A. HYATT ON TETRABRANCHIATE CEPHALOPODS.

VII. On the Parallelism between the different stages of Life in the Individual and those in the entire Group of the Molluscous order Tetrabranchiata. By ALPHEUS HYATT.

Read February 21, 1866.

HERETOFORE all investigators of the morphological changes taking place in the individual during its life have directed their attention wholly to the examination of the younger stages, while the body is increasing in bulk, and the various organs are developing from an immature to a more or less matured condition.

The importance of continuing such researches throughout the entire life of the individual has not yet attracted the attention of naturalists, although, as I hope to show, the modifications which succeed the embryological stages, during the adult period and old age, or period of decline in the individual, are not less significant, or less worthy of the deepest study.

No one, with the exception of Alcide D'Orbigny, has yet attempted to describe systematically all the metamorphoses of an individual from its ovarian origin to its death, and even he has not detected the correlations which exist between these metamorphoses and the gradual changes which mark the course of life in the group, from its beginning in time to its extinction. D'Orbigny's observations were made upon the Ammonites, and having been engaged myself, for the past six years, in arranging the magnificent collections of Cephalopods belonging to the Museum of Comparative Zoölogy at Cambridge, Massachusetts, I have had ample means of testing the truth of his statements upon European specimens. The Museum collections are very richly furnished with Ammonites, nearly every species represented by a large number of individuals, and comprising, among others, the former cabinets of Prof. Bronn, L. de Koninck, M. Boucault, M. Duval, a large and choice selection purchased from Dr. A. Krantz of Bonn, and a suite of exchanges from the Museum of Stuttgardt. These having been placed temporarily in my charge, to be arranged in the show-cases designed for them, I availed myself of this favorable opportunity, while connected with the Museum in the capacity of a student, and since my graduation, to scrutinize closely the account given by D'Orbigny of the young, adult, and period of decline of the Ammonite.

These studies ¹ finally led me to compare the characteristics of the period of decline the individual with the adult features of allied species in the hope of finding similar correlations to those so successfully worked out by Von Baer, Professor Louis Agassiz, and others, between the development of the young and the permanent states of simpler organizations. That correlations of a definable nature exist, I have no longer any doubt; and after completing the partial comparisons hitherto made only between the young of the Ammonites and the shells preceding them in time, I hope to show that the life of the individual, so far as the shell and its internal structure indicate what its metamorphoses were, displays during its rise and decline, phenomena correlative with the rise and decline of the collective life of the group to which it immediately belongs.

D'Orbigny divides the life of the individual into five periods, distinguishable from each

¹ I have also undertaken, at the suggestion of Professor Agassiz, a Catalogue of the Ammonites, the first part of which is now ready for the press and only waiting his return from

other by the external characteristics of the shell: ¹ namely, the first period, or " période embryonnaire," during which it is smooth and the abdomen ² round; the second period, or "première période d'accroissement," which is marked by the advent of the tubercles, or ribs and keel, if there are to be any upon the adult shell; the third period, or " dernière période d'accroissement," during which the tubercles, or ribs and the keel, are fully developed, and the whorl takes on its adult configuration; the fourth period, or " première période de dégénérescence," during which the ribs or tubercles begin to separate more widely and become depressed; and the fifth period, or " deuxième période de dégénérescence," when all these ornaments are obsolete, and the exterior is smooth again as in the young.

The recapitulation in which he sums up the results of this remarkably original and unique series of observations is equally truthful and instructive. The following paragraph conveys the sense of the original, though the piquancy and force of the French is lost in the translation.

"These modifications are not due to chance, but to decided and regularly occurring periodical metamorphoses, which affect the larger number of the Ammonites, and which invariably operate in a regular order of succession. In fact, each one, although smooth in the youngest period, covers itself at a later time in the course of growth with tubercles around the umbilicus, afterwards with ribs, striations, or tubercles, upon the back (abdomen). It is then in the adult stage. Having arrived at the maximum of external complication, all these ornaments begin to show signs of alteration; it degenerates; its striations and dorsal (abdominal) ribs first disappear; then follow its lateral ribs or tubercles, and in old age it becomes fully as simple externally as it was during the embryonic period."

The accomplished author of the "Paléontologie Française," however, did not extend his researches to the internal organization beyond a merely casual notice of the simplicity of the lobes of the septa in the young; and, also, positively denied that these parts were affected by old age: "ne montrent qu'une complication toujours croissante et jamais de dégénérescence."⁸

Robert Owen, the great comparative anatomist, states that the young Ammonite has an embryonic stage of development, when its septa resemble a Ceratite,⁴ but besides this, three more periods can be traced, — one in the young, one in the adult of all shells, and the other in the old age of a limited number of forms, making altogether four periods of septal growth.

The first period, corresponding with D'Orbigny's "période embryonnaire" of the external characteristics, has simple septa curved like those of *Goniatites Marcellensis*, or any of the Nautilini, and the siphon occupies an abdominal position, giving rise to an exceedingly shallow abdominal lobe. The second, the equivalent, with reference to the more complicated adult septa, of the second period of D'Orbigny in the development of the ex-

1 Alcide D'Orbigny, Pal. Française, Terr. Crét. Ceph., p. 377.

dans les dernières cloisons qu' une Ammonite a formées avant sa mort, et parait être la suite d'une maladie ou de la vieillesse."

⁴ Robert Owen. Paleontology, p. 103, 2d ed., 1861. The same authority (p. 99) also states, that "the sutures of an Ammonite are at first very slightly lobed, and become progressively more complex; so that specimens of the same species have been referred to three genera — Goniatites, Ceratites, and Ammonites, according to their age."

² D'Orbigny calls the outer part of the whorl the back, but in common with Pictet and Agassiz I would regard it as the abdomen.

³ D'Orbigny, *Op. cit.* p. 396, 2°. On the preceding page, however, he partially contradicts this assertion by doubtfully referring certain changes of the septa either to sickness at the approach of death, or to old age, "Ce cas a lieu généralement

ternal ornaments, and of the Ceratitic period of Owen, has a deeper abdominal lobe, and the lateral portions of the septa bent into a number of pectinated, club-shaped lobes like those of Ceratites nodosus. This period is not invariably coincident with the first appearance of the tubercles; on the contrary, it often precedes them, occurring while the shell is still smooth, as in Amm. Kridion D'Orb., or Amm. Beechei Sow. It is rare, however, to find a shell in which the septa have attained to any considerable degree of complication before the beginning of the tubercular period. The third period is always partly coincident with the third period of the external ornaments. It includes the septa from the time they acquire their Ammonitic lobes until they begin to degenerate in old age, and usually accompanies the ornaments through the entire course of their adult complication. The fourth period is not always distinguishable; thus Amm. heterophyllus, Amm. primordialis, and the like, which habitually increase the radii of the spiral throughout life, present no very decided marks of septal degradation in the oldest parts of their shells. In those species, however, such as the Planulati and Maerocephali, in which the radii of the spiral in the old decrease, the size of the whorl also diminishes, consequently crowding the lobes together, narrowing the breadth of the cells and preventing the formation of new auxiliary lobes. In fact, the complexity and number of the lobes seem to depend wholly upon the unceasing expansion of the whorls. There is then more room for them, and they either broaden, or an additional number of auxiliary lobes are added, as in the old of any of the more involute species of the Arietes, Faleiferi, Dentati, Fimbriati, or Heterophylli. When the recession of the spiral takes place among the keeled Ammonites it may occasion the atrophy of the keel and an approximation to the aspect of species having rounded abdomens, as in the example given by D'Orbigny and Pictet of Amm. varicosus Sow., which loses its keel in the old, and resembles some of the Capricorni (Amm. planieosta).¹ There is, therefore, a general agreement between the mutations of the septa and form of the whorl, with those of the superficial characteristics of the shell; sufficient, indeed, to show that all the parts are more or less interdependent, and have at least four distinct periods during which they are mutually modified, viz: two periods of development, one adult period, and one old age period. The fourth period of the septa, when it does occur, is necessarily coincident with the fourth and fifth periods of the external ornaments, since the last two invariably accompany the diminution in bulk of the old whorl, and the degradation of the septa during the fourth period also depends upon the contraction of the interior caused by this diminution.

The correlations of these periodical revolutions in the life of the individual with those displayed on a greater scale in the life of the entire order of Tetrabranchiates in time, are wonderfully harmonious and precise. They open a vista through which the individual may be viewed in a new and unexpected light; standing side by side with its own series of forms, it seems to embody the same biological law; not only rising and declining within the narrow limits of its separate existence as they do in their totality, but varying the characteristics of its different periods reciprocally with the more extensive changes of the entire series.

The general agreement of the life of the individual and the life of the group are evident and need no extended explanations; but for the purpose of entering more minutely into these comparisons, it will be necessary to give a summary of the principal points in the history of the order. The Tetrabranchiates are specially suitable for an inquiry like the present. With the exception of two species now living, they are extinct, and the possibilities of their structural combinations were exhausted even before the extinction of the Cretaceous fauna. The shells, also, are not simple, like those of others of their own subkingdom, but are provided with a series of partitions or septa, which afford additional means of verifying the observations made upon their superficial characteristics. The objections usually urged against the accuracy of investigations founded solely upon the shell, cannot, therefore, have the same weight, when they are supported, as in the Tetrabranchiates, by the evidence of internal structures. In some respects shells are the most satisfactory of all animal remains. While the bones of the extinct Vertebrata, the casings of the Echini and Crustacea, and other fossils, give us in each specimen but one period or stage of growth, shells embody in nearly every well-preserved example a history of the individual from its earliest period to its death. The shell, indeed, is but a single organ, but then it retains the impression of the contour and many of the minor peculiarities of the softer parts, and when we have another set of internal hard partitions of acknowledged importance, there is but slight danger of overrating the value of their evidence.

The Nautiloids commence in the Silurian with aberrant genera, such as Orthoceras, Phragmoceras, Gyroceras, Lituites and others, and these gradually die out until they are no longer to be found in the Jurassic. The normal discoidal Nautili begin in the Upper Silurian with two species¹ and gradually gain in numbers, amounting in the Carboniferous to upwards of thirty-eight species, and then decrease until but two species survive in the seas of the present day. The greatest variety in the form of the adult whorls and the most complicated ornamentation is exhibited at this epoch, when the number of the species and the vital energies of the series are at their maximum. There are globular, keeled, channelled, flattened, smooth and tuberculated species, - all those essential differences of the adult whorl which vary its form but one, the complete involution of the spiral. Subsequently these ornamented and keeled species gradually disappear before the striated and ribbed Nautili of the Jura and Cretaceous, and the latter before the smooth Nautili, which have been slowly gaining in number and importance ever since their first appearance in the Silurian. There are only six of these in the Tertiary, whereas there are about cleven smooth species, according to Giebel, in the Cretaceous.² Thus while their predominance in the Tertiary is significant of the extinction of the more highly ornamented species of the Nautili, their falling off in number shows the whole of the Nautiloids to be approaching their dissolution.

The same laws, however, do not obtain with regard to the greater or less involution of the shell and the complication of the septa. The Nautili of the Carboniferous and preceding geological formations are not involute, but those of the Jura and succeeding formations have the umbilicus more or less covered by the enveloping whorls; the septa are reciprocally progressive, and attain their highest complication in the angular lobes of *Nautilus ziczue* of the Tertiary. Thus during the decline of the Nautiloids, both in the number and in the variety of the form and ornamentation of their whorls, the very species that indicate this decline are becoming more complicated in respect to the involution of the whorls and the formation of the lateral lobes.

This sustained progression corresponds precisely with what may be observed among the individuals of the series. From the earliest period they perpetually lengthen the radii of

¹ Mentioned by M. Barrande in "Étage E" of Bohemia. Quart. Journ. Geol. Soc., London, Vol. X. (Translation).

² Giebel, Fauna der Vorwelt, Ceph. iii. 1852.

the spiral, increasing the bulk of the whorls and deepening the flexures of the septa. Age, indeed, seems to produce no greater impression upon these features in the individual than it does in the whole group. There is every reason for supposing, also, that in its other characteristics the shell agrees equally well with the decline in the whole group of the ornamented species and their replacement by smooth shells.

If the growth of the ornamented carboniferous shells agrees in any manner with their representatives, the ornamented and keeled Ammonites, the adult ornaments either entirely vanish or become partially obsolete in the old. We should then have in any one individual three periods answering to the three periods in the general life of the series : the youngest period with its bent, non-enveloping, smooth tube, and simple septa resembling a Phragmoceras, or a Cyrtoceras among the aberrant genera; the adult period with its profusion of ornaments especially belonging to the epoch of its occurrence and the returning smoothness foreshadowing the smooth shells of the last days of the entire series.

I have not yet had an opportunity of examining any specimens of the ornamented Nautili which betrayed evidences of senile degeneration; but this is not surprising, since among hundreds of Ammonites it is often impossible to pick out one specimen which presents a complete history of its own life.

The Ammonoids are the opponents of the Nantiloids, expressing in every step of their serial arrangement opposition to the latter, reproducing the same forms, but in such succession, that they are removed from their prototypes among the Nautiloids to the greatest possible degree both of time and organization. For this reason, and because the word has been used to designate similar phenomena by others, I shall call this general repetition of form morphological polarity, whether it be in the young and old periods of the individual or of the group.

The series under consideration begins in the Devonian with the normal discoidal shells¹ of the Clymeniæ, and mounting step by step in the complication of the septa, the multiplicity of the forms and the number of species, reaches its culmination in the Jurassic and dies out with the Cretaceous.

The number of species in the Jurassic, according to D'Orbigny, are in the aggregate about two hundred and twenty-two, whereas those of the Cretaceous are but one hundred and forty-four, making an excess in the Jura of seventy-eight species.² The researches of the same indefatigable paleontologist have demonstrated that the Ammonites differ from the Nautili in the suddenness with which they disappear, having, according to his "Prodrome de Paléontologie," upwards of forty-two species in their last geological horizon, the "Sénonien." The aberrant genera, on the contrary, first announce themselves with two species of straight shells of the genus Bactrites in the Devonian, and progressing very slowly do not arrive at the maximum number of species until the close of their career in the "Sénonien." Out of eighty-six in the Cretaceous, about fifty, or more than one half, are confined to this formation, and exceed the normal forms only by some eight species. Many of these aberrant genera are precise repetitions of the aberrant Nautiloids, which in the Silurian were, also, numerically superior to the normal Nautili. The Baculite, for instance, is a straight cone like the Orthoceratite; the Turrilite is a turbinated form

1 There can be but little doubt of the affinity of the Clymenian, has well-defined abdominal and lateral lobes,

² D'Orbigny, Prod. de Paléontologie, Vol. III., 1850.

Clymenia with the Ammonoids, since the discovery of the which are undeniable Ammonitic characteristics. Clymenia pseudogoniatites (Guido Sandberger, Beobacht. über d. Clym. Wiesbaden, 1853) This species, an undoubted

similar to Trochoceras; the Crioceras an open coil answering to Lituites; the Toxoceras a curved tube like Cyrtoceras, and so on. Most of these are exclusively Cretaceous and, as will be shown presently, are at the head of the Ammonitic series. Thus those approximating to the normal, discoidal Nautili in form are next to them in time, and those approximating to the beginning aberrant Nautiloid are the farthest removed. The Ammonoids, therefore, are in every respect polar to the Nautiloids, and entirely revolutionize the succession of the latter. This is equally well exemplified in the morphological sequence of their structure. The Orthoceratite, on account of its simple concave septa, straight cone, and priority of geological position, may be considered as the elementary form. Between it and the involute discoidal Nautili, we find the Cyrtoceras and Phragmoceras somewhat more bent, and the septa with very shallow lateral lobes; the Gyroceras with a very loosely coiled shell, and the lateral lobes deeper; Lituites closely coiled with two shallow lateral lobes; and lastly, the discoidal Nautili leading to the involute Nautilus ziczac, and its angular lateral lobes and rounded cells. Among the Ammonoids, there are the Clymeniæ simulating in the lowest species, such as Clymenia lavigata, the open umbilieus, almost dorsal siphon and simple lateral flexures of the Trocholites or Lituites, and in the highest, Clymenia pscudogoniatites, having perfect angular lateral and abdominal lobes. Next the Goniatites and Ceratites, with their more involute forms and numerous lobes and cells, and the keeled Ammonites with a greater variety of forms and foliated lobes, and then the group of Ammonites with round abdomens which precede the tubular aberrant genera and connect them with the discoidal Ammonites. Lastly, the aberrant genera themselves, which are successively more and more open from the Scaphites, as will be shown farther on, to the perfectly straight Baculites. This of course is not strictly their connection, because no directly traceable linear series exists, but only the general resolution of the elements of form as determined by the special affinities of the septa. Morphologically, therefore, and with regard to the general sequence in time and structure, the aberrant Nautiloids are to the discoidal Nautili as uncoiled cones to involute cones, and the discoidal Ammonites to the aberrant Ammonoids as involute cones to uncoiled cones. In other words, if we wish to look at the order as a whole we may consider the straight Orthoceratite as coiling upon itself and producing the discoidal shells, and these uncoiling to generate its structurally antithetical but polar form, the straight Baculite.

The senile period of the individual may be contrasted with the young, as the Ammonoids were with the Nautiloids, and its polarity to the young expressed in nearly the same phraseology which was used to describe the morphological inversion of the two series by simply substituting the terms "old age" for "Ammonoids," "rising period" for "Nautiloids," and "characteristics" for "forms."

Thus it may be said that the old age of the individual is the opponent of the rising period, expressing in every step opposition to the latter and reproducing the same characteristics, but in such succession that they are removed from their prototypical characteristics to the greatest possible degree both of time and organization. Thus; the external ornaments, as previously stated, in dying out pass through a series of changes which are inversely the same as those by which they came into being, and the periods most alike are the two smooth ones situated at the extremes of individual life. The polar forms are morphologically unrolled Ammonites, and in dying out pass through a series of forms which are inversely the same as those by which the Nautili came into being; and the forms most alike are the two straight cones, the Orthoceratite and the Baculite, situated at the extremes of the collective life of the order. The forms of the order and the characteristics of the isolated shell both undergo, after their vital powers are expended, a reversion which approximates the aspect of the exterior of the shell and the forms of the order to their original simplicity.

Farther; during the rising period of individual growth the septa are constantly complicating to correspond with the equally constant increase of the radii of the whorls, but in old age, as previously stated, the septa deteriorate because the whorl becomes more tubular. The order also during its rising period has constantly complicating septa, and in its decline, when the whorls become more tubular and less involute among the aberrant genera, these parts present marks of degradation and have fewer lobes than the involute shells, not above six in all, — which is the number usually found in the young Ammonite at the Ceratitic period.

The old septa of the shell of the individual retain much of the adult complication, parting only with those characteristics which are immediately influenced by the degradational changes in the breadth of the whorl. The lobes and cells may be crowded together or otherwise modified, but they still hold, even in extreme old age, to the Ammonitic foliations, and never become smooth again as in the young, however much the whorl may be rounded or otherwise brought to resemble the young. In the order, also, though the polar forms so closely copy their prototypes and the septa have fewer lobes to correspond with the degraded character of the whorl, yet they never lose the Ammonitic foliations, or repeat the smooth septa of the prototypical Nautiloids.

Thus the polarities of the individual are exhibited in the same manner as those of the whole order with reference both to time and mode of occurrence, agreeing even in the negative features last described, in the extent to which the septa may be changed by the degradation in form of the old whorl and the decadence of the entire group. These polarities, however, are not so complete as some which may be made by contrasting the life of the individual as a whole with that of the order, and thus bringing into view not only the agreement of polarities but the agreement of the intermediate adult period.

The Tetrabranchiata, as regards their progress in time, have four periods of greatest expansion: the first, in the Silurian; the second, in the Carboniferous; the third, in the Jurassic; and the fourth, in the Cretaceous. These are the epoch of geological history, when the four separate groups had their maxima of development, as previously estimated by the number of species, the multiplicity of their forms, and their profuse ornamentation. They show that the groups, although parallel with each other in the general phenomena of life, — namely, having a beginning in time, from which they augment in complication and in numbers and then die out, — nevertheless do not perform their cycles together, but each by itself, and arrive at their maxima regularly in the order of their zoölogical rank. The aberrant Nautiloids have, according to D'Orbigny,¹ about one hundred and fourteen species in the Silurian, decline to (about) sixty-four in the Carboniferous, and to (about) fourteen in the succeeding strata, and are absent, as previously remarked, in the Jura. They therefore predominate over the Nautili, which amount to thirty-eight species in the Carboniferous, and only (about) eight species in the strata intervening between that and the Jura, until they are replaced by the Nautili in the last named formation.

The Ammonites in the Jura, as previously stated, run up to more than two hundred

species and, therefore, vastly surpass their predecessors the discoidal Nautili, which are represented by only a few more than twenty species in the same formation. The aberrant Ammonoids differ from their prototypes in one respect: they do not outnumber the discoidal shells in the Cretaceous, as the aberrant Nautiloids of the Silurian did the normal forms of their special group, but the normal Ammonites have much the largest number, being as one hundred and forty-four to eighty-six. In the last horizon of the Cretaceous, it is true that the polar forms exceed them, as has been shown, by about eight species, but this is only sufficient to demonstrate that the latter are gaining, and does not afford margin enough for the assumption that their superiority is comparable with the vast predominance of the aberrant Nautiloids in the Silurian. Although the polarity is here less accurate than in other respects, the succession of the four epochs resembles the succession of the four periods of the individual both in number and their general structural peculiarities.

The first epoch of the order is especially the era of rounded, and, in the majority of the species, unornamented shells with simple septa; the second is the era of ornamentation, and the septa are steadily complicating; in the third the complication of the septa, the ornamentation, and the number of species, about twice that of any other epoch, all combine to make it the zenith of development in the order; the fourth is distinguishable from all the preceding as the era of retrogression in the form and partially in the septa.

The four periods of the individual are similarly arranged and have comparable characteristics. As has been previously stated, the first is smooth and rounded with simple septa; the second tuberculated and the septa more complicated; the third was the only one in which the septa, form, and ornamentation simultaneously attained the climax of individual complication; the fourth, when amounting to anything more important than the loss of a few ornaments, was marked by the retrogression of the whorl to a more tubular aspect, and by the partial degradation of the septa.

This exhausts the correlations between the individual as a unit and the whole order. There yet remain, however, those which may be traced in the proportions of the embryonic, adult, and old age features of the shell; by their aid we shall be able to perceive the extraordinary correspondence of the life of the individual with its position in the structural scale.

The adult period of the individual is evidently that which differs most from all the rest, since these, as has been shown, are inversely repeated on either side, and it alone remains non-conformable to any other.

Examining the order, it is not difficult to perceive that at the epoch of the Jura, corresponding to the adult period of the individual, the Ammonites depart to the utmost extent from their polar types the Orthoceratite and the Baculite, since, as we have also seen, this epoch is remarkable for the combination of all the elements of complication and their simultaneous arrival at the maximum of vital intensity.

It is also most remarkable, that the growth of the individual itself is strictly conformable with this law, being more homogeneous or embryonic in the Orthoceratite, heterogeneous or continuing to increase the diversity of the adult from its own young throughout life at the era of greatest vital intensity among the Ammonites, and more homogeneous or embryonic again in the Baculite. An adult Orthoceras has precisely the same concave septa and round whorl as the young; the septa of an Ammonite may vary among the keeled group from four rounded to eighteen foliated lobes, and the form from an open coil to a completely covered umbilicus (*Amm. discoides* Ziet., *Amm. discus* Sow.), or among the smooth

round-backed group from four to twenty-two (Amm. Calypso D'Orb.); the septa of a Baculite, however, retain the embryonic number of four or six lobes and have precisely the same form in the adult and in the young.

This law proves that there is a direct connection between the position of a shell in the completed cycle of the life of this order and its own development. Those shells occupying the extremes of the cycle, the polar forms, being more embryonic than the intermediate forms, although in regard to geological sequence and structural position one of the extremes must be of a higher zoölogical rank.¹

There is, however, another and more striking correlation between the Ammonites of the Jurassic era and the adult period of individual growth. All the shells of earlier eras among Ammonoids, such as those of the Clymeniæ, Goniatites, and Ceratites, are deficient in senile characteristics. The radii of their whorls do not diminish in old age, nor do their septa or ornamentation show any signs of degradation; each successive species adds something to the increment of complication, and there are no visible traces of a failing vitality, so far as I know, either in the individual or in the group to which it belongs. But in the same manner that the individual begins to show signs of decay during the adult period do the Ammonoids begin to produce individuals and species with well-marked senile characteristics at the moment when they reach their maximum of development in the Jura. Doubtless the softer parts were affected by the decline of the vital powers of the individual among the earlier series, above mentioned, but the changes were not such as to visibly affect the shell or the septa.

Among the Nautiloids, also, this law appears to hold, since, as previously described, they maintain the progressive complication of their septa throughout the series, and if there are any signs of senile degradation they must be found among the ornamented species of the Carboniferous, when the group reaches its fullest expansion. Within itself this series may, as I have inferred, correspond with the changes of the different periods in an ornamented individual of the Carboniferous; but with regard to the order of Tetrabranchiates it is eminently a "progressive series." It forms the organic base of the order, as the Clymeniæ form the organic base of the Ammonoids; but while it completes the cycle of its life they do not, but are cut off after existing for a limited time in the midst of their growth. The Nautiloids, in fact, are dying a natural death of decay; whereas the Clymenia, Goniatites, and Ceratites were for the most part abruptly destroyed at the end of the Devonian, Carboniferous, and Triassic epochs. The concentration, also, of the whole progress of the Nautiloids within the boundaries of one small group, the Clymenia, as will be seen presently, confirms their progressive nature and shows them, notwithstanding their wide-spread distribution, to be but little more than an equivalent of the latter.

The first septum of Nautilus Pompilius, and also of Nautilus lineatus from the Inferior Oölite, and of Nautilus bohemicus Barrande, according to D'Orbigny's figure, has an abdominal cell, and the lateral portions slightly sinuous, and the siphonal aperture even at this early age is central. The striations are broader externally than internally, indicating from the apex the tendency towards the spiriform mode of growth.

The presence of the siphon shows that the young does not repeat the siphonless adult

tively a higher organization, although, as here stated, the adult may be quite embryonic and differ but little in the charac-

¹ That this "higher zoological rank" also implies rela- teristics of the shell from its own young, may be seen by reterring to the last page of this article.

² D'Orbigny, Op. cit. Terr. Jurass. Ceph., pl. 31, p. 156; Barrande, Op. cit.

condition of some of the lower genera, such as Endoceras. There is, however, a faint reference, perhaps, to such species as *Tretoceras bisiphonatum*, caused by a minute dorsal lobe in the young of *N. Pompilius*, which from its position and general appearance might be homologized with the dorsal chambers of that species.¹ The plainly convex septa, equable striations, and straight mode of growth of the Orthoceras is also omitted, the young shell being wholly devoid of resemblance to these simplest forms. It is presumable that in their earlier periods the ova have characteristics in common; but certainly after these egg phases are past, if there are resemblances between the embryonic Nautilus and the adult Endoceras or Orthoceras, they are too transient to make any impression either upon the mode of growth, the septa, or the curvature of the shell.

Entering upon the Ammonoid series, the first member of it, the Clymeniæ, confined to a single geological epoch, the Devonian, centres within the boundaries of one small series of shells like *Clymenia lærigata*, that are separable from Trocholites only through their external outline, which is flatter or more definitely discoidal than the spiral of the latter, and the *Clymenia pseudogoniatites*, which we ascertained to be a true Ammonoid.² The range of the complication is greater, so far as the septa are concerned, than that traversed by the Nautiloids in almost the whole of geological time from the Silurian to the Tertiary. A still more decided concentration is exhibited in the last named species, every individual of which, according to Guido Sandberger's figures, begins life with the simple septa of a *Clymenia lærigata* and crowds all the essential steps of the entire advance into its younger periods. Whether the Clymeniæ are true Ammonoids or not is of no material consequence; certainly, in one division, and, finally, in the young of one individual of that division, and in a proportionately shorter time, they bring together by successive concentrations the results of the progress of the Nautilian septa, and proceed in the adult to make a yet greater advance in another direction towards the more highly constituted Ammonoids.

The Goniatites do not repeat in their young the position of the siphon in the Clymenia, although the septa may be quite as simple as they are in *Clymenia lavigata*. It is possible that the siphon may alter its place in the young of such simply septate species as *Goniatites mareellensis* Van., but this is exceedingly doubtful, since in species as simple as *Goniatites discoideus* Hall, the siphon is ventral at an early period of growth. The range of complication is greater than among the Clymeniæ, being from *Goniatites mareellensis* with two shallow lateral lobes to *Goniatites ceratitoides*, which closely approaches the Ceratites in the shape and number of its club-shaped lobes. The development of the septa accords with the growth of the same parts in the Clymeniæ, since among the lower species it takes a longer period to bring the lobes and cells to their full development than in the higher. Thus in *Goniatites mareellensis* the septa have about the same embryological curves throughout; in *G. lamed* Sand., a more complicated species with two angular lateral and one large divided ventral lobe, they take on the adult aspect during the second or third whorl, having passed through a stage equivalent to the adult period of *G. mareellensis* during the first whorl; and in *G. crenistria* Phill, a still more advanced species, the changes are introduced even more

Nautiloids, with C. pseudogoniatites, through such species as C. binodosa, sublævis, or costellata, all of Munster, which have the angulated Clymenian septa in the adult, but are like the adult C. lævigata in the young, both in the external striations, form of the whorl, and curvature of the septa.

¹ This homology seems to confirm Mr. Salter's opinion, that the dorsal (his ventral) chamber is wholly independent of the siphon. (Salter on Tretoceras. *Journ. Geol. Society*, London, 1858.)

² I connect *Clymenia lavigata*, which, together with its allied species, has been placed by several authors among the

rapidly. The development varies, also, among the Ammonites, according to the adult com-

plication of the septa, the siphon being constantly ventral. As has been described, there is a goniatitic and ceratitic stage, and these are both passed through almost invariably in the first whorl, and in some highly complicated species, such as *Amm. discoides Ziet.*, or *Amm. Beechei* Sow., the septa are deeply foliated in the young.

In both the Goniatites and the Ammonites the central position of the siphon, so conspicuous among the Nautiloids and Clymeniæ, is passed over, and left out in the course of growth, and the development of the septa accelerated in proportion to the position of the shell. Thus among the Clymeniæ, as a rule, it is slower than among Goniatites, and slower in the latter than in the Ammonites; although in each division there are, also, differences in the rapidity with which the development proceeds, proportioned to the zoölogical rank of the species.

In minor series we find the same principle; thus the younger periods of Amm. hybrida, covering about two thirds of the spiral, have the large, squarely set ribs of the full-grown Amm. planicosta, but the adult is remarkable for its flattened sides and Beechean ribs and tubercles. Next in serial order is a species, Amm. appressus nobis, MSS.¹ which has the same Planicostan markings in the young, but they do not take up more than about one third of the spiral, and the rest of the shell is adorned with true Beechean ornaments. This species is absolutely smaller than Amm. hybrida, and the shell more involute and flatter.

Finally, we have Amm. Henleyi, with a very faint Planicostan aspect at a much earlier period, caused by the prominence of ribs crossing the abdomen and nearly the entire spiral with the Beechean ornaments, and finally Amm. Beechei itself, devoid of all resemblance to Planicosta. It is smooth and round at the youngest period, and in course of growth assumes the tubercles, the narrow bifurcating ribs and flattened sides of its species, wholly ignoring the Planicostan stage of the lower members of its own series. This series is one among the Ammonites, in which I have observed no marks of decadence; all is progress, and the phenomena are precisely the same as those brought out in the earlier eras of the rising period of the structure of the Ammonids. The young of higher species are thus constantly accelerating their development, and reducing to a more and more embryonic condition or passing entirely over the stages of growth corresponding to the adult periods of preceding or lower species.

In other words, there is an unceasing concentration of the adult characteristics of lower species in the young of higher species, and a consequent displacement of other embryonic features which had themselves, also, previously belonged to the adult periods of still lower forms.

This law, applied to such groups as have been mentioned, produces a steady upward advance of the complication. The adult differences of the individuals or species being absorbed into the young of succeeding species, these last must necessarily add to them by growth greater differences, which in turn become embryonic, and so on; but when the same law acts upon some series whose individuals alter the shell in old age, precisely the reverse occurs, and a general decline takes place. The old age characteristics, in due course of time or structure, become embryonic, and finally affect the entire growth and aspect of the higher members of the series.

The Arietes of the Lower Lias, arranged according to their zoölogical affinities, have first

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in order such species as Amm. Ceras and Amm. Conybeari, which are non-involute, like the Clymeniae or lower Nautili, and have smooth ribs with a keeled and channelled abdomen; then Amm. Bucklandi, Amm. bisuleatus, Amm. Brookei Sow., which differ from the first in their tuberculated ribs; and finally Amm. Brookei Zieten, Amm. obtusus, Amm. stellaris, and Amm. Collenctii, devoid of tubercles and with the ribs more or less depressed near the abdomen. This part, also, becomes narrower than in the preceding species, and in the adult of the last three its channels are lost and the keel is almost obsolete. The deterioration is so extensive and perfect, that Amm. Collenctii has been deemed by some authorities one of the Clypeiformi with a smooth, acute abdomen. Both Amm. stellaris and Amm. Collenctii are more involute than the others, but they have similar septa, and it is difficult to draw the line between the former and some varieties of Amm. obtusus, an undoubted Arietian; the thick, depressed ribs of Amm. stellaris are traceable, also, upon the sides of Amm. Collenctii, although, of course, one degree nearer to absolute atrophy.

In the old of *Amm. Bucklandi* or *Amm. Brookei* Sow., the prominently keeled, flat, and deeply channelled abdomen, and the projecting. tuberculated ribs of the adult may be observed giving way to a narrower abdomen, with a depressed keel and without channels, the ribs obsolete near the abdomen and the aspect of the whorl in transverse section changing from the rectangularity of the adult to a trigonal outline. The increase of the radii of the spiral and the continued complication of the septa are not interfered with, and the shells show no perceptible signs of senility.

These old age peculiarities are identical with those distinguishing the adult of Amm. Brookei Ziet., (which is a totally different species from Amm. Brookei Sow., separable by reason of the trigonal outline of the whorl and the depressed, smooth ribs of the adult) and Amm. tenuis nob. MSS.¹ The latter, however, is deeply channelled in the adult, while the former is so only at an earlier stage, but they both repeat in the young the rectangular whorl of the preceding species. Amm. stellaris has the keel and channels more distinct in the young than in the adult, but the form of the whorl shifts at an early period to the senile trigonal aspect and becomes quite involute in the adult. The last is the only characteristic which is not identical with the old of Amm. Brookei Ziet. In Amm. Collenotii the rectangular whorl is entirely left out of the growth, the transition being gradual from the round embryonic to the senile trigonal, and the channels are only faintly marked in the young. The whole shell is an exaggeration of the old age tendencies of Amm. bisulcatus or Amm. Brookei Zieten, and the adult is a counterpart of the extreme old age of the involute Amm. stellaris, when the ribs are almost wholly obsolete and the sides are partially smooth. Amm. stellaris and Amm. Collenotii, therefore, are the old age forms of the Arietes series, and they, also, complete the senile tendency shown in the old individual of the lower forms by becoming more involute, — that is, by increasing the radii of the spiral in greater proportion than any other species, and thus responding, as the heads of the series, to the unceasing increase of the radii in the spirals of Amm. Bucklandi and the like.

Following the keeled group upwards, the "homomorphs" of the old age forms of the Arietes are found to acquire greater importance, until in the Cretaceous they are represented by an entire series of smooth, involute shells with acute abdomens and no channels.

In the Lower Lias all of the Arietes, with the exception of the two senile forms, are noninvolute. The Amalthei of the Middle Lias, however, have but one species, Amm. Hawsker-

¹ Also to be published in the Museum Bulletin.

ensis with an open umbilicus, the rest, including Amm. costatus, vittatus, and margaritatus, are progressively more involute with more complicated septa, and their abdomen more acute. Succeeding these are the Falciferi of the Upper Lias, which have but two species, Ann. Walcotii and Amm. bifrons, that simulate Amm. Hawskerensis and the Arietes, and then a long list of others, first with acute abdomens and open umbilici, as in Anum. striatulus, then more involute as in Amm. radians and serpentinus, and finally with the internal whorls entirely hidden, as in Amm. discoideus and Amm. elegans. The remaining strata of the Jura contain but two or three, like Amm. eyeloides D'Orb., and some of the so-called varieties of Amm. Murchisonia, which have the abdomen channelled and keeled; their enrolment in all cases, however, that have come under my eye, is more involute than the generality of the Arietes. The Cristati and Clypeiformi constitute the Cretaceous series. The first has a few species, such as Amm. influtus and Amm. tricarinatus, which repeat the narrow-whorled Arietes, but only one species, Amm. tricarinatus, has the umbilicus sufficiently open to emulate with any accuracy the non-involution of Amm. Walcotii of the Falciferi, or Amm. Conybeari of the Arietes. The rest are all more involute, and have, in proportion to the radial breadth of the whorls, narrower abdomens. The second series is wholly composed of shells which initate the old age involution, the smoothness, the obsolescing keel, the obsolete channels, the acute abdomen and trigonal whorl of Amm. stellaris and Amm. Collenotii.

Besides these, other instances might be taken demonstrating the incorporation of the degradational characteristics of the individual into the higher forms of succeeding groups, but the brevity of my remarks does not admit such a full illustration of the subject.

One more example is needed, however, to establish the fact, that this incorporation of old age tendencies in the growth of succeeding shells becomes more complete not only as we approach the upper boundaries of the life of the order, but, also, in proportion to our proximity to the termination of the structural cycle among the polar forms.

The senile characteristics of the Clypeiformi are brought out in a manner closely analogous with those of the smooth Nautili, the progress of the septa and form of the whorl in complicating themselves is not sufficiently impaired to afford well-marked degradations, but in the series of shells with round abdomens, like Amm. Humphriesianus, a different element is introduced. With them the entire organization appears to have finished its advance and to have begun its morphological decline; the adult era of the collective life of the order is passed, and the coming of its old age era fairly announced. The old of Amm. Humphriesianus of the Inferior Oolite, as noticed by D'Orbigny,¹ varies the rate of increase in the length of the radii of the spiral, and ceases to augment the volume of the whorl, which is less involute and more tubular than in the adult. This is attended, as we have seen, by a narrowing of the cells consequent upon the lessening of the space which the lobes have for their expansion. The diminution of the radii in the old of Ann. dimorphus and Amm. Sauzei, also, of the Inferior Oolite, is more abrupt, and if persisted in would project the last portion of the whorl after the fashion of a Scaphites, or Crioceras. Ascending to the Great Oolite, we find two singular species of the same series, Amm. microstoma and Amm. bullatus, which are eccentric from an early period. The chambers of Amm. microstoma, as they are successively built and left behind in course of growth, become more tubular, and describe curves within the limits of the ideal prolongation of the regular spiral. These chambers are not reabsorbed but remain undisturbed, the animal building onward

1 D'Orbigny, Récherches sur les Ammonites.

from their contracted apertures, and spreading out after each contraction into a broader whorl, which again contracts, and so on. By this process the spiral is reduced to a succession of circular segments, and the symmetry of the logarithmic curve, in which the discoidal forms usually revolve, entirely destroyed. Each segment tends to strike off at a tangent from the main direction of the spiral, but is turned back again toward the centre of revolution at every new season of growth. *Amm. bullatus* caps this series, and the spiral is so deformed by the successive segments, that from the side it has a spherically triangular aspect. The old age features of *Amm. Humphriesianus* are in this way adopted even at a young stage in *Amm. microstoma*, and eventually obliterate the regularity of the spiral in *Amm. bullatus*, because the old age degeneration of the whorl in the first is but a permanent chamber of the same general character with the successive permanent chambers of the two last members of the series.

Amm. terebratus of the Oxford Clay stands intermediate, geologically and zoölogically, between these and the aberrant genus Scaphites of the Cretaceous. The last chamber in which the animal lives bends upon itself, making an acute angle with the preceding portion of the whorl; and since these chambers are probably present at each arrest of development and reabsorbed, as in Scaphites, when the season for growth again returns, the likeness to the latter is perfect. The curve of the last chamber is much within the prolongation of the spiral, and shows the same tendency that was perceived in the growth of Amm. microstoma to depart from, and then return toward, the centre of revolution.

The Scaphites come next, and with them the latter part of the whorl actually does strike off at a tangent, but they nevertheless obey the same law, and are forced at last to turn upon themselves toward the centre, forming a kind of shepherd's crook. The whorl is usually more or less flattened, until near the mouth, where it gradually lessens in size and becomes more tubular. They may have upwards of ten lobes as in the adult (*Scaphites constrictus*). Ancyloceras has the whorl tubular throughout, but generally flattened somewhat laterally, and the tangential departure of Scaphites is not only greatly exaggerated in the shepherd's crook of the adult and old, but its effect can be observed in the earliest periods of some species, such as *Ancyloceras Matheronianus* D'Orb., their whorls being separated from the very beginning. None of the species have more than six lobes. The whorl of Hamites has a rounder outline, as a rule, than in Ancyloceras, and the departure is so excessive that the spiral is lost in a succession of straight tubes, making a double shepherd's crook, and there are never more than six lobes to the septa.

In Ptychoceras the shell is yet farther reduced to a single straight shaft with one crook, and in Baculites even this is gone, the spiral tendency of the growth not having sufficient power to produce even the approximation to its former mode of revolution still evident in Ptychoceras. The straight tubular cone, with its usual complement of four to six septal lobes, is all that remains.

The senile tendency of *Amm. Humphriesianus* has gradually culminated in these successive growths until the degeneration of the septa and shell which were primarily indicated in the Inferior Oolite have terminated, as we have previously remarked, in completely uncoiled and rounded whorls and in a number of lobes reduced to the embryonic formula of four or six.

Notwithstanding the accuracy with which these correlations may be followed upward in time throughout the Ammonoid series, they do not necessarily indicate any priority in time for those species which primarily produce the senile characteristics, except in this general series. In other series, such as the Arietes of the Lower Lias, we have in the same formation, and side by side, embryonic, adult, and old age forms, and among the Nautiloids the old age forms actually precede in the Silurian the great display of the fully ornamented adult forms of the Carboniferous.

I can only claim, therefore, that there is a correspondence between the manifestations of decline in the individual and in the degradational features of the group, whether these appear early or late in time.

It may be said that the smoothness of the Lævigati in the Nautilian series is entirely due to a retention of embryonic characters throughout life; and their early advent in the Silurian certainly affords good grounds for such a conclusion. On the other hand, however, their development, omitting as it does the characteristics of the straight Endoceras and Orthoceras, seems to identify them with such undoubtedly senile species as *Amm. obtusus*, or *Amm. stellaris*. The resemblance of the adult features of such species to the old age characteristics of lower species are too clear to be accounted for by an arrest of development; unless, indeed, we can assert that the resemblance of the old and young in the same shell is due to an arrest of development, which would be a manifest absurdity.

I have been dealing so far with but one organ, the shell; and notwithstanding the utmost care and frequent reviews of the specimens themselves, I have found that the facts always revealed the same laws, and ever more decidedly. But some time since I satisfied myself that if the softer parts had been preserved, one of my conclusions would have received important qualifications. In order to obtain an adequate illustration of this, I will conclude with one or two examples from existing animals.

Mr. Morse, besides elucidating the general homologies of the Saccata, shows with the greatest clearness that the Cephalopod is very similar in form to the Polyzoon, although completely reversing its structure.¹ Thus, while both are sacs closed at one end by a disc perforated by the mouth and fringed with a circular crown of tentacles, and their alimentary canals bent in a similar way and opening in the vicinity of the mouths, one is a perfectly cephalized, and the other an anti-cephalic type. The nerve-mass of the Cephalopod is situated at the anterior, and in the Polyzoon at the posterior pole; and while in the former the anus and intestine are on the ventral side, in the latter they are on the dorsal side. By entirely revolving the positions of the principal organs a morphological polarity is established in the Cephalopod; which being the structural reverse of the Polyzoon is yet so alike in shape, that either a longitudinal or transverse section of the body has the same outline. The element of time being eliminated, these polarities are related morphologically to the intermediate members or classes, as the aberrant Ammonoids and Nantiloids were to the normal forms; they are organically removed from each other to the greatest possible degree, being at the extremes of the Saccate type.

It will be remembered, also, that the polarities were brought about by a revolution of the straight cone into an involute cone, and subsequently from the involute to a straight cone again. The intermediate steps of the revolution of the organs between the Polyzoa and Cephalopoda exhibit the action of the same law.

Mr. Morse's figures in the single plate attached to his paper give us a distinct idea of the successive changes in this remarkable series of transformations. The anus remains more or less posterior, and the oral region with the other organs is carried by a cephalic concentration towards the anterior pole of the Brachiopoda; the anus remains posterior and the oral region is yet more anterior in the Ascidia; the anus is posterior and the oral region opens at the anterior end in the Lamellibranchiata. At this point the revolution of the mouth stops, it having been transferred from the posterior pole of the Polyzoon to the anterior pole of the Lamellibranchiate along the ventral side, and the revolution of the anus may be said to begin. This follows the mouth along the ventral side and in the Gasteropoda and Cephalopoda opens in proximity to the latter on that side, thus completing the inversion.

What effect old age may have upon the individual, and what may be its correlations with polarities upon such a vast scale, are questions that I am at present unable to answer in a satisfactory manner.

One fact, however, is worthy of notice and exceedingly suggestive. The initiatory transformations described above are due to cephalic concentration, a retraction of the whole body within the cœnœcial or mantle region. This is the permanent position of the Polyzoon at the two extremes of its life, during its old age, and while it is still an embryo.1 The Brachiopoda have been homologized by Mr. Morse and myself,² and the Ascidia by Prof. Allman³ with an invaginated Polyzoon on account of this very cephalic concentration; and what is still more curious, the Brachiopoda, which most nearly resemble the invaginated individuals of the Polyzoa, are those that betray an old age peculiarity. It is well known that the old individuals are more globular than the adult or young,⁴ and the forms which have the simple dorsal flexure of the intestine and the oral disc or lophophore extended into horse-shoe shaped arms fringed with tentacles, as in the Hypocrepian Polyzoa, are the Waldheimia, and Terebratula, - exceedingly globular and deep shells. Whatever may be the value of these suggestions, it certainly seems that the Polyzoa assume in old age, as described by Milne Edwards in the genus Eschara, a much higher state, withdrawing themselves into their cephalic regions, and in this condition are more closely allied to the Brachiopoda or Ascidia than at any previous time of life.

There are other polarities which are similarly placed in their respective divisions. The Dibranchiate Cephalopoda are, also, the polar forms of the Pteropoda, which are at the foot of the series of cephalized Saccata. The general aspect, the arrangement and position of the oral region, and the disposition of the internal organs, are similar in both. The Limacidæ are the polar forms of the Nudibranchiata, the former ending the series of intermediate shell-covered Pulmonifera, and the latter beginning the series of shell-covered Branchifera. The shell-bearing Pulmonifera, and Branchifera have equivalent features and are the normal turbinated Gasteropoda. The polar extremes, where all the viscera and the coniform mantle of the turbinated Gasteropoda are condensed into the cavity of the foot, have a much more embryonic appearance than the intermediate norms. According to the observations of Lereboullet upon the development of Limneus stagnalis,⁵ the foot is observable at a very early age, before the internal organs, with the exception of the alimentary sac, are defined, or the spiral tendency of the growth is manifested; and the whole yolk, in fact, is first only part of a creeping disc. The Medibranchiata and Limacidæ are only creeping discs, with the viscera in place of the yolk, and must, therefore, mor-

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¹ Milne Edwards. Annales des Sci. Nat. Tom. vi. 1836.

² Hyatt. Observations on Polyzoa. Proc. Essex Inst. Vols. iv. and v. 1865-6.

³ Prof. Allman. Monogr. Fresh Water Polyzoa, Lond., 1856.

⁴ Woodward. Recent and Fossil Shells, p. 213.

⁵ Lereboullet. Embryol. du Limnée des Étangs., Ann. Sci. Nat., 4° Sér. Tom. xviii. 1862.

phologically be deemed more embryonic than the normal spiriform and turbinated shells, notwithstanding the elevated structural position and functional superiority of the Limacidæ. We reduced the morphological polarities of the Tetrabranchiata to the same law. It was, however, impossible then, in dealing with the shell alone, to perceive, as we did in this or in the case of the reversional polarity of the Cephalopod to the Polyzoon, that the polar forms might be structurally and functionally higher than the norms, although the latter might be, with respect to the structure of some parts and their general morphological peculiarities, less embryonic and apparently more complicated. There is undoubtedly a direct structural degeneration of the septa and form among the aberrant Ammonoids; but it is probable that their structure as a whole is deserving a higher zoölogical rank than the seemingly more complicated Ammonites; just as the Cephalopoda or the Limacidæ are secured in their respective positions by the balance of the organization, in spite of their morphological reversions to prototypic forms.

These remarks being simply preliminary, I have not thought it appropriate or necessary to discuss doubtful points of classification, or to extend the subject to all its applications, preferring to leave a fuller consideration until I shall have completed the publication of the catalogue of the Cephalopoda, referred to previously as partly ready for publication in the *Bulletin* of the Museum of Comparative Zoölogy. Facts, however, have been brought out which sufficiently show that there are correlations between the two modes of manifesting vitality in the cycle of a single life and that of the collective life of the group to which the individual belongs.