grabau and Burnett Smith among the Gastropoda; of Lang and Cumings among the Bryozoa; of Ruedemann among the graptolites; and of Beecher, Girty, Lang and others among the corals. To many of these researches I shall refer later.

I am also not unmindful of the fact that many of those who are not primarily paleontologists recognize the fact that development does not terminate with the completion of the embryonic stages, and that recapitulation may be legitimately looked for in epembryonic as well as embryonic stages, or that it may be sought in epembryonic stages, even though masked or falsified in embryonic stages. It is true, of course, that some speak of a comparison of *ontogeny* and phylogeny when, judging by the context, they mean a comparison between *embryogeny* and phylogeny. There arises here a question of definition: does the biogenetic law mean that the *ontogeny* is a recapitulation of the phylogeny, or does it mean that the *embryogeny* is a recapitulation of the phylogeny? If we take the general consensus of opinion we shall find for the former definition, and if we take the words of Haeckel, whose statement of the law is the one usually quoted, we shall again find for the former definition. I believe that, as a matter of fact, no one would maintain that the second definition is correct, however much he might forget in his studies to take the epembryonic stages into consideration.

Nor would I create the impression that the embryologists and zoologists have utterly deserted the paleontologists in their support of the recapitulation theory. Several recent papers give considerable aid and comfort to those of us who still believe in recapitulation. I shall introduce here the conclusions of three of these workers, more particularly because it will afford me an opportunity to correct what I hold to be another error of those who oppose the theory.

One of the most interesting pieces of evidence that has recently been adduced in favor of the idea that ontogeny recapitulates phylogeny is to be found in a paper by Griggs on "Juvenile Kelps" (28). It is not my purpose, however, to discuss the very interesting evidence which he has recorded, but rather to quote his remarks on the views of His and Morgan, and his general conclusions. His maintains that the reason why ontogeny seems to recapitulate phylogeny is because the stages in development are, as Griggs paraphrases it, "only the physiologically necessary steps for the formation of the adult body from its earliest stage, which in most cases is the egg." With the ideas of Morgan as expressed in his valuable book on "Evolution and Adaptation" we are all familiar. He holds that organisms repeat in their development, not adult stages, but only embryonic stages of their ancestors. To this idea he has given the name of "repetition."

On this point of the recapitulation of embryonic conditions Griggs makes the following pertinent statements: "In the toothless animals, the whale and the bird, the development of teeth in the jaws is entirely unnecessary * * * it may even be said to hinder the attainment of the adult condition. The same is true of the mammalian gill slits and of most structures which have in the past attracted attention in connection with the recapitulation theory. As the ancestral period when such structures were fully developed in the adult becomes more and more remote, the tendency to inherit them becomes less and less, because of the cumulative impulses given to the heritage by the nearer ancestors. Consequently they are successively less and less developed. Any gradual loss of inheritance can, in the nature of the case, take place only from the mature condition backward toward the beginning of the life cycle; otherwise we should have adult structures with no ontogenetic history. Therefore we can understand why it is that in many cases only the embryonic stages of ancestral history persist in the ontogeny." In a foot note he says: "The cutting off of end stages in the development of organs has

given rise to the idea that the adult stages are 'pushed back into the embryo.' Such a misconception easily arose from the loose language in which the facts have often been expressed. Thus the embryogeny will be gradually shortened by the omission of more and more of the superfluous ancestral stages; and it will tend finally to retain only such stages as are necessary to the attainment of the adult form." Morgan and His, he maintains, have confused morphology and physiology. "The recapitulation theory has nothing to do with physiology; it is purely a matter of morphology."

In conclusion Griggs says: "Taking all the evidence into consideration, it seems to the writer that we are bound to conclude that though organisms are subject to adaptations at any stage of their life cycles and may gradually cut out superfluous stages, yet, except as some such tendency has operated to change the heritage, the development of the individual does recapitulate the history of the race * * * recapitulation must take place if there is any force which tends to make offspring like parent, if heredity is of any importance in moulding the forms of organisms. On the other hand, if there is any variability of transmutation of individuals in stages other than the adult end stages of the life cycles, the recapitulation cannot be perfect, but must be marred at every stage where secondary change has taken place." I shall return later to some of the points raised by Griggs in the above statements.

Another eminent worker, Dr. Eigenmann, says at the close of a paper on the eyes of the blind vertebrates of North America (20): "We have seen in the preceding pages that the foundations of the eye [of *Amblyopsis*] are normally laid, but that the superstructure instead of continuing the plan with new material, completes it out of the material provided for the foundations, and that in fact not even all of this (lens) material enters into the structure of the adult eye. The development of the foundations of the eye is phylogenic, the stages beyond the foundations are direct."

The third writer, Dr. Zeleny (64), in his paper on "Compensatory Regulation," in a discussion of the development and regeneration of the opercula in serpulids, says that the morphologic series is so complete as to make sufficient ground for the conclusion that the opercula arose in the course of phylogeny as modified branchia. The ontogenetic series, he says, *corresponds very closely with the probable phylogenetic series.* Speaking of the regeneratory development he says: "The course of re-

generatory development is characterized by great condensation and direct-
ness of the development. There is no trace of the branchial stage, and
the development of the two rows of processes of the terminal cup does
not follow the ontogenetic order."

His final conclusion is as follows: "The data furnished, therefore,
by the opercula of the serpulids give a fairly close agreement between
the ontogenetic stages and the probable phylogenetic ones as determined
by the usual criteria. The regeneratory development, however, follows a
course which may be modified by the character of the operation that
leads to the regeneration." By the "usual criteria" he means morphology,
etc., so that he cannot be accused of the *circulus vitiosus*.

Those who wish to review the detailed evidence given in the above
papers, bearing on the theory of recapitulation, will, of course, consult
the original papers. My main reason for quoting them is, as stated above,
because of their bearing on what seem to me to be grave errors in the
reasoning of His, Morgan and Montgomery and others who have adopted
similar views. The error seems to me to be, as pointed out by Griggs, in
the confusion of morphology and physiology. The adult characters that
are supposed to be recapitulated in the ontogeny, as well as the characters
in ontogeny that are supposed to represent them, are morphological
characters solely. It matters not what new function they may have come
to serve, nor by what physiologic process they have come to make their
appearance in the recapitulating organism. The confusion arising from
this source colors all the argument of Montgomery, in which he endeav-
ors to prove that new specific characters must have some representation
in the ovum—a view which we must certainly agree with—and that there-
fore "the whole row" of cells from the ovum to the adult must be differ-
ent. We grant that "The whole row" *is* different in some way, physiolog-
ically different, different in its play of energies; but it may conceivably
be morphologically identical up to the very point where the new
character is added. It is just as easy to conceive that the energy,
or whatever we choose to call it, that is at a certain stage in develop-
ment to produce a certain rib or spine or color-band on the shell of a
gastropod, may be handed through the row of cells reaching up to the
given stage, without producing a single recognizable morphologic change
in the row, as compared with the individual that is not to possess the new
character, as it is to conceive the opposite. The argument for the one
view is just as certainly *a priori* as the argument for the other view. It

is also perfectly conceivable that the morphology of the *individual cells* in the row might differ after the acquisition of the new character (in so far as this assumption is required by recent cytological studies), and yet not a single organ or part of the organism be different up to the stage in ontogeny when the new character appears. Unless, therefore, a change in the energies of the cells *inevitably necessitates* a change in the morphology of all the cells or of all the organs which they compose, the argument of Montgomery proves nothing.

As to the argument of His and others, that the supposedly ancestral stages are merely the physiologically necessary stages in the development of the individual; it again, as Griggs points out, confuses morphology with physiology, and is open to the further objection that it is directly opposed to the facts. Why, for example, should the condition of perfect blindness, with complete loss of all the essential structures of the eye, be attainable only by the round-about way of first developing the foundations of a normal eye? Why should a serpulid be able to regenerate a perfect operculum in a manner entirely different from, and even opposed to the ontogenesis of the organ, if there is any physiologically necessary way in which that particular individual or that particular organ must develop? The thing that makes it necessary for development to take a certain course in a given individual is the fact that the development has taken that same course in the ancestors. This species of coercion may, to be sure, be relaxed, and the development take some other course, but it is usually relaxed with extreme slowness, and after many generations have passed.

If inheritance were perfect, the individual would take exactly the same course in development as its ancestors. That it does not do this in all cases is, as Griggs points out, a more remarkable fact than that in other cases it should follow the ancestral mode of development so closely. Griggs explains the loss of inheritance as due to a progressive condensation of the ontogeny by the "omission of more and more of the superfluous ancestral stages." This is the well-known law of acceleration or tachygenesis. Like most embryologists, however, he misconceives the law, as shown by the foot-note quoted above. Embryologists are especially prone to limit the law of acceleration in development to the skipping or omission of steps, and the consequent shortening of development. This is not in keeping with the views of Hyatt, who first definitely formulated the law; and, as all paleobiologists know, it is not in keeping with the

facts. Hyatt (31) says: "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 stages according to the law of acceleration, until they either become embryonic or are crowded out of the organization and replaced in the development by characters of later origin." A more concise statement of the law is as follows: "The substages of development in ontogeny are the bearers of distal characters in inverse proportion and of proximal characters in direct proportion to their removal in time and position from the protoconch, or last embryonic stage" (31).

According to the definitions just quoted, acceleration involves not only the omission of characters, in some cases (and this is the only sort of acceleration that most embryologists seem to recognize), but it involves also condensation without omission, by crowding more into a given portion of the ontogeny, or again by "telescoping" of characters, as Grabau (25) calls it, so that characters that originally appeared in succession, come to appear simultaneously. In other words acceleration may be by *elimination*, by *condensation*, without change in the order of appearance of characters, or, third, by *telescoping*. The latter is condensation with change in the order of appearance, or as commonly expressed, unequal acceleration. It is probable that paleobiologists have erred in giving too much emphasis to the principle of earlier inheritance, involved in the law, just as embryologists and morphologists have erred in entirely neglecting this phase of inheritance. As conceived by the paleobiologist, the law of acceleration is an explanation of recapitulation, as well as an explanation of the failure to recapitulate.

Another factor in inheritance has been given the name of retardation by Cope (15). By the operation of this factor, characters that appear late in the ontogeny may disappear in descendants because development terminates before the given character is reached. In this way, it is conceived, the ontogeny may be shortened and simplified, and many ancestral characters lost entirely. The result of the continued operation of retardation would be retrogression. That is, the given form, if it continued to repeat the remoter ancestral stages in the early part of its ontogeny, and continued at the same time to drop off the later ancestral stages, by failing to proceed far enough in its development, would ultimately come to resemble the remote rather than the nearer ancestors. Manifestly the retarded forms do not recapitulate the lost characters, so

that here, also, as in the omission of characters in the earlier stages of ontogeny, the heritage is incomplete.

Of the complications of inheritance that arise from larval adaptations, intra-uterine adaptations, and special adaptations arising in later life, I shall not speak. All of these have been repeatedly discussed (see for example Smith 57), and are well understood. Against all of these the paleobiologist must be on his guard. All of these factors tend to make the parallelism between ontogeny and phylogeny inexact, as long ago pointed out by Cope (15). Yet in spite of the operation of these factors, the cases in which there is clear evidence of recapitulation are so numerous, and so well known to the paleobiologist, that were it not for the continually reiterated statements of certain embryologists that there is no such thing as recapitulation, I should hesitate to again point them out. I shall now take up the evidence according to the groups of organisms in which it has been ascertained; and I once more remind the reader that most of this evidence applies to the epembryonic and not to the embryonic stages.

II.

Cephalopoda.—The only existing representative of the great group of Tetrabranchiata, the class to which nearly all of the fossil cephalopods belong, is the *Nautilus*. The genus *Nautilus* is a striking example of the persistence of a primitive type. It belongs to the more primitive branch of the tetrabranchs, from which, according to all the evidence, the marvelously complex ammonities, on the one hand, and the modern naked cephalopods are descended. Nautilus is the only tetrabranch of which the entire ontogeny, including the embryonic stages, is known.

This lack, however, in the case of the fossil genera is not as serious as might be supposed, for the reason that even in these ancient forms all of the growth stages from the latest embryonic (phylembryonic) stage to the adult are preserved in every complete individual shell. An inspection of the *Nautilus* shell makes this at once apparent, for the earlier stages of the shell are surrounded and protected by the later, and no part of the shell is lost or resorbed. In the straight and loosely coiled shells only, such for example as *Orthoceras, Cyrtoceras, etc.,* is the case different; and even here, barring injury, or the dehiscence of the earlier chambers, every post-embryonic stage is preserved. From a study, therefore, of a single shell, we are able to make out perfectly all of the epembryonic de-

velopment in that part of the organism that was most vitally affected by the environment, and which must therefore indicate most perfectly the lines along which the evolution proceeded.

If the initial portion of the shell of *Nautilus* be examined, it will be found to be characterized by a scar or cicatrix. In the same region of the shells of ammonites and some Nautiloidea (*Orthoceras*), instead of this cicatrix, there is present a minute, bulbous or bag-like shell, attached to the apex of the shell proper. If in the case of *Orthoceras*, as shown by Hyatt (31), this bulb, or protoconch be broken away, there is exposed a scar (cicatrix) precisely similar to that of *Nautilus*. The initial shell or protoconch is therefore substantially the same in all of the Tetrabranchiata, and is supposed to point to a "septa-less and chamberless form similar to the protoconch" as the common ancestor of these two great divisions of the Tetrabranchiata; and possibly, as Hyatt suggests of the Cephalopoda, Pteropoda and Gastropoda (31). The protoconch represents the latest of the true embryonic stages, namely the phylembryo.

Succeeding this early stage are the stages of the shell proper.[1] In *Nautilus* the early nepionic portion of the shell, which includes the formation of the first three septa, is only slightly curved (cyrtoceraform). Up to the stage of the formation of the second septum, the shell is in fact nearly straight (orthorceraform). The first septum has an apically directed caecum, and the second septum an apically directed closed tube, the closed apical end of which fits into the caecum of the first septum. This tube is the beginning of the siphuncle. Since the tube fits closely into the caecum, the two together form a continuous tube, in which the apical end or bottom of the siphuncular tube forms a partition or septum, so that as Hyatt points out, the resemblance "of this early stage to the adult structures of *Diphragmoceras* becomes perfectly clear." (31)

In the later nepionic stages (i. e., after the formation of the third septum) the shell is rather sharply bent (the gyroceran curve), so that near the close of the first volution the whorl is brought back into contact with the apex of the conch. This manner of growth results in leaving an empty space or *umbilical perforation* between the two halves of the first volution. In the ancient coiled Nautiloidea there appears at the beginning of this (neanic) stage, when the whorls come into contact, a de-

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[1] The stages from this point on are termed by Hyatt (31), and following him by practically all paleobiologists at the present time, the *nepionic, neanic, ephebic* and *gerontic* stages; meaning respectively, the infantile, youthful, mature and old age stages of growth.

pression or groove in the dorsum of the whorl, where it rests against the venter of the preceding whorl. This is the *impressed zone*. In the modern *Nautilus*, however, this furrow or impressed zone begins in the early nepionic stage, *before the whorls have come into contact*. This occurs also in the nautilian shells of the Carboniferous, Jurassic, Cretaceous and Tertiary.

Of this truly remarkable feature of cephalopod development, Hyatt says: "When one ascends in the same genetic series to the more specialized nautilian involved shells this purely acquired character becomes, through the action of tachygenesis, forced back, appearing as a rule in the nepionic stage before the whorls touch. It is therefore, in these forms entirely independent of the mechanical cause, the pressure of one whorl upon another, which first originated it. One need only add that this configuration of the dorsum is never found in the adults of any ancient and normally uncoiled shells, so far as I know, nor so far as have been figured." (31)

Without reviewing any of the further interesting details of the ontogeny of *Nautilus*, enough has been said to make it evident that if there is any truth in recapitulation, the development of *Nautilus* would indicate (disregarding the protoconchal characters) an ancestral line that contained, first straight or slightly arched, then loosely coiled, and finally closely coiled shells, and that the earliest of these possessed a septate siphuncle. That the geological series of shells indicates the same thing every paleontologist knows perfectly well. The development of *Nautilus* also affords one of the most perfect illustrations of the law of tachygenesis, in the earlier inheritance of the impressed zone, known in the whole animal kingdom.

One further illustration, from the Cephalopoda, of the parallelism of ontogeny and phylogeny must suffice. This illustration is drawn from the genus *Placenticeras*, one of the complex Ammonites of the Cretaceous. The development of this genus has been beautifully worked out by Professor J. P. Smith (58). The species *P. pacificum* comes from the Chico formation of the Upper Cretaceous. The following account applies to the development of this species and is drawn from the paper by Smith, cited above.

The earliest shelled stage was probably passed before the animal was hatched. This is the protoconch or phylembryo. It is a smooth, oval, bulbous body, similar to that of all the later ammonites. It probably rep-

resents an "adaptive form, due to life in the egg, and does not represent any ancient ancestral genus, for none of the early cephalopods were shaped like this."

"With the formation of the first septum, the young ammonite has taken its place among the chambered cephalopods, and has become, for the time being, a nautiloid, although it is not possible . . . . to correlate it with any special genus. . . . . The first septum . . . . is nautilian in character, but the siphuncle begins inside the protoconch with a siphonal knob, or caecum, and the protoconch itself is calcareous. These are two characters that the nautiloids even to this day, have never yet acquired. . . . . We have in this stage ammonite characters pushed back by unequal acceleration [telescoping], until they occur contemporaneously with more *remote* ancestral characters."

There is no sign of an umbilical perforation as in the *Nautilus*, described above, a fact which again shows the degree of acceleration of these ammonites.

With the second septum the ammonite characters are assumed. The shell at this stage is "distinctly goniatitic," but also possesses characters, introduced by acceleration, that belong to later genera. The evidence indicating the goniatitic as well as later stages to be mentioned, is mainly the character of the suture lines. "At about five-eighths of a coil . . . . the larva has reached a stage correlative with the goniatites of the Upper Carboniferous." This stage is quickly passed, and the goniatitic characters are lost and characters transitional to the ammonite stage make their appearance. "At one and one-twelfth coils the shell is transitional from the glyphioceran stage to what resembles closely the genus *Nannites* of the Trias." In regard to this stage Smith says: "If it had not been said that this was a minute shell taken out of an older individual, any paleontologist would refer it without hesitation to the Glyphioceratidæ, and probably to . . . . *Pronannites*, of the Lower Carboniferous." This stage lasts about one-half revolution.

In the neanic stage, at one and seven-twelfths coils, the shell resembles very strongly *Cymbites*, or some related genus of the Lower Jurassic. The first signs of shell sculpture occur in this stage. In the next stage the sculpture becomes stronger, and the shell assumes a decidedly aegoceran appearance. From two up to two and one-quarter coils, the shell resembles in most respects the stock to which *Perisphinctes* belongs, and this is accordingly called the perisphinctes stage. During this

stage the sides of the shell become more flattened, and the abdominal shoulders squarer, the varices frequent, and strong intermediate ribs appear on the sides and abdomen.

In the next (*Cosmoceras*) stage "the ribs no longer cross the abdomen, but end in tubercles on the abdominal shoulders, forming well defined shoulder keels, with a furrow between them." Near the beginning of the fourth coil the ribs are reduced to mere faint undulations and fine sickle-shaped striae on the sides of the umbilicus, while the external tubercles become almost obsolete, forming mere notches on the continuous abdominal keels. Specific characters begin to appear here. This may be taken as the beginning of the *Hoplites* stage. The septa have not reached the complete development of the genus.

The umbilical knots begin at this stage, and growing stronger, become a characteristic feature of the adult *Placenticeras*. "*Placenticeras pacificum* at this stage is wholly unlike *P. californicum*, with which it is associated, being much more compressed and discoidal, with narrow abdomen, flatter sides, much less distinct sculpture, and narrower umbilicus, although in the earlier adolescent periods both species are very much alike." The shell passes from this stage by gradual changes into the adult *Placenticeras*.

Professor Smith's conclusions are of especial interest. He says: "The development of *Placenticeras* shows that it is possible, in spite of dogmatic assertions to the contrary, to decipher the race history of an animal in its individual ontogeny."[1]

[1] For further illustrations of recapitulation among the Cephalopoda, the student should consult the following papers : Branco, W., Beiträge zur Entwicklungsgeschichte der fossilen Cephalopoden, *Paleontographica,* vols. xxvi, xxvii, 1879, '80. Buckman, S. S., Monograph of the Inferior Oolite Ammonites, *Paleontographical Society,* 1887-'96. Hyatt, A., Paralellism of the individual and the order among tetrabranchiate Mollusks, *Mem. Bos. Soc. Nat. Hist.,* vol. i, 1866 ; Fossil cephalopods of the Museum of Comparative Zoology, *Bull. Mus. Comp. Zool.,* vol. iii, 1872 ; Genesis of the Arietidæ, *Smithsonian Contr. to Knowl.,* vol. xxvi, 1889 ; Phylogeny of an acquired characteristic, *Proc. Am. Phil. Soc.,* vol. xxxii ; Cephalopoda, in *Text Book of Paleontology* by Zittel (Eastman trans.), 1899. Hyatt, A., and Smith, J. P., Triassic cephalopod genera of North America, *U. S. Geol. Surv. Prof. Paper* No. 40, 1905. Karpinsky, A., Ueber die Ammoneien der Artinsk-Stufe, *Mem. Acad. Sci. Imp. St. Petersburg,* vol. xxxvii, No. 2, 1889. Neumayr, M., Die Ammoniten der Kreide und die Systematik der Ammonitiden, *Zeitschr. der Deutch. Geol. Ges.,* 1875 ; Ueber unvermittelt auftretende Cephalopodentypen im Jura Mittel-Europas, *Jahrb. d. K. K. Geol. Reichs. Wien,* vol. xxviii, 1878. Smith, J. P., The development of Glyphioceras and the phylogeny of the Glyphioceratidæ, *Proc. Calif. Acad. Sci.,* (3) *Geol.,* vol. i, 1897 ; The Development of Lytoceras and Phylloceras, *Ibid.,* 1898 ; Larval stages of Schloenbachia, *Jour. Morphology,* vol. xvi, 1899 ; The Carboniferous Ammonoids of America, Monog. U. S. G. S., No. xlii, 1903. Würtenburger. R., Studien über die Stammgeschichte der Ammoniten, Leipzic, 1880.

Pelecypoda.—The classic memoir of Jackson (32) on the phylogeny of the Pelecypoda brings together numerous illustrations of recapitulation among the members of this class of animals. Jackson's conclusions are well-known, and I shall therefore review them very briefly.

From a study of a large number of genera representing widely divergent members of the Pelecypoda, Jackson concludes that there is present throughout the group an embryonic shell, which he calls the "prodissoconch" (a term correlative with the term protoconch of the Cephalopoda and Gastropoda), and which is a simple bivalved, equivalve shell. At this (phylembryonic) stage of development there are two adductor muscles, even in genera in which the adult have only one adductor. That is, the prodissoconch is dimyarian even though the adult animal may be monomyarian. In the Aviculidæ and their allies (*Ostrea, Avicula, Perna, Pecten, Plicatula, Anomia*) the prodissoconch very closely resembles in form the primitive genus *Nucula.* The anatomical characters of the prodissoconch also bear out this resemblance. It is therefore inferred that some such type as *Nucula* is the primitive ancestor of the Aviculidæ, and possibly of the Pelecypoda. The paleontological and anatomical evidence supports this conclusion.

We have here, then, in the Aviculidæ and their allies, a group of monomyarians, some of them, as *Ostrea, Plicatula,* and *Anomia,* of very aberrant form, the representation in the ontogeny of a dimyarian stage, which, from all the evidence, actually characterized the adults of the ancestors of the group. Whether or not *Nucula* is the actual ancestor of this group of pelecypoda, it is quite certain that the earliest pelecypods were of the same general form as the prodissoconch, and that they were dimyarian.

In the same paper Jackson has shown in a masterly manner that the ostreaform shape of the shell, which characterizes many more or less widely separated genera of pelecypods, is due to "the mechanical conditions of direct cemented fixation." These ostreaform shells are very variously derived, and should, if there is anything in the theory of recapitulation, each show in the young stages, before the valves have become fixed, the distinctive adult characters of its particular ancestor. In this case we are relieved from the danger of arguing in a circle by the fact that the genetic relations of most of the forms are fairly well known from lines of evidence other than the ontogeny. The following specific cases cited by Jackson are of especial interest.

Mulleria lobata, a member of the Unionidæ, "is so remarkably like an oyster (in the adult) that it has been called the fresh-water oyster. In the monomyarian adult . . . . the shell is rough and irregular with a deep attached and flattish free valve, and a specimen in the Museum of Comparative Zoology is indistinguishable in shape from forms commonly found in *Ostrea virginiana*. . . . . The young shell of *Mulleria* . . . . is Anodon-shaped, equivalvular and dimyarian as described by authors."

Hinnites is another genus which has the ostreaform adult. "In the young it is free and pectiniform, but in the adult . . . . so close is the likeness to an oyster that in the synonomy of the genus it has been named *Ostrea* and *Ostracites*." In *Hinnites cortesi* of the Tertiary, in the neanic stage, the right valve is purely pectiniform. "It has the well-developed ears, deep byssal sinus, and an evenly plicated shell which at this stage is nearly or quite equivalvular." With the period of attachment a most marked change in the valves takes place and the adult becomes deeply concave (in the right attached valve) and highly ostreaform. The byssal notch is filled up and "completely wiped out of existence."

In genera such as *Ostrea* and *Plicatula*, where fixation takes place at the close of the prodissoconch stage, the succeeding stages give very little indication of the ancestry, owing to the extensive modification of the shell as soon as fixation takes place. According to Dall *Ostrea* is derived from the Pteriidæ.

Spondylus is another genus in which cementation has caused extensive modification of the valves in the adult. Fixation takes place at the close of the nepionic period. Therefore this genus may be expected to afford some evidence of recapitulation. The first nepionic stage of *Spondylus* is decidedly pectiniform. It has a long hinge-line and a deep byssal sinus. After fixation, in the first stages of irregular growth, the byssal notch is soldered over, and eradicated in a manner similar to *Hinnites*.

Another illustration of recapitulation among the Pelecypoda is the case of *Pecten* itself. Of this genus Jackson says: "In the development of the modern *Pecten* we find in the first stages of dissoconch growth a form of shell . . . . presenting characters which make it referable in ancestral origin to *Rhombopteria*, a member of the true Aviculidæ, later succeeded by a growth . . . . bearing marked features referable in origin to an ancestral genus *Pterinopecten*. . . . . Still later a stage

exists . . . . which is referable in its inherited form to *Aviculopecten*, and finally the true *Pecten* features characteristic of the adult . . . . are established. The geological sequence of these several groups is in the order indicated by the development of *Pecten*. We have, therefore, a clear case of the ontogeny of an individual illustrating the phylogeny of the group."

Gastropoda.—For studies of the Gastropoda in which growth stages have especially been taken into consideration we are indebted chiefly to Grabau (22, 23, 24, 25) and Burnett Smith (53, 54, 55, 56). My illustrations of recapitulation among the members of this class will be drawn, therefore, from the writings of these two authors.

It is commonly known that the apical whorl of the gastropod shell may differ materially from the succeeding portions of the shell (conch), being smooth and without ornament in cases where the conch is highly sculptured, or in some forms, as *Acmaea* and *Crepidula*, being coiled, although the adult shell is patelliform and non-coiled. To this apical whorl the name "protoconch" has come to be applied, a name which, as we have already seen, is also applied to the embryonic shell of the Cephalopoda. Grabau (22) has suggested the use of the name "protorteconch" in place of protoconch for the initial shell of the gastropods.

The protoconch of the existing Gastropoda is more variable than that of the Cephalopoda, as would be expected from the highly specialized nature of most of the extant representatives of the class. In most cases there is no definite line of demarkation between the protoconch and the conch, but in a few cases, as in *Fusus*, etc., the "end of the protoconch is strongly marked by the existence of a pronounced varix and an abrupt change of ornamentation." (22) "The early whorls of the protoconch . . . . are smooth rounded coils of the type found in adult *Natica*. . . . . In the majority of cases the initial whorl is minute, while the succeeding ones enlarge gradually and regularly. In some types the initial whorl is large and swollen. . . . . This type of protoconch has been termed 'bulbous' by Dall (19). The naticoid form of protoconch is in general umbilicated, and it is probable that at least the earlier portion of the protoconch is umbilicated in the majority of gastropods.

"From the characters of the initial whorls of the protoconch we may argue that the radicle of the coiled gatropods must have been a naticoid type with a well-marked umbilicus. Such a type is found in *Straparollina remota* Billings, one of the earliest coiled gastropods of the Etcheminian

or Lower Cambrian of the Atlantic border province of North America. That it is not the most primitive type of gastropod is suggested by the consideration that the earliest stage . . . . of the protoconch is not coiled, but rather cap-shaped like modern *Patella*. Such primitive types are found in Lower Cambrian species which have variously been referred to *Platyceras*, *Scenella*, or *Stenotheca*, owing to the want of sufficient characteristics to define their exact relations." (22.)

From the above it appears that the early protoconch stages indicate an ancestor of the simple, smooth shelled, umbilicated type exemplified by *Straparollina*, and that this is actually the only type of coiled gastropod characteristic of the basal Cambrian. It is also likely from paleontological evidence that the very earliest type of gastropod possessed a conical or cornucopia-shaped shell of the *Scenella* type.[1] Such an ancestry is, according to Grabau, suggested by the cap-shaped earliest stage of the protoconch.[2]

One of the most completely worked-out cases of recapitulation among Gastropoda that has come to my knowledge is that of the races of *Athleta petrosa* Con. and its allies. The phylogeny of this group of gastropods has been very fully studied by Burnett Smith (54), from whose paper the following account is drawn.

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[1] Sardeson (50) suggests that the gastropod ancestor was an "asymmetrical long conical shell" of the pteropod type. He may be right, but even so, I do not see that his conclusion would in the least invalidate the conclusions of Grabau in regard to the phylogenetic significance of the protoconch, although Sardeson seems to think so. Grabau says very plainly that the coiled shell is probably not the most primitive type of shell, and he points out the fact (quoted above) that the initial portion of the protoconch is cap-shaped and may indicate some such remote ancestor as the Cambrian forms referred to the genera *Platyceras*, *Stenotheca*, and *Scenella*. Whether this patelliform ancestor was in turn derived from a long conical shell, or whether on the other hand the coiled type of shell was derived directly from the "long conical" shell without the mediation of a patelliform ancestor, does not materially affect the conclusions that at a very remote time a coiled gastropod radicle was established from which practically all modern gastropods were derived. To my mind the conclusion that the ultimate ancestor of the Gastropoda was a "long conical" shell is by no means established.

[2] Burnett Smith (55) concludes from a study of the Tertiary species of the genus *Athleta* that "we can say for this restricted normal group at least that the apex is not only a variable feature, but the most variable feature which the shells furnish." In a footnote he says "The author is thoroughly convinced that the features of the apex must be used in classification with great caution." The variations which he cites in this and other papers (54, 55, 56) seem to be chiefly in the size of the protoconch, and the degree to which acceleration has caused conchal characters to appear in the later protoconchal stages. His caution, however, in regard to the classificatory value of the protoconch, should put students of the gastropods on their guard against a too free use of this portion of the shell in the establishing of genera.

The species under consideration occur in the Gulf Eocene, extending nearly throughout it. They have heretofore been referred to the genus *Volutilithes*, but are placed by Smith (55) in the genus *Athleta*. Smith states that the material at his disposal was very complete, and enabled him to study large series of individuals, very carefully collected with reference to horizon. The stratigraphy of the formations from which they came is also well understood. These favorable conditions of study, it may be remarked, are especially important in the present connection, because they enabled Smith to trace out the evolution of the forms practically continuously from zone to zone, without being chiefly dependent on ontogeny for indications of their relationships. Another fortunate circumstance is the fact that this author is disposed to use the evidence from ontogeny with the utmost discretion, everywhere checking it by an appeal to the morphological and geological series.

In the forms under consideration, the first two or three whorls are smooth and rounded, constituting the smooth or protoconchal stage. "The first ornamental feature to appear on the smooth, rounded whorl is the transverse rib, that is, a slight elevation of the whorl which runs across it from suture to suture. These early ribs are invariably curved slightly, and each one is simple and uniform from suture to suture. The curved ribs persist as a rule for about a quarter or a half of a whorl, or even for a much less space. . . . . The curved rib stage . . . . has been found in every species and race dealt with in this paper. The curved ribs, after about one-third of a whorl, change abruptly into the straight ribs of what has been designated the cancellated stage."

"The cancellated condition is found more or less well developed in all the different races. In the primitive races it may persist as a constant feature to the end of the individual's life; but in most forms it covers only a few whorls and is more variable than the preceding curved rib stage." The end of the cancellated stage is much less definite than the beginning. It is followed by the "spiny stage." In this stage the shoulder tubercle is sharp and spine-like. Other tubercles have disappeared, and this portion of the shell is therefore no longer cancellated. Succeeding the spiny stage, there may be a senile stage.

In the base of the Eocene at Matthew's Landing, Alabama, occurs a species, *Athleta limopsis*, which from its primitive characters, and its position at the base of the Eocene, Smith regards as the ancestor of the races and species which he deals with in his paper. This form presents

no stages later than the cancellated stage. There is also very little individual variation. Associated with *A. limopsis* is the species *A. rugatus*. In its earlier stages this species very closely resembles *A. limopsis*, but "differs radically . . . . from that form with the progress of its ontogeny." In its later whorls it presents evidence, though not extreme, of senility. It has no spiny stage.

The next species *A. petrosa*, represents an assemblage of races connected by many intergrading forms. These races range upward from the Nanfalia beds to the Jackson beds of the Eocene. Several of them are senile races, and in the adult strikingly different from the ancestral form, *A. limopsis*. Smith says, however, that the young of all the races "are remarkably uniform and constant. The early whorls indicate clearly that they are all descended from a cancelated ancestor, and bear a strong resemblance . . . . to the characters of *A. limopsis*." Some of the senile races of *petrosa* are profoundly modified in the adult, as for example, the Hatchetigbee race, derived from the main stock through the Bell's Landing and Wood's Bluff races. Yet their derivation from the main stock is shown by intermediate forms, and the young of the terminal races greatly resemble the ancestral form. In the Jackson race, which is the terminal member of the main stock, the last two whorls are spiny, and the last whorl shows some senile characters at its close. "This race shows a regular and even ontogeny." Acceleration has carried the curved rib stage back to the beginning of the third whorl, whereas in the ancestral *A. limopsis* this stage begins near the close of the fourth whorl.

Smith has graphically expressed the main developmental and phylogenetic changes in the following diagram:

	1	2	3	4	5	6	7	8	9	10	11	12
A. limopsis. Matthew's Landing race..	...	...	A	B	...	...	...	C	...	...	...	Lower Eocene.
A. petrosa. Gregg's Landing race....	...	A	...	B	...	C	...	...	D and I	D and I	...	E Slight.
A. petrosa. Jackson race	A	...	B	...	C	...	...	...	D	D and E	...	E never extreme. Upper Eocene.

In the above diagram the figures across the top stand for the number of the whorl of the shell, and the letters indicate the different ontogenetic stages as follows:

> A—Smooth stage.
> B—Curved rib stage.
> C—Cancellated stage.
> D—Spiny stage.
> E—Senile stage.
> I—Individual variation.

The acceleration of the Jackson race is beautifully brought out in this diagram, and as its correlative, the recapitulation in the earlier ontogeny of the later races, of the adult characters of the ancestral race. The individual variations may occur on any part of the shell, but usually follow stage C.[1]

Brachiopoda.—Among the members of this class there is a wealth of illustrations of recapitulation. I can only select a few cases that have been worked out in such a way that the relationships of the forms are indicated by the morphological and geological series as well as by the ontogeny. The pioneer student of the correlation of ontogeny and phylogeny among the brachiopods was Beecher, whose refined researches in paleobiology have never been excelled and rarely equaled.

The developing brachiopod, in the later embryonic stages, secretes in the mantle on opposite sides of the body two shell plates, which by peripheral growth ultimately meet at the edges and form the initial shelly investment of the animal. This initial shell to which Beecher has given the name "protegulum" (6) is of very simple form, consisting substantially of two convex plates of semicircular plan, gaping at the posterior straight edges. Through this gap between the two valves the pedicle (organ of attachment) projects. At first the pedicle occupies the full width of the valves, but subsequent peripheral growth of the shell with-

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[1] For additional studies of the gastropoda from the developmental standpoint see the following: Koken, E., Ueber der Gastropoden vom Cambrium bis zur Trias., *Jahrb. für Mineral. Geol. u. Pal.*, 1889, Beil. Bd. vi. Linden, Gräfen M. von, Die Entwicklung der Skulptur und der Zeichnung bei den Gehausschnecken des Meeres, *Zeitschr. Wiss. Zool.*, vol. lxi. 1896. Grabau, A. W., Studies of Gastropoda II, Fulgar and Sycotypus, *Am. Nat.*, vol. xxxvii, 1903; Phylogeny of Fusus and its allies, *Smithsonian Miscell. Coll.*, vol. xliv, 1904; Studies of Gastropoda III on Orthogenetic variation, *Am. Nat.*, vol. xli, 1907. Smith, Burnett, Phylogeny of the species of Fulgur with remarks on an abnormal specimen of Fulgur canaliculatum and sexual dimorphism in Fulgur carica, *Proc. Acad. Nat. Sci. Phila.*, vol. liv, 1902; Senility among Gastropods, *Proc. Acad. Nat. Sci. Phila.*, vol. lvii, 1905; Phylogeny of the races of Volutilithes petrosus, *Proc. Acad. Nat. Sci. Phila.*, March, 1906; A new species of Athleta and a note on the morphology of Athleta petrosa, *Proc. Acad. Nat. Sci. Phila.*, May, 1907; A contribution to the morphology of Pyrula, *Proc. Acad. Nat. Sci. Phila.*, May, 1907.

out corresponding enlargement of the pedicle, leaves the latter restricted
to a notch (delthyrium) in the posterior margins of the valves, providing
the peripheral growth is about equal on all anterior and lateral radii.
If the shell growth is greater in the anterior direction, the shell becomes
pointed, the pedicle (posterior) end remaining of about the original
width. If the shell growth is mainly in the lateral directions, the shell
becomes wide, with a long straight hinge, of which the pedicle opening
forms a very small proportion. Whatever may be the later growth of the
shell, all the earlier stages are preserved, except in cases where the beaks
are injured or resorbed by the encroachment of the pedicle in adult and
senile stages. The growth of the shell is entirely by additions at the mar-
gins or on the inner surface. It follows that the protegulum may in ex-
ceptionally well preserved material be seen intact at the beaks of the
adult shell. It is often seen at the apices of young shells.

Searching for the phylogenetic significance of the protegulum, Beecher
(6) ascertained that certain of the earliest known brachiopods approxi-
mate very closely in form to the protegulum, and he selected the genus
Paterina (*Iphidea*) as the radicle of the class. It has since been shown
that *Paterina* is not the most primitive known brachiopod.[1] It is still
true, however, that the most primitive brachiopods known are of the
same general form and type as *Paterina*, in fact they approximate more
closely, if anything, than that genus, to the form of the protegulum. It
may be very safely concluded, therefore, from the geological evidence,
that the primitive brachiopod was actually of the type indicated by the
protegulum.

Beecher says of *Paterina:* "In mature specimens, all lines of growth,
from the nucleal shell to the margin, are unvaryingly parallel and con-
centric, terminating abruptly at the cardinal line. In other words, no
changes occur in the outlines or proportions of the shell during growth,
through the nepionic and neanic stages up to and including the com-
pleted ephebic condition. The resemblance of this form to the protegulum
of other brachiopods is very marked and significant, as it represents a
mature type having only the common embryonal features of other genera."

Among the Brachiopoda, as among the Pelecypoda there are a number
of forms in which the condition of very close fixation or of burrowing has

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[1] Walcott (62) seems to reserve this distinction for his genus *Rustella*. Pater-
ina is by him made a subgenus of the genus *Micromitra*. These forms are all
placed in the superfamily *Rustellacea.*

given rise to extremely aberrant types. One of the most extreme of these
types is the genus *Proboscidella*. The adults of this genus bear a very
marked resemblance to the Pelecypod genus *Aspergillum*. In the early
neanic stages *Proboscidella* resembles an ordinary *Productus*, from which
genus the type is known to have descended. *Orbiculoidea* is a genus
originating in the Ordovician, and extending through the Mesozoic. The
first stage is paterina-like, the second resembles *Obolella*, the third is like
Schizocrania, and adult growth brings in the characters of *Orbiculoidea*.
The geological order of these genera is the same as the ontogenetic order
of *Orbiculoidea*.

Of *Orbiculoidea* and its allies Beecher (7) says: "The early stages
of Paleozoic *Orbiculoidea* have straight hinge-lines and marginal beaks,
and in the adult stages of the shell the beaks are usually subcentral and
the growth holoperipheral. This adult discinoid form, which originated
and was acquired, through the conditions of fixation of the animals, has
been accelerated in the recent *Discinisca* so that it appears in a free-swim-
ming larval stage. Thus a character acquired in adolescent and adult
stages in a Paleozoic species, through the mechanical conditions of growth,
appears by acceleration in the larval stages of later forms before the as-
sumption of the condition of fixation which first produced this character."

In the higher genera of the Terebratellidæ, the ontogeny recapitulates
the phylogeny with remarkable fidelity, as pointed out by Beecher (7).
This example has become classic, so that it is scarcely necessary to re-
peat the details. I shall give Beecher's conclusions in his own words.
He says: "In each line of progression [the austral and boreal subfami-
lies] in the Terebratellidæ, the acceleration of the period of reproduction,
by the influence of environment, threw off genera which do 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 representa-
tive in a lower genus. Moreover the lower genera are not merely equiva-
lent to or in exact parallelism with, the early stages of the higher, but
they express a permanent type of structure, as far as these genera are
concerned, and after reaching maturity do not show a tendency to at-
tain higher phases of development, but thicken the shell and cardinal
process, absorb the deltidial plates, and exhibit all the evidences of
senility."

Raymond (46) has pointed out a number of interesting cases of recapitulation. The very common and well-known Devonian Spirifer, *S. mucronatus*, has the cardinal extremities in the adult very acute (mucronate), sometimes, indeed, drawn out into needle-like points; while the number of plications may be thirty or more. In the neanic stage these transversely elongated spirifers pass through forms corresponding to the adults of certain Niagara species. The adult of *S. crispus*, corresponds very closely in shape, number of plications, and shell index with these young specimens of *S. mucronatus*.

Shimer and Grabau (51) have shown that in the upper part of the Hamilton series of Thedford, Ontario, there occurs a variety of *Spirifer mucronatus*, which though not mucronate at all in the adult, is "extremely mucronate" in the neanic stage. At this stage also there is evidence of the median plication of the sinus, another charactertistic of the adult of the normal *S. mucronatus*. In the adult of the Thedford variety this median plication has disappeared. The geological and morphological evidence of the derivation of this form of *S. mucronatus* is complete.

I have pointed out an exactly similar case in the variety *senex* of *Platystrophia acutilirata* (16). This variety occurs in the upper part of the Whitewater division of the Richmond series of Indiana and Ohio. *Platystrophia acutilirata*, as is well known, is very mucronate in the adult, resembling in its general outline, *Spirifer mucronatus*. It was in fact at first referred to the genus *Delthyris (Spirifer)*. The normal form is shown by an unusually closely graded series of intermediate forms to be descended from *P. laticosta*, and it repeats the adult characters of the latter very faithfully in its late neanic stage, becoming always more mucronate as development proceeds. The upper Whitewater form, var. *senex*, frequently has entirely lost, in the adult stages, the acute angulation of the cardinal extremities, so that the lateral and cardinal edges make a right, or nearly a right angle. In the young (neanic) stages of *P. senex*, however, the shell is decidedly mucronate, so that these young shells exactly resemble the normal *Platystrophia acutilirata* of the lower Whitewater and Liberty formations. *P. senex*, it may be remarked, is a well defined form, and its derivation from *P. acutilirata* is beyond question, since it is connected with the latter by every gradation.

Another interesting case of recapitulation among the brachiopods has been worked out with great care by Mr. F. C. Greene (27). In this case also no pains was spared to ascertain the relationships of the various

forms by tracing them continuously from zone to zone, and by a comparison of the morphological characters of the adults. The group studied by Greene is that of *Chonetes granulifer*, from the Upper Carboniferous rocks of Kansas. Here the forms from the higher zones repeat in their ontogeny the characters of forms from the lower zones with great fidelity. The very young stages also recall very forcibly the species of *Chonetes* from the Devonian. *Chonetes granulifer* is also very interesting from the fact that the first hinge-spines appear very much earlier in the ontogeny than is the case in the Devonian species studied by Raymond (46), therefore showing a considerable degree of acceleration of this character during the interval from the Devonian to the Upper Carboniferous.

Other interesting cases of recapitulation among brachiopods have been pointed out by Beecher and Schuchert (12) in the development of the brachial apparatus in *Dielasma* and *Zygospira*.[1]

Trilobita.—Studies of the early stages of the development of trilobites have been published by Barrande (3, 4), Walcott (59, 60, 61), Beecher (8, 9), Matthew (39, 40, 41) and others, but for indication of the correlation of the ontogeny and the phylogeny in this class we are almost entirely indebted to Beecher. In his papers on "Larval Stages of Trilobites" (8), and a "Natural Classification of the Trilobites" (9), he has not only pointed out the remarkable way in which characters are recapitulated in this class, but has also proposed what is probably to be regarded as the most perfect example of a phylogenetic classification of a group of organisms, in existence.

The earliest developmental stage of trilobites that has ever been found (barring supposed trilobite eggs) is the larval stage or "protaspis," as it is called by Beecher (8). The protaspis is a minute body of ovate or discoid shape, and about a millimeter in length. This larval stage has

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[1] For additional examples of recapitulation among the brachiopods see the following: Beecher, C. E., Studies in Evolution (a series of collected papers), Scribners, 1901. Beecher, C. E., and Clarke, J. M., The Development of some Silurian Brachiopoda, *Mem. N. Y. State Mus.,* No. I, 1889. Beecher, C. E., and Schuchert, C., Development of the shell and brachial supports in Dielasma and Zygospira, *Proc. Biol. Soc. Washington,* vol. viii, 1893. Cumings, E. R., The morphogenesis of Platystrophia; A study of the Evolution of a Paleozoic Brachiopod, *Am. Jour. Sci.,* vol. xv, 1903. Raymond, P. E., The developmental change in some common Devonian brachiopods, *Am. Jour. Sci.,* vol. xvii, 1904. Greene, F. C., The development of the Carboniferous brachiopod Chonetes granulifer. Owen, *Jour. Geol.,* vol. xvi, 1908. Buckman, S. S., Homeomorphy among Jurassic Brachiopoda, *Proc. Cotteswold Nat. Field Club,* vol. xii, 1901.

been seen in a sufficiently representative series of genera to make it reasonably certain that it is the common larval type among the trilobites.

It is pretty well established that the eye of crustaceans has migrated from the ventral to the dorsal surface of the cephalon. At an intermediate stage in this process the eyes would appear on the margins of the cephalon. If this has been the history of the eye, the most primitive larvae should show no evidence of eyes on the dorsal surface, and since the eye is on the inner margin of the free cheek, there should be no evidence of the free cheek. This is exactly the case in the youngest larvae of *Ptychoparia, Solenopleura* and *Liostracus,* "which are the most primitive genera whose protaspis is known. The eye-line is present in the later larval and adolescent stages of these genera, and persists to the adult condition. In *Sao* it has been pushed forward to the earliest protaspis, and is also found in the two known larval stages of *Triarthrus. Sao* retains the eye-line throughout life, but in *Triarthrus* the adult has no traces of it, and none of the higher and later genera studied has an eye-line at any stage of development." This character according to Matthews, is characteristic of the Cambrian trilobites. In its phylogenesis in later trilobites it disappears first from the adult stages, and is finally lost from the entire ontogeny. The eyes appear on the margin of the cephalon in the last larval stage of *Ptychoparia, Solenopleura, Liostracus, Sao,* and *Triarthrus.* In the later genera the eyes are present "in all the protaspis stages, and persist to the mature, or ephebic condition, moving in from the margin to near the sides of the glabella."

According to Beecher (8) "A number of genera present adult characters which agree closely with some of the larval features [of later genera]. The main features of the cephalon in the simple protaspis forms of *Solenopleura, Liostracus,* and *Ptychoparia* are retained to maturity in such genera as *Carausia* and *Acontheus,* which have the glabella expanded in front, joining and forming the anterior margin. They are also without eyes or eye-line. *Ctenocephalus* retains the archaic glabella to maturity, and likewise shows eye-lines and the beginnings of the free cheeks (larval *Sao*). *Conocoryphe* and *Ptychoparia* are still further advanced in having the glabella rounded in front, and terminated within the margin (larva of *Triarthrus).* These facts and others of a similar nature show that there are characters appearing in the adults of later and higher genera, which successively make their appearance in the protaspis stage, sometimes to the exclusion or modification of structures present in the most primitive

larvae. Thus the larvae of *Dalmanites* and *Proetus*, with their prominent eyes, and glabella distinctly terminated and rounded in front, have characters which do not appear in the larval stages of ancient genera, but which may appear in their adult stages. Evidently such modifications have been acquired by the action of the law of earlier inheritance or tachygenesis."

Bryozoa.—My studies (17, 18) were the first to show that there is in the bryozoan colony a definite recapitulation of ancestral characters, and that in this particular the colony behaves as an individual. This same fact was very clearly pointed out by Ruedemann (47) two years earlier in the Graptolites, and I take pleasure in quoting his very explicit statement. He says: "Furthermore the fact that the thecæ within the same colony show a gradation from phylogenetically older to younger forms, and therefore analogous to the organ of a growing individual, pass through ancestral stages, as, e. g., do the septa of a cephalopod shell, demonstrates how closely the zooids of this colony were united into one organism, and that practically they were more the organs of an individual than the component of a colony. . . . . . If the graptolites so closely approached the morphologic value of an individual, it may be expected that, like an individual, the whole colony has its ontogeny and repassed ancestral stages."

My studies, referred to above, brought out the fact that the bryozoan colony begins as a minute hemispherical body, the "protœcium" which is the earliest exoskeletal stage of the first individual of the colony. This protœcium (basal disc) is very conspicuous in the Cyclostomata, and also in the ancient Cryptostomata (as shown in *Fenestella*).[1] It can not be definitely asserted that the protœcium corresponds to any ancestral bryozoan, but the marked resemblance of the zoœcia of some of the ancient *Stomatopora* of the Ordovician to the protœcium is at least very suggestive.

The ancestrula, or first complete individual of the colony, has long been known to present characters more similar to those of ancestral forms

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[1] I first used the term protœcium as the designation of the first individual of the colony, and in this sense it would be exactly equivalent to the term ancestrula of Jullien. In a later paper (18) I restricted the term to the basal disc (of Barrois) which is the calicified wall of the metamorphosed and histolyzed embryo in its earliest sedentary stage. Out of this basal disc the first normal individual arises by a process stirctly analogous to budding. In this sense, therefore, the term protœcium is exactly correlative with the terms protegulum, protoconch, prodissoconch, etc.

than the characters of the ephebastic zoœcia (see Nitsche 44, and Pergens 45). I have succeeded in finding evidence (18) that this is true to a notable extent in the ancient *Fenestella*, where the tubular ancestrula bears a striking resemblance to the simple tubular ephebastic zoœcia of the Cyclostomata, from which group there is every reason to believe the Cryptostomata are descended.

It is also pointed out by Nitsche and Pergens *(loc. cit.)* that the earlier budding habit of the colony is similar to ancestral types. In my own studies I was able to show that the early budding habit is very uniform in the most diverse types of Bryozoa, and that it corresponds to the budding habit that prevails throughout the astogeny of the reptant stomatoporas.

In *Fenestella* my studies indicate that the earlier individuals (nepiastic) of the colony are very different from the adult (ephebastic) individuals and are strikingly similar to the ephebastic individuals of certain Cyclostomata that are on morphological grounds, as pointed out by Ulrich (63), probably ancestral. And again, the early neanastic zoœcia of the Devonian fenestellas studied are almost exactly like to the ephebastic zoœcia of the fenestellas of the Niagara series. Unpublished studies indicate that in the Fenestellas of the Upper Carboniferous the neanastic stage is more abbreviated, and that the adult type of zoœcia follows more closely upon the nepionic type.

Dr. Lang of the British Museum has published very interesting studies of the Stomatoporas and Eleids of the Mesozoic (35, 36, 37), and has come independently to exactly the same conclusions as the writer in regard to the development of the colony, and the relations of astogeny and phylogeny among the Bryozoa. He says (35), "The development of the colony is comparable with and follows the same laws as the development of the individual." And again: "Among Jurassic forms of *Stomatopora* and *Proboscina* it has been found that when any given character, such, for instance, as the ratio of the length of the zoœcium to its breadth, is followed from the first zoœcium to the last, that it has a progressive development, or anagenesis, reaches a maximum, or acme, and often may be seen to have a retrogressive development, or katagenesis, in the ultimate branches of the zoarium."

Lang has paid especial attention to the manner of branching in Jurassic stomatoporas. The nearly universal method of branching in the Jurassic members of this group is by dichotomy. This according to Lang may

be by one or other of three types as follows: In type I the two zoœcia are separate throughout their entire length, only touching at their bases. In type II they are contiguous throughout their length, and in the intermediate type they are contiguous for part of their length. To a large extent correlated with these types of dichotomy is the angle of divergence of the branches.

In all the Jurassic stomatoporas and in a few proboscinas the first dichotomy is according to type I, and at a very wide angle (180°). The second dichotomy, in the majority of cases, is also according to type I, with an angle of 120°. The next is commonly only 90°, the next 60°, and the next 45°, all according to type I. "In primitive [Jurassic] forms the branching never gets beyond type I with a small angle. In the majority of forms, however, sooner or later the intermediate type of branching comes in, and in a great many forms this type is the final one. In a few cases of *Stomatopora*, and in all *Proboscina*, type II is at some time or other reached, and remains the ultimate form of branching of the zoarium. This sequence namely, Type I—Intermediate type—Type II, is invariably followed." (35).

In primitive *Proboscina* (a genus derived from *Stomatopora*) the first dichotomies are according to type I. "In the typical forms of *Proboscina* the early stages have been so condensed according to the law of acceleration (Tachygenesis), that the first dichotomy is formed on type II. . . . . In the more advanced types of *Proboscina* . . . . the arrangement of peristomes is irregular from the first." This is the typical arrangement for *Berenicea*, a derived genus of which *Stomatopora* and *Proboscina* are the first two terms. It is worthy of notice that while in the Jurassic forms of *Stomatopora* type II is not very common, it is extremely common in the Cretaceous forms.[1]

Graptolites.—The beautiful researches of Ruedemann in this group have shown us, as pointed out above, that the graptolite colony closely approaches the morphologic value of an individual, and that, like the individual, it presents definite ontogenetic (astogenetic) stages. Ruedemann (47) applies to the colonial development the terminology proposed by

[1] For studies in the zoarial development of Bryozoa see Cumings, E. R., The development of some Paleozoic Bryozoa, *Am. Jour. Sci.*, vol. xvii, 1904; Development of Fenestella, *Am. Jour. Sci.*, vol xx, 1905.   Lang, W. D., The Jurassic forms of the 'genera' Stomatopora and Proboscina, *Geol. Mag.*, Dec. v, vol. i, 1904; The Reptant Eleid Polyzoa, *Geol. Mag.* Dec. v, vol. iii, 1906; Stomatopora antiqua, Haime, and its related Liassic forms, *Geol. Mag.*, Dec. v, vol. ii. 1905.

Hyatt (31). In a later paper, however, he approves the terminology introduced by me, and proposes to call the development of the colony the astogeny (48).

The embryonic stage of the graptolites is represented by the initial portion of the sicula (first zooid), according to Ruedemann; and Holm (29) asserts that the more pointed end of the sicula "corresponds to the original chitinous covering of the free zooid germ or embryo." This initial part of the sicula, according to Ruedemann, holds a position similar to the protoconch of the cephalopod shell.

In part I of his splendid monograph of the Graptolites (48) of New York, at page 530, Ruedemann says: "It has been pointed out in a former publication that not only did there exist in the graptolites ontogenetic growth stages in the development of the individual zooids, ... *but the rhabdosomes in toto and in their parts, the branches, seem also to pass through stages which suggest phylogenetically preceding forms.*"

Of the various ways in which these astogenetic stages express themselves, Ruedemann mentions the following: "The original direction of growth of the branches of the Dichograptidæ has been in the approximate continuation of the sicula, i. e., an ascending erect position as long as the rhabdosomes were sessile, on the ground. These became pendant when the graptolites attached themselves in a suspended position to seaweeds, as numerous hydroids do today. To restore to the zooids their original . . . . erect position, the branches began now to recurve . . . . [becoming progressively horizontal, reflexed, reclined and recumbent] . . . . We find now in the majority of the Dichograptidæ with the above cited growth directions of the branches, that the latter still retain their original dependent direction, in the proximal parts in some species . . . . while in others by the law of acceleration, the dependent proximal direction has already changed into a horizontal one . . . . the change in direction becoming progressively more abrupt as the final direction of the branches becomes reclined . . . . or recumbent. . . . . The branches pass hence, in their development, through different directions representing ontogenetic stages that repeat stations in their phylogenetic development." (48.)

An analogous fact is found in the character of the thecæ. "A comparison of the form of the thecæ of the youngest dichograptid genera . . . . with that of the older and presumably phylogenetically preced-

ing genera . . . . shows that in general the older genera have the more tubular, simpler thecæ, with the less protected apertural margins. It is, hence, apparent that the stolonal or earlier thecæ of the rhabdosomes represent indeed the older types of thecal form." (48.)

Other Classes.—The case of the larva of *Antedon* has already been referred to. As pointed out by Bather (1), the stem ossicles of the larval *Antedon* are of a complex and specialized type, and in a general way resemble the stem ossicles of the Bourgueticrinidæ of the Upper Cretaceous. It is held by Bather that the structures of the adult ancestors have been pushed back by acceleration to the larval stages of the existing *Antedon*.

Recapitulation is also shown in the anal plate of *Antedon*. The anal plate appears between two of the radials and on the same level with them. Subsequently it is lifted out from between the radials, and the latter close beneath it. Still later the anal plate is resorbed entirely. That this is the recapitulation of an adult character and not of a larval character, as contended by Hurst, is shown by the fact that the oldest crinoids do not possess the anal plate at all. It appears from paleontological evidence that this plate first appeared above the level of the radials, that it gradually sank down between the two posterior radials, and that at a far later period (at about the close of the Paleozoic) it gradually passed upward again as it does in *Antedon*, and eventually disappeared.

Jackson has shown that there is good evidence of recapitulation among the fossil echinoids (33). In most regions of the echinoid the development is obscured by the more or less extensive resorption, but the plates of the corona may show by their position and number, the course of development. Jackson holds that the introduction of columns of plates, both interambulacral, and ambulacral, in *Melonites*, etc., indicates the stages of growth through which the individual has passed in its development. He shows that two columns of ambulacral plates "may be accepted as the usual characteristic of the whole class, which finds its representative in the majority of the adults, in nearly all young, and in the adult of the simplest and oldest known type, *Bothriocidaris*."

Interambulacral areas originate ventrally in a single plate. Only one genus is known, however, that has a single row of plates in the adult, namely *Bothriocidaris*. This is the simplest known and "perhaps the simplest conceivable echinoid."

In *Goniocidaris* the interambulacral plates of the adult are approximately hexagonal in form instead of pentagonal. "The relative form of the plates in young *Goniocidaris* is almost exactly the same as in the primitive type, *Bothriocidaris*."

"The early stage in which we find a single interambulacral plate, together with two ambulacral plates, in each area is so important that it is desirable to give it a name, the protechinus stage. The protechinus is an early stage in developing Echini, belonging to the phylembryonic period, in which the essential features of the echinoid structure are first evinced. . . . . This protechinoid stage of Echinoderms is comparable as a stage in growth to a similar stage which is expressed in the protegulum of brachiopods, the protoconch of cephalous mollusks, the prodissoconch of pelecypods, and the protaspis of trilobites." (33.)

Miss Smith (Mrs. Alexander Shannon) has shown very conclusively the exact resemblance of the form of the young *Pentremites conoideus* to the adult *Codaster* (52). In *Codaster* the conical form, narrowest at the base and enlarging upward, is maintained throughout life. In *Pentremites* only the early stages of growth have this form, while the adult is broadest at the base and narrowest at the top.

This evidence from development would, according to the theory of recapitulation, indicate that *Codaster* stands in an ancestral relation to *Pentremites*, and it is therefore of importance to the theory that Bather (2) from other evidence has independently reached the same conclusion as Miss Smith in regard to the relationship of the two forms.[1]

Among corals Beecher (5) has worked out the development of *Pleurodictyum lenticulare* and concludes that the first neanic stage, in the manner of growth and the structure of the corallum, is very suggestive of *Aulopora*, and should be given considerable significance." Girty (21) comes to the same conclusion from a study of *Favosites forbesi*, etc.

Bernard (14) has shown that the coral colony in similar fashion to the bryozoan colony and the graptolite colony behaves as an individual. In another paper (13) he has recognized as the first growth stage of the

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[1] Bather's conclusion was published in 1900, and Miss Smith's paper in 1906. The latter, however, was not aware of Bather's views as to the relationships of these two forms, so that the conclusions of the two workers, arrived at independently and from different lines of evidence are all the more important and convincing. Bather says in a review of Miss Smith's paper that he considers Pentremites as the "extreme link in the series *Codaster—Phaenoschisma—Cryptoschisma—Orophocrinus—Pentremitidea—Pentremites*."

coral skeleton the "prototheka," or basal cup of the first individual of the colony.[1]

Lang (38) has written a very suggestive paper on growth stages of British species of corals, in which he points out the fact that the ontogenetic stages are repeated in each rejuvenescence (branching?), and suggests that we have here an example of localized stages in development (see Jackson 34). It may be remarked at this point that Ruedemann has also detected localized stages in graptolites (47, 48), and Lang in Bryozoa (36). Lang also, in the paper on corals, concludes that there is recapitulation in the coral genera studied by him, of ancestral characters, and he gives a table illustrating this.[2]

Summary.—Paleontologists almost universally accept the theory of recapitulation. Its chief critics have been embryologists. The reason for the difference in attitude is probably to be sought in the fact that the former ordinarily compare epembryonic stages with adult characters of geologically older species, while the latter too often compare embryonic stages with the adult stages of existing species. It is also to be noted that in recapitulation we have to do with morphological and not with physiological characters, and that the row of cells from the egg to the adult may be morphologically the same in two organisms, while being at the same time physiologically different. Until it can be shown that two organisms morphologically different in the adult must of necessity be morphologically different at all stages, the argument of Montgomery, Hurst and others proves nothing.

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[1] The term *prototheka* was proposed simultaneously (January, 1904) by Bernard and myself for the earliest skeletal structure of the coral colony. We have used it, however, in a slightly different sense. Bernard applies it not only to the first individual of the colony, but also to the basal plates or cups of later individuals. I intended to restrict it to the basal cup of the first individual. The references are as follows : Bernard. H. M., The prototheka of the Madreporaria, with special reference to the genera Calostylis, Linds., and Mosleya, Quelch. *Ann. Mag. Nat. Hist.,* Ser. 7, vol. xiii, Jan. 1904. Cumings, E. R., The development of some Paleozoic Bryozoa. *Am. Jour. Sci.,* vol. xvii, Jan., 1904 (footnote, p. 74).

[2] This so-called rejuvenescence in corals appears to be a species of budding, in which the bud is directly superimposed upon the parent. It is fission occurring in a horizontal plane. as suggested by Bernard (14), and the new skeleton is in direct continuity with the old. This is the same idea exactly as that advanced by Ulrich some years ago (63) to account for the diaphragms of the Bryozoa Trepostomata. In the case of the Trepostomata the zoœcium is frequently operculate (ex. *Callopora*). and there is good evidence that the bud grows up through the operculum hence leaving it behind as the floor of the new individual.

In the Cephalopoda, Pelecypoda, Gastropoda, Brachiopoda, Trilobita, Bryozoa, Graptolites, Echinoderms and Corals, examples are pointed out in which there is clear and unmistakable evidence of recapitulation. In most of these cases it is the epembryonic and not the embryonic stages that are the basis of comparison.

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