CHAPTER XII.

Development—Relations of Reproduction and Development—Structure of the Ovum in relation to its Development — Primary Stage of the Developmental Process—Formation of the Blastoderm—Community of First Stage of Development—Von Baer's Law of Development—Second Stage of Special Development —Varieties of Ova—Development as seen in the various Subkingdoms—Nature of the Process in *Protozoa*—Third Stage of Development—" Nutritive Development "—Metamorphosis— " Retrograde " Development and Metamorphosis.

We have already noticed, in considering the subject of reproduction, the earlier or preparatory phases and actions which mark the production of a new individual or being. We have thus been led to notice that, throughout the animal series, the conditions under which the true sexual process of reproduction is effected, are primarily and essentially the same. These conditions are the contact of the " ovum " of the female with the " spermatozoids " of the male, and the subsequent and successful fertilisation of the germ, from which the future being is evolved. The process by which this evolution is accomplished is investigated under our present subject, that of *Development*, which thus may be said to chronicle the progress of those after-changes in the ovum that take their origin from the successful performance of the reproductive act.

And throughout the wide domain of physiological science there exists no subject of greater interest and importance than the present; involving as it does the tracing of the primitive germ after its fecundation through the various stages by which it gradually advances from the faint exhibition of vitality to the full maturity of adult and independent existence.

Our present aim will be most satisfactorily attained if we direct our attention to the phenomena of development in the highest animal forms, and thereafter extend our knowledge in a brief generalisation of the process of development throughout the leading or primary groups of the animal series; noticing, also, the various views which from time to time, and at various periods in scientific history, have been entertained respecting the chief points in the developmental process.

The structure of the ovum, and the disposition of its coverings, have been already described; but the essential points included in this description are worthy of being recapitulated in the present instance. Prior to impregnation, and as it lies in the "ovarium" or "ovary," we find the ovum (Fig. 21, C) surrounded by the coverings derived from the "ovisac" or vesicle in which it is developed and contained. Primarily, the ovum consists simply of the "germinal vesicle" and "germinal spot" (Fig. 21, B, *c d*). But gradually, and as development proceeds, we find the substance of the "yolk" or "vitellus" (*b*) to be formed around the primitive germinal centre; and then, finally, the "zona pellucida," or "vitellary membrane" (*a*), a nearly structureless membrane surrounding and enclosing the other and more important parts of the ovum, is developed, and the essential parts and structure of the egg are thus completed.

It is, however, to be borne in mind, that the structure thus described, is characteristic only of the "ovarian" ovum; that is, of the ovum as it lies in the ovary, and before any changes consequent upon impregnation take place. The parts thus enumerated, as already remarked in treating of reproduction, are common to the ova of all animal forms. Of these essential and common parts, however, the germinal vesicle and germ-spot are those which constitute the most important structures of the ovum, and which consequently are the seat of the important changes induced by the occurrence and progress of the developmental process.

To these primary and essential parts there are generally added, in the course of purely "ovarian" development, various structures, partaking of the nature of coverings or envelopes to the ovum. The nature, number, and disposition of these coverings vary greatly throughout the animal series; indeed, the differences between the ova of different forms may be regarded as depending almost entirely upon the varied nature of the ovular envelopes. Thus we find the ovum of *Mammalia* embedded in its "Graäfian vesicle" or "ovisac," which is bounded externally by an outer and inner tunic (Fig. 21, C, *g*); whilst closely applied to the inner tunic we find a layer of cellular matter known as the "granular membrane" (*f*), which near the ovum becomes developed to form a cellular investment to it, known as the "discus proligerus" or "granular zone" (*d*). And finally, imbedded within this latter structure, we find the ovum (*a*) itself, occupying a position generally near the external surface or "periphery" of the ovisac. The ovisac, in common with a number of similar and neighbouring vesicles, is embedded in the general tissue or "stroma" (*h*) of the ovarium.

In birds, we observe an illustration of the changes in the structure of an ovum, which a variation in the disposition of its envelopes or coverings may induce. The "yolk" of the Bird's ovum is of large size when compared with the "vitellus" of the Mammal; and the "vitellary membrane" is closely applied to the tunics of the "ovisac," no intervening "granular membrane" or "discus proligerus" being found in the ovarian ovum of the Bird. The characteristic coverings of the ovum in this latter case are formed and added to it in its descent through the oviduct. These coverings in the ovum of the Bird consist of the "albumen" or "white" of the egg; of the shell; and of the membranes pertaining to this latter structure. In their simplest form these latter parts constitute the "chorion" of the egg.

In size ova vary greatly; those of the highest animals being exceedingly minute; whilst in Reptiles, Birds, Fishes, and in many *Invertebrata*, we find limits of size, extending from a considerable magnitude to a small or even minute bulk. These remarks, however, apply chiefly to the envelopes and extrinsic parts of the ovum; the essential parts, namely the "germinal vesicle" and "germinal spot," preserving a very constant uniformity of size and minuteness throughout the series.

Regarding the constant and unvarying occurrence of the elements of sexual reproduction throughout the entire animal series, there is now little reason to entertain any doubt. The earlier ideas entertained on this subject did not assume the presence, in the lower forms, of organs strictly homologous and analogous with the ovaria and spermaria of the higher members of the series; but extended generalisation and research have fully proved in every instance, save in the *Protozoa*, the presence of true reproductive elements. And even in the case of *Protozoan* forms, there appears reason to believe that they are not entirely destitute of means, whereby a process very nearly resembling that of true sexual reproduction may be performed. Modern research has demonstrated the existence in the *Protozoa* of a developmental process, which, so far as the mere exhibition of phenomena is concerned, appears to imitate and fulfil, in the closest manner, the ascertained conditions and stages of development in higher forms. And if the "nucleus" and "nucleolus" of the *Protozoa*,—structures of almost invariable occurrence throughout the sub-kingdom (Fig. 22, A, *n*)—be considered equivalent to, and homologous with, the ovarium and spermarium of other animals, there can be little doubt that the phases of reproductive development witnessed in those lower forms are essentially those in which, as true animal forms, we should expect them to participate. The community of the process of development and reproduction, so far as all other animals are concerned, would tend to strengthen the belief and supposition that the *Protozoa*, in addition to the ascertained asexual modes of reproduction, should also possess the means for carrying on the truly sexual form of the process.

The subject and phenomena of development admit of a natural division into three successive groups or stages. The first of these divisions or stages includes those primary phenomena which are exhibited from the moment of impregnation, to the stage in development known as the "formation of the blastodermic membrane." The second and succeeding stage may be conveniently considered as including those phenomena and actions which mark the evolution of the new being, from the first appearance of the special and characteristic features of the embryo to the termination of embryonic life in its "birth," when the period of development proper may be said to end. The third stage or period includes the consideration of those ulterior changes, in form or structure, which the new being may undergo between the period of birth and the assumption or attainment of the adult, mature, and perfect form. This latter stage, therefore, embraces the investigation of the phenomena of "nutritive development" or "growth," and may be said in this way to be somewhat intermediate between the processes of reproduction and development on the one hand, and that of ordinary nutrition on the other.

To the details included under each of these three divisions we may devote such attention as the limits and nature of our present inquiries will allow; since it must be borne in mind that the present subject involves considerations of a highly technical nature, and which may more properly be considered as falling to the province of the comparative physiologist. Still it is necessary for the due information of the beginner in zoological studies, that some general ideas on the subject of development should be obtained; the clearer and better appreciation of many systematic points relating to this process being thereby greatly facilitated.

The first or primary stage of the developmental process extends from the time of impregnation of the ovum to the period of formation of the structure known as the "blastodermic membrane," or simply as the "blastoderm." The changes and phenomena observed in this first stage are essentially the same in the development of the ova of all animals; and therefore, by gaining a correct idea of the primary process in any one animal form, we become acquainted with the essential changes which take place in the early development of the ovum of any other animal. A very remarkable community of type is thus characteristic of animal development in its primary stages; and this fact, to be presently exemplified, is particularly worthy of being borne in mind; since its due recognition serves to refute and correct certain ideas and theories which formerly gave rise to much misconception regarding the entire subject of development.

We thus become aware of the important fact, that the ovum of any vertebrate, mollusc, annulose animal, cœlenterate,—and in all probability of any protozoön also,—exhibits in its earlier development a series of changes exactly corresponding in kind to those observed in the ovum belonging to any higher or lower type or sub-kingdom. The precursory phenomena observed in the ovum of the Mammal, in this way, correspond to those witnessed in the development of the *Cœlenterate Molluscous*, or of any other impregnated animal germ. Development in its earlier stages is thus essentially and invariably *general*. The changes therein observed are common to the entire animal series. Where differences exist, they are merely those of degree, and not of kind. Variations in the manner in which the plan of development may be executed, depending upon slight structural modifications, either in the ovum or in the circumstances of its development, do not affect the primary and typical course through which that development in its early history must proceed.

To the stages included in this first or primary development the collective term of "segmentation of the yolk" has been applied. As implied by this term, the process chiefly affects the "yolk mass" or "vitellus" of the "ovum;" and it also includes in its extent the "germinal vesicle" and "germinal spot," in which latter structures the essential parts of the ovum have been already remarked to reside.

In the ovum of the mammal, after impregnation, the initiatory stages of development are ushered in by the disappearance of the "germinal vesicle" (Fig. 21, C, *c*), and its contained "germinal spot;" the place of the

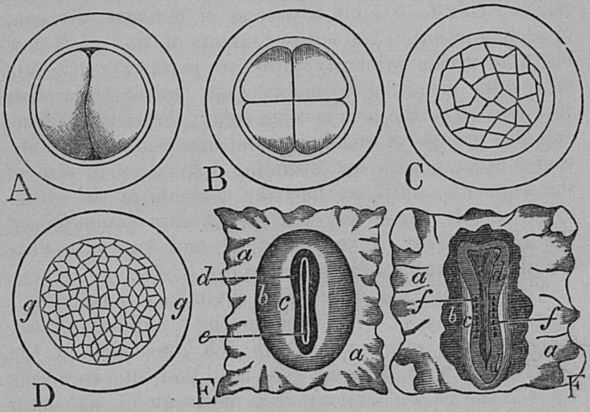

Fig. 25. Development of Mammalian Ovum.

A, First stage of segmentation of mammalian egg, showing its division into two halves. B, Second stage, in which the two primary segments are divided to form four. C, More advanced stage, in which the process of division has produced numerous segments. D, Complete segmentation of egg, known as the "mulberry-like condition;" *g g*, "zona pellucida" or "vitellary membrane." E, Progress of development as seen in ovum of dog (after Bischoff): *a a*, germinal membrane; *b*, area vasculosa; *c*, area pellucida; *d*, dorsal laminæ; *e*, primitive groove, bounded by the substance from which the cerebro-spinal nervous system is formed. F, Further development of E (Bischoff): *a a*, *b*, layers of germinal membrane; *c*, area vasculosa; *d d*, dorsal laminæ: *e*, placed on primitive groove, showing at its upper portion a dilatation corresponding to the primitive divisions of the brain; *f f*, vertebral plates or rudimentary vertebræ.

primary vesicle or cell, according to the majority of competent opinions, being taken by another and newly-formed cell, also of minute structure, and to which the general name of "embryo-cell" has been given. This "embryo-cell,"—so termed, because, from subsequent changes in its substance the future being may be said to be evolved —at first bears the same relation to the "yolk" as did the germ-vesicle and spot. Around the "embryo-cell" the yolk speedily gathers, and then, by a process of "cytogenesis" or cell-multiplication, we find the embryo-cell and yolk to exhibit a process of cleavage, division, or segmentation. The entire contents of the ovum now begin to divide primarily into two parts (Fig. 25, A); these two primitive segments soon resolve themselves into four (B); the four become eight; the eight sixteen; and this process of successive and increasing multiplication continues, with corresponding diminution in size of the segments, until we find the contents of the entire ovum finally presenting the appearance produced by the high degree of segmentation, and known as the "mulberry-like" condition of the egg (C D).

The "zona pellucida" or "vitellary membrane" (Fig. 25, D *g g*), still encloses the "mulberry-mass," and the next stage consists in the conversion of the segments of this mulberry-like condition into true cells by the formation around each segment of an outer envelope or cell-wall; the included portion of the yolk forming the cell-contents, whilst the little segment itself occupies the position of the central particle or "nucleus."

These newly-formed cells, which thus result from the segmentation of the yolk, now tend to arrange themselves, as represented in Fig. 26, A, *b b*, around the external surface or periphery of the yolk; there to form a membrane or cellular structure of considerable thickness, lining the internal aspect of the "vitellary membrane" (Fig. 26, A, *a a*), and leaving the interior or central portion of the yolk filled with a clear albuminous liquid. Thus we find the ovum in its present stage to consist, firstly, of the outer and original "vitellary membrane" (*a a*); secondly, of an inner membrane (*b b*), formed by the aggregation, near the periphery of the yolk, of the primitive cells resulting from its segmentation, and variously known as the "germinal membrane," "blastoderm," or "blastodermic vesicle," (Bischoff); whilst, lastly, we have the interior of the ovum occupied by the clear fluid already referred to.

With the formation of the "blastoderm" or "germinal membrane," the first stage of development may be said to terminate, and up to this point, therefore, the phases of development through which we have traced

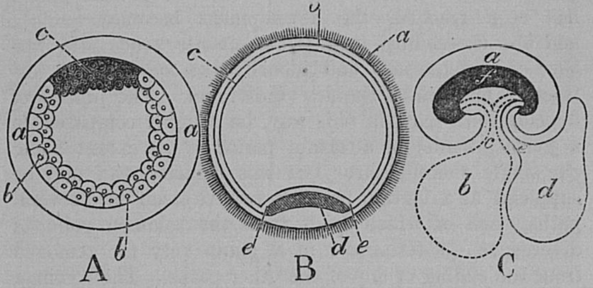

Fig. 26. DEVELOPMENT OF MAMMALIAN OVUM.

A, Formation of "blastoderm" or germinal membrane (*b b*), after complete segmentation, and appearance of germinal area (*c*): *a a*, vitellary membrane. B, Further development of ovum, showing vitellary membrane (*a*), covered with villosities, and constituting the "chorion;" *b*, cutaneous or serous layer of germinal membrane; *c*, mucous layer of germinal membrane; *d*, further development of germinal area to form the embryonic mass; *e e*, elevation of serous layer to form the dorsal laminæ. C, Relation of the embryonic sacs: *a*, inner layer of amnion, immediately investing the embryo (*f*); *b*, umbilical vesicle with its vitelline duct (*c*); *d*, allantois and its duct or "urachus" (*e*), which afterwards becomes the urinary bladder; *f*, embryo. (The figures are purely diagrammatic.)

the Mammalian ovum are common in a greater or less degree to the ova of all other animals. The succeeding series of changes, the consideration of which belongs to the second division of our subject, commence with the formation, at one point of the blastoderm, of an opaque spot (Fig. 26, A *c*), known as the "germinal area" or "area germinativa." This "area" becomes the seat of the more special phases of development, which the second division of the subject will lead us to consider.

Whilst, therefore, the ova of all animals exemplify the same stages of development up to the period of mulberry-segmentation and formation of the blastoderm, the similarity or homogeneity of developmental phases stops short at this point; and the development then assumes the ulterior phases characteristic of the particular type of being about to be evolved from the germ. Development up to the period of formation of the blastoderm is thus general to the entire animal series. After this period has been reached, the development becomes *special;* and the succeeding progress of events tends still further to differentiate and identify the special and distinctive features of the new individual. The process of development, may, in this way, be roughly compared to a journey made for a certain period of its extent along one single thoroughfare; but this primary road may be supposed at a certain point to resolve itself into several paths, each of which leads from the common point of divergence, to terminate in a point very far removed from the ending of any of the other paths. The common road corresponds to the primary process or earlier stages of development; the common point of divergence represents the stage of formation of the blastoderm; and the diverging paths represent the various tracts or directions, that is, the various sub-kingdoms or types, the distinctive characters of which will be evolved by the subsequent progress of development.

On the proper appreciation of these points depends the clear conception of Von Baēr's great law of development, the import of which lies in the enunciation of the principle we have just been enforcing—namely, that "development proceeds from the general to the special," or that 'the more special and characteristic features, progressively evolve themselves out of the more common and general.' The true and full import and value of such a generalisation is best observed when we consider the erroneous nature of the views and theories which its discovery tended to suppress. Thus, it was formerly supposed, that—taking the case of the human embryo as an example—the ovum of man passed in its development through successive phases, each of which corresponded to the *adult* or permanent condition of the inferior types of structure seen in the animal series. Or, referring the case to its actual details, it was supposed that the human embryo in its earliest stage of development corresponded to the simple protoplasmic body of the *Protozoön;* then as development proceeded, it was believed to evolve the features of the *Cœlenterate;* next appeared the characters of the *Annulose* animal; then it became like a *Mollusc*, and finally evinced the characters of the *Vertebrata*, passing in its latter stages through the successive forms of the fish, reptile, bird, and then assuming the aspects of the mammal and of man.

Such an idea is therefore embodied in Serres' phase, that "human development or organogenesis is a transitory comparative anatomy, as, in its turn, comparative anatomy is a fixed and permanent state of the organogenesis of man." In other words, the human ovum in its development exhibited a moving or panoramic view of the leading types of structure seen in the animal world; whilst these types, in turn, presented us with fixed views or stages of the progress of embryonic development in man. Such a theory, if proved to be true and worthy of belief, would materially tend to support and strengthen the hypotheses of evolution; since the embryology of the human form would present us with evidence of the gradual evolution of the higher forms from lower types of structure, substantiated and repeated in the cycle of development itself. But clearer views of the bearings of morphology upon development have shown us that the fixed structural type of an organism becomes demonstrable at a very early period in its embryonic history; that period corresponding to the formation of the "blastoderm;" and the evolution being thus not one of successive types, but in reality of the one and particular type to which the ovum belongs, and of which, consequently, the future being will become a member.

Thus the human embryo, immediately after the formation of the blastoderm, evinces the special characters of the vertebrate type of structure alone; and the progress of development only tends the further to specialise the already fixed and distinct type, and to develop the characteristic features successively of the mammal and of man. Similarly with the ovum of the Fish, Amphibian, Reptile, or Bird. The vertebrate type, and no other, is first evinced after the point of divergence common to all ova has been reached; and thereafter development specialises itself most highly in the case of the Bird, next in the case of the Reptile, still less highly in the case of the Amphibian, and least highly of all in the case of the Fish.

We thus see that not only is the type of structure to which any animal form belongs, distinctly specialised in the first instance, but its exact place and rank in the type itself are further determined by the degree of specialisation to which development may proceed. The first phase or tendency of development is therefore a morphological one, whilst its second phase is as distinctly physiological. In this way are the respective features of type, class, order, genus, and species, successively evolved. Hence, Von Baer's generalisation marks a significant era in the progress of philosophical biology. It gave a fresh impetus to the progress of research into the phases of development throughout the entire animal series; and at the same time constituted a new and important test and aid for the further generalisations and laws of morphology and physiology.

The unity of type, as displayed by the process of development, is further exemplified by instances in which the adult and permanent condition of a form low in the type is represented by the early or embryonic stages of another animal belonging to the same type or sub-kingdom, but of higher organisation than the former. Thus the young condition of a Crab, one of the higher *Crustaceans*, resembles the permanent condition of many of the lower Crustacea. And among the *Mollusca*, we find the well-known example of the young condition of many *Gasteropoda*, representing the permanent and adult condition of the *Pteropoda*—the former class represented by the Whelks, Snails, Sea-Lemons, etc.; whilst the latter group embraces a number of forms of minute size, which swim on the surface of the sea by means of a pair of wing-like organs or "fins."

Development, however, in the case of the crab becomes more highly specialised than in the case of the lower *Crustacean*. And, similarly, in the *Gasteropoda* the process of development, which at one stage produced a form resembling the adult *Pteropod*, continues beyond this stage, and eventually evolves a form of a much higher organisation than the last-mentioned animal. Nor has such a series of phenomena escaped the notice of the evolutionist, who, naturally enough, enlists these observations in the defence and support of his theory. But the transient likeness of a higher form to the mature state of a being lower in the type or sub-kingdom is susceptible of explanation on the ground of mere unity of type, and apart from any considerations respecting the common or connected origin of the forms. The likeness implies a morphological relationship apart from questions of origin or descent; and the explanation of the evolutionist is as insufficient to account for such resemblances as it is to explain why certain forms should evince a higher degree of specialisation than others, or why, for that matter of it, a *Vertebrate* ovum as yet unspecialised, should in one case tend, by development, to evolve the body of a fish, or, in another case, the form of a man.

The consideration of the second of the three stages into which we divided the process of development leads us to notice, in brief detail, the phenomena exemplified in the production from the primitive blastoderm of the characteristic embryonic form; and of the subsequent phases which culminate in the full development and birth of the embryo.

The first stage of development terminated with the formation of the blastoderm, and we had traced the production from the blastodermic surface of the "area germinativa" or "germinal area" (Fig. 26, A, *c*), in the substance of which the form of the embryo first appears. The blastoderm itself now becomes the seat of active change. We observe its rapid increase in thickness by the development of its cell-structures; and finally we can trace its subdivision into two distinct layers, each of which forms a primary and formative tissue in the embryonic form.

The outer or upper of these blastodermic layers is termed the "serous," "cutaneous," or "animal" layer (Fig. 26, B, *b*), since from this structure the rudiments of the vertebral column, the cerebro-spinal nervous axis, and the epidermis or general skin of the body are produced. The inner layer is known as the "mucous" or "vegetative" layer (Fig. 26, B, *c c*), and from this latter the general textures of the alimentary or nutritive system are formed. Latterly, and between these two primitive layers, a third and intermediate layer is developed, and to this third structure the term "vascular layer," or "vascular membrane," is given; the blood-vascular or circulatory apparatus, and other structures, being evolved from this particular source.

By the specialisation of these primary layers the entire embryonic form is ultimately produced, but the changes that ensue on the formation of the blastoderm have their more immediate seat in the "area germinativa," which we have already seen to be formed in the substance of the "germinal membrane" (Fig. 26, A, *c*). Within the "germinal area" a clear spot is next observed to form. This latter has, from its appearance, been accordingly termed the "area pellucida" (Fig. 25, E, *c*); and around the "area pellucida" the cells combine to form a marginal border, known as the "area vasculosa" (Fig. 25, E, *b*).

The "serous" and "mucous" layers of the germ both participate in the formation of these structures; but it is in connection with the "serous" layer of the "germinal area" that the next phase of development is observed to occur; this latter phase consisting in the formation of the so-called "primitive groove" or "trace" (Fig. 25, E, *e*). By the "primitive groove" is meant the shallow groove (*e*) formed in the centre of the "germinal area," and which lies between two projecting ridges of the serous layer (Fig. 26, B, *e e*), known as the "laminæ dorsales." Gradually these "laminæ" (Fig. 25, E, *d*) alter in form, and in consequence change the conformation of the "groove" they enclose, until they finally become of an elliptical shape, and unite together, thus converting the shallow "groove" into a tube or canal.

In the floor of the tube so formed the rudiments of the brain and spinal cord (Fig. 25, F, *e*) are next developed. Whilst beneath the floor of the tube the embryonic structure known as the "notochord," or "chorda dorsalis" (*e e*), is produced; this latter structure being replaced in greater part, and as the being advances towards maturity, by the vertebral column or spine. The first rudiments of the vertebral column itself make their appearance at this stage on the sides of the "primitive groove" in the form of square-shaped cells (Fig. 25, F, *f f*), which are known to the embryologist by the name of "primitive vertebræ."

The "dorsal laminæ," therefore, form the upper or "neural" tube of the *Vertebrate* body, and from the "laminæ dorsales" other two processes, or "ventral laminæ," are in turn produced downwards. And these latter, uniting below in the middle line, form a second tube parallel with the first-formed or "neural" canal. This second tube constitutes the "visceral" tube of the *Vertebrate* body, and forms the thoracic and abdominal cavities of the future being. In the primitive visceral cavity thus produced the rudimentary digestive tract is developed from the "mucous" layer, and the general outline of the body may in this way be said to have been sketched.

In connection with these three distinct layers of the germinal substance, of which the embryonic form is at first exclusively composed, we have to notice three distinct "sacs" or "vesicles," which make their appearance at an early stage of development, and which subserve each a special function in the embryonic economy. From the outer portion of the "serous" layer of the embryo the first of these sacs takes origin. This sac or vesicle is of a double nature, the outer fold becoming continuous with the "vitellary membrane," whilst the inner fold forms a protective sac, in which the embryo is contained. This serous sac is known as the "amnion" (Fig. 26, C, *a*), and it secretes a fluid termed the "amniotic fluid," or "liquor amnii," in which the embryo (*f*) floats and is contained.

The mucous layer, in turn, gives origin to the "umbilical vesicle" or "yolk-sac" (Fig. 26, C, *b*); a structure which communicates with the abdominal cavity by means of a constricted neck-like portion, known as the "vitelline duct" (*c*). The "umbilical vesicle" contains the unabsorbed portion of the yolk or "vitellus," and contributes directly to the nutrition of the embryonic form.

Lastly, from the "vascular" or intermediate layer of the "germinal membrane," a third sac is developed, and to this latter vesicle the term "allantois" has been applied. The "allantois" (Fig. 26, C, *d*) springs from the lower surface of the embryo, and communicates with the digestive tract, and with the rudimentary kidneys, or "Wolffian bodies," as they are termed. The function of the "allantois" is undoubtedly that of a respiratory organ, and in this capacity it serves to bring the blood of the embryo in contact with the external air, thus providing for its due aëration. In Birds the "allantois" assumes a large size and a high importance in the economy of the embryo. But in most *Mammalia* we find the "allantois" in connection with the "chorion," giving origin to a new and distinct structure, known as the "placenta;" the latter organ assuming the functions which formerly devolved upon the "allantois" itself. The portion of the "allantois" contained within the abdominal cavity, together with its pedicle or "urachus" (*e*), become finally converted, by the process of ulterior development, into the urinary bladder of the adult form.

The last structure in connection with the purely embryonic appendages which may here be alluded to is that known as the "chorion." This term is applied to the external envelopes of the embryo, constituted in chief by the ultimate development of the "vitelline membrane of the germ." The outer surface of the "chorion" at an early stage of development becomes shaggy or villous in appearance, from the presence of a number of minute projections or tufts (Fig. 26, B, *a*). These tuft-like processes, or "villi," gradually become more complicated and branched, and appear to subserve the function of nutrition in its earliest phase, by absorbing from the maternal surfaces the fluids necessary for the sustenance of the embryo. And finally, in the Mammal, we find the "allantois" becoming associated with the "chorion," to form the structure already alluded to under the name of the "placenta; on which latter organ the function of respiration, in the later stages of embryonic existence, chiefly, if not wholly, devolves.

The tracing, from the primary tissues, of the after-development of the various organs and systems of the body, falls to the province of the comparative anatomist and physiologist; and such an inquiry presents details of too technical a character for enumeration or description in the present work. The second stage progresses from these more general to more special developments, and terminates in the "birth" of the fully-developed embryo; that is, with its evolution from the maternal surfaces at a period when it is fitted to carry on the separate existence of the individual. Embryonic life thus ends, and individual existence begins.

The period at which the birth of the embryo may take place varies greatly throughout the animal series, as also does the entire duration of the developmental process. The relationship between the parent-body and the embryonic form also varies widely throughout the animal creation. Thus, in the lower forms of animal life, the ova, in the majority of instances, are not only impregnated external to the body, but the entire process of development is carried on in a manner entirely independent of parental care. To this rule there are, among the lower forms, undoubted exceptions; but the fact is, notwithstanding such exceptional cases, of the most generally applicable kind. In the lower forms we therefore find nothing approaching to that intimate connection between parent and offspring which is witnessed among the higher *Vertebrates.*

The *Vertebrata* exhibit in turn wide differences in the process of development, so far at any rate as relates to the duration of the developmental period, and to the relation between the parent and the impregnated germ. Thus in the Fishes, as constituting the lowest class of the Vertebrate sub-kingdom, the ova are generally impregnated without the body, and the subsequent development of the fecundated germ also takes place independently of, and external to, the parent-organism. Those forms which thus produce eggs, from which the young are afterwards developed, are known as "oviparous" animals. Some fishes and certain reptiles are "ovo-viviparous;" that is, the eggs are retained within the parent-body until the young are ready to be produced or hatched. In Birds, we find the "oviparous" mode of development united to a peculiar exhibition of parental care, by means of which the eggs are hatched through the warmth of the parent-body. In the bird the process of external development is carried out on the part of the parent to the same extent that internal development is shared in by the parent among the *Mammalia.* Impregnation in such cases, as also in the "ovo-viviparous" mode of development, may, and generally does, take place within the body of the parent, the ova being fertilised by the introduction within the female body of the male element. Lastly, in *Mammalia*, we find the "viviparous" mode of development exemplifying the highest form of relation between parent and embryo. Impregnation in this latter case is invariably internal, and the development of the ovum is also carried on within the maternal organism until the period of embryonic maturity is attained, when the new being is born alive into the world; this last feature constituting the essential part of the "viviparous" form of development. In conformity with this high specialisation of the process, we find corresponding adaptations of structure both in the ovum and in the structure of the parent-organism; these adaptations contrasting in the most striking manner with the analogous arrangements witnessed in lower forms. It is, however, peculiarly the province of the systematic zoologist to investigate the relative homologies and structure of the reproductive systems throughout the series of animal forms.

Finally, it is to be borne in mind that the mere manner of impregnation, or mode of development, is of secondary importance so far as the recognition and distinction of the truly "sexual" form of the reproductive process is concerned. We have already seen that the essential part of this process consists in the mere contact of the sperm-cell of the male with the germ-cell of the female; and it is therefore immaterial to the performance and constitution of the sexual reproductive act whether the contact or impregnation be effected external or internal to the body, or whether development be carried on without or within the parent-organism. The observation thus detailed will be found of value, since the relations between the processes of reproduction and development are exceedingly susceptible of mistake and confusion.

It has already been pointed out that the "germ vesicle" and "germinal spot," together with the "yolk" and "vitellary membrane," constitute the essential parts of every true ovum. And whilst this general statement is thoroughly correct, it is at the same time worthy of remembrance that the relative development of these parts, both before and after impregnation, varies greatly throughout the animal series. The comparative physiologist has accordingly been accustomed to divide ova into three great groups, taking the relative development and transformation of the "yolk" as the basis of his classification. Thus the first group includes those ova in which the entire yolk becomes segmented in the process of development; and of this group the egg of the Mammal may be cited as a typical representative. The second group, typified by the egg of the bird, and by that of many Invertebrate forms, embraces those ova in which only a portion of the yolk undergoes segmentation. Whilst the third group includes ova in which the process of cleavage, relatively to the yolk, appears to vary greatly; the results of segmentation being, in a certain degree, intermediate to those seen in the other two groups. The generally large size of the yolk in all classes of the animal series, save the *Mammalia*, has reference to the peculiar mode of development of the lower forms. The yolk constitutes, in all save the *Mammalia*, the source of nutritive supply to the embryo, whilst in these higher forms the embryonic form is nourished directly from the maternal tissues and fluids,—the large size, as well as the nutritive function of the yolk-mass, being thus rendered entirely useless in the Mammalian economy.

In briefly tracing the progress of development throughout the great subdivisions of the animal series we have firstly to consider the *Protozoa*, as in all probability presenting us with the same series of primary stages of development that we observe in the other sub-kingdoms; although further research is required ere we can make this statement as one of absolute certainty. Analogy alone would lead us, as previously remarked, to refer to the typical process of segmentation certain phenomena observed in the reproductive processes of the *Protozoa*.

Thus in *Gregarina*, one of the lowest of *Protozoan* forms

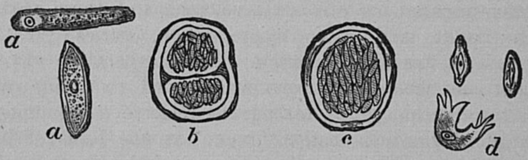

Fig. 27. GREGARINIDA.

Development of *Gregarina*: *a a*, adult *Gregarina*; *b*, encysted condition of *Gregarina* undergoing the reproductive process, showing "pseudonavicellæ" contained within the cyst; *c*, more advanced stage of *b*, the septum or partition having disappeared; *d*, free "pseudonavicellæ" escaping from cyst (*c*) by its rupture.

(Fig. 27, *a a*), we observe a series of phases in the course of the reproductive process which very closely resembles the stages of yolk segmentation in the ova of higher forms. Two *Gregarinæ* may be observed to coalesce together—or the series of changes about to be described may take place in a single individual—and the contained nucleus is observed to disappear. The organism now assumes a globular or spherical form, and appears to consist of a cyst-like body surrounded by a thickened wall. Soon the interior of this cyst becomes divided, apparently by a process of segmentation, into a number of spindle-shaped bodies (*b c*), to which the term "pseudonavicellæ" has been applied. By the subsequent rupture of the cyst, the "pseudonavicellæ" escape (*d*), and appear to require but little additional development to change them into the likeness of true *Gregarinæ*, resembling in every way the organism from which they sprang.

In considering the above and similar phenomena there does not appear any insuperable difficulty or objection to the idea that a lowly-specialised form of the developmental process of higher forms is therein represented. Analogy would thus seem to indicate that the *Gregarina*, in its reproductive phase, assumes the functions and form of a true ovum; the contained nucleus and nucleolus corresponding to the germ-vesicle and germinal spot. The disappearance of the nucleus would appear to represent the dissolution of the "germinal vesicle;" whilst the succeeding process by which the pseudonavicellæ are produced might, and not inaptly, be regarded as corresponding to the process of ovular segmentation. The stage of rupture of the Gregarina cyst would similarly correspond to the formation of the blastoderm in the ordinary ovum; the *Protozoan* development proceeding no further than this stage, but resulting, in virtue of its low degree of specialisation, in the simple evolution and production of the new beings.

In other and higher *Protozoa* a similar, and, in some cases, a better marked series of phenomena has been observed. Although, therefore, it would be inadmissible and premature to assert that the sexual process of reproduction and of ovular development is actually carried on in the *Protozoa*, we are sufficiently justified in stating that there are strong reasons, analogical and otherwise, for assuming that the processes known and ascertained to be present without exception in the higher groups of animal life, should be at least represented in these humbler forms. We cannot expect, it is true, that the process in the *Protozoa* should be as highly specialised as in the higher types. *Protozoan* development cannot be assumed or expected to attain the degree of specialisation evinced by that of the *Cœlenterate*, any more than the development of the *Cœlenterate* could be expected to be of as complicated or advanced a nature as that of the *Vertebrate*. It would appear, however, that this expectation has led observers to overlook the actual details of the process as it occurs in the *Protozoa;* and accordingly we find the idea strongly promulgated that the process of sexual reproduction, and of consequent development, is entirely absent or wanting throughout the lowest sub-kingdom or type of structure. But when we carefully notice the actual phenomena, and also observe the sequence in which these phenomena appear, it must be allowed that they more nearly approach and imitate the process of true ovular development than any other process in the living organism. If, on the contrary, we reject even the mere analogy of this process with that of ordinary "ovular" development, we necessarily place the *Protozoa* as unnatural exceptions to the most general and universal of rules; and, at the same time, leave the nature of the process observed in these forms entirely unexplained and unaccounted for.

The higher and succeeding sub-kingdoms present us with the characteristic phases of development we have already investigated. In the *Cœlenterata* the primitive blastoderm, formed after the segmentation of the yolk, divides into the two typical layers, the inner or "mucous," and the outer or "serous" layer. Cœlenterate development, beyond mere consolidation and fixation of external form, proceeds no further than this. The inner layer of the primitive blastoderm goes to form the "endoderm" of the perfect Cœlenterate (Fig. 8, *b*), whilst the outer blastodermic layer develops into the "ectoderm" or outer tissue of the perfect organism (Fig. 12, B, *a b*). There results, therefore, from this development, no specialisation of either neural or hæmal centres, and but a very imperfect development of the alimentary tract; since we have already seen, in our definition of the *Cœlenterate* type (Fig. 12, B), that the stomach-sac or digestive cavity (*e*) of these forms communicates freely with the cavity of the body (*f*).

The cavity formed in the early Cœlenterate embryo, after the separation of the blastodermic layers, corresponds to the somatic or body cavity of the perfect organism. The embryo would appear to be developed generally from the greater portion of the fertilised ovum; the initiatory stages of development being ushered in by the division or segmentation of the germ-vesicle. The embryonic form usually appears as a free-swimming ciliated body (Fig. 24, E), in the history of which the changes already described are soon manifested, and finally result in the production of the new being. The ova in *Cœlenterata* are further said to be, in the majority of instances, unprovided with a "vitellary membrane."

So far, therefore, as *Cœlenterate* development proceeds, it appears to present but little advance upon the phases seen in the *Protozoa*, the developmental nature of which phases we have already suggested and advocated. The *Protozoan* path, which diverges from the common point in the previously single developmental road, stops short at a very limited distance from the point of divergence; whilst the *Cœlenterate* road proceeds a little further, and leads us to more specialised detail. But the *Cœlenterate* path, in turn, stops short of the tracts leading to higher types of structure at a stage of its extent even earlier than that at which the *Protozoan* road ceases to be comparable with that of the *Cœlenterate*.

In the *Annulosa*, after the segmentation of the ovum, we find the characteristic and special phase of development to result in the transverse division of the primitive blastoderm ; the distinctive body-division of the annulose form being thus foreshadowed. The neural or nervous region becomes first developed, and the mouth soon comes to open on the lower or neural aspect of the body, towards which side the limbs are also turned.

In the *Mollusca*, the blastoderm is destitute of the definite segmentation so typical of the preceding type, and the hæmal or blood-vascular centres appear first in order of development. The mouth in this type of structure also opens on the neural aspect of the body.

Finally, in the *Vertebrata*, we have noticed that the appearance of the "primitive groove," with its dorsal and ventral "laminæ," constitute the special features of Vertebrate development, as distinguished from that of all other forms ; the mouth in *Vertebrata* being developed on the hæmal aspect of the body, towards which side of the body the limbs are directed. The neural region is first developed in the evolution of the Vertebrate form.

The third stage into which the subject of Development may be divided has reference to certain processes or phases incidental to the early life of many organisms, whereby they undergo a secondary development, generally possessing a more or less intimate connection with the nutrition and growth of the individual, and with certain subsequent and ulterior functions which the individual may be called upon to subserve. Viewed in this light, the third division of the subject may appropriately be termed that of *Nutritive Development.*

The principal series of phenomena which fall to be considered under this third division are those included under the general term of "transformation" or "metamorphosis." By this term we imply the series of changes through which an organism passes after its birth, and in its transition from the immature state in which it was produced, to the attainment of the mature and adult form. The form which undergoes this metamorphic process is therefore produced or evolved from the egg in an immature state of development ; the secondary development which it undergoes roughly representing or corresponding to the latter period of the developmental process, which, in ordinary cases, is carried on within the egg. The phenomena of "metamorphosis" are intimately associated with the process of nutrition, in that we see these phenomena most fully exemplified in cases where, from rapidity of development, or from insufficient nutritive supply on the part of the parent, or from both of these causes, the young form is prematurely introduced into the external world, in so far, at least, as its nutrition and growth are concerned. The process of "metamorphosis" also bears, as will be presently shown, a close connection with that of reproduction; inasmuch as the reproductive organs of the form thus prematurely produced partake of the imperfect development common to the entire form; and these latter organs, during the process of nutritive development, attain their full perfection, and thus arrive at maturity only when the fully-mature state has been reached. Hence the form which is the subject of the metamorphic process is generally sexless; or, if the reproductive organs be present, they are functionally useless. On the other hand, when the function of nutrition has been in a manner concluded, and when the being assumes its perfect and adult phase of existence, the reproductive function is then perfected and subserved. The probationary period passed in the metamorphic process is thus devoted to the assumption of those nutritive energies which the performance of the reproductive function will tend to waste and dissipate. We here notice an illustration of the law alluded to when treating of reproduction, and which has been elucidated by Spencer, Carpenter, and others—namely, that the functions of nutrition and reproduction act antagonistically and in opposition to each other.

As implied by the term "metamorphosis," the immature organism undergoes successive changes of form and structure; these changes affecting not merely superficial organs and parts, but involving the deeper-seated structures of the body. Although, therefore, the process of metamorphosis has been compared to the latter stages of ordinary development, the analogy between the cases is by no means perfect or complete. Thus, in the course of ordinary development, we have new parts or organs added successively to those which were already formed; these developed structures, with a few changes dependent on the process of ordinary growth, remaining to form definite parts, not only of the embryo, but also of the adult being. But in the metamorphic process we find that the embryonic organs characteristic of one stage of the process generally disappear, and are replaced by new and totally diverse structures, morphologically, as well as functionally, different from those of the preceding stage. And the process thus involves more than that of ordinary development. It necessitates and implies almost complete change, not only of external form, but also of internal structure; the phases of ordinary development tending to produce merely new and stable parts which do not alter, save in the processes of nutrition and growth.

Examples of the process of "metamorphosis" are plentifully scattered throughout the *Invertebrate* series. Among the *Annulosa, Annuloida, and Mollusca,* we find many illustrations of the process, the first-mentioned group probably presenting the greater number, and at the same time the most typical examples.

A familiar illustration of the process of metamorphosis is witnessed in the development of the Butterflies and Moths (Fig. 28), or in the case of the Beetles. From the egg of the Butterfly comes forth a crawling grub or caterpillar, known technically as the "Larva" (*a*). The preliminary stages of development have resulted in the production of this form, the structure of which is comparable in detail to that of a highly-organised worm; a creature this as unlike the perfect insect as could well be conceived. And as it resembles not the perfect form in appearance, so neither has it any kinship with its life or habits. It possesses a mouth fitted for mastication, and a digestive system adapted for the elaboration of a dietary different from that of the perfect form. It is provided with six true legs, and also with a number of fleshy locomotive appendages, known as "prolegs." And it is also generally furnished with an organ for the production of silk-material, which is used in the latter stage of its larval existence, to form a case or "cocoon" for its body.

The larval form, so constructed, spends its life wholly in the performance of the nutritive process. It eats voraciously, and usually increases enormously in bulk, changing its skin many times in the course of its exist-

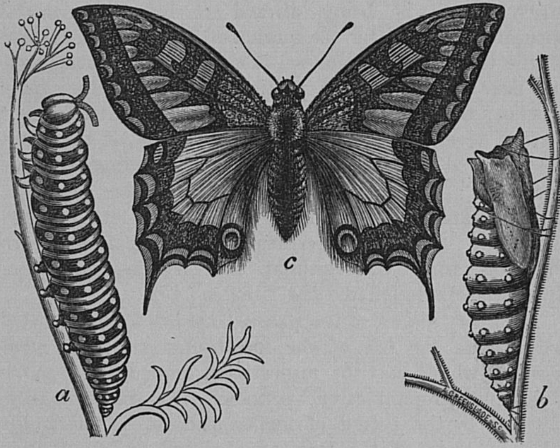

Fig. 28. Development and Metamorphosis.

Metamorphosis of the Swallow-tailed Butterfly (*Papilio Machaon*): *a*, Larva or Caterpillar; *b*, Pupa; *c*, Imago, or perfect form.

ence, to meet the exigencies of increasing size, the process of moulting being known as that of "ecdysis;" and so rapidly does it grow, that at the termination of this period of existence it will generally be found to have increased very many times in size from its original dimensions.

The larval stage is terminated by the preparation of a case-like structure or "cocoon," which varies widely in form and nature, throughout the insect-class. And in this cocoon it proceeds to enclose its body, and thus enters upon the second period of its metamorphic existence.

This second stage is known as that of the "pupa" or "chrysalis" (*b*). Viewed externally, the period would seem to be one of perfect quiescence, but changes of important extent are meanwhile proceeding within the pupa-case. The elements of the larval form are gradually being transformed into those of the adult. The masticatory mouth is being altered to form a suctorial apparatus, adapted for the suction of flower-juices, instead of the trituration of leaves. The digestive, circulatory, and nervous systems also participate in the metamorphic process; the reproductive organs similarly attain their perfect development; the rudimentary legs of the larva are replaced by those of the adult; the wings are now developed; and at the fitting period the pupa-case ruptures, and a bright, new, and perfect form escapes therefrom. This perfect creature, exercising its new-born functions amid the sunlight and flowers, has been appropriately designated the "imago" (*c*).

A cursory review of the phases thus briefly enumerated will divide the life of the insect-form into two great periods, which may be respectively named the "nutritive" and "reproductive" periods. The former is constituted by the period of metamorphosis, in which the whole energies of the form are devoted to its nutritive supply. The reproductive stage is constituted by the life of the perfect insect; and during this period we find the energies of the being devoted to the active perpetuation of the species. And recognising this division of the periods of functional activity in the light of the remarks already made when entering upon the subject of metamorphosis, we lastly observe that the process of metamorphosis is most fully exemplified in those cases where the demands upon the reproductive energies are very great, and where the existence or nature of the perfect form is generally of an ephemeral kind. The life of the perfect insect is, as a rule, of but short and limited duration; and we find this relative arrangement of the nutritive and reproductive periods of its life forming a most admirable illustration of the adaptive cycle, according to which the whole series of functions in the living organism operate and are arranged.

Among the *Crustacea*, we find the crabs and other forms exemplifying the metamorphic process; whilst among the *Annuloida*, as already noticed (Fig. 13), the *Echinodermata* exemplify a kindred series of developmental phases. In the latter instance we observe the "provisional larva" of the Echinoderm, furnishing a structure out of the materials of which the perfect form is built up and evolved. Such a phase, however, exemplifies the metamorphosis in a less perfect degree than does the case of the insect; the larval form of the Echinoderm being more truly of a provisional or temporary nature, and not possessing the same intimate relations with the perfect form as those borne by the larva of the insect to the adult "imago."

The term "retrograde" or "recurrent" development, is applied to certain cases of development, in which we find the larval or embryonic form presenting us with a structure evidently superior to that seen in the adult and perfect organism; the development of the adult apparently retrogressing from that of the larva. Thus, among *Crustacea*, the *Balani* or "Sea-acorns," and many allied forms, are free and locomotive in their earlier stages, and are then provided with eyes, organs of sense, and locomotive organs, and are otherwise adapted for an active existence. In their adult condition they become fixed and sessile, and are destitute of the organs of sense and appendages with which the embryonic form was provided. This "retrograde development" extends to all the structures of the body save the reproductive organs, which are developed in the adult form alone. In all probability the series of changes thus witnessed, and which are apparently so strange and inexplicable, have a close relationship with the reproductive or sexual phases of these forms; although regarding the exact nature of such a relationship we possess no definite knowledge.

The phenomena of "retrograde development" are also witnessed in cases of the conversion of healthy or normal tissues into diseased or abnormal textures; the pathologist, however, in such cases, being generally able to definitely determine the exciting or predisposing causes of the abnormal action.

The term "retrograde metamorphosis" has been given to a series of changes which a form, in itself of transitional nature, may undergo after the performance of its particular function or functions. Thus in the case of the Medusoid embryo of *Hydroid* zoophytes (Fig. 24, D), we occasionally notice that, after the performance of its reproductive function, the *Medusa* loses its bright crystalline appearance, shrivels up, and presents us with a form curiously altered from that in which we formerly beheld it; and in this state it may continue for a longer or shorter period prior to its dissolving away in the surrounding water.

The terms "retrograde metamorphosis" and "retrograde development" are frequently used as synonymous; but it appears to be more consistent with a correct rendering of their significance and relative meaning to distinguish between these terms. We should thus limit the term "retrograde *development*" to the distinction of phenomena, in which forms as adults, evince a retrogression in development from that seen in their embryonic state; the phrase being thus applied to organisms possessing a fixed, or at any rate more than a merely transitional nature. Thus the young *Balanus* or *Epizoön* is a form of distinct entity undergoing development. And similarly the expression "retrograde *metamorphosis*" should be limited to identify conditions, in which a form, in itself of merely transitory nature, exemplifies a retrogression. The retrogression in the *Medusa* is thus one not of "development," but merely of "metamorphosis;" the metamorphic retrogression in this latter case merely presaging the final dissolution of the transitory form.