
In this chapter Darwin presents strong evidence and logical thinking in support of gradual evolutionary change linking the members of all taxonomic group into a genealogical series. Why are all smaller groups of animals and plants, like species and families, naturally placed within larger groups, like orders, classes, and phyla? Why are the members of different classes of organisms so different from each other? Why can all living and extinct organisms be grouped together within the same few major taxonomic categories? Why are embryological characteristics so often used in grouping organisms? Why are identical larval stages so often found in such a wide variety of adult organisms? Why are atrophied or only partially developed, currently functionless organs so useful in placing organisms into their proper groups? Why are characteristics of seemingly minor physiological importance to an organism often so useful in classification? Why are some body parts that different animals use for greatly different purposes constructed on the same basic pattern? The most rational explanation for these and related questions is simple, says Darwin: The explanation is that all organisms living today have descended from common ancestors, with a great deal of change and extinction occurring over time. Thus our natural classification reflects a “community of descent.”

From the most remote period in the history of the world, people have noticed that living organisms resemble each other in descending degrees, so that groups of organisms lie within
other groups of organisms. The group Vertebrata, for example, contains seven other major groups, including the bony fish (Osteichthyes), the frogs and salamanders (Amphibia), the birds (Aves), and mammals (Mammalia, including humans). And each of those groups contains other groups. The Mammalia, for example, contains at least two major subgroups--marsupials and placental mammals. This classification of organisms, with groups contained within other groups, is not arbitrary, unlike the way that stars have been grouped to form constellations. The existence of these animal and plant groupings would have been of little significance if one group had been adapted to live exclusively on land and another for life in water; or one to feed on flesh, and another to feed on vegetable matter; and so forth. But the actual groupings are quite different: indeed, it is notorious how commonly the members of even any one sub-group differ in their lifestyles.

In Chapters 2 (on variation) and 4 (on natural selection), I attempted to show that within each country it is the most wide-ranging, much diffused, and common species---that is, the dominant species belonging to the larger genera in each class of organisms--that show the most variation in traits among individuals. It is these varieties that will ultimately become converted into new and distinct species; thus I have called these varieties “incipient species.” And these, on the principles of inheritance, tend to eventually produce other new and dominant species. Consequently, the groups that are now large and which generally include many dominant species tend to go on increasing in size over time. I further attempted to show that from the varying offspring of each species always trying to occupy as many and as different ecological niches¹ as

¹Darwin referred to what we now call “niches” as “places in the economy of nature.”
possible in nature, they tend constantly to diverge in character. This latter conclusion is supported by observing the great diversity of forms which, in any small area, come to compete mostly closely with each other and by certain facts in naturalization.

I also attempted to show that there is a steady tendency for the forms that are increasing in number and diverging in character to eventually supplant and exterminate the preceding, less divergent and less improved forms. If you turn to Figure 4.11 (reprinted below, from page 93 of *The Readable Darwin, Vol. 1*), which illustrates the action of these several principles that I have already discussed in detail, you will see that the modified descendants of any one ancestor inevitably become broken up over time into groups within groups. In the diagram, each letter (e.g., a, q, or b) on the uppermost line may represent one genus that includes a number of species, and all of the first eight genera along this upper line form together one taxonomic class, for all are descended from a single ancient parent (a member of original genus A) and, consequently, have inherited something in common. But the three genera on the left hand side of the figure (a-14, q-14, p-14) also have, on this same principle, much in common, and form a sub-family distinct from that containing the next two genera to the right (b-14 and f-14), which diverged from a different parent at the 5th stage of descent.

The members of these first five genera shown in the diagram also have much in common with each other, though less than when grouped in sub-families; and they form a family distinct from that containing the three genera (o-14, e-14, and m-14) still farther to the right in the diagram, which diverged from the other descendants of parent A at an even earlier period.
And all of the genera descended from ancestor (A) form a taxonomic order distinct from that which includes the genera descended from ancestor (I). So here we have many species descended from a single ancestor grouped into genera; and the genera are distributed among various sub-families, families, and orders, all under one great class. The grand fact of the natural subordination of living organisms into groups within groups which, from its familiarity, does not always strike us sufficiently, is in my judgment thus explained.
No doubt we could classify organic beings in many ways, as with all other objects, either artificially by single characters, or more naturally by a number of characters. We know, for instance, that minerals and the chemical elements can be thus arranged. In the case of minerals and elements, of course, the grouping has nothing to do with genealogical succession, and no cause can presently be assigned for their falling into groups. But with organic beings the case is different, and the view that I have just given above explains their natural arrangement in groups within groups very well. Indeed, no other explanation of this grouping has ever been attempted.

Naturalists, as we have seen, try to arrange the species, genera, and families in each class based on what is called the “Natural System.” But what is meant by such a “natural system”? Some authors look at it merely as a scheme for arranging together those living objects that are most like each other and for separating those that are most unlike each other, or as an artificial method of enunciating, as briefly as possible, various general propositions—giving in a single sentence the characteristics that all mammals have in common, for instance, and in another sentence stating the characteristics that all carnivores have in common, and then that all members of the dog genus have in common. And then, just by adding another sentence, they can give a full description for each kind of dog. The ingenuity and utility of this system are indisputable. But many naturalists think that something more is meant by this Natural System; they believe that it reveals the plan of the Creator. But unless it is be specified what is meant by “the plan of the Creator,” it seems to me that nothing is added to our knowledge. Expressions such as that famous one by the Swedish taxonomist Carl Linnaeus, namely that “the characteristics do not make the genus, but that the genus gives the characteristics,” seem to imply that some deeper bond is included in our classification system than mere resemblances. I believe that this is indeed the case, and that community of descent—the only known potential cause of close
similarity between groups of organic beings—is the bond that is partially revealed to us by our classifications.

Now let us consider the rules followed in classification, and the difficulties that are encountered if one believes that classification either gives some unknown “plan of creation,” or is simply a scheme for making general statements and placing together the forms which most resemble each other.

In ancient times, it was thought that those parts of the structure that determined the habits of life and the general place of each being in the economy of nature would be very important in classification; but nothing can be more false. No one regards the external similarity of a mouse and a shrew to be of any importance in classification, or that between a dugong and a whale, or between a whale and a fish. Those resemblances, though so intimately connected with the whole life of the being, are ranked as merely "adaptive or analogical characters." We shall return to this issue later. It may even be given as a general rule, that the less any part of an animal or plant’s organization is concerned with specialized habits, the more important it becomes for classification. For example, Sir Richard Owen, in speaking of the dugong, says, "The generative organs, being those which are most remotely related to the habits and food of an animal, I have always regarded as affording very clear indications of its true affinities. We are least likely in the modifications of these organs to mistake a merely adaptive for an essential character." With plants, how remarkable it is that the organs of vegetation, on which their nutrition and life depend, are of such little significance in suggesting relationships for classification, whereas the reproductive organs, along with their products, in the form of seeds and embryos, are of paramount importance! So again, in formerly discussing certain morphological characters that are not functionally important to an organism, we have seen that they are often of the highest
service in classification. This depends on their constancy throughout many allied groups; and their constancy chiefly depends on any slight deviations not having been preserved and accumulated by natural selection, which acts only on characters that affect survival and reproductive success.

That the mere physiological importance of an organ does not determine its value for classification is almost proven by the fact that in allied groups, in which the same organ seems to have nearly the same physiological value in all members, its value in classification is widely different. No naturalist can have worked with any group without being struck with this fact; and it has been fully acknowledged in the writings of almost every author. It will suffice to quote the highest authority, the Scottish botanist Robert Brown, who, in speaking of certain organs in the plant family Proteaceae, says that their importance in determining what genera they belong to "like that of all their parts, not only in this, but, as I apprehend in every natural family, is very unequal, and in some cases seems to be entirely lost." Again, in another work he says that the genera belonging to the plant family Connaraceae "differ in having one or more ovaria, in the existence or absence of albumen, in the imbricate or valvular aestivation. Any one of these characters singly is frequently of more than generic importance, though here even, when all taken together, they appear insufficient to separate members of the genus Cnestis from those of the genus Connarus." Let me give an example among insects: in one great division of the large insect order Hymenoptera, which includes the ants, wasps, and bees, the antennae, as Westwood has remarked, are extremely constant in structure, while in another division they differ much, and the differences

---

2 These flowering plants—about 1,000 species—are found mostly in tropical and subtropical parts of the southern hemisphere.

3 Two genera of tropical flowering plants found in the family Conaraceae.
are of quite subordinate value in classification. Yet no one will say that the antennae found in these two divisions of organisms belonging to the same order are of unequal physiological importance. *Any number of instances could be given of an important organ differing in how useful it is for purposes of classification within the same group of organisms.*

Similarly, no one will say that rudimentary or atrophied organs are of high physiological or vital importance to the organism that has them; yet, undoubtedly, organs in this condition are often of much value in classification. No one will dispute that the rudimentary teeth in the upper jaws of young ruminants\(^4\), and certain rudimentary bones of the leg, are extremely useful in demonstrating the close affinity between cows, sheep, deer and other ruminants and pachyderms, such as elephants and the rhinoceros. Similarly, Robert Brown has strongly insisted that the position of the rudimentary florets of grasses is of the highest importance in classifying them.

Numerous instances could be given of characters derived from parts that must be considered of very trifling physiological importance but that are universally admitted as being most useful in defining major groups. Here are some examples: whether or not there is an open passage from the nostrils to the mouth, the only character that, according to Sir Richard Owen, absolutely distinguishes fishes from reptiles; the inflection of the angle of the lower jaw in kangaroos, wallabies, and other marsupials; the manner in which the wings of insects are folded; mere color in certain algae; mere pubescence (soft down or fine short hairs on the leaves and stems of plants) on parts of the flower in grasses; and the nature of the skin covering among vertebrates—whether it is hair or feathers, for example. If the duck-billed platypus had been

---

\(^4\) Mammals such as cows, goats and sheep, that have a specialized stomach capable of fermenting ingested food before it is digested. There are about 150 ruminant species alive today around the world.
covered with feathers instead of hair, this external and trifling character would have been considered by naturalists to be an important aid in determining how closely related this strange creature is to birds.

**How important such trifling characters are for purposes of classification depends mainly on their being correlated with many other characters of more or less importance.**

The value indeed of an aggregate of characters is very evident in natural history. Thus it has often been remarked that a species may depart from its allies in several characters, both of high physiological importance and of almost universal prevalence, and yet leave us in no doubt where it should be ranked. Indeed, a classification founded on any single character, however important it may be, has always failed; for no part of the organization is invariably constant. The importance of an aggregate of characters, even when none are especially important by themselves, explains the aphorism enunciated by Linnaeus, namely, that the characters do not give the genus, but the genus gives the character; for this seems founded on the appreciation of many trifling points of resemblance, too slight to be defined. Certain tropical and subtropical flowering plants belonging to the family Malpighiaceae bear both perfect and degraded flowers; in the latter, as the French botanist Adrien-Henri de Jussieu has remarked, "The greater number of the characters proper to the species, to the genus, to the family, to the class, disappear, and thus laugh at our classification." When the asphead tree *Aspicarpa* produced in France, during several years, only these degraded flowers, which departed so wonderfully in a number of the most important points of structure from the accepted representatives of the order, yet M. Richard sagaciously saw, as A.-H.de Jussieu observes, that this genus should nevertheless be retained among the Malpighiaceae. This case well illustrates the spirit of our classifications.
When naturalists are at work, they do not trouble themselves about the physiological value of the characters they are using in defining a group or in allocating any particular species to a particular group. If they find a character that is nearly uniform, and that is common to a great number of forms, and not common to others, they use it as one of high value in classifying; if common to some lesser number, they use it as of subordinate value. This principle has been broadly confessed by some naturalists to be the true one for classifying organisms; and by none more clearly than by that excellent botanist, Augustin Saint-Hilaire. If several trifling characters are always found in combination, though no apparent bond of connection can be discovered between them, special value is set on them. In most groups of animals, important organs, such as those for propelling the blood, or for aerating it, or those for propagating the race, are found to be nearly uniform among species and are considered to be especially useful in classification; but in some groups all of these most important vital organs are found to offer characters of quite subordinate value. Thus, as Fritz Müller has lately remarked, all members of the ostracod genus *Cypridina* are furnished with a heart, while in the closely allied genera *Cypris* and *Cytherea*, there is no such organ; similarly, one species of *Cypridina* has well-developed gills, while another species is destitute of them.

---

5 A famous German biologist who spent much of his life studying natural history in the forests of Brazil. The phenomenon of “Müllerian mimicry” is named after him.

6 Ostracods are small, aquatic crustacean, a major arthropod group that also includes such larger organisms as krill, crabs, lobsters, and shrimp.
We can see why characters derived from the embryo should be of equal importance with those derived from the adult, for a natural classification of course includes organisms at all ages and stages of development. But it is by no means obvious, on the ordinary view, why the structure of the embryo should ever be more important for this purpose than that of the adult, which alone plays its full part in the economy of nature. Yet it has been strongly urged by those great naturalists, Henri Milne Edwards and Louis Agassiz, that embryological characters are the most important of all in deducing relationships; and this doctrine has very generally been admitted as true. There are, of course some exceptions owing to the adaptive characters of larvae not having been excluded; in order to show this, Fritz Müller, for example, tried using such characters alone in arranging the various members of the great class of crustaceans, and the arrangement did not prove a natural one.

**But there can be no doubt that early embryonic characters are of the highest value for classification, and not only with animals but with plants as well.** Thus the main divisions of flowering plants are in fact founded on differences in embryonic characteristics--on the number and position of the cotyledons, for example, and on the mode of development of the rudimentary shoot of an embryonic plant (the plumule) and the first part of the plant that emerges from the seed (the radicle)\(^7\). We can immediately see why these characters possess so high a value in classification, for the natural system is genealogical in its arrangement. Indeed, our classifications are often plainly influenced by chains of affinities. Nothing can be easier than to define a number of characters common to all birds; but with crustaceans, any such definition has hitherto been found impossible. There are crustaceans at the opposite ends of the series that have

---

\(^7\) The cotyledon is an embryonic leaf, while the radical grows downward into the soil, serving to anchor the seed.
hardly a character in common; yet the species at both ends, from being plainly allied to others within the grouping, and these to others, and so onwards, can be recognized as unequivocally belonging to this, and to no other class of arthropods.

Geographical distribution has often been used—though perhaps not quite logically—in classification, particularly in very large groups of closely related forms. The Dutch zoologist Coenraad Temminck insists on the utility or even necessity of this practice for certain groups of birds; and it has been followed by several entomologists and botanists as well.

Finally, with respect to the comparative value of the various groupings of species, such as orders, suborders, families, subfamilies, and genera, they seem to be, at least at present, almost arbitrary. Indeed, several of the best botanists have strongly insisted on their arbitrary value. I could easily give examples among plants and insects of groups that were first ranked by experienced naturalists as only genera, and which were later raised to the rank of a subfamily or family; this has not been done because further research has detected important structural differences that were initially overlooked, but rather because numerous allied species, with slightly different grades of difference, have been subsequently discovered.

All of the foregoing rules and aids and difficulties in classification may be explained, if I do not greatly deceive myself, on the view that our natural system is founded on descent with modification—that the characters which naturalists consider as showing true affinity between any two or more species are those which have been inherited from a common parent. That is, all true classification is genealogical, and community of descent is the hidden bond that naturalists have been unconsciously seeking, and not some unknown plan of creation, or the mere putting together and separating of objects that are more or less alike.
But I must explain my meaning more fully. Although I believe that the ARRANGEMENT of the groups within each class, in due subordination and relation to each other, must be strictly genealogical in order to be natural, I also believe that the AMOUNT of difference in the several branches or groups, though allied to the same degree in blood with their common ancient ancestor, may differ greatly, depending on how much modification they have undergone over time. This is expressed by the various species being ranked under different genera, families, sections or orders. To better understand my meaning, please take the trouble to refer to the diagram in Chapter 4⁸.

We will suppose that the letters A to L along the bottom of the figure represent allied genera that existed during the Silurian epoch⁹, and that all descended from some still earlier form. In three of these genera (A, F, and I), a species has transmitted modified descendants to the present day, represented by the fifteen genera (a-14 to z1-4) on the uppermost horizontal line. Now, all of these modified descendants from a single species are related in blood or descent to the same degree; they may metaphorically be called cousins to the same millionth degree. And yet they differ widely and to different degrees from each other. The forms descended from ancestor A, now broken up into two or three families of species, constitute a distinct order from those descended from ancestor I, whose descendants are now also broken up into two families. Nor can the existing species descended from ancestor A be placed in the same genus with the parent A, or those from ancestral parent I with parent I. But the members of existing genus F14 may be supposed to have been only slightly modified, and it will then rank with the parent genus F, just as some few still-living organisms belong to genera found in Silurian deposits. Thus that the comparative value of the

---

⁸ See page 4 of the present chapter, for a copy of that figure.

⁹ The Silurian geological period ran from about 444 million years ago to the beginning of the Devonian period, about 419 million years ago.
differences between these organic beings, which are all related to each other to the same degree in blood, has come to be widely different. Nevertheless, their genealogical arrangement remains strictly true, not only at the present time, but at each successive period of descent. All the modified descendants from ancestor A will have inherited something in common from their common parent, as will all the descendants from ancestor I; so will it be with each subordinate branch of descendants at each successive stage. If, however, we suppose any descendant of ancestor A or of ancestor I to have become so much modified as to have lost all traces of its parentage, its true place in the natural system will be lost to us, as seems to have occurred with some few existing organisms. All the descendants of genus F, along its whole line of descent, are supposed to have been but little modified, and they still form a single genus. But this genus, though much isolated, will still occupy its proper intermediate position.

The representation of the groups as given in the two-dimensional diagram, is really much too simple. The branches ought to have diverged in all directions. If the names of the groups had been simply written down in a linear series the representation would have been even less natural; and it is notoriously impossible to represent in a series, on a flat surface, the affinities that we discover in nature among the members of the same group. Thus, the natural system is genealogical in its arrangement, like a pedigree. But the amount of modification that the different groups have undergone has to be expressed by ranking them under different groups and subgroups, which we refer to as genera, subfamilies, families, sections, orders, and classes.

We can perhaps better understand this view of classification as a genealogical series by considering the case of human languages. If we possessed a perfect pedigree of mankind—showing exactly how each race is related to the other races and the order of their formation—
genealogical arrangement of the human races would afford the best classification of the various languages now spoken throughout the world; and if all extinct languages, and all intermediate and slowly changing dialects, were to be included, such an arrangement would be the only possible one. Yet it might be that some ancient languages had altered very little over time and had given rise to only a few new languages, whilst others had become altered a great deal, owing to the spreading, isolation, and state of civilization of the several co-descended races, and had thus given rise to many new dialects and new languages, all arising from the same initial tongue. The various degrees of difference between the languages of the same initial stock would have to be expressed by groups within groups. But the proper or even the only possible arrangement would still be genealogical; and this would be strictly natural, as it would connect together all languages, extinct and recent, by the closest affinities, and would give the relationships and origin of each tongue.

In confirmation of this view, let us glance at the classification of varieties that are known or believed to be descended from a single species. These are grouped under the species name, with the sub-varieties being grouped under the name of the particular varieties and, in some cases, as with the domestic pigeon, with several other grades of difference. Nearly the same rules are followed as in classifying species. Authors have insisted on the necessity of arranging such varieties on a natural instead of an artificial system. We are cautioned, for instance, not to class two varieties of the pineapple together merely because their fruit, though the most important part, happens to be nearly identical. No one puts the Swedish and common turnip together, even though the esculent and thickened stems are so similar.

Whatever part is found to be most constant is used in classing varieties. The great agriculturist William Marshall, for example, says that the cattle’s horns are very useful for this
purpose because they are less variable than the shape or color of the body, whereas with sheep
the horns are much less useful because they vary more among individuals. In classing varieties, I
realize that if we had an actual pedigree, a genealogical classification would be universally
preferred; and that has in fact been attempted in some cases. For we might feel sure, whether
there had been more or less modification, that the principle of inheritance would keep together
those forms that were allied in the greatest number of points. In tumbler pigeons, though some of
the sub-varieties differ in the important character of the length of their beak, yet all are kept
together in the same named group from having the common habit of tumbling in the air. But the
short-faced breed of tumbler pigeon has nearly or even completely lost this habit of tumbling;
even so, without any thought on the subject, these pigeons are kept in the same group. Why?
Because they are all clearly related by blood and are alike in some other respects, and thus
clearly belong to this tumbler variety.

With species in a state of nature, every naturalist has in fact unintentionally brought
descent into his classification, for he includes both sexes in the basic category of species. And
yet how enormously the two sexes sometimes differ in their most important characteristics is
known to every naturalist: scarcely a single fact can be predicated in common for adult males
and hermaphrodite individuals of certain barnacle species, and yet no one dreams of
categorizing them as separate species. Among orchids, plants that were for a long time placed
in three distinct genera (*Monachanthus, Myanthus, and Catasetum*) were immediately considered
to simply be varieties of a single species once it was known that all three types of flowers were
sometimes produced on the same plant; indeed, I have now shown that they are the male, female,
and hermaphrodite forms of the same species.
Similarly, the naturalist includes as one species the various larval stages of the same individual, however much they may differ from each other and from the adult. The same is true with the so-called alternate generations\(^\text{10}\) described for some parasitic worms by the Danish biologist Japetus Steenstrup, which can only in a technical sense be considered as the same individual, as they look so very different from each other and have such very different lives; he includes monsters and varieties as belonging to the same one species, not from their partial resemblance to the parent-form, but because they are all descended from it.

As descent from an original ancestor has universally been used in classing together the individuals of the same species, though the males and females and larvae are sometimes extremely different; and as it has also been used in classing varieties that have undergone a certain (and sometimes a considerable) amount of modification, may not this same element of descent have been unconsciously used in grouping species under genera, and genera under higher groups, all under the so-called natural system? I believe it has been unconsciously thus used. Indeed this is the only way that I can understand the several rules and guides that have been followed by our best systematists. As we have no written pedigrees, we are forced to trace community of descent by resemblances of any kind. Therefore, we choose those characters that are the least likely to have been modified in relation to the conditions of life to which each species has been recently exposed. Rudimentary structures on this view are as good as, or even sometimes better than other parts of an organism’s organization. We care not how

\(^{10}\) Here Darwin refers to an alteration between phases of sexual and asexual reproduction, not the alteration of diploid and haploid stages seen in some plants and algae.
trifling a character may be—let it be the mere inflection of the angle of the jaw, the manner in which an insect's wing is folded, whether the skin be covered by hair or feathers—if it prevail throughout many and different species, especially those having very different habits of life, it assumes high value for showing relationships; for we can account for its presence in so many forms with such different habits only by inheritance from a common parent. We may err in this respect in regard to single points of structure, but when several characters, let them be ever so trifling, concur throughout a large group of beings having different habits we may feel almost sure, on the theory of descent, that these characters have been inherited from an ancient common ancestor; such aggregated characters clearly have special value in classification.

We can now understand why a species, or a group of species, may depart from its relatives in several of its most important characteristics and yet still be confidently classed with them. This may be done with confidence—and is often done—as long as a sufficient number of other characters, let them be ever so unimportant, betrays the hidden bond showing community of descent. Even if two forms have not a single character in common, if these extreme forms are nevertheless connected together by a chain of intermediate groups, we may at once infer their community of descent and put them all into the same taxonomic category. As we find organs of high physiological importance—those which serve to preserve life under the most diverse environmental conditions—are generally the most constant, we attach special value to them; but if these same organs, in another group or section of a group, are found to differ much, we at once value them less in our classification. Later in this chapter we shall see why embryological characters are so especially useful in classification. Geographical distribution may sometimes also be brought usefully into play in classifying large genera, because all the species of the same
genus, inhabiting any distinct and isolated region, are in all probability descended from the same ancestral parents.

**Analogical Resemblances**

We can understand, on the above views, the very important distinction between real genealogical relationships and analogical resemblances caused simply by independent adaptations to the same environmental selective agents. Lamarck first called attention to this subject, and he has been ably followed by Macleay and others. The resemblance in the shape of the body and in the fin-like anterior limbs between dugongs and whales, for example, and between these two orders of mammals and fishes, are merely analogical (i.e., not indicating an evolutionary relationship). So is the resemblance between a mouse and a shrew-mouse (genus *Sorex*), which belong to different orders as is the still closer resemblance, insisted on by the English biologist St. George Jackson Mivart\(^1\), between the mouse and a small marsupial animal (genus *Antechinus*) of Australia. These latter resemblances may be easily accounted for, I believe, by adaptation for similarly active movements through thickets and herbage, and with concealment from enemies.

Among insects there are innumerable instances of such misclassification. For example, Linnaeus, misled by external appearances, actually classified a homopterous insect\(^2\) as a moth. We see something of the same kind even with our domestic varieties, as in the strikingly similar body shapes of the body in the improved breeds of the Chinese and common pig, which are descended from what turn out to be entirely different ancestral species, and in the similarly

---

\(^1\) Mivart was initially an ardent follower of Darwin’s theory of natural selection, but later become one of its fiercest opponents.

\(^2\) The homopterans include apids, cicadas, leaf hoppers, and scale insects, all of which have sucking mouthparts.
thickened stems of the common and specifically distinct Swedish turnip. The resemblance between the greyhound and the race-horse is hardly more fanciful than the analogies that have been drawn by some authors between other widely different animals.

On the view of characters being of real importance for classification only if they reveal descent from a common ancestor, we can clearly understand why analogical or adaptive characters, although of the utmost importance to the welfare of the organisms that possesses them, are almost valueless to the systematist. For animals belonging to two very separate and distinct lines of descent may have gradually become adapted to similar conditions, and thus have gradually assumed a close external resemblance; but such resemblances will not reveal—in fact will rather tend to conceal—their actual degree of blood-relationship. We can thus also understand the apparent paradox, that the very same characters are merely analogous with each other—and thus of no value in assessing relationships—when the members of one group are compared with the members of another group, but give true affinities when the members of the same group are compared with each other: thus the shape of the body and the fin-like limbs are merely analogous characteristics when whales are compared with fishes, being independent adaptations in both classes for swimming through the water; but between the several members of the whale family, the shape of the body and the fin-like limbs offer characters exhibiting true genealogical affinity: for as those parts are so nearly similar throughout the whole family, we cannot doubt that they have been inherited from a common ancestor. And so it is with fishes.

Numerous cases could be given of striking resemblances between single parts or organs that have been adapted for the same functions in quite distinct beings. A good instance is afforded by the close resemblance of the jaws of the dog and the Tasmanian wolf (Thylacinus
cynocephalus)

--animals that are placed widely apart in the natural classification system. But this resemblance is confined to general appearance, as in the prominence of the canines and in the cutting shape of the molar teeth. Closer inspection reveals that the teeth really differ a great deal in these two groups of animals: thus the dog has on each side of the upper jaw four pre-molars and only two molars, while Thylacinus has three pre-molars and four molars. The molars also differ greatly in the two animals in their relative size and structure. The adult dentition is preceded by a widely different milk dentition. Anyone may, of course, deny that the teeth in either case have been adapted for tearing flesh through the natural selection of successive variations; but if this be admitted in the one case, it is unintelligible to me that it should be denied in the other. I am glad to find that so high an authority as Professor William Henry Flower has come to this same conclusion.

The extraordinary cases given in Chapter 6 (“Difficulties with the Theory”) of widely different types of fishes possessing electric organs, of widely different insects possessing luminous organs, and of orchids and asclepiads both having pollen-masses with viscid discs, come under this same head of analogical resemblances. These cases are so wonderful that they were introduced by sceptics as difficulties or objections to our theory! In all such cases some fundamental difference in the growth or development of the parts, and generally in their matured structure, can be detected, indicating independent origins of the structures in the different groups. The end gained is the same, but the means, though appearing superficially to be the same, are essentially different. The principle formerly alluded to under the term of “analogical

---

13 The Tasmanian wolf is no more: it was rare in 1965, and extinct by 1982.

14 William Flower was a leading authority on mammals. In 1884 he was appointed as Director of the British Museum of Natural History in London, upon the retirement of Sir Richard Owen.
variation” has probably often come into play in these cases; that is, the members of the same
class, although only distantly allied, have inherited so much in common in their constitution that
they are apt to vary under similar exciting causes in a similar manner; and this would obviously
aid in the acquisition through natural selection of parts or organs strikingly like each other,
independently of their direct inheritance from a common ancestor.

As species belonging to different classes have often been adapted by successive slight
modifications to live under nearly similar circumstances--to inhabit, for instance, the three
distinctly different elements of land, air and water--we can perhaps understand how it is that a
numerical parallelism has sometimes been observed between the subgroups of distinct classes. A
naturalist, struck with a parallelism of this nature, by arbitrarily raising or sinking the value of
the groups in several classes (and all our experience shows that their valuation is as yet
arbitrary), could easily extend the parallelism over a wide range; and thus the septenary, quinary,
quaternary and ternary classifications have probably arisen.

There is another and especially curious class of cases in which a close external
resemblance between organisms that are not closely related to each other does not depend on
adaptation to similar habits of life, but has been gained for the sake of protection. I allude here to
the wonderful manner in which certain butterflies imitate, as first described by Mr. Henry Walter
Bates\(^\text{15}\), other and quite distinct butterfly species. This excellent observer has shown that in some
districts of South America, where, for instance, a clearwing butterfly species (genus *Ithomia*)
abounds in gaudy swarms, another butterfly, belonging to a different genus (*Leptalis*), is often

\(^{15}\) Have you ever heard of Batesian mimicry, in which one group of otherwise defenseless
organisms comes to possess the physical warning signals that characterize a different,
chemically-defended species? That’s the Bates that Darwin is talking about here, based on work
that Bates did in the rainforests of Brazil mostly in the1850’s.
found mingled in the same flock; and the latter so closely resembles the clearwing butterfly in every shade and stripe of color, and even in the shape of its wings, that Mr. Bates, with his eyes sharpened by eleven years of collecting, was, though always on his guard, continually deceived as to which species an individual belonged. When the mocker (i.e., the imitating) butterfly and the mocked (i.e., the imitated butterfly) are caught and compared, they are found to be very different in their essential structure, and to belong not only to distinctly different genera, but often to distinctly different families. Had this mimicry occurred in only one or two instances, it might have been passed over as a strange coincidence. But, if we proceed from a region where one *Leptalis* butterfly imitates an *Ithomia* butterfly, another mocking and mocked species belonging to the same two genera, equally close in their resemblance, may be found. Altogether no less than ten genera have been found that include some butterfly species that closely imitate other butterfly species. The mockers and the mocked always inhabit the same region; we never find an imitator living far from the form that it imitates. The mockers are almost invariably rare insects, whereas the mocked species in almost every case abounds in swarms. In the same district in which a species of *Leptalis* closely imitates a species of *Ithomia*, there are sometimes other lepidopterans mimicking the same *Ithomia* species: thus in the same place, butterfly species of three different genera and even a moth are found that all closely resemble a butterfly species that belongs to a fourth genus. It deserves special notice that many of the mimicking forms of the *Leptalis* butterfly, as well as of the mimicked forms, can be shown by a graduated series to be merely varieties of the same species, while others are undoubtedly distinct species. But why, it may be asked, are certain forms treated as the mimicked and others as the mimickers? Mr. Bates satisfactorily answers this question by showing that the form which is imitated keeps the usual
dress characteristic of the group to which it belongs, while the counterfeits have changed their
dress and no longer resemble their closest relatives.

We are next led to enquire why certain butterflies and moths so often assume the dress of
a different and quite distinct form; why, to the perplexity of naturalists, has nature condescended
to such tricks of the stage? Mr. Bates has, no doubt, hit on the true explanation. The mocked
forms, which always abound in numbers, must habitually escape destruction to a large extent,
otherwise they could not exist in such swarms. A large amount of evidence has now been
collected showing that they are distasteful to birds and other insect-devouring animals. On the
other hand, the mocking forms that inhabit the same district are comparatively rare, and belong
to rare groups; hence, they must suffer habitually from some danger, for otherwise, from the
number of eggs laid by all butterflies, they would in three or four generations swarm over the
whole country.

Now if a member of one of these persecuted and rare groups were to assume a dress so
similar to that of a well-protected, chemically-defended species that it continually deceived the
practiced eyes of an entomologist, it would often deceive predaceous birds and insects as well,
and thus often escape being eaten. Mr. Bates may almost be said to have actually witnessed the
process by which the mimickers have come to so closely resemble the mimicked; for he found
that some of the forms of the *Leptalis* butterfly that mimic so many other butterflies varied in an
extreme degree. In one district several varieties were found, and of these one alone resembled, to
a certain extent, the common *Ithomia* butterfly of the same district. In another district there were	wo or three varieties, one of which was much commoner than the others, and this one closely
mocked another form of *Ithomia*. From facts of this nature, Mr. Bates concludes that the *Leptalis*
first varies, and when a variety happens to resemble in some degree any common, chemically-
protected butterfly inhabiting the same district, this variety, from its resemblance to a flourishing and little persecuted kind, has a better chance of escaping destruction from predaceous birds and insects, and is consequently more likely to survive, "the less perfect degrees of resemblance being generation after generation eliminated, and only the others left to propagate their kind."

Here indeed we have an excellent illustration of natural selection in action.

Messrs. Robert Wallace and the British-South African entomologist Roland Trimen have likewise described several equally striking cases of imitation among the lepidopterans of the Malay Archipelago and Africa, and with some other insects. Mr. Wallace has also detected one such case with birds, although we have no examples involving the larger quadrupeds\textsuperscript{16}. The much greater frequency of imitation with insects than with other animals is probably a consequence of their small size. For one thing insects cannot defend themselves physically, excepting indeed the kinds furnished with a stinger, and I have never heard of an instance of such kinds mocking other insects, though they themselves are mocked by other species. Neither can insects easily escape by flight from the larger animals that prey on them. Therefore, speaking metaphorically, insects are reduced, like most weak creatures, to trickery and dissimulation: imitate a chemically-defended species, and become less vulnerable yourself.

It should be observed that the process of imitation probably never took place between forms that were widely dissimilar in color. But, starting with species that already resemble each other somewhat, a closer and closer resemblance, if beneficial, could readily be gained by the above means, and if the imitated form was subsequently and gradually modified through any agency, the imitating form would be led along the same track and thus be altered to almost any

\textsuperscript{16} Four-legged vertebrates, such as cattle, dogs and cats, and lizards
extent, so that it might ultimately assume an appearance or coloring wholly unlike that of the other members of the family to which it belonged.

There is, however, some difficulty with this explanation, for it is necessary to suppose in some cases that ancient members belonging to several distinct groups, before they had diverged to their present extent, accidentally resembled a member of another and protected group closely enough to afford some slight protection, this having given the basis for the subsequent, gradual acquisition of the most perfect resemblance.

On the Nature of the Affinities Connecting Organic Beings

As the modified descendants of dominant species belonging to the larger genera tend to inherit the advantages that made the groups to which they belong large and their parents dominant, they are almost sure to spread widely and to seize on more and more places in the economy of nature. The larger and more dominant groups within each class thus tend to go on increasing in size over time, and consequently supplant many smaller and feeble groups. Thus we can account for the fact that all organisms, both recent and extinct, are included within a few great orders and still fewer classes. To show just how few the higher groups are in number, and how widely they are spread throughout the world, consider this striking fact: the discovery and exploration of Australia has not added a single insect species belonging to a new class, and the same is true for the vegetable kingdom; and as I have learned from Dr. Hooker, it has added only two or three families of small size, all within existing classes.

In the chapter on geological succession (Chapter 11) I attempted to show, on the principle of each group having generally diverged much in character during the long-continued process of
modification, how it is that the more ancient forms of life often present characters that are to some degree intermediate between those of existing groups. A few of the old and intermediate forms have transmitted to the present day descendants that are but little modified from their ancestors; these constitute our so-called aberrant groups. The more aberrant any form is, the greater must be the number of connecting forms that have been exterminated and utterly lost. And we have evidence of aberrant groups having suffered severely from extinction, for they are almost always represented by extremely few species; and such species as do occur are generally very distinct from each other, which again implies extinction of the intermediate forms. The genera *Ornithorhynchus* (the duck-billed platypus) and *Lepidosiren* (the South-African lungfish), for example, would not have been less aberrant had each been represented by a dozen species, instead of as they are at present by a single species, or by two or three. We can, I think, account for this fact only by looking at aberrant groups as forms that have been largely conquered and exterminated by more successful competitors, with just a few members still preserved under unusually favorable conditions.

The English naturalist Mr. George Robert Waterhouse\(^{17}\) has remarked that when a member belonging to one group of animals exhibits an affinity to a quite distinct group, this affinity in most cases is general and not special: thus, according to Mr. Waterhouse, of all rodents, the bizcacha\(^{18}\) is most nearly related to marsupials; but in the points in which it

\(^{17}\) Years before the first edition of *The Origin of Species* was published, Waterhouse had been invited to accompany Darwin on the voyage of the Beagle, but had declined to do so. He later took possession of Darwin’s collection of mammals and beetles at the British Museum of Natural History, and wrote a book about the natural history of mammals.

\(^{18}\) These are also called viscachas; this is an informal group comprising two genera of chinchillas, which resemble rabbits, but have longer tails.
approaches this order, its relations are general, that is, not to any one marsupial species more
than to another. As these points of affinity are believed to be real and not merely adaptive and
representing convergent evolution, they must be due, in accordance with our view, to inheritance
from a common ancestor. Therefore, we must suppose either that all rodents, including the
bizcacha, branched off from some ancient marsupial ancestor, which will naturally have been
more or less intermediate in character with respect to all existing marsupials; or that both rodents
and marsupials branched off from a common ancestor, and that both groups have since
undergone much modification in divergent directions. On either view we must suppose that the
bizcacha has retained, by inheritance, more of the character of its ancient ancestor than have
other rodents; and therefore it will not be specially related to any one existing marsupial species,
but indirectly to all (or nearly all) marsupials, from having partially retained the character of their
common ancestor or of some early member of the group. On the other hand, of all marsupials, as
Mr. Waterhouse has remarked, members of the genus *Phascolomys*\(^\text{19}\) resemble most nearly not
any one species, but rather the general order of rodents. In this case, however, it may be strongly
suspected that the resemblance is only analogous, owing to *Phascolomys* having become adapted
to habits very similar to those of a rodent. The elder De Candolle has made nearly similar
observations on the general nature of the affinities of distinct families of plants.

On the principle of the multiplication and gradual divergence in character of the species
descended from a common ancestor, together with their retention by inheritance of some
characters in common, we can understand the excessively complex and radiating affinities by

---

\(^{19}\) *Phascolonus* was a genus of prehistoric Australian marsupials in the wombat family. The largest species,
*Phascolonus gigas*, weighed as much as 200 kg (450 lb). *Phascolonus* existed alongside an even larger marsupial,
*Diprotodon*, which weighed as much as three tons and was distantly related to wombats. Both disappeared at the
end of the Late Pleistocene in a Quaternary extinction event, together with many other large Australian animals.
which all the members of the same family or higher group are connected together. For the common ancestor of a whole family that is now broken up by extinction into distinct groups and subgroups will have transmitted some of its characters, modified in various ways and to various degrees, to all of the descendant species; consequently, these will all be related to each other by circuitous lines of affinity of various lengths (as may be seen in the diagram that I have been so often referring to), mounting up through many predecessors. As it is difficult to show the blood-relationship between the numerous kindred of any ancient and noble human family, even by the aid of a genealogical tree, and almost impossible to do so without this aid, we can understand how extraordinary difficult it is for naturalists to describe, without the aid of a diagram, the various affinities that they perceive to exist between the many living and extinct members of any one great natural class of organisms.

**Extinction, as we have seen in Chapter 4, has played an important part in defining and widening the gaps between the various groups in each class of organisms.** We may thus understand why classes of organisms are so distinct from each other--for instance, why birds are so distinctly different from all other vertebrate animals--by the belief that the many ancient forms of life that formerly connected the various early ancestors have been utterly lost. At one point in time, the early ancestors of birds were connected with the early ancestors of the other, and at that time less differentiated, vertebrate classes. Those intermediate forms are now extinct.

There has been much less extinction of the forms of life that once connected fishes with Batrachians. There has been still less within some whole classes, for instance the Crustacea, for here the most wonderfully diverse forms are still linked together by a long and only partially broken chain of affinities. Extinction has only defined the groups: it has by no means made them. For if every form that has ever lived on this earth were suddenly to reappear, a natural
classification, or at least a natural arrangement, would be possible. We can easily see this by turning to the diagram from Chapter 4 mentioned previously: the letters A to L can be thought to represent eleven ancient Silurian genera, some of which have produced large groups of modified descendants, with every link in each branch and sub-branch still alive, and the links not greater than those between existing varieties. In this case it would be quite impossible to give definitions distinguishing the several members of the several groups from their more immediate parents and descendants. Yet the arrangement in the diagram would still hold good and would be natural, for, on the principle of inheritance, all the forms that descended, for instance, from ancestor A, would have something in common. In a tree we can distinguish this or that branch, though at the actual fork the two unite and blend together. Although we could not, as I have said, define the several groups, we could nevertheless pick out types, or forms, representing most of the characters of each group, whether large or small, and thus give a general idea of the value of the differences between them. This is what we should be driven to if we were ever to succeed in collecting all the forms in any one class that have lived throughout all time and space. Assuredly we shall never succeed in making so perfect a collection. Nevertheless, in certain classes, we are making progress toward this end; and Milne Edwards has lately insisted, in an able and recent paper, on the high importance of looking to types, whether or not we can separate and define the groups to which such types belong.

Finally, we have seen that natural selection, which follows from the struggle for existence and which almost inevitably leads to extinction and divergence of character in the descendants of any one parent-species, explains that great and universal feature in the affinities of all organic beings, namely, their subordination in group within group. We use the element of descent in classing the individuals of both sexes and of all ages under one species, even though they may
have but few characters in common; we use descent in classifying acknowledged varieties as members of a particular species, however different they may be from their parents. I believe that this element of descent is the hidden bond of connection that naturalists have sought under the term of “the Natural System.” On this idea of the natural system being, in so far as it has been perfected, genealogical in its arrangement, with the grades of difference expressed by the terms genera, families, orders, etc., we can understand the source of the rules that we are compelled to follow in our system of classification. We can understand 1) why we value certain resemblances far more than others; 2) why we use rudimentary and useless organs, or others of trifling physiological importance, in deducing affiliations; 3) why, in finding the relations between one group and another, we summarily reject analogous or adaptive characters, and yet 4) why we can use these same characters within the limits of the same group. We can also clearly see how it is that all living and extinct forms can be grouped together within a few great taxonomic classes, and how the several members of each class are connected together by the most complex and radiating lines of affinities. We shall probably never disentangle the inextricable web of the affinities between the members of any one class; but when we have a distinct object in view, and do not simply look to some unknown “plan of creation,” we may hope to make sure but slow progress toward this end.²⁰

Professor Haeckel in his "Generelle Morphologie" and other works, has recently brought his great knowledge and abilities to bear on what he calls “phylogeny,” or the lines of descent of all organic beings from ancient ancestors. In drawing up the several series, he trusts chiefly to embryological characters, but receives aid from homologous and rudimentary organs, as well as

²⁰ The current availability of sophisticated molecular techniques and data analysis is now finally allowing us to do just that.
from the successive periods at which the various forms of life are believed to have first appeared in our geological formations. He has thus boldly made a great beginning, and shows us how classification will be treated in the future.

Morphology

We have seen that the members of any one class of organisms, independently of their habits of life, resemble each other in the general plan of their organization. This resemblance is often expressed by the term "unity of type," or by saying that the several parts and organs in the different species of the class are "homologous". The whole subject is included under the general term of Morphology. This is one of the most interesting departments of natural history, and may almost be said to be its very soul. What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should include similar bones, in the same relative positions to each other? And how curious it is, that the hind feet of the kangaroo, which are so well fitted for bounding over the open plains; and those of the climbing, leaf-eating koala, equally well fitted for grasping the branches of trees; and those of the ground-dwelling, insect or root-eating, bandicoots; and those of some other Australian marsupials, should all be constructed on the same extraordinary plan, namely with the bones of the second and third digits extremely slender and enveloped within the same skin, so that they appear as a single toe furnished with two claws. Notwithstanding this similarity of pattern, it is obvious that the hind feet of these several animals are used for as widely different

---

21 This term is still used today, and refers to traits with a common evolutionary origin; i.e., traits that have evolved from a common ancestor.
purposes as it is possible to conceive. The case is rendered all the more striking by the American opossums, which follow nearly the same habits of life as some of their Australian relatives, and yet have their feet constructed on the ordinary plan. Professor Flower, from whom these statements are taken, remarks in conclusion, "We may call this ‘conformity to type’, without getting much nearer to an explanation of the phenomenon;" and he then adds "but is it not powerfully suggestive of true relationship, of inheritance from a common ancestor?"

Geoffroy St. Hilaire has strongly insisted on the high importance of relative position or connection in homologous parts; they may differ to almost any extent in form and size and yet remain connected together in the same invariable order. We never find, for instance, the bones of the arm and forearm, or of the thigh and leg, transposed in any individual. That explains why the same names can be given to the homologous bones in widely different animals. We see the same great law in the construction of the mouths of insects: what can be more different than the immensely long spiral proboscis of a sphinx-moth, the curious folded proboscis of a bee or bug, and the great jaws of a beetle? Yet all these organs, although serving for such widely different purposes, are formed by infinitely numerous modifications of an upper lip, mandibles, and two pairs of maxillae. The same law governs the construction of the mouths and limbs of all the different crustaceans. And so it is with the many different flowers of plants.

Nothing can be more hopeless than to attempt to explain this similarity of pattern in members of the same class by utility or by the doctrine of final causes. The hopelessness of the attempt has been expressly admitted by Richard Owen in his most interesting work on the "Nature of Limbs." On the ordinary view of the independent creation of each being, we can only say that so it is: that it has pleased the Creator to construct all the animals and plants in each great class on a uniform plan. But this is not a scientific explanation.
On the other hand, the explanation is pretty simple on the theory of the selection of successive slight modifications in successive generations, each being profitable in some way to the modified form, but often also affecting, by correlation, other parts of the organism’s organization. In changes of this nature, there will be little or no tendency to alter the original pattern, or to transpose any of the parts. The bones of a limb might be shortened and flattened to any extent, becoming at the same time enveloped in thick membrane so as to serve as a fin; or a webbed hand might have all its bones, or certain bones, lengthened to any extent, with the membrane connecting them increased, so as to serve as a wing; yet none of these modifications would alter the framework of the bones or the relative connection of the parts. If we suppose that an early ancestor—the archetype, as it may be called—of all mammals, birds, and reptiles had its limbs constructed on the existing general pattern, for whatever purpose they served, we can at once understand the plain signification of the homologous construction of the limbs in all members of the class. And so it is with the mouths of insects: we have only to suppose that their common ancient ancestor had an upper lip, mandibles, and two pairs of maxillae, these parts being perhaps very simple in form; natural selection, over enormous periods of time, will then account for the infinite diversity in structure and function of the mouths of insects that we see today. Nevertheless, it is conceivable that the general pattern of an organ might become so much obscured as to be finally lost, by the reduction and ultimately by the complete abortion of certain parts, by the fusion of other parts, or by the doubling or multiplication of others, variations that we know to be within the limits of possibility. In the paddles of the gigantic extinct sea-lizards, for example, and in the mouths of certain suckorial crustaceans, the general pattern seems thus to have become partially obscured.
Here is another and equally curious branch of our subject: namely, “serial homologies,” which involves comparing the different parts or organs in the same individual rather than of the same parts or organs in different members of the same class. Most physiologists believe that the bones of the skull are homologous—that is, corresponding in number and in relative connection with the elemental parts of a certain number of vertebrae. The anterior and posterior limbs in all members of the higher vertebrate classes are plainly homologous. So it is with the wonderfully complex jaws and legs of crustaceans: they are built on the same basic plan in the members of all species. Similarly, the relative position of the sepals, petals, stamens, and pistils of a flower, as well as their intimate structure, makes sense only on the view that they consist of modified leaves arranged in a spire. In monstrous plants, we often get direct evidence of the possibility of one organ being transformed into another; and we can actually see, during the early or embryonic stages in the development of flowers, as well as in crustaceans and many other animals, that organs which become extremely different when mature are exactly alike earlier in development.

How inexplicable are such cases of serial homologies on the ordinary view of special creation! Why should the vertebrate brain be enclosed in a box composed of such numerous and such extraordinarily shaped pieces of bone apparently representing vertebrae? As Owen has remarked, the benefit derived from the yielding of the separate pieces of the mammalian skull during child-birth will by no means explain why the skulls of birds and reptiles are constructed in the same way. And why should similar bones have been created to form both the wing and the leg of a bat, structures used for totally different purposes, namely flying and walking? And why should one crustacean species that has an extremely complex mouth formed of many parts consequently always have fewer legs; or conversely, why should those crustacean species with many legs have simpler mouths? And with flowers, why should the sepals, petals, stamens, and
pistils in each flower, though fitted for such distinct purposes, all be constructed on the same pattern?

On the theory of natural selection, we can, to a certain extent, answer these questions. We need not consider here how the bodies of some animals first became divided into a series of segments, or how they became divided into right and left sides, with corresponding organs, for such questions are almost beyond investigation. Some serial structures probably result from cells multiplying by division, entailing the multiplication of the parts developed from such cells. It must suffice for our purpose to bear in mind that an indefinite repetition of the same part or organ is common, as Professor Owen has remarked, in all of the less specialized forms; therefore the unknown ancestor of the Vertebrata probably possessed many vertebrae; the unknown ancestor of the Articulata\textsuperscript{22}, many segments; and the unknown ancestor of flowering plants, many leaves arranged in one or more spires. We have also formerly seen that parts that are repeated many times in an organism are eminently liable to vary, not only in number, but also in form. Consequently, such parts, being already present in considerable numbers and being highly variable, would naturally provide the materials needed for adaptation to widely different purposes; yet they would generally retain, through the force of inheritance, plain traces of their original or fundamental resemblance. They would retain this resemblance all the more, as the variations that afforded the basis for their subsequent modification through natural selection would tend from the first to be similar, as the parts are alike in the early stages of growth, and would be subjected to nearly the same environmental conditions. Such parts, whether more or less modified, unless their common origin became wholly obscured, would be “serially homologous”.

\textsuperscript{22} An older taxonomic grouping that related the annelids and arthropods, both of which have many segments.
Among the molluscs (members of the phylum Mollusca), although the parts in distinct species can be shown to be homologous, only a few serial homologies can be indicated, such as the eight shell plates of chitons; that is, we are seldom able to say whether one part is homologous with another part in the same individual. And we can understand this fact quite easily, as among the molluscs, even in the least complex members of the group, we do not find nearly so much indefinite repetition of any one part as we find in the other great classes of the animal and vegetable kingdoms.

But morphology is a much more complex subject than it at first appears, as has been shown in a recent and remarkable paper by Mr. E. Ray Lankester. Mr. Lancester has drawn an important distinction between certain classes of cases that have all been equally ranked by naturalists as homologous. He proposes to call those structures that resemble each other in different animals, owing to their descent with modification from a common ancestor "homogenous"; resemblances that cannot thus be accounted for in that way, he proposes to call "homoplastic". For instance, he believes that the hearts of birds and mammals are as a whole homogenous--that is, they have all been derived over an enormous number of generations from a common ancestor. On the other hand, he believes that the four cavities of the heart in those two groups are homoplastic--that is, that they have been independently developed. Mr. Lankester also gives as evidence the close resemblance of the parts on the right and left sides of the body, as in humans, and in the successive segments of the same individual animal, as in earthworms; and here we have parts commonly called “homologous” but which bear no relation to the descent of distinct species from a common ancestor. Homoplastic structures are the same as those that I have referred to as analogous modifications or resemblances. Their formation may be attributed in part to distinct organisms--or to distinct parts of the same organism--having varied in an
analogous manner, and in part to similar modifications having been preserved for the same
general purpose or function, of which many instances have been given.

Naturalists frequently speak of the vertebrate skull as being formed of modified
vertebrae; and of the jaws of crabs as being modified legs; and of the stamens and pistils of
flowers as modified leaves. But it would in most cases be more correct, as Professor Huxley has
remarked, to speak of both skull and vertebrae, jaws and legs, and so forth as having been
modified, not one from the other as they now exist, but rather from some common and simpler
structure. Most naturalists, however, use such language only in a metaphorical sense: they are far
from meaning that during many generations of descent, primordial organs of any kind--vertebrae
in the one case and legs in the other, for example--have actually been converted into skulls or
jaws. Yet so strong is the appearance of this having occurred that naturalists can hardly avoid
employing language that has this very clear implication. But according to the views I have
presented here, such language may in fact be used literally! The wonderful fact of the jaws of a
 crab retaining numerous characters of true, but extremely simple legs, for instance, is at least in
part explained by recognizing that they probably did indeed retain those characteristics through
inheritance, over the course of many, many generations.

Development and Embryology

This is one of the most important subjects in the whole round of natural history. The
metamorphosis of insects, with which everyone is familiar, is generally abrupt, with transitions
from one stage to the next; but the transformations are actually numerous and gradual, although
concealed. A certain ephemeral insect\(^{23}\) (the “Mayfly,” *Chloeôn*) molts more than 20 times during its development, as shown by Sir J. Lubbock, and undergoes a certain amount of change each time; and in this case we see the act of metamorphosis performed in a very gradual manner. Many insects, and especially certain crustaceans, show us what wonderful changes of structure can be effected during development. Such changes, however, reach their acme in the so-called alternate generations of some of the lower animals. It is, for instance, an astonishing fact that a delicate branching hydrozoan, studded with polyps that resemble small sea anemones and attached to a submerged rock, should produce, first by budding and then by transverse division, a host of huge floating jellyfish! These jellyfish then go on to produce eggs, from which are hatched swimming microscopic larvae that eventually attach themselves to rocks and soon develop into branching polyps again… and so on in an endless cycle.

The idea that the processes of alternating generations and of ordinary metamorphosis are essentially identical has been greatly strengthened by Wagner's discovery that the larva or maggot of a certain small fly (*Cecidomyia*) asexually produces other larvae, and these larvae eventually develop into mature males and females and go on to propagate their kind in the ordinary manner by eggs and sperm. It may be worth notice that when Wagner's remarkable discovery was first announced, I was asked how was it possible to account for the larvae of this fly having acquired the power of a sexual reproduction. As long as the case remained unique no answer could be given. But now Grimm has shown that another fly, a species in the non-biting midge genus *Chironomus*, reproduces itself in nearly the same manner, and he believes that this occurs frequently among other species in the order. The main difference here is that it is the pupa, and not the larva, of

\(^{23}\) Members of the insect order Ephemoptera; the larval stages may live for years, but the adults rarely live for more than a day.
*Chironomus* that has this power; and Grimm further shows that this case, to a certain extent, "unites that of the Cecidomyia with the parthenogenesis of the Coccidae;" the term parthenogenesis implying here that the mature females of the Coccidae are capable of producing fertile eggs without any contribution from the male. Certain animals belonging to several classes are now known to have the power of ordinary reproduction at an unusually early age; and we have only to accelerate parthenogenetic reproduction by gradual steps to an earlier and earlier age--*Chironomus* showing us an almost exactly intermediate stage, viz., that of the pupa--and we can perhaps account for the marvelous case of the Cecidomyia.

It has already been stated that various parts may be exactly alike in the same individual during an early embryonic period, but become widely different and serve for widely different purposes in the adult. **So again it has been shown that although the embryos of the most distinct species belonging to the same class are generally closely similar, they become, when fully developed, widely dissimilar.** A better proof of this latter fact cannot be given than by the embryologist Karl von Baer’s statement that "the embryos of mammalia, of birds, lizards and snakes, probably also of turtles, are in the earliest states exceedingly like one another, both as a whole and in how their parts develop; so much so, in fact, that we can often distinguish the embryos of these widely different groups only by their size. In my possession are two little preserved embryos whose names I didn’t attach to the vials, and at present I am quite unable to say to what class of vertebrates they belong. They may be lizards or small birds, or even very young mammals, so complete is the similarity in the mode of formation of the head and trunk in these different animals. The extremities, however, are still absent in these embryos. But even if they had existed in the earliest stage of their development we should learn nothing, for the feet of
lizards and mammals, the wings and feet of birds, no less than the hands and feet of man, all arise from the same fundamental form."

The larvae of most crustaceans, at corresponding stages of development, closely resemble each other even though the adults may look very different; and so it is with very many other animals. A trace of the law of embryonic resemblance occasionally lasts until a rather late age: thus birds of the same genus, and of allied genera, often resemble each other in their immature plumage; we see this, for example, in the spotted feathers of young thrushes. In the cat tribe, most of the species when adult are striped or spotted in lines; and stripes or spots can be plainly distinguished in the whelp of the lion and the puma. We occasionally, though rarely, see something of the same kind in plants; thus the first leaves of the gorse plant (also known as the “furze,” genus *Ulex*) and the first leaves of the phyllodineous acacias, are produced on both sides of the stem or divided like the ordinary leaves of the pea and bean family, *Leguminosae*.

The points of structure in which the embryos of widely different animals within the same class resemble each other are often unrelated to their environmental conditions. We cannot, for instance, suppose that the peculiar loop-like courses of the arteries near the branchial slits during the embryonic development of vertebrates are related to similar conditions—in the young mammal that is nourished in the womb of its mother, in the egg of the bird that is hatched in a nest, and in the spawn of a frog under water. We have no more reason to believe in such a relation than we have to believe that the similar bones in the hand of a man, wing of a bat, and fin of a porpoise are related to similar conditions of life. And no one supposes that the stripes on a young lion, or the spots on the young blackbird, are of any use to these animals.

---

24 Members of the pea family, *Fabaceae.*
The case, however, is different when an animal, during any part of its embryonic career, is active and free-living, and has to provide for itself. The period of activity may come on earlier or later in life; but whenever it comes on, the adaptation of the larva to its conditions of life is just as perfect and as beautiful as in the adult animal. Sir J. Lubbock has recently shown in just how important a manner this has acted in his remarks on the close similarity of the larvae of some insects belonging to very different orders, and on the dissimilarity of the larvae of other insects within the same order, according to their habits of life. Owing to such adaptations the similarity of the larvae of allied animals is sometimes greatly obscured, especially when there is a division of labor during the different stages of development, as when the same larva has to search for food during one stage of development, and has to search for a place to attach during another stage. Cases can even be given of the larvae of allied species, or groups of species, differing more from each other than do the adults. In most cases, however, the larvae, though active, still obey, more or less closely, the law of common embryonic resemblance. Barnacles (intriguing members of the arthropod superclass Crustacea) afford a good example of this: even the illustrious Cuvier did not perceive that a barnacle was in fact a crustacean. But even a glance at the larva shows this in an unmistakable manner. So again the two main divisions of barnacles—the stalked and directly-attached barnacles—though differing widely in external appearance, have larvae that are, in all stages of their development, barely distinguishable from each other.

Embryos generally increase in organization as they develop. I use this expression even though I am aware that it is hardly possible to define clearly what is meant by an organism’s organization being “higher” or “lower”. But probably no one will dispute that a butterfly is higher (i.e., more complex in organization) than a caterpillar. In some cases, however, the mature animal must be considered as lower in the scale than the larva, as with certain parasitic
crustaceans. Let us consider barnacles once again: the larvae in the first stage have three pairs of locomotive appendages, a simple single eye, and a probosciformed mouth, with which they must feed a great deal, for they increase much in size as they develop. In the second larval stage of barnacle development, similar to the chrysalis stage of butterflies, the “cyprid” larva now has six pairs of beautifully constructed swimming legs, a pair of magnificent compound eyes, and extremely complex antennae. And yet, they have a closed and imperfect mouth in that stage, and cannot feed at all: the larva’s sole function, at this stage, is simply to explore solid surfaces, using their well-developed organs of sense, and to reach by their active powers of swimming a proper place on which to attach and to undergo their final metamorphosis to adult form. When this is completed they are fixed in that place for the rest of their lives: their legs are now converted into prehensile organs for feeding, and they indeed again obtain a well-constructed mouth. But they have no antennae, and their two complex larval eyes are now reconverted into a minute, single, simple eye-spot. In this last and complete state, adult barnacles may be considered as either more highly or more lowly organized than they were in the larval condition. But in some barnacle genera, some larvae become developed into simultaneous hermaphrodites having the ordinary structure, while others develop into what I have called “complemental males,” in which the male is now a mere sack that lives for only a short time and has neither mouth, stomach, or any other organ of importance, excepting those for reproduction.

We are so used to seeing a difference in structure between the embryo and the adult that we are tempted to look at this difference as in some necessary manner contingent on growth. But there is no reason why, for instance, the wing of a bat or the fin of a porpoise should not have been sketched out with all their parts in proper proportion as soon as any part became visible in

25 Each individual has both male and female reproductive organs.
embryonic development. In some whole groups of animals and in certain members of other
groups this is indeed the case, and the embryo does not differ widely from the adult at any stage
of development. Owen, for example, has remarked in regard to cuttle-fish26, “there is no
metamorphosis; the cephalopodic character of the animal is manifested long before the parts of
the embryo are completed.” Terrestrial snails and fresh-water crustaceans are born having their
proper forms, while the marine members of the same two great classes pass through considerable
and often great changes during their development. Spiders, again, barely undergo any
metamorphosis. In contrast, the larvae of most insects pass through a worm-like “caterpillar”
stage, whether they are active and adapted to diversified lifestyles and habitats or are inactive
from being placed in the midst of proper nutriment or from being fed by their parents; but in
some few cases, as in that of aphids, if we look to Professor Huxley’s admirable drawings of the
development of this insect, we see hardly any trace of the worm-like stage.

Sometimes it is only the earlier developmental stages that fail to appear. Thus, Fritz
Müller has made the remarkable discovery that the larvae of certain shrimp-like crustaceans first
develop into a simple nauplius larva and after passing through two or more zoeal stages, then
through a “mysis” stage before finally metamorphosing one last time to acquire their mature
structure. Now in the whole great malacostracan order to which these crustaceans belong, no
other member is as yet known to first develop as a nauplius larva, although many appear as
zoeas; nevertheless, Müller argues that if there had been no suppression of development in other
malacostracans, all crustaceans would have first developed as nauplii.

26 Cuttlefish are cephalopod molluscs, closely related to octopus and squid.
How, then, can we explain these several facts in embryology—namely, 1) the very general, though not universal, difference in structure between the embryo and the adult; 2) the various parts in the same individual embryo, which ultimately become very unlike and serve for diverse purposes, being very similar in early development; 3) the common, but not invariable, resemblance between the embryos or larvae of species belonging to the same class that look very different from each other as adults; 4) the embryo often retaining, while within the egg or womb, structures that are of no use to it, either at that or at a later period of life; 5) larvae that have to provide for their own wants being perfectly adapted to the conditions surrounding them; and lastly, 6) the fact of certain larvae being more structurally complex than the mature animal into which they develop? I believe that all these facts can be explained as follows.

It is commonly assumed that slight variations or individual differences seen among adults of any particular group necessarily appear early in development. We have little evidence on this point, but what we have certainly points the other way; for it is notorious that breeders of cattle, horses, and various fancy animals, cannot positively tell, until some time after birth, what will be the strengths and weaknesses of their young animals. We see this plainly in our own children; we cannot tell early on whether a child will be tall or short, or what his or her precise features will be. The question is not at what period of life any variation may have been caused, but rather at what period the effects are displayed. The cause may have acted, and I believe often has acted, on one or both parents before the act of generation. It is worth noticing that it is of no importance to a very young animal, as long as it is nourished and protected by its parent, whether most of its characters are acquired a little earlier or later in life. It would not matter, for instance, whether a bird that obtained its food by having a much-curved beak as an adult possessed a beak of this shape when young, as long as it was fed by its parents during that time.
As I stated in chapter 1, at whatever age any variation first appears in the development of the parent, it tends to reappear at a corresponding age in their offspring. Certain variations can only appear at corresponding ages; for instance, peculiarities in the caterpillar, cocoon, or imago states of the silk-moth can’t appear at other stages of development; or, again, in the full-grown horns of cattle. But variations which, for all that we can see, might have appeared equally well either earlier or later in life than we see them appear, likewise tend to reappear at a corresponding age in the offspring and parent. I am far from meaning that this is invariably the case, but it is a worthy generalization.

These two principles, namely, that slight variations generally appear at a not very early period of life and are inherited by offspring at a corresponding not early period in the next generation, explain, I believe, all the leading facts in embryology mentioned above. But first let us look at a few analogous cases in our domestic varieties. Some authors who have written on dogs maintain that the greyhound and bull-dog, though so different, are really closely related varieties and have descended from the same wild ancestral stock. I was therefore curious to see how far their puppies differed from each other. I was told by breeders that the puppies differed just as much as their parents, and this, judging by the eye, did seem to be almost to be the case. But on actually measuring the adult dogs and their six-day-old puppies, I found that the puppies had not yet acquired nearly their full amount of proportional difference. Similarly, I was told that the foals of cart and race-horses--breeds that have been almost wholly formed by careful selection over many generations under domestication--differed as much as the full-grown animals; but having had careful measurements made of the dams and of three-day-old colts of both race horses and heavy cart-horses, I find that this is by no means the case.
As we have conclusive evidence that all breeds of pigeon are descended from a single wild species, I compared the young pigeons within twelve hours after being hatched with characteristics of their parents. I carefully measured the proportions (but will not here give the details) of the beak, width of mouth, length of nostril and of eyelid, and size of feet and length of leg in the wild parent species and in pouters, fantails, runts, barbs, dragons, carriers, and tumblers. Now, some of these birds, when mature, differ in so extraordinary a manner in the length and form of the beak and in other characters, that they would certainly have been ranked as belonging to distinctly different genera if found in nature. But when the nestling birds of these several breeds were placed in a row, though most of them could just be distinguished, the proportional differences in the above specified points were incomparably less than in the full-grown birds. Some characteristic points of difference among the breeds--for instance, differences in the width of mouth--could hardly be detected at all in the young. I did, however, find one remarkable exception to the rule: the young of the short-faced tumbler differed from the young of the wild rock-pigeon and of the other breeds in almost exactly the same proportions as in the adult stage.

These facts are explained by the above two principles. Breeders select their dogs, horses, pigeons, etc., for breeding when their subjects are nearly grown up. They care not at all whether the desired qualities are acquired earlier or later in life, as long as the full-grown animal possesses them. And the cases just given, particularly that of the pigeons, show that the characteristic differences that have been accumulated by man's selection and that give value to his breeds do not generally appear at a very early period of life, and are inherited at a correspondingly not early period in development. But the case of the short-faced tumbler, which already possessed its proper characters when only twelve hours old, proves that this is not the
universal rule; for here the characteristic differences must either have appeared at an earlier period than usual or, if not so, the differences must have been inherited, not at a corresponding age, but at an earlier age.

Now, let us apply these two principles to species in nature. Let us take a group of birds, descended from some ancient form and modified through natural selection for different lifestyles. Then, from the many slight successive variations having supervened in the several species at a not early age, and having been inherited at a corresponding age, the young will have become but little modified, and they will still resemble each other much more closely than do the adults, just as we have seen with the breeds of the pigeon. We may extend this view to widely distinct structures and to whole classes of organisms. The fore-limbs, for instance, which once served as legs to a remote ancestor, may have become, through a long course of modification, adapted in one descendant to act as hands, in another as paddles, in another as wings; but on the above two principles the fore-limbs will not have been much modified in the embryos of these several forms, despite the great differences in fore-limb structure in adults. Whatever influence long continued use or disuse may have had in modifying the limbs or other parts of any species, this will chiefly or solely have affected it when nearly mature, when it was compelled to use its full powers to gain its own living; and the effects thus produced will have been transmitted to the offspring at a corresponding nearly mature age, as explained in a previous chapter. Thus the young will not be modified, or will be modified only in a slight degree, through the effects of the increased use or disuse of parts.27

---

27 As noted previously, there is still no evidence for this Lamarckian idea that structural changes gained through the use or disuse of parts are transmitted to offspring.
With some animals the successive variations may have supervened at a very early period of life, or the steps may have been inherited by offspring at an earlier age than that at which they first occurred. In either of these cases the young or embryo will closely resemble the mature parent-form, as indeed we have seen with the short-faced tumbler. And this is the rule of development in certain whole groups, or in certain sub-groups alone, as with cuttlefish, land-snails, fresh-water crustaceans, spiders, and some insects. With respect to the final cause of the young in such groups not passing through any metamorphosis, we can see that this would follow from the following contingencies: namely, from the young having to provide at a very early age for their own wants, and from their following the life-style of their parents; for in this case it would be indispensable for their existence that they should be modified in the same manner as their parents. Again, with respect to the singular fact that many terrestrial and freshwater animals do not undergo any metamorphosis in their development, while marine members of the same groups typically do pass through such transformations, Fritz Müller has suggested that the process of slowly modifying and adapting an animal to live on the land or in freshwater, instead of in the sea, would be greatly simplified by its not passing through any larval stage; for it is not probable that places well-adapted for both the larval and mature stages, under such new and greatly changed habits of life, would commonly be found unoccupied or ill-occupied by other organisms. In this case the gradual acquisition of the adult structure at an earlier and earlier age would be favored by natural selection… and all traces of former metamorphoses would finally be lost from the life history.

If, on the other hand, the young of some animal benefitted by following habits of life slightly different from those of the parent-form, and consequently to be constructed on a slightly different plan, or if it benefitted a larva that already looked different from its parent to change
still further, then, on the principle of inheritance at corresponding ages, the young or the larvae might be rendered by natural selection more and more different from their parents to any conceivable extent. Differences in the larva might also become correlated with successive stages of its development; so that the larva, in the first stage, might come to differ greatly from the larva in the second stage, as is the case with many animals. The adult might also become adapted for sites or habits in which organs of locomotion or of the senses, etc., would be useless; and in this case the metamorphosis would be retrograde, involving the loss of such organs and capabilities.

From the remarks just made we can see how by changes of structure in the young, in conformity with changes in lifestyles, together with inheritance at corresponding ages, animals might come to pass through stages of development that are perfectly distinct from the ancient condition of their adult ancestors. Most of our best authorities are now convinced that the various larval and pupal stages of insects have thus been acquired through adaptation, and not through simple inheritance from some ancient form. The curious case of Sitaris--a blister beetle that passes through certain unusual stages of development--will illustrate how this might occur. The first larval form is described by the French entomologist M. Jean-Henri Fabre as an active, minute insect that is furnished with six legs, two long antennae, and four eyes. These larvae hatch in the nests of bees. In the spring, when the male bees emerge from their burrows, which they do before the females, the blister beetle larvae spring on them, and afterwards crawl onto the females while they are still paired with the males. As soon as the female bee deposits her eggs on the surface of the honey stored in the cells, the Sitaris larvae leap onto the eggs and devour them. Afterwards the larvae undergo a complete change: their eyes disappear; their legs and antennae become rudimentary, and they feed on honey. Now they more closely resemble
ordinary insect larvae; ultimately they undergo a further transformation, and finally emerge as the perfect, normal beetle.

Now if an insect undergoing transformations like those exhibited by *Sitaris* were to become the ancestor of a whole new class of insects, the course of development of this new class would be widely different from that of any of our existing insects; certainly the first larval stage would not represent the former condition of any adult and ancient form.

On the other hand it is highly probable that with many animals the embryonic or larval stages give us a very good idea of what the ancestor of the whole group looked like as an adult. Among crustaceans, forms wonderfully distinct from each other, namely sectorial parasites, barnacles, entomostracans\(^{28}\), and even members of the Malacostraca all appear at first as minute, swimming nauplius larvae; and as these larvae live and feed in the open sea, and are not adapted for any peculiar habits of life, it is probable that an independent adult animal resembling a nauplius once existed, a very long time ago, and subsequently produced, along several divergent lines of descent, the above-named great crustacean groups. Similarly, the embryos of mammals, birds, fishes and reptiles seem very likely to be the modified descendants of some ancient ancestor that as an adult possessed gills, a swim-bladder, four fin-like limbs, and a long tail, all fitted for an aquatic life.

As all organic beings—both extinct and recent--which have ever lived can be arranged within a few great classes; and as all within each class have, according to our theory, been connected together by fine gradations, the best, and--if our collections were nearly perfect--the only possible arrangement, would be genealogical, descent from a common ancestor being the

\(^{28}\) Entomostracans were at the time one of two major groups of crustaceans, including copepods, ostracods, and branchiopods. Other crustaceans were included in the other major subgroup, the Malacostraca.
hidden bond of connection that naturalists have been seeking under the term of the “Natural System”. On this view we can understand how it is that, in the eyes of most naturalists, the structure of the embryo is even more important for classification than that of the adult. In two or more groups of animals, however much the adults may differ from each other in structure and habits if they pass through closely similar embryonic stages, we may feel assured that they are all descended from one and the same ancestor, and are therefore closely related. **Thus, similarities in embryonic structure reveal community of descent.**

On the other hand, dissimilarities in embryonic development do not disprove community of descent: the developmental stages may have been suppressed in one of any two groups, or may have been so greatly modified through adaptation to new habits of life as to be no longer recognizable. Even in groups in which the adults have been modified to an extreme degree, community of origin is often revealed by the structure of the larvae. We have seen, for instance, that barnacles, though externally so like oysters and other shellfish, are at once known by their larvae to be crustaceans. As the embryo often shows us more or less plainly the structure of the less modified and ancient ancestor of the group, we can see why the adults of ancient and extinct forms so often resemble the embryos of existing species of the same class. Agassiz believes this to be a universal law of nature; we may hope hereafter to see that law proved true. It can, however, be proven true only in those cases in which the ancient state of the group’s ancestor has not been wholly obliterated, either by successive variations having supervened at a very early period of growth, or by such variations having been inherited at an earlier age than that at which they first appeared. It should also be borne in mind that although the law may very well be true, it may remain for a long period--or forever--incapable of being convincingly proven, owing to the geological record not extending far enough back in time. The law will not strictly hold good
in those cases in which an ancient form became adapted in its larval state to some special line of life, and transmitted the same larval state to a whole group of descendants; for such larvae will not resemble any still more ancient form in its adult state.

Thus, it seems to me that the leading facts in embryology, which are second to none in importance, are explained very simply as follows: variations in the many descendants from some particular ancient ancestor, having appeared at a not very early period of life, have been inherited at a corresponding period. The study of embryology rises greatly in interest when we look at the embryo as a picture, more or less obscured, of the ancestor--either in its adult or larval state--of all the members of the same great class.

**Rudimentary, Atrophied, and Aborted Organs**

Organs or parts in this strange condition, bearing the plain stamp of uselessness, are extremely common, or even general, throughout nature. It would be impossible to name any one of the higher animals in which some part or other is not now in a rudimentary condition. Among the mammals, for instance, the males possess rudimentary mammary glands; in snakes one lobe of the lungs is rudimentary; in birds the small, freely-moving alula on the leading edge of the wings of modern (and some extinct) birds (also called the "bastard-wing") may safely be considered as a rudimentary digit, and in some species the whole wing is so far rudimentary that it cannot be used for flight. And what can be more curious than the presence of teeth in fetal whales, which when grown up have not a tooth in their heads; or the teeth, which never cut through the gums, in the upper jaws of unborn calves?

Rudimentary organs plainly declare their origin and meaning in various ways. There are beetles belonging to closely related species, or even to the same identical species, which have
either full-sized and perfect wings, or mere rudiments of membrane that often lie under normal wing-covers firmly soldered together; and in these cases it is impossible to doubt that the rudiments represent wings. Rudimentary organs sometimes retain their potentiality; this occasionally occurs with the mammaries of some male mammals, which have been known to become well-developed and to secrete milk. So again in the udders of the cow genus *Bos*, there are normally four developed and two rudimentary teats; but the latter in our domestic cows sometimes become well-developed and yield milk. In regard to plants, the petals are sometimes rudimentary and sometimes well developed in different individuals of the same species. In certain plants that have separate sexes, Kolreuter found that by crossing one species in which the male flowers included a rudiment of a seed-producing pistil with a hermaphrodite species having of course a well-developed pistil, the pistil rudiment in the hybrid offspring was much larger; this clearly shows that the rudimentary and perfect pistils are essentially alike in nature.

An animal may also possess some parts in a perfect state, perfectly developed, and yet they may be useless, and thus in this sense still be considered to be “rudimentary.” For example, the tadpole of the common salamander or water-newt, as Mr. G.H. Lewes remarks, "has gills, and passes its existence in the water; but the *Salamandra atra*, which lives high up among the mountains, brings forth its young full-formed, with no specialized free-living larval stage\(^29\). This animal never lives in the water. Yet if we open a gravid female, we find tadpoles inside her with exquisitely feathered gills; and when placed in water they swim about like the tadpoles of the water-newt. Obviously this aquatic organization of the tadpole has no reference to the future life

---

\(^{29}\) This is now referred to as “direct development:” the embryo develops directly into the adult morphology without passing through a free-living larval stage.
of the animal, nor has it any adaptation to its embryonic condition; it has solely reference to ancestral adaptations, it repeats a phase in the development of its progenitors."

An organ that serves two different purposes may become rudimentary or utterly aborted for one—even the more important—purpose, and yet remain perfectly efficient for the other. Thus, in plants, the role of the female pistil is to allow the pollen-tubes to reach the ovules within the ovarium. The pistil consists of a stigma supported on the style. But in some members of the widespread angiosperm family Compositae, the male florets, which of course cannot be fecundated, have a rudimentary pistil, for it is not crowned with a stigma; but the style remains well developed and is clothed in the usual manner with hairs that serve to brush the pollen out of the surrounding and conjoined anthers. Again, an organ may become rudimentary for its proper purpose and be used instead for a distinctly different one: in certain fishes, for example, the swim-bladder seems to be rudimentary for its proper function of achieving buoyancy, but has become converted into a nascent breathing organ or lung. Many similar instances could be given.

Useful organs, however little they may be developed, ought not to be considered as rudimentary unless we have reason to suppose that they were formerly more highly developed. They may be in an early stage of development progressing towards further development. On the other hand, truly rudimentary organs are either quite useless, such as teeth that never cut through the gums, or almost useless, such as the wings of an ostrich, which serve merely as sails. As organs in this condition would formerly, when even less well-developed, have been of even less use than at present, they cannot formerly have been produced through variation and natural

---

30 This is a very good example of something that makes sense only in the context of evolution. The adults are fully terrestrial, and their offspring are born as miniatures of the adults. And yet there is a well-formed tadpole larva in the life-history, which basically metamorphoses before birth.

31 Includes daisies, asters, and sunflowers.
selection, which acts solely by the preservation of useful modifications. They have instead been partially retained by the power of inheritance, and relate to a former state of things when they did perform a useful function. It is, however, often difficult to distinguish between rudimentary organs and nascent organs—organs at an early stage of evolutionary development; for we can judge only by analogy whether a part is capable of further development, in which case it deserves to be called “nascent”. Organs in this condition will always be somewhat rare; for beings thus provided will commonly have been replaced by their successors with the same organ in a more perfect state, and consequently will have become extinct long ago. The penguin’s wing, for example, is of high service to the animal, acting as a fin when the penguin is swimming; it could, therefore, represent the nascent state of the wing. Not that I believe this to be the case: it is more probably a reduced organ, modified for a new function. But a nascent function is still an interesting possibility. The wings of the flightless kiwi bird in New Zealand (genus *Apteryx*), on the other hand, is quite useless, and is truly rudimentary. Richard Owen considers the simple filamentary limbs of the South American lungfish, *Lepidosiren paradoxa*, as the "beginnings of organs which attain full functional development in higher vertebrates."

However, according to the view lately advocated by Dr. Gunther, they are probably the remnants of a formerly better-developed condition, consisting of the persistent axis of a fin, with the lateral rays or branches aborted. The mammary glands of the duck-billed platypus of Australia (*Ornithorhynchus anatinus*) may be considered, in comparison with the udders of a cow, as in a nascent condition. Similarly, the egg-retaining ovigerous frena” of certain barnacles that no longer provide attachment to the developing eggs (“ova”) and are feebly developed, are probably nascent branchiae.
Rudimentary organs found in individuals of a single species are very liable to vary in their degree of development and in other respects in closely related species; the extent to which the same organ has been reduced occasionally differs a good deal. This latter fact is well exemplified by the state of development in the wings of female moths belonging to the same family. Rudimentary organs may be utterly aborted; this implies that in certain animals or plants, parts are entirely absent, where analogy would lead us to expect to find in them, and which are occasionally found in monstrous individuals. Although in most species found within the plant family Scrophulariaceae, the fifth stamen is utterly aborted, yet we may conclude that a fifth stamen once existed, for a rudiment of it is found in many other species within the family; in fact, this rudiment occasionally becomes perfectly developed, as is sometimes seen in the common snap-dragon. In tracing the homologies of any part in different members of the same class of organisms, nothing is more common, or, more useful in understanding the relations of the parts than the discovery of rudiments. This is well shown in the drawings given by Richard Owen of the leg bones of the horse, ox, and rhinoceros, which show very clearly that all are related.

Rudimentary organs, such as teeth in the upper jaws of whales and in cows, sheep and other ruminants, can often be detected in the embryo, but wholly disappear as development continues. It is also, I believe, a universal rule that a rudimentary part is larger in the embryo, relative to the adjoining parts, than in the adult; thus the organ at this early age is less rudimentary, or cannot even be said to be rudimentary in any degree. Hence rudimentary organs in the adult are often said to have retained their embryonic condition.

I have now given the leading facts with respect to rudimentary organs. In reflecting on them, all readers must be struck with astonishment: for the same reasoning power which tells us
that most body parts and organs are exquisitely adapted for certain purposes tells us with equal
plainness that rudimentary or atrophied organs are imperfect and useless. In works on natural
history, rudimentary organs are generally said to have been created "for the sake of symmetry,"
or in order "to complete the scheme of nature." But this is merely a restatement of the fact, not an
explanation. Nor is it consistent with itself. The boa-constrictor, for example, has rudiments of
hind limbs and of a pelvis; if it be said that these bones have been retained "to complete the
scheme of nature," why, as Professor Weismann asks, have they not been retained by other
snakes, which do not possess even a vestige of these same bones?

What would we think about an astronomer who maintained that satellites revolve in
elliptic courses round their planets "for the sake of symmetry," because the planets thus revolve
round the sun? An eminent physiologist (who I will not name) accounts for the presence of
rudimentary organs by supposing that they serve to excrete matter in excess, or matter injurious
to the an organism’s physiology; but can we suppose that the minute papilla, which often
represents the pistil in male flowers, and which is formed of mere cellular tissue, can act in that
same way, and for the same reasons? Can we suppose that rudimentary teeth, which are
subsequently absorbed as development proceeds, are beneficial to the rapidly growing embryonic
calf by removing matter so precious as phosphate of lime? When a man's fingers have been
amputated, imperfect nails have been known to appear on the stumps; I could as soon believe
that these vestiges of nails are developed in order to excrete horny matter as that the rudimentary
nails on the fin of the manatee have been developed for this same purpose!

On the view of descent with modification, however, the origin of rudimentary organs is
comparatively simple, and we can understand to a large extent the laws governing their imperfect
development. We have plenty of cases of rudimentary organs in our domestic productions, as for
example, the stump of a tail in our otherwise tailless breeds; the vestige of an ear in earless breeds of sheep; the reappearance of minute dangling horns in otherwise hornless breeds of cattle, particularly (according to William Youatt\textsuperscript{32}) in young animals; and the state of the whole flower in the cauliflower. We often see rudiments of various parts in monsters; but I doubt whether any of these cases throw light on the origin of rudimentary organs in a state of nature, other than by simply showing that rudiments can indeed be produced; for the balance of evidence clearly indicates that species under nature do not undergo great and abrupt changes. But we learn from the study of our domestic productions that the disuse of parts leads to their reduced size, and that the result is inherited.

It seems likely that disuse of organs has been the main agent in rendering them rudimentary. It would at first lead by slow steps to the more and more complete reduction of a part, until at last it became rudimentary, as in the case of the eyes of animals that inhabit dark caverns, and of the wings of birds inhabiting oceanic islands, which have seldom been forced by beasts of prey to take flight, and have thus ultimately lost the power of flying. Again, an organ that is useful under certain conditions might become injurious under others, as with the wings of beetles living on small and exposed islands; and in this case natural selection will have aided in reducing the organ, until it was rendered harmless and rudimentary.

Any change in structure and function that can be brought about by small stages is within the power of natural selection to accomplish, so that an organ rendered useless or injurious for

\textsuperscript{32} William Youatt (1776–1847) was a British veterinarian who wrote a series of books on the management and diseases of farm animals, including cattle.
one purpose through changed habits of life might be subsequently modified and used for a very
different purpose. An organ might also be retained for just one of its several former functions.
Organs that were originally formed by the aid of natural selection may well be variable when
rendered useless, for their variations can no longer be checked by natural selection. All of this
agrees well with what we see in nature. Moreover, at whatever period of life either disuse or
selection reduces an organ-- and this will generally be when the being has come to maturity and
begins to exert its full powers of action--the principle of inheritance at corresponding ages will
tend to reproduce the organ in its reduced state at the same mature age, but will seldom affect it
in the embryo. Thus we can understand the greater size of rudimentary organs in the embryo in
comparison with the adjoining parts, and their lesser relative size in the adult. If, for instance, the
digit of an adult animal was used less and less during many generations, owing to some change
of habits, or if an organ or gland was less and less functionally exercised, we may infer that it
would gradually become reduced in size in the adult descendants of this animal, but would retain
nearly its original standard of development in the embryo.

There remains, however, the following difficulty. After an organ has ceased being used
and has become in consequence much reduced, how can it be still further reduced in size until
the merest vestige is left; and how can it be finally quite obliterated? It is scarcely possible that
disuse can go on producing any further effect after the organ has once been rendered
functionless. Some additional explanation is required here, but unfortunately I cannot give it. If,
for instance, it could be proved that every part of the organization tends to vary in a greater
degree towards diminution than toward augmentation of size, then we should be able to
understand how an organ that has become useless would be rendered, independently of the
effects of disuse, rudimentary, and would at last be wholly suppressed; for the variations towards
diminished size would no longer be checked by natural selection. The principle of the economy of growth, explained in a former chapter, by which the materials forming any part, if not useful to the possessor, are saved as far as is possible, will perhaps come into play in rendering a useless part rudimentary. But this principle will almost necessarily be confined to the earlier stages in the process of reduction; for we cannot suppose that a minute papilla, for instance, representing in a male flower the pistil of the female flower and formed merely of cellular tissue, could be further reduced or absorbed for the sake of economizing nutriment.

Finally, as rudimentary organs--by whatever steps they may have been degraded into their present useless condition--are a record of a former state of things and have been retained solely through the power of inheritance, we can understand (on the genealogical view of classification) how it is that systematists, in trying to place organisms in their proper places in the natural system, have often found rudimentary parts as useful as, or even sometimes more useful than, parts of high physiological importance. Rudimentary organs may be compared with letters that are still retained in the spelling of a word, even though they are no longer pronounced; they nevertheless serve as a clue for the word’s derivation. On the view of descent with modification, we may conclude that the existence of organs in a rudimentary, imperfect, and useless condition, or quite aborted, far from presenting a strange difficulty, as they assuredly do on the old doctrine of special creation, might even have been anticipated in accordance with the views explained here.

SUMMARY

In this chapter I have attempted to show all of the following: 1) the rules followed and the difficulties encountered by naturalists in their classifications; 2) that all organic beings
throughout all time are arranged in groups within groups; 3) that all living and extinct organisms are united into a few grand classes by complex, radiating, and circuitous lines of affinities; 4) that the characters of greatest value are those that are constant and prevalent, whether of high or of the most trifling importance, or, as with rudimentary organs, of no functional importance at all; 5) the wide opposition in value between analogical or adaptive characters, and characters based on true affinity. All naturally follow if we admit the common parentage of allied forms together with their modification through variation and natural selection, with the contingencies of extinction and divergence of character. In considering this view of classification, it should be borne in mind that the element of descent has long been universally used in ranking together the sexes, ages, dimorphic forms, and acknowledged varieties of the same species, however much they may differ from each other in structure. If we extend the use of this element of descent—the one certainly known cause of similarity between and among organic beings—we shall understand what is meant by the Natural System: it is genealogical in its attempted arrangement, with the levels of acquired difference marked by the terms varieties, species, genera, families, orders, and classes.

On this same view of descent with modification, most of the great facts in Morphology also become intelligible—whether we look to the same pattern displayed by the different species within a single class of organisms in their homologous organs, to whatever purpose applied, or to the serial and lateral homologies in each individual animal and plant.

On the principle of successive slight variations being inherited by offspring at a corresponding period in development, we can understand the leading facts in embryology: the close resemblance in the individual embryo of the parts which are homologous, and which when
matured become widely different in structure and function; and the resemblance of the homologous parts or organs in allied—though distinct—species, though fitted in the adult state for habits as different as is possible. Larvae are active embryos that have become specially modified to a greater or less degree in relation to their habits of life, with their modifications inherited at a corresponding early age. On these same principles, and bearing in mind that when organs are reduced in size, either from disuse or through natural selection, it will generally be at that period of life when the being has to provide for its own wants, and bearing in mind how strong is the force of inheritance, we might even have anticipated the occurrence of rudimentary organs. The importance of embryological characters and of rudimentary organs in classification makes perfectly good sense on the view that a natural arrangement must be genealogical.

Finally, the several classes of facts that have been considered in this chapter seem to me to proclaim very plainly that the innumerable species, genera, and families with which this world is inhabited are all descended, each within its own class or group, from common parents, and have all been gradually modified over the long course of descent to the present day. I should without hesitation adopt this view, even if it were unsupported by any other facts or arguments.