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THE PRIMARY FACTORS OF ORGANIC EVOLUTION

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OF

ORGANIC EVOLUTION

BY

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PREFACE.

THE present book is an attempt to select from the mass of facts accumulated by biologists, those which, in the author's opinion, throw a clear light on the problem of organic evolution, and especially that of the animal kingdom. As the actual lines of descent can be finally demonstrated chiefly from paleontologic research, I have drawn a large part of my evidence from this source. Of course, the restriction imposed by limited space has compelled the omission of a great many facts which have an important bearing on the problem. I have preferred the paleontologic evidence for another reason. Darwin and the writers of his immediate school have drawn most of their evidence from facts which are embraced in the science of œcology. Weismann and writers of his type draw most of their evidence from the facts of embryology. The mass of facts recently brought to light in the field of paleontology, especially in the United States, remained to be presented, and the evidence they contain interwoven with that derived from the sources mentioned.

Many of the zoölogists of this country, in common with many of those of other nations, have found reason for believing that the factors of evolution which were first clearly formulated by Lamarck, are really such. This view is taken in the following pages, and the book may be regarded as containing a plea on their behalf. In other words, the argument is constructive and not destructive. The attempt is made to show what we know, rather than what we do not know. This is proper at this time, since, in my opinion, a certain amount of evidence has accumulated to demonstrate the doctrine here defended, and which I have defended as a working hypothesis for twenty-five years.

In the following pages I have cited many authors who have contributed to the result, but it has been impossible to cite all who have written on one part or another of the subject. If some very meritorious essays have not been cited, it has been generally because I have confined myself to those in which facts or doctrines were first presented, and have not had so much occasion to refer to those of later date.

Mr. Romanes, in his posthumous book, Volume II. of his *Darwin, and After Darwin* on *Post-Darwinian Questions*, expresses the following opinion of the position which has been taken by the Neo-Lamarckians of this country. He says that they do not distinguish between the "statement of facts in terms of a proposition, and an explanation of them in terms of causality." Had Mr. Romanes been acquainted with the literature of the subject published in America and elsewhere during the last three years, he would have had reason to change this view of the case. I think he would have found in it demonstration "in terms of causality."

At the outset it must be stated that a knowledge of the history of organic evolution rests primarily on the science of morphology, and secondarily on the kinematics of the growth of organic structures. The phenomenon to be explained is the genealogical succession, or phylogeny of organisms; and the access to this subject is through the sciences of paleontology and embryology. The phenomena of the functioning of the organism, or physiology, are only incidentally referred to, as not the real object of inquiry. Since organic species are much more numerous than the tissues of which they are composed, organogenesis must claim attention more largely than histogenesis. It is true that histogenesis is fundamental, but it is a science as yet in its early infancy, and little space can be given to it. The exact *how* of organic evolution will never be finally solved, however, until our knowledge of histogenesis is complete.

The research depicted in the following pages has proceeded on the assumption that every variation in the characteristics of organic beings, however slight, has a direct efficient cause. This assumption is sustained by all rational and philosophical considerations. Any theory of evolution which omits the explanation of the causes of variations is faulty at the basis. Hence the theory of selection cannot answer the question which we seek to solve, although it embraces an important factor in the production of the general result of evolution.

In the search for the factors of evolution, we must have first a knowledge of the course of evolution. This can only be obtained in a final and positive form by investigation of the succession of life. The record of this succession is contained in the sedimentary deposits of the earth's crust, and is necessarily imperfect. Advance in knowledge in this direction has, however, been very great of recent years, so that some parts of the genealogical tree are tolerably or quite complete. We hope reasonably for continued progress in this direction, and if the future is to be judged of by the past, the number of gaps in our knowledge will be greatly lessened. In the absence of the paleontologic record, we necessarily rely on the embryologic, which contains a recapitulation of it. The imperfections of the embryonic record are, however, great, and this record differs from the paleontologic in that no future discovery in embryology can correct its irregularities. On the contrary every paleontologic discovery is an addition to positive genealogy. If the present work has any merit, it is derived from the fact that the basis of the argument is the paleontologic record.

E. D. COPE.

PHILADELPHIA, November 1, 1895.

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INTRODUCTION.

THE doctrine of evolution may be defined as the teaching which holds that creation has been and is accomplished by the agency of the energies which are intrinsic in the evolving matter, and without the interference of agencies which are external to it. It holds this to be true of the combinations and forms of inorganic nature, and of those of organic nature as well. Whether the intrinsic energies which accomplish evolution be forms of radiant or other energy only, acting inversely as the square of the distance, and without consciousness, or whether they be energies whose direction is affected by the presence of con sciousness, the energy is a property of the physical basis of tridimensional matter, and is not outside of it, according to the doctrine we are about to consider.

As a view of nature from an especial standpoint, evolution takes its place as a distinct science. The science of evolution is the science of creation, and is as such to be distinguished broadly from the sciences which consider the other operations of nature, or the functioning of nature, which are not processes of creation, but processes of destruction. This contrast is especially obvious in organic evolution, where the two processes go on side by side, and are often closely intermingled, as for instance in muscular action, where both destruction of proteids and growth of muscular tissue result from the same acts, or use. Physiology, or the science of functions, concerns itself chiefly with destruction, and hence physiologists are especially prone to be insensible to the phenomena and laws of progressive evolution. The building of the embryo, remains a sealed book to the physiologist unless he take into account the allied biological science of evolution, as resting on the facts of botany, zoölogy, and paleontology. In his reflections on the relations of mind to matter he is likely to see only the destructive functioning of tissue, and not the history of the building of the same during the ages of geological time.

J. B. P. A. Lamarck[1] thus contrasts the theories of direct creation, and creation by evolution. The former asserts: "That nature or its author in creating animals has foreseen all possible kinds of circumstances in which they may have to live, and has given to each species a permanent organization as well as a predetermined form, invariable in its parts; that it forces each species to live in the place and the climate where one finds them, and to preserve there the habits which it has." He then states his own, or the evolutionary, opinion to be: "That nature in producing successively all species of animals, commencing with the most imperfect or simple, and terminating its work with the most perfect, has gradually complicated their organization; and these animals spreading themselves gradually into all habitable regions of the globe,—each species has been subjected to the influence of the circumstances in which it is; and these have produced the habits which we observe, and the modifications of

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[1] *Philosophie Zoologique*, Paris, 1809, Vol. I., Chap. VII.

its parts." On an earlier page of the same chapter, Lamarck thus formulates the laws of organic evolution, to which his name has been attached.

First law. "In every animal which has not passed the time of its development, the frequent and sustained employment of an organ gradually strengthens it, develops and enlarges it, and gives it power proportional to the duration of its use; while the constant disuse of a like organ weakens it, insensibly deteriorates it, progressively reduces its functions, and finally causes it to disappear."

Second law. "All that nature acquires or loses in individuals by the influence of circumstances to which the race has been exposed for a long time, and in consequence of the influence of the predominate employment of such an organ, or of the influence of disuse of such part, she preserves by generation, in new individuals which spring from it, providing the acquired changes be common to both sexes, or to those which have produced new individuals."

We have here a theory of the origin of characters; viz., of the increased development or loss of parts as a result of use or disuse. We have also the theory that the peculiarities thus acquired are transmitted to the succeeding generation by inheritance.

The next formal statement of the efficient cause of organic evolution was presented by Messrs. Charles Darwin and Alfred R. Wallace in 1859.[1] The cause assigned is natural selection, and Mr. Darwin thus states what is meant by this expression in his work *The Origin of Species.*[2] "If under changing conditions of life organic beings present individual differences

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[1] *Proceedings of the Linnean Society of London.*

[2] Ed. 1872, p. 102.

in almost any part of their structure, and this cannot be disputed; if there be, owing to their geometrical rate of increase, a severe struggle for life at some age, season, or year, and this certainly cannot be disputed; then considering the infinite complexity of the relations of all organic beings to each other and to their conditions of life, causing an infinite diversity of structure, constitution, and habits, to be advantageous to them, it would be a most extraordinary fact if no variations had ever occurred useful to each being's own welfare, in the same manner as so many variations have occurred useful to man. But if variations useful to any organic being ever do occur, assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance, these will tend to produce offspring similarly characterized. This principle of preservation, or the survival of the fittest, I have called natural selection. It leads to the improvement of each creature in relation to its organic and inorganic conditions of life; and consequently in most cases, to what must be regarded as an advance in organization. Nevertheless, low and simple forms will long endure if well fitted for their simple conditions of life."

It is readily perceived that this statement makes no attempt to account for the origin of variations, but that it simply formulates, as observed by Mr. Darwin, the doctrine of survival of such variations as are most useful to their possessors. This fact is more distinctly pointed out in the same work (p. 63) where the author remarks: "Several writers have misapprehended or objected to the term natural selection. Some have even imagined that natural selection induces variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life. No one objects to agriculturists speaking of the potent effects of man's selection, and in this case the individual differences given by nature, which man for some object selects, must of necessity first occur." It is evident then that Mr. Darwin did not attempt to account for the origin of variations, but that the service rendered by him and by Mr. Wallace to the doctrine of evolution consists in the demonstration of the reality of natural selection. Darwin also assumes in the statement first quoted above, the inheritance of acquired characters.

In 1865 the *Principles of Biology* of Herbert Spencer appeared. In this work the attempt is made to set forth the laws of organic evolution, in a way which represents an advance beyond the positions of his predecessors. He adopts and harmonizes both the Lamarckian and Darwinian doctrines, and is at times more specific in his application of Lamarck's doctrine of the stimulus of the environment, and of use, than was Lamarck himself. Very often, however, Spencer contents himself with generalities; or takes refuge in the "instability of the homogeneous," as an efficient cause. This phrase, however, like his other one, "the unknowable," is but a makeshift of temporary ignorance, and is neglected by Spencer himself, when he can see his way through it. He approaches the cause of the varied forms of leaves of plants in this language:[1] "And it will also be remembered that these equalities and inequalities of development correspond with the equalities and inequalities in the incidence of forces." Language of similar significant but rather indefinite import is frequently used throughout this volume.

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[1] *The Principles of Biology*, by Herbert Spencer, Amer. Ed., 1873, II., p. 143.

But in some cases Spencer is more specific. With reference to the inequality in the basal lobes of the erect leaves of Tilia and other plants, he says:[1] "A considerable deviation from bilateral symmetry may be seen in a leaf which habitually so carries itself that the half on the one side of the midrib is more shaded than the other half. The drooping branches of the lime show us leaves so arranged and so modified. On examining their attitudes and their relations one to another, it will be found that each leaf is so inclined that the half of it next the shoot grows over the shoot and gets plenty of light; while the other half so hangs down that it comes a good deal into the shade of the preceding leaf. The result is that having learned which fall into these positions, the species profits by a large development of the exposed halves; and by survival of the fittest acting along with the direct effect of extra exposure, this modification becomes established." In his discussion of the origin of the characters of animals, Spencer is also sometimes specific. Respecting the development of muscular insertions he remarks:[2] "Anatomists easily discriminate between the bones of a strong man and those of a weak man by the greater development of those ridges and crests to which the muscles are attached; and naturalists on comparing the remains of domesticated animals with those of wild animals of the same species, find kindred differences. The first of these facts shows unmistakably the immediate effect of function on structure, and, by obvious alliance with it, the second may be held to do the same, both implying that the deposit of dense substance capable of great resistance habitually takes

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[1] *Op. cit.*, p. 143.

[2] *Loc. cit.*, p. 200.

place at points where the tension is excessive." Quite as specific is his ascription of the forms of epithelial cells to definite causes, as follows:[1] "Just the equalities and inequalities of dimensions among aggregated cells, are here caused by the equalities and inequalities among their mutual pressures in different directions; so though less manifestly, the equalities and inequalities of dimensions among other aggregated cells, are caused by the equalities and inequalities of the osmatic, chemical, thermal, and other forces besides the mechanical, to which their different positions subject them."

In spite of this not infrequent definiteness, Mr. Spencer occasionally falls into the error of ascribing the origin of structures to natural selection, as in the case of the forms of flowers,[2] and the armor-plates of paleozoic fishes.[3] Spencer assumes the inheritance of acquired characters throughout.

In 1866 Haeckel's *Schöpfungsgeschichte* appeared. In this work the author presents a mass of evidence which sustains the doctrine of evolution, and he combines the views of Lamarck and Darwin into a general system. He says:[4] "We should, on account of the grand proofs just enumerated, have to adopt Lamarck's theory of descent for the explanation of biological phenomena, even if we did not possess Darwin's theory of selection. The one is so completely and directly proved by the other, and established by mechanical causes, that there remains nothing to be desired. The laws of inheritance and adaptation are universally acknowl-

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[1] *Op. cit.*, p. 260.

[2] *Op. cit.*, p. 153.

[3] *Op. cit.*, p. 288.

[4] *The History of Creation*, Amer. Edition, II., p. 355.

edged physiological facts, the former traceable to propagation, the latter to the nutrition of organisms." Apart from the statement that adaptation is traceable "to the nutrition of organisms," we find nothing in Haeckel's earlier writings which attempts the explanation of the origin of variations, beyond the general position assumed by Lamarck. The distinctive merit of Haeckel is his formulation of phylogeny. Much of this was speculative at the time he wrote, but so far as the Vertebrata are concerned, it has been largely confirmed by subsequent discovery.

Up to this period, the form in which the doctrine of evolution had been presented, was general in its application; that is, without exact reference to the structural definitions of natural taxonomic groups. No attempt was made to show the modes of the origin of any particular class, order, or genus, and only in the most general way in the case of a few species, by Mr. Darwin. Phylogeny was untried, except by Haeckel; and this distinguished author did not attempt to account specifically for the origins of the divisions whose filiations he set forth.

In the year in which Haeckel's work above cited appeared, Professor Hyatt of Boston and myself took the first step towards the formulization of a rational theory of the origin of variation, which should accord with specific examples of taxonomy. Quite independently, we selected the simple series presented by the characters of genera in their natural relations, Hyatt in the cephalopodous Mollusca, and I in the Batrachia Salientia. It is probable that Hyatt's[1] article was published shortly before mine. He says of the genera of Cephalopoda: "In other words, there is an increasing

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[1] *Memoirs Boston Society Natural History*, 1866, p. 193.

concentration of the adult characteristics in the young of higher species and a consequent displacement of other embryonic features which had themselves also previously belonged to the adult period of still lower forms." My own language is:[1] "That the presence, rudimental condition, or absence of a given generic character can be accounted for on the hypothesis of a greater rapidity of development in the individuals of the species of the extreme type, such stimulus being more and more vigorous in the individuals of the types as we advance towards the same, or by a reversed impulse[2] of development, where the extreme is characterized by absence or 'mutilation' of characters." The phenomena of the aggregation of characters in progressive evolution, and the loss of characters in retrogressive evolution, were termed by me acceleration and retardation in an essay published in 1869.[3] In these papers by Professor Hyatt and myself is found the first attempt to show by concrete examples of natural taxonomy, that the variations that result in evolution are not multifarious or promiscuous, but definite and direct, contrary to the method which seeks no origin for variations other than natural selection. In other words, these publications constitute the first essays in systematic evolution that appeared. By the discovery of the paleontologic succession of modifications of the articulations of the vertebrate, and especially mammalian skeleton, I first furnished an actual demonstration of the reality of the Lamarckian factor of use, or mo-

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[1] *Transactions American Philosophical Society*, 1866, p. 398; reprinted in *The Origin of the Fittest*, p. 92.

[2] The expression "reversed" is unfortunate, *diminished* being the proper word to convey the meaning intended.

[3] *The Origin of Genera*, Philadelphia, 1869.

tion, as friction, impact, and strain, as an efficient cause of evolution.[1] This demonstration led me to the necessary inference that when the agency directive of motion is consciousness, this also has been an important factor of evolution, in demonstration of the supposition of Erasmus Darwin.[2] Hyatt has demonstrated first on paleontologic evidence, the inheritance of a mechanically acquired character. Important contributions to corresponding histories of the Mollusca have been made by Hyatt,[3] Dall,[4] Jackson,[5] and Beecher.[6] Many other contributions, into which the paleontologic evidence does not enter, have also been made by various authors in Europe and America.

The authors quoted up to this point had all assumed that the progress of evolution depends on the inheritance by the offspring of new characters acquired by the parent, and had believed that such is the fact in ordinary experience. In 1883, Weismann, in an essay on heredity, announced the opinion that characters acquired by the body could not be transmitted to the reproductive cells, and could not therefore be inherited. This doctrine rests on the relation of the germ-cells to those of the rest of the body, which is expressed in the following language of his predecessor Jaeger: "Through a great series of generations the

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[1] "The Origin of the Hard Parts of Mammalia," *American Journal of Morphology*, 1889, p. 137.

[2] *Origin of the Fittest*, 1887, p. 357.

[3] "Phylogeny of an Acquired Characteristic," *Proc. Amer. Philosophical Society*, 1893, p. 349; "The Genesis of the Arietidæ," *Memoirs Mus. Compar. Zoölogy*, Cambridge, Mass., 1889, XVI., No. 3.

[4] Dall, W. H., "The Hinge of Pelecypods and Its Development, *Amer. Jour. Sci. Arts*, 1889, XXXVIII., p. 445.

[5] Jackson, R. T., "Phylogeny of the Pelecypoda, the Aviculidæ, and Their Allies," *Memoirs Boston Society Natural History*, 1890, IV., p. 277.

[6] *American Journal Sci. Arts*, 1893.

germinal protoplasm retains its specific properties, dividing in every reproduction into an ontogenetic portion and a phylogenetic portion, which is reserved to form the reproductive material of the mature offspring. This reservation of the phylogenetic material I described as the continuity of the germ-protoplasm. . . . Encapsuled in the ontogenetic material the phylogenetic protoplasm is sheltered from external influences, and retains its specific and embryonic characters." In other words, the reproductive cells are removed from the influence of those stimuli which affect and effect growth in the cells of the other parts of the body, so that no character acquired by the rest of the body can be inherited. The bearing of this theory on evolution is thus stated by Weismann:[1] "The origin of hereditary individual variations cannot indeed be found in the higher organisms, the metazoa and metaphyta, but is to be sought for in the lowest, the unicellular." "The formation of new species, which among the lower protozoa could be achieved without amphigony (sexual union), could only be attained by means of this process in the metazoa and metaphyta. It was only in this way that hereditary individual differences could arise and persist." In other words, variation in organic beings above the unicellular forms, has been and is, introduced only by sexual reproduction.

The conclusions of Weismann were derived principally from embryologic research, and his disciples have been chiefly recruited from embryologists. These conclusions have been supported by extensive and exhaustive investigations, which have added greatly to our knowledge of the subject. In order to account for

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[1] *Essays*, p. 296. For a complete account of Weismann's views, see *The Germ-Plasm*, 1893.

the appearance of characters in the embryonic succession, through influences confined to the germ-plasma, Weismann invented a theory which requires the presence of distinct molecular aggregates within it, which represent the potentialities or causes. To these he has given the names of ids, idants, determinants, etc. As Weismann's contribution to evolution has been confined to the department of heredity, I will consider it more particularly in the third part of this book, which is devoted to that subject.

Weismann has, however, subsequently modified his views to a considerable extent. He has always admitted the doctrine of Lamarck to be applicable to the evolution of the types of unicellular organisms. His experiments on the effect of temperature on the production of changes of color in butterflies, showed that such changes were not only effected, but were sometimes inherited. This he endeavors to explain as follows.[1] "Many climatic variations may be due wholly or in part, to the simultaneous variation of corresponding determinants in some parts of the soma and in the germ-plasm of the reproductive cells." This is an admission of the doctrine which in 1890 I called Diplogenesis,[2] and which is adopted in the present work. It appears to have been first propounded by Galton in 1875. In the chapter on Heredity I hope to offer some reasons for believing that the suggestion of Galton embraces the true doctrine of heredity.

From what has preceded, two distinct lines of thought explanatory of the fact of organic evolution may be discerned. In one of these the variations of organisms which constitute progressive and regressive

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[1] *The Germ Plasm*, Contemporary Science Series, 1893, p. 406.

[2] *American Naturalist*, Dec., 1889; published in 1890.

evolution appear fortuitously, and those which are beneficial survive by natural selection, while those which are not so, disappear. Characters both beneficial and useless or harmless, which are acquired by the adult organism, are not transmitted to the young, so that no education in habit or structure acquired by the adult, has any influence in altering the course of evolution. This is the doctrine of Preformation. From this point of view the cause of the variations of organisms has yet to be discovered.

The other point of view sees in variation the direct result of stimuli from within or without the organism ; and holds that evolution consists of the inheritance of such variations and the survival of the fit through natural selection. This is the doctrine of Epigenesis. To this I would add that in so far as sensations or states of consciousness are present, they constitute a factor in the process, since they enable an organism to modify or change its stimuli. The position of each of these schools on each of the questions to which reference has been made, may be placed in opposition as follows :

1. Variations appear in definite directions.	1. Variations are promiscuous or multifarious.
2. Variations are caused by the interaction of the organic being and its environment.	2. Variations are "congenital" or are caused by mingling of male and female germ-plasmas.
3. Acquired variations may be inherited.	3. Acquired variations cannot be inherited.
4. Variations survive directly as they are adapted to changing environments. (Natural selection.)	4. Variations survive directly as they are adapted to changing environments. (Natural selection.)

5. Movements of the organism are caused or directed by sensation and other conscious states.	5. Movements of organism are not caused by sensation or conscious states, but are a survival through natural selection from multifarious movements.
6. Habitual movements are derived from conscious experience.	6. Habitual movements are produced by natural selection.
7. The rational mind is developed by experience, through memory and classification.	7. The rational mind is developed by natural selection from multifarious mental activities.

It is not the object of the present book to present all the available evidence on both sides of each of the questions above enumerated. I propose merely to submit certain facts, in support of the doctrines contained in the left-hand column of the above table. My aim will be to show in the first place, that variations of character are the effect of physical causes; and second, that such variations are inherited. The facts adduced in support of these propositions will be necessarily principally drawn from my own studies in the anatomy, ontology, and paleontology of the Vertebrata. It will be my aim, moreover, to co-ordinate the facts of evolution with those of systematic biology, so that the result may be as clearly presented as possible. The failure to do this by the founders of evolutionary doctrine has given their work a lack of precision, which has been felt by systematic biologists. The detailed application of the principles of Lamarck and Darwin has been the work of their successors, and has necessarily thrown much new light on the principles themselves. In pursuing the object above stated, I shall be obliged to consider briefly in the following pages, the validity of the general propositions on which the doctrine of evolution rests. Less space will be given, however, to those which are less relevant, than to those which are more relevant to the doctrine of neo-Lamarckism.

PART I.

THE NATURE OF VARIATION.

PRELIMINARY.

THE structural relations of organisms may be expressed in the following canons:[1]

1. *Homology.*—This means that organic beings are composed of corresponding parts; that the variations of an original and fixed number of elements constitute their only differences. A part large in one animal may be small in another, or *vice versa*; or complex in one and simple in another. The analysis of animals with skeletons, or Vertebrata, has yielded several hundred original elements, out of which the twenty-eight thousand included species are constructed. The study of homologies is thus an extended one, and is far from complete at the present day.

2. *Successional Relation.*—This expresses the fact that species naturally arrange themselves into series in consequence of an order of excess and deficiency in some feature or features. Thus species with three toes naturally intervene between those with one and four toes. So with the number of chambers of the heart, of segments of the body, the skeleton, etc. There are greater series and lesser or included series, and mistakes are easily made by taking the one for the other.

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[1] *Origin of the Fittest*, p. 6. The laws here stated are as expressive of the relations of plants as of animals.

3. *Parallelism.*—This states that all organisms in their embryonic and later growth pass through stages which recapitulate the successive permanent conditions of their ancestry. Hence those which traverse fewer stages resemble or are *parallel* with the young of those which traverse more numerous stages. This is the broad statement, and is qualified by the details.

4. *Teleology.*—This is the law of fitness of structures for their special uses, and it expresses broadly the general adaptations of an animal to its home and habits.

The first and fourth of the laws above enumerated are taken for granted as generally accepted, and are not especially considered in the following pages. The second law, that of successional relation, is discussed and illustrated under the two heads of Variation and Phylogeny; the first expressing contemporary relations, and the second, successive relations in time. The third law, or that of parallelism, is considered in a chapter devoted to that subject.

CHAPTER I—ON VARIATION.

PRELIMINARY.

ALL species are not equally variable. Some species vary little or not at all, even under domestication. Thus the varieties of the turkey (*Meleagris gallopavo*) and the guinea-fowl (*Numida meleagris*) are few, and are confined to albinistic or melanistic conditions. The barnyard fowl (*Gallus sp.*), on the other hand, varies enormously, as does also the pigeon (*Columba livia*). Among domesticated Mammalia the variations of cats (*Felis domestica*) are few as compared with those of dogs (*Canis sp.*). Variability is not peculiar to domesticated animals. A large proportion of animals and plants are, in a state of nature, variable, and some of these are much more so than others. The common garter-snake (*Eutænia sirtalis*) varies exceedingly, while the variations of the allied ribband snake (*Eutænia saurita*) are minute or none. But little variation has been observed in the polar bear (*Ursus maritimus*), while the common bear (*U. arctos*) presents many varieties. Similar conditions are found among fishes. Thus the larger species of pike, the muskallonge (*Lucius nobilior*), the pike (*L. estor*), and the pickerel (*L. vermiculatus*) are constant in their characters, while the small pickerel (*L. vermiculatus*) presents numerous varieties.

Many of the varieties of the animals referred to inhabit the same territory, although some are restricted to particular regions. Of geographical varieties or races much is known. As a rule, all widely distributed species present them. Examples are the brown bear of the Northern Hemisphere (*Ursus arctos*); the cobra di capello snake of the warmer parts of Asia (*Naja tripudians*), and that of Africa (*Naja haje*). In North America the king-snake (*Ophibolus getulus*) and the milk-snake (*Osceola doliata*) are represented by distinct races in different regions. On the other hand, the copperhead (*Ancistrodon contortrix*) and the Eastern rattlesnake (*Crotalus horridus*), which have a wide range, scarcely vary at all. The chub (*Hybopsis biguttatus*) is an example of a fish distributed everywhere east of the Rocky Mountains, which presents scarcely any variation.

Variations are not promiscuous or multifarious, but are of certain definite kinds or in certain directions. Thus amid all their varieties, dogs never present black cross-bands on the back like those of the dog-opossum (*Thylacinus cynocephalus*) of Tasmania, nor do they present ocellated spots like those of the leopard, nor longitudinal stripes like those of certain squirrels. The same is true of the many varieties of cattle (*Bos taurus*), and of numerous other mammalia. Domestic fowls never vary to blue or green, colors which are common to many other birds; nor are canaries known to produce blue or red natural sports. All variations are in the first place necessarily restricted by the existing characters of the ancestor; but beyond this it is evident that other conditions determine the nature of the variation. It is not supposable, for instance, that the pale tints of animals which live in dry regions originated by an accident or without a determining cause. The increased amount of dark pigment observed in animals which dwell in especially humid regions must have a corresponding cause, and it is naturally to be supposed, of a kind the opposite of that which produces the pale colors.

I shall adduce some illustrations which show that color variations in species, as well as structural variations in higher groups, have appeared in certain definite series, and observe a successional relation to each other, which may or may not coincide with geographical conditions. The same relation is observed in the order of appearance of variations on the body.

Eimer and Weismann have shown that the gradual modification of color markings has originated in lizards and in caterpillars at the posterior end of the body and has gradually extended forwards. This has been discovered both by comparisons of the variations of the adults, and by studies of the order of their appearance in ontogenetic growth. Eimer shows that longitudinal bands have been produced in some animals by the confluence of spots placed in transverse series, which themselves are the remains of interrupted transverse bands. Thus he believes that the spots of the leopard group of the large cats were derived from the breaking up of transverse bands of the character of those now possessed by the tiger. The uniform coloration of the lion is the result of the obliteration of the spots. Traces of these spots may be distinctly seen in lions' cubs.

In plants variation is said to be equally definite by Henslow. He says: "In 1847 Professor J. Buckman sowed the seed of the wild parsnip in the garden of the Agricultural College at Cirencester. The seeds began to vary, but in the same way, though in different degrees. By selecting seed from the best rooted plants the acquired 'somatic' characters of an enlarged root, glabrous leaves, etc., became fixed and hereditary; and the 'Student,' as he called it, having been 'improved' by Messrs. Sutton and Sons, is still regarded as 'the best in the trade.' This is *definite variation*, according to Darwin's definition, for those weeded out did not differ from the selected, morphologically, except in degree, the variations towards improvement not being quite fast enough to entitle them to survive."

Finally I wish especially to point out that variation in animals, and probably in plants, (with which I am not so familiar,) gives no ground for believing that "sports" have any considerable influence on the course of evolution. This is apparent whether we view the serial lines of variations of specific, generic, or higher characters; or whether we trace the phylogeny of the animal and vegetable types by means of the paleontological record. The method of evolution has apparently been one of successional increment or decrement of parts along definite lines. More or less abruptness in some of the steps of this succession there may have been; since a definite amount of energy expended in a given direction at a given point of history might produce a much greater effect than the same amount expended at some other period or point of evolution. This might be due to the release of stored energy, which could only be accomplished by a coincidence of circumstances. A simple illustration of the phenomenon of abrupt metamorphosis is to be found in the passage of matter from the gaseous to the liquid, and from the liquid to the solid state. I have stated the case in the following language:[1]

"As one or more periods in the life of every species is characterized by a greater rapidity of development" (ontogenetic) "than the remainder; so in proportion to the approximation of such a period to the epoch of maturity or reproduction is the offspring liable to variation. During the periods corresponding to those between the rapid metamorphoses, the characters of the genus would be preserved unaltered, though the period of change would be ever approaching. Hence the transformation of genera may have been rapid and abrupt, and the intervening periods of persistency very long. Thus, while change is really progressing, the external features remain unchanged at other than those points, which may be called *expression points*. Now the *expression point* of a new generic type is reached when its appearance in the adult falls so far prior to the period of reproduction as to transmit it to the offspring and their descendants."

1. VARIATIONS OF SPECIFIC CHARACTERS.

a. Variations in the Coleopterous Genus Cicindela.

Dr. George H. Horn has traced the variations in the color patterns of the elytra of the North American species of this abundant and well-known genus. He shows that they form series, in the following language:[2]

"Any one in glancing over this series will perceive that there is a great similarity of marking between many species. This similarity, which may be considered as the type of marking, and is illustrated by

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[1] *Origin of the Fittest*, p. 79.

[2] *Entomological News*, Philadelphia, Feb., 1892, p. 25.

No. 1 of the accompanying plate (Fig. 1) is the underlying pattern from which all the forms observed in our Cicindela have been derived.

“Before going further it is well to present the following propositions that the argument and the illustrations may be understood.

“1. The *type* of marking is the same in all our species.

“2. Assuming a well-marked species as a central type the markings vary.

a. by a progressive spreading of the white,

b. by a gradual thinning or absorption of the white,

c, by a fragmentation of the markings,

d, by linear supplementary extension.

“3. Many species are practically invariable. These fall in two series.

a. those of the normal type, as *vulgaris*, *hirticollis*, and *tenuisignata*,

b, those in which some modification of the type has become permanent, probably through isolation, as *marginipennis*, *togata*, and *lemniscata*.

“4. Those species which vary, do so in one direction only. That is, supposing a species begins typically with markings similar to *vulgaris*, the variation may be either in the direction of thickening and increase of white, as in *hyperborea*, *generosa*, and others, or in the direction of thinning or fragmentation of the white with perhaps an entire loss of markings as in *hæmorrhagica*, *splendida*, or *obsoleta*.

“The first two propositions must be considered as applying to the species of the genus collectively, the last two to the species separately.

“The accompanying plate has been prepared to illustrate these propositions. It must, however, be

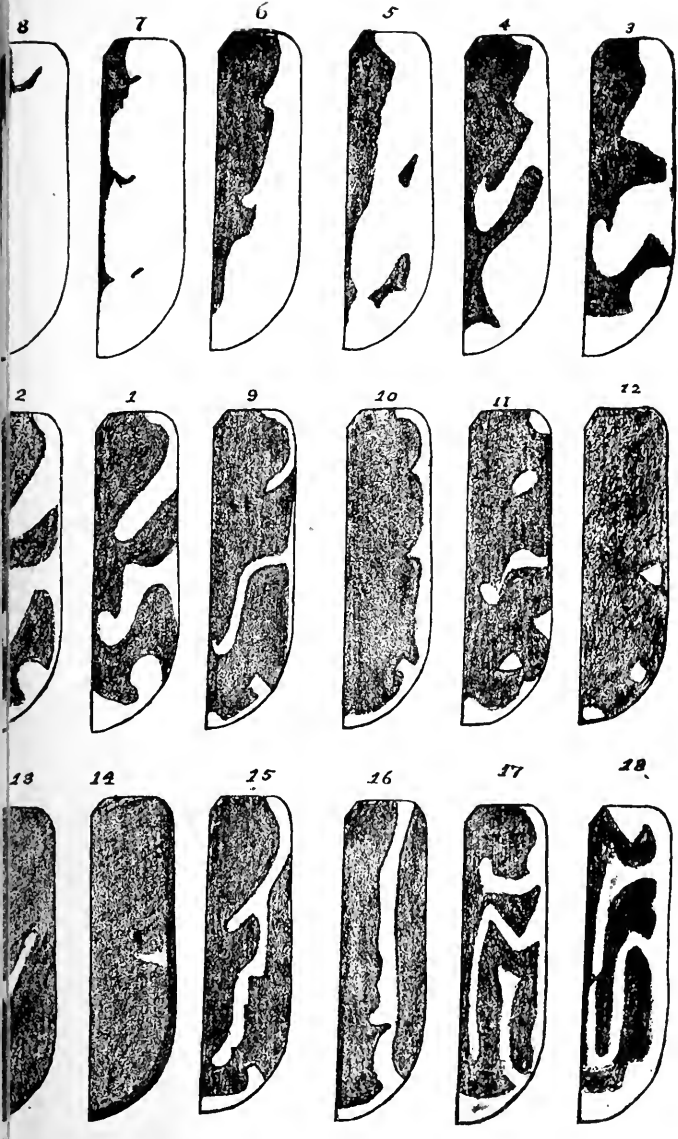

Fig. 1.—Horn on Cicindela.

understood that, in tracing the derivations from the typical, it is not possible to use one species, as these modifications go on gradually through a number of species, one sometimes beginning where another ends.

'In the plate, No. 1 represents *vulgaris*, which is a fairly typical species, following through *generosa* (2–3), *pamphila* (4), *hyperborea* var. (5), *togata* (6), *gratiosa* (7), *canosa* (8), we finally arrive at a perfect white elytron as seen in some varieties of *dorsalis*.

"Following in the other direction through *tenuisignata* (9), *marginipennis* (10), *hentzii* (11), *sexguttata* (12), *hæmorrhagica* (13), and *splendida* var. (14), it will be observed that through a gradual thinning or absorption of the markings, or by their fragmentation and obliteration, we arrive at the opposite result of elytra without any white markings whatever, as in many forms of *obsoleta*, *scutellaris*, *punctulata*, and *hæmorrhagica*.

"Those species which vary from the type in having the markings broken into spots, as in 12-*guttata* or *hentzii*, may lose the spots by a gradual decrease of size, so that they all seem to disappear nearly at the same time; or the spots may disappear successively, those on the disc being the first to go, while the marginal spots remain.

"From our series it would be difficult to say which spot is the most persistent, but it is probably the lunule, as there are more with entirely dark elytra with slight traces of this spot than with any other, as shown in *abdominalis* and *punctulata*.

"Forms like *lemniscata* (16) seem very far removed from the type, but many forms of *imperfecta* (15) show how the markings gradually leave the margin and tend by fusion to form a vitta at first somewhat oblique, but finally becoming nearly median.

"The last two figures on the plate represent the markings of *gabbii* (17) and *saulcyi* (18), in which the ends of the bands or lunules are greatly prolonged. The latter form, which represents *dorsalis* as well, is but rarely seen so perfectly marked, the tendency being toward a greater extension of the white. The other species is scarcely variable, although equally a coast form.

"Those species which retain a permanent divergence from the normal standard, such as *togata* (6) or *lemniscata* (16), are doubtless descendants from a normal type which has varied, and in which a variety has become isolated and perpetuated itself."

The accompanying plate is copied from the original drawing by Dr. Horn, and which accompanies the paper now cited.

b. Variations in the Osceola doliata.

The Milk-Snake, *Osceola doliata* Linn., ranges in North America over the Eastern, Central, and Austroriparian districts, and is absent from the Sonoran and Pacific districts. It is found also in the humid regions of Mexico and Central America, as far as the Isthmus of Darien. Beyond this point it does not occur, but a very similar snake (*Opheomorphus mimus*) is found in New Grenada.

I have called attention to the color variations of this species in a brief paragraph in the introduction to my check list of Batrachia and Reptilia in North America, 1875,[1] and have given the characters of the

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[1] *Bulletin of the U. S. National Museum*, No. I, p. 4.

color types, or subspecies, in an analytical key, in a "Review of the Characters and Variations of the Snakes of North America," 1892.[1] I have also given a series of figures representing the North American color forms, for which I am indebted to the United States National Museum, which are here reproduced.

Before going further into the patterns of the *Osceola doliata*, I give a synoptic key of them.

I. No yellow band posteriorly from orbit (a yellow half-collar).
  a. Dorsal spots or saddles (red) open at the side, the borders of adjacent spots forming pairs of black rings.
    Interspaces between red saddles open below; scales not black-tipped; front more or less black; first black ring on nape only: *O. d. coccinea.*
    Interspaces between red saddles closed by black spot below; scales black tipped; front black; first black ring complete: *O. d. polyzona.*
    Interspaces not closed; rings, including first, complete on belly; first yellow band crossing occipital plates; front black; scales not black-tipped: *O. d. conjuncta.*
  aa. Dorsal spots closed at the sides below, forming saddles.
    b. Saddles closed by a single black tract on the middle of the belly; no spots between the saddles.
      Dorsal spots undivided medially; front black; first black ring complete: *O. d. annulata.*
      Dorsal spots divided longitudinally by a median black connection; front black: *O. d. gentilis.*
    bb. Inferior borders of saddles separate and not confluent with each other.
      Saddles completed on gastrosteges; no alternating spots; no black collar: *O. d. parallela.*
      Saddles completed on gastrosteges; spots opposite intervals forming a single series on the middle line of the belly: *O. d. syspila.*
      Saddles completed above the gastrosteges; alternating spots which do not meet on the middle line of the belly: *O. d. doliata.*

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[1] *Proceedings of the U. S. National Museum*, XIV, p. 589 608.

II. A yellow band posteriorly from orbit, bounded below by a black or brown one.

a. Saddle spots closed laterally on gastrosteges; alternate spots entirely on gastrosteges.

A half collar behind parietal plates, no superciliary stripe: *O. d. temporalis.*

aa. Saddle spots closed above gastrosteges; alternate spots on scales.

A half collar nearly or quite touching occipital plates, no bands; alternate spots partly on gastrosteges: *O. d. collaris.*

Neck with longitudinal bands; alternate spots partly on gastrosteges: *O. d. clerica.*

Neck with bands; alternate spots entirely on scales: *O. d. triangula.*

In Fig. 2 are represented vertical, lateral, and inferior views of parts of the body of the subspecies *triangula*, taken from a specimen in my collection from Westchester County, New York, which I owe to the kindness of my friend, Mr. T. H. Mead.

The characters of this form are seen in (1) the presence of a light band extending from the posterior angle of the eye downward and backward, which is bounded by a black border above and below; (2) a black cross-band on the posterior border of the prefrontal plates; (3) chevron shaped mark with the apex on the posterior part of the frontal plate, whose limbs extend posteriorly as a band on each side of the neck, where they are fused together, and continue as a single, broad band for a short distance; (4) a series of lateral spots which do not extend beyond the scales on to the gastrosteges, and which alternate with the dorsal spots; (5) a series of spots on the ends of the gastrosteges which alternate with the last mentioned; (6) a series of spots on the centers of the gastrosteges which alternate with the spots mentioned under (5).

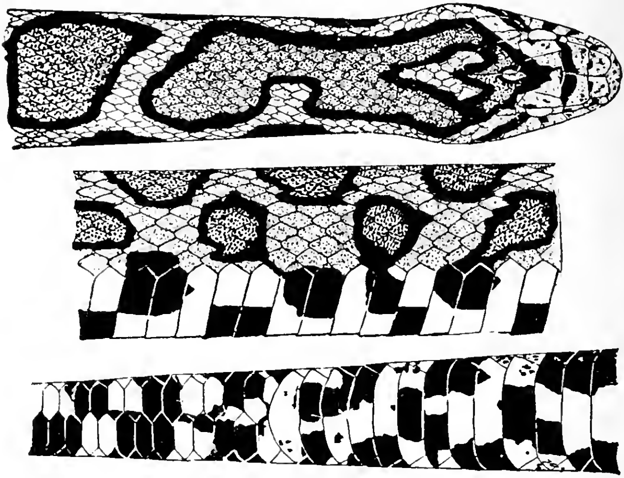


Fig. 2. *Osceola doliata triangula.*

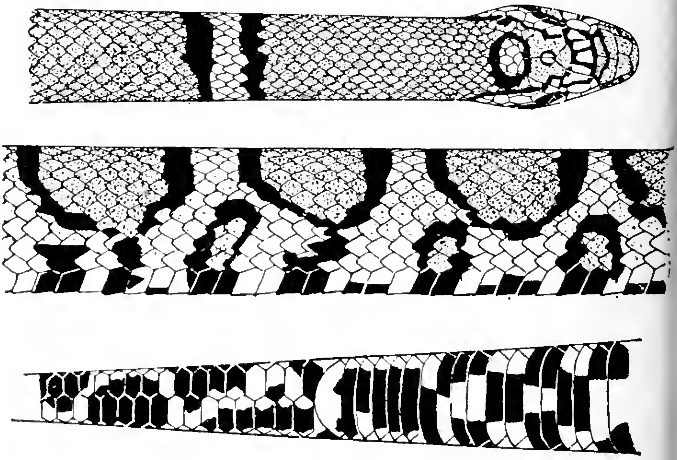


Fig. 3. *Osceola doliata clerica.*

The ground color in this form is gray, and the spots are a rich brown with black borders. The belly has a white ground color.

In Fig. 3 we have the subspecies *clerica*, where the following modifications appear. The fusion of the limbs of the chevron is more complete, and the dorsal spots are more expanded transversely. They extend to within two or three scales of the gastrosteges, while in the form *triangulus* they are five scales distant. The alternate spots touch the gastrosteges. This figure is taken from a specimen in the Museum of the Philadelphia Academy from southern Illinois.

In Fig. 4 we have an individual from Elmira, Illinois, which illustrates the characters of the form *collaris*. Here the chevrons are distinct from the first dorsal spot, whose anterior black border forms a half collar on the neck. This specimen is instructive, as it displays the last connection between the chevron and the first spot, in a black line on each side. This is wanting in the typical *collaris*.

The collar of ground color is complete in its anterior border, as well as the posterior in the form *temporalis* (Fig. 5), owing to the disappearance of the chevron. The transverse band on the prefrontals has also disappeared. The anterior extremity of the postorbital stripe is cut off, and consists of a spot of ground color. The dorsal saddle spots are wider, reaching the gastrosteges, while the intermediate spots are exclusively gastrostegal. The spots which alternate with them, have fused on the middle line. Fig. 5 is from a specimen from the State of Delaware.

In subspecies *doliata* the postocular stripe has disappeared, and the chevron is replaced by a black patch on the parietal and temporal plates. In other respects

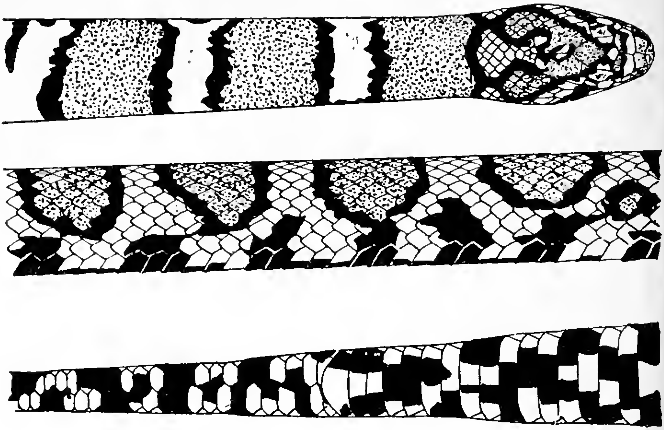


Fig. 4. *Osceola doliata collaris.*

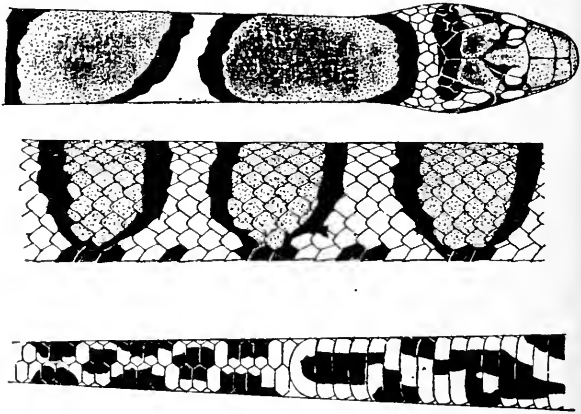


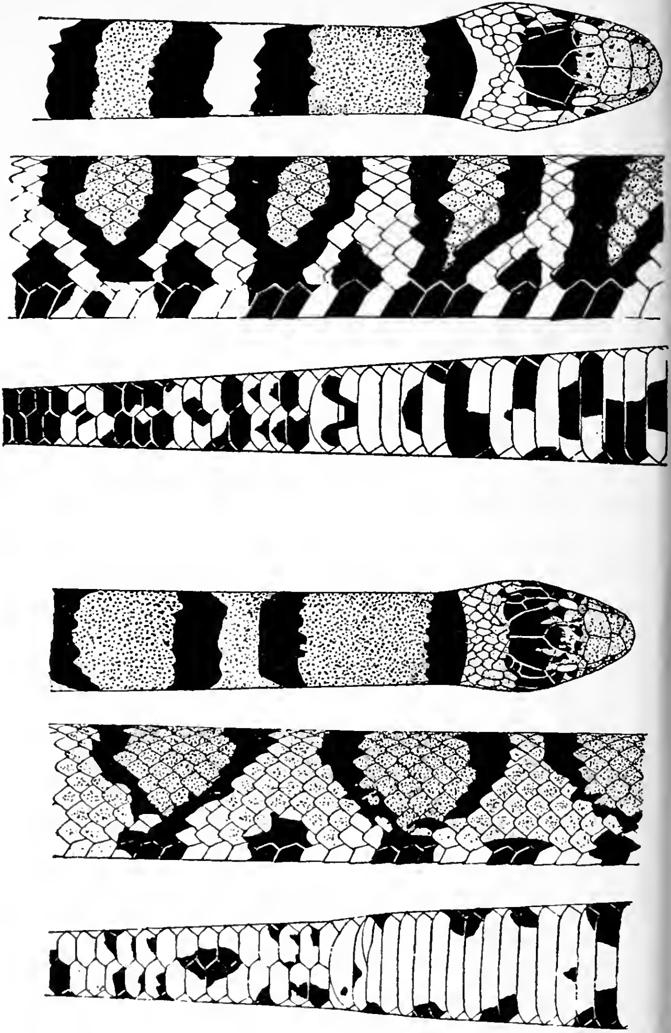
Fig. 5. *Osceola doliata temporalis.*

this form is more like the form *collaris.* The dorsal saddle spots are separated by a row or two of scales from the gastrosteges, and their alternating spots are partly on the scales. The ground color in this form, as in the *temporalis*, approaches red. This is the form of the tier of states between latitude 40° and the Gulf States.

The subspecies *syspila* is represented in Fig. 8. The head pattern is like that of *doliata* with the black patch more or less reduced—in the specimen figured being represented by a cross stripe. The dorsal saddle spots are more expanded than in any form yet encountered, their lateral borders being completed below the scales and entirely on the gastrosteges. The alternate spots now meet and fuse on the middle line of the abdomen, and the second series of alternating spots has disappeared. This is distinctively a southern form, extending west to central Oklahoma.

The dorsal saddles are so far extended in the next subspecies, *parallela*, as to form two parallel stripes with a narrow strip of ground color between, on the middle line of the abdomen. The alternating spots have disappeared. In the specimen figured, which is from Florida, and is in the United States National Museum, the supraocular spots seen in *temporalis*, are indicated. The ground color is red. Black begins to appear on the head.

From the form *syspila* two types of color modification may be traced. One of these brings the borders of the saddle spots together on the median line, forming a median black stripe ; this is the subspecies *annulata*, which belongs to western Texas and the adjacent parts of Mexico. The top of the head is black (Fig. 10). In the other, the lateral borders of the saddle



Figs. 6–7. *Osceola doliata doliata.*

spots have disappeared altogether, so that the body is more or less completely encircled by pairs of black rings, the alternating spots having disappeared. This might be supposed to have resulted from a continuation of the process by which the alternating spots have disappeared, and the edges of the saddles been brought closer and closer together. The continued transverse extension of the spot color would finally obliterate the lateral borders completely, as actually occurs in this last form, the *coccinea* of authors, which is the common type of the Gulf Coast. But the black has not covered the head and muzzle of this form as in the *annulata*. These regions are on the contrary red, as is the spot color generally, while the ground color is pale yellow.

A tendency to a development of black pigment in the saddle spots is seen in two other forms. The subspecies *gentilis* resembles *annulata*, but has a black longitudinal dorsal band which divides each saddle spot in two equal halves. This is a rare form, only known from the Indian Territory. The common Mexican form (*polyzona*) has the paired rings of *coccinea*, the black head of *annulata*, but each scale of the red intervals is tipped with black.

The relations of these forms may be expressed in a tabular form, given on page 39.

The main series corresponds with a distribution in latitude, commencing with the *triangula* of New England and New York, and passing gradually to the *coccinea* of the Gulf Coast regions, and *polyzona* of Mexico and Central America. The forms of the right-hand column are (except the *parallela*) from the central warmer parts of the continent.

This series of color-forms of the *Osceola doliata*

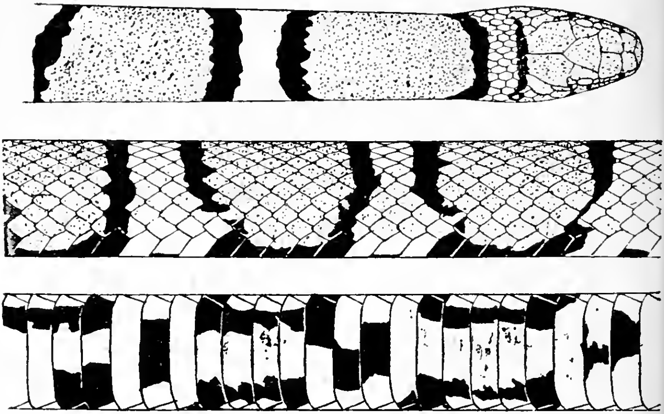


Fig. 8. *Osceola doliata syspila.*

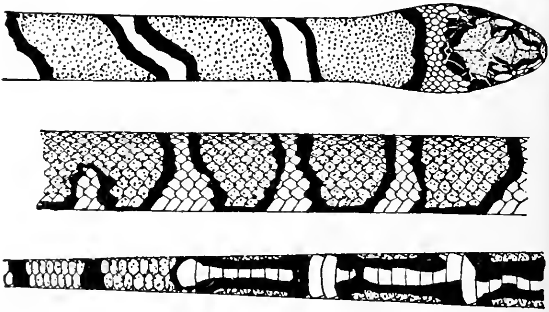
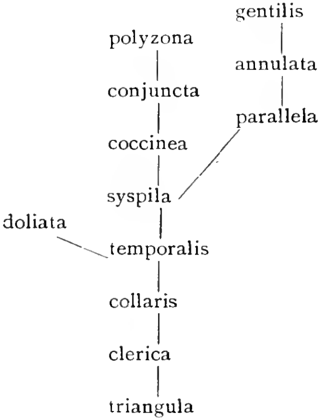


Fig. 9. *Osceola doliata parallela.*

demonstrates the following points. First: the color-variation is determinate and not indeterminate. It consists in, *a*, the successive enlargement of the dorsal spots toward, to, and across, the belly; *b*, the diminution and extinction of the longitudinal stripes on the head; *c*, do. of the spots of the inferior surface of the body; *d*, in the increase of red in the color of the dorsal spots, coincidentally with the changes mentioned. Second: these color-changes follow parallels of latitude, the red color and accompanying changes developing from north to south. Third: so far as regards eastern North America, there is a diminution of size in passing from north to south; the *O. d. coccinea* being the smallest of the subspecies. In Mexico, the size is recovered, as the *O. d. polyzona* equals in dimensions the *O. d. triangula*.



The young of the northern *O. d. triangula* presents the colors of the dorsal spots nearly as brilliant as those of the southern *O. d. coccinea*, and they fade

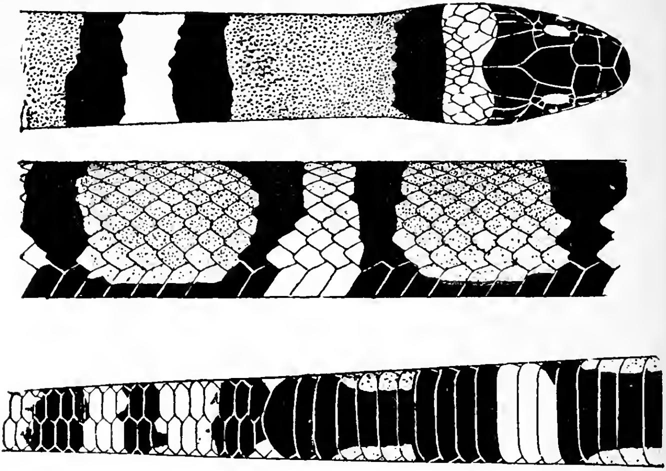


Fig. 10. *Osceola doliata annulata.*

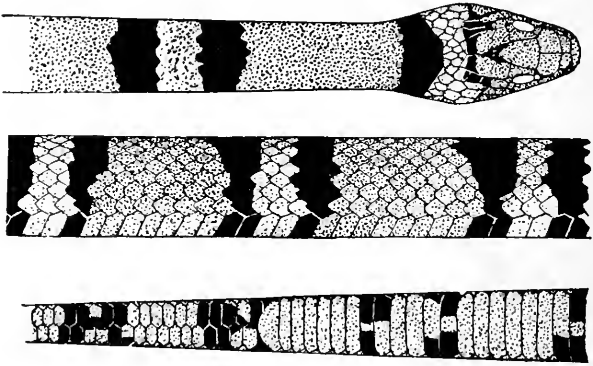


Fig. 11. *Osceola doliata coccinea.*

with age to the adult character. The pattern in the young at the period of hatching is the same as that of the adult.

c. *Color-Variations in Cnemidophorus.*

Another illustration of the nature of color-variation is to be found in certain species of the lacertilian genera Cnemidophorus in America, and Lacerta in Europe. In both genera the color-markings differ in the same individual at different ages, and the age at which the adult coloration is assumed, differs in different localities. Some of the species, e. g., *Cnemidophorus sexlineatus*, never abandon the coloration of the young of other species and subspecies. The same condition is characteristic of the *C. deppei* of Mexico, the *C. lemniscatus* of Brazil, and other species. The process of color-modification in the *C. tessellatus* and *C. gularis* of North America is, as I have pointed out,[1] as follows: The young are longitudinally striped with from two to four stripes on each side of the middle line. With increasing age, light spots appear between the stripes in the dark interspaces. In a later stage these spots increase in transverse diameter, breaking up the dark bands into spots. In some of the forms these dark spots extend themselves transversely and unite with each other, forming black cross-stripes of greater or less length. Thus we have before us the process by which a longitudinally striped coloration is transformed into a transversely striped one.

The large number of specimens of the *C. tessellatus* and *C gularis* in the National Museum collection show that the breaking up of the striped coloration appears

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[1] *Proceeds. Amer. Philos. Soc.*, 1885, p. 283. *Transac. Amer. Philos. Soc* 1892, p. 27.

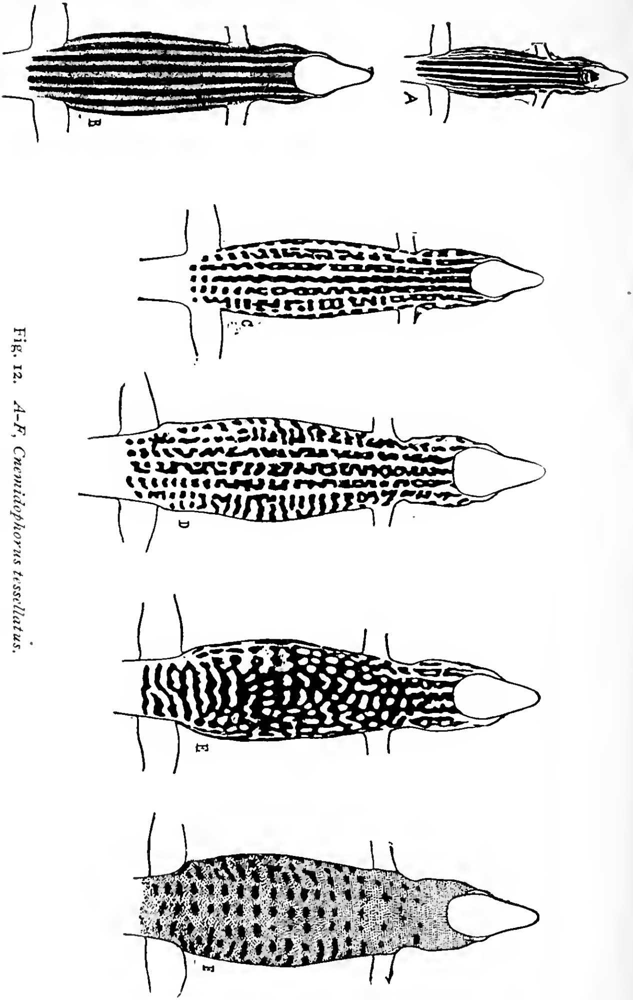

Fig. 12. *A–F, Cnemidophorus tessellatus.*

first at the posterior part of the dorsal region (i. e., the sacral and lumbar). The confluence of the spots appears there first; and finally (*C. gularis semifasciatus*), where the color markings disappear, leaving a uniform hue, this also appears first at the posterior part of the

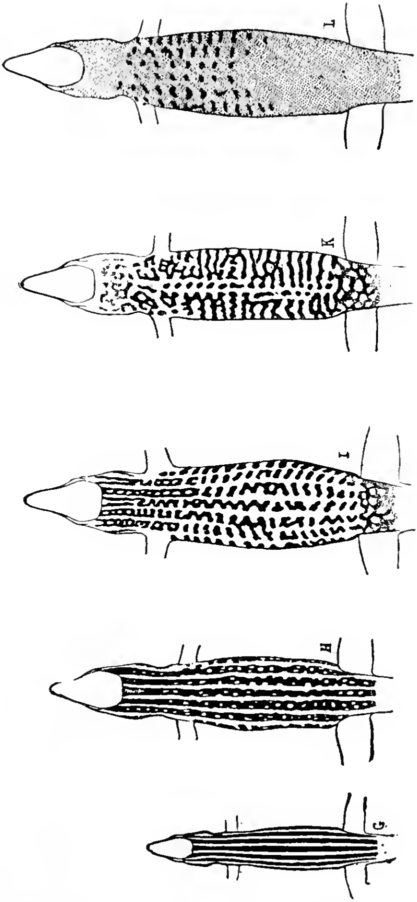

Fig. 13. G–L, *Cnemidophorus gularis.*

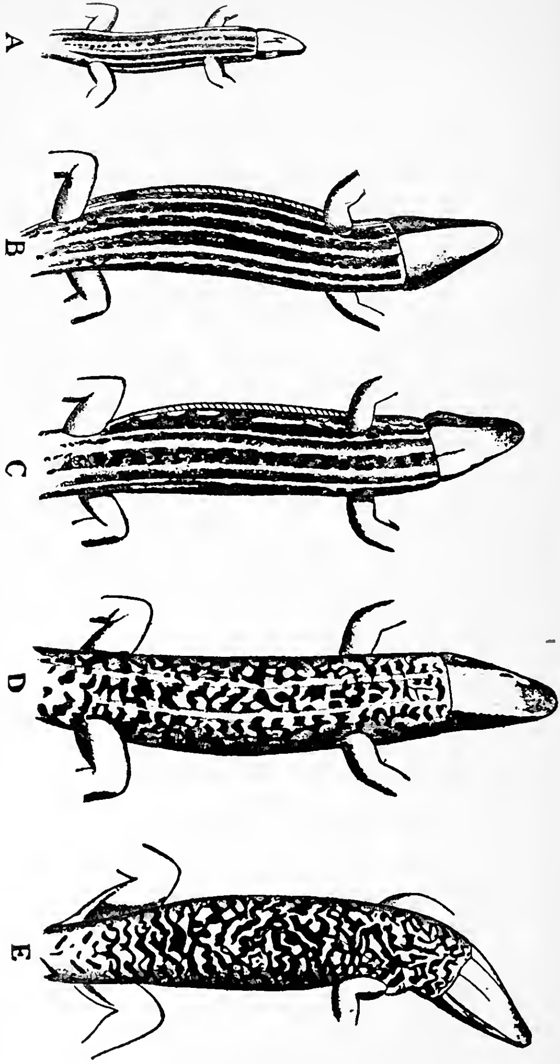

Fig. 14. *Lacerta muralis.*

body. In the *C. tessellatus rubidus* the dark spots disappear first on the anterior regions.

According to Eimer,[1] among many color-variations of the *Lacerta muralis* there exists a series of types closely similar to those observed by me to characterize the two species of Cnemidophorus mentioned. I give figures of these series in all three species. It will be observed that in the second and third forms (B and C) of the *L. muralis*, the pale portions of the dark stripes do not assume the very light hue of the ground color as they do in the corresponding phase of the *Cnemidophorus tessellatus* (C and D, Fig. 12), but this intermediate condition is exactly paralleled by the subspecies *mariarum* of the *Cnemidophorus gularis*. The correspondences are represented in the table on page 46.

There are some color forms in the *Lacerta muralis* which are not repeated in the North American Cnemidophori, particularly those which result in a strong contrast between the dorsal colors as a whole and the darker lateral colors, as a band. The color variety, No. 7, of the Cnemidophori is not reported by Eimer as occurring in the *Lacerta muralis*.

The variations from one to four form a direct series, and so do those represented by Nos. 1, 2, 3, and 5. Such variations cannot be regarded as promiscuous, especially when the same process of change is to be observed in three different species, one of which inhabits a continent remote from the other two.

d. Variations in North American Birds and Mammals in Relation to Locality.

The distinguished zoölogist, Dr. J. A. Allen of New York, has made a thorough study of this subject with

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[1] *Archiv für Naturgeschichte*, 1881, p. 239.

	Cnem. tessellatus.	*Cnem. gularis.*	*Other Cnemidoph'i.*	*Lacerta muralis.*
1. Longitudinally striped...........	*C. t. perplexus.*		*C. octolineatus.* *C. sexlineatus.*	*L. m. campestris.*
2. Dark interspaces pale spotted.....	*C. t. tessellatus α.*	*C g. gularis α.*	*C. labialis.* *C. septemvittatus.*	
3. Dark interspaces divided by light color........................	*C. t tessellatus β.*	*C. g. scalaris α.*	*C. grahamii.*	*L. m. albiventris.* *L. m. striatomaculata.*
4. Dark spots confluent transversely, forming crossbars.............	*C. t. tessellatus γ.*	*C. g. scalaris β.* *C. g. costatus.*		*L. m. reticulata.* *L. m. tigris.*
5. Light spots not confluent; light stripes broken up; pattern reticulated........................	*C. t. melanostethus.*		*C. variolosus.*	*L. m. punctulato-fasciata.*
6. Dark stripes interrupted by darker color.........................		*C. t. mariarum.*		*L. m. maculostria α.*
7. Dark spots separate and on a brown ground...	*C. t. rubidus.*	*C. g. semifasciatus.*		

ample material at his disposal. Following lines already laid down by Prof. Spencer F. Baird, Dr. Allen has shown that variations in form, size, and color are directly related to latitude, and that they are not promiscuous or multifarious, but are definite and graded. I make the following extract from a summary of the subject published by him in *The Radical Review* (New Bedford, Mass.) for May, 1877:

"Geographical variation, as exhibited by the mammals and birds of North America, may be summarized under the following heads, namely: (1) variation in general size, (2) in the size of peripheral parts, and (3) in color; the latter being subdivisible into (*a*) variation in color with latitude, and (*b*) with longitude. As a rule, the mammals and birds of North America increase in size from the south northward. This is true, not only of the individual representatives of each species, but generally the largest species of each genus and family are northern. There are, however, some strongly marked exceptions, in which the increase in size is in the opposite direction, or southward. There is for this an obvious explanation, as will be presently shown; the increase being found to be almost invariably toward the region where the type or group to which the species belongs receives its greatest numerical development, and where the species are also most specialized. Hence the representatives of a given species increase in size toward its hypothetical center of distribution, which is in most cases doubtless also its original center of dispersal. Consequently there is frequently a double decadence in size within specific groups, and both in size, and numerically in the case of species, when the center of development of the group to which they belong is in the warm-temperate or tropical regions. This may be illustrated by reference to the distribution of the higher classes of vertebrates in North America. Among the species occurring north of Mexico there are very few that may not be supposed to have had a northern origin; and the fact that some are circumpolar in their distribution, while most of the others (especially among the mammals) have congeneric Old World allies further strengthens the theory of their northern origin. Not only do individuals of the same species increase in size toward the north, but the same is true of the species of different genera. Again, in the exceptional cases of increase in size southward, the species belong to southern types, or, more correctly, to types having their center of development within or near the intertropical regions, where occur, not only the greatest number of the specific representatives of the type, but also the largest.

"For more detailed illustration we may take three families of the North American Carnivora; namely, the Canidæ (wolves and foxes), the Felidæ (lynxes and wild cats), and the Procyonidæ (raccoons). The first two are to some extent cosmopolitan, while the third is strictly American. The Canidæ have their largest specific representatives, the world over, in the temperate or colder latitudes. In North America the family is represented by six species,[1] the smallest of which (speaking generally) are southern, and the largest northern. Four of them are among the most widely distributed of North American mammals, two (the gray wolf and the common fox) being circumpolar species; another (the Arctic fox) is also circumpolar, but

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[1] The gray wolf (*Canis lupus*), the coyote (*C. latrans*), the Arctic fox (*Vulpes lagopus*), the common fox (*V. alopex*), the kit fox (*V. velox*), and the gray fox (*V. cinereoargentatus*).

is confined to high latitudes. The three widest-ranging species (the gray wolf, the common fox, and the gray fox) are those which present the most marked variation in size. Taking the skull as the basis of comparison, it is found that the common wolf is fully one-fifth larger in the northern parts of British America and Alaska than it is in Northern Mexico, where it finds the southern limit of its habitat. Between the largest northern skull and the largest southern skull there is a difference of *about thirty-five per cent. of the mean size!* Specimens from the intermediate region show a gradual intergradation between these extremes, although many of the examples from the upper Missouri country are nearly as large as those from the extreme North.

"The common fox, though occurring as far north as the wolf, is much more restricted in its southward range, especially along the Atlantic coast, and presents a correspondingly smaller amount of variation in size. The Alaskan animal, however, averages about one-tenth larger than the average size of specimens from New England. In the gray fox, whose habitat extends from Pennsylvania southward to Yucatan, the average length of the skull decreases from about five inches in Pennsylvania to considerably less than four in Central America—a difference equal to about thirty per cent. of the mean size for the species.

"The Felidæ, unlike the Canidæ, reach their greatest development, as respects both the number and the size of the species, in the intertropical regions. This family has but a single typical representative—the panther (*Felis concolor*)—north of Mexico, and this ranges only to about the northern boundary ot the United States. The other North American representatives of the family are the lynxes, which, in some of their varieties, range from Alaska to Mexico. They form, however, the most northern, as well as the most specialized or 'aberrant,' type of the family. While they vary greatly in color, as well as in the length and texture of the pelage, at different localities, they afford a most remarkable exception to all laws of variation in size with locality; for a large series of skulls, representing localities as widely separated as Louisiana, Northern Mexico, and California, on the one hand, and Alaska and the Mackenzie River district on the other, as well as various intermediate localities, reveals no appreciable difference in size throughout this wide area. The true cats, however, as the panther and the ocelots, are found to greatly increase in size southward, or toward the metropolis of the family. The panther ranges from the Northern States southward over most of South America. Skulls from the Adirondack region of New York have an average length of about seven and a half inches, the length increasing to eight and three-quarters in Louisiana and Texas, from beyond which points there is lack of data. The ocelot (*Felis pardalis*) finds its northern limit near the Rio Grande of Texas, and ranges thence southward far into South America. The average size of Costa Rican examples is about one-fifth greater than that of specimens from the Rio Grande.

Instances of increase in size northward among the Carnivora of North America are so generally the rule that further space need not be taken in recounting examples in detail. It may suffice to state that the badger (*Taxidea americana*), the marten (*Mustela americana*), the fisher (*M. pennanti*), the wolverine (*Gulo luscus*), and the ermine (*Putorius ermineus*)—all northern types—afford examples of variations in size strictly parallel with that already noticed as occurring in the foxes and wolves.

"To refer briefly to other groups, it may be stated that the Cervidæ (deer family) are mainly rather northern in their distribution; that the largest species occur in the colder zones, and that individuals of the same species increase rapidly in size toward the north. Some of the species, in fact, afford some of the most striking instances of northward increase in size; among which are the Virginia deer and its several representatives in the interior of the continent and on the Pacific Slope. It is also noteworthy that the most obviously distinctive characteristic of the group—the large, annually deciduous antlers—reaches its greatest development at the northward. Thus all the northern species, as the moose, the elk, and the caribou, have branching antlers of immense size, while the antlers are relatively much smaller in the species inhabiting the middle region of the continent, and are reduced to a rudimentary condition—a simple, slender, sharp spike, or a small and singly forked one—in the tropical species; the antlers declining in size much more rapidly than the general size of the animal. This is true in individuals of the same species as well as of the species collectively.

"The Glires (the squirrels, marmots, spermophiles mice, and their affines) offer the same illustrations in respect to the law of increase in size as the species already mentioned, the size sometimes increasing to the southward, but more generally to the northward, since the greater number of the species belong decidedly to northern types. There is no more striking instance known among mammals of variation in size with locality than that afforded by the flying squirrels, in which the northern race is more than one-half larger than the southern; yet the two extremes are found to pass so gradually the one into the other, that it is hardly possible to define even a southern and a northern geographical race, except on the almost wholly arbitrary ground of difference in size. The species, moreover, is one of the most widely distributed, ranging from the Arctic regions (the northern limit of forests) to Central America.

"Among birds the local differences in size are almost as strongly marked as among mammals, and in the main, follow the same general law. A decided increase in size southward, however, or toward the warmer latitudes, occurs more rarely than in mammals, although several well-marked instances are known. The increase is generally northward, and is often very strongly marked. The greatest difference between northern and southern races occurs, as in mammals, in the species whose breeding-stations embrace a wide range of latitude. In species which breed from Northern New England to Florida, the southern forms are not only smaller, but are also quite different in color and in other features. This is eminently the case in the common quail (*Ortyx virginianus*), the meadow-lark (*Sturnella magna*), the purple grackle (*Quiscalus purpureus*), the red-winged blackbird (*Agelaeus phaeniceus*), the golden-winged woodpecker (*Colaptes auratus*), the towhee (*Pipilo erythrophthalmus*), the Carolina dove (*Zenædura macrura*), and in numerous other species; and is quite appreciable in the blue-jay (*Cyanurus cristatus*), the crow (*Corvus americanus*), in most of the woodpeckers, in the titmice, numerous sparrows, and several thrushes and warblers, the variation often amounting to from ten to fifteen per cent. of the average size of the species.

"As a general rule, certain parts of the organisms vary more than does general size, there being a marked tendency to enlargement of peripheral parts under high temperature, or toward the tropics,—hence southward in North America. This is more readily seen in birds than in mammals, in consequence, mainly, of their peculiar type of structure. In mammals it is manifested occasionally in the size of the ears and feet, and in the horns of bovines, but especially and more generally in the pelage. At the northward, in individuals of the same species, the hairs are longer and softer, the under fur more abundant, and the ears and the soles of the feet better clothed. This is not only true of individuals of the same species, but of northern species collectively as compared with their nearest southern allies. Southern individuals retain permanently, in many cases, the sparsely clothed ears and the naked soles that characterize northern individuals only in summer, as is notably the case among the different squirrels and sphermophiles.

"In mammals which have the external ear largely developed—as in the wolves, foxes, some of the deer, and especially the hares,—the larger size of this organ in southern as compared with northern individuals of the same species is often strikingly apparent. It is more especially marked, however, in species inhabiting extensive open plains and semi-desert regions. The little wood hare, or gray rabbit (*Lepus sylvaticus*), affords a case in point. This species is represented, in some of its varieties, across the whole breadth of the continent, and from the northern border of the United States southward to Central America, but in different regions by geographical races or subspecies. In addition to certain differences of color and general size, the ears vary still more strongly. In the form inhabiting the Great Plains, commonly known as the little sage-brush hare (*L. sylvaticus nuttalli*), the ears are considerably longer than in the eastern variety, and increase in size from the north southward, reaching their greatest development in Western Arizona and the desert region further westward and southward, where the variety is characterized mainly by the large size of its ears, which are in this race nearly twice the size they attain in the eastern variety. In the long-eared 'jackass' hares of the plains, the ear likewise increases in size to the southward. In *Lepus callotis*, for example, which ranges from Wyoming southward far into Mexico, the ear is about one-fourth to one-third larger in the southern examples than in the northern. The little brown hare of the Pacific Coast (*L. trowbridgei*) presents a similar increase in the size of the ear southward, as does, to a less extent, the prairie hare (*L. campestris*). Not only are all of the long-eared species of American hares confined to the open plains of the arid interior of the continent, but over this same region is the tendency to an enlargement of the ear southward stronger than elsewhere. It is also of interest in this connection that the largest-eared hares of the Old World occur over similar open, half-desert regions, as do also the largest-eared foxes. On our western plains, the deer are represented by a large-eared species. Among the domestic races of cattle, those of the warm temperate and intertropical regions have much larger and longer horns than those of northern countries; as is shown by a comparison of the Texan, Mexican, and South American breeds, with the northern stock, or those of the South of Europe with the more northern races. In the wild species of the Old World, the southern or sub-tropical are remarkable for the large size of their horns. The horns of the American prong-horn (*Antilocapra americana*) are also much larger at southern than at northern localities.[1] Naturalists have also recorded the existence of larger feet in many of the smaller North American Mammalia at the southward than at the northward, among individuals of the same species, especially among the wild mice, in some of the squirrels, the opossum and raccoon, as well as in other species.

"In birds, the enlargement of peripheral parts, especially of the bill, claws, and tail, is far more obvious and more general than in mammals. The bill is particularly susceptible to variation in this regard,—in many instances being very much larger, among individuals of unquestionably the same species, at the southward than at the northward. This accords with the general fact that all the ornithic types in which the bill is remarkably enlarged occur in the intertropical regions. The southward enlargement of the bill within specific groups may be illustrated by reference to almost any group of North American birds, or to those of any portion of the continent. As in other features of geographical variation, the greatest differences in the size of the bill are met with among species having the widest distribution in latitude. Among the species inhabiting eastern North America we find several strik-

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[1] The deer tribe, in which the antlers increase in size toward the north, offer an apparent exception to the rule of increase in size of peripheral parts toward the tropics. The antlers of the deer, however, are merely seasonal appendages, being annually cast and renewed, and are thus entirely different physiologically from the horns of bovines, which retain a high degree of vitality throughout the life of the animal.

ing examples of this enlargement among the sparrows, black-birds, thrushes, crows, wrens, and warblers, in the quail, the meadow-lark, the golden-winged woodpecker, etc. Generally the bill, in the slender-billed forms, becomes longer, more attenuated, and more decurved (in individuals specifically the same) in passing from the New England States southward to Florida, while in those which have a short, thick, conical bill there is a general increase in its size so that the southern representatives of a species, as a rule, have thicker and longer bills than their northern relatives, though the birds themselves are smaller. There is thus not only generally a relative, but often an absolute, increase in the size of the bill in the southern races. The species of the Pacific Coast and of the interior afford similar illustrations, in some cases more marked even than in any of the eastern species. More rarely, but still quite frequently, is there a similar increase in the size of the feet and claws.

"The tail, also, affords an equally striking example of the enlargement of peripheral parts southward. Referring again to the birds of the Atlantic Coast, many of the above-named species have the tail absolutely longer at southern localities than at northern, and quite often relatively longer. Thus while the general size decreases, the length of the tail is wholly maintained, or decreases less than the general size; but, in some cases, while the general size is one-tenth or more smaller at the south, the tail is ten to fifteen per cent. longer than in the larger northern birds. Some western species are even more remarkable in this respect; and in consequence mainly of this fact the southern types have been varietally separated from the shorter-tailed northern forms of the same species.

"Variations in color with locality are still more obvious, particularly among birds, in which the colors are more positive, the contrasts of tints greater, and the markings consequently better defined than is usually the case in mammals. The soft finely-divided covering of the latter is poorly fitted for the display of the delicate pencilings and the lustrous, prismatic hues that so often characterize birds. Mammals, however, present many striking instances of geographical variation in color.

"As already stated, geographical variations in color may be conveniently considered under two heads. While the variation with latitude consists mainly in a nearly uniform increase in one direction, the variation observed in passing from the Atlantic Coast westward is more complex. In either case, however, the variation results primarily from nearly the same causes, which are obviously climatic, and depend mainly upon the relative humidity, or the hygrometric conditions of the different climatal areas of the continent. In respect to the first, or latitudinal variation, the tendency is always toward an increase in intensity of coloration southward. Not only do the primary colors become deepened in this direction, but dusky and blackish tints become stronger or more intense, iridescent hues become more lustrous, and dark markings, as spots and streaks or transverse bars, acquire greater area. Conversely, white or light markings become more restricted. In passing westward a general and gradual blanching of the colors is met with on leaving the wooded regions east of the Mississippi, the loss of color increasing with the increasing aridity of the climate and the absence of forests, the greatest pallor occurring over the almost rainless and semi-desert regions of the Great Basin and Colorado Desert. On the Pacific Slope, north of California, the color again increases, with a tendency to heavy, sombre tints over the rainy, heavily-wooded region of the Northwest Coast."[1]

2. VARIATION IN STRUCTURAL CHARACTERS.

Modifications of structural characters may appear quite independently of variation of specific ones. Indeed, generic characters have at times changed completely without the appearance of corresponding changes in the more superficial characters which define the species. Thus changes in the dentition of some of the Mammalia appear within the limits of species, which, should they become permanent, would entitle the two sets of individuals which display the different dentitions to be placed in different genera.

Some striking examples of how generic characters may undergo metamorphosis without corresponding changes in specific characters, have been brought to light by Dr. William H. Dall among the Brachiopodous Mollusca. Some of the species of different genera can scarcely be distinguished, except by comparison of their generic characters. I have cited the axolotls as illustrative of this phenomenon. Here the same species may reproduce as a permanent larva, or as an adult. Duméril has shown that the North American salamander (*Amblystoma tigrinum*) can lay and fertilize eggs before the metamorphosis is passed. I have since observed that the females of the allied species of Amblystomidæ, the *Chondrotus tenebrosus* B. and G., of California contain mature eggs ready for de-

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[1] *The Radical Review*, May, 1877.

posit, and have supposed that this species has also the same power.[1] The difference between such larvæ and the adult which has passed the metamorphosis is great. It extends not merely to the branchial processes, but to the splenial teeth, which are shed, and to the palatopterygoid arch, which is absorbed, and to the posterior ceratobranchial and epibranchial cartilages, which are absorbed. In the larva of the *C. tenebrosus* the palatopterygoid arches and epibranchials are ossified, so that the probability of its being able to maintain an independent existence as a larva is greater than in the case of the *A. tigrinum*. In this type, then, each species displays variations concomitant with reproductive maturity, which are not only of generic, but of family significance. In a third species, the *Siredon mexicanum*, no metamorphosis has yet been shown to take place, so that it is probable that it reproduces ordinarily while in the branchiferous stage. Yet it is only specifically different from the larva of the *Amblystoma tigrinum*.

Excellent illustrations of the serial appearance of generic characters may be seen in the family of the dogs (Canidae). In the true genus Canis, the dental formula is, I. $\frac{3}{3}$; C. $\frac{1}{1}$; P. m. $\frac{4}{4}$; M. $\frac{2}{3}$. The inferior sectorial (m. 1) has a metaconid, and the second inferior true molar has two roots. It not unfrequently happens, however, that the last inferior molar (m. 3) is wanting; and in some cases the inferior m. 2 has but one root. When in addition to this, as in some of the black-and-tans, in the Mexican naked dog, and in the pug, the inferior m: 1 loses its metaconid, we have the genus Synagodus. Occasionally the pug dog, and frequently the Mexican dog, loses one of its premolars

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[1] *Batrachia of North America*, 1888, p. 113, Pl. xxii, xxiii.

from both jaws. The Japanese spaniel goes still further, and usually loses also its second superior true molar and frequently another premolar from each jaw; and we then have a dentition which indicates a third genus, which has been called Dysodus. Its dental formula is I. $\frac{3}{3}$; C. $\frac{1}{1}$; P. m. $\frac{2}{2}$–$\frac{3}{3}$; m. $\frac{1}{2}$. Transitions between this and the normal dentition of Canis, in all respects can be found in the smaller domesticated dogs. And these modifications are not pathological, but simply express a rapid metamorphosis of the dentition towards the reduced formula which is characteristic of the cats. And while the most characteristic dentitions belong to particular species (or races) of dogs, many of the single modifications are both absent and present in dogs of the same species or race. And these are the kind of characters which are observed to mark the slow progress during long geologic ages, of mammals of various other groups. These modifications are not promiscuous, but are in the direct line of change which has characterized all Mammalia during geologic time; i. e., the reduction of the numbers of the molar teeth. And in greater detail, the loss of metaconid of the inferior sectorial, and loss of posterior true molars, are the exact losses which the carnivorous type has undergone in the evolution of the cats.

A significant modification of the third superior premolar has been observed by Dr. Horace Jayne to be occasionally met with in the domestic cat. Sometimes an internal cusp (deuterocone), with a corresponding root is developed, giving rise to a tritubercular crown.

Similar observations have been made on the dentition of man, which presents two phenomena of variation of opposite phylogenetic significance. I have shown[1] that most of the Indo-European race, together with the Esquimaux, present a reversion to a lemurine form in the second and third superior molars, and sometimes, in the case of the Esquimaux, in the first superior molar also. I have also shown,[2] after a study of the dentition of the extinct Mammalia, that the more complex molars of later placental orders, have been derived from a tritubercular type, which prevailed throughout the earth just before the opening of the Eocene period. In the line of human and quadrumanous phylogeny, the lemurs of the Eocene period presented this type of molar in the upper jaw, and mostly continue to do so to the present time. The true monkeys, however, added the fourth tubercle or hypocone, in accordance with the developmental law in Mammalia generally, and the apes and men of the lower races present the same characteristic. Now, in the yellow race the hypocone of the last molar is generally wanting, while in the white race it is usual to find it absent from both the second and third molars. In this we have a case of reversion.

The reduction of the third (last) superior molar, and of the inferior as well, has gone further in the white race, since the tooth is frequently abnormally small, abortive, or totally wanting. The external superior incisor has a similar history, although its reduction and loss is not nearly so frequent as that of the last molars. These losses from the dental series are not of the nature of reversions, since the number of teeth is more and more numerous as we recede in time along the line of human ancestry. It is, on the contrary, the continuation of a process which has been,

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[1] *American Journal of Morphology*, 1888, p. 7.

[2] *American Naturalist*, 1884, p. 350; *Origin of the Fittest*, 1887, p. 347.

as already remarked, common to all the Mammalia, of reduction in the number of teeth. Thus men with fewer teeth are more advanced than those with more numerous ones; while people with tritubercular superior molars have reverted to an ancient type; and both results are probably attained by the same physiologic process, i. e. defect of nutrition. It is to be remembered also, in connection with our argument, that these dental variations are modifications of generic characters, and that they are in definite directions, and are not promiscuous. With regard to the question as to whether dental variations in man are promiscuous or not, we have better opportunities of investigation than in the case of the lower animals generally. It may be safely asserted that the dental variations above cited are by far the most frequent in man, and that all others put together are relatively insignificant.

3. SUCCESSIONAL RELATION.

As the biologic types are variations become permanent, it is important to examine how the former stand related to each other. These relations express the direction which variation has taken, and throw a great deal of light on the nature of the process. That existing types of all grades are the result of the isolation of variations of species, is shown by the frequent examples of incomplete isolation, which follows inconstancy of the definitive characters. Groups of individuals which display this partial isolation are termed subspecies.

As an illustration of the mingling of isolated groups of individuals (species) with imperfectly isolated groups (subspecies), in a single genus, I refer to the American garter-snake (genus Eutaenia B. and G.). An examination of several hundred individuals of this genus yielded the following results: I found seventeen groups of individuals, which could be said to be completely isolated in characters, with very few exceptions. Eight other groups (species) are probably isolated, but they are not represented by a sufficiently large number of specimens to yield a satisfactory demonstration. Of the seventeen, four species embrace fifteen non-isolated geographical forms (subspecies), besides the typical forms (eight of which are included under the *E. sirtalis*); and two others include three color forms easily recognizable, besides the typical ones. Similar phenomena are presented in every part of the animal and vegetable kingdoms.

One of the most instructive natural divisions for the study of taxonomic relations as the result of variation, on account of the simplicity of the relations presented, is the Batrachia Salientia, or the order of Batrachia to which belong the toads, frogs, etc. Omitting the very restricted suborders of the Aglossa and Gastrechmia, the Batrachia Salientia fall into two divisions, which differ only in the structure of the lower portion of their scapular arch, or shoulder-girdle. In the one the opposite halves are capable of movements which contract or expand the capacity of the thorax; in the other the opposite halves abut against each other so as to be incapable of movement, thus preserving the size of the thoracic cavity. But during the early stages, the frogs of this division have the movable shoulder-girdle which characterizes those of the other division, the consolidation constituting a modification superadded in attaining maturity. Furthermore, young *Salientia* are toothless, and one section of the species with embryonic shoulder-girdle never acquire teeth. The suborder with embryonic shoulder-girdle is called the *Arcifera*, and that which is advanced in this respect is the *Firmisternia.* Now the frogs of each of these divisions present nearly similar scales of development of another part of the skeleton, viz., the bones of the top of the skull. We find some in which one of these bones (ethmoid) is represented by cartilage only, and the frontoparietals and nasals are represented by only a narrow strip of bone each. In the next type the ethmoid is ossified; in the next, we have the frontoparietal completely ossified, and the nasals range from narrow strips to complete roofs; in the fourth station on the line, these bones are rough, with a hyperostosis of their surfaces; and in the next set of species this ossification fills the skin, which is thus no longer separable from the cranial bones; in

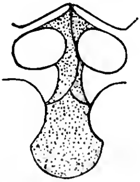

Fig. 15.

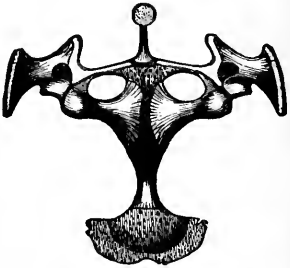

Fig. 17.

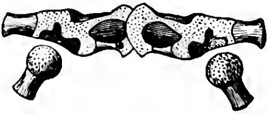

Fig. 16.

SHOULDER-GIRDLES OF "ANURA."

Fig. 15.—Of the Arciferous type (*Phyllomedusa bicolor*). Fig. 16, *Rana temporaria*, tadpole with budding limbs. Fig. 17, do., adult. Figs. 16 and 17 from Parker.

the sixth form the ossification is extended so as to roof in the temporal muscles and inclose the orbits behind, while in the rare seventh and last stage, the tympanum is also inclosed behind by bone. Now all of these types are not found in all of the families of the *Salientia*, but the greater number of them are. Six principal families, four of which belong to the *Arcifera*, are named in the diagram below, and three or four others might have been added. I do not give the names of the genera which are defined as above described, referring to the explanation of the cuts for them, but indicate them by the numbers attached in the plate, which correspond to those of the definitions above given. A zero mark signifies the absence or non-discovery of a generic type.

	Sternum embryonic. Arcifera.				Sternum complete
	Toothless.	Toothed.			Firmisternia.
	Bufonidæ.	Scaphiopidæ.	Cystignathidæ.	Hylidæ.	Ranidæ.
1—	1	0	1	1	0
2—	2	2	2	2	0
3—	3	0	3	3	3
4—	4	4	4	4	4
5—	5	5	0	5	5
6—	6	6	6	6	6
7—	7	0	0	0	0

It is evident, from what has preceded, that a perfecting of the shoulder-girdle in any of the species of the arciferous columns would place it in the series of *Firmisternia*. An accession of teeth in a species of the division *Bufonidæ* would make it one of the *Scaphiopidæ*; while a small amount of change in the ossification of the bones of the skull would transfer a species from one to another of the generic stations represented by the numbers of the columns from one to seven.

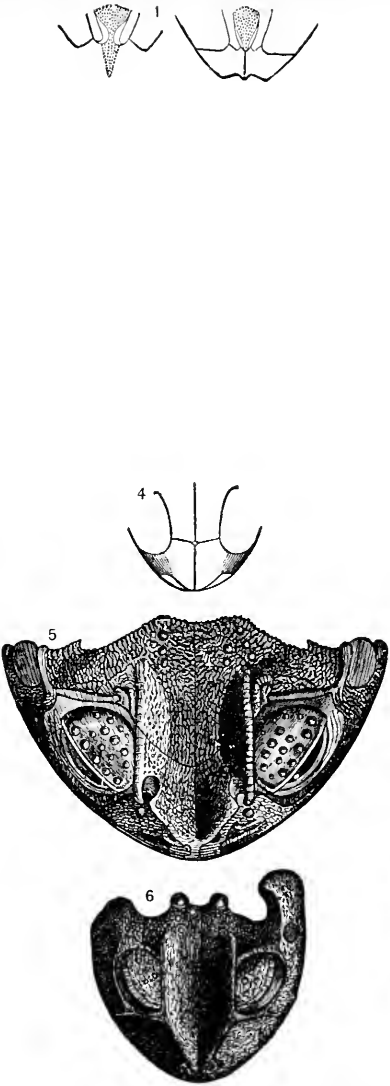

Fig. 18.
Bufonidæ.

Fig. 19.
Scaphiopidæ and Pelobatidæ.

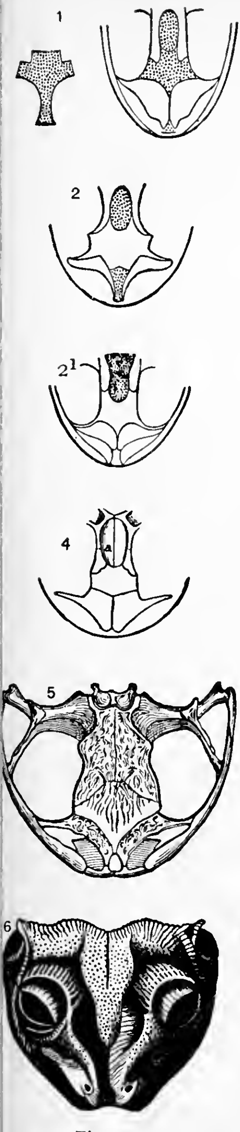

Fig. 20.
Hylidæ.

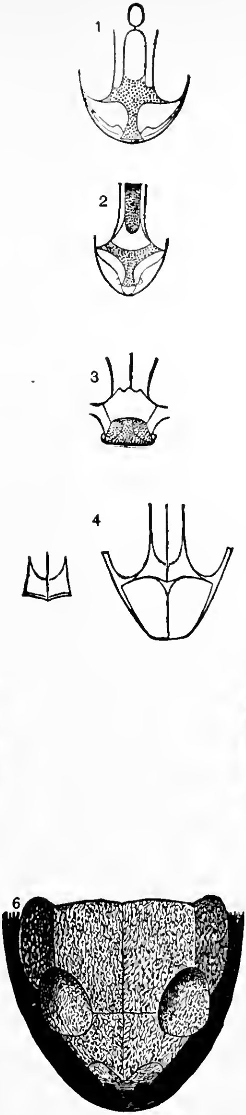

Fig. 21.
Cystignathidæ.

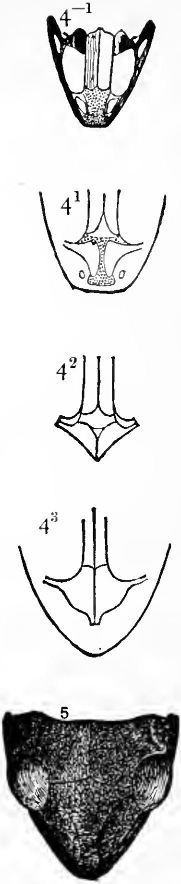

Fig. 22.
Ranidæ.

That the above generic divisions have been actually developed from each other is demonstrated by the occurrence of occasional intermediate forms. Thus no generic distinction can be maintained between types third and fourth in the family of toads (Bufonidæ), so complete is the transition between them. In Hylidæ and Cystignathidæ occasional transitions between types second and third occur. In the Scaphiopidæ the subspecies *Spea hammondii intermontana* sometimes has the frontoparietal fontanelle open, sometimes closed. I have seen some adult specimens of *Rana virescens austricola* from Central America with the ethmoid bone unossified above, as in the genus Ranula. The rugose cranium is only acquired in old age of some of the species of Polypedates of India. Yet these genera are as

EXPLANATION OF CUTS OF CRANIA OF SALIENTIA.

The numbers in each column correspond with the types of ossification mentioned in the text, and are the same as those in the table of families given in the same connection. The power numbers attached to No. 4, represent the degree of ossification of the nasal bone, except -1, which signifies unossified ethmoid. Most of the cuts are original.

Fig. 18.—Bufonidæ.—No. 1, anterior part of skull of *Chelydobatrachus gouldii* Gray, from Australia. No. 4, do. of *Schismaderma carens* Smith, South Africa. No. 5, top of head of *Peltaphryne peltacephala* D. and B., Cuba. No. 7, top of head of *Otaspis empusa* Cope, Cuba.

Fig. 19.—Scaphiopidæ and Pelobatidæ.—No. 2, diagram of top of cranium of *Didocus calcaratus* Micahelles, Spain. No. 5, skull of *Scaphiopus holbrookii* Harl., United States. No. 6, skull of *Cultripes provincialis*, from France, after Dugès.

Fig. 20.—Hylidæ.—No. 1, *Thoropa miliaris* Spix., Brazil. No. 2, *Hypsiboas doumercii* D. and B., Surinam. No. 2^1, *Hypsiboas punctatus* Schn., Brazil. No. 4^4, *Scytopis venulosus* Daudin, Brazil. No. 5, *Osteocephalus planiceps* Cope, E. Peru. No. 6, *Trachycephalus geographicus* D. and B., after Steindachner.

Fig. 21.—Cystignathidæ.—No. 1, *Eusophus nebulosus* Gir., Chili. No. 2, *Borborocœtes tasmaniensis* Gthr., Tasmania. No. 3, *Elosia nasus* Licht., Brazil. No. 4, *Hylodes oxyrhynchus* D. and B., West Indies. No. 6, *Calyptocephalus gayi* D. and B., Chili.

Fig. 22.—Ranidæ.—No. 4^{-1}, *Ranula chrysoprasina* Cope, Costa Rica. No. 4^1, *Rana clamata* Daud., N. America. No. 4^2, *Rana agilis* Thomas, Europe. No. 4^3, *Rana hexadactyla* Less., India No. 5, *Polypedates quadrilineatus* D. and B., Ceylon.

well defined as closely allied genera in most natural divisions.

It is seldom that so many stages of developmental series survive so as to be contemporaries, as in this case of the Batrachia Salientia. In order to obtain such series we usually have to explore the ages of the past. In the higher groups this is also the case, but here we have also occasional examples of the persistence of fairly complete series. Such a one is presented by the suborder Artiodactyla of the Diplarthrous Ungulate Mammalia. I give the definitions of the succession of the existing families.

I. Molars bunodont (tubercular); superior incisors generally present. No cannon or naviculocuboid bones.

Lateral toes well developed; *Hippopotamidæ.*

Lateral toes rudimental; *Suidæ.*

II. Molars selenodont (crescent-bearing). (Lateral toes rudimental or wanting).

A. Premolars with one row of lobes.

No naviculocuboid bone; one superior incisor; a cannon bone; *Camelidæ.*

A naviculocuboid bone; no superior incisor; (cannon bone variable); *Tragulidæ.*

AA. Premolars with two rows of tubercles; a naviculocuboid and cannon bones; no incisors above.

Premolar iii with only one row of lobes; canine teeth, no horns; *Moschidæ.*

Premolar iii with two rows of lobes; fixed horns; no canines above; *Bovidæ.*

Premolar iii with two rows of lobes; horns deciduous; *Cervidæ.*

In this suborder we see a gradual complication of the structure of the molar teeth, and a loss of the incisors. In the limbs we observe the successive loss of the lateral digits, and the fusion of elements,—as the metapodials into cannon bones, and the elements of the tarsus, and, what is not stated in the above table, of the carpus also. Finally there is the remarkable development of horns on the head. When we come to examine the phylogeny of this order we will find how completely these characters are the result of the fixation of variations which have appeared in past geologic ages, and how various are the combinations and modifications presented by the extinct types.

Few natural groups permit of representation of their subdivisions in linear series. The only correct representation is in the form of a branching tree, and this cannot be well done in flat projection on the pages of a book. Each branch taken by itself, however, yields itself for a longer or shorter space to linear treatment.

For an example of such linear series in higher groups I turn again to the Batrachia Salientia. Here the two suborders of the Arcifera and Firmisternia present the following interesting parallels:

<table>
<tr><th>ARCIFERA.</th><th>FIRMISTERNIA</th></tr>
<tr><td colspan="2">I. Without teeth.</td></tr>
<tr><td colspan="2"><i>a.</i> With sacral diapophyses dilated.</td></tr>
<tr><td>Bufonidæ.</td><td>Brevicipitidæ.
Engystomidæ.
Phryniscidæ.</td></tr>
<tr><td colspan="2"><i>aa.</i> Sacral diapophyses cylindric.</td></tr>
<tr><td>Dendrophryniscidæ.</td><td>Dendrobatidæ</td></tr>
<tr><td colspan="2">II. With premaxillary and maxillary teeth only.</td></tr>
<tr><td colspan="2"><i>a.</i> With sacral diapophyses dilated.</td></tr>
<tr><td>Pelodytidæ
Pelobatidæ
Hylidæ</td><td>Dyscophidæ.
Cophylidæ.</td></tr>
<tr><td colspan="2"><i>aa.</i> With sacral diapophyses cylindric.</td></tr>
<tr><td>Cystignathidæ.</td><td>Colostethidæ.
Ranidæ.</td></tr>
</table>

III. Teeth in both jaws.

a. Sacral diapophyses not dilated.

Amphignathodontidæ Hemiphractidæ ..... }	.... Ceratobatrachidæ.

In strict reference to the structure of the hind feet the following parallels may be drawn:

FIRMISTERNIA.	RANIDÆ.	ARCIFERA.
External metatarsal free :		
Aquatic.	Rana.	Pseudis.
Subfossorial.	Hoplobatrachus.	Mixophyes.
External metatarsal attached :		
Feet webbed—		
Burrowing.	Pyxicephalus.	Ceratophrys.
Arboreal (vom. teeth).	Leptopelis.	Hyla.
Arboreal (no v. teeth).	Hyperolius.	Hylella.
Aquatic.	Heteroglossa.	Acris.
Feet not webbed—		
Terrestrial.	Cassina.	Cystignathus.
Terrestrial, spurred.	Hemimantis.	Paludicola.

Parallel series like those of the Arcifera and Firmisternia I have termed "homologous," and the corresponding terms of such series I have called "heterologous."[1] Such corresponding phylogenetic series are homologous to each other, while their terms or genera are heterologous in their relation to corresponding terms of other phyla. In such cases the genera or terms of a series owe their resemblances to each other to inheritance; but they owe their resemblances to their corresponding or heterologous genera, to identical evolutionary influences. Subsequently to my proposal to use the above terms, Prof. E. R. Lankester proposed the word "homogenous" to express what is conveyed by my term homologous, and "homoplastic" to express the sense of heterologous. For the two con-

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[1] "Origin of Genera," *Proceedings Philadelphia Academy*, 1868, p. 281.

ditions he coined the words "homogeny" and "homoplassy." The terms introduced by Lankester differ from mine in that they convey implications as to the origin of the respective conditions.

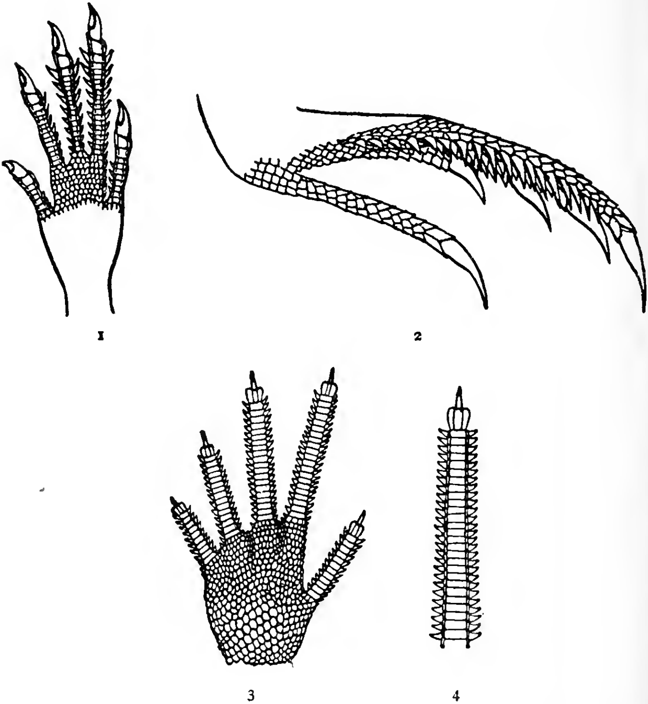


Fig. 23.—Feet of (1–2) *Uma scoparia* Cope, from near Tucson, Arizona, and (2–3) *Ptenopus garrulus* Smith, from South Africa. No. 1, manus; No. 2, pes; Nos. 3–4, pes. Nos. 1–2, original; Nos. 3–4, from Boulenger.

An illustration of homoplassy is to be seen in the spines on the head, tail, and feet of lizards which inhabit desert regions. The parallelism between Phrynosoma of the American dry regions, and the Moloch of the corresponding climates of Australia has been already noted. In the deserts of Asia, South Africa, and North America some of the lizards exhibit a great elongation of the lateral scales of the digits on one or both extremities. These become fringes of spines, freely articulated at their bases with the integument. By penetrating the sand, they increase the hold on its yielding surface, and greatly improve the speed of their movements. The genera in which this structure is conspicuous in the three localities in question, belong to as many distinct families. Thus in Asia it is the genus Phrynocephalus of the family Agamidæ; in South Africa it is Ptenopus of the Gecconidæ; while in North America it is Uma of the Iguanidæ. I give figures of the feet of Ptenopus and Uma for comparison. (Fig. 23.) Phrynocephalus is more like Uma than is Ptenopus.

In the succeeding chapters of this book many illustrations of the serial relation of characters will be given, so that it is not necessary to occupy more space with the subject here.

CHAPTER II.—PHYLOGENY.

1. GENERAL PHYLOGENY.

THE actual phylogeny or genealogy of organisms can only be positively determined by paleontologic research. We have been able in this way to obtain numerous lines of descent of animals and some general results as to the genealogic relations of the primary types of animals and plants. Many forms of both animals and plants are and have been without those hard parts which are susceptible of preservation in the formations of the earth's crust, so that no trace of their existence remains to us. In these cases our resort is embryologic investigation, since the embryonic history is a more or less complete recapitulation of the types of the past ages, from which the existing ones are descended. But since many representatives of the ancient and primitive forms of life still remain on the earth, we can trace, by the study of their structure, the larger features of general phylogeny. So far as we have compared the results derived from these three lines, it has been found that they coincide in their indications. We have in this a satisfactory proof that our conclusions are trustworthy contributions to the knowledge of the history of life.

The study of phylogeny shows that the evolution of life-forms has been from the simple to the complex, and from the generalized to the specialized. These two forms of expression are not identical. In the phrase, "from the simple to the complex," is implied an ascending scale of evolution. In the phrase, "from the generalized to the specialized," we may include both progressive and retrogressive evolution. Retrogressive or degenerative evolution has been a frequent phenomenon in the past, and scarcely an organism exists which does not display degeneracy in some detail of its structure. Progressive evolution has, however, not been prevented by the frequent occurrence of an opposite process; and, indeed, degeneracy of parts, or of types of life, have been necessary to the advance of other and better organs or forms.

It is necessary to an understanding of the laws of evolution to get beforehand some idea of what that evolution has actually been. I will, therefore, give a general outline of the phylogeny of plants and animals, and will thus illustrate the subject in full detail in the case of the Vertebrata, where our facilities are especially good.

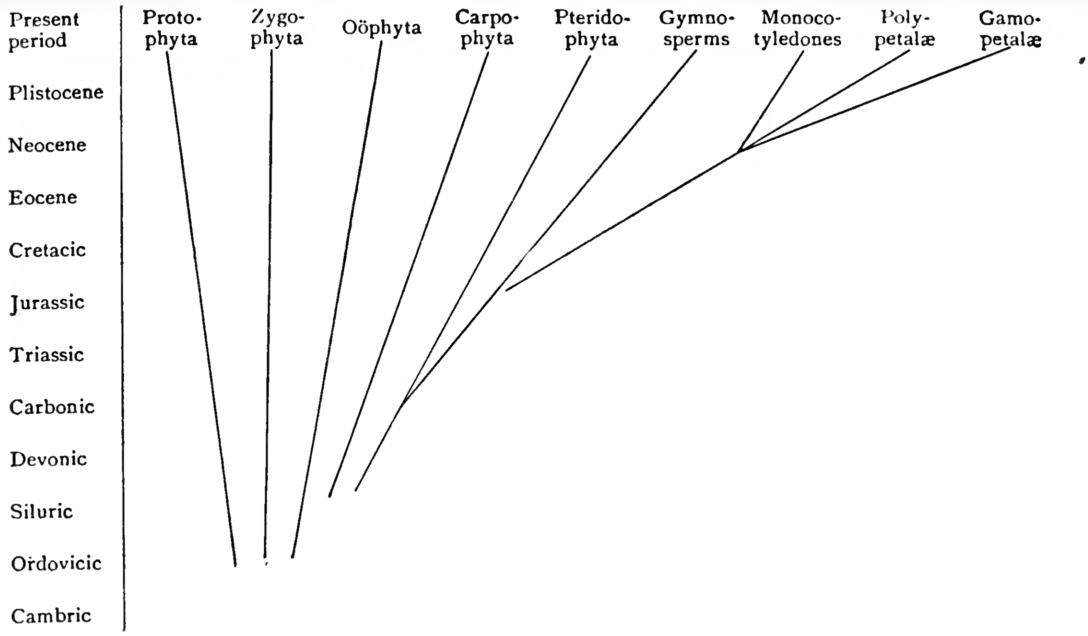
It is well known that the Protophyta and the Protozoa are not distinguishable by any sharp line of demarcation. Chlorophyll, which is so characteristic of plants, is absent from many of the lowest forms, including the entire class of Fungi, while it is present in a few of the lowest animals. The capacity for motion from place to place, so general in animals, at least in their earlier stages, is present in the earlier stages of some of the Algæ, and is universal, except at the period of reproduction, in the Myxomycetes. If it be denied that the latter are plants, then they are animals which do not reproduce by the ordinary process of fission, but by spores, which are borne together in a mass, or in a sporangium distinguished from the rest of the body. A distinction between the lower animals and plants is that the former introduce their food at a definite, though it may be a variable, point of the body; while plants absorb their nutriment in solution at all points. It is however demonstrated that some animals (many parasites) nourish themselves in the same manner as do plants; and in their early stages the Myxomycetes have the feeding habit of the lowest animals (Amœbæ). Both animals and plants from a morphological point of view have a common origin, in a nucleated, undivided, more or less globular piece of protoplasm or sarcode.

From freely moving Protophyta of this form, the vegetable kingdom took its rise. They first of all assumed a sessile position on the earth, and became what one may call earth-parasites. This abandonment of free mobility we cannot hesitate to regard as the efficient cause of a degenerate line of evolution. There can be no doubt about this, since fixity of habitat at once limits enormously the range of active influences which tend to modify an organism, whether they proceed from within it or from without it. The subsequent inclosure of the protoplasm in a structure of cellulose removes them from many of the stimuli which have so potent an influence in the life-history of animals, and the storage of other substances, as proteids, gums, resins, etc., in their cells, still further emphasizes the distinction.

From this beginning, progress in plants is seen chiefly in the modifications of their methods of reproduction. This function is the aim of the vegetable kingdom so far as their own condition is concerned.

Incidentally they are, however, essential to the existence of the animal kingdom, since they alone elaborate protoplasm and proteids from inorganic nature. In the simplest plants there is no sexuality, and reproduction is effected by spores which are mere fragments of the parental protoplasm (Protophyta). In the next stage sexual conjugation is necessary, but the sexes do not differ from each other in characters (Zygophyta). In the third stage (Oöphyta) the sexes are distinct, and the reproductive elements are distinguished as female germ-cell and male antheridium. In the remaining types of plants a distinct set of individuals, the prothallia, is produced by cell-division, whose function is sexual reproduction, thus constituting an alternation of generations. These plants may be entirely cellular (Carpophyta), or may be furnished with vascular canals. Of the latter the male and female prothallia may be naked and free (Pteridophyta or ferns, etc.), or may be enclosed in modified leaves, or flowers, the Phænogamia or flowering plants.

For the reasons already mentioned the order of "successional relation" above pointed out, is likely to prove to be the order of appearance of plants in time, and that such is the fact is demonstrated by their paleontology. In the earliest beds in which plants are positively known to occur, the Ordovician, we have only Algæ (Zygophyta and Oöphyta). In the Siluric we have a great predominance of the same classes, a very few species of which appear to have formed great erect stems. In the next period, the Devonic, probable Carpophyta are present, while the vascular Pteridophyta appear for the first time, and in considerable numbers. A few members of the gymnospermous Phænogamia (Coniferæ) appear. In the Carbonic pe-


Present period
Plistocene
Neocene
Eocene
Cretacic
Jurassic
Triassic
Carbonic
Devonic
Siluric
Ordovicic
Cambric
Protophyta
Zygophyta
Oöphyta
Carpophyta
Pteridophyta
Gymnosperms
Monocotyledones
Polypetalæ
Gamopetalæ

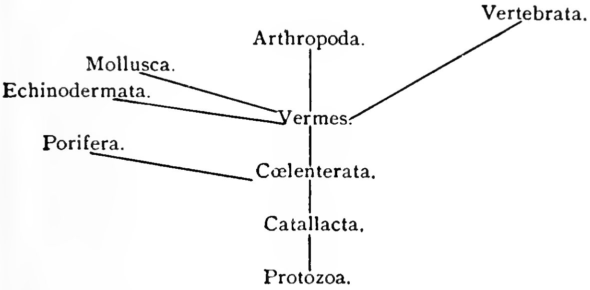
riod, the greatest known development of the Pteridophyta (Lycopodia, ferns, Equiseta) took place, while the Gymnosperms were still represented by a few genera. Their period of development or acme arrived in the Mesozoic ages, and the Pteridophyta underwent a corresponding reduction of numbers and importance. Not until the upper Cretaceous epoch did the Angiospermous Phanerogams with their attractive flowers appear, and from that period to the present they have gained and maintained the ascendency. In accordance with the mode of origin of tubular flowers by the fusion of the separate petals of polypetalous forms, we find that the former succeeded the latter in time.

We may review this brief sketch of the paleontology of plants in the preceding phylogenetic table.

Turning now to the animal kingdom, its order of succession may also be perceived in existing species. As with plants we commence with unicellular asexual forms (Protozoa). Some of these increase by division only (Rhizopoda), while others must occasionally conjugate, since, according to Maupas, the reproductive energy is exhausted by continued self-division (Infusoria). Such structural specializations as the highest of the Protozoa possess, are merely vacuities or processes of their material, for the purpose of internal or external motion. In the second grade of organization animals are multicellular, or composed of more than one protoplasmic unit. The simplest of these, as Volvox, contains no specialized organs, but seems like a colony of Protozoa, although all its cells are not exactly alike (Ryder). An appreciable advance of structure defines the next class, the Cœlenterata. Here the multicellular mass contains a distinct digestive chamber, from which usually radiate tubes towards the periphery, which distribute the products of digestion. The first nervous threads appear. But there is as yet no body cavity which should form a sac in which the organs of nutrition and reproduction should be suspended. The Porifera (sponges) appear to be a much modified form of this type.

This grade of specialization belongs to the greater number of the five succeeding classes, the Echinodermata, Vermes, Mollusca, Arthropoda, and Vertebrata. Where it is absent from a few of the three lower classes, it is supposed to have disappeared by degeneracy. The Echinodermata come first in consideration. In these animals the form inclines to be radiated and the nervous system presents no single axis, but consists of branches which radiate from a ring surrounding the oral extremity of the digestive canal. In the second type, the general form is longitudinal and may be segmented, and a nervous axis may extend longitudinally from one or more points on the œsophageal ring. These are the Vermes (true worms). Embryology indicates clearly the common origin of the Echinodermata and the Vermes. No line of descent can be traced from the former, but from the latter we have traced the remaining branches of animals, three in number. Lowest of these is the Mollusca. The form of the body is sac-like, and the nervous system displays, typically, besides the œsophageal ring, a second ring, consisting of lateral commissures, making a single median ganglion of the foot. The body is not segmented, and there are no jointed limbs. In the second branch, that of the Arthropoda, the body is longitudinal and segmented, and segmented limbs are present. There is a median nervous axis, proceeding from the œsophageal ring along the inferior axis of the body, connecting several ganglia, (with some exceptions where the ganglia are fused or wanting). There is no internal skeleton. In the last and highest branch, that of the Vertebrata, the body is longitudinal and is segmented. It has a longitudinal nervous axis on the superior middle line, which is supported below by an axis of resistant material, usually bone, which forms the axis of an internal skeleton. Segmented limbs are present.

The lines of descent of these branches indicated by embryology are as follows:



The above series present a history which is, on the whole, very different from that already described as characterizing the vegetable kingdom. Between the first and last terms of the series, there is exhibited a great progressive advance in all the higher features of life. These are mobility, and such control over the environment as it gives; and sensibility, through the development of a nervous system, which gives control over the movements. The highest development is that of mental characteristics, as emotions and intelligence, which are especially seen in the higher Vertebrata.

This progress has not been accomplished without much degeneracy by the way. All of the branches display divisions which have become sessile, and some of them are almost altogether so. Among Cœlenterata the Actinozoa are fixed, and often develop a calcareous skeleton. Many of the Hydroids are sessile. The great branch of the Echinodermata has its locomotive powers greatly curtailed, and many of them are permanently sessile. The same is true of the Mollusca. Both divisions are at one side of the line of progressive evolution as a consequence of this tendency. The Vermes display in their free representatives the conditions of progressive evolution. Being longitudinal and bilateral, one extremity becomes differentiated by first contact with the environment, as the seat of special senses, the basis having been secured by the location there of the nervous centers and ring. The Arthropoda present us with a great development of locomotive organs, and of special senses. As a whole, they have not made a considerable advance into the possession of the higher animal mental capacities, but display various degeneracies or degenerate tendencies among themselves. The moderately specialized as to structure are the most intelligent. These are the Hymenoptera, which display mental capacity superior to that of many Vertebrata. The latter branch, although presenting one sessile type, the Urochorda, has produced in its highest class, the Mammalia, the most general elevation in this, the highest of animal functions. This intelligence is in most of the types expended in preserving themselves from destruction against hostile environments, and the conquest of nature thus effected is remarkable from a physical point of view, but is an end of no great elevation of purpose from a mental standpoint. It is only in the most intelligent of the Mammalia, and in man, that we behold social and intellectual qualities which express something more than a mere routine of material existence.

Since Protozoa are very fragile, even when possessed of shells of mineral salts, we cannot expect to discover the actual date of their first appearance on the earth. Nevertheless they have been recently discovered in the later Archæan (= Huronian) beds of France. Some of the simplest Cœlenterata, however, (the Actinozoa), have deposited lime salts in the septa of their digestive chambers, and in some instances over their entire surface, so that their preservation has been assured. Thus we can prove that the simplest coral animals appear in the oldest rocks of sedimentary origin, the Cambric. Probably Vermes, and positively Echinodermata, Mollusca, and Arthropoda (Trilobita), also appear in the Cambric. Vertebrata appear definitely in the Siluric ; their supposed appearance in the Ordovicic being very doubtful.

The paleontologic history conforms to the systematic order in so far as it shows that the Cœlenterata appeared first, and the Vertebrata last, in time. A more complete correspondence between the two histories is found in the divisions of these branches, and I will take up the Vertebrata as the one of whose beginning we know the most, and are likely to know more.

2. THE PHYLOGENY OF THE VERTEBRATA.

a. Phylogeny of the Classes.

As the illustrations of evolution in the present work are mainly drawn from the Vertebrata, I go somewhat into detail in discussing the phylogeny of that branch.

They present the advantage, that, since they appeared last of the animal kingdom in time, we can obtain a clearer view of their beginnings than in the case of the other great branches.

Before going into the subject I wish to call attention to a prevalent source of error in the construction of phylogenies. This is the confusion of ideas general among naturalists who are not at the same time competent systematists, as to the subordination of characters. All correct phylogenetic inference depends on a correct appreciation of the value of characters. Failing this, error and confusion result. If, for instance, it is alleged that such a genus is ancestral to another genus, it is often forgotten that the descent of generic character, and not specific character, is meant. The usual type of critic attempts to contradict such hypothesis by showing some incongruity in *specific* characters; a matter which is quite irrelevant to the issue. Thus Madame Pavlov finds that *Hippotherium mediterraneum* is not the ancestor of *Equus caballus*, and comes promptly to the conclusion that the genus Hippotherium is not ancestral to the genus Equus. This is a *non sequitur*, for there are perhaps twenty species of Hippotherium, some of which are almost certain to have been ancestral to species of American Equus. In like manner, if it is alleged that the condylarthrous Mammalia are ancestral to the Diplarthra, if it should happen that no known genus of the former fits exactly the position of ancestor to any genus of the latter, in our present state of knowledge, the contention is not thereby vitiated, and it is implied that such genus will certainly be found. If it is also alleged that Condylarthra have been the ancestors of the anthropoid line, if some of the known genera of the former turn out to have no clavicle, a bone which is possessed by the latter, it is only to be concluded that the early lemuroids were derived from Condylarthra which possessed a clavicle. And in the discussion of the descent of one order from another, care must be taken that family, generic, and even specific characters are not imported into the discussion.

It is this confusion of ideas on the part of both phylogenists and their critics, that has brought phylogenetic schemes into a discredit in some quarters, which is sometimes deserved and sometimes undeserved. Embryologists are especially apt to construct impossible phylogenies, as they are generally not systematists, and frequently not anatomists. An excellent illustration of an impossible phylogeny is that of the fishes published a few years ago by the embryologist Dr. Beard. As an illustration of clean-cut phylogeny without confusion, I cite that of Haeckel; which I have shown to be, as regards the Vertebrata, mainly correct.

In attempting to ascertain the course of evolution of the Vertebrata, and to construct phylogenetic diagrams which shall express this history, among the difficulties arising from deficient information one is especially prominent. As is well known, there are many types in all the orders of the Vertebrata which present us with rudimentary organs, as rudimental digits, feet or limbs, rudimental fins, teeth, and wings. There is scarcely an organ or part which is not somewhere in a rudimental and more or less useless condition. The difficulty which these cases present is, simply, whether they be persistent primitive conditions, to be regarded as ancestral types which have survived to the present time, or whether, on the other hand, they be results of a process of degeneration, and therefore of comparatively modern origin. The question, in brief, is, whether these creatures presenting these features be primitive ancestors or degenerate descendants.

A great deal of light has been happily thrown on this question, as regards the Vertebrata, by the recent work done in North American paleontology. The lines of descent of many of the minor groups have been positively determined, and the phylogenetic connections of most of the primary divisions or classes have been made out. The result of these investigations has been to prove that the evolution of the Vertebrata has proceeded not only on lines of acceleration, but also on lines of retardation. That is, that evolution has been not only progressive, but at times retrogressive.

The Amphioxus (genus Branchiostoma) is generally regarded as the ancestral vertebrate. There are many reasons why this position must be accepted, although it possesses a few secondary modifications. Whether Branchiostoma derived its descent from an annelid worm, or from a tunicate, is a vexed question. Brooks[1] remarks as to this, "Up to this point I believe that the ancestral history of the tunicates was identical with that of the vertebrates; for the hepatic cœcum, the dilated pharynx, the pharyngeal clefts, the hypopharyngeal gland, and the peripharyngeal bands, have been inherited by all the Chordata (Vertebrata), and have impressed themselves so firmly in their organization that even the highest vertebrates still retain them, either as vestiges or as organs which have been fitted to new functions. I believe, however, that while they were acquired before the tunicates diverged from the chordate (vertebrate) stem, they were acquired by an

[1] *Studies from the Laboratory of the Johns Hopkins University*, 1893, p. 175.

organism whose environment and habits of life were essentially like those of the modern Appendicularia.' Appendicularia is well known as the tunicate which retains throughout life, the notochord and tail which characterize the larvæ of other Tunicata.

Omitting from consideration the two classes above mentioned (Acrania and Tunicata), whose remains have not yet been certainly found in a fossil state, there remain the following: the Pisces, Batrachia, Monocondylia, and Mammalia.[1]

I have traced the origin[2] of the Mammalia to the theromorous reptiles of the Permian epoch, and these to the Cotylosauria. The latter include the Pelycosauria, Procolophonina, Anomodontia, and perhaps other orders. In the Cotylosauria the temporal region is roofed over, which roof is reduced in the Pelycosauria to one postorbital arch of the skull, and this is the zygomatic of the Mammalia. In both Reptilia and Mammalia (excepting Prototheria and Procolophonina[3]) the coracoid element is of reduced size, and is co-ossified with the scapula. In both (except Cotylosauria) the capitular articulation of the ribs is intercentral. In both the humerus has distal condyles and epicondyles, and there is an entepicondylar foramen in the Pelycosauria as in the lower Mammalia. The posterior foot

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[1] See *The Evolution of the Vertebrata Progressive and Retrogressive: Amer. Naturalist*, 1885. Dohrn, *Der Ursprung der Wirbelthiere und das Princip des Functionwechsels*, Leipsic, 1875. "On the Phylogeny of the Vertebrata," Cope, *American Naturalist*, Dec., 1884. See also the following references: *American Naturalist*, 1884, p. 1136; *Proceedings of the Academy of Philadelphia*, 1867, p. 234; *Proceedings American Philosophical Society*, 1884, p. 585; *American Naturalist*, 1884, p. 27; *Proceedings American Association for the Advancement of Science*, XIX, 1871, p. 233; *Proceedings American Philosophical Society*, 1882, p. 447; *American Naturalist*, 1884, pp. 261 and 1121; *Report U. S. Geol. Survey W. of 100th Mer.*, G. M. Wheeler, 1877, IV, 2, p. 282.

[2] *Proceedings American Philosophical Society*, 1884, p. 43.

[3] Seeley, *Philos. Trans. Royal Society*, 1889, 269.

is constructed in the Pelycosauria almost exactly like that of the Prototheria. The single occipital condyle of the reptiles is not found in the Mammalia, but in some of the Lacertilia (Uroplates, Gecco) there are two condyles, the median (basioccipital) portion of the single condyle being rudimental, and Seeley has recently shown that it is deeply divided at the middle in the Permian Cynognathidae of South Africa.. The Pelycosauria could not, however, have given origin to the Prototheria, since in that subclass of mammals there is a well-developed coracoid. But in the Procolophonina this element is developed as in the Prototheria. Moreover, the Pelycosauria and the Procolophonina have the interclavicle, which is an element of membranous origin, while in the Prototheria we have the corresponding cartilage bone, the episternum. This element is present in the Permian order of the Cotylosauria, which is nearly related to the Pelycosauria. This order has, however, single-headed ribs, springing from the diapophyses, which is not usual in the Mammalia. But in some Cotylosauria the diapophyses are short, and in the Monotremata the postcervical ribs are single-headed, so this character is not an insurmountable one. It is evident that the Mammalia were derived from some type probably referable to a Permian reptilian order of the Theromorous series, although to which one is not yet known.

The Reptilia have been supposed by Haeckel to have taken their origin from the Batrachia. I have indicated that it is probable that the batrachian order, which stands in this relation to the Reptilia, is the Embolomeri of the Permian epoch. This conclusion rests on the following considerations. The reptilian order of the Cotylosauria approaches the Batrachia of the subclass Stegocephali in the overroofing of the posterior regions of the skull; in the presence of vomerine teeth, and in the absence of obturator foramen of the pelvis. In some Cotylosauria (Diadectidæ) the stegocephalian tabular bone of the skull is well developed. But in the Cotylosauria, the vertebral column consists mainly of centra, while in the Stegocephali it consists entirely or partly of intercentra. But in the Embolomeri the centra are well developed, and are larger than the intercentra anterior to the pelvis. Hence this is the only order of Stegocephali from which the Reptilia could have been derived.

Haeckel derived the Batrachia from the Dipnoi (Dipneusta), and I followed him in this belief, being strengthened in it by Huxley's ascription of an autostylic suspensorium of the mandible[1] to both divisions. This phylogeny is questioned by Pollard[2] and by Kingsley,[3] who would see the ancestry of the Batrachia in the crossopterygian fishes on embryological grounds derived from a study of Polypterus. In support of their view I would cite the absence of the maxillary arch in the Dipnoi, and its full development in the Stegocephali, which are the ancestral Batrachia. The large development of the dorsal and anal fins in the Dipnoi is not favorable to the Haeckelian view; nor do the paired fins approach as nearly to the limbs of Batrachia as do those of some other fishes. It has been shown by Huxley that the suspensorium of the Batrachia is hyostylic in its earliest stages, and that it becomes autostylic at a later period of development.

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[1] *Proceedings Zoölogical Society of London*, 1876, p. 59.

[2] *Anatomischer Anzeiger*, VI, p. 338, 1891.

[3] *American Naturalist*, 1892, p. 679. Kingsley would also derive the Dipnoi from Crossopterygia.

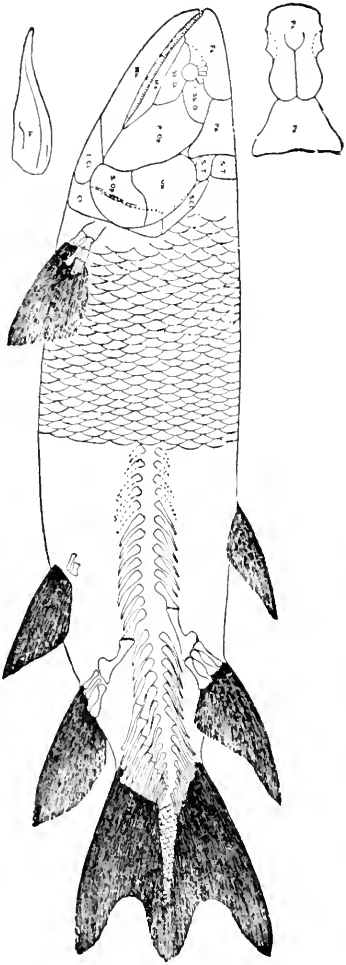

Fig. 24.—*Eusthenopterum foordii* Whiteaves; ⅓ natural size. Devonian of New Brunswick. From Whiteaves.

The Batrachia may then have originated from a hyostylic teleostomous (i. e., one with complete maxillary arch) fish. Among Teleostomata we naturally look for forms with limbs which approach nearest the batrachian type, and in which median fins are feeble or wanting. Such are the Rhipidopterygia (formerly included in the Crossopterygia), which include the families of Holoptychiidæ, Tristichopteridæ, Osteolepididæ, Cœlacanthidæ, and perhaps some others. These families, except the last, abounded in the waters of the Devonian period, at the time when the ancestors of the Batrachia also existed. All of them agree in possessing the median fins of greatly reduced proportions, and the mesodermal or internal elements of the paired fins more like the limbs of the Batrachia than are those of any known fishes. The constitution of the superior cranial wall is a good deal like that of the stegocephalous Batrachia. The characters of the fins can be learned from the accompanying figure of the *Eusthenopterum foordii* Whiteaves, one of the Tristichopteridæ. The pectoral fin well-nigh realizes Gegenbaur's theory of the derivation of the Chiropterygium from the Archipterygium.

The ancestral type of fishes is probably the acanthodean order of the subclass of sharks (Elasmobranchii).[1] Like other sharks, they are hyostylic and have no maxillary arch or cranial bones. They have the ptychopterygium, which is the primitive type of fin. In this fin the osseous elements which support the fin-rays are enclosed within the body-wall, the rays only being free. Such a fin sustains the hypothesis that the paired fins are parts of primitively continuous

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[1] As represented by the Cladodontidae; see Dean, *Trans. N. Y. Acad. Sci.*, 1893, p. 124, and Cope, *American Naturalist*, 1893, p. 999.

longitudinal folds. This hypothesis is further sustained by the acanthodean genus Climatius, where a series of spines intervenes between the paired fins in line with them. From what the Acanthodeans can have been descended is at present conjectural. They trace their ancestry ultimately to Branchiostoma (Amphioxus) through forms not yet discovered. This ge-

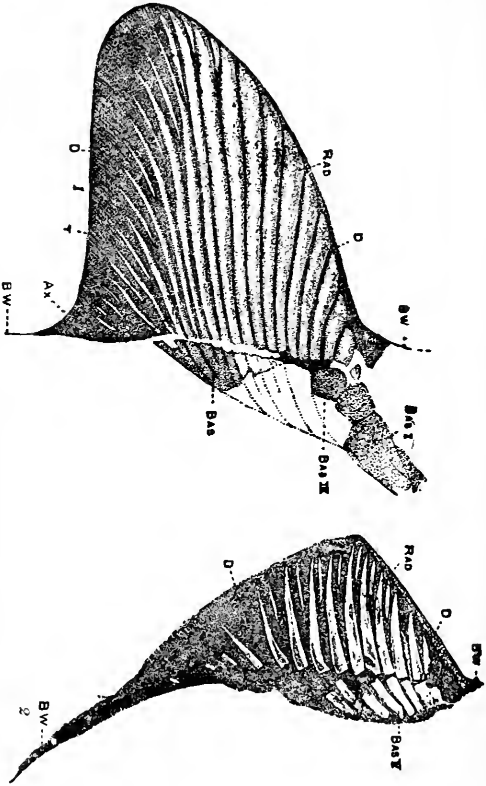
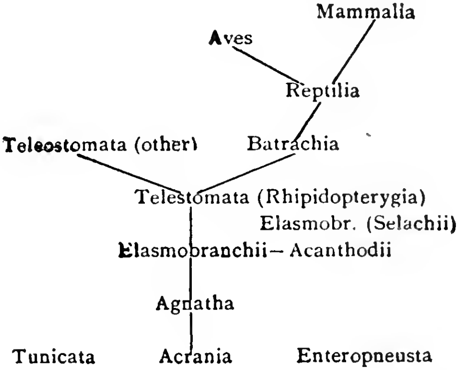


Fig. 25.—Paired fins of *Cladoselache Dean.* from the Carbonic of Ohio. No. 1, pectoral, No. 2, ventral fins. *BW*, body wall; *Ax*, axilla; *Bas*, basilar elements; *Rad*, "*radials*"; *T*, actinotrichia; *D*, dermal margin. From Dean.

nus represents the class Acrania, which is the ancestor of craniate Vertebrata.

The phylogeny of the Vertebrata may be represented diagrammatically as follows:



The Vertebrata exhibit the most unmistakable gradation in the characters of the circulatory system. It has long been the custom to define the classes by means of these characters, taken in connection with those of the skeleton. Commencing in the Leptocardii with the simple tube, we have two chambers in the Marsipobranchii and fishes; three in the Batrachia and Reptilia; and four in the Aves and Mammalia. The aorta-roots commence as numerous pairs of branchial arteries in the Leptocardii; we see seven in the Marsipobranchi, five in the fishes (with number reduced in some); four and three in Batrachia, where they generally cease to perform branchial functions; two and one on each side in Reptilia; the right-hand one in birds, and the left-hand one in Mammalia. This order is clearly an ascending one throughout. It consists of, first, a transition from adaptation to an aquatic, to an aërial respiration; and, second, an increase in the power to aërate and distribute a circulating fluid of increased quantity, and of increased calorific capacity. In other words, the circulation passes from the cold to the hot-blooded type coincidentally with the changes of structure above enumerated. The accession of a capacity to maintain a fixed temperature while that of the surrounding medium changes, is an important advance in animal economy.

The brain and nervous system also display a general progressive ascent. Leaving the brainless Acrania, the Marsipobranchs and fishes present us with small hemispheres with thin cortex, larger optic lobes, and well-developed cerebellum. The hemispheres are really larger than they appear to be, as Rabl Rückard has shown[1] that the supposed hemispheres are only corpora striata. But the superior walls are membranous, and support on their internal side only a layer of epithelial cells, as in the embryos of other Vertebrata, instead of the gray substance. So that, although we find that the cerebellum is really smaller in the Batrachia and most Reptilia than in the fishes, the better development of the hemispheres in the former gives them the preeminence. The Elasmobranchii show themselves superior to many of the fishes in the large size of their corpora restiformia and cerebellum. The Reptilia constitute an advance on the Batrachia. In the latter the optic thalami are, with some exceptions, of greater diameter than the hemispheres, while the reverse is generally true of the reptiles. The crocodiles display much superiority over the other reptiles in the larger cerebellum, with rudimental lateral lobes. The greater development of the hemispheres in birds is well known,

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[1] *Biologisches Centralblatt*, 1884, p. 449.

while the general superiority of the brain of the living Mammalia over all other vertebrates is admitted.

The consideration of the successive relations of the skeleton in the classes of vertebrates embraces, of course, only the characters which distinguish those classes. These are not numerous. They embrace the structure of the axis of the skull; of the ear-bones; of the suspensors of the lower jaw; of the scapular arch and anterior limb, and of the pelvic arch and posterior limb. Other characters are numerous, but do not enter into consideration at this time.

The persistence of the primitive cartilage in any part of the skeleton is, embryologically speaking, a mark of inferiority. From a physiological or functional standpoint it has the same significance, since it is far less effective both for support and for movement than is the segmented osseous skeleton. That this is a prevalent condition of the lower Vertebrata is well known. The bony fishes and Batrachia have but little of the primitive cartilage remaining, and the quantity is still more reduced in the higher classes. Systematically, then, the vertebrate series is in this respect an ascending one. The Acrania are membranous; the Marsipobranchii and most of the Elasmobranchii cartilaginous; the other Pisces and the Batrachia have the basicranial axis cartilaginous, so that it is not until the Reptilia are reached that we have osseous sphenoid and presphenoid bones, such as characterize the birds and mammals. The vertebral column follows more or less inexactly the history of the base of the skull, but its characters do not define the classes.

As regards the suspensor of the lower jaw, the scale is in the main ascending. We witness a gradual change in the segmentation of the mandibular visceral arch of the skull, which clearly has for its object such a concentration of the parts as will produce the greatest effectiveness of the biting function. This is accomplished by reducing the number of the segments, so as to bring the resistance of the teeth nearer to the power, that is, the masseter and related muscles, and their base of attachment, the brain-case. This is seen in

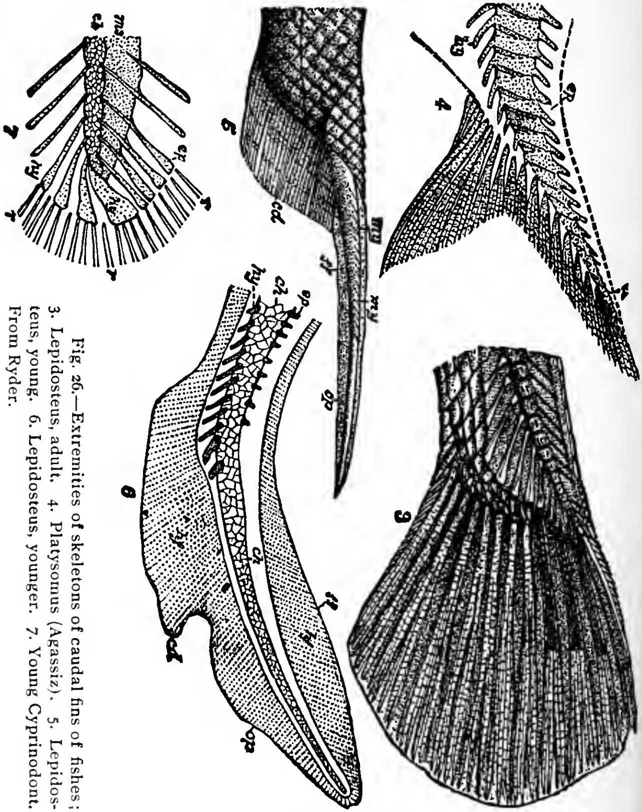

Fig. 26.—Extremities of skeletons of caudal fins of fishes; 3. Lepidosteus, adult. 4. Platysomus (Agassiz). 5. Lepidosteus, young. 6. Lepidosteus, younger. 7. Young Cyprinodont. From Ryder.

bony vertebrates in the reduction of the segments between the lower jaw proper and the skull, from four to none. In the fishes we have the hyomandibular, the symplectic, the inferior quadrate, and the articular. In the Batrachia, reptiles and birds, we have the quadrate and articular only, while in the Mammalia these elements also are wanting.

The examination of the pectoral and pelvic arches reveals a successive modification of the adaptation of the parts to the mechanical needs of the limbs. In this regard the air-breathing types display wide diversity from the gill-bearing types or fishes. In the latter, the lateral elements unite below without the intervention of a median element or sternum, while in the former the sternum, or parts of it, is generally present. Either arrangement is susceptible of much mechanical strength, as witness the siluroid fishes on the one hand, and the mole on the other. The numerous segments of the fishes' pectoral arch must, however, be an element of weakness, so that from a mechanical standpoint it must take the lowest place. The presence of sternal elements, with both clavicle, epicoracoid, and coracoid bones on each side, gives the Reptilia the highest place for mechanical strength. The loss of the bony coracoid seen in the tailed Batrachia, and loss of coracoid and epicoracoid in the Mammalia, constitute an element of weakness. The line is not then one of uniform ascent in this respect.

The absence of pelvis, or its extremely rudimental condition, in fishes, places them at the foot of the line in this respect. The forward extension of the ilium in some Batrachia and in the Mammalia, is to be compared with its backward direction in Reptilia, and its extension both ways in the birds. These conditions are all derived by descent from a strictly intermediate position in the Batrachia and Reptilia of the Permian epoch. The anterior direction must be regarded as having the mechanical advantage over the posterior direction, since it shortens the vertebral column and brings the grip of the posterior nearer to the anterior feet. The prevalence of the latter condition in the Mammalia enables them to stand clear of the ground, while the Reptilia move with the abdomen resting upon it, excepting the higher Dinosauria, where the arrangement is as in birds. As regards the inferior arches of the pelvis, the Mammalia have the advantage again, in the strong bony median symphysis connecting the ischium and pubis.[1] This character, universal among the land Vertebrata of the Permian epoch, has been lost by the modern Reptilia and birds, and is retained only by the Mammalia. So the lines, excepting the mammalian, have *degenerated* in every direction in the characters of the pelvis.

The limbs of the Pisces are as well adapted to their environment as are those of the land Vertebrata; but, from an embryological standpoint, their structure is inferior. The primitive rays are less modified in the fin than in the limb; and limbs themselves display a constantly increasing differentiation of parts, commencing with the Batrachia and ending with the Mammalia. The details of these modifications belong to the history of the contents of the classes, however, rather than to the succession of the Vertebrata as a whole.

In review, it may be said that a comparison of the characters which define the classes of the vertebrates shows that this branch of the animal kingdom has

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[1] This is an advantage as a protection during gestation.

made with the ages successive steps of progress from lower to higher conditions. This progress has not been without exception, since, as regards the construction of the scapular arch, the Mammalia have retrograded from the reptilian standard as a whole.

In subsequent pages I shall take up the lines of the classes separately.

b. The Line of the Pisces.

The fishes form various series and subseries, and the tracing of all of them is not yet practicable, owing to the deficiency in our knowledge of the earliest or ancestral forms. Thus the origins of the three subclasses, Holocephali, Dipnoi, and Elasmobranchii, are lost in the obscurity of the early Paleozoic ages. The genus Paleospondylus of Traquair from the Carboniferous probably represents an Agnathous type from which all fishes may have sprung, although the genus, as now known, has not sufficient antiquity to claim this place. It may be a near descendant of the amphioxus.

A comparison of the four subclasses of fishes shows that they are related in pairs. The Holocephali and Dipnoi have no distinct suspensory segment for the lower jaw, while the Elasmobranchii and Teleostomata have such a separate element. The latter, therefore, present one step in the direction of complication beyond the former. It is, however, asserted by Huxley[1] that the absence of suspensorium is due to its appropriation by the hyoid arch in the Holocephali, and its rudimental condition in the Dipnoi. If this be the case, the Holocephali and Dipnoi are peculiar speciali-

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[1] *Proceedings Zoölogical Society*, London, 1876, p. 45.

zations at one side of the main line of descent of the fishes. We look then for the ancestral type of the true fishes among the Elasmobranchii, and of these the Ichthyotomi display the greatest resemblances to the Teleostomata in all respects.[1]

Too little is known of the history of the subclasses, excepting the Teleostomata, for us to be able to say much of the direction of the descent of their contained orders. On the sharks much light is shed by the discovery of characters of the genus Cladodus Agass., in which the support of the paired fins consists of a metapterygium, which is enclosed in a lateral fold of the body wall, and which gives rise to simple external basilar rods only. Of the Teleostomata a much clearer history is accessible. It has four primary divisions or tribes which differ solely in the structure of the supports of the fins. In the first division, the Crossopterygia, the anterior limbs have numerous basilar bones which are supported on a peduncle of axial bones. The posterior limbs are similar. In the second division, or Podopterygia (the sturgeons, etc.), the posterior limbs remain the same, while the anterior limbs have undergone a great abbreviation in the loss of the axial bones and the reduction of the number and length of the basilar bones. In the third group, or Actinopterygia, both limbs have undergone reduction, the basilar bones in the posterior fin being almost all atrophied, while those of the fore limb are much reduced in number. In the fourth superorder, the Rhipidopterygia, the axial supports of the median fins are greatly reduced in number, presenting a marked contrast to the other superorders ; while the axial elements

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[1] See *Proceedings American Philosophical Society*, 1884, p. 572, on the genus Didymodus.

of the paired fins are present and primitive, and resemble those of one of the suborders of sharks.

The phylogeny of the Teleostomata, as indicated by the fin-structure, will commence with the Crossopterygia. From this group the Podopterygia may be theoretically derived, and from these the Actinopterygia. The Rhipidopterygia appear to be a side group, not in the main piscine line. But the oldest known Crossopterygia are from the Carboniferous, while the Rhipidopterygia are abundant in the Devonian. Moreover, the superorder Actinopterygia, with its contracted fins, may have appeared in the Carboniferous, while the Podopterygia (Palæoniscidæ) certainly did so.

The descent of the fishes in general has witnessed, then, a contraction of the limbs to a very small compass, and their substitution by a system of accessory dermal radii. This has been an ever-widening divergence from the type of the higher Vertebrata, and from this standpoint, and also a view of the "loss of parts without complementary addition of other parts," may be regarded as a process of degeneration.

Taking up the great division of the Actinopterygia, which embraces most of the species of living fishes, we can trace the direction of descent largely by reference to their systematic relations when we have no fossils to guide us.

The three subtribes adopted by Jordan represent three series of the true fishes which indicate lines of descent. The Holostei include the remainder of the old ganoids after the subtraction of the Rhipidopterygia, the Crossopterygia, and the Podopterygia. They resemble these forms in the muscular bulbus arteriosus of the heart, in the chiasm of the optic nerves, and in the greater distinctness of the metapterygium. The two former characters are complexities which the two other divisions do not possess, and which, as descendants coming later in time, must be regarded as inferior, and therefore to that extent degenerate. Of these divisions the Malacopterygia approach nearest the Holostei, and are indeed not distinctly definable without exceptions. The third division, or Acanthopterygia, shows a marked advance beyond the others in : (1) the obliteration of the primitive trachea, or ductus pneumaticus, which connects the swim-bladder and œsophagus ; (2) the advance of the ventral fins from the abdomen forward to the throat ; (3) the separation of the parietal bones by the supraoccipital ; (4) the presence of numerous spinous rays in the fins ; and (5) the roughening of the edges of the scales, forming the ctenoid type. There are more or less numerous exceptions to all of these characters. The changes are all further divergencies from the other vertebrate classes, or away from the general line of ascent of the vertebrate series taken as a whole. The end gained is specialization ; but whether the series can be called either distinctively progressive or retrogressive, is not so clear. The development of osseous spines, rough scales, and other weapons of defense, together with the generally superior energy and tone which prevail among the Acanthopterygia, characterize them as superior to the Malacopterygia, but their departure from the ascending line of the Vertebrata has another appearance.

The descent of the Acanthopterygian fishes has probably been from Holostean ancestors, both with and without the intervention of Malacopterygian forms. This is indicated by increase in the number of basilar bones[1] in the fins of families which have pectoral ventral fins, and in the extinct genus Dorypterus.[2]

The Malacopterygia display three or four distinct lines of descent. The simplest type is represented by the order Isospondyli, and paleontology indicates clearly that this order is also the oldest, as it dates from the Trias at least. In one line the anterior dorsal vertebræ have become complicated, and form an interlocking mass which is intimately connected with the sense of equilibrium in the water. This series commences with the Characinidæ, passes through the Cyprinidæ, and ends with the Siluridæ. The arrangements for equilibration constitute a superadded complication, and to these are added in the Siluroids defensive spines and armor. Some of this order, however, are distinctly degenerate, as the soft purblind Ageniosus, and the parasitic Stegophilus and Vandellia, which are nearly blind, without weapons, and with greatly reduced fins.

The next line (the Haplomi, pike, etc.) loses the precoracoid arch and has the parietal bones separated, both characters of the Acanthopterygia. This group was apparently abundant during the Cretaceous period, and it may have given origin to many of the Acanthopterygia.

Another line also loses the precoracoid, but in other respects diverges totally from the Acanthopterygia and all other Malacopterygia. This is the line of the eels. They next lose the connection between the scapular arch and the skull, which is followed by the loss of the pectoral fin. The ventral fin disappeared sooner. The palatine bones and teeth disappear, and the suspensor

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[1] See Cope "On the Homologies of the Fins of Fishes"; *American Naturalist*, 1890, p. 401.

[2] See *Proceedings of the American Association for the Advancement of Science*, 1878, p. 297.

of the lower jaw grows longer and loses its symplectic element. The opercular bones grow smaller, and some of them disappear. The ossification of most of the hyoid elements disappears, and some of their cartilaginous bases even vanish. These forms are the marine eels or Colocephali. The most extraordinary example of specialization and degeneracy is seen in the abyssal eels of the family Eurypharyngidæ. Here all the degenerate features above mentioned are present in excess, and others are added, as the loss of ossification of a part of the skull, almost total obliteration of the hyoid and scapular arches, and the semi-notochordal condition of the vertebral column, etc.

The Acanthopterygia nearest the Malacopterygia have abdominal ventral fins, and belong to several orders. It is such types as these that may be supposed to have been derived directly from Holostean ancestors. They appear in the Cretaceous period (Dercetidæ), along with the types that connect with the Malacopterygia (Haplomi). Intermediate forms between these and typical Acanthopterygii occur in the Eocene (Trichophanes, Erismatopterus), showing several lines of descent. The Dercetidæ belong apparently to the order Hemibranchi, while the Eocene genera named belong apparently to the Aphododiridæ, the immediate ancestor of the highest Physoclysti, the Percomorphi. The order Hemibranchi is a series of much interest. Its members lose the membrane of their dorsal spinous fin (Gasterosteidæ), and then the fin itself (Fistularia, Pegasus). The branchial apparatus has undergone, as in the eels, successive deossification (by retardation), and this in direct relation to the degree with which the body comes to be protected by bony shields, reaching the greatest defect in the Amphisilidæ. One more downward step is seen in the next succeeding order of the Lophobranchii. The branchial hyoid apparatus is reduced to a few cartilaginous pieces, and the branchial fringes are much reduced in size. In the Hippocampidæ the caudal fin disappears and the tail becomes a prehensile organ by the aid of which the species lead a sedentary life. The mouth is much contracted and becomes the anterior orifice of a suctorial tube. This is a second line of unmistakable degeneracy among true fishes.

The Acanthopterygia with pectoral ventral fins present us with perhaps ten important ordinal or subordinal divisions. Until the paleontology of this series is better known, we shall have difficulty in constructing phylogenies. Some of the lines may, however, be made out. The accompanying diagram will assist in understanding them.

The Anacanthini present a general weakening of the organization in the less firmness of the osseous tissue and the frequent reduction in the size and character of the fins. The caudal vertebræ are of the diphycercal type. As this group does not appear early in geological time, and as it is largely represented now in the abyssal ocean fauna, there is every reason to regard it as a degenerate type.[1] The Heterosomata (flounders) found it convenient to lie on one side, a habit which would appear to result from a want of motive energy. The fins are very inefficient organs of movement in them, and they are certainly no rivals for swift-swimming fishes in the struggle for existence, excepting as they conceal themselves. In order to see the better while unseen, the inferior eye has turned in-

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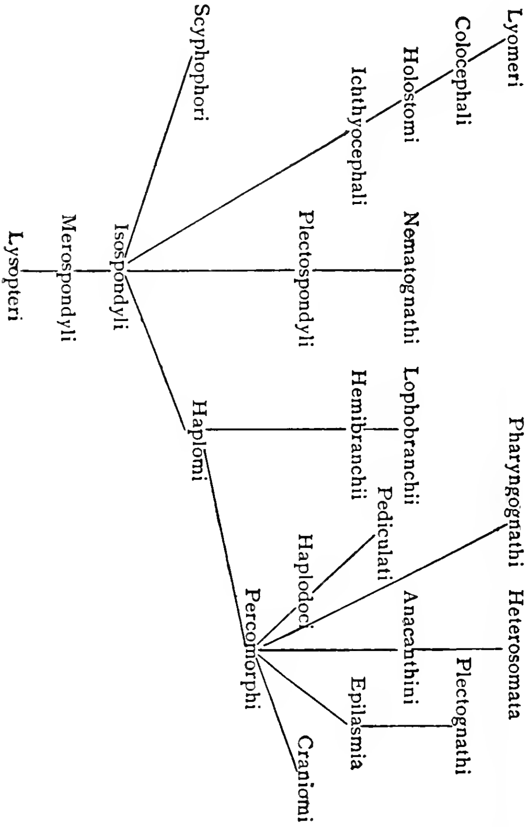
[1] The general characters of the deep-sea fish-fauna are those of degeneracy.

ward, i. e., upward, and finally has penetrated to the superior surface, so that both eyes are on one side. This peculiarity would be incredible, if we did not know of



its existence, and is an illustration of the extraordinary powers of accommodation possessed by nature. The Heterosomata (flatfishes) can only be considered a degenerate group. The scyphobranch line presents a specialization of the superior pharyngeal bones, which is continued by the Haplodoci (Batrachidæ). This cannot be called a degenerate line, although the fin-rays are soft.

The double bony floor of the skull of the distegous percomorph fishes is a complication which places them at the summit of the line of true fishes. At the summit of this division must be placed the Pharyngognathi, which fill an important rôle in the economy of the tropical seas, and the fresh waters of the Southern Hemisphere. By means of their powerful grinding pharyngeal apparatus they can reduce vegetable and animal food inaccessible to other fishes. The result is seen in their multifarious species and innumerable individuals decked in gorgeous colors, and often reaching considerable size. This is the royal suborder of fishes, and there is no reason why they should not continue to increase in importance in the present fauna.

Very different is the line of the Plectognathi. The probable ancestors of this division, the Epelasmia (Chætodontidæ, etc.), are also abundant in the tropical seas, and are among the most brilliantly colored of fishes. One of their peculiarities is seen in a shortening of the brain-case and prolongation of the jaws downward and forward. The utility of this arrangement is probably to enable them to procure their food from the holes and cavities of the coral reefs, among which they dwell. In some of the genera the muzzle has become tubular (Chelmo), and is actually used as a blow-gun by which insects are secured by shooting them with drops of water. This shortening of the basicranial axis has produced a corresponding abbreviation of the hyoid apparatus. The superior pharyngeal bones are so crowded as to have become a series of vertical plates like the leaves of a book. These characters are further developed in the Plectognathi. The brain-case is very small, the face is very elongate, and the mouth is much contracted. The bones surrounding it in each jaw are coössified. The axial elements (pubes) of the posterior fins unite together, become very elongate, and lose the natatory portion. In one group (Orthagoriscidæ) the posterior part of the vertebral column is lost, and the caudal fin is a nearly useless rudiment. In the Ostraciontidæ (which may have had a different origin, as the pharyngeal bones are not contracted) the natatory powers are much reduced, and the body is inclosed in an osseous carapace so as to be capable of very little movement. The entire order is deficient in osseous tissue, the bones being thin and weak. It is a marked case of degeneracy.

There are several evident instances of sporadic degeneracy in other orders. One of these is the case of the family of the Icosteidæ, fishes from deep waters off the coast of California. Although members of the Percomorphi, the skeleton in the two genera Icosteus and Icichthys is unossified, and is perfectly flexible. Approximations to this state of things are seen in the parasitic genus Cyclopterus, and in the ribbon-fishes, Trachypteridæ.

Thus nearly all the main lines of the Acanthopterygii are degenerate; the exceptions are those that terminate in the Scombridæ (mackerel), Serranidæ, and Scaridæ (Pharyngognathi).

c. The Line of the Batrachia.

We know Batrachia first in the Coal Measures. They reach a great development in the Permian epoch, and are represented by large species in the Triassic period. From that time they diminish in numbers, and at the present day form an insignificant part of the vertebrate fauna of the earth. The history of their succession is told by a table of classification such as I give below:

I. Supraoccipital, tabular, and supramastoid bones present. Propodial bones distinct. STEGOCEPHALI.
    Vertebral centra, including atlas, segmented, one set of segments together supporting one arch; *Rhachitomi.*
    Vertebræ segmented, the superior and inferior segments each complete, forming two centra to each arch; *Embolomeri.*
    Vertebral centra, including atlas, not segmented, one to each arch; *Microsauri.*

II. Supraoccipital and supramastoid bones wanting. Frontal and propodial bones distinct; URODELA.
  a. An os tabulare.
    A palatine arch and separate caudal vertebræ; *Proteida*
  aa. No os tabulare.
    A maxillary arch; palatine arch imperfect; nasals, premaxillaries and caudal vertebræ distinct; *Pseudosauria.*[1]
    No maxillary or palatine arches; nasals and premaxillary, also caudal vertebræ, distinct; *Trachystomata.*

III. Supraoccipital, tabular, and supramastoid bones wanting. Frontals and parietals connate; propodial bones and caudal vertebræ confluent; SALIENTIA.
    Premaxillaries distinct from nasals; no palatine arch; astragalus and calcaneum elongate, forming a distinct segment of the limb; *Anura.*

The probable phylogeny of these orders as imperfectly indicated by paleontology is exhibited in the diagram on the following page.

An examination of the above tables shows that there has been in the history of the batrachian class a reduction in the number of the elements composing

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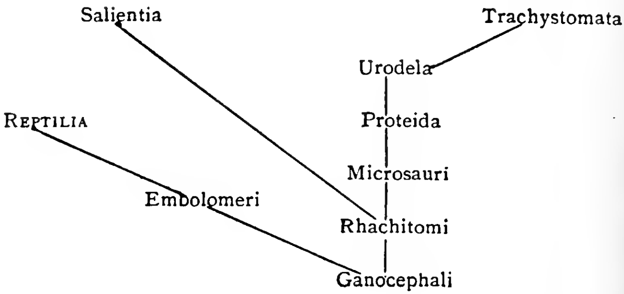
[1] Includes the Gymnophiona.

the skull, both by loss and by fusion with each other. It also shows that the vertebræ have passed from a notochordal state with segmented centra, to biconcave centra, and finally to ball-and-socket centra, with a great reduction of numbers. It is also the fact that the earlier forms (those of the Permian epoch) show the most mammalian characters of the tarsus and of the pelvis. The later forms, the salamanders, show a more generalized form of carpus and tarsus and of pelvis also. In the latest forms, the Anura, the carpus and tarsus are reduced through loss of parts, except



that the astragalus and calcaneum are phenomenally elongate. We have then, in the batrachian series, a somewhat mixed kind of change; but it principally consists of concentration and consolidation of parts. The question as to whether this process is one of progression or retrogression may be answered as follows· If degeneracy consists in "the loss of parts without complementary addition of other parts," then the batrachian line is a degenerate line. This is only partly true of the vertebral column, which presents the most primitive characters in the early, Permian, genera (Rhachitomi). If departure from the nearest approximation to the Mammalia is degeneracy, then the changes in this class come partly under that head. The scapular and pelvic arches of the Rachitomi are more mammalian than are those of any of their successors; the carpus and tarsus are less so than that of the Anura.

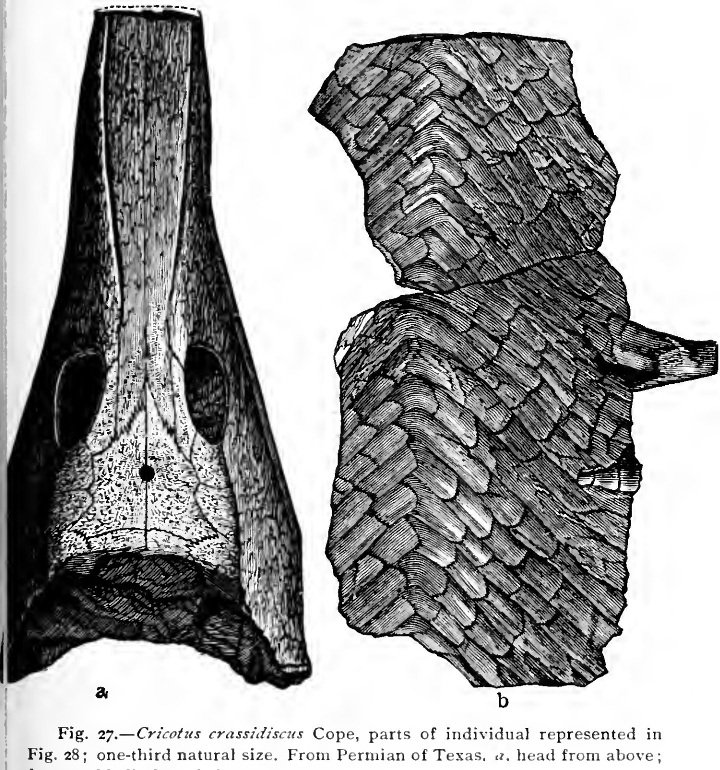


Fig. 27.—*Cricotus crassidiscus* Cope, parts of individual represented in Fig. 28; one-third natural size. From Permian of Texas. *a*, head from above; *b*, part of belly from below. From Cope.

There are several groups which show special marks of degeneracy. Such are the reduced maxillary bones

Fig. 28.—*Cricotus crassidiscus* Cope, vertebral column and pelvis; three-tenths natural size. Cope Coll. from the Permian formation of Texas. Fig. *a*, proatlas; *b*, *c*, cervical centra and intercentra; *d*, *e*, *f*, *g*, caudal centra; *is*, ischium; *il*, ilium; *Pu*, pubis; *is*, ischium.

and persistent gills of the Proteïda; the absence of the maxillary bones and the presence of gills in the Trachystomata; the loss of a pair of legs and feebleness of the remaining pair in the same; and the extreme reduction of the limbs in Amphiuma, and their total loss in the Cæciliidæ. Such I must also regard, with Lankester, the persistent branchiæ of the siredons. I may add that in the brain of the proteïd Necturus the hemispheres are relatively larger than in the Anura, which are at the end of the line.

It must be concluded, then, that in many respects the Batrachia have undergone degeneracy with the passage of time.

d. The Reptilian Line.

As in the case of the Batrachia, the easiest way of obtaining a general view of the history of this class is by throwing their principal structural characters into a tabular form. As in the case of that class, I commence with the oldest forms and end with the latest in the order of time, which, as usual, corresponds, with the order of structure. I except from this the first order, the Ichthyopterygia, which we do not know prior to the Triassic period:

I. The quadrate bone united with the adjacent elements by suture.
  A. Temporal region of skull with a bony roof; no postorbital bars.
    Supramastoid bone present; an interclavicle; limbs ambulatory; *Cotylosauria.*
  AA. Cranium with one postorbital bar; no sternum. (Synaptosauria.)
  a. Paroccipital bone distinct.
    A supramastoid bone; ribs two-headed on centrum; carpals and tarsals not distinct in form from metapodials; *Ichthyopterygia.*

No supramastoid; sub- and postpelvic ossifications; interclavicle and clavicles separated from and below scapular arch; ribs one-headed on centrum; coracoid large, free posteriorly; *Testudinata.*

aa. Paroccipital bone not distinct.

Ribs one or two-headed, capitulum intercentral; clavicles and interclavicles forming part of shoulder-girdle; scapula simple; pubis and ischium plate-like with small or no obturator foramen; no sub- or post-pelvic bones; no supramastoid; *Theromora.*

Supramastoid present; ribs one-headed; scapula triradiate; no sternum; pubis and ischium plate-like; no sub- or postpelvic bones; *Plesiosauria.*

AAA. Cranium with two postorbital bars; a sternum. (Archosauria.)

Paroccipital bone not distinct; no supramastoid.

Ribs two-headed; no interclavicle; external anterior digits greatly elongate to support a patagium; *Ornithosauria.*

Ribs two-headed; no interclavicle; acetabulum perforate; limbs ambulatory; *Dinosauria.*

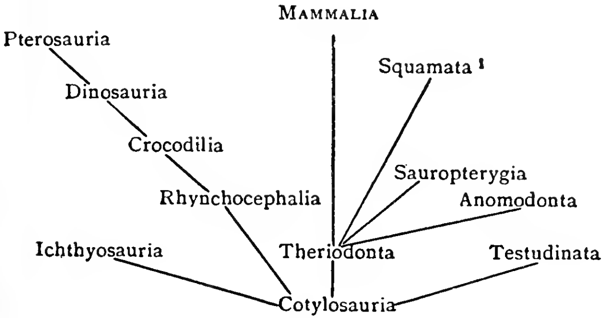
Ribs two-headed; an interclavicle; acetabulum closed; feet ambulatory; *Crocodilia.*

Ribs one headed; an interclavicle; acetabulum closed; feet ambulatory; *Rhynchocephalia.*

II. The quadrate loosely articulated with the adjacent elements, and only proximally. (Streptostylica.)

One postorbital bar, when present; a paroccipital; supramastoid not distinct; ribs one-headed; *Squamata.*

An inspection of the characters of these ten orders, and their consideration in connection with their geological history, will give a definite idea as to the character of their evolution. The history of the class, and therefore the discussion of the question, is limited in time to the period which has elapsed since the Permian epoch inclusive, for it is then that the Reptilia enter the field of our knowledge. During this period two remarkable orders of reptiles inhabited the earth, those of the Cotylosauria and of the Theromora. The important character and rôle of these types may be inferred from the fact that the Cotylosauria are structurally nearer to the Batrachia and the Theromora to the Mammalia than any other, and the former presents characters which render it probable that all the other reptiles derived their being from them. The phylogeny may be thus expressed:



It is extremely probable that the characters of the posterior parts of the cranium of reptiles, as seen in the osseous bars posterior to the orbit, were derived by a kind of natural trephining of the cranial roof of the primitive order of the Cotylosauria. This order has left remains in the Permian beds of North America, South Africa, and Germany. This is the theory of Baur,[3] and I have rendered it probable by researches on the Permian genera of North America.[4]

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[1] Some unknown type of Pythonomorpha will represent the ancestor of the Ophidia, while it is uncertain whether this order originated from the Theriodonta or the Rhynchocephalia.

[2] The Theromora include the Pelycosauria, Theriodonta, Anomodonta, and other suborders.

[3] *American Journal of Morphology*, 1889, p. 471.

[4] *Trans. Amer. Philos. Society*, 1892, p. 13; *American Naturalist*, 1892, p. 407.

The diagrams on pages 117–119 illustrate the successive changes in the structure of the posterior region of the skull in the types mentioned. The orders and suborders Pseudosuchia, Rhynchocephalia, Ichthyopterygia, Dinosauria, Crocodilia, Sauropterygia, and Testudinata commence at the beginning of Mesozoic time, after the Permian had closed. The Squamata (lizards and snakes) commence, so far as is certainly known, in the later Mesozoic, in the Cretaceous period.

The line which terminated in the Lacertilia and Ophidia (Squamata) may have originated directly from the Theriodonta, or it may have descended from the Rhynchocephalia. It departs from the former type in two respects:

First, in the loss of the capitular articulation of the ribs, and, second, in the gradual elongation and final freedom of the suspensory bone of the lower jaw (the os quadratum). In so departing from the Theromora, it also departs from the mammalian type. The ribs assume the less perfect kind of attachment which the mammals only exhibit in some of the whales, and the articulation of the lower jaw loses in strength, while it gains in extensibility, as is seen in the development of the line of the eels among fishes. The end of this series, the snakes, must therefore be said to be the result of a process of creation by degeneration, and their lack of scapular arch and fore limb and usual lack of pelvic arch and hind limb are confirmatory evidence of the truth of this view of the case.

Secondly, as regards the ossification of the anterior part of the brain-case. This is deficient in some of the Theromora, the ancestral series, which resemble in this, as in many other things, the contemporary Batrachia. The late orders mostly have the anterior walls

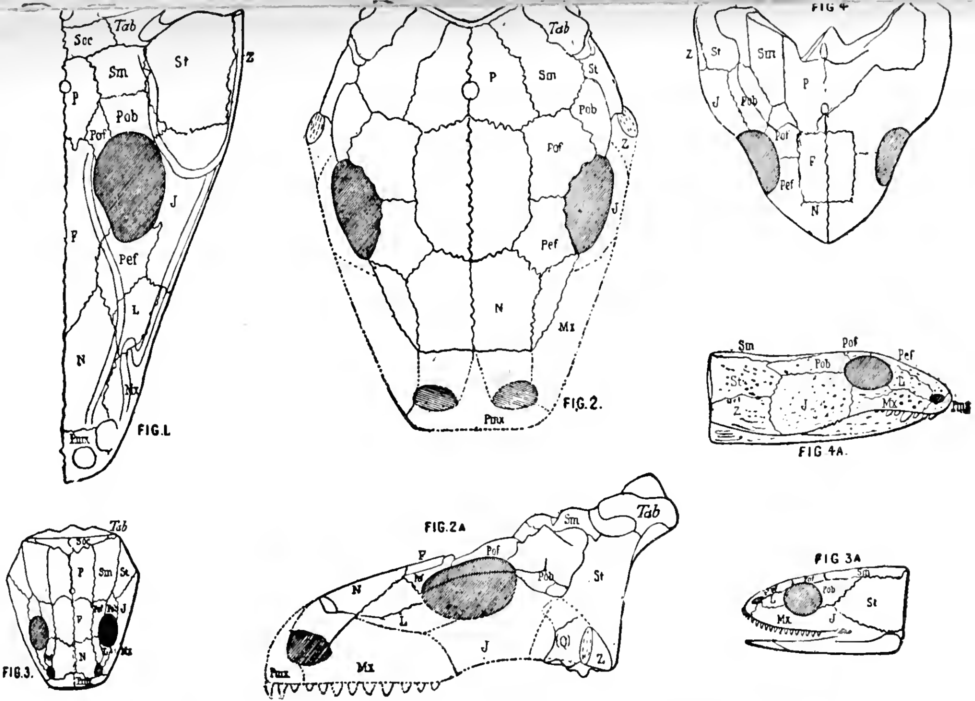

Fig. 29.—1. *Mastodonsaurus* Jaeger. 2. *Chilonyx* Cope. 3. *Pariotichus* Cope. 4. *Pantylus* Cope.—Fig. 1, Stegocephalian Figs. 2-4, Cotylosaurians.

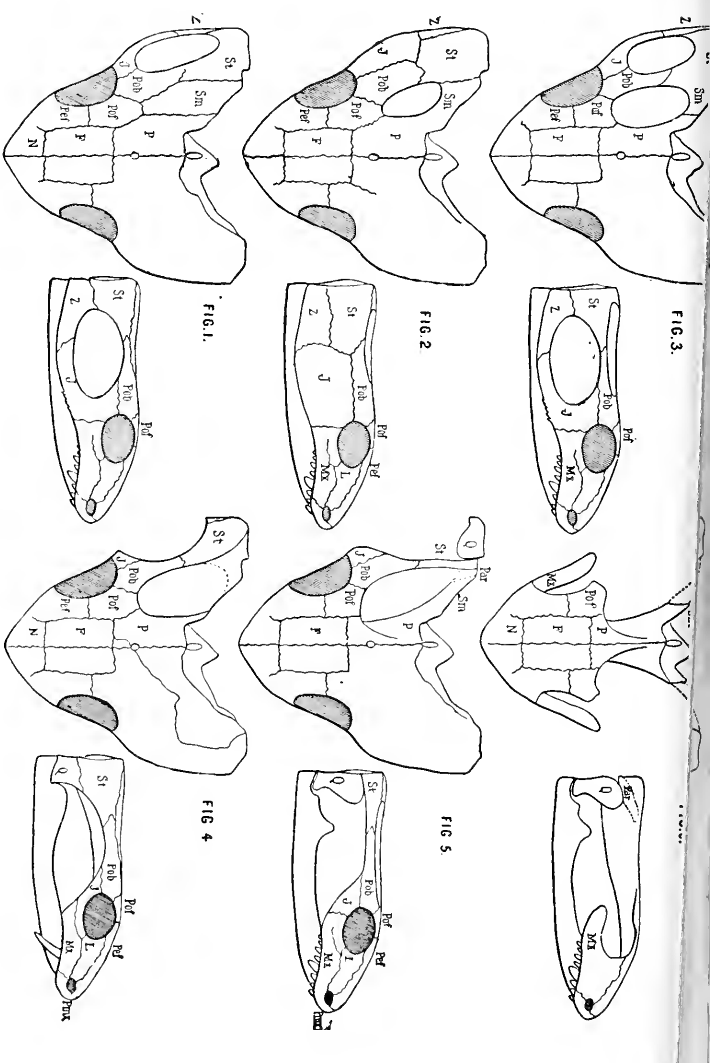

FIG. 1.

FIG. 2

FIG. 3.

FIG 4

FIG 5.

Fig. 30.—1. *Pelycosauria.* 2. *Pseudosuchia.* 3. *Rhynchocephalia.* 4. *Anomodontia.* 5. *Lacertilia.* 6. *Ophidia.*

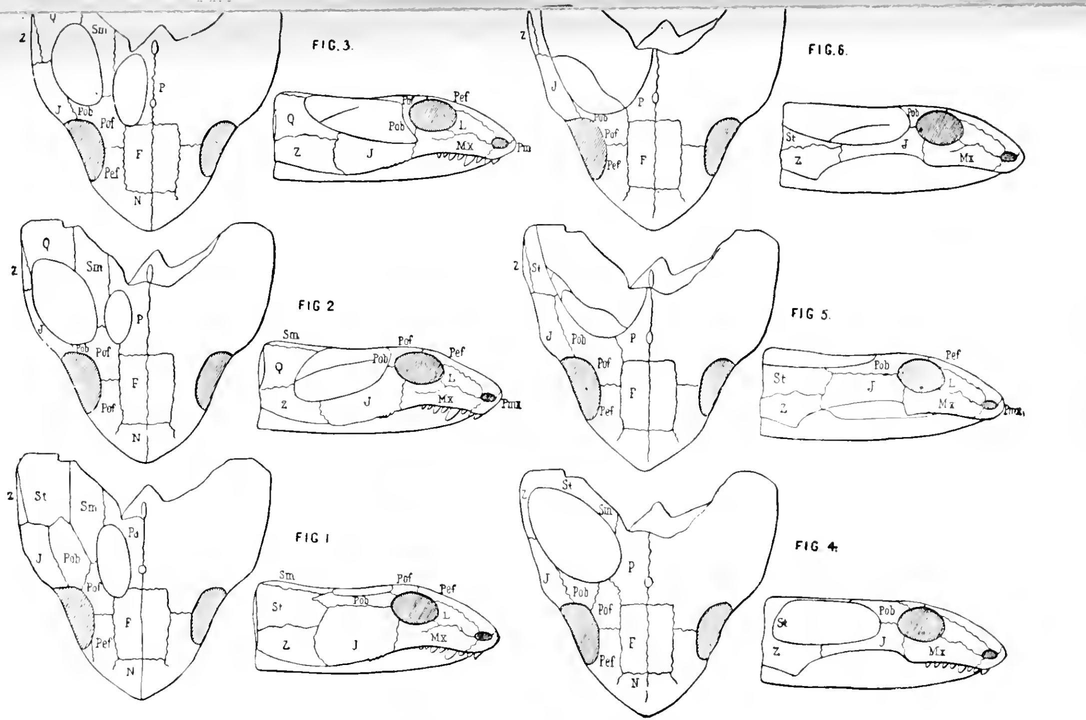
FIG. 3. FIG. 6. FIG 2 FIG 5. FIG 1 FIG 4.

Fig. 31.—1. *Ichthyopterygia.* 2. *Dinosauria.* 3. *Crocodilia.* 4. *Sauropterygia.* 5 6 *Testudinata*

membranous, but, in the streptostylicate series at the end, the skull in the snakes becomes entirely closed in front. In this respect, then, the latter may be said to be the highest or most perfect order.

As regards the scapular arch, including the sternum, no order possesses as many elements as thoroughly articulated for the use of the anterior leg as the Permian Theromora (excepting in the suborder Pelycosauria). In all the orders there is loss of parts, excepting only in the Ornithosauria and the Lacertilia. In the former the adaptation is to flying. The latter retain nearly the theromorous type. An especial side development is the modification of abdominal bones into three pairs of peculiar elements to be united with part of the scapular arch into a plastron, and the inclusion of the coracoid above them, seen in the Testudinata.

The pelvic arch has a more simple history. Again, in the Theromora we have the nearest approach to the Mammalia. The only other order which displays similar characters is the Ornithosauria (Dimorphodon, according to Seeley). In the Dinosauria we have a side modification which is an adaptation to the erect or bipedal mode of progression, the inferior bones being thrown backward so as to support the viscera in a more posterior position in birds. This is an obvious necessity to a bipedal animal where the vertebral column is not perpendicular. And it is from the Triassic Dinosauria that I suppose the birds to have arisen. The main line of the Reptilia, however, departs from both the mammalian and the avian type and loses in strength as compared with the former. In the latest orders, the Pythonomorpha and Ophidia, the pelvis is rudimental or absent.

As regards the limbs, the degeneracy is well marked. No reptilian order of later ages approaches so near to the Mammalia in these parts as do the Permian Theromora. This approximation is seen in the internal epicondylar foramen and well-developed condyles of the humerus, and in the well-differentiated seven bones of the tarsus. The epicondylar foramen is only retained in later reptiles in the rhynchocephalian Sphenodon (Dollo); and the condyles of the Dinosauria and all of the other orders, excepting the Ornithosauria and some Lacertilia, are greatly wanting in the strong characterization seen in the Theromora. The posterior foot seems to have stamped out the greater part of the tarsus in the huge Dinosauria, and it is reduced, though to a less degree, in all the other orders. In the paddled Plesiosauria, dwellers in the sea, the tarsus and carpus have lost all characterization, probably by a process of degeneracy, as in the mammalian whales. This is to be inferred from the comparatively late period of their appearance in time. The still more unspecialized feet and limbs of the Ichthyosaurus (Ichthyopterygia) can not yet be ascribed to degeneracy, for their history is too little known. At the end of the line, the snakes present us with another evidence of degeneracy. But few have a pelvic arch (Glauconiidæ Peters), while very few (Peropoda) have any trace of a posterior limb.

The vertebræ are not introduced into the definitions of the orders, since they are not so exclusively distinctive as many other parts of the skeleton. They nevertheless must not be overlooked. As in the Batrachia, the Permian orders show inferiority in the deficient ossification of the centrum. Many of the Theromora are notochordal, a character not found in any later order of reptiles excepting in a few Lacertilia (Gecconidæ). They thus differ from the Mammalia, whose characters are approached more nearly by some of the terrestrial Dinosauria in this respect. Leaving this order, we soon reach the prevalant ball-and-socket type of the majority of Reptilia. This strong kind of articulation is a need which accompanies the more elongated column which itself results at first from the posterior direction of the ilium. In the order with the longest column, the Ophidia, a second articulation, the zygosphen, is introduced. The mechanical value of the later reptilian vertebral structure is obvious, and in this respect the class may be said to present a higher or more perfect condition than the Mammalia.

In review it may be said of the reptilian line, that it exhibits marked degeneracy in its skeletal structure since the Permian epoch ; the exception to this statement being in the nature of the articulations of the vertebræ. And this specialization is an adaptation to one of the conditions of degeneracy, viz., the weakening and final loss of the limbs and the arches to which they are attached.

The history of the development of the brain in the Reptilia presents some interesting facts. In the diadectid family of the Permian Cotylosauria it is smaller than in a *Boa constrictor*, but larger than in some of the Jurassic Dinosauria. Marsh has shown that some of the latter possess brains with relatively very narrow hemispheres, so that in this organ those gigantic reptiles were degenerate, while the existing streptostylicate orders have advanced beyond their Permian ancestors.

There are many remarkable cases of what may now be safely called degradation to be seen in the contents of the orders of reptiles.[1] Among tortoises may be cited the loss of one or two series of phalanges in several especially terrestrial families of the Testudinidæ. The cases among the Lacertilia are the most remarkable. The entire families of the Pygopodidæ, the Anniellidæ, the Anelytropidæ, and the Dibamidæ are degraded from superior forms. In the Anguidæ, Teidæ, and Scincidæ, we have series of forms whose steps are measured by the loss of a pair of limbs, or of from one to all the digits, and even to all the limbs. In some series the surangular bone is lost. In others the eye diminishes in size, loses its lids, loses the folds of the epidermis which distinguish the cornea, and finally is entirely obscured by the closure of the ophthalmic orifice in the true skin.[2] Among the snakes a similar degradation of the organs of sight has taken place in two suborders, which live underground, and often in ants' nests. The Tortricidæ and Uropeltidæ are burrowing-snakes which display some of the earlier stages of this process. One genus of the true colubrine snakes even (according to Günther) has the eyes obscured as completely as those of the inferior types above named (genus Typhlogeophis.)

e. The Avian Line.

The paleontology of the birds not being well known, our conclusions respecting the character of their evolution must be very incomplete. A few lines of succession are, however, quite obvious, and some of them are clearly lines of progress, and others are lines of re-

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[1] Such forms in the Lacertilia have been regarded as degradational by Lankester and Boulanger.

[2] A table of the degenerate forms of Lacertilia is given in the chapter on Catagenesis.

trogression. The first bird we know at all completely, is the celebrated Archeopteryx of the Solenhofen slates of the Jurassic period. In its elongate series of caudal vertebræ and the persistent digits of the anterior limbs we have a clear indication of the process of change which has produced the true birds, and we can see that it involves a specialization of a very pronounced sort. The later forms described by Seeley and Marsh from the Cretaceous beds of England and North America, some of which have biconcave vertebræ, and all probably, the American forms certainly, possessed teeth. This latter character was evidently speedily lost, and others more characteristic of the subclass became the field of developmental change. The parts which subsequently attained especial development are the wings and their appendages; the feet and their envelopes, and the vocal organs. Taking all things into consideration, the greatest sum of progress has been made by the perching birds, whose feet have become effective organs for grasping, whose vocal organs are most perfect, and whose flight is generally good, and often very good. In these birds also the circulatory system is most modified, in the loss of one of the carotid arteries.

The power of flight, the especially avian character, has been developed most irregularly, as it appears in all the orders in especial cases. This is apparent so early as in the Cretaceous toothed birds already mentioned. According to Marsh, the Hesperornithidæ have rudimental wings, while these organs are well developed in the Ichthyornithidæ. They are well developed among natatorial forms in the albatrosses and frigate pelicans, and in the skuas, gulls, and terns, and are rudimental in their allies, the auks. They are developed among rasorial types in the sand-grouse, and, among the adjacent forms, the pigeons. Then

Fig. 32.—*Archæopteryx lithographica,* from the middle Oölite of Bavaria.

among the lower Passeres, the humming-birds exceed all birds in their powers of flight, and the swifts and some of the Caprimulgidæ are highly developed in this respect. Among the higher or true song birds, the swallows form a notable example. With these high specializations occur some remarkable deficiencies. Such are the reduction of the feet in the Caprimulgidæ, swifts, and swallows, and the fœtal character of the bill in the same families. In the syndactyle families, represented by the kingfishers, the condition of the feet is evidently the result of a process of degeneration.

A great many significant points may be observed in the developmental history of the epidermic structures, especially in the feathers. The scale of change in this respect is in general a rising one, though various kinds of exceptions and variations occur. In the development of the rectrices (tail-feathers) there are genera of the wading and rasorial types, and even in the insessorial series, where those feathers are of primitive structure (Menuridæ), are greatly reduced, or absolutely wanting. These are cases of degeneracy.

There is no doubt that the avian series is in general an ascending one.

f. The Mammalian Line.

Discoveries in paleontology have so far invalidated the accepted definitions of the orders of this class that it is difficult to give a clearly cut analysis, especially from the skeleton alone. The following scheme, therefore, while it expresses the natural groupings and affinities, is defective, in that some of the definitions are not without exceptions:[1]

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[1] This classification of the Mammalia was first published by the writer in the *American Naturalist* for 1885; was improved in the same, 1889 (October); and appeared in a Syllabus of Lectures of the University of Pennsylvania, July, 1891.

I. A large coracoid bone articulating with the sternum. An interclavicle (Prototheria).

Epicoracoid and marsupial bones; fibula articulating with proximal end of astragalus: 1. *Monotremata.*

II. Coracoid a small process coössified with the scapula (Eutheria).

α. Marsupial bones; palate with perforations (uterus divided; placenta and corpus callosum rudimental or wanting; cerebral hemispheres small and generally smooth).

But one deciduous molar tooth: 2. *Marsupialia*

αα. No marsupial bones; palate generally entire (placenta and corpus callosum well developed).

β. Anterior limb reduced to more or less inflexible paddles posterior limbs wanting (Mutilata).

Elbow-joint fixed; carpals discoid, and with the digits separated by cartilage; lower jaw without ascending ramus: 3. *Cetacea.*

Elbow-joint flexible; carpals and phalanges with normal articulations; lower jaw with ascending ramus: 4. *Sirenia.*

ββ. Anterior limbs with flexible joints. Ungual phalanges compressed and pointed[1] (Unguiculata).

γ. Feet taxeopodous (with exceptions in the carpus).

δ. Teeth without enamel; generally no incisors.

Limbs not volant; hemispheres small, smooth: 5. *Edentata*

δδ. Teeth with enamel; incisors generally present.

No postglenoid process; mandibular condyle not transverse; limbs not volant; hemispheres small, smooth: 6. *Glires*

Anterior limbs volant; hemispheres small, smooth: 7. *Chiroptera*

A postglenoid process; mandibular condyle transverse; limbs not volant; no scapholunar bone[2]; hemispheres small, smooth: 8. *Bunotheria.*[3]

A postglenoid process; limbs not volant, with a scapholunar bone; hemispheres larger, convoluted: 9. *Carnivora.*

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[1] Except Mesonychiidæ.

[2] Except Erinaceus and Talpa.

[3] With the suborders Pantotheria, Creodonta, Insectivora, and Tillodonta

$\gamma\gamma$. Feet diplarthrous.

Limbs ambulatory; a postglenoid process; molars quadritubercular: 10. *Ancylopoda.*

$\beta\beta\beta$. Anterior limbs with flexible joints and distinct digits; ungual phalanges not compressed and acute at apex[1] (Ungulata[2]).

ε. Tarsal bones in linear series; carpals generally in linear series.

Limbs ambulatory; teeth with enamel: 11. *Taxeopoda.*[3]

$\varepsilon\varepsilon$. Carpal series alternating; tarsal series linear.

Limbs ambulatory; median digits longest; teeth with enamel: 12. *Toxodontia.*

$\varepsilon\varepsilon\varepsilon$. Tarsal series alternating; carpals linear.

Cuboid bone partly supporting navicular, not in contact with astragalus: 13. *Proboscidia.*

$\varepsilon\varepsilon\varepsilon\varepsilon$. Both tarsal and carpal series more or less alternating.

Os magnum not supporting scaphoides; cuboid supporting astragalus; superior molars tritubercular: 14. *Amblypoda.*

Os magnum supporting scaphoides; superior molars quadritubercular:[4] 15. *Diplarthra.*[5]

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[1] Except the Hapalidæ.

[2] Lamarck, *Zoologie Philosophique*, 1809.

[3] This order has the following suborders:

Carpal series linear; no intermedium; tibia not interlocking with astragalus; no anapophyses; incisors rooted; hallux not opposable: *Condylarthra.*

Carpal series linear; an intermedium; tibia interlocking with astragalus; hallux not opposable: *Hyracoidea.*

An intermedium; fibula not interlocking; anapophyses; hallux opposable; incisors growing from persistent pulps: *Daubentonioidea.*

An intermedium; fibula not interlocking; anapophyses; hallux opposable; incisors rooted; carpus generally linear: *Quadrumana.*

No intermedium;[6] nor anapophyses; carpal rows alternating; incisors rooted: *Anthropomorpha.*[7]

The only difference between the Taxeopoda and the Bunotheria is in the unguliform terminal phalanges of the former as compared with the clawed or unguiculate form in the latter. The marmosets among the former division are, however, furnished with typical claws.

[4] Except Trigonolestes.

[5] This order includes the suborders Perissodactyla and Artiodactyla. It is the Ungulata of some authors.

[6] Except in Simia and Hylobates.

[7] Includes the Anthropoid apes and man.

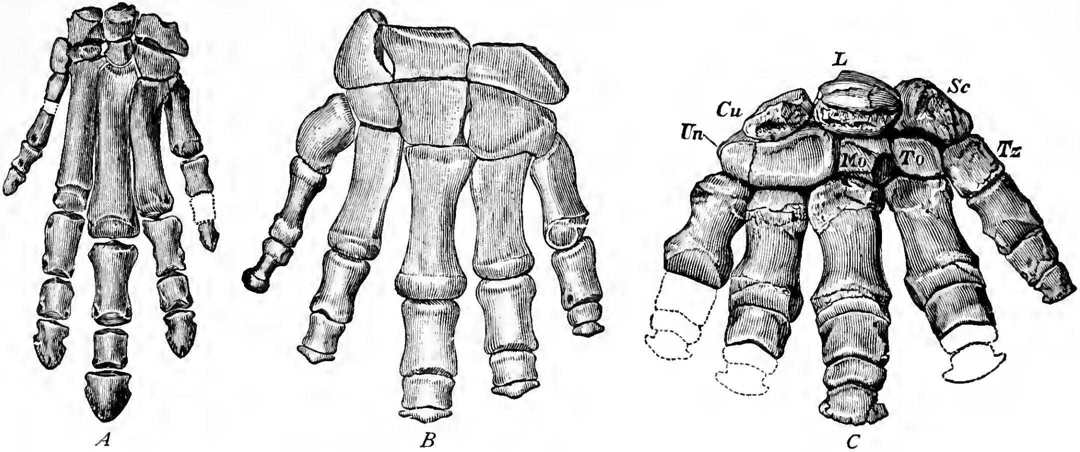

Fig. 33.—Ungulata, anterior feet. *A*, Phenacodus; *B*, Elephas; *C*, Coryphodon.

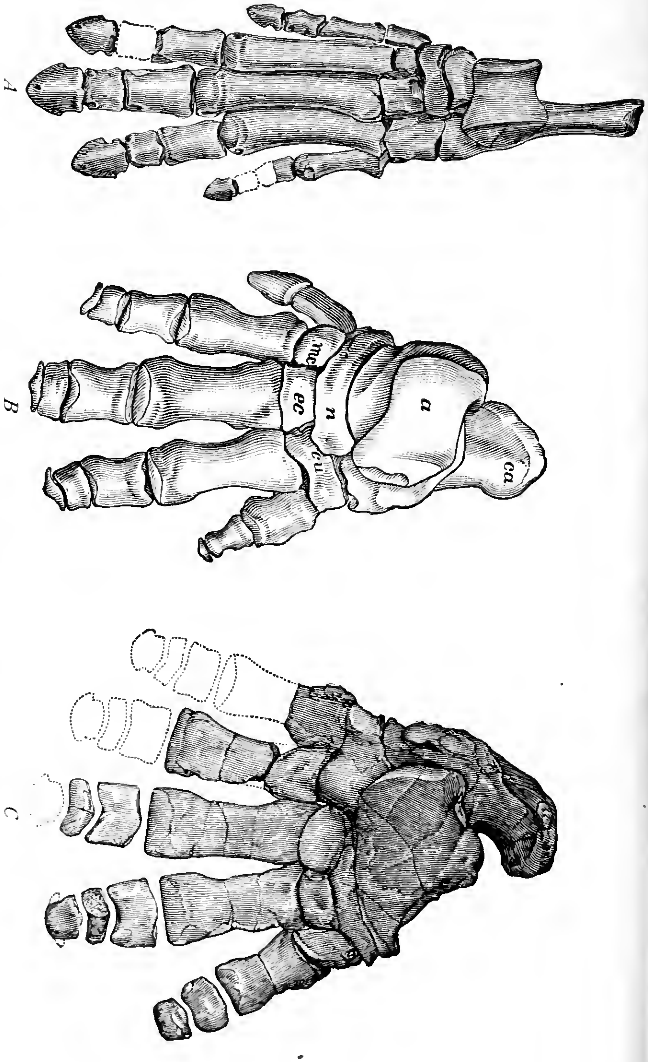

Fig. 34.—Ungulata, posterior feet. *A*, Phenacodus; *B*, Elephas; *C*, Coryphodon.

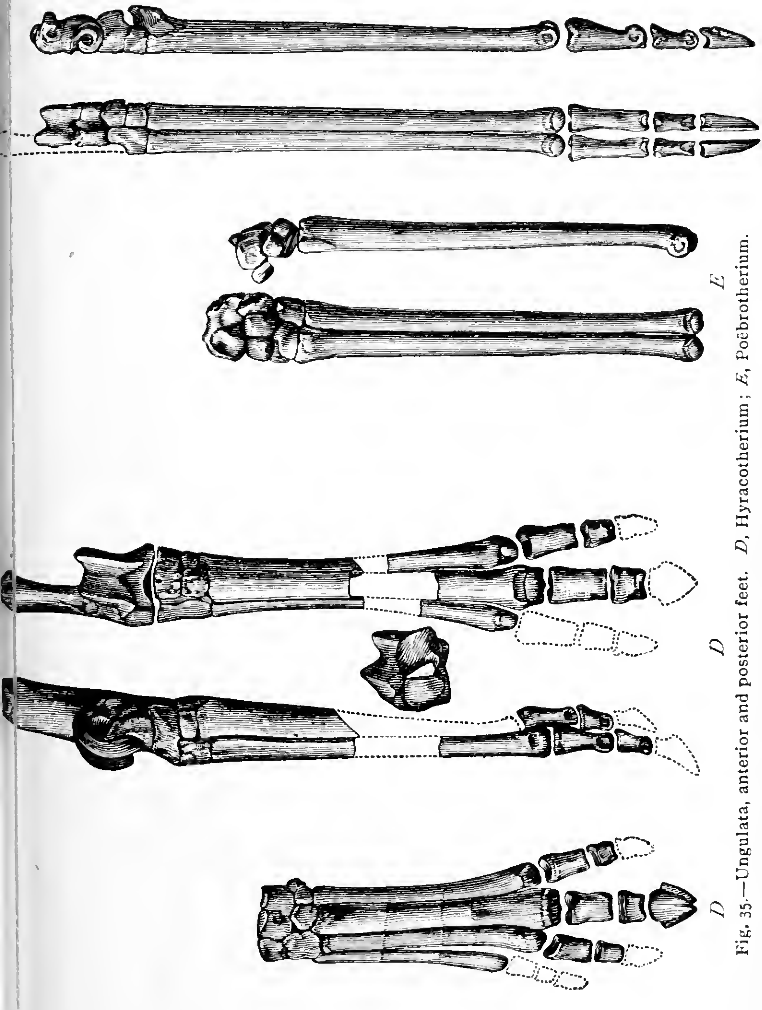

Fig. 35.—Ungulata, anterior and posterior feet. *D*, Hyracotherium; *E*, Poëbrotherium.

The characters of the skeleton of the order Monotremata show that it is nearest of kin to the Reptilia, and many subordinate characters, especially of the extremities, point to the Theromora as its ancestral source.[1] In the general characters the Marsupialia naturally follow in a rising scale, as proved by the increasing perfection of the reproductive system. The Monodelphia follow with improvements in the reproductive system and the brain, as indicated in the table above given. The oldest Monodelphia were, in respect to the structure of the brain, much like the Marsupialia, and some of the existing orders resemble them in some parts of their brain-structure. Such are the Condylarthra and Amblypoda of extinct groups, and the Bunotheria, Edentata, Glires, and Chiroptera, recent and extinct. The characters of the brains of Amblypoda and some Creodonta are, in their superficial characters, even inferior to existing marsupials. The divided uterus of the recent forms named, also gives them the position next to the Marsupialia. In the Carnivora, Hyracoidea, and Proboscidia, a decided advance in both brain-structure and reproductive system is evident. The hemispheres increase in size, and they become convoluted. A uterus is formed, and the testes become external, etc. In the Quadrumana and Anthropomorpha the culmination in these parts of the structure is reached, excepting only that, in the lack of separation of the genital and urinary efferent ducts, the males are inferior to those of many of the Artiodactyla. This history displays a rising scale for the Mammalia.[2]

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[1] *Proceedings American Philosoph. Society*, 1884, p. 43. *Antea*, p. 87.

[2] See the evidence for evolution in the history of the extinct Mammalia *Proceedings of the American Association for the Advancement of Science*, 1883.

Looking at the skeleton, we observe the following successional modifications:

First, as to the feet, and (A) the digits. The Condylarthra have five digits on both feet, and they are plantigrade. This character is retained in their descendants of the lines of Anthropomorpha, Quadrumana, and Hyracoidea, also in the Bunotheria, Edentata, and most of the Glires. In some of the Amblypoda and in the Proboscidia the palm and heel are a little raised. In the Carnivora and Diplarthra the heel is raised, often very high, above the ground, and the number of toes is diminished, as is well known, to two in the Artiodactyla and one in the Perissodactyla. (B) The tarsus and carpus. In the Condylarthra and most of the Creodonta the bones of the two series in the carpus and tarsus are opposite each other, so as to form continuous and separate longitudinal series of bones. This continues to be the case in the Hyracoidea and many of the Quadrumana, but in the anthropoid apes and man the second row is displaced inwards so as to alternate with the first row, thus interrupting the series in the longitudinal direction, and forming a stronger structure than that of the Condylarthra. In the bunotherian, rodent, and edentate series, the tarsus continues to be without alternation, as in the Condylarthra, and is generally identical in the Carnivora. In the hoofed series proper it undergoes change. In the Proboscidia the carpus continues linear, while the tarsus alternates. In the Amblypoda the tarsus alternates in another fashion, and the carpal bones are on the inner side linear, and on the outer side alternating. The complete interlocking by universal alternation of the two carpal series is only found in the Diplarthra. (C) As to the ankle-joint. In most of the Condylarthra

Fig. 36.—*Phenacodus vortmanii*, representative of the order Condylarthra, two-ninths natural size.

it is a flat joint or not tongued or grooved. In most of the Carnivora, in a few Glires, and in all Diplarthra, it is deeply tongued and grooved, forming a more perfect and stronger joint than in the other orders, where the surfaces of the tibia and astragalus are flat. (D) In the highest forms of the Rodentia and Diplarthra the fibula and ulna become more or less coössified with the tibia and radius, and their middle portions become attenuated or disappear.

Secondly, as regards the vertebræ. The mutual articulations (zygapophyses) in the Condylarthra have flat and nearly horizontal surfaces. In higher forms, especially of the ungulate series, they become curved, the posterior turning upward and outward, and the anterior embracing them on the external side. In the higher Diplarthra this curvature is followed by another curvature of the postzygapophysis upward and outward, so that the vertical section of the face of this process is an S. Thus is formed a very close and secure joint, such as is nowhere seen in any other Vertebrata.

Thirdly, as regards the dentition. Of the two types of Monotremata, the Tachyglossus, and the Platypus, the known genera of the former possess no teeth, and the known genus of the latter possesses only a single corneous epidermic grinder succeeding two deciduous molars, like those of certain extinct forms, in each jaw. As the theromorous reptiles from which these are descended have well-developed teeth, their condition is evidently one of degeneration. We probably have their ancestors in the Multituberculata, which range from Triassic to lower Eocene time in both hemispheres. In the marsupial order we have a great range of dental structure, which almost epitomizes that of the monodelph orders. The dentition of the carnivorous forms is creodont; that of the kangaroos is perissodactyle, and that of the wombats is rodent. Other forms repeat the Insectivora. I therefore consider the placental series especially. I have already shown that the greater number of the types of this series have derived the characters of their molar teeth from the stages of the following succession. First, a simple cone or reptilian crown, alternating with that of the other jaw. Second, a cone with anterior and posterior lateral denticles. Third, the denticles rotated to the inner side of the crown below, and outer side above forming with the principal (median) cone a three-sided prism, with tritubercular apex, which alternates with that of the opposite jaw. Fourth, development of a heel projecting from the posterior base of the lower jaw, which, in mastication, meets the crown of the superior, forming a tubercular-sectorial inferior molar. From this stage the carnivorous and sectorial dentition is derived, the tritubercular type being retained. Fifth, the development of a posterior inner cusp in the superior molar, and the elevation of the heel in the inferior molar, with the loss of the anterior inner cusp. Thus the molars become quadritubercular, and opposite. This is the type of many of the Taxeopoda, including the Quadrumana and Insectivora as well as the inferior Diplarthra. The higher Taxeopoda (Hyracoidea) and Diplarthra add various complexities. Thus the tubercles become flattened and then concave, so as to form V's in the section produced by wearing; or they are joined by cross-folds, forming various patterns, of which the most specialized is that of the horse. In the Proboscidia the latter

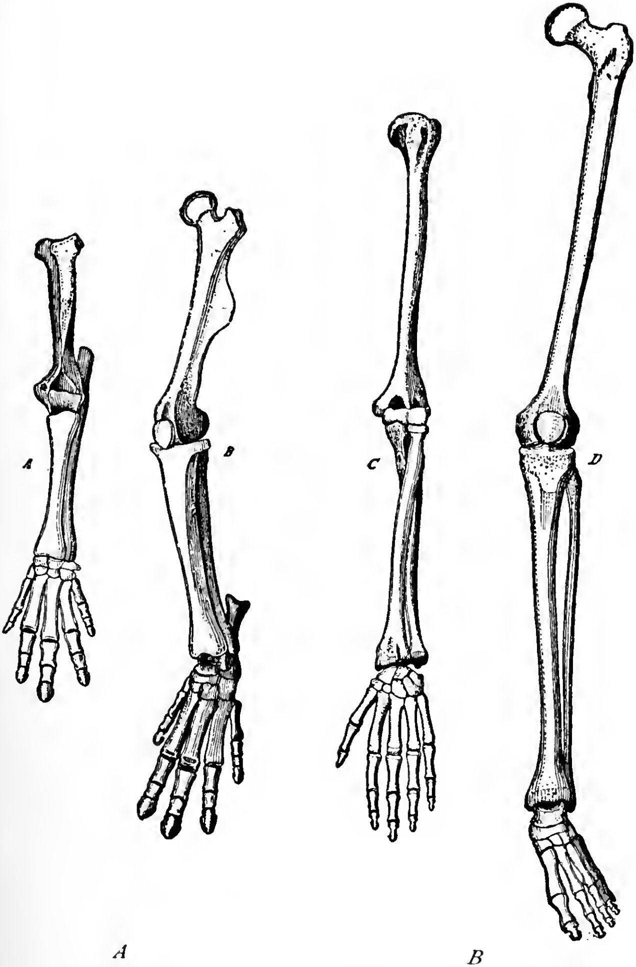

Fig. 37.—*A*, *Phenacodus primævus*, fore and hind limbs; *B*, *Homo sapiens*, fore and hind limbs.

become multiplied so as to produce numerous cross-crests.

The molars of some of the Sirenia are like that of some of the Ungulata, especially of the tapirine group, while in others the teeth consist of cylinders. In the Cetacea the molars of the oldest (Eocene and Miocene) types are but two-rooted and compressed, having much the form of the premolars of other Mammalia. In existing forms a few have simple conical teeth, while in a considerable number teeth are entirely wanting.

g. General Review of the Phylogeny of Mammalia.

In the accompanying table some of the characters of the mammalian skeleton above described are thrown into a tabular form. They are exhibited in the order of their appearance in geological time, beginning with the oldest horizon at the bottom of the left-hand column. Continued primitive types are enclosed in brackets. These relations were pointed out by me in 1883,[1] and every discovery made since that date has confirmed their correctness. Some characters of the Mesozoic Mammalia are now added.

Paleontology has cleared up the phylogeny of most of the mammalian orders, but some of them remain as yet unexplained. This is the case with the Cetacea, the Sirenia, and the Edentata. The Marsupialia can be supposed with much probability to have come off from the Monotremata, but there is but little paleontological evidence to sustain the hypothesis. Little progress has been made in unravelling the phylogeny

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[1] *Proceedings American Assoc. Adv. Science*, p. 40. The successional gradation in the limbs and teeth was announced by me in 1873 (*Proceeds. Academy Philadelphia*, p. 371, and *Journal of the Academy*, 1874, p. 20), and that in the size of the hemispheres of the brain by Marsh in 1874 (*American Journal Sci. Arts*, p. 66).

FORMATION.	NO. TOES.	FEET.	ASTRAGALUS.	CARPUS AND TARSUS. UNGULATA.	RADIUS. UNGULATA.	SUPERIOR MOLARS.	ZYGAPOPHYSES.	BRAIN.
RECENT......	1-1	Digitigrade.	Grooved.	Interlocking.	Faceted.	4-tubercles,	Doubly involute.	Hemispheres
MIOCENE.....	2-2	(Plantigrade.)	**(Flat.)**	(Opposite.)		crested and	Singly involute.	larger, convo-
Upper..........	3-3					cemented.		luted.
(Loup Fork.)	4-4							
	(5-5)							
Middle..........	2-2	Digitigrade.	Grooved.	Interlocking.	Faceted.	4-tubercles, and	Singly involute.	Hemispheres
(John Day.)	3-3				Smooth.	crested.	Doubly involute.	larger, convo-
	4-4							luted.
Lower.........	3-3	Digitigrade.	Grooved.	Interlocking.	Smooth.	4-tubercles, and	? Singly involute.	Hemispheres
(White River.)	4-3	Plantigrade.			Faceted.	crested.		small; and
	4-4							larger.
EOCENE......	3-3	(Digitigrade.)	Grooved.	Opposite.	Smooth.	4-tubercles.	Singly involute.	
Middle..........	4-3	Plantigrade.	(Flat.)	Interlocking.		3-tubercles, and	Plane.	Hemispheres
(Bridger.)	4-5					crested.		small.
	5-5							
Lower..........	4-3	Plantigrade.	Flat.	Opposite.	Smooth.	4-tubercles.	Plane.	Hemispheres
(Wasatch.)	4-5	(Digitigrade.)	(Grooved.)	Interlocking.		3-tubercles, a	Singly involute.	small; mesen-
						few crested.		cephalon some-
CRETACEOUS..	5-5							times exposed.
Upper...........	5-5	Plantigrade.	Flat.	Opposite.	Smooth.	3-tubercles.	Plane	Mesencephalon
(Puerco.)						(4-tubercles,		exposed; hemi-
						none crested.)		spheres small
(Laramie.)			Flat.			Tritubercular.		and smoother.
JURASSIC.....						Tritubercular.		
						Triconodont.		
TRIASSIC.....						Protodont.		

of the Cetacea and Sirenia. The results attained by the study of the paleontology of the other orders may be summarized as follows:

First. It is probable that the common ancestors of the placental and implacental lines of Mammalia are known to us in some of the types of the Jurassic period. Whether they were marsupial in the sense of possessing an external pouch for the young or not, is immaterial. They were probably marsupial in brain characters, in the structure of their reproductive system, and in the absence of placenta. To this source the existing polyprotodont marsupials may be traced, through such forms as Myrmecobius. The multituberculate type has a contemporary history, and one distinct from that of the Polyprotodontia, and its ancestry has not yet been discovered. Their earliest forms (of the Jurassic and Triassic) are already highly specialized. They probably represent the Monotremata of their time.

Second. The immediate didelphian ancestors of the monodelphous Mammalia have not yet been certainly discovered. In the oldest of the latter (of the Puerco epoch) numerous points of approach to the insectivorous Jurassic forms occur, especially in the prevalent trituberculy of the molars in both epochs.

Third. The phylogeny of the clawed group has been traced back to a common ordinal form which has been called the Bunotheria. Of these the most generalized are the Creodonta, from which we may trace the Carnivora, the Insectivora, and the Tillodonta, and probably all other Unguiculata. The Ancylopoda only have undergone the alternation of the carpal and tarsal bones, which obtains in the diplarthrous Ungulata.

Fourth. The phylogeny of the hoofed groups carries us back to the order Condylarthra, the hoofed cotemporary of the Bunotheria. The even and odd toed hoofed mammals are traceable back to the Amblypoda, whose oldest representatives are the Pantodonta of the Puerco. The Proboscidia and Hyracoidea come directly from the Condylarthra. Moreover, the phalanges of the lemurs are not distinguishable by any important characters from the hoofs of the Hyracoidea and Condylarthra. Not only this, but the structure of the foot in these three groups is identical in regard to the mode of articulation of the first and second rows of the tarsal and carpal bones.

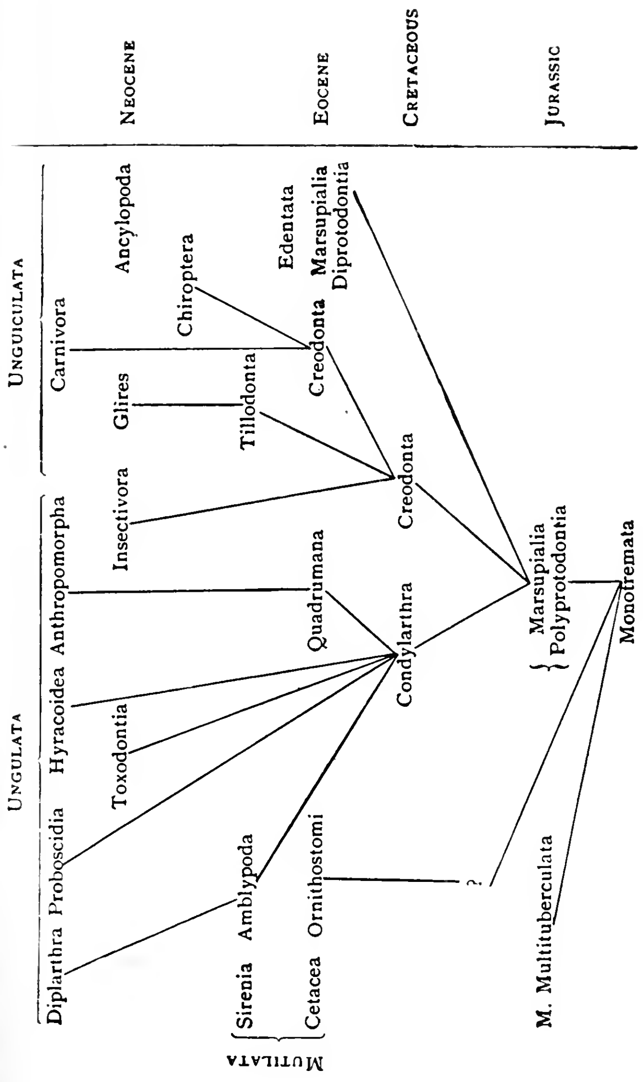
Fifth. The characters of the feet of the Condylarthra agree with those of unguiculate placental Mammalia, and bind the two series together. The synthesis of the ungulate and unguiculate lines is accomplished by exceptions to the characters which define them. Thus the hoofs of Pantolambda (Amblypoda), Periptychus (Condylarthra), and Mesonyx (Creodonta) do not differ by any marked character. Claws occur in the Hapalidæ of the quadrumanous line, and the ungues of some Glires are absolutely intermediate between the hoofs and claws. Many Edentata have claws on the fore feet and hoofs on the hind feet. The Condylarthra with tritubercular molar teeth are then traceable to Bunotheria with tritubercular teeth, of which many are known from the Puerco beds; and the quadritubercular forms from corresponding quadritubercular or tritubercular Bunotheria, of which latter, some are known.

Sixth. The anthropoid line may be traced directly through the lemurs to the Condylarthra. The changes which have taken place in the skeleton are slight, and consist among other points in a rotation of the second row of carpal bones inwards on the first row, in the anthropoid apes and man, similar to that which has occurred among the Ungulata, but it has not become so pronounced.

As a result we get the general phylogenetic scheme as shown on the following page.

In this diagram, divisions of greater and lesser rank are mixed, so as to display better some of the relationships. Thus all the divisions whose names stand on the right side of the middle vertical line are unguiculates; and those on the left side of the line, excepting Sirenia and Cetacea, are ungulates. The three names in the middle vertical line are those of the suborders of the Taxeopoda.

A review of the characters of the existing Mammalia as compared with those of their extinct ancestors displays a great deal of improvement in many ways, and but few instances of retrogression. The succession in time of the Monotremata, the Marsupialia, and the Monodelphia, is a succession of advance in all the characters of the soft parts and of the skeleton which define them (see table of classification). As to the monotremes themselves, it is more than probable that the order has degenerated in some respects in producing the existing types. The history of the Monotremata is not made out, but the earliest forms of which we know the skeleton, Polymastodon (Cope) of the Lower Eocene, is as specialized as the most specialized recent forms. The dentition of the Jurassic forms, Plagiaulax, etc., is quite specialized also, but not more so than that of the kangaroos. The premolars are more specialized, the true molars less specialized than in those animals. The history of Marsu-


NEOCENE
EOCENE
CRETACEOUS
JURASSIC
UNGUICULATA
UNGULATA
MUTILATA
Carnivora
Ancylopoda
Chiroptera
Edentata
Marsupialia Diprotodontia
Creodonta
Glires
Tillodonta
Creodonta
Insectivora
Anthropomorpha
Quadrumana
Marsupialia
Polyprotodontia
Monotremata
Hyracoidea
Toxodontia
Condylarthra
Diplarthra
Proboscidia
Amblypoda
Ornithostomi
?
M. Multituberculata
Sirenia
Cetacea

pialia indicates that the primitive types were all insectivorous, and possessed a larger number of molars than any of the recent forms. The latter have then followed the same course as the placentals in the reduction of the number of teeth and specialization of those that remain.

Coming to the Monodelphia, the increase in the size and complication of the brain, both of the cerebellum and the hemispheres, is a remarkable evidence of advance. But one retrogressive line in this respect is known, viz., that of the order Amblypoda,[1] where the brain has become relatively smaller with the passage of time. The successive changes in the structure of the feet are all in one direction, viz., in the reduction of the number of the toes, the elevation of the heel, and the creation of tongue and groove joints where plain surfaces had previously existed. The diminution in the number of toes might be regarded as a degeneracy, but the loss is accompanied by a proportional gain in the size of the toes that remain. In every respect the progressive change in the feet is an advance. In the carpus and tarsus we have a gradual extension of the second row of bones on the first, to the inner side. In the highest and latest orders this process is most complete, and, as it results in a more perfect mechanical arrangement, the change is clearly an advance. The same progressive improvement is seen in the development of distinct facets in the cubito-carpal articulation, and of a tongue and groove ("trochlear crest") in the elbow-joint. In the vertebræ the development of the interlocking zygapophysial articulations is a clear advance.

Progress is generally noticeable in the dental struc-

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[1] See *Naturalist*, Jan., 1885, p. 55.

tures; for, the earliest dentitions are the most simple, and the later the more complex. Some of the types retain the primitive tritubercular molars, as the Centetidæ, shrews, and some lemurs, and most Carnivora (above), but the quadritubercular and its derivative forms are by far the most common type in the recent fauna. The forms that produced the complicated modifications in the Proboscidia and Diplarthra appeared latest in time, and the most complex genera, Elephas, Bos, and Equus, the latest of all. The extreme sectorial modifications of the tritubercular type, as seen in the Hyænidæ and the Felidæ, are the latest of their line also.

Some cases of degeneracy are, however, apparent in the monodelphous Mammalia. The loss of pelvis and posterior limbs in the two mutilate orders is clearly a degenerate character, since there can be no doubt that they have descended from forms with those parts of the skeleton present. The reduction of flexibility seen in the limbs of the Sirenia and the loss of this character in the fore limbs of the Cetacea are features of degeneracy for the same reason. The teeth in both orders have undergone degenerate evolution; in the later and existing forms of the Cetacea even to extinction.

The Edentata have undergone degeneration. This is chiefly apparent in the teeth, which are deprived of enamel, and which are wanting from the premaxillary bone. A suborder of the Bunotheria, the Tillodonta of the Lower Eocene period, display a great reduction of enamel on the molar teeth, so that in much-worn examples it appears to be wanting. Its place is taken by an extensive coat of cementum, as is seen in Edentata, and the roots of the teeth are often undivided as in that order.

Local or sporadic cases of degenerate loss of parts are seen in various parts of the mammalian series, such as toothless Mammalia wherever they occur. Such are cases where the teeth become extremely simple, as in the honey-eating masupial Tarsipes, the carnivore Proteles, the pteropod bats, and the aye-aye. Also where teeth are lost from the series, as in the canine genus Dysodus, and in man. The loss of the hallux and pollex without corresponding gain, in various genera, may be regarded in the same light.

In conclusion, the progressive may be compared with the retrogressive evolution of the Vertebrata, as follows: In the earlier periods and with the lower forms, retrogressive evolution predominated. In the higher classes progressive evolution has predominated. When we consider the history of the first class of vertebrates, the Tunicata, in this respect, and compare it with that of the last class, the Mammalia, the contrast is very great.

h. The Phylogeny of the Horse.

As an example of special phylogeny I select that of the horse, because it is the most completely represented by specimens in our museums.

I have already pointed out that the alternate type of carpus and tarsus of the Diplarthra has been derived from the linear of the Taxeopoda by a displacement inwards of the bones of their second rows. In the posterior foot this has changed the convex surface of the head of the astragalus into a bifacetted face. Thus was the condylarthrous astragalus modified into that of the Diplarthra. At the beginning of the line of the horses we find the condylarthrous genus of the Wasatch Eocene, Phenacodus Cope, to differ in this way from the perissodactylous genus Hyracotherium Owen. Phenacodontidæ are indicated as the ancestors of all the Ungulata by their character as "bunodont pentadactyle plantigrades," characters in which they agree with the ancestors of all placental mammals. That they are not the ancestors of all the latter is shown by the fact that their molar type is quadritubercular; but one has to go backwards but a short distance in time to the Puerco epoch, to find their tritubercular ancestors. Between these and Phenacodus, comes the quadritubercular genus Euprotogonia Cope, of the Puerco, which has simpler premolar teeth.

Between Phenacodus and Hyracotherium there is room for two or more genera with fully facetted carpals and tarsals, longer feet, and a rudimental first toe on the anterior foot, and first and fifth toes on the hind foot. In Hyracotherium these digits have disappeared. Further, in Hyracotherium the internal cusps of the molars are more or less connected with the external by low and indistinct ridges, which in the superior molars include the small intermediate tubercles or conules. Thus is the lophodont dentition foreshadowed. Hyracotherium was a contemporary of Phenacodus and continued later in Eocene time. Some of its forms developed an increased complexity of the last premolars in both jaws, forming the genus Pliolophus, and foreshadowing the development of molar-like premolars, which is so characteristic of the later members of the horse line. In the genus Epihippus Marsh, of one epoch later in time (the Uinta), two such premolars are developed in each jaw. We have seen very short interspaces next the canine teeth in Phenacodus, and these have become longer in Hyracotherium and Epihippus.

With the opening of the Neocene age, we have the descendant of Epihippus in Mesohippus Marsh, which differs from its predecessor as follows. There are but three toes on all the feet; three premolars resemble the true molars; the crests which connect the internal pair of cusps with the external in both jaws, are much more elevated, and soon form on wearing a part of the pattern of the crown. Hyracotherium already walked on the ends of its toes, and the feet of Mesohippus continue the character. The crowns of all the molars are short like those of its ancestors. In the Middle Neocene formations we have the genus Anchitherium Kaup, where the incisor teeth show the addition of a ridge or cingulum round the inner side, which bounds a cup; forming the cupped incisors so characteristic of the horses. The species have been all the while growing gradually larger.

Towards the end of Neocene time important progress was made. In the Loup Fork epoch the three toed horses were very numerous in species, but their lateral toes were all much shortened so that they did not reach the ground. The crests of the molar teeth were much stronger, and in the superior series the conules had assumed a greater importance, extending themselves posteriorly from the transverse crests, and showing crescentic sections, resembling those of the outer cusps, with which they are parallel. The anterior conule extended so far posteriorly as to join the posterior one, resembling in this respect also the anterior external cusp. So the crown came to have six modified cusps of which the two inner are the smallest and remain unconnected with each other. The crowns of the molars vary in length in these later three-toed horses. Some are short like the Anchitheriums, and others are longer, approaching the true horses. In the valleys between these high cusps cement is deposited, as in the true horses and other mammals with long-crowned molars. There are two types of these later three-toed horses. In one the posterior inner cusp is not joined to the conule by a transverse crest (genus Hippotherium Kaup), or it is so joined (genus Protohippus Leidy).

Plistocene times witnessed the perfection of the horse line. The lateral toes dwindled into splints concealed beneath the skin. The crowns of the molar teeth became very long, and in the upper jaw the inner posterior tubercle, now a column, joined the adjacent conule, and became extended very much in fore and aft diameter. The small anterior premolar disappeared, and the canines became the mark of the male sex only, in general. The lower molars acquire some additional complications, and the feet are longer than in any of its ancestors. The genus Equus L. is finished, and remains a permanent member of the human epoch, from which its only relatives, the rhinoceros and the tapir, are gradually disappearing.

This history may be duplicated in manner and mode, by the lines of the camels, the dogs and bears, the cats, the beaver, etc.

Examination of all these genealogical lines reveals a certain definiteness of end and directness of approach. We discover no accessions of characters which are afterwards lost, as would naturally occur as a result of undirected variation. Nor do we discover anything like the appearance of sports along the line, the word sport being used in the sense of a variation widely divergent from its immediate ancestor. On the contrary, the more thorough becomes our knowledge of the series, the more evident does it become that progressive evolution has advanced by minute increments along a definite line, and that variations off this line have not exerted an appreciable influence on the result.

i. The Phylogeny of Man.

In man the feet retain the pentadactyle plantigrade type with scarcely grooved astragalo-tibial articulation, which characterizes the Mammalia of the Puerco epoch, and most of those of the Lower Eocene.[1] His dentition is not lophodont, but is simply bunodont, like that of the Phenacodontidæ of the Lower Eocene. It is only in the structure of the brain and the reproductive system that man shows an advance over the Eocene type. In the former he greatly excels any mammal that has appeared since; a superiority already apparent in one of his early ancestors, the anaptamorphous lemur of the Lower Eocene. In the reproductive system he is about on a par with the higher Artiodactyla, although the male, in the persistent union of the genital and urinary efferent ducts is not so much specialized as some of the latter, where they are distinct. It is an interesting fact that man displays in his dentition strong tendencies to a greater specialization by simplification beyond the ordinary quadrumanous type, by reduction in the number of the true molars and incisors. Thus the $\text{M}.^{\underline{3}}$ is not unfrequently absent in the highest races, and some families display a rudimental condition and absence of the $\text{I}.^{\underline{2}}$.

Much importance attaches to the composition of the molar dentition. Many years ago, Owen[2] called

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[1] This fact was first pointed out by myself in the *Penn Monthly Magazine*, 1875; see *Origin of the Fittest*, p. 268.

[2] *Odontography*, 1840–5, p. 454.

attention to the fact that in the dark races the roots of the last superior molar are distinct from each other, while in the Indo-Europeans they are known to be more or less fused together. These now well-known characteristics of human dentition constitute one of the examples of transition from a simian to a human

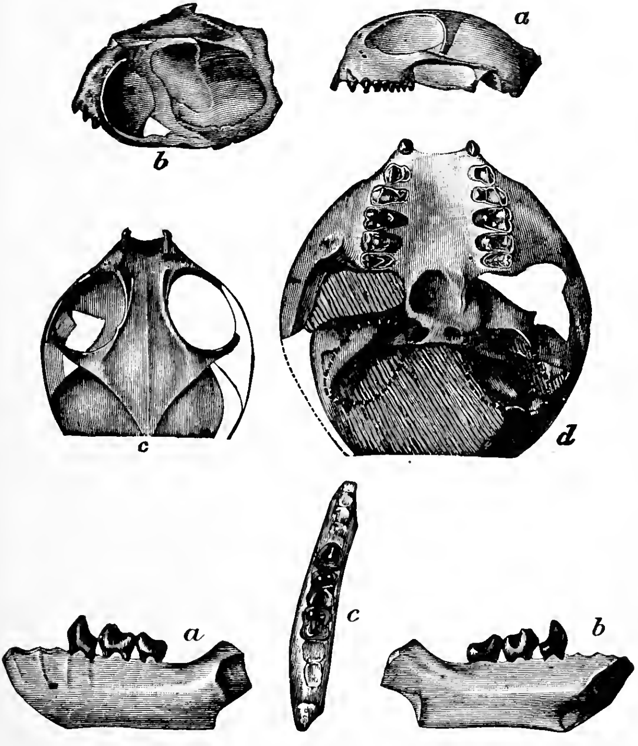

Fig. 38.—Fig *a*, skull of *Anaptomorphus homunculus* Cope, natural size. Fig. *b*, same, oblique view, displaying the large cerebral hemispheres. Fig. *c*, superior view of skull, natural size. Fig. *d*, inferior view, three-halves natural size. Lower figs. *a*, *b*, and *c*, left branch of lower jaw of *Anaptomorphus æmulus* Cope, twice natural size; *a*, from left side; *b*, inner side; *c*, from above.

type. I have pointed out a corresponding modification in the structure of the crown of the superior true molars, viz.: the transition from a quadritubercular to a tritubercular structure in passing from the lower to the higher races. As this point has some interesting implications in the earlier phylogeny of man, and as its value has been disputed, I give it a little attention.

The facts of the case are as follows: I have demonstrated[1] the fact that all forms of dentition exhibited by the eutherian mammals have been derived from a primitive tritubercular type. Professor Osborn says that he expects to be able to do the same for the multituberculate (? Prototherian) dentition. I have also shown that man exhibits a tendency to revert from his primitive quadritubercular molar to this tritubercular type.[2] As to the significance of these facts, I have expressed the view that this acquisition of a tritubercular molar is a reversion to the lemurine type. This conclusion is necessary because the lemurs are the last of the families in the line of the ancestry of man which present this dentition. The monkeys and anthropoid apes are all quadritubercular, except a few limited collateral branches of the former, which still retain the lemurine type. There are also a few collateral types of lemurs which have acquired one or more quadritubercular molars, but they are not typical. In many tritubercular mammals, a precocious form or two can be found, which has acquired the fourth tubercle. But the further back we go in time, the fewer they become, until, in the Puerco fauna, of eighty-two species of

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[1] *Proceeds. Amer. Philos. Soc.*, Dec., 1883; *Origin of the Fittest*, 1887, pp 245, 347, 359.

[2] *American Journal of Morphology*, II., 1883, p. 7.

eutherian mammals, but four have true quadritubercular superior molars.

I take this opportunity of saying, however, that reversion is not necessarily a result of heredity. It may be simply a retrogression on a line of advance already laid down. What influence lemurine heredity may have had in the case of man, it is not easy to know. But it must be borne in mind that various forms of degeneracy of molar teeth are possible other than the resumption of the tritubercular type, yet the normal reduction generally presented is just this lemurine and primitive eutherian condition. The simplicity of the elements involved, has something, but not everything, to do with this reversion.

Dr. Paul Topinard has made an investigation[1] of the characters of the crowns of the molars in man, and has reached general conclusions identical with my own. He remarks (p. 665): "It is demonstrated, in conclusion, that the teeth of man are, at present, in process of transformation, and that in some future which is remote the inferior molars shall certainly be quadricuspid, and the superior molars tricuspid. It will be curious to have the statistics as to prehistoric man; unfortunately, their crania are rare, and their molars generally much worn." In the details of his examination, there are some divergencies from my results. Thus he finds the quadritubercular second and third superior molar relatively of more frequent occurrence in Europeans than I did. But the absence of Europeo-Americans from his tables reduces the percentage of tritubercular in the Indo-Europeans. He makes no report of Esquimaux. Had he observed this type, he would have found a higher per cent. of tritubercular

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2 *L'Anthropologie*, 1892, p. 641 (Nov., Dec.).

upper molars than in any race that he has recorded. He confirms my conclusion as to the high percentage of quadritubercular superior molars in the Malays, Polynesians, and Melanesians.

The relation of this fact to phylogeny is to confirm Haeckel's hypothesis of the lemurine ancestry of man. I have advanced the further hypothesis that the Anthropomorpha (which include man and the anthropoid apes) have been derived directly from the lemurs, without passing through the monkeys proper. This close association of man with the apes, is based on various considerations. One of them is that the skeleton of the anthropoid apes more nearly resembles that of man in the most important respects than it does that of the monkeys. This is especially true of the vertebral column, where the anapophyses are wanting in the Anthropomorpha (insignificant rudiments remaining on one or two vertebræ, as pointed out by Mivart), while they are well developed in the monkeys and lemurs. The molar teeth of the apes and man resemble each other more than either do those of the monkeys, since they lack the crests which connect the cusps, which are general in the latter.

The frequent presence of the tritubercular molar in man suggests the superior claim of the lemurs over the monkeys to the position of ancestor. Another significant fact pointing in the same direction is the existence of large-brained lemurs with a very anthropoid dentition (Anaptomorphidæ) in our Eocene beds, which have the dental formula of man and the Old World monkeys and apes. This resemblance is very remarkable, much exceeding that lately observed by Ameghino in certain extinct forms of monkeys in Patagonia, which appear to be ancestors of the existing South American monkeys (Cebidæ), and possibly of the Old World monkeys also. The superior molars of the Anaptomorphus are tritubercular, while the premolars, canines, and incisors are essentially anthropomorphous, and rather human than simian. Anaptomorphus is probably at the same time the ancestor of the Malaysian lemurine genus Tarsius, and M. Topinard remarks that Tarsius has as good claims to be regarded as ancestral to Homo as Anaptomorphus. But M. Topinard must be aware that in the existing genus the character of the canine and incisive dentition is very unlike that of the Anaptomorphus and Homo. It is specialized in a different direction. The dentition of Anaptomorphus being so generalized as compared with Tarsius, I suspect that its skeleton will be found to present corresponding characters. Of course, if it be found hereafter to have the foot structure of Tarsius (which I do not anticipate), it cannot be included in the ancestry of the Anthropomorpha.

It must be further observed that the ancestral line of the Anthropomorpha cannot be traced through any existing type of Lemuridæ, but through the extinct forms of the Eocene period.[1] This is on account of the peculiar specialization of the inferior canines, which are incisor-like, and because of the peculiar character of the incisors themselves, in the modern lemurs in the restricted sense. But we have numerous lemurine types of the Eocene of both America and Europe which satisfy the conditions exactly, so far as the dentition is concerned. These are mostly referable to the family Adapidæ.

Unfortunately, we do not know the entire skeletons

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[1] *On the Primitive Types of the Orders of the Mammalia Educabilia*, 1873, p. 8.

of these Eocene lemurs, but as far as we have them (genera Tomitherium and Adapis) they are monkey-like. But we have what is almost as useful, the skeleton of their Eocene and Puerco ancestors, the Condylarthra. I long since pointed out that the latter order (not the genus Phenacodus, as Lydekker has represented me as saying) must be the ancestors of the lemurs, basing my views expressly on the general structure of the Phenacodus, Periptychus, and Meniscotherium. The structure of the ungual phalanges of Periptychus is very significant, and even more so is that in Meniscotherium, as recently shown by Marsh,

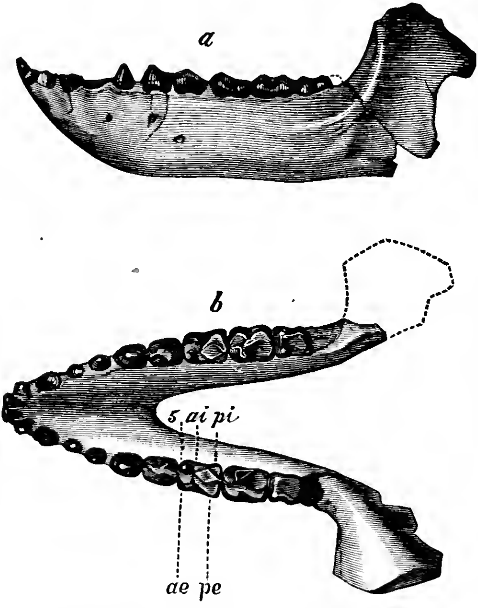

Fig. 39.—*Tomitherium rostratum* Cope, one of the Adapidæ, mandible, natural size; *a*, from left side; *b*, from above. Original, from Report U. S. Geol. Survey Terrs., Vol. III.

who adopts (without credit) my hypothesis of lemurine affinities of the Condylarthra (which he renames the Mesodactyla). From Condylarthra back to Creodonta is an easy transition, and I have always assumed that the Creodonta were derived from generalized polyprotodont Mursupialia. This view has been entirely confirmed by the recent discoveries of Ameghino in Patagonia, where he has found forms whose remains may be referred with equal propriety to the one group or the other. M. Topinard has been rather hasty in reaching the marsupial ancestry in supposing that Phenacodus belongs to that order. All the evidence shows that Phenacodus is a generalized ungulate placental.

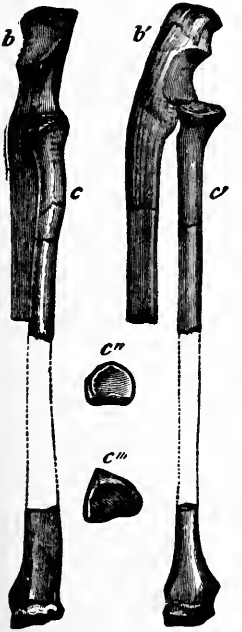

Fig. 40.—*Tomitherium rostratum* Cope, fore arm, five-sixths natural size. Original, *b*, ulna; *c*, radius.

To return to the more immediate ancestry of man. I have expressed,[1] and now maintain as a working hypothesis, that all the Anthropomorpha were descended from the Eocene lemuroids. In my system[2] the Anthropomorpha includes the two families Hominidæ and Simiidæ. The sole difference between these families is seen in the structure of the posterior foot; the Simiidæ having the

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[1] *American Naturalist*, 1885, p. 467.

[2] *Origin of the Fittest*, 1887, p. 346, from *American Naturalist*, 1885, p. 346, where the classification of the Taxeopoda should be in a foot-note; *loc. cit.*, 1889, October.

hallux opposable, while in the Hominidæ the hallux is not opposable. This is not a strong character, since it depends on a slight difference in the form of the entocuneiform bone. In some vertebrates, as the tree-frogs, the same and similar characters (genus Phyllomedusa) are not regarded as of family value. It is then highly probable that Homo is descended from some form of the Anthropomorpha now extinct, and probably unknown at present, although we do not yet know all the characters of some extinct supposed Simiidæ, of which fragments only remain to us. It cannot now be determined whether man and the Simiidæ were both descended from a genus with opposable hallux, or without opposable hallux, or whether from a genus presenting an

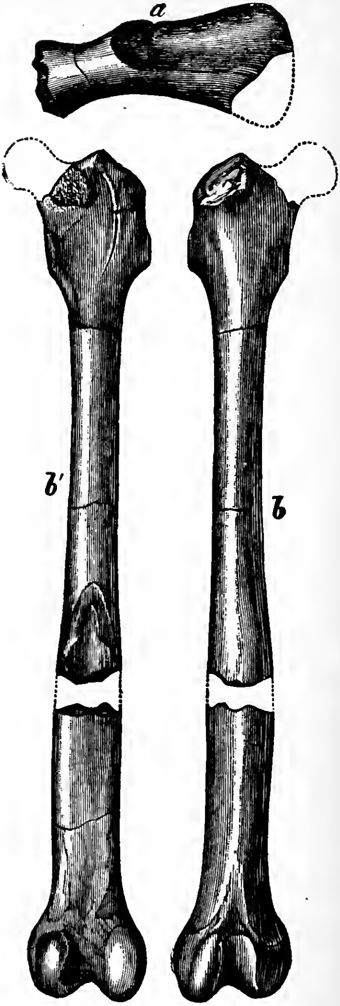

Fig. 41.—*Tomitherium rostratum* Cope, five-sixths natural size; *a*, ilium; *b*, femur. Original.

intermediate character in this respect. This genus was, in any case, distinct from either of the two existing genera of Simiidæ, Simia and Hylobates, since these present varied combinations of anthropoid resemblances and differences, of generic and specific value.

Professor Virchow in a late address[1] has thrown down the gage to the evolutionary anthropologists by asserting that "scientific anthropology begins with living races," adding "that the first step in the construction of the doctrine of transformism will be the explanation of the way the human races have been formed," etc. But the only way of solving the latter problem will be by the discovery of the ancestral races, which are extinct. The ad captandum remarks of the learned professor as to deriving an Aryan from a Negro, etc., remind one of the criticisms directed at the doctrine of evolution when it was first presented to the public, as to a horse never producing a cow, etc. It is well known to Professor Virchow that human races present greater or less approximations to the simian type in various respects. Such are the flat coössified nasal bones of the Bushmen; the quadritubercular molars of the Polynesians; the flat ilia and prognathous jaws of the Negro; the flat shinbones of various races; the divergent hallux of some aborigines of farther India, etc. Professor Virchow states that the Neanderthal man is a diseased subject, but the disease has evidently not destroyed his race characters; and in his address he ignores the important and well-authenticated discovery of the man and woman of Spy. These observations are reinforced by recent discovery of a similar man by DuBois at Trinil

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[1] *Popular Science Monthly*, January, 1893, p. 373, translated.

in the island of Java. To these ancient people I will now devote some space.

What had been long suspected is now established,

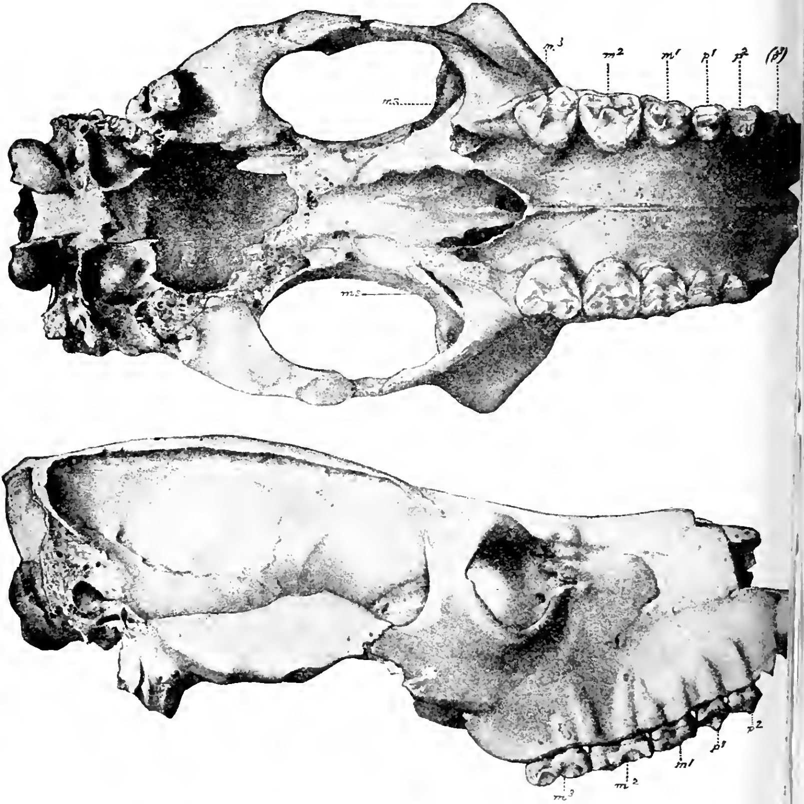

Fig. 42.—*Megaladapis madagascariensis* Forsyth Major, ½ natural size; lemuroid from Pl
tocene bed of Madagascar, with tritubercular superior molars. From Forsyth Major.

through the discovery and descriptions of Messrs. Fraipont and Lohest of Liège; viz. that there dwelt in Europe during Paleolithic times a race of men which possessed a greater number of simioid characteristics than any which has been discovered elsewhere. The important discovery in the grotto of Spy of two skeletons, almost complete, served to unify knowledge of this race, which had previously rested on isolated fragments only. These skeletons proved what had been previously only surmised, that the lower jaws of Naulette, and of Shipka, and probably the skeleton of Neanderthal, belong to one and the same race. The simian characters of these parts of the skeleton are well known. These are the enormous superciliary ridges and glabella; the retreating frontal region; the thickness of the cranial wall; the massive mandibular ramus with rudimentary chin, and the large size of the posterior molars. Messrs. Fraipont and Lohest have added other characters to these, viz.: the tibia shorter than in any other known human race; the sigmoid flexure of the femur; the divergent curvature of the bones of the fore-arm, and most important, a very

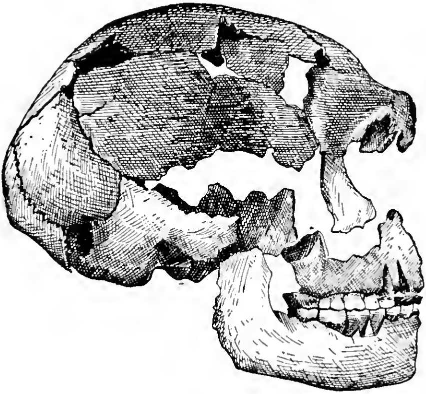

Fig. 43.—Skull of the man of Spy. From Prof. G. F. Wright's *Man and the Glacial Period.* From a photograph.

peculiar form of the posterior face of the mandibular symphysis, already pointed out by Topinard in the jaw of Naulette. On these characters the following remarks may be made.[1]

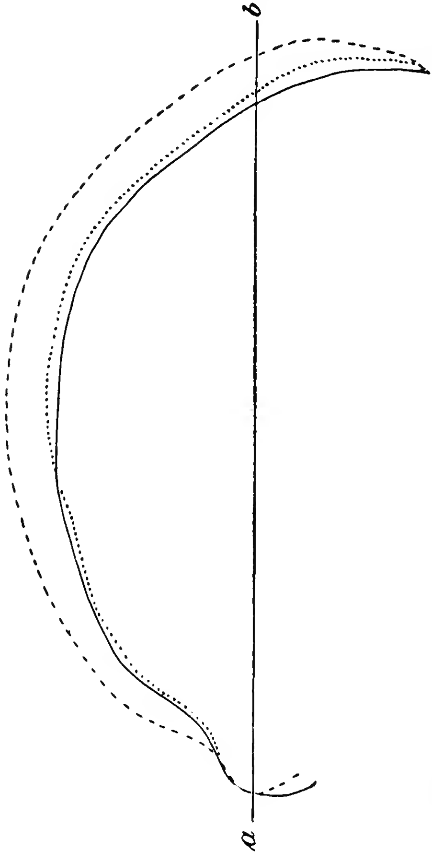

Fig. 44.—Outlines of calvaria; of the Neanderthal man in solid line; of the Spy man No. 1 in dots, and of the Spy man No. 2 in broken line. From Fraipont and Lohest.

I. The prominent superciliary crests, which are

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[1] *Archives Belges de Biologie*, VII., 1886, p. 731, Gand.

characteristic of the Neanderthal race. No existing race presents such a development, neither the Papuans, Australians, nor Negroes of any race. But we find the superciliary crests and underlying sinuses identical in adult female orangs and chimpanzees and young male gorillas. In the female chimpanzees the crests are almost inferior in size to those of the man of Spy.

II. The retreating forehead of the two crania of Spy is not found in any existing human race, while it is typical of that of Neanderthal. It is characteristic of female orangs and gorillas and of the young males of both species, and of adult males and female chimpanzees. It appears in existing men in rare and isolated cases; [probably as survivals].

III. The prominent transverse superior semicircular crest of the occipital bone is found in existing races among the Fellahs of Africa and the Nigritos. It is characteristic of the Neanderthal skulls, and presents exactly the same characters as the young male and female orang and gorilla and young male and adult female of the chimpanzee.

IV. No human race presents the characters of the lower jaw exhibited by those of Spy, Naulette, and Shipka. In this part of their osteology the anthropoids depart widely from man, the most conspicuous point in the latter being the presence of a chin. Accordingly, the angle formed by the anterior face of the symphysis with the inferior border of the horizontal ramus, is less than a right angle in man, and much more than a right angle in the anthropoids. According to Topinard, this angle in fifteen Parisians is 71.4°; in fifteen African Negroes, 82.2°; in fifteen Neocaledonians, 83.9°; in the jaw of Naulette, 94°. In the best preserved jaw of Spy the angle is 107°, if measured from the inferior symphysial border, or 90° if measured from the inferior border of the ramus. There is no chin in the jaw of the Spy race, and the large angle approaches without nearly equaling that of the

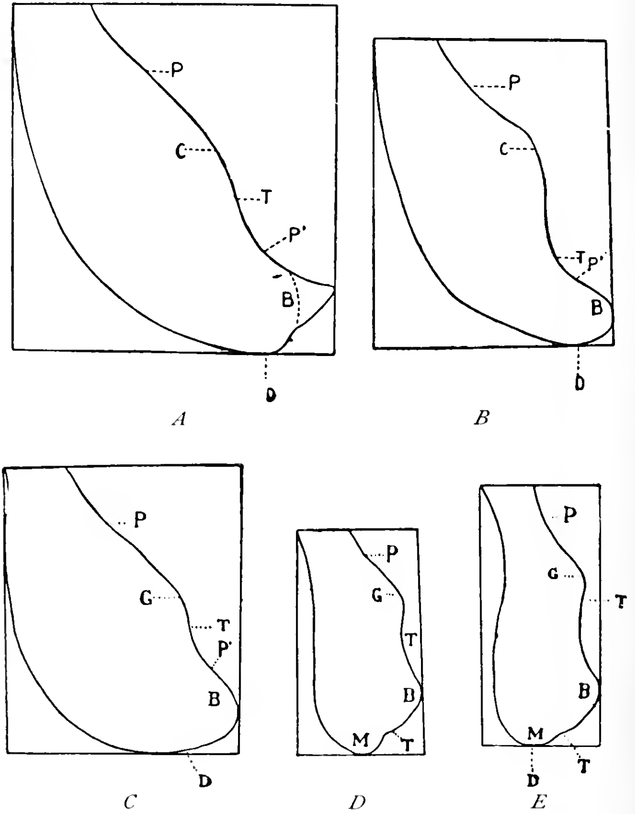

Fig. 45.—Vertical sections of symphysis mandibuli of gorilla (Fig. *A*), and orang (Fig. *B*), of chimpanzee (Fig. *C*), of Spy man No. 1 (Fig. *D*), and Spy man No. 2 (Fig. *E*). From Fraipont and Lohest.

anthropoids. But the posterior face of the symphysis presents the most remarkable peculiarity. In the symphysis of the apes (Fig. 54, *A*, *B*, *C*) the posterior border is a continuous slope from the alveolar border to the inferior margin, interrupted by a slight concavity below the middle. In the human jaw this line slopes backward to near the middle, where are situated the small tuberosities for the insertion of the genioglossal muscles. (B in the accompanying figures.) The surface then slopes rapidly forward to pass into the narrow inferior border of the chin (Fig. 46, *F*, *G*). In the jaws Naulette and Spy the structure is exactly intermediate between the two, and quite different from both (Fig. 45, *D*, *E*). It commences above with a posterior slope similar to that of the apes, exhibiting what is called by Topinard "internal prognathism," as it appears in the lower human races. The surface then descends abruptly, forming a vertical concavity, which is bounded a considerable distance below by another protuberance, the insertion of the genioglossal muscles. This concavity is not present in the human symphysis, while it is less developed in the simian. The surface then slopes forward, as in the human symphysis, but this portion is shorter than in human jaws generally. It is represented by a convex face in the simian jaw. This character, taken in connection with the others cited, goes a long way toward justifying the separation of the Neanderthal race as a distant species, as has been done by some author under the name of *Homo neanderthalensis*. This name is objectionable but must be retained.

To these observations Messrs. Fraipont and Lohest add the following.

V. The curvature of the ulna and radius, which produces a wide interosseous space, is not found in any human race, but is common to the apes. On the contrary, the shortness of these bones is entirely human.

VI. The anterior convexity of the femur, with its round section, is only found among living races among the Nigritos of the Philippine Islands. It is seen in a less degree in femora of Neolithic men, and occasional instances are seen among existing Europeans. It is the normal condition in the apes.

VII. The tibia is shorter in its relation to the femur than in any human race, and is more robust than in most of them. This character, with the oval section, while not identical with what is seen in the apes, forms an approximation to it.

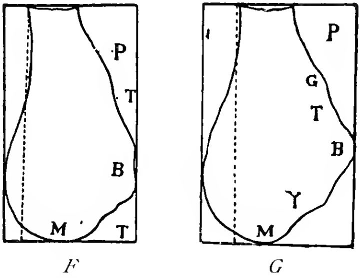

Fig. 46.—Sections of symphysis mandibuli of modern Liègois (Fig. *F*) and of an ancient Parisian (Fig. *G*). From Fraipont and Lohest.

Messrs. Fraipont and Lohest have pointed out the general characters of the dentition of the man of Spy. They show that the molars increase in size posteriorly to the same extent that they do in the apes, which is the reverse of what is usual in man, where they diminish posteriorly, or, in a few lower races (Australians, etc.), remain equal. They show that the superior molars are all quadritubercular, and that the internal root

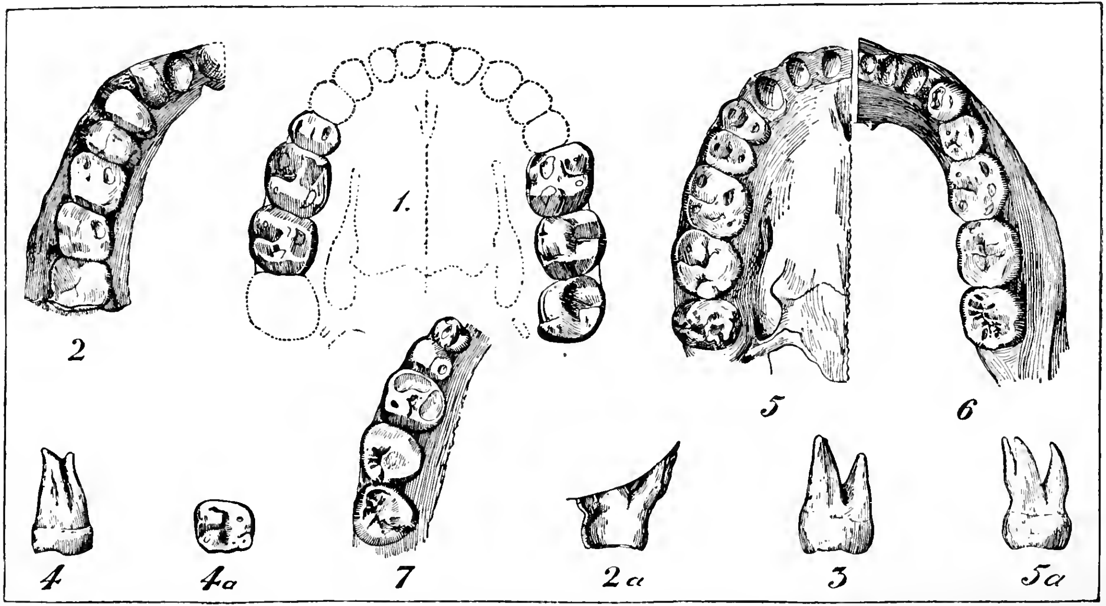

Fig. 47.—Molar teeth of man. 1-2, man and woman of Spy; 3, Maori; 4, Tahitian; 5-6, Fan, 7, Esquimau.

is distinct in all of them. Through the kindness of M. Lohest I received casts and photographs of these teeth, and I give here figures of the former (Fig. 47), which are more satisfactory than those in the memoir from which I have already quoted so fully, where, indeed, the grinding faces are not represented at all.

The figures accompanying[1] show the large size of the last superior molar, which exceeds in its proportions those of the corresponding tooth in the chimpanzee. The fourth tubercle, or hypocone, is especially large. In the male the crowns are more produced posteriorly than in man generally, and remind one of the character seen in the orang. The strong divergence of the internal root of the last molar is shown in No. 2 *a*, and the corresponding character in a Maori and a Fan from tropical Africa is shown in Nos. 3 and 5 *a*. The quadritubercular crown of the last superior molar of a Tahitian is shown in No. 4 *a*; and the roots, which are exceptionally fused nearly as much as in the typical Indo-European, are shown in No. 4.

Dr. Eugene Dubois of the Army of the Netherlands has recently published in Batavia, Java, in a brochure in quarto, an account of some bones of an interesting quadrumanous mammal allied to man, which were found in a sedimentary bed of material of volcanic origin of probably Plistocene age, near a village called Trinil. The remains consist of a calvarium which includes the supraorbital ridges and a part of the occiput; a last superior upper molar, and a femur. The tooth was found close to the skull and belongs probably to the same individual as the latter, while the reference of the femur is more uncertain, as it was found some fifty feet distant.

[1] From *The American Naturalist*, April, 1893.

The characters of the skull are closely similar to those of the men of Neanderthal and of Spy, but the walls are not so thick as those of the former, and more nearly resemble those of the latter. The frontal region is, therefore, much depressed, and it is also much constricted posterior to the postorbital borders. The sutures are obliterated. Dr. Dubois states that the cranial capacity is just double that of the gorilla, and two-thirds that of the lowest normal of man, bridging the gap which has long separated the latter from the apes. Thus the capacity of the former is 500 cubic centimetres, and the latter is 1500 cubic centimetres. In the Java man the capacity is 1000 cubic centimetres. The last upper molar has widely divergent roots, as in apes and inferior races of man, and the crown is large, with the cusps not clearly differentiated, showing a character commonly observed in the lower molars of the gorilla. The femur is long, straight, and entirely human. This discovery of Dr. Dubois adds to our knowledge of the physical characters of the Paleolithic man, and especially to his geographical range.

As regards the proper appellation of this being, Dr. Dubois is not happy. He proposes for him a new genus Pithecanthropus (after Haeckel), and even a new family, Pithecanthropidæ, without having shown that he is not a member of the genus Homo. It is not certain that he is not an individual of the species *Homo neanderthalensis*. His cranial capacity is less, it is true, than that of the man of Spy, but Virchow has pointed out that some of the Nigritos possess a remarkably small cranial capacity, as little as 950 cubic centimetres, and an inhabitant of New Britain only 860 cubic centimetres, a capacity even smaller than that of the man of Trinil. Until we learn the characters of the lower jaw of the latter we shall be in doubt as to whether this individual pertains to the *Homo sapiens* or the *Homo neanderthalensis*.

The characters of the dentition, cranium, and limbs which have been observed in the Paleolithic man, are not without parallel in existing races, though the characters do not generally occur together in the latter. The supposition that all the Paleolithic men so far found are all pathological subjects is not a probable solution of the question, although this type was no doubt subject to pathological conditions such as have been found in the leg-bones of the men of Neanderthal and Trinil. The characters of the symphysis of the lower jaw are quite sufficient to separate the Neanderthal man as a distinct species of the genus Homo.[1] This character is not pathological but it is zoölogical, and places that species between *Homo sapiens* and the apes.

In conclusion, it may be observed that we have in the *Homo neanderthalensis* a greater number of simian characteristics than exist in any of the known races of the *Homo sapiens*, although, so far as known, he belongs to the genus Homo. The posterior foot, so far as preserved, indicates this to be the case. The foot-character, which distinguishes the genera Homo and Simia still remains. There is still, to use the language of Fraipont and Lohest, "an abyss" between the man of Spy and the highest ape; though, from a zoölogical point of view, it is not a wide one.

The flints which were discovered in the stratum of cave deposit containing the human remains, are of the Paleolithic type known as Mousterien in France, which

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[1] This view was first insisted on in an article on the Genealogy of Man in the *American Naturalist*, 1893, p. 331.

are of later origin than the Celléen or older Paleolithic. The older Paleolithic man is not yet known. It is interesting to observe that these flints (Mousterien) are of the same form as the obsidian implements which I collected at Fossil Lake, in Oregon, with the bones of extinct llamas, horses, elephants, sloth, etc. The animals which accompanied the man of Spy are, *Cœlodonta antiquitatis* (wooly rhinoceros), *Equus caballus*, *Cervus elaphus*, *Cervus tarandus*, *Bos primigenius*, *Elephas primigenius*, *Ursus spelæus*, *Meles taxus*, *Hyæna spelæa* ; five extinct and four existing species.

As the evidence now stands, the most primitive and simian of human races inhabited the Old World. No trace of the *Homo neanderthalensis* has been found in America. As, however, Paleolithic implements are found in all continents, we may anticipate that this or some similar species of man will be discovered there also. The genealogy of man may be then represented as follows :

CLASS & BRANCH	ORDER AND FAMILY.	GEOL. SYSTEM
Mammalia	Hominidæ	Plistocene
	Simiidæ	Neocene
	Adapidæ	Eocene
	Condylarthra	Cretaceous
	Creodonta	
	Marsupialia polyprotodontia	Jurassic
	Monotremata	Triassic
Reptilia	Theromora	Carbonic
Batrachia	Batrachia Stegocephali	Carbonic
Pisces	Teleostomi Rhipidopterygia	
	Elasmobranchii Ichthyotomi	
Agnatha	[1]	
Cephalochorda	Leptocardii	
Vermes	[1]	
Cœlenterata	[1]	
Protozoa	[1]	

[1] Subordinate type not specified.

3. THE LAW OF THE UNSPECIALIZED.

The facts cited in the preceding parts of this chapter show that the phylogenetic lines have not been continuous, but that they may be represented by a system of dichotomy. In other words, the point of departure of the progressive lines of one period of time has not been from the terminal types of the lines of preceding ages, but from points farther back in the series. Thus it is not the highly developed or specialized plants which have given origin to the animal kingdom, but the lowest forms or Protophyta, which are not distinguishable from the Protozoa. Among animals it is not the specialized Arthropoda or Mollusca which present the closest affiliations with the Vertebrata, but the simple Vermes or Tunicata, from which the origin of the latter may be traced. In the Vertebrata it is not the higher fishes (Actinopterygia) which offer the closest points of affinity to the succeeding batrachian class, but that more generalized type of the Devonic period, the Rhipidopterygia, which probably occupies that position. The modern types of Batrachia (Urodela, Salientia) have plainly not furnished the starting-point for the reptiles, but the ancient order of the Stegocephali, which are also fish-like, is evidently their source. The Reptilia of the Permian present us with types with fish-like vertebræ (Cotylosauria, Pelycosauria), from which the class Mammalia may be distinctly traced. The later reptiles diverged farther and farther from the mammalian type with the advance of geologic time. The same principle has been found to be true in tracing the history of the subdivisions of the great classes, in the preceding section.

Agassiz and Dana pointed out this fact in taxonomy, and I expressed it as an evolutionary law under the name of the "Doctrine of the Unspecialized." This describes the fact that the highly developed, or specialized types of one geologic period have not been the parents of the types of succeeding periods, but that the descent has been derived from the less specialized of preceding ages. No better example of this law can be found than man himself, who preserves in his general structure the type that was prevalent during the Eocene period, adding thereto his superior brain-structure.

The validity of this law is due to the fact that the specialized types of all periods have been generally incapable of adaptation to the changed conditions which characterized the advent of new periods. Changes of climate and food consequent on disturbances of the earth's crust have rendered existence impossible to many plants and animals, and have rendered life precarious to others. Such changes have been often especially severe in their effects on species of large size, which required food in large quantities. The results have been degeneracy or extinction. On the other hand plants and animals of unspecialized habits have survived. For instance, plants not especially restricted to definite soils, temperatures, or degrees of humidity, would survive changes in these respects better than those that have been so restricted. Animals of omnivorous food-habits would survive where those which required special foods, would die. Species of small size would survive a scarcity of food, while large ones would perish. It is true, as observed by Marsh, that the lines of descent of Mammalia have originated or been continued through forms of small size. The same is true of all other Vertebrata.

It is not to be inferred from the reality of the law of "the unspecialized" that each period has been dependent on the simplest of preceding forms of life for its population. Definite progress has been made, and highly specialized characters have been gradually developed, and have passed successfully through the vicissitudes of geologic revolutions. But these have not been the *most* specialized of their respective ages. They have presented a combination of effective structure with plasticity, which has enabled them to adapt themselves to changed conditions.

In a large number of cases in each geologic age forms have been successful in the struggle for existence through the adoption of some mode of life parasitic on other living beings. Such habits reduce the struggle to a minimum, and the result has been always degeneracy. In other cases it is to be supposed that extremely favorable conditions of food, with absence of enemies, would have occurred, in which the struggle would have been almost nil. Degeneracy would follow this condition also. On the other hand, extreme severity of the struggle cannot have been favorable to propagation and survival, so that here also we have a probable cause of degeneracy. Degeneracy is a fact of evolution, as already remarked, and its character is that of an extreme specialization, which has been, like an overperfection of structure, unfavorable to survival.

In general, then, it has been the "golden mean" of character which has presented the most favorable condition of survival, in the long run.

CHAPTER III.—PARALLELISM.

IT IS now generally recognized that the successive types of organic beings present characters which are traversed in the embryonic life of those which attain the greatest complexity of development, and which occupy the highest places in the scale of life. This fact was observed by the early embryologists, as Von Baer and Agassiz, who did not admit its bearing on the doctrine of evolution. But Darwin and Spencer understood its significance, and Haeckel, Hyatt, and the writer applied it directly to the explanation of phylogeny. At the present time one of the chief aims of the science of embryology is to discover the record of the history of the past, recapitulated in the stages of embryonic life, and to unravel the phylogenesis of plants and animals by this method. The utility of these researches is attested by the results which they have attained, though for obvious reasons, these are not as definite and conclusive as those which are derived from paleontology. The general conclusion is however justified, i. e., that the records of embryology and paleontology are closely similar, and that any discordance between them may be explained on comprehensible principles.

A number of illustrations of the parallelism between taxonomy, ontogeny, and phylogeny may now be given.

1. PARALLELISM IN THE BRACHIOPODA.

For the following abstract I am indebted to Mr. C. E. Beecher of New Haven, whose excellent work in this field is well known.

The parallelism between the ontogeny and phylogeny in the Brachiopoda has been worked out in numerous instances.[1] To illustrate these, some more or less familiar genera may be taken as characteristic examples.

Lingula has been shown by Hall and Clarke (*Pal. New York*, Vol. VIII., 1892) to have had its inception in the Ordovician. In the ontogeny of both recent and fossil forms, the first shelled stage has a straight hinge line, nearly equal in length to the width of the shell. This stage may be correlated with the more ancient genus Paterina from the lowest Cambrian. Subsequent growth produces a form resembling Obolella, a Cambrian and Ordovician genus. Then the linguloid type of structure appears at an adolescent period, and is completed at maturity. Thus, Lingula has ontogenetic stages corresponding to (1) Paterina, (2) Obolella, and (3) Lingula, of which the first two occur as adult forms in geological formations older than any known Lingula.

Paterina represents the radicle of the brachiopods.

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[1] C. E. Beecher, "Development of the Brachiopoda," Part I., Introduction, *Amer. Journ. Sci.*, Vol, XLI., April, 1891; "Development of the Brachiopoda," Part II., Classification of the Stages of Growth and Decline, *Amer. Jour. Sci.*, Vol. XLIV., August, 1892; "Development of Bilobites," *Amer. Jour. Sci.*, Vol. XLII., July, 1891; "Revision of the Families of Loop-bearing Brachiopoda," *Trans. Conn. Acad. Sci.*, Vol. IX., May, 1893.

It shows no separate stages of growth in the shell, is found in the oldest fossiliferous rocks, and corresponds to the embryonic shelled condition (protegulum) of other brachiopods.

The genus Orbiculoidea of the Discinidæ first appears in the Ordovician and continues through the Mesozoic. The early stages in the ontogeny of an individual are as in Lingula, first a paterina stage, followed by an obolella stage. Then from the mechanical conditions of growth a Schizocrania-like stage follows, and completed growth results in Orbiculoidea.

The elongate form of the shell in Lingula, as well as in many other genera, is determined by the length of the pedicle and freedom of motion. The discinoid or discoid of Orbiculoidea and Discinisca among the brachiopods, and Anomia among pelecypods, is determined by the horizontal position of the valves, which are attached to an object of support by a more or less flexible, very short organ, a pedicle or byssus, without calcareous cementation. This mode of growth is characteristic of all the discinoid genera, but, as already shown, the early stages of Paleozoic Orbiculoidea have straight hinge lines and marginal beaks, and in the adult stages of the shell the beaks are usually subcentral and the growth holoperipheral. This adult discinoid form, which originated and was acquired through the conditions of fixation of the animal, has been accelerated in the recent Discinisca, so that it appears in a free-swimming larval stage. Thus, a character acquired in adolescent and adult stages of Paleozoic species through the mechanical conditions of growth, appears by acceleration in larval stages of later forms before the assumption of the condition of fixation which first produced this character.

The two chief subfamilies of the Terebratellidæ undergo complicated series of metamorphoses in their brachial structure. Generic characters are based upon the form and disposition of the brachia and their supports. The highest genera in one subfamily, which is austral in distribution, pass through stages correlated with the adult structure in the genera Gwynia, Cistella, Bouchardia, Megerlina, Magas, Magasell, and Terebratella, and reach their final development in Magellania and Neothyris. The higher genera in another subfamily, boreal in distribution, pass through metamorphoses correlated with the adult structures of Gwynia, Cistella, Platidia, Ismenia, Mühlfeldtia, Terebratalia, and Dallina. The first two stages in both subfamilies are related in the same manner to Gwynia and Cistella. The subsequent stages are different except the last two, so that the Magellania structure is similar in all respects to the Dallina structure, and Terebratella is like Terebratalia. Therefore Magellania and Terebratella are respectively the exact morphological equivalent to, or are in exact parallelism with Dallina and Terebratalia.

The stages of growth of the genera belonging to the two subfamilies Dallininæ and Magellaniinæ are further correlated in the accompanying tables.

The simplest genus Gwynia, as far as known, passes through no brachial metamorphoses, and has the same structure throughout the adolescent period, up to and including the mature condition. In the ontogeny of Cistella the gwyniform stage, through acceleration, has become a larval condition. In Platidia, the cistelliform structure is accelerated to the immature period, and in Ismenia (representing an ismeniform type of structure in the higher genera), the gwyniform and cistelliform stages are larval, and the platidiform represents

MORPHOGENY FROM GWYNIA TO DALLINA.

PERIODS	STAGES	STAGES	STAGES	STAGES	STAGES	STAGES	STAGES
Larval	gwyniform?	gwyniform	gwyniform	gwyniform	gwyniform	gwyniform	gwyniform
				cistelliform	cistelliform	cistelliform	cistelliform
Adolescent	gwyniform	cistelliform	cistelliform	platidiform	platidiform	platidiform	platidiform
					ismeniform	ismeniform	ismeniform
						mühlfeldtiform	mühlfeldtiform
							terebrataliform
Mature	*Gwynia*	*Cistella*	*Platidia*	*Ismenia*	*Mühlfeldtia*	*Terebratalia*	*Dallina*

MORPHOGENY FROM GWYNIA TO MAGELLANIA.

PERIODS	STAGES	STAGES	STAGES	STAGES	STAGES	STAGES	STAGES	STAGES
Larval	gwyniform	gwyniform	gwyniform	gwyniform	gwyniform	gwyniform	gwyniform	gwyniform
				cistelliform	cistelliform	cistelliform	cistelliform	cistelliform
Adolescent	gwyniform	cistelliform	cistelliform	bouchardiform	bouchardiform	bouchardiform	bouchardiform	bouchardiform
					megerliniform	megerliniform	megerliniform	megerliniform
						magadiform	magadiform	magadiform
							magaselliform	magaselliform
								terebratelliform
Mature	*Gwynia*	*Cistella*	*Bouchardia*	*Megerlina*	*Magas*	*Magasella*	*Terebratella*	*Magellania*

an adolescent condition. Similar comparisons may be made in the other genera. Progressively through each series, the adult structure of any genus forms the last immature stage of the next higher, until the highest member in its ontogeny represents serially, in its stages of growth, all the adult structures, with the larval and immature stages of the simpler genera. It is evident that in the identification of specimens belonging to the Terebratellidæ, whether recent or fossil, the strict specific characters must be given first consideration. Species, therefore, must be based upon surface ornaments, form, and color, within certain limits, and genera only upon structural features developed through a definite series of changes, the results of which are permanent in individuals evidently fully adult.

In each line of progression in the Terebratellidæ, the acceleration of the period of reproduction, by the influence of environment, threw off genera which did not go through the complete series of metamorphoses, but are otherwise fully adult, and even may show reversional tendencies due to old age; so that nearly every stage passed through by the higher genera has a fixed representative in a lower genus. Moreover, the lower genera are not merely equivalent to, or in exact parallelism with the early stages of the higher, but they express a permanent type of structure, as far as these genera are concerned, and after reaching maturity do not show a tendency to attain higher phases of development, but thicken the shell and cardinal process, absorb the deltidial plates, and exhibit all the evidences of senility.

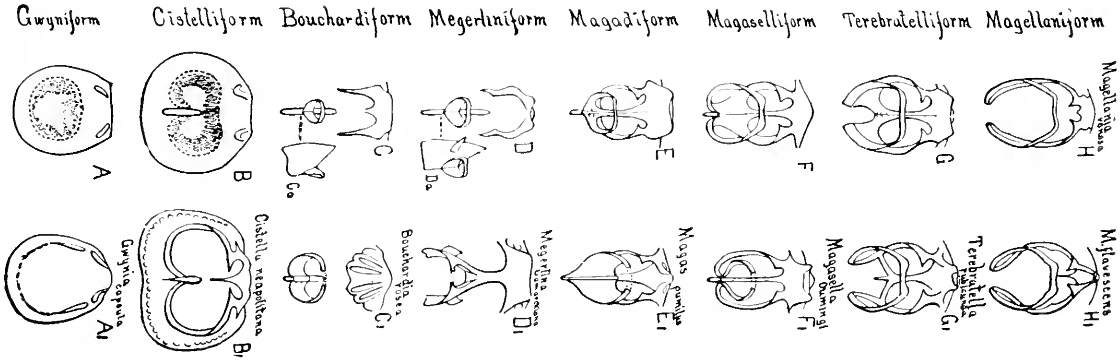

Fig. 48.—Parallelism in Brachiopoda; ontogeny and phylogeny of Magellania. (From Beecher.)

2. PARALLELISM IN THE CEPHALOPODA.

Among Mollusca it is well known that the Cephalopoda form a number of series of remarkable regularity, the advance being, in the first place, in the complication of the folds of the external margins of the septa, and, in the second place, in the degree of involution of one or both extremities of the shell to the spiral ; third, in the position of the siphon.

Alpheus Hyatt, in an important essay on this subject,[1] points out that the less complex forms are in many cases identical with the undeveloped conditions of the more complex. He says : "There is a direct connection between the position of a shell, in the completed cycle of the life of this order, and its own development. Those shells occupying the extremes of the cycle" (in time), "the polar forms, being more embryonic than the intermediate forms. The first epoch of the order is especially the era of rounded, and, in the majority of the species, of unornamented shells with simple septa ; the second is the era of ornamentation, and the septa are steadily complicating ; in the third the complication of the septa, the ornamentation, and the number of species, about twice that of any other epoch, all combine to make it the zenith of development in the order ; the fourth is distinguishable from all the preceding as the era of retrogression in the form, and partially in the septa.

"The four periods of the individual are similarly arranged, and have comparable characteristics. As

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[1] *Memoirs of the Boston Society for Natural History*, 1866, p. 193. Hyatt was followed by Würtenberger in *Ausland*, 1873, who entirely confirmed his conclusions.

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

I am indebted to Professor Hyatt for the following more detailed account of the results of his researches in this interesting field. The evidence as to the nature of evolution derived from the Cephalopoda is more complete than that obtained from any other source.

"Every group of nautiloids passes through, during its evolution in time, either a part or the whole of a certain series of changes. These modifications consist: first, of a straight or nearly straight cone, orthoceran; second, a curved cone, cyrtoceran; third, a coiled cone, gyroceran, which does not come in contact at any point; fourth, a coiled cone, nautilian, which does come in contact at the termination of the first volution and then during further growth remains in about the same condition, all of the internal whorls being visible as in a flat coil of rope; fifth, a coiled cone, involute-nautilian, which also comes in contact like the fourth but then the whorl growing with greater rapidity spreads internally, covering up more or less of the internal volutions sometimes to such an extent that even the centre is concealed from view. The examples which I have myself seen of the fifth kind range from the Silurian to the Nautili of the existing fauna, some being present in every period, and of other kinds, the first, second, and third kinds die out gradually, diminishing in the Devonian and Carboniferous and ultimately ceasing their existence altogether in the Trias. The fourth ceases in the Cretaceous, and the fifth alone survives in the Tertiaries and is still living in the *Nautilus umbilicatus* and *pompilus*, and two other species.

"Wherever found, the young of shells of the fifth kind are at first orthoceran or cyrtoceran like the first and second kind, then gyroceran in curvature like the third class, and then they become more or less rapidly nautilian like the fourth class in succeeding stages. In Silurian, Devonian, and Carboniferous forms this succession is so marked that about all of the young shells of the fifth class may be described as palingenetic, that is as cyrtoceran, gyroceran, nautilian, and then involute-nautilian in their individual or ontogenetic development. In the Trias, Jura, Cretaceous, Tertiary, and present, as the fifth class increases in numbers, there is a decided tendency to shorten and supersede the gyroceran or third stage and introduce the fourth kind or the tendency to spread by growth inwards, at earlier stages.

"The characteristics of the sutures are correlative with these stages of development, and it may be said in a general way, that all other characteristics correlate more or less when studied comparatively in different series with the differences in the curvature and coiling of the whorls. The curvature and amount of involution is therefore the most important single characteristic of the nautiloids, so far as the comparative study of change by evolution is concerned, whether the whole order be considered statistically as above, i. e. with reference to the existence or non-existence of certain forms orthoceran, cyrtoceran, etc., or genetically, i. e. with sole regard to the evolution of distinct series which may be traced from their origin to their termination in time.

"Of these last there are some in every period traceable with more or less completeness by gradations of adults back to orthoceran or cyrtoceran ancestors. Of these series of adults, some pass through only the orthoceran and cyrtoceran modifications, others have the orthoceran, cyrtoceran, gyroceran, and nautilian, but those having the latter and the nautilian-involute are of extreme rarity until the Carboniferous is reached. After this the nautilian shells begin to predominate in every series, ultimately becoming the sole representatives of genetic series.

"Such series are, of course, frequently so closely parallel that it is possible to follow them, and show they are distinct only by means of certain genetic characters, the apertures, the structure of the siphuncle, the sutures and septa, and sometimes, although very rarely, all of these internal characters may show differences peculiar to some one genetic series in which the regular gamut of forms is passed through in the usual succession. Neglect of the comparative study of the stages of development and decline, and of the obvious parallelisms between these and adults of ancestral forms, have caused naturalists, notably Barrande, to make artificial classifications in which about all straight forms, with the exception of some in which the siphuncles were notably distinct to be classed as Orthoceras, most of second kind as Cyrtoceras, most of the third kind as Gyroceras, most of the fourth and fifth kinds as Nautilus.

"To such authors the involute-nautilian forms of the Silurian and the existing fauna were considered to be only specifically distinct, although any prolonged study and comparison of the young would have shown that they were widely separated in development and really only morphic equivalents evolved from entirely distinct ancestors.

"A good example of this is the Eudoceratidæ[1] including the Silurian and Devonian Eudoceras and Tripteroceras, and probably gyroceran form Edaphoceras of the Carboniferous and the close-coiled nautilian shells of Endolobus of the Carboniferous. The peculiar forms of this series and their remarkable sutures enable the observer to follow the line both in the gradations of the adults and by means of the parallelisms of the development.

"Another good series easily distinguished by the remarkable sculpture of the shells is Zittelloceras of the Silurian with cyrtoceran forms, and the gyroceran and nautilian Halloceras of the Devonian.

"One of the best is Thoraceras, a rough spinous cone of the Silurian, Devonian, and Carboniferous, which has straight and cyrtoceran shells; the gyroceran Triboloceras of the Carboniferous, and the nautilian shells of Vestinautilus and its allies in the same period.

"There is no possible explanation of the parallelisms of development of these nautilian shells and the adult stages of others except heredity in the same genetic series. It is useless to waste time in discussion unless the facts are specifically denied after having been properly reëxamined.

"When the ammonoids are taken up, it is easy to demonstrate[2] by the study of the young of the Gonia-

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[1] "Genera of Fossil Cephalopods," *Proc. Bost. Soc. Nat. Hist*,, p. 287.

[2] See "Genera of Fossil Cephalopods," *Proc. Bost. Soc. Nat. Hist.*, XXII., 1883, p. 303.

titinæ that they had straight forms among their ancestors and that these forms have a central siphuncle and suture as among nautiloids. The Devonian Goniatitinæ and some of the Carboniferous forms had also gyroceran forms and loosely coiled nautilian forms, indicating an ancestry with similar cones, but at these stages the siphuncle is invariably ventral as in the adults. The young of all of the Ammonitinæ, however involute the shell may afterwards become, have an invariably straight or curved cyrtoceran cone in the apical part, and when they come in contact by growth, the first whorl or whorls are equally invariably open coils like the coils of the fourth grade in nautiloids. The fifth kind of shell, the involute-nautilian, follows in precisely similar succession to what it does in the ontogeny of nautiloids. Farther than this the degree of involution increases according to the species, with age, and the amount of this involution is often an important part of the specific diagnosis.

"Among Ammonitinæ one finds at once that there are no orthoceran or cyrtoceran shells except among the large group designated by the author as Bactrites. This genus begins early in the Silurian with shells that are not distinguishable from true Orthoceras except by having the siphuncle in adults and later stages close to the venter. Some of these forms have no bulb or protoconch and have a large scar on the apex as in true Orthoceras, others have a calcareous bulb or protoconch on the apex as in true Ammonitinæ. There are also open or gyroceran shells in the adults of the genus Mimoceras which are repeated in the young of Anarcestes and other genera of Goniatitinæ figured in my 'Embryology of Fossil Cephalopods.'[1]

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[1] *Bull. Mus. Comp. Zoöl.*, III.

The shells of the Ammonitinæ, however, are of the fourth and fifth kinds almost exclusively, and in following out the separate genetic series one has to distinguish the progressive gradations by means of the greater or less amount of involution even in the Goniatitinæ of the Devonian and Carboniferous.

"There are also some very remarkable facts showing that the coiling is closer in the Mesozoic than in the Paleozoic forms as a matter of hereditary derivation. The young of the Silurian and Devonian forms have the open, slowly coiling whorls figured by Sandberger and Barrande and repeated by myself as referred to above, but the young of all Mesozoic forms are close coiled so far as known. This is shown in the centre of the umbilicus by the perforation or central opening which is extremely large in most of the Paleozoic Gonititinæ but becomes almost obliterated in the true Ammonitinæ of the Jura.

"In tracing parallels between development of the individual and the series among Ammonitinæ it has been found by Branco and the author, that in ornamented shells the young are first like a nautilus in the sutures, then have a goniatitic stage like the first representatives of the order of ammonoids in the Paleozoic, and that during these stages it is invariably smooth and similar in general form to these same ancestors. After this nepionic stage is passed through the sutures and the characteristics alter with greater or less rapidity, but the stages show decisive parallelisms with the immediate ancestors of the same genetic series. Some of the best examples of palingenetic development of this kind, where the later stages of growth present parallels with proximate ancestors, are cited in my 'Genesis of the Ariëtidæ'[1] and others have been given by Buckman and Würtenburger.

"Some of the most remarkable occur in the least expected quarters. As usual, when one has a true law, it leads him into conclusions that are, perhaps, more surprising to himself than to his readers, or to any subsequent investigator. This was certainly my own case in being led to recognise the perfect examples of parallelisms in retrogressive series. Quenstedt and all students since his time agree that the so-called genera Crioceras, Hamites, Ancyloceras, Baculites, forms that are successively more and more uncoiled until in Baculites they are absolutely straight cones, were derived from normal, close-coiled, involute-nautilian shells of the Ammonitinæ. Their young have been repeatedly shown to be close-coiled and they grade into the normal progressive shells by all of their adult characters.

"The ultimate fact in this demonstration has been added by Dr. Amos Brown in the discovery of a close coiled nepionic stage in the straight Baculites of the Cretaceous, the only form whose development had not been ascertained and whose exact relations had not been determined.

"It is now admitted by all students of Ammonitinæ that these retrogressive groups are not true genera; but that as first demonstrated by Quenstedt, Baculites, Crioceras, etc., are retrogressive stages in the evolution of distinct genetic series and that they do not exist as natural groups of species. In other words, different genetic series of the Ammonitinæ die out by passing through a series of modifications which are parallel and which are just the reverse of the parallel

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[1] *Smithson. Contrib.*, 673, p. 41 et seq.

series of the orthoceran, cyrtoceran, gyroceran shells with which each distinct complete genetic series of nautiloids arose in time.

"While the nautiloids coil up in their progressive evolution and the Ammonitinæ increase this coiling up tendency in the primitive and progressive forms of each genetic series, the latter in becoming retrogressive reverse the processes of progressive evolution. They become more and more uncoiled, each complete retrogressive series ending with a straight cone. All other characters correlate with this uncoiling and in a general way may be said to degenerate in greater or less proportion to the amount of the uncoiling. To make this extraordinary picture complete it is only necessary to add that these retrogressive series followed out to their ultimate development are distinctly parallel with changes or stages of modification taking place in the senile stages of individuals of the same genetic group.

"In old age the highly ornamented shell gradually parts with its spines and other ornaments, the whorls slowly diminish, the involution decreases and eventually in extreme age it becomes separated from the spiral and completely rounded and smooth. The aperture becomes correlatively modified, and also the sutures. If an old ammonite could have its life prolonged, it would become Baculites, and the full-grown part of the shell would, in some forms of Lytoceratinæ be very similar to the minute nepionic shell of the Baculites as described and figured by Dr. Brown. If now the coiled adult part of this imaginary shell were broken off and lost, the straight senile fragment would be referred to the old genus Baculites. The morphic characters of the gerontic or old-age stage of ontogeny are therefore parallel with the forms evolved in the paraplastic or retrogressive stage of evolution of the phylum. In other words, the morphic modifications which may occur as permanent, specific, and generic characters in the adults of retrogressive descendants of any progressive individuals may be predicted from the study of the similar changes that take place in the senile stages of the progressive individuals. As it has been stated by the writer on several occasions, the embryonic, nepionic, and later stages of development up to the adult repeat with greater or less clearness in proportion to their removal in time and organization from the point of the origin of the genetic group to which they belong the permanent characteristic of their ancestors; the adult gives the existing essential differentials acquired by its own species, genus, and group, being the index according to the time of its occurrence of the progression or retrogression of its group; the old, in its invariably retrogressive course, indicates the path that must be followed by degraded series after the acme of the group to which the individual belongs has been reached. This, of course, is a generalized statement of the correlations of the ontogenic cycle and the phylocycle when they occur as in the Ammonitinæ, but it will be found eventually that this law is true of all animals to some degree. It is obvious from all past experience that every law of correlation of structures cannot be true in any one group without being found more or less in all organisms. I have therefore ventured upon the basis of this and Beecher's, Clarke's, and Schuchert's researches among Brachiopoda, corals, and trilobites, Dr. Jackson's among pelecypods, and after the confirmations by the independent researches of Würtenburger and Buckman among Ammonitinæ, and those of Bather among crinoids, to designate the complete study of the correlations of the ontocycle and phylocycle as Bioplastology. Bioplastology is easily separable from the study of growth, and from that of heredity, for which last I have proposed the term Genesiology,[1] and from that of Ctetology or the study of the origin of acquired characteristics. By properly defining these different branches of research it is practicable to see that bioplastology includes the results of the action of growth, the laws of growth, as well as those of genesiology and ctetology, but has a field entirely distinct from all of these in so far as it deals essentially with the study of parallelism in all its phases."

The parallelism of the gyroceras with an early stage of all coiled Cephalopoda is represented in Fig. 119 page 410, as illustrative of the inheritance of an acquired character.

3. PARALLELISM IN THE VERTEBRATA.

Parallels between the ontogeny and phylogeny are well known in the Vertebrata. The primary relations of the Vertebrata are discernible in the successive types of structure of the nervous system, and of the skeleton, but most clearly in those presented by the circulatory system. It is well known that the central organ—the heart, is, in the amphioxus, a straight tube. In the next higher group, the Marsipobranchii (lampreys), it is a bent tube, with a constriction which divides it into two chambers. In the Pisces (fishes) the heart is composed of two chambers related to each other in a reversed longitudinal direction. In the Ba-

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[1] See *Proceedings of the Boston Society of Natural History*, 1893, p. 59.

trachia and Reptilia the cephalad (auricular) division is divided into two chambers by a septum; while in the birds and Mammalia the caudad division (ventricle) is also so divided, making four chambers in all.

The sources of the great vessels which distribute the blood to the body and return it to the heart, display the same successional relation of types. In the Acrania (amphioxus), the Marsipobranchii, and most of the fishes, the vessel (truncus communis) which receives the blood from the central organ, gives off several branches on each side, which are distributed to skeletal bars or arches which are in immediate contact with water, which aerates the blood. They then return, and, first sending the carotids anteriorly, unite dorsad to the heart, and form the aorta posteriorly. In the Batrachia, where aerial respiration succeeds to an aquatic one during the life of the animal, the number of the vessels contributing to form the aorta is reduced from five to three in the sucessive types. One of the arches is aborted as an arch, and sends the circulating fluid to the modified swim-bladder of the fish, or lung, where it is aerated. This aerated blood is returned to the heart with non-aerated blood from other organs, and the mixture is sent throughout the body. In the reptiles we have essentially the same system, but the aorta-origins are reduced to two, and one, on each side. Next a division of the truncus communis ensues, which corresponds functionally with that in the ventricle, so that the impure blood from one auricle is sent into the ventricle (right) which communicates with the lung; and the aerated blood is then returned to the other auricle, which pours its contents into the left auricle, which drives it into the aorta, and thus throughout the body. Thus pure or

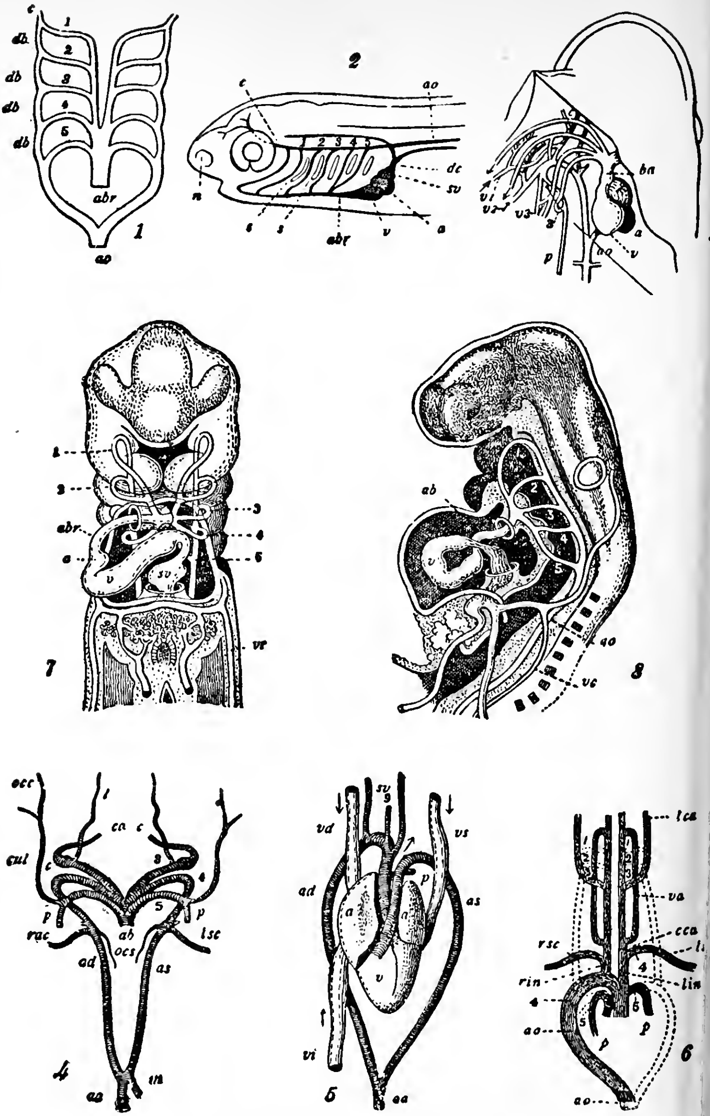

Fig. 49.—Circulatory systems; 1–2, fish; 3–4, batrachian; 5, reptile; 6, bird; from Gegenbaur. Figs. 7–8, human fœtus, from His.

aerated blood is distributed to the organs, and all but one of the old roots of the aorta have ceased to function as such.

This evolutionary succession is preserved with much fidelity in the ontogeny of the respective classes of Vertebrata. The representatives of each class pass through the stages which are permanent in the classes below them in the series. The Mammalia, as the highest class, pass through all the stages. (Fig. 49.) This series coincides also with phylogenetic succession. The order of appearance in time of the Vertebrata is, first Agnatha, then Pisces, Batrachia, Reptilia, and Mammalia.

In all the details of structure the same relation may be observed. Referring to the illustrations of phylogeny and variation of character described in the preceding pages, many of the characters definitive of natural divisions have been observed to appear in the course of the embryonic life of those types which possess them. Those of greater systematic significance appear earlier, and those of less importance in a taxonomic sense, later. I select some illustrations of this principle.

I have shown that the primitive type of superior molar in the placental Mammalia is tritubercular, the fourth tubercle being added internally and posteriorly in the later forms. Dr. Taeker has recently observed that in the development of the superior molars in the horse, at an early stage the crown is tritubercular, and that the fourth cusp or hypocone is subsequently added, as in the phylogenetic history. As the horse presents the most complex molar among Mammalia, this survival of the record is interesting.

In the Artiodactyla and Edentata which lack superior incisor teeth, rudiments of them can be found in the early stages. We now know early extinct forms of both of these types where these teeth are permanent throughout life. In the toothless whalebone whales the same phenomenon has been observed.

It is well known that the highest deer (Cervidæ) add an antler to the simple spike horn in the third year, and an additional antler with each successive year for several years. Also they develop a basal snag of the antler (see Cuvier, *Ossem. Fossiles* ; Gray, *Catal. Brit. Mus.*) at the third year. Now a majority of those of the New World (genera Cariacus, Coassus) never develop it except in "abnormal" cases in the most vigorous maturity of the most northern Cariacus (*C. virginianus*); while the South American Coassus retains to adult age the simple horn of the second year of Cervus.

Among the higher Cervidæ, Rusa and Axis never assume characters beyond an equivalent of the fourth year of Cervus. In Dama the characters are on the other hand assumed more rapidly than in Cervus, its third year corresponding to the fourth of the latter, and the development in after years of a broad plate of bone, with points, being substituted for the addition of the corresponding snags, thus commencing another series.

Returning to the American deer, we have Blastocerus, whose antlers are identical with those of the fourth year of Cariacus.

The oldest known deer (Palæomeryx) have no horns, or they are undivided.

Among Batrachia excellent illustrations are furnished by the two series of Salientia, the Arcifera and the Firmisternia.

The firmisternial structure is a modification of the arciferous, which comes later in the history of growth, and probably also in geological time. During the early stages the Firmisternia have the movable shoulder girdle which characterizes those of the arciferous division, the consolidation constituting a modification superadded in attaining maturity. Furthermore, young Salientia are toothless, and one section of the species of Arcifera never acquire teeth. In these (the Bu-

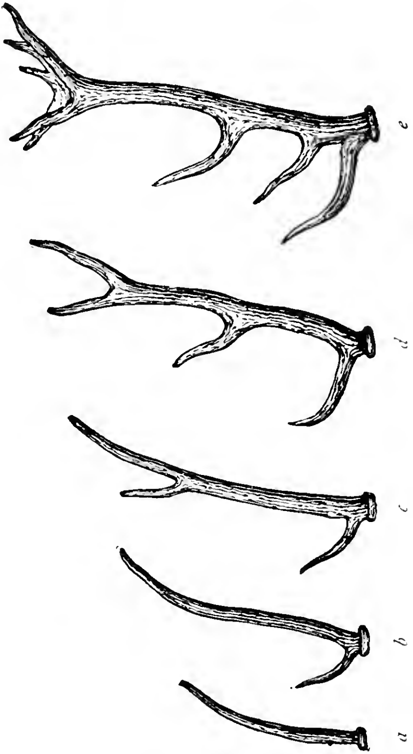

Fig. 50.—Succession of horns of *Cervus elaphus* L. from Gaudry. *a*, second year represented by permanent horn of Coassus; *b*, third year represented by permanent horn of Furcifer; *c*, fourth year represented by permanent horn of Rusa; *d*, fifth year; *e*, sixth year.

fonidæ) we have a group which is imperfect in two points instead of one.

The genera of these salientian suborders exhibited on a preceding page as forming indentical series in five different families (pp. 66–67) are related to each other as developmental stages in the history of the genera that attain the extreme development on each line. For example we select the family Hylidæ of which the terminal genus is Trachycephalus. Nearly allied to it is the genus Osteocephalus, which differs in the normal exostosis of the cranium not involving the derm, as it does in the former. Close to this is Scytopis, where the fully ossified cranium is not covered by an exostosis. Next below Scytopis is Hyla, where the upper surface of the cranium is not ossified at all, but is a membranous roof over a great fontanelle. Still more imperfect is Hylella, which differs from Hyla in the absence of vomerine teeth. Now, the genus Trachycephalus, after losing its tail and branchiæ, possesses

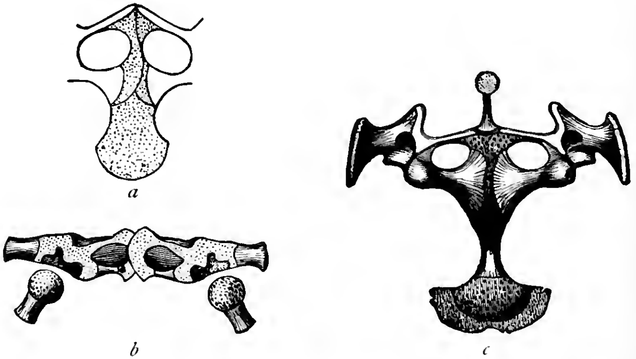

Fig. 51.—Shoulder girdles of Anura ; *a*, of the arciferous type (*Phyllomedusa bicolor*) ; *b*, *Rana temporaria*, tadpole with budding limbs; *c*, do., adult, firmisternial type ; *b* and *c* from Parker.

all the characters possessed by the genera Hylella and Hyla, either at or just before the mature state of the latter, as the ethmoid bone is not always ossified in advance of the parietals. It soon, however, becomes a Scytopis, next an Osteocephalus, and finally a Trachycephalus. It belongs successively to these genera, for an exhaustive anatomical examination has failed to reveal any characters by which, during these stages, it could be distinguished from these genera. The same succession in development of the genera of the other families is well known, the genus Otaspis of the Bufonidæ attaining a point beyond any of the others, in the enclosure of its membranum tympani posteriorly by dermoössification.

Finally reaching in our review the relations of specific characters, the readers will call to mind that the species of the lacertilian genus Cnemidophorus (page 41) are either striped, spotted, or cross-banded, and that the *Lacerta muralis* agrees with them in this respect. It was also shown that the young of all the species are striped, and that the cross-banded forms pass through not only a striped, but an intermediate spotted stage, before attaining the adult coloration.

The young of spotted salamanders are without spots (genera Amblystoma and Salamandra e g.) ; so that unspotted species resemble the young of the spotted. In many species of birds of more or less uniform patterns of coloration, the young are spotted. In some of these the females remain spotted throughout adult life. In some other species both sexes retain the spotted coloration of the young. The young of most deer are spotted. In the fallow-deer (Axis) the adults retain the spotted coloration, thus resembling the young of most of the species.

3. INEXACT PARALLELISM OR CÆNOGENY.

When the early or transitional stage of a higher form is exactly the same as a permanent lower form, the parallelism is said to be "exact." Such is the relation of a *Cnemidophorus gularis scalaris* to a *Cnemidophorus gularis gularis* as to color characters ; and of an *Amblystoma tigrinum* to a permanent breeding *Siredon lichenoides* in characters of higher structural value.

When the transitional stage of the higher only resembles the lower form in some one or more features, but not in all, the parallelism is said to be "inexact." It is evident that "exact parallelism" can only exist between ancestor and descendant in the same restricted line, and can be therefore only demonstrated in the case of the nearest relatives, between which a perfect phylogeny is known. So soon as new subordinate characters are assumed, or a change in the order of appearance of characters supervenes, the parallelism becomes "inexact," and such is the kind of parallelism usually observed. And it is more inexact the more widely removed in relationship are the forms compared. Thus the parallelism between the embryo man with five branchial slits, and the adult shark, is very inexact ; but that between a true fish and a shark is much less inexact. That between a higher and a lower shark is still more exact, and so on. Exact parallelism in growth is called by Haeckel palingenesis or palingeny. The growth which has, through changes introduced subsequent to the origin of a line of descent, become inexact, or "falsified," is termed by the same author cænogenesis or cænogeny.

The superposition of characters which constitutes evolution, means that more numerous characters are possessed by the higher than the lower types. This involves a greater number of changes during the ontogenetic growth of each individual of the higher type. In other words, characters acquired during the phylogenetic history are continually assumed by the progressive form at earlier and earlier periods of life. This process has been metaphorically termed by Professor Alpheus Hyatt and myself "acceleration." All progressive organic evolution is by acceleration, as here described. Retrogressive evolution may be accomplished by a retardation in the rate of growth of the taxonomic characters, so that instead of adding, and accumulating them, those already possessed are gradually dropped; the adults repeating in a reversed order the progressive series, and approaching more and more the primitive embryonic stages. This process I have termed "retardation." Retardation is not however, always exact, even in retracing a true phylogenetic line, whence in such instances the process may not be correctly described as retardation. Professor Hyatt has applied to such types the term "senile," and gerontic; and to the resulting condition, the term "senility." His observations on this subject have been made on Mollusca, and principally on the Cephalopoda, and are of fundamental importance in this connection.

The history of a type which has passed through a full cycle of life, from its earliest appearance to its extinction, is divided by Haeckel into three stages, viz.: those of its rise; full vigor, as displayed by predominance of variations and numbers; and decadence. For these stages he uses the expressions Anaplasis, Metaplasis, and Cataplasis. For the processes which bring about the first and last of these conditions, Professor Hyatt has used the terms Anagenesis and Catagenesis. Catagenesis is equivalent to degeneracy and has played an important part in organic evolution. I had used the term previously to Professor Hyatt for the same process, but with a wider application; extending its use to inorganic nature as well.[1] (See Chapter IV. of this book.)

Embryology has, however, revealed another series of phenomena which in many instances obscure the simplicity of the problem of ontogeny as presented in the preceding pages. It was the merit of Haeckel to generalize from the facts brought to light by this science, so as to present the relations which subsist between the primitive stages of all multicellular animals. This is known as the Gastræa theory. He showed that the primitive gastric cavity of all such animals is produced by an invagination of a portion of the surface of a primitive sphere or morula, which results from the segmentation of the oösperm. This hollow half-sphere he termed the gastrula, and the theoretical primitive animal which corresponds to it he called the Gastræa. Marine animals very similar to this Gastræa have been discovered. Haeckel showed, however, that gastrulas are not all alike, since they differ in the extent to which the segmentation of the oösperm may be carried, and the rate of segmentation of different parts of it. Thus early do inexact parallelisms arise. From this point onwards special peculiarities of the various developmental lines appear, some of which have especial reference to the necessities of embryonic life. Hence the trochosphere stage of so many

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[1] *Origin of the Fittest*, p. 422.

invertebrate forms, and the nauplius and zoæa of the Crustacea.

Such are the statoblasts which are resting-stages for the embryos of fresh-water sponges and Polyzoa, and the glochidia of the Unionidæ, which are wanting in the marine forms of the same orders. Such are the amnion and allantois of certain Vertebrata and the placenta of certain Mammalia, which have no reference to any structures but their own residua, found in the adults of those animals.

A remarkable instance of this state of things appears in the history of the evolution of the insects. It is quite impossible to understand this history without believing that the larval and pupal states of the highest insects are the results of a process of degeneracy which has affected the middle periods of growth, but not the mature results. The earliest insects are the Orthoptera, which have active aggressive larvæ and pupæ, undergoing the least changes in their metamorphosis (Ametabola), and never getting beyond the primitive mandibulate condition at the end. The metamorphosis of the jawed Neuroptera is little more marked, and they are one of the oldest orders.

The highest orders with jaws undergo a marked metamorphosis (Coleoptera, Hymenoptera), the Hymenoptera even requiring artificial intervention in some instances to make it successful. Finally, the most specialized orders, the suctorial Diptera and Lepidoptera, especially the latter, present us with very unprotected more or less parasitic larval stages, both active and inactive. These animals have evidently degenerated, but not so as to prevent their completing a metamorphosis necessary for purposes of reproduction. As is well known, many imagines (Saturniidæ, Œstridæ) can perform no other function, and soon die, while in some Diptera the incomplete larvæ themselves reproduce, so that the metamorphosis is never completed.

This history is parallel to that proposed by Dohrn to account for the origin of the Ammocœtes larval stage of the Marsipobranchii. He supposes this form to be more degenerate than the corresponding stage of its probable ancestral type in the ancestral line of the Vertebrata. An inactive life in mud is supposed by Dohrn to have been the effective cause. An inactive life on the leaves of plants, or in dead carcases, has probably been the cause of the same phenomenon in the Lepidoptera and Diptera.

Thus we have developed an ontogeny within an ontogeny, and a phylogeny within a phylogeny. These facts do not, however, affect the general result in the least. They only show us that the persistent larvæ of those animals which possess them, have a history of their own, subject to the same laws of evolution as the adults. It results that in many cases the phylogeny can only be determined by the discovery and investigation of the ancestors themselves, as they are preserved in the crust of the earth. In all cases this discovery confirms and establishes such definite conclusions as may be derived from embryology. It is also clear that on the discovery of phylogenetic series it becomes at once possible to determine the nature of defective types. It becomes possible to ascertain whether their rudimental parts represent the beginnings of organs, or whether they are the result of a process of degeneration of organs once well developed.

An excellent illustration of inexact parallelism is to be found on comparison of man with the lower Vertebrata. I have pointed out[1] that in the structure of his extremities and dentition, he agrees with the type of Mammalia prevalent during the Eocene period (cfr. Phenacodus). Hence in these respects he resembles the immature stages of those mammals which have undergone special modifications of limbs and extremities, such as Ungulata in which cænogeny has not obliterated the early stages from the embryonic record. These forms are probably extinct. I have also shown[2] that in the shape of his head man resembles the embryos of all Vertebrata, in the protuberant forehead, and vertical face and jaws. In this part of the structure most Vertebrata have grown farther from the embryonic type than has man, so that the human face may be truly said to be the result of a process of retardation. Nevertheless, in the structure of his nervous, circulatory, and for the most part, of his reproductive system, man stands at the summit of the Vertebrata. It is in those parts of his structure that are necessary to supremacy by force of body only, that man is retarded and embryonic.

5. OBJECTIONS TO THE DOCTRINE OF PARALLELISM.

An objection to the theory of parallelism in its full sense has been recently put forward by Mr. C. Herbert Hurst.[3] He says, "My object now is to show that in neither case can a record of the variation at any one stage of evolution be preserved in the ontogeny, much less can the ontogeny come to be a series of

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[1] "The Relation of Man to the Tertiary Mammalia," *Penn Monthly*, 1875; *Origin of the Fittest*, 268.

[2] "The Developmental Significance of Human Physiognomy," *American Naturalist*, June, 1883; *Origin of the Fittest*, 1887, p. 281.

[3] *Natural Science*, 1893, p. 195.

stages representing in proper chronological order some of the stages of adult structure which have been passed through in the course of evolution." Again: "The early stages of the fish embryo are very like those of the bird embryo. These two do correspond to each other. The statement that the embryonic structure of a bird follows a course which is from beginning to end roughly parallel with, but somewhat divergent from, the course followed by a fish, is borne out by the actual facts. A bird does not develop into a fish and then into a reptile, and then into a bird. There is no fish-stage, no reptile-stage, in its ontogeny. The adult resembles an adult fish only very remotely. Every earlier stage resembles the corresponding earlier stage of the fish more closely. There is a parallelism between the two ontogenies. *There is no parallelism between the ontogeny and the phylogeny of either a bird or any other animal whatever.* A seeming parallelism will fall through when closely examined." "The promise that this theory gave of serving as the guide to knowledge of past history without the labor involved in paleontological research, was indeed tempting: and where the royal road to learning has been shown by it, it is not surprising that some zoölogists should have entered for the race along this road. To what goal that road has led may be learned by a comparison of the numerous theories as to the ancestry of the 'Chordata' which have been put forward by those who have adopted the theory without enquiring as to its validity."

I have made this quotation as showing the point of view from which the doctrine of parallelism when incorrectly stated may be assailed. There is truth in the author's accusation that embryologists who have not used their results with proper caution, have been frequently led to incorrect and even absurd results. The errors of this class of biologists are mainly due to their ignorance of species in the adult state, and their ignorance of systematic biology or taxonomy. They profess to regard this branch of the science as only suitable for beginners, and as comparatively unimportant, as compared with their own; yet one might as well attempt the study of philology without a knowledge of alphabets, as to study phylogeny without the knowledge of natural taxonomy. The correct discrimination of species, genera, etc., imposes much greater burdens on the faculty of judgment, than does anything to be found in any science which includes observation and record only. But Mr. Hurst's statement is somewhat overdrawn, and he does not give embryologists the credit which is due to their theory of recapitulation. I think he will find the following, which I wrote in 1872[1] to be a correct statement of the facts, and a fair induction as to principles.

"The smaller the number of structural characters which separate two species when adult, the more nearly will the less complete of the series be identical with an incomplete stage of the higher species. As we compare species which are more and more different, the more necessarily must we confine the assertion of parallelism to single parts of the animals, and less to the whole animal. When we reach species as far removed as man and a shark, which are separated by the extent of the series of vertebrated animals, we can only say that the infant man is identical in its numerous origins of the arteries from the heart, and in the cartilaginous skeletal tissue, with the class of

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[1] *Penn Monthly*, 1872. *Origin of the Fittest*, 1887, p. 8.

sharks, and in but few other respects. But the importance of this consideration must be seen from the fact that it is *on single characters of this kind that the divisions of the zoölogist depend.* Hence we can say truly that one order is identical with an incomplete stage of another order, though the species of the one may never at the present time bear the same relation in their entirety to the species of the other. Still more frequently can we say that such a genus is the same in character as a stage passed by the next higher genus; but when we can say this of species, it is because their distinction is almost gone. It will then depend on the opinion of the naturalist as to whether the repressed characters are permanent or not. Parallelism is then reduced to this definition: that each separate character of every kind, which we find in a species, represents a more or less complete stage of the fullest growth of which the character appears to be capable. In proportion as those characters in one species are contrasted with those of another by reason of their number, by so much must we confine our comparison to the characters alone, and the divisions they represent; but when the contrast is reduced by reason of the fewness of differing characters, so much the more truly can we say that the one species is really a suppressed or incomplete form of the other The denial of this principle by the authorities cited has been in consequence of this relation having been assigned to orders and classes, when the statement should have been confined *to single characters,* and divisions characterized by them. There seems, however, to have been a want of exercise of the classifying quality or power of 'abstraction' of the mind on the part of the objectors."

It is nevertheless true that the records brought to light by embryologists are very imperfect, and have to be carefully interpreted in order to furnish reliable evidence as to the phylogeny of the species examined. An illustration of this is the fact that the species characters appear in many embryos before those which define the order or the family, although it is certain that the latter appeared first in the order of time. Most of the important conclusions as to the phylogeny of Vertebrata demonstrated by paleontology have never been observed by embryologists in the records of the species studied by them. Thus I have shown that it is certain that in the amniote vertebrates the intercentrum of the vertebral column has been replaced by the centrum; yet no evidence of this fact has been observed by an embryologist. If we could study the embryonic development of the vertebral column of the Permian and Triassic Reptilia, the transition would be observed, but in recent forms cænogeny has progressed so far that no trace of the stage where the intercentrum existed can be found.

Again I have demonstrated by paleontological evidence that the lines of the ungulate Mammalia originated from a bunodont pentadactyle plantigrade ancestor; but embryonic research has failed to discover the preservation of a record of this fact in the ungulates at present existing. The embryo of the horse is not pentadactyle, nor even tridactyle, although tridactyle horses persisted late in geologic time. Nor has embryonic research demonstrated a four-toed stage in the Bovidæ (oxen, etc.), although there is no doubt that they descended directly from an ancestor so characterized. Any number of similar cases might be cited to show the prevalence of inexact parallelism or cænogeny. If we could study the embryology of the many extinct forms of life, the missing stages would all be found, but as we have not the opportunity of pursuing this important research, we have to rely on paleontology for our phylogeny. Paleontology is and always will be imperfect, but all that we get is palingeny, or the phylogeny itself, and not an inverted and distorted record of it.

CHAPTER IV.—CATAGENESIS.

WE HAVE been principally occupied so far with progressive evolution or anagenesis. Reference has, however, been made to retrogressive evolution or degeneracy, in Chapter III., in describing the evolution of the Vertebrata, and will be in Chapter V., under the caption "Disuse in Mammalia." Degeneracy has, however, played a more important part in creation than would be suspected from these references, and I propose in the present chapter to go more fully into its phenomena, which, in the broadest sense, I have called collectively Catagenesis.

As evidence for degeneracy as a factor in evolution we naturally appeal first to examples in the life histories of plants and animals which are known to us; and then examine the records of the past, in the light thus gained, for evidence of degeneracy in vegetable and animal phylogeny. In both directions we are met by an *embarras de richesse*, and a few conspicuous cases will have to suffice.

The parasitic copepod Crustacea undergo a retrograde metamorphosis, which commences at different periods of the growth history of different genera. Says Claus: "Many parasitic Copepoda, however, pass over the series of nauplius forms [which are traversed by other copepods] and the larva, as soon as hatched, undergoes a moult, and appears at once in the youngest Cyclops form with antennæ adapted for adhering, and mouth-parts for piercing. From this stage they undergo a retrogressive metamorphosis, in which they become attached to a host, lose more or less completely the segmentation of the body, which grows irregular in shape, cast off their swimming feet, and even lose the eye, which was originally present (*Lernæapoda*). The males, however, in such cases often remain small and dwarfed, and adhere, frequently more than one, firmly to the body of the female in the region of the genital opening. In the *Lernæa* such pigmy males were for a long time vainly sought for upon the very peculiarly shaped body of the large female (Fig. 52), which carries egg-tubes.

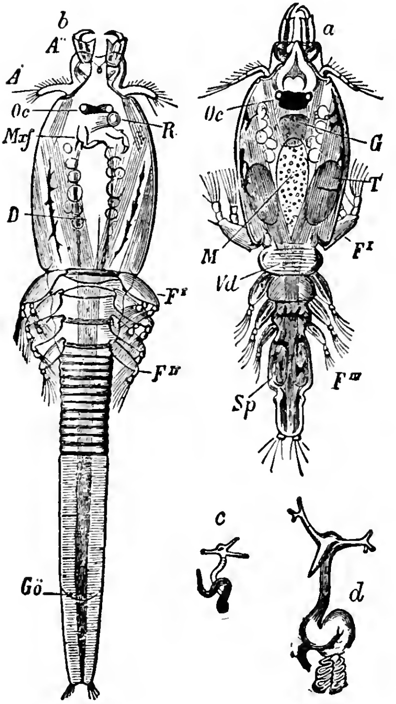

Fig. 52.—*Lernæa branchialis*; *a*, male; *b*, non-degenerate female; *c*, female after fertilization undergoing metamorphosis; *d*, *do.* with egg sacs, natural size. From Claus.

At last it was discovered that the small Cyclops-like males lead an independent life and swim about freely by means of their four pairs of swimming feet, and that the females in their copulatory stage resemble the males, and that it is only after copulation that they (the females) become parasitic and undergo the considerable increase in size and modification of form which characterizes the female with egg-tubes."

A degeneracy of the females of a remarkable character occurs in the insects of the order Strepsiptera. Here the female during the larval stage, bores its way into the body of a hymenopterous insect and soon undergoes a moult. At this time they shed their three pairs of well-developed legs, and become a parasitic maggot, which lives on the body of the host. The males do not undergo this degeneracy but retain the six legs and two pairs of wings common to the class Insecta.

A notorious example of degeneracy among the Mollusca is offered by the *Entoconcha mirabilis*. Says J. S. Kingsley: "So greatly has parasitism altered the form of the body, and all of the organs, that the proper position of this form among the gastropods is far from certain, some placing it near Natica. Indeed, were it not for the characters afforded by the young, its position among the Mollusca would not be suspected. Some thirty years ago [before 1885] Johannes Müller found in some specimens of *Synapta digitata* an internal worm-like parasite, attached by one extremity to the alimentary canal, while the other end hung free in the perivisceral cavity." "In one specimen of Synapta out of one or two hundred this strange form occurs. It is a sac, the upper part bearing the female, and the lower the male reproductive organs, while the centre of the body serves for a while as a broodpouch, the embryos later passing out from an opening at the free end of the body of the parent. The eggs undergo a tolerably regular development, producing a velum, shell, and operculum, the later stages being found free in the body-cavity of the host."

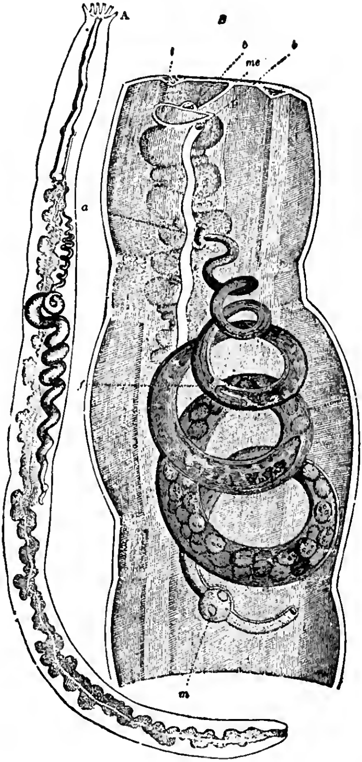

Fig. 53.—A *Synapta digitata* with parasitic Entoconcha; *B*, a portion of Synapta, with Entoconcha (*F*) enlarged; *a*, point of attachment; *b*, blood vessels; *f*, female portion; *i*, intestine; *m*, male portion; *me*, mesentery. From Kingsley.

The preceding examples illustrate the degenerating or catagenetic effect of a parasitic life. We will now observe the corresponding effect of a sedentary life, which may be called earth-parasitism. As an example of this I select the well-known case of the lowest of the Vertebrata, the Tunicata.

The embryo ascidian has the form of a tadpole-like larva which swims actively through the sea by vibrating its long tail. After a short free-swimming existence the fully developed, tailed larva fixes itself by its anterior adhering papillæ to some foreign object, and then undergoes a remarkable series of retrogressive changes, which convert it into the adult ascidian. The tail atrophies, until nothing is left but some fatty cells in the posterior part of the trunk. The adhering papillæ disappear and are replaced functionally by a growth of the test over neighboring objects. The nervous system with its sense-organs atrophies, until it is reduced to the single small ganglion placed on the dorsal edge of the pharynx, and a slight nerve-cord running for a short distance posteriorly. Slight changes in the shape of the body and a further growth and differentiation of the branchial sac, peribranchial cavity, and other organs now produce gradually the structure found in the adult ascidian (Herdman). It is, however, to be noted that in the order Larvacea, this retrograde metamorphosis does not take place. It embraces the single family Appendiculariidæ, which includes Tunicata which preserve the tail, notochord, and other larval features, and lead a free-swimming existence in the ocean.

On the Tunicata, Herdman makes the following general observations. "(1) In the ascidian embryo all the more important organs (e. g. notochord, neural canal, archenteron) are formed in essentially the same manner as they are in amphioxus and other Chordata. (2) The free-swimming tailed larva possesses the essential characters of the Chordata, inasmuch as it has a longitudinal skeletal axis (the notochord), separating a dorsally placed nervous system (the neural canal) from a ventral alimentary canal (archenteron); and therefore during this period of its life history the animal belongs to the Chordata. (2) The Chordata larva is more highly organized than the adult ascidian, and therefore the changes by which the latter is produced

	DIPLOGLOSSA			LEPT	
	Pygopodidæ	Zonuridæ	Anguidæ	Teidæ	Gerrhosaurida
I. Limbs, two pair *a*. Digits 5-4				Tejus	
b. Digits 4-5				Tretioscineus Micrablepharus Gymopthalmus	
c. Digits 4-4			Sauresia	Scolecosaurus	Saurophis
d. Digits 4-3					
e. Digits 3-4					
f. Digits 3-3				Microdactylus	
g. Digits 3-2				Herpetochalcis	
h. Digits 2-4					
i. Digits 2-3					
j. Digits 2-2					
k. One or both monodactyle		Chamæsaura	Panolopus	Cophias Ophiognomon	Cætia
II. Fore limbs only				Propus (digits o	
III. Hind limbs only	Pygopus Cryptodelma Delma Pletholax Aprasia Lialis	Mancus	Pseudopus Opheodes Hyalosaurus		
IV. No limbs			Opheosaurus Dopasia Anguis		

GLOSSA				ANNIELLOIDEA	ANNULATI
Scincidæ	Acontiidæ	Dibamidæ	Anelytropsidæ	Anniellidæ	
Hagria					
Heteropus Ristella Menetia					
Gongyloseps Chiamela Rhinoseineus Tetradactylus Miculia Chalcidoseps Blepharactisis Sphenops					
Zygnopsis					
Allodactylus					
Tridentulus Chalcides Hemiergis Siaphus Phaneropis Sepomorphus Sphenoscineus Sepsina	Nessia				
Hemipodium					
Anisoterma					
Lerista Eumecia Heteromeles					
Dimeropus Chelomeles					
Brachystopus Oncopus Brachymeles Anomalopus Coloscincus Furcillus Dicloniscus	Evesia				
					Euchirotidæ (digits 3–5)
llochirus umerlia Scelotes oridia Podoclonium		Dibamus			
Opheoscincus Herpetosaura epophis Herpetoseps Opheomorus	Acontias Typhlacontias		Anelytropsis Feylinia Typhlosaurus	Anniella	Amphisbæna Rhineura Lepidosternum Trogonophidæ

from the former may be regarded as a process of degeneration. The important conclusion drawn from all this is, that the Tunicata are the degenerate descendants of a group of the primitive Chordata" (=Vertebrata).

The degeneracy of the Tunicata follows immediately their assumption of the sessile condition. Some of the degenerate forms which are not sessile, are supposed to be the free descendants of sessile forms.

Among the craniate Vertebrata, most conspicuous examples of degeneracy are to be seen in the reduction and loss of limbs in certain Batrachia and in many Reptilia. In both classes successive loss of phalanges and digits form series in several groups of salamanders and lizards, and in both these orders there are forms with the limbs rudimental or altogether wanting. In Batrachia, the genus Amphiuma displays rudimental limbs with minute digits numbering two or three on each limb. In the Cæciliidæ, the limbs are wanting. Both types are subterranean in their habits. I give the annexed table of the Lacertilia with degenerate limbs, which it will be observed are found in eleven distinct families. (Pp. 216–217.)

Finally, in the snakes (Ophidia) the limbs have totally disappeared, rudiments only remaining in the boas and pythons and their allies.

Paleontology renders it clear that this reduction is a case of degeneracy, since both the Ophidia and Lacertilia can be traced to Reptilia of the Permian epoch, which have well-developed limbs. This degeneracy is allied to subterranean or terrestrial habits. It is probable that the primitive snakes sought concealment in cavities of the earth and beneath rocks and logs, and spent much of their time in narrow quarters, where limbs would be of no use to them. Some of them, the Angiostomata, are now subterranean in their habits, and most of them are blind, or nearly so. These forms present rudiments of limbs, which leads to the supposition that they are near to the ancestral types. From such forms they developed a type which has proved competent to compete successfully with other vertebrates on the ground, in the water, and in the trees of the forest.

From what has gone before it is now clear that while kinetogenesis is a factor in progressive evolution, the reverse process, or akinetogenesis, is as definite a factor in degeneracy. The evidence derived from parasitism and sedentary modes of life is conclusive in this direction.

I now cite another example of catagenesis which throws much light on the origin of the vegetable kingdom. I have advanced the hypothesis[1] that plants are the degenerate descendants of protozoan animal ancestors, and I will now produce some of the evidence on which the hypothesis rests. The Myxomycetes or Mycetozoa occupy debatable ground between the vegetable and animal kingdoms. They seem at one period of their history to pertain to the former and at another to the latter.

These organic beings are claimed by both botanists and zoölogists, the former placing them with the Fungi, the latter including them in the Protozoa. The fact is that in their mature form they enter the Fungi, while in their early stages they are Protozoa. They have distinct reproductive structures, which produce spores. From each spore issues a "flagellula," which is a simple cell with a flagellum, not apparently

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[1] *Origin of the Fittest*, pp. 431–432.

different from a monad. The flagellum is early lost, and the cell is then termed an amœbula, since it does not differ materially from an amœba. Its movements are similar, and it puts forth short pseudopodia. When these amœbulæ come in contact with each other they fuse, often in large numbers, forming a continuous gelatinous sheet, the plasmodium (Fig. 54), which may have several square inches, and even feet of surface. At the proper time reproductive organs form on this surface in the form of capsules (sporangia), which may or may not be supported on peduncles, and

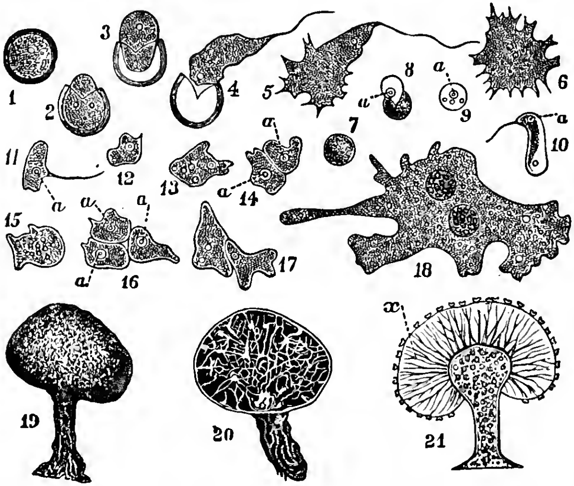

Fig. 54.—Mycetozoa (from Lankester after Du Bary). 1-6, Germination of spore (1) of *Trichea varia*, showing the emerging flagellula; (4-5) and its conversion into an amœbula (6). 7-18, Series leading from spore to plasmodium phase of *Chondrioderma difforma*; 7, spore; 10, flagellula; 12, amœbula; 14, apposition of two amœbulæ; 15-17, fusions; 18, plasmodium. 19-20, Spore-fruit (cyst) of *Physarum leucophæum* × 25; the former from the surface, the latter in section with the spores removed to show the sustentacular network or capillitium. 21, Section of the spore-cyst of *Dydymium squamulosum*, with the spores removed to show the radiating capillitium *x*, and the stalk.

which are filled with minute cyst-like masses of protoplasm, or spores. As already stated, these spores give issue to flagellula.

We have in the life of the Mycetozoa, if not the actual origin of the vegetable from the animal kingdom, a case closely similar to it in a collateral phylum. The process is one of degeneracy through the assumption of a sessile life, or earth-parasitism ; an example of akinetogenesis. The paleontology of animals has absolutely established the fact that the predecessors of all characteristic or specialized types have been unspecialized or generalized types, "neither one thing nor another." It may then be regarded as almost certain that the ancestors of the present higher types of plants were more animal-like than they; that the forms displaying automatic movements were more numerous, and the difficulty of deciding on the vegetable or animal nature of a living organism greater than it is now. Hence it may be concluded that "animal" bathmism has from time to time undergone retrograde metamorphosis producing as a result the permanent form of life which we call vegetable. Given spontaneous movement (i. e. growth) and surrounding conditions, and the resultant product must be structures adapted to their surroundings, just as the plastic clay is fitted to its mould. And this is essentially the distinguishing character of vegetable teleology as compared with animal. In the average plant we see adaptation to conditions permitted by unconscious nutrition and reproduction ; in the animal, adaptation to a greater variety of conditions, due to the presence of sensation or consciousness.

In closing Part I. of this book, I desire to point out the conclusion which has, I think, been reached.

It has been proved, as it appears to me, that the variation which has resulted in evolution has not been multifarious or promiscuous, but in definite directions. It has been shown that phylogeny exhibits a progressive advance along certain main lines, instead of having been indefinite and multifarious in direction.

It is not denied that many lines of variation have been at one geologic period and another discontinued. It is also true that certain divergences from the main lines have appeared, and that minor and secondary variations have occurred. Such variations do not seem to have had any material effect on the general course of evolution. In many cases such variations from main lines might be compared to the undulations in the course of a stream, which nevertheless seeks its lowest level in spite of all temporary obstacles. Professor Scott has termed these temporary variations "nutations," in an able article on the subject.[1] "Sports" seem to have been of no importance in evolution whatever.

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[1] *American Journal Sci. Arts*, Vol. XLVIII., 1894, p. 355.

PART II.

THE CAUSES OF VARIATION.

PRELIMINARY.

IN Part II., which treats of the causes of variations, I propose to cite examples of the direct modifying effect of external influences on the characters of individual animals and plants. These influences fall naturally into two classes, viz., the physico-chemical (molecular), and the mechanical (molar). The modifications so presented are supposed to be the result of the action of the causes in question, continued throughout geologic time. To the two types of influence which thus express themselves in evolution, I have given the names Physiogenesis[1] and Kinetogenesis. The inheritance of character is assumed in this section, and the reason for so doing will be considered later, in the third section of this book.

In the animal kingdom we may reasonably suppose that kinetogenesis is more potent as an efficient cause of evolution than physiogenesis. In the vegetable kingdom it is quite evident that evolution is more usually physiogenetic than kinetogenetic. Atmospheric and terrestrial conditions play a major rôle in the

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[1] "The Energy of Evolution," *American Naturalist*, March, 1894. "The Origin of Structural Variations" in *New Occasions*, Chicago, May, 1894. C. H. Kerr & Co.

determination of plant-structure, but motion has also had an important influence. The motion, however, has originated in small degree in the plant itself, but has been derived from without. Some importance must be ascribed to the effects of winds, but the principal source of the especial strains to which plants have been subjected, has been the insect world. Insects have been inhabitants of land-plants since their origin in early Paleozoic ages, and the mutual relations of plants and insects have ever been intimate. As has been insisted by Müller and Henslow, the uses to which the floral organs have been put by hymenopterous and other insects have been probably a principal cause of the forms assumed by the former. From this direction has been derived the kinetogenetic influence in plant evolution. The few independent movements displayed by plants may have had some influence on the evolution of their structure. We have no reason as yet to suppose that such movements have any other than purely physical factors.

CHAPTER V.—PHYSIOGENESIS.

BOTANISTS and gardeners are familiar with the effects of physical causes in producing modifications in the characters of plants. That modifications so produced have become hereditary is known to be the fact, and we may therefore infer that the evolution of plant forms has been produced in large degree by similar agencies in past geological ages. Says Henslow:[1] "M. Carrière raised the radish of cultivation, *Raphanus sativus* L., from the wild species, *R. raphanistum* L., and moreover found that the turnip-rooted form resulted from growing it in a heavy soil, and the long-rooted one in a light soil. Pliny records the same fact as practised in Greece in his day, saying that the male (turnip form) could be produced from the female (long form) by growing it in a "cloggy soil." The rule may be laid down that a species [of plant] may be constant as long as its environment is constant, but no longer. I have changed the spiny *Ononis spinosa* L., the rest-harrow, both by cuttings and by seed into a spineless form, undistinguishable from the species *O. repens* L. in two years; but it would have, I doubt

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[1] *Natural Science*, 1894, pp. 259-260.

not, at once reverted to the *O. spinosa* if I had replanted it on the poor soil from which I took it. It seems, therefore, to be a very hazardous and fallacious method of testing the value of specific or other characters by cultivation. A wild plant may or may not change at once. Thus the carrot, *Daucus carota* L., proved refractory with Buckman, but not with Vilmorin, who converted this *annual* into a hereditary *biennial* by sowing the seed late in the season, till the character of flowering in the second season became fixed."

The prevalence of spinous plants in dry and desert regions has often been described.[1] The same is true of reptiles, although spines appear on some species in fertile regions. Spines of plants are believed to be twigs, petioles, leaves, etc., partially aborted under the influence of drought, or the absence of the water necessary to the tissues of the parts in question. Wallace points out, however, that there are spinous plants in humid climates, citing the Gleditschia (honey locust) as an example. The spines of such plants may be survivals of periods of drought in previous geologic ages. Or desiccation of certain parts of a plant might be a form of abortion of those parts, a phenomenon which is confined to no region, and is evidently due to causes other than drought in some cases. Henslow (*l. c.*) says: "They [spines] originate, I maintain, as a mere accidental and inevitable result of the arrest of the organ in question, such arrest being *mainly* due to drought."

One of the best expositions of the influence of the physical characters of the environment on the structure of animals is to be found in Semper's work, *Ani-*

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[1] *Natural Science*, 1894, September, p. 179.

mal Life, to which I refer my readers for a fuller exposition than can be given here.

a. Relation of the Size of Shells of Mollusca to the Environment.

It has been observed that both in natural conditions and in confinement; shells of fresh-water Mollusca grow to a larger size in larger bodies of water, and become reduced in size as the bulk of water in which they live is reduced. Varigny has shown that the reduced size follows a reduction of the air-surface of the water rather than a reduction of the actual bulk, though the two conditions may often coincide. He also shows that, other things being equal, the size of individuals is inversely as their numbers in a given enclosure.

b. The Conversion of Artemia Into Branchinecta.[1]

In 1871 the spring flood broke down the barriers separating the two different lakes of the salt works near Odessa, diluting the water in the lower portion to 8° Beaumé, and also introducing into it a large number of the brine shrimp, *Artemia salina.* After the restoration of the embankment, the water rapidly increased in density, until in September, 1874, it reached 25° of Beaumé's scale, and began to deposit salt. With this increase in density, a gradual change was noticed in the characters of the Artemiæ, until late in the summer of 1874 forms were produced which had all the characters of a supposed distinct species, *A. muelhausenii.* The reverse experiment was then tried. A small quantity of the water was then gradually diluted,

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[1] Abstracted from an account by J. S. Kingsley, *Standard Natural History*, Vol. II.

by M. Vladimir Schmankewitsch, who conducted the experiments, and though continued for only a few weeks, a change in the direction of *A. salina* was very apparent. Led by these experiments, he tried still others. Taking *Artemia salina*, which lives in brine of moderate strength, he gradually diluted the water, and obtained as a result a form which is known as *Branchinecta schæfferii*, the last segment of the abdomen having become divided into two. Nor is this change produced by artificial means alone. The salt pools near Odessa, after a number of years of continued washing, became converted into fresh-water pools, and with the gradual change in character, *Artemia salina* produced first a species known as *Branchinecta spinosa*, and at a still lower density *Branchinecta ferox*, and another species described as *B. media*. Here not only new species were produced, but a new genus.

c. The Production of Colors in Lepidopterous Pupæ.

The following important contribution to this subject has been made by Poulton.[1] As an illustration of the direct effect of the environment in the production of color-changes, it is of the greatest value. Several lepidopterists, among others Weismann and Merrifield, had shown that by exposing the pupæ of butterflies to low temperatures material changes in the coloration of the mature insects can be produced. Says Poulton: "In 1867 Mr. T. W. Wood exhibited to the Entomological Society of London a number of chrysalides of the large and small garden white butterflies (*Pieris brassicæ* and *P. rapæ*), which corresponded in color to the surfaces to which they were attached. Dark pupæ

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[1] *The Colors of Animals*, International Scientific Series, Vol. LXVIII, by E. B. Poulton, London, 1890.

had been found on tarred fences and in subdued light; light ones on light surfaces; while green leaves were shown to produce green chrysalides, at any rate in certain cases.

"During the following nineteen years, gradual confirmation of Mr. Wood's central position was afforded. In 1873 Professor Meldola supported the observations upon the chrysalides of the "garden whites." He compared large numbers of individuals and found that the pupæ upon black fences were darker than those upon walls.

"In 1874 a paper by Mrs. M. E. Barber, and communicated by Mr. Darwin to the Entomological Society of London, was printed in the transactions of that society. Mrs. Barber had experimented with a common South African swallow-tailed butterfly (*Papilia nireus*), and had found the chrysalis wonderfully sensitive to the colors of its environment. When the pupæ were attached among the deep green leaves of the food-plant, orange, they were of a similar color; when fixed to dead branches covered with withered, pale, yellowish-green leaves, they resembled the latter. One of the caterpillars affixed itself to the wood frame of the case, and then became a yellowish pupa of the same color as the wooden frame.

"Mr. Maurel Weale also showed that the color of certain other South African pupæ can be modified, and Mr. Roland Trimen made some experiments upon another African swallow-tail (*Papilio demoleus*) confirmatory of Mrs. Barber's observations. He covered the sides of the cage with bands of many colors, and found that green, yellow, and reddish-brown tints were resembled by the pupæ, while black made them rather darker. Bright red and blue had no effect. The larvæ did not exercise any choice, but fixed themselves indiscriminately to colors which their pupa could resemble and those which they could not. In the natural conditions the latter would not exist, for the pupæ can imitate all the colors of their normal environments.

"I began work with the common peacock butterfly (*Vanessa io*), of which the chrysalis appears in two forms, being commonly dark gray, but more rarely, bright yellowish-green; both forms are gilded, especially the latter. Only six caterpillars could be obtained, and these were placed in glass cylinders surrounded by yellowish-green tissue-paper. Five of them became chrysalides of the corresponding color; the sixth was removed immediately after the caterpillar skin had been thrown off, and was placed in a dark box lined with black paper, but it subsequently deepened into a green pupa exactly like the others. Obviously the surroundings had exercised their influence before the pupa was removed.

"Being unable to attain more larvæ of the peacock, I worked upon the allied small tortoise-shell butterfly (*Vanessa urticæ*), which can be obtained in immense numbers. In the experiments conducted in 1886, over seven hundred chrysalides of this species were obtained and their colors recorded. Green surroundings were first employed in the hope that a green form of pupa, unknown in the natural state, might be obtained. The results were, however, highly irregular, and there seemed to be no susceptibility to the color. The pupæ were, however, somewhat darker than usual, and this result suggested a trial of black surroundings, from which the strongest effects were at once witnessed: the pupæ were as a rule extremely dark, with only the smallest trace, and often no trace at all, of the golden spots which are so conspicuous in the lighter forms. These results suggested the use of white surroundings, which appeared likely to produce the most opposite effects. The colors of nearly one hundred and fifty chrysalides obtained under such conditions were very surprising. Not only was the black coloring matter as a rule absent, so that the pupæ were light-colored, but there was often an immense development of the golden spots, so that in many cases the whole surface of the pupæ glittered with an apparent metallic lustre. So remarkable was the appearance that a physicist, to whom I showed the chrysalides, suggested that I had played him a trick and had covered them with gold-leaf.

"These remarkable results led to the use of a gilt back-ground as even more likely to produce and intensify the glittering appearance. By this reasoning I was led to make the experiment which had been suggested by Mr. Wood nineteen years before. The results quite justified the reasoning, for a much higher percentage of gilded chrysalides, and still more remarkable individual instances, were obtained among the pupæ which were treated in this way.

"These observations and experiments had been made when I began to work at the subject in 1886: they appeared to prove that the power certainly exists, but nothing was really known as to the manner in which the adjustment is effected. Mr. S. W. Wood's original suggestion, that the 'skin of the pupa is photographically sensitive for a few hours only after the caterpillar's skin has been shed,' was accepted by most of those who had worked at the subject. And yet the suggestion rested upon no shadow of proof; it depended upon a tempting but overstrained analogy to the darkening of the sensitive photographic plate under the action of light. But the analogy was unreal, for, as Professor Meldola stated in the discussion which followed Mrs. Barber's paper, 'the action of light upon the sensitive skin of a pupa has no analogy with its action on any known photographic chemical. No known substance retains permanently the color reflected on it by adjacent objects.' The supposed 'photographic sensitiveness' of chrysalides was one of those deceptively feasible suggestions which are not tested because of their apparent probability. It would have been very easy to transfer a freshly formed pupa from one color to another which is known to produce an opposite effect upon it; and yet if this simple experiment had been made the theory would have collapsed, for the pupa would have been found to resemble the first color and not the second. Furthermore, Mr. Wood's suggestion raised the difficulty that chrysalides which had become exposed in the course of a dark night would have no opportunity of resembling the surrounding surfaces, for the pupal colors deepen very quickly into their permanent condition.

"Having thus defined the time of susceptibility. the next question was to ascertain the organ or part of the larva which is sensitive. At first it appeared likely that the larvæ might be influenced through their eyes (ocelli), of which they have six on each side of the head. Hence, in many experiments the eyes of some of the larvæ were covered with an innocuous black opaque varnish, and they, together with an equal number of normal larvæ from the same company, were placed in gilt or white surroundings. The pupæ from both sets of larvæ were, however, always equally light-colored. It then seemed possible, although highly improbable, that the varnish itself might act as a stimulus similar to that caused by gilt or white surroundings, and therefore the experiments were repeated with black surroundings in darkness, but the pupæ of the two sets were again almost identical, so that it appeared certain that the eyes can have nothing to do with the influence.

"It then seemed possible that the large branching bristles, with which the larvæ are covered, might contain some organ which was affected by surrounding colors, but experiments in which half of the larvæ were deprived of their bristles showed conclusively that the sensitive organs must have some other position, for the pupæ from both sets of larvæ were identical.

"I was thus driven to the conclusion that the general surface of the skin of the caterpillar is sensitive to color during stage ii, and part of stage iii. In order to test this conclusion, I wished to subject the body of the same larvæ to two conflicting colors, such as black and gold, producing the most opposite effects upon the pupa. Such an experiment, if successfully carried out, would decide some important points. If the part of the body containing the head was not more sensitive than the other part, a valuable confirmation of the blinding experiments would be afforded. Mrs. Barber's suggestion that particolored pupæ may be produced by the influence of two colors would be tested in a very complete manner; if particolored pupæ were obtained, it seemed probable that the light acts directly upon the skin, but if they could not be obtained, it seemed more probable that the light influences the termination of nerves in the skin, and that the pupal colors are produced through the medium of the nervous system. The experiments were conducted in two ways. In the first, the larvæ were induced to suspend themselves from sheets of clear glass, by placing them in wide shallow boxes, so that the ascent to the glass roof was easily accomplished. As soon as suspension (stage iii.) had taken place, each larva was covered with a cardboard tube, divided into two chambers by a horizontal partition, which was fixed rather below the middle. There was a central hole in the partition just large enough to admit the body of the larva. The tube was fixed to the glass sheet with glue; the upper chamber was lined with one color, e. g. gilt, and the lower chamber with the opposite color, e. g. black, with which the outside of the cylinder was also covered, in case the larva should stretch its head beyond the lower edge. The partition was fixed at such a height that the larval head and rather less than half of the total surface of skin were contained in the lower chamber, while rather more than half of the skin surface was contained in the upper chamber.

"The second method of conducting the conflicting color experiments was superior in the more equal illumination of the upper and lower colors. The bottom of a shallow wooden box was covered with alternate areas of black and gilt papers, and partitions were fixed along the lines where the two colors came in contact. Each partition was gilt toward the gilt surface, and black toward the black surface, and was perforated close to the bottom of the box with holes that would just admit the body of a larva. The box was then placed in a vertical position towards a strong light, so that the partitions became strong shelves, while the black and gilt surfaces were uppermost alternately. As soon as a larva was suspended to a glass sheet, the boss of silk was carefully scraped off and was pinned on the upper color, above one of the holes, so that the head and first five body-rings passed through the hole on to the color beneath, which tended to produce opposite effects. Other larvæ were similarly fixed between the shelves upon one color only, so as to afford a comparison with the results of the conflicting colors.

"A careful comparison of all the pupæ obtained in the conflicting color experiments showed that, when the illumination of the two surfaces was equal, the effective results were produced by that color to which the larger area of skin had been exposed, whether the head formed part of that area or not. Particolored pupæ were never obtained. It therefore appears to be certain that the skin of the larva is influenced by surrounding colors during the sensitive period, and it is also probable that the effects are wrought through the medium of the nervous system. The latter conclusion receives further confirmation from other observations."

Professor Poulton has since produced remarkable color-changes in the larvæ of Lepidoptera by confining them to the branches of plants of distinct colors. Thus geometrid larvæ confined to the stems of a black color, became correspondingly dark; while those restricted to white twigs became very pale. These larvæ, and, still more strikingly, those of *Cossus ligniperda*, when confined on branches which supported lichens, became of variegated colors, corresponding with those of the lichens, and affording an admirable means of concealment.

d. The Effect of Light on the Colors of Flatfishes.

It is well known that the side of the body which is uppermost in the normal position in the flatfishes (Pleuronectidæ) is colored generally with dark tints, and frequently with a distinct pattern, while the lower side is white. This is due to the absence from the lower side of the chromatophoræ or pigment-containing cells, which are abundant on the upper side. The young fish has chromatophoræ on both sides as it has its eyes also in the normal position, but as the fish turns the left side upwards and the right eye gradually rotates to the left side, the chromatophoræ disappear from the right side, which thus becomes colorless.

Prof. J. T. Cunningham[1] experimented with young flounders taken at the beginning or middle of their metamorphosis, by placing a mirror below the aquarium in which they were kept, at an angle of 45°, and cutting off the light from above by an opaque cover. In the great majority of the specimens treated in this way, after several months, although no effect was produced upon the eyes, more or less of the skin of the lower side was pigmented. He thus showed that the absence of pigment on that side in the normal fish is due to its position in shadow, where little light can reach it.

e. The Effect of Feeding on Color in Birds.

Mr. F. E. Beddard cites the following remarkable example of the direct effect of internal physical causes in producing change of coloration.[2]

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[1] *Zoologischer Anzeiger*, 1891.

[2] *Animal Coloration, an Account of the Principal Facts and Theories Relating to the Colors and Markings of Animals.* By Frank E. Beddard, M. A. Oxon., F. R. S. E. With Four Colored Plates; and Wood-Cuts in the Text. London. Swan Sonnenschein & Co. New York: Macmillan & Co. 1892.

"That the yellow color of canaries can be altered to an orange red by mixing cayenne pepper with their food, has been known for a long time. This curious fact was first discovered in England, as was also the fact that the different races of canaries vary in their susceptibility to the action of the pepper; some kinds are more, others are less, affected, while one race is absolutely without any power of having its coloration altered by these means. The color-change is produced by feeding the newly hatched young with the pepper conveyed in their food or the old birds while sitting upon the nest are furnished with food containing the cayenne, which they in turn feed their offspring. The color change can, in fact, be only brought about in very young birds whose feathers are not completely matured; it is quite impossible to produce any alteration upon the full-grown canary. Clearly, therefore, here is an instance of the direct effect of food upon color. An interesting paper upon the subject, which has also furnished me with the facts already mentioned, has lately appeared,[1] and it will be of interest to give some account of the author's (Dr. Sauermann's) experiments for reasons that will appear. Cayenne pepper, of course, is a composite substance, from which a number of distinct chemical substances can be extracted: the red color is caused by a pigment termed capsicin, which can be separated from the pepper; and it might easily be supposed that the change from yellow to red in the feathers of the canary was simply caused by a transference of the pigment, as in the cases mentioned on page 127; but Dr. Sauermann shows that it is not so. Yellow-colored canaries were

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[1] *Archiv für Anatomie und Physiologie.* 1889. Physiologische Abtheilung, 543.

not in the very slightest degree affected by the pigment alone; but, curiously enough, particolored birds did react,—the brown parts of the feathers became distinctly lighter in hue. It is a fatty substance (triolein) which appears to convey the pigment, and to produce thus a changing of the color from yellow to red; and further experiments were made with other birds, showing that it is not only canaries which are influenced by their food in this way. Some white fowls, belonging to a special breed, showed traces of yellow among the feathers after feeding with cayenne; but in this case there were not racial but individual differences in susceptibility, for all the specimens of birds experimented with did not react to the stimulus.

"A similar series of experiments was made with some other colors: it was found with carmine that the yellow color was destroyed and the birds became white. This unexpected effect is explained by the fact that a mixture of violet and yellow produces white. The fact that the fatty constituent, triolein, plays the chief part in the coloring of the feathers may perhaps help to explain the very singular fact that the Amazon parrots change from green to yellow when fed upon the fat of certain fishes.

"With regard to the white fowls referred to, the experiments made by Dr. Sauermann were particularly interesting. The interest lies in the fact that the pigment was not absorbed equally by all the feathers; only special tracts were affected; the breast feathers, for instance, became red, while the head remained white. It is therefore quite credible that in a state of nature partial alteration of color may be produced by a change of diet."

In a chapter of Dr. Beddard's book relating to protective resemblances will be found an account of several examples of animals which have apparently acquired a resemblance to their surroundings by the transference of pigment to their bodies in their food.

f. The Blindness of Cave-Animals.

Neo-Lamarckian writers have always ascribed the absence or rudimentary condition of the eyes characteristic of animals which dwell exclusively in caves, to disuse consequent on the absence of light. Lamarck ascribed the rudimentary condition of the eyes in the mole to this cause. As the removal of so important an organ as the eye is not accomplished in a single generation, the element of heredity enters the proposition. This subject is reserved for Part Third of this book; nevertheless, for the present suspending judgment as to this question, it has been rendered exceedingly probable by embryological investigations into the history of dwellers in darkness, that the Neo-Lamarckian view is the correct one.[1] Says Packard:

"In my essay on *The Cave Fauna of North America* (p. 139), I record the fact that in the young of the blind crayfish (*Oreonectes pellucidus*), the eyes of the young are perceptibly larger in proportion to the rest of the body than in the adult, the young specimen observed being about half an inch in length. Previously to this, Dr. Tellkampf, in 1844, remarked that 'the eyes are rudimentary in the adults, but are larger in the young.' Mr. S. Garman states, regarding the blind Cambarus of the Missouri Cave: 'Very young specimens of *C. setosus* correspond better with the adults of *C. bartonii*; their eyes are more prominent in these

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[1] I am indebted for a *résumé* of this subject to Packard, *American Naturalist*, 1884, p. 735.

stages, and appear to lack but the pigment.' In the blind cave-shrimp (Troglocaris) of Austria, Dr. Joseph discovered that the embryo in the egg is provided with eyes.

"In this connection should be recalled the observations of Semper in his *Animal Life* (pp. 80, 81) on *Pinnotheres holothuriæ*, which lives in the 'water-lungs' of holothurians, where, of course, there is an absence of light. The zoëa of this form has large 'well-developed eyes of the typical character. Even when they enter the animal they still preserve these eyes; but as they grow they gradually become blind or half-blind, the brow grows forward over the eyes, and finally covers them so completely that, in the oldest individuals, not the slightest trace of them, or of the pigment, is to be seen through the thick skin, while, at the same time, the eyes seem to undergo a more or less extensive retrogressive metamorphosis.'

"In this connection may be mentioned the case of the burrowing blind shrimp (*Callianassa stimpsonii*), which has been found by Prof. H. C. Bumpus, at Wood's Holl, Mass., living in holes at a depth of between one and two feet. He has kindly given me a specimen of the shrimp, which is blind, with reduced eyes, smaller in proportion to the body than those of the blind crayfish. He has also obtained the eggs, and has found that the embryos are provided with distinct black, pigmented eyes, which can be seen through the egg-shell.

"Recently, Zeller has studied the embryology of the Proteus of Adelsberg Cave, and has confirmed the statement of Michahelles, who, in 1831, discovered that the eyes of this animal are more distinct in the young and somewhat larger than in the adult. We quote and translate from Zeller's account:

"'The development of the eyes is very remarkable; they are immediately perceived and present themselves as small, but entirely black and clearly drawn circular points, with a slit which is very narrow, and yet, at the same time, well defined, and which penetrates from the lower circumference out to the middle.

"'Indeed, one can hardly doubt that this astonishing development of the eye has been accomplished by the influence of light, as has also the pigmentation of the skin, the reddish-white ground-color of which appears thickly studded with very small brownish-gray points mixed with detached white ones, over the upper surface of the head and over the back, down over the sides of the yellowish abdomen. Even on the edge of the fins (*Flossensaum*) the pigment is found. On the other hand, there is a whitish spot over the snout, as is likewise the case in the adult creatures which have been colored by the light. Both the under surface of the head and the entire abdomen are shown free from pigment like the limbs. . . .

"'I cannot specify very exactly as to when the pigmentation of the skin begins, but, in any case, it is very early, and often earlier that the first beginning of the eyes can be discovered. The latter occurs toward the end of the twelfth week, at which time a thin, light gray line, which still appears overgrown, may be perceived, forming a half-circle, open underneath. Then while this line subsequently becomes clearer and darker, and its ends grow further under and towards each other, there also takes place simultaneously a progression of the pigment larger towards the middle point, and the circle finally seems closed and filled up to the narrow slit mentioned above, which proceeds from the lower circumference and penetrates to the middle of the eye' (pp. 570, 571).

"But the most striking discovery bearing on this subject is that of the condition of the eyes in the embryo and young compared with the adult of the blind goby of San Diego.

"In his essay on *The Fishes of San Diego*, Professor Eigenmann briefly refers to and gives four figures (Fig. 55) of the embryo of Typhlogobius, Mr. C. L. Bragg having been fortunate enough to discover the egg in the summer of 1891. 'The eyes develop normally, and those of No. 4 differ in no way from the eyes of other fish embryos.' In this case, then, we have the simplest and clearest possible proof of the descent of this blind fish from individuals with eyes as perfect as those of its congeners.

"We have been permitted by the Director of the United States National Museum to reproduce Professor Eigenmann's excellent figures on the embryo, which tell the story of degeneration of the eye from simple disease of the organ, the species being exposed to conditions of life strikingly different from those of its family living in the same bay.

"Before the discovery of the eggs, the youngest individual ever seen is represented in Fig. 55, No. 1, its eyes being, though small, yet distinct, and 'apparently functional.'

"From these data it is obvious that future embryological study on cave-animals will farther demonstrate their origin from ancestors with normal eyes."

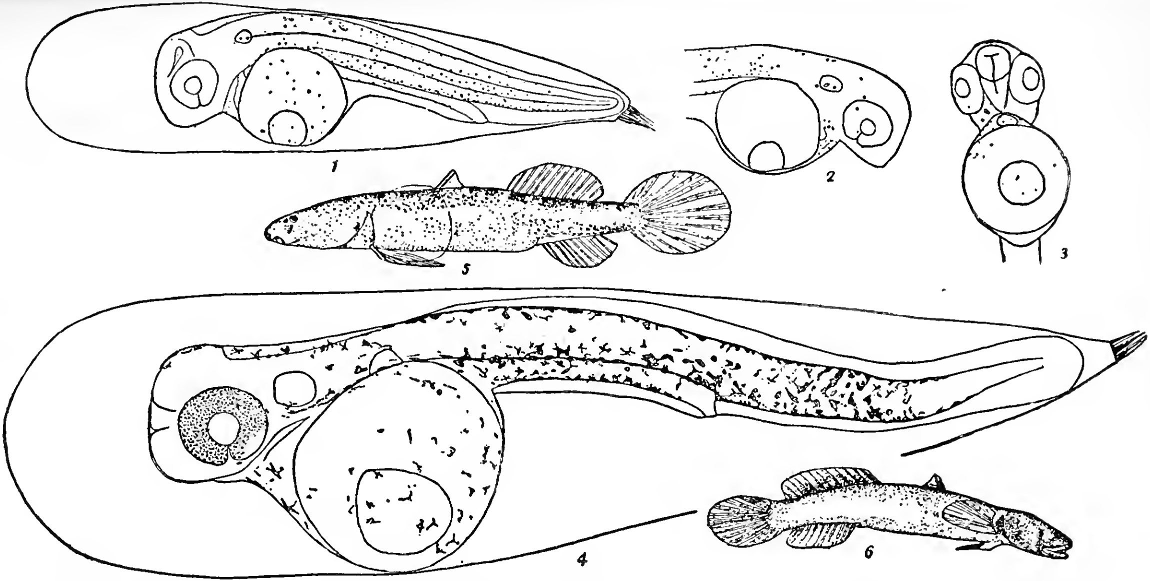

Fig. 55.—*Typhlogobius californiensis* Steind.; showing obliteration of eye in course of growth from the egg to maturity. Adapted from Eigenmann. No. 1. The youngest *Typhlogobius* seen; Zeiss A and 2. No. 2. The head of an older one from the side. No. 3. The head of one similar to No. 3, seen from below. No. 4. Another larva forty-eight hours older than No. 1; the oldest one seen; it is still inclosed in its club-shaped zona. No. 5. Young *Typhlogobius*; ×4 2-9, showing color-markings and the eye. No. 6. Adult *Typhlogobius*, natural size, in the position usually assumed in the aquarium.

CHAPTER VI.—KINETOGENESIS.

UNDER the head of kinetogenesis (development by motion) comes the consideration of the effect of use and disuse. Use necessarily conditions the evolution of useful characters. These characters are such by reason of their adaptation to the life-functions of the beings which possess them. It is perfectly well known, however, that all plants and animals possess more or less numerous peculiarities which are not useful to their possessors. Such are the mammæ of male animals; the incisions forming palmate or pectinate leaves and petals of plants; rudimental organs of all kinds; great elongation of the vertebral column, especially of the caudal series in certain species; patches of color, or of hairs, at particular places, etc. These, and many others may be arranged in divisions according to their probable origin, as follows:

I. Excess of growth energy.

Examples: the recurved tusks of the mammoth, babirussa, etc.; the elongate feathers of some birds, etc.

II. Defect of growth-energy.

1. Atavism: examples; the tritubercular superior molar of certain races of man.

2. Degeneracy from disuse: examples; the rudimental legs and digits of numerous lizards.
3. Degeneracy from disuse and complementary excess elsewhere: examples; reduction in number of molars and incisors in man; reduced mammæ in male Mammalia; reduction of lateral digits in the true horses (Equus).
4. Physico-chemical causes: here must be probably included various color-patches and color-tints, for which no other explanation is accessible.

Darwin considers several of the above conditions, and endeavors to explain some of them as consequences of natural selection. Equivalent to the Section I. above, he enumerates extraordinary developments of particular parts.[1] He says, "A part developed in any species in an extraordinary degree or manner in comparison with the same part in an allied species, tends to be highly variable." He does not attempt any explanation of the origin of such characters, except through natural selection. Of the characters coming under Section II. above, he says, "Multiple, rudimentary and lowly organized structures are variable." Of these he remarks, "I presume that lowness here means that the several parts of the organism have been but little specialized for particular functions; and as long as the same part has to perform diversified work, we can perhaps see why it should remain variable, that is, why natural selection should not have preserved or rejected each little deviation of form so carefully as when the part has to serve for some one special purpose." Here Mr. Darwin well illustrates his unwillingness to look to disuse as the cause of the conditions he describes. Under "Compensation and Economy of Growth" he quotes from Goethe that "In order to

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[1] *The Origin of Species*, Ed. 1872, p. 119.

spend on one side, nature is forced to economize on the other side." I have expressed the same view in the following language:[1]

"*The complementary diminution* of growth-nutrition follows the excess of the same in a new locality or organ, of necessity, if the whole amount of which an animal is capable be, as I believe, fixed. In this way are explained the cases of retardation of character seen in most higher types. The discovery of truly complementary parts is a matter of nice observation and experiment." An apparent illustration is that of the increase of the median digits in the diplarthrous Ungulata contemporaneously with the diminution and atrophy of the lateral digits. This is, however, an example of the relative effects of use and disuse, which proceed contemporaneously, and it is probable that most if not all cases of complementary growth-relations may be expressed in this way. Thus the orthognathism of the higher human races is accompanied by full frontal development, the two modifications constituting a retardation of the postembryonic growth of the face. But this change can be traced to use, increased brain action enlarging that organ, and expanding its osseous case, probably at the expense of lime salts which would otherwise go to the jaws. Reduction of teeth in Artiodactyla and in man cannot be regarded as a useful character in itself, but it is complementary to the development of other characters which are useful.

Under the same head may come perhaps, the facts included by Mr. Darwin under the head of "Correlated Variation." Of these he says, "I mean by this expression that the whole organization is so tied together

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[1] "Method of Creation," *Proceedings of the American Philosophical Society*, 1871, p, 257; *Origin of the Fittest*, 1887, p. 201.

during its growth and development, that when slight variations in any one part occur, and are accumulated through natural selection, other parts become modified." After referring to various characters of composite and unbelliferous plants in illustration of such a law, he says (*l. c.*, p. 116), "Hence modifications of structure, viewed by systematists as of high value, may be wholly due to the laws of variation and correlation, without being, so far as we can judge, of the slightest service to the species." Here Mr. Darwin admits the insufficiency of natural selection as an explanation of the origin of such characters; for he says (p. 119), "Natural selection, it should never be forgotten, can act solely for the advantage of each being." He goes further, and admits (p. 114) that the Lamarckian doctrine has some claims to credence, where he says, "On the whole we may conclude that habit, or use and disuse, have in some cases, played a considerable part in the modification of the constitution and structure; but that the effects have often been largely combined with, and sometimes overmastered by the natural selection of innate variations."

1. KINETOGENESIS OF MUSCLE.

The fundamental condition of the molar movements of organic beings is the contractility of protoplasm. In the Amœba this contractility is a generally diffused characteristic of its body-substance, and this is the case with Rhizopoda generally. In higher Protozoa the contractility is already especially developed in certain regions where most needed for the movement of the body in definite directions; generally immediately beneath the denser sarcode of the external surface. In

Stentor this substance presents the appearance of longitudinal threads; in Gregarina they encircle the body. From these simple beginnings we can follow the muscular tissue to its various expressions in all classes of animals; to the concentric threads of the Cœlenterata; to the longitudinal bundles beneath the integument of worms; and the variously directed masses attached to the external skeleton of the Arthropoda, and the internal skeleton of the Vertebrata. The ease with which muscular tissue is grown in the higher animals under use, permits us to infer that its development in all animals has been due to the same cause. Muscular structure is directly related to the needs of the structures to which it is attached, in the performance of movements. In rudimental limbs muscles are reduced in both size and number, distinct slips or bodies becoming fused. In enlarged limbs the reverse process takes place. Muscular bellies increase in size, and in number by subdivision. The muscular system in the middle and higher Vertebrata is variable, and its plasticity to the stimuli to movements is well known. It is evident that definite muscular bands have been developed in the lines of resistance which it has been necessary to overcome in moving the body or parts of it. The movable segments which have become adapted for contact with the surrounding media, by development of hardness or extent of surface, as limbs (feet, wings), and jaws, have naturally become the points of origin of the most efficient muscular bands. No one can doubt the mutual stimuli which the muscular and skeletal systems have exchanged during the process of evolution, since they are necessary to each other from a mechanical point of view.

Hüter,[1] a distinguished specialist in the diseases of the joints, gives the following positive information as to the easy formation of new modifications of muscular structure:

"Muscular tissue everywhere possesses the capacity to shorten itself in consequence of continued approximation of its points of insertion; that is, to become shorter by the disappearance of tissue, in proportion to the duration of the approximation. This law is of the greatest importance for the muscular contraction of joints, that is, for such restriction of the freedom of movement of the articulations as has its origin in muscular movements. We have experimental opportunities for the observation of this fact, such as the effect of a stiff bandage on an articulation. When it is necessary, in consequence of a fracture of the fore-arm, to fix the elbow-joint for several weeks in a right-angled flexure, we find on the removal of the bandage that the power of extension of the fore-arm has been much restricted. That the cause is nutritive change is proven by the fact that considerable force of muscular contraction is necessary before the normal extension can be effected."

Similar phenomena are to be observed in consequence of a prolonged lying in bed, where no injury to the innervation exists.

"The muscles adapt themselves to the permanent positions of the articulations, as in joint-contractions which are due to muscular paralysis. Those muscles which are habitually stretched, increase in length, while those whose insertions are approximated, are shortened, producing joint-contraction." He then goes

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[1] Hüter, "Studien an den Extremitätengelenken Neugeborener und Erwachsener." Virchow's *Archiv für pathologische Anatomie*, Bd. XXV., 6-8.

on to describe the effect of such fixation of joints on the bones themselves, to which I will refer on a later page, under the head of the origin of articular surfaces.

Professor Eimer of Tübingen has given us a synopsis of the nature of the evolution of the characters of the muscular tissue, which is highly instructive, and of which I present here an abstract.[1] The conclusions reached by Eimer are derived from a general study of the subject, both in the laboratory and in the literature. He says:

"(1) It is apparently continued contractions of the protoplasm in definite directions, which have produced muscular masses. Since plants do not display continuous and vigorous movements, they have not developed muscular bodies.

"(2) Undoubted facts indicate that from a primitively identical substance muscular tissue has developed in the direction of effective contractions, while connective tissue has developed where no contractions have been present.

"(3) Muscle-masses first appeared almost everywhere in the external layer of the contractile region:

"*a*, in Protozoa in the outer layer of the body;
"*b*, in Metazoa in the tegumentary sheath of the body.
"*c*, They consist first either of muscle-cells, or muscle-fibers, from which develop mantle muscle-cells and mantle muscle-fibers. Mantle muscle-fibers compose the otherwise highly developed striped muscles of

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[1] "Die Entstehung und Ausbildung des Muskelgewebes, insbesondere der Querstreifung desselben als Wirkung der Thätigkeit betrachtet." *Zeitschrift für wissenschaftliche Zoologie*, LIII., Suppl., 1892, p. 67.

Arthropoda, and some Vertebrata (Batrachia). And when the entire muscle-fiber is divided into fibrillæ, there can appear an external layer of muscular threads.

"(4) That muscle cells and fibers first appear in the external stratum of the active body of animals, is due to the especially active movements necessary to this part of the body. This is a simple mechanical consequence of the fact, that in a more or less longitudinally extended body of protoplasm, whether it be Protozoön or worm, or muscle-cell or muscle-fiber, that its movements must be more vigorous on the external than the internal portion of it. Therefore, the former would first display muscular structure.

"(5) If the first stage is the development of masses of plasma, which display contraction in definite directions, the next step is the division of such masses into muscle-threads or fibrillæ. These threads must be regarded as a result of contractions, whose inequality produces subdivisions of the original mass. A compound structure is also more effective than a simple one in effecting contractions.

"(6) The next stage of evolution of muscular tissue consists of the appearance of the cross-striping. The mechanical effect of the cross-striping is to distribute the contractility equally throughout the length of the fiber. The contractions of the unstriped muscular fiber are less vigorous, and also less uniformly distributed than those of the striped fiber. *The cross-striping is a result of contractions.* It commences as simple undulations of the surface of the fiber. The contraction of the plasma is wave-like and is propagated rapidly through the fiber, and is not due to a flow and return of the contained protoplasm. The frequent repetition of these local contractions and enlargement of the fiber have resulted in a permanent difference in its intimate structure, the alternate waves becoming fixed as cross-bands."

As evidence of the truth of this proposition, (6), Eimer cites many facts. In the muscles of the Mollusca, striped fibers occur in those forms, as Pecten, where the closing of the shell is especially vigorous, this being their mode of progress through the water. In other forms, where the muscles have no such vigorous use, the fibers are smooth. In Arthropoda, the muscles of the legs of swiftly running forms are striped, while those of the alimentary canal are smooth. It is a general law that muscles which have energetic contractions are striped, while those in which the contractions are slow or feeble, are smooth. In the common house-fly, Eimer records some remarkable observations. Flies examined in winter, during the period of torpidity, were found to have the fibers of the thoracic muscles smooth. With advance of the spring the striping gradually made its appearance, and in the summer it was fully developed. An artificial imitation of winter, by refrigeration in an ice-cellar, caused the cross-striping to disappear. The striping in some other animals is shown by Eimer to be strongly influenced by physical conditions.

In fact, muscular tissue is highly plastic, and as it is directly under the control of nervous or equivalent stimuli, the effect of the latter in building structure is evident. That the motion communicated to the hard parts through the agency of the muscular system is effective in building the hard structures will be shown in a subsequent section.

2. KINETOGENESIS IN MOLLUSCA.

a. The Origin of the Plaits in the Columella of the Gastropoda.

Mr. W. H. Dall has developed the mechanics of evolution in the Gastropoda, and I quote extracts from one of his papers to show the harmony of his views with those of other Neo-Lamarckians.[1] "The question which first arises is as to the origin of the columellar plications and their function. In considering the dynamic relations of the animal to its shell we may obtain satisfaction on this point. In the fusiform Rhachiglossa an anatomical difference exists to which I believe attention has not hitherto been called. Indeed, unless the principles of dynamic evolution are granted, it is a difference which would appear to have little or no significance. These principles, however, afford a key which seems to unlock this and many other mysteries. In the recent forms of this sort the adductor muscle, which in all gastropods is attached to the columella at a certain distance within the aperture, is attached *deeper within the shell* than in non-plicate forms. The point of attachment may be an entire turn, or even more, behind the aperture, while in short globose few-whorled shells and in the non-plicate forms it is, as a general rule, little more than half a turn behind the aperture.

"Now let us consider the dynamics of the case. We have, reduced to its ultimate terms, a twisted, shelly, hollow cone, subangulate or even channelled at two ex-

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[1] *Transactions of the Wagner Free Institute of Science*, Philadelphia, Aug., 1890, p. 58.

tremes corresponding to the canal and the posterior commissure of the body and outer lip. Inside of this we have a thin, loose epithelial cone, the mantle, of which the external surface, especially toward the margin, is shell-secreting; lastly, inside of the mantle-cone we have a more or less solid third cone, consisting of the foot and other external parts of the body of the animal, which can be extended beyond the mantle-cone outwardly, as the mantle-cone can be beyond the shell-cone. The body-cone and the mantle-cone are attached at one of the angles of the shell-cone some distance within the opening of the spiral of the latter. The two outer cones constitute a loose, flexible funnel within a rigid, inflexible funnel, while the body-cone forms a solid, elastic stopper inside of all.

"What will happen according to mechanical principles (which can be tested by anybody with the simplest apparatus) when the mantle-cone is withdrawn into a part of the shell-cone too small for the natural diameter of the contracted mantle-cone? It must wrinkle longitudinally. Where will the wrinkles come? They will come at the angles of the shell-cone first; they will be most numerous toward the aperture, since toward the aperture the mantle-cone enlarges disproportionately to the caliber of the shell, owing to its processes, the natural fold of the canal, etc., etc.; the deepest and strongest wrinkles will be on the pillar, owing to the fact that the attachment of the adductor prevents perfect freedom in wrinkling and the groove of the canal will mechanically induce the first fold in that vicinity. The most numerous small wrinkles will be near the aperture opposite the pillar, because of the mantle-edge this is the most expanded part, and there will be a tendency to a ridge near the angle of the posterior commissure. Repeated dragging of a shell-secreting surface, thus wrinkled, over a surface fitted to receive such secretion, will result in the elevated shelly ridges which on the pillar we call plications; and on the outer lip liræ, if long, or teeth, if short. The commonly existing subsutural internal ridge on the body of the shell near the posterior commissure will mark the special conditions in that part of the aperture.

"When the secreting surface is thus wrinkled or corrugated longitudinally, the wrinkles and the concave folds between them will be directed in the sense or direction in which the body moves in emerging from or withdrawing to the whorl. The summits of the convex wrinkles will be appressed more or less forcibly against the shell-wall exterior to them in which they are confined. The semi-fluid, limy secretion of which the shell-lining is built up, exuding from the whole surface of the mantle, will be rubbed away from the lines of the summits of the wrinkles and tend to accumulate in lines corresponding to the concave furrows between the wrinkles. This secretion hardens rapidly and these lines would become somewhat elevated ridges which would by their presence (when once initiated)

Fig. 56.—*Fusus parilis* Con. the body whorl opened, displaying non-plicate columella. From Dall.

tend to maintain the furrows and wrinkles in the same place with relation to the thus-initiated liræ, as these elevated lines are called when on the outer lip; or plaits, when situated on the pillar.

"The modification referred to generally takes place during resting stages of the animal's growth, since while the animal is rapidly extending its coil the secretions seem to be directed toward the extreme margin, and the general mantle-surface resumes its secretive function (or the latter becomes active) somewhat later, after the formation of a definite varix, or thickened margin; indicating a resting stage in the animal's career. It is probable also that during rapid growth there is less compression of the tissues than during the resting-stages. The external sculpture and some of the modifications of the aperture are connected with the functions of the extreme edge of the mantle; those we are at present considering relate more especially to the function of its general surface by which the layer which lines the whorls, the pillar, plaits, and liræ are solely secreted and deposited.

"In species with the abductor attached to the pillar near the aperture, the wrinkles would be fewer, and their action, if any, confined to the vicinity of the margin of the aperture. The deeper the attachment, the greater will be the compression of the secreting surface and the distance over which it is constantly dragged back and forth, and the consequent length of the ridges of shelly matter deposited. If the inner or mantle-cone had the whole cavity to itself, it is evident that it could and would infold itself in a manner which might not appress its folds against the inner surface of the rigid outer or shell-cone. But there the mass of the solid and elastic foot and external body comes into play, and by its withdrawal inward forces the wrinkled mantle-cone against the shell. The mantle is thus confined between a rigid outer and an elastic inner surface, with the result that it cannot recoil from the former and that a certain uniformity of size and direction is imposed upon the wrinkles, except where the recess of the canal allows them to become more emphatic, or to a less degree the posterior angle permits a slight expansion. The mechanical principles involved may be readily illustrated by the experiment of pulling a handkerchief through the neck of a bottle, or funnel, followed by a cork in the center. Of course, the more nearly the apparatus conforms to the form and twist of a spiral shell, the more nearly the results will approximate those of nature. It is difficult, however, to find any artificial tissue which will correspond in elasticity, or capacity for partial self-contraction, to the living tissues concerned in nature. Hence, an exact conformity is not to be expected, though the mechanical principles may be reasonably well illustrated.

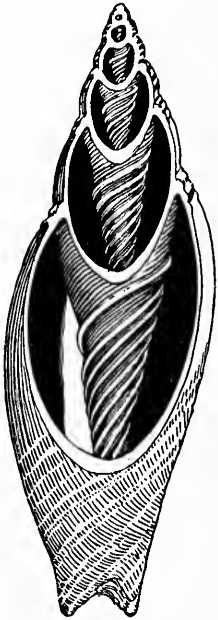

Fig. 57.—*Mitra lineolata* Heilprin, the body-whorl opened, showing the plications of the columella. From Dall.

"A comparison of specimens will show that the results exhibited agree with marvellous precision with the results called for by the preceding hypothesis, based on the dynamical status of the bodies concerned, their motions and secretions. The agreement is so complete as to amount to a demonstration, though in certain cases there may be complications which need additional explanation.

"A point which may be noted in regard to the Volutidæ, to which my attention was called by Mr. Pilsbry, is that in this group the mantle is greatly extended, and there would be more of it to be wrinkled than in such forms as Buccinum, etc. It may be added that the forms in which we note the beginning of plaits for this family, many of them, such as Liopeplum and Volutomorpha, had the mantle so extended as to deposit a coat of enamel over the whole shell, as in the modern Cypræa, so that here we have an additional reason why plication should be emphasized in this group.

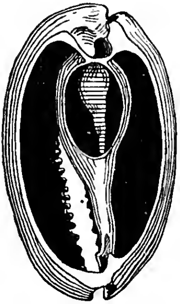

Fig. 58.—*Siphocypræa problematica* Heilprin; body-whorl opened, showing plications of lips. From Dall.

"Of course, as before noted, the mechanical principles are the same in any group of gastropods, but among those in which the wrinkling is confined to the region of the aperture, or those shells which are lirate or dentate, as opposed to plicate, several other principles come into play which may be briefly referred to in passing. In the first place, those species which have a very extended mantle, with hardly an exception have a lirate aperture (Oliva, Olivella, Cypræa, Trivia, etc.). With species in which there is a widely expanded mantle and yet no lirations, it will usually be found that the mantle is not entirely withdrawn into the shell in such forms, or is permanently external to the shell (many

Opisthobranchs, Marseniidæ, Sigaretus, Harpa, etc.). In a group like the Cypræidæ, where nearly all the species are lirate on both lips, there are a few which want these liræ, and these are species which have a wider aperture in the adult than most of the genus, and in which we should expect the wrinkles to be less emphatic."

b. Mechanical Origin of Characters in the Lamellibranchs (Pelecypoda).

Dr. Robert T. Jackson has pointed out[1] the history of the characters of the retractor muscle and some of those of the list, of bivalve Mollusca. I take the following abstract of his conclusions: "In the development of pelecypods we find in a late embryonic stage (the phylembryonic) that the shell has a straight hinge-line. This is characteristic of Ostrea (Fig. 59), Cardium, Anodonta, and so many widely separated genera that it apparently represents a primitive ancestral condition common to the whole class. Embryology shows that the bivalve shell doubtless arose from the splitting on the median line of a primitive univalvular ancestor. If that ancestor had a saddle-shaped[2] or a cup-shaped[3] shell, as is probable, the first result of the introduction of a hinge in the median line would have been to straighten the shell on the hinge-line. This is a simple problem in mechanics, for if one tries to break by flexion a piece of metal which is saddle-shaped or cup-shaped, it will tend to form a straight line on the axis of flexion. A parallel case is seen in the development of a bivalve shell in ancient crus-

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[1] *Memoirs of the Boston Society of Natural History*, Vol. IV., No. 8, p. 277 July, 1890; *American Naturalist*, 1891, p. 11.

[2] Characteristic of young Dentalium.

[3] Characteristic of the extreme young of cephalous mollusks.

taceans. The ancient Ostracoda, Leperditia, Aristozoe, etc., have a straight hinge-line and subcircular valves, which are united dorsally by a ligament. The resulting form of the early condition of the bivalvular shell in these two distinct classes is so strikingly similar, that it lends weight to our supposition that the form is induced by the mechanical conditions of the case.

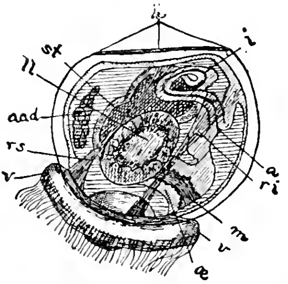

Fig. 59.—*Ostrea edulis*, embryo; *a ad*, anterior adductor muscle; *m*, mouth; *a*, anus; *v*, velum; *h*, hinge of shell. (After Huxley.)

"I think that the adductor muscles which close the valves may also be demonstrated to be the necessary consequence of the bivalvular condition. In the phylembryo stage (Fig. 59) the valves are closed by a single adductor muscle, which is the simplest condition mechanically possible to effect the desired end.[1] This muscle does not seem homologous with any muscle in other classes of mollusks, and is probably developed from the mantle muscles as a consequence of the conditions of the case. In support of this view, bivalvular crustaceans may again be cited. They have an analogous adductor muscle, developed, of course, on an entirely different line of descent, but under closely similar mechanical conditions. At the completed prodissoconch stage in all pelecypods, as far as known, there are two adductor muscles, a second one having developed in the posterior portion of the body. In later life the anterior, the posterior, or both adductors

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[1] This early adductor appears in the same position in many genera, and is apparently characteristic of the class. It is the anterior of the two adductors found in the later stages; but it may be retained or lost in the adult.

may be retained, reduced, or lost, according as the persistence or changes in correlated anatomical features retain in use or bring into disuse the muscles in question.

"Let us look at examples of the retention or loss of the adductors. In typical dimyarian pelecypods, as in Mya (Fig. 60) or Venus, the adductors lie toward either end of the longer axis of the shell. As the hinge occupies a position on the borders of the shell about midway between the adductors, both muscles are nearly or quite in a position to be equally functional in closing the valves. As a result, both muscles are of about the same size. The condition described is that existent in the completed prodissoconch stage in all pelecypods, as far as known. In later life, however, a revolution of the axes of the soft parts may take place, so that the antero-posterior axis (represented by a line drawn through the mouth and middle of the posterior adductor muscle), instead of being parallel to the hinge-axis (the axis of motion of the valves) as in dimyarians, may present a greater or less degree of divergence from the parallel. In progressive series,

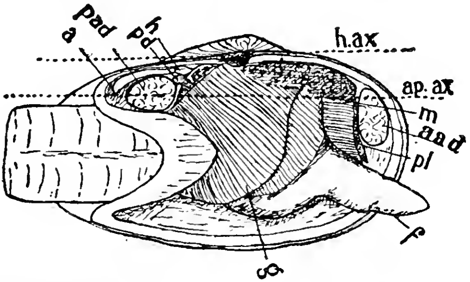

Fig. 60.—*Mya arenaria.* Lettering: *ap ax*, antero posterior axis; *h ax*, hinge axis; *a ad*, anterior, and *p ad*, posterior adductor muscle; *m*. mouth; *pl*, palps; *a*, anus; *g*, gills; *pd*, pedal muscle; *f*, foot; *b*, byssus; *h*, heart.

as in Modiola (Fig. 61), Perna, etc., as the adductor muscle is brought nearer and nearer to the hinge-line,

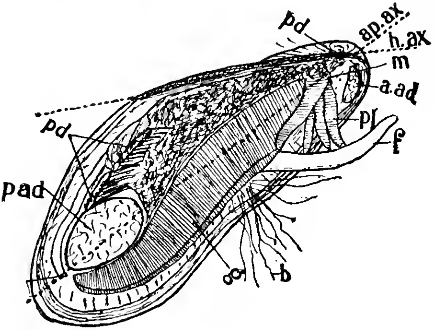

Fig. 61.—*Modiola plicatula*. Lettering same as in Fig. 60.

where its mechanical action is less and less effectual in closing the valves, we find that it is more and more reduced until it finally disappears from disuse and atrophy, as in Ostrea (Fig. 62), and Pecten. Conversely, the posterior adductor in the same series in the revolution of the axes is pushed farther and farther from the hinge-line and nearer to the central plane of the valves, where its mechanical action is most effectual in closing the valves. With its increase in functional activity the muscle increases in size. The revolved position of the axes, and the consequent reduction or loss of the anterior adductor and increase of the posterior adductor, is

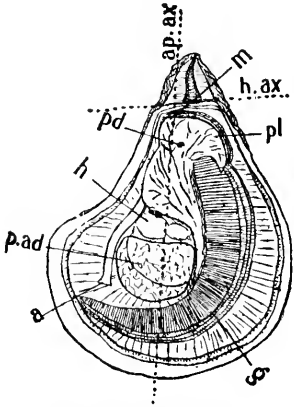

Fig. 62.—*Ostrea virginiana*. Lettering same as in Fig. 60.

found in many widely separated genera of pelecypods, as Ostrea, Mulleria, and Tridacna; thus proving the development of the same features on different lines of descent.[1] In Aspergillum the two valves have concresced so as to form a truly univalvular, tubular shell, so that the adductors would evidently be functionless if existent. The posterior adductor has disappeared and the anterior is reduced to a few disconnected shreds (Fisher), though evidently existent in the young, as attested by the form of the shell in the nepionic stage.

"Ordinarily there are two posterior retractor-muscles of the foot in pelecypods, one situated on either side. In adult Pecten either the left retractor alone exists, or both retractors are wanting (the left doubtless always exists in the young). In studies of young *Pecten irradians*, I found that the animal always crawled while lying on the right side, with the foot extended through the notch in the lower valve and pressed against the surface of support. It is evident that while crawling in this position the left retractor is in the plane of traction, and it is retained; on the other hand, the right retractor would not be in the plane of traction, and it has disappeared through disuse and atrophy.[2] A similar disappearance of the right retractors of the foot is seen in *Anomia glabra*, and is explained on similar bases of argument.

"In *Mya arenaria* we find a highly elongated siphon. In the young the siphon hardly extends beyond the borders of the valves, and then the animal lives at or

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[1] Dr. B. Sharp and I published almost simultaneously closely similar views on the mechanical aspect of the relative size of the adductors. See *Proceeds. Phila. Acad.*, 1888, p. 122, and *Proceeds. Boston Soc. Nat. Hist.*, Vol. XXIII., 1888, p. 538.

[2] Both retractors doubtless exist in the prodissoconch stage of Pecten and allies.

close to the surface. In progressive growth, as the animal burrows deeper, the siphon elongates, until it attains a length many times the total length of the valves. The ontogeny of the individual and the paleontology of the family both show that Mya came from a form with a very abbreviated siphon, and it seems evident that the long siphon of this genus was brought about by the effort to reach the surface, induced by the habit of deep burial.

"The tendency to equalize the form of growth in a horizontal plane in relation to the force of gravity acting in a perpendicular plane, or the geomalic tendency of Professor Hyatt,[1] is seen markedly in pelecypods. In forms which crawl on the free borders of the valves the right and left growth in relation to the perpendicular is obvious, and agrees with the right and left sides of the animal. In Pecten the animal at rest lies on the right valve, and swims or flies with the right valve lowermost. Here equalization to the right and left of the perpendicular line passing through the center of gravity is very marked (especially in the Vola division of the group); but the induced right and left aspect corresponds to the dorsal and ventral sides of the animal, —not the right and left sides, as in the former case. Lima, a near ally of Pecten, swims with the edges of the valves perpendicular. In this case the geomalic growth corresponds to the right and left sides of the animal.

"The oyster has a deep or spoon-shaped attached valve and a flat or flatter free valve. This form, or a modification of it, we find to be characteristic of all

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[1] "Transformations of Planorbis at Steinheim, with Remarks on the Effects of Gravity Upon the Forms of Shells and Animals." *Proceeds. A. A. A. S.*, Vol. XXIX., 1880.

pelecypods which are attached to a foreign object of support by the cementation of one valve. All are highly modified, and are strikingly different from the normal form seen in locomotive types of the group. The oyster may be taken as the type of the form adopted by attached pelecypods. The two valves are unequal, the attached valve being concave, the free valve flat; but they are not only unequal, they are often very dissimilar,—as different as if they belonged to a distinct species in what would be considered typical forms. This is remarkable as a case of acquired and inherited characteristics finding very different expression in the two valves of a group belonging to a class typically equivalvular. The attached valve is the most highly modified, and the free valve is least modified, retaining more fully ancestral characters. Therefore, it is to the free young before fixation takes place and to the free, least-modified valve that we must turn in tracing genetic relations of attached groups. Another characteristic of attached pelecypods is camerated structure, which is most frequent and extensive in the thick attached valve. The form as above described is characteristic of the Ostreidæ, Hinnites, Spondylus, and Plicatula, Dimya, Pernostrea, Aetheria, and Mulleria; and Chama and its near allies. These various genera, though ostreiform in the adult, are equivalvular and of totally distinct form in the free young. The several types cited are from widely separated families of pelecypods, yet all, under the same given conditions, adopt a closely similar form, which is strong proof that common forces acting on all alike have induced the resulting form. What the forces are that have induced this form it is not easy to see from the study of this form alone; but the ostrean form is the base of a series, from the summit of which we get a clearer view."

c. Mechanical Origin of the Impressed Zone in Cephalopoda.

Prof. Alpheus Hyatt has shown that the groove on the dorsum or inside of each coil of the Cephalopoda is due to the pressure exercised by contact with the ventral side of the coil within it. He has shown that this groove persists in cases where the shell in the course of evolution has become more or less unwound, and he regards this as an example of the inheritance of a mechanically acquired character. This subject is presented in greater detail in the part of this book devoted to heredity.

3. KINETOGENESIS IN VERMES AND ARTHROPODA.

It is believed with good reason that the Arthropoda have descended from some of the forms included in the branch Vermes, and perhaps Peripatus furnishes the nearest living approach to that type. The ancestor, whatever it may have been, developed limbs from processes of the body-wall, and used them to aid in progression. Peripatus has soft flexible limbs, and a non-chitinous integument generally. With the beginning of induration of the integument, segmentation would immediately appear, for the movements of the body and limbs would interrupt the deposit at such points as would experience the greatest flexure. The muscular system would initiate the process, since flexure depends on its contractions, and its presence in animals prior to the induration of the integuments in the order of phylogeny, furnishes the condition required. It is a matter of detail how the diverse segmentations of existing forms were produced. We can believe, however, that, as in Vertebrata, there has been a gradual elimination of less important segments of the limbs, until the highest mechanical efficiency was attained. We well know how the segments of the head and body have been modified by fusion, etc.

Prof. B. L. Sharp has shown the mechanical conditions of segmentation in Arthropoda as follows:[1]

"It occurred to me that if the theory [of kinetogenesis] had a general application, some additional proofs could be shown to exist among the invertebrates, where we have the action of muscular force upon hard and resisting parts of the skeleton. Those which present the best study for this purpose appear to be the crustaceans, where we find an immense variety of articulations in the body and in the limbs; highly complicated locked joints, others allowing motion in but one plane, as well as loose joints, where the hard parts scarcely come in contact with one another, and cases of degeneration of the hard parts, leading to total disappearance of a previously existing joint.

"In the Anneiides, from which, there is no doubt, the arthropod branch sprang, we find no deposit of inorganic salts in the epidermis. The outer layer of the body is generally of a horn-like character, adhering closely to the secretive cells of the epidermis, very flexible, and thrown into folds by the vermicular motion of its possessor. In the leeches the body consists of a flexible cylinder, made up of two sets of muscles, an outer longitudinal cylinder and an inner cylinder of circular fibers, the contraction of which causes the animal to increase in length, while shortening is ef-

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[1] *American Naturalist*, 1893, p. 89.

fected by the contraction of the longitudinal layer. The external surface of the medicinal leech, for example, is thrown into a regular series of very fine folds, extending across the longitudinal axis of the body. These folds do not correspond in numbers to the somites of the body, which are not indicated externally, five, six, or more of them belonging to one somite. When the animal shortens its length, these folds are deepened and the segments thrown closely together; when extension takes place, the folds are flattened, spread open, although not wholly disappearing, as they are a fixed quantity, so to speak. I believe these folds are due to mechanical action; by the disposition of the different fibers of the longitudinal series, in being inserted in a series of planes bounded by the valleys between the folds, this being aided by some of the circular fibers which pass through the longitudinal sheath, and find their attachment to the bases of the valleys.

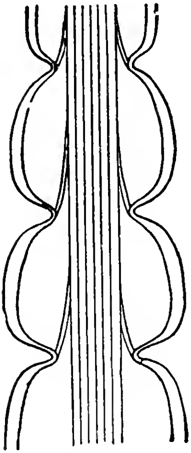

Fig. 63.—Diagrammatic representation of the segments of the leech, showing the folds, valleys, and muscular fibers.

"Starting from this point, and supposing the regularity of the folds to have become established from preëxisting folds by the regularity and stress of muscular action, we can conceive that when deposits of calcareous matter took place, rings similarly formed by a folding of a soft skin would receive that deposit at the most prominent portion of this fold, the convex face, and not in the protected valleys, as there would be more friction or pressure from external causes, and no deposits would take place in the valleys themselves, because they would not be subject to external friction, and their continual flexion would prevent any such deposits. Should such a deposit take place in the valleys, there would be a stiffening of the whole surface, which would defeat motion. In fact, in the leech the cuticle is already much thicker on the crests of the folds than in the valleys.

"In the more primitive Crustacea, we find the animal made up of rings extending over the whole length of the body, similar to the rings of the leech, save that there is but one ring to one somite, and instead of a perpendicular valley between the folds, this valley has an inward and a forward direction, allowing the anterior edge of a caudad ring to fit into the posterior edge of a cephalad ring.

"In the higher Crustacea, several of the anterior rings have coalesced and form a solid shield which is known as the carapace. This has no doubt arisen by the lessening of the action between the anterior rings when the posterior portion of the body became the more active propelling organ. As the action ceased forward the valleys came to rest, and became exposed to friction and pressure, and consequently a deposit of calcareous matter took place producing the stiffening above hinted at.

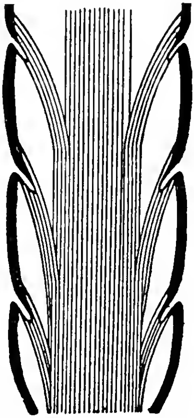
Fig. 64. — Diagrammatic representation of the rings of a primitive crustacean, showing the action of the muscles.

"The formation of jointed appendages from parapodic paddles of the annelids can be followed out in the same manner, since the manner of mutual relation of the segments is the same as in the case of the body-segments.

"It has been stated that in the leech the folds do not correspond in number to the somites of the body, while they do in the Crustacea. All annelids do not move by means of a muscular system built upon the plan found in the leech. In many the circular layer has to a large extent disappeared, for the longitudino-circular plan is undoubtedly ante-annelidan. The movement of the free medusoid forms, and of the Ctenophora, is the result of a modified arrangement of this plan.

"With the disappearance of the circular layer, we find a peculiar modification of the longitudinal layer. This layer becomes broken up and the fibers act in moving the setæ, which answer to limbs. In a segment of a setiferous annelid, we may observe that the longitudinal muscles of the somite in section at the position of the seta are arranged like the letter 'V' in the fork of which the seta lies, the fibers to the left (anterior) pull the seta externally backward, those on the right (posterior) pull the seta forward. The introduction of the setæ, the origin of which I do not here attempt to explain, has no doubt been, together with the establishment of the external segmentation, a strong factor in causing the breaking up of the muscular tube into sections (myotomes), which by use and consequent increase have extended each arm of the 'V' into the segment on each side, while the insertion of the end of the seta has caused a break in the muscle by the formation of an aponurosis. This gives us the peculiar disposition of a myotome to extend across the union of two somites.

"If we examine the segments of the so-called abdomen of the macrurous Crustacea, as the lobster, we will find that the anterior face of one abdominal ring is pulled into the posterior orifice of the ring lying anterior to it, forming a kind of tubular ball and socket-joint, but with a flexible part of the integument with no calcareous deposit, folded upon itself, and acting physiologically as a tubular *ligamentum teres*. On examining the different joints, we will find that commencing at a fixed point, as at the base of the thorax, the movable ring of the first abdominal somite is *pulled into* the fixed part. Then the first abdominal somite becomes the fixed point for the movable ring posterior to it, and so on, so that we find that as the rings proceed away from the thorax, each is pulled into the opening of the one in advance. This is true of all those forms where the abdomen is well formed, strong, and an active organ in the economy of the animal; when this organ, the abdomen, ceases to be an active organ of motion, as in the burrowing forms, as in Callianassa, Gebia, some of the Squillidæ, etc., or where it is folded upon the sternum of the thoracic region, the muscles becoming weaker through disuse, the rings are not subject to the powerful muscular strain, and they as a rule overlap but little, if at all, but lie so that the edge of one ring rests upon the edge of another. In those forms where degeneration of the abdomen has proceeded so far as not to have even the usual deposit of calcareous matter, as in the hermit crabs, there are simply indications of rings on the abdomen, and this organ is but little more than a fleshy sac containing some of the viscera, and supplied with a few muscles which act together, with the form of the organ, to keep the abdomen curled so that it may hold as a hook, the animal within the molluscan shell which it habitually inhabits.

"When the limbs are examined, the same rule will be found to hold good, viz.: that the movable part is pulled into the fixed part. A modification of this is well illustrated in the evolution of the large chelæ. In some forms, take for example Ibacus, the first pair, and in fact all of the thoracic limbs end in a sharp-pointed segment, there being not the slightest suggestion of a chela. In Crangon, on the other hand, the terminal segment is pulled against the broad face of the penultimate one thus making a shift for a chela. In the Stomatopoda this step has been developed, for the last segment can be drawn against the whole length of the penultimate one (which is sometimes grooved to protect the points of the spines of the latter) and forms with it a very effective grasping organ. The continual use of the terminal segment, the increase of the muscular power will tend to draw this terminal segment backward (into) on the penultimate which enlarges with the increase of bulk of muscle, so that a well-developed chela, as in the lobster is found, where the ultimate segment is pulled backward to about the middle of the penultimate segment."

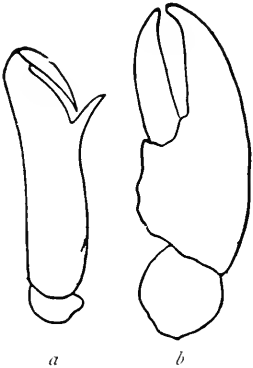

Fig. 65.—Diagrams of, *a*, hand of a form of Crangon; *b*, hand of a form of Astacus.

4. KINETOGENESIS IN THE VERTEBRATA.

I have already adduced the evidence in support of the doctrine that the structures of the hard parts of invertebrates have been produced by muscular movements. In turning to the Vertebrata we shall find that the evidence indicating that the details of their hard parts have had a similar origin, is quite convincing. This branch of the animal kingdom presents two distinct advantages for this study. First, we have a more complete paleontologic series than in any other. Second, we have the best opportunity for observation and experiment on their growth processes, since we ourselves, and our companions of the domesticated animals, belong to this branch of the animal kingdom.

I shall show first, the conditions under which abnormal articulations of the skeleton have been formed; and then the process involved in the formation of normal articulations. I shall then apply these facts to the phylogeny of the Mammalia as we know it, and then in a more general way to the Vertebrata as a whole.

i. KINETOGENESIS OF OSSEOUS TISSUE.

a. Abnormal Articulations.

Hütter, from whom I have quoted under the head of "Kinetogenesis of Muscle," thus describes the effect of abnormal conditions of joints on the articular surfaces of the bones which form them. He says: "We have abundant opportunity to investigate the change of condition which the joints undergo during a year of fixed muscular contraction.

"The ligaments and bursæ undergo similar changes to those described for the muscles concerned. They elongate at points where the articular surfaces are spread apart, and correspondingly shorten where the flexure produces a folding. These changes proceed more slowly than those of the muscles and tendons. Very remarkable are the changes undergone by the articular cartilages. When a joint is permanently flexed, a part of the extremity of each bone is separated from contact with the other, and the articulation is finally destroyed at this point, because the cartilage begins to vanish. One must conclude that the existence of the articular cartilages is dependent on their mutual contact; for dislocated articular surfaces which remain in contact with soft tissues only, lose their cartilaginous covering. . . . Finally it is possible by a consideration of the etiology of the effects of joint contractions to reach some hitherto unnoticed conclusions regarding the changes of articular surfaces, and bone forms. The results of joint-contraction are most conspicuous when the latter occurs in childhood. During maturity, a dislocation which causes an articular border or prominence to rest abnormally on the opposed articular face in the act of walking, will be followed by the penetration of the former into the latter, and a deformation of the articulation; but the corresponding changes under like conditions in the growing skeleton are much more conspicuous."

Hütter thus describes the formation of new articular surfaces as a consequence of dislocation of joints. "If the head of the femur or humerus leaves its socket, and rests on the side of the ilium or the scapula, the periosteum of the bone which receives the new impact is excited to active bone-production, and the result is the deposit of new osseous tissue. The thin bones become thicker, not uniformly, but in correspondence with the periphery of the head of the humerus or femur, rather than with the point of contact of the latter. This point is irritated, but the contact of the ball restrains osseous deposit. So it occurs that gradually a new socket is developed, whose mechanical relations correspond exactly with those of the articulating bone. The head also acquires a strictly spherical shape, by such contractions and atrophies as are necessary to produce that result. Further, cartilage appears in the place of the periosteum of the socket, which functions like the primitive articular cartilage. It is characteristic of both connective and periosteal tissue to develop cartilage under the stimulus of continued friction of hard surfaces, such as occurs in dislocations and fractures."

These observations of Hütter have been confirmed by Henke, Reyher, Moll, and Lesshaft. Henke and Reyher state that the artificial prevention of flexure of articulations in young dogs renders them immobile, and their restraint of flexure to one direction, results in a curving of the articular faces in that direction.

I cite here two examples of modifications of structure under abnormal conditions which imposed new impacts and strains on the parts. I have described these cases, which are examples of false elbow-joints in man and in the horse, in the *Proceedings of the American Philosophical Society* for 1892.

In the first case, that of the human elbow, the cubitus was luxated posteriorly, so that the humeral condyles articulate with the ulna anterior to the coronoid process. The head of the radius is in contact with the external epicondyle on its posterior inferior face. The results are as follows. A new coronoid process was developed in front of the abnormal position of the humeral condyle to an elevation above the shaft of the ulna exceeding that of the normal coronoid. Between it and the normal coronoid was developed a perfectly functional cotylus which embraces the humeral condyle like the normal cotylus. The latter has its articular surface, buried under osseous deposit, so as to be no longer visible. The region of contact between the head of the radius and the external epicondyles, has developed in the latter a large articular cotylus which permits of both rotary and vertical movement of the former. The articular surface of the humeral condyles, except where in articulation with the ulna, is roughened, and partially overgrown with exostoses, so as to alter its form to a great extent. The opportunity of examining this specimen I owe to Provost Pepper of the University of Pennsylvania, in whose museum it is preserved.

In the case of the horse's elbow, the luxation of the cubitus is inward, so that the olecranon articulates with the external epicondylar surface, and the humeral condyles are not adapted to the head of the radius; their internal border falling considerably internal to the inner border of the radius. The horse from which this specimen was derived lived for two years after the luxation took place, and became able to use the limb in some degree. The effect on the articulation is as follows.

A large part of the inferior extremity of the posterior rib of the shaft of the humerus, which is the place of insertion of the external *flexor metacarpi* muscle, has been removed, so as to present a wedge-shaped outline with the apex downward. This removal permits the close articulation of the inner face of the olecranal process with the epicondyle, which has developed a considerable articular face, on which movement takes place in extension and flexion. The posterior border of this face has developed a ridge which borders the facet behind, and retains the olecranon in place. Two other facets are developed on the humeral condyles, and two on the head of the radius. The most important of the latter is a bevel of the external part of the surface to the border, due to the contact of the expanded internal humeral condyle. The articular face of the olecranon is much depressed in consequence of its articulation with the external epicondyle of the humerus. Besides these new and changed facets, the effect of the luxation is seen in the development of osseous crests at the points of insertion of the articular ligaments. One of these on the humerus has been already referred to. Another is concentric with and posterior to the internal humeral facet of the olecranar process, and serves as a guide to the humeral crest above described. A third is an extensive osseous deposit on the internal face of the head of the radius, which partially builds an extension of the head of the radius, which if completed would articulate with the overhanging portion of the internal humeral condyle. A third modification of normal structure is similar to that observed in the human elbow. It consists of osseous deposit beneath the synovial bursa at points where the luxation causes a gaping of the surfaces. This occurs at the trochlear groove of the head of the radius, which is partially filled up with exostosis.

The preceding observations lead to the following conclusions:

First. Continued excessive friction removes osseous tissue from the points of contact until complete

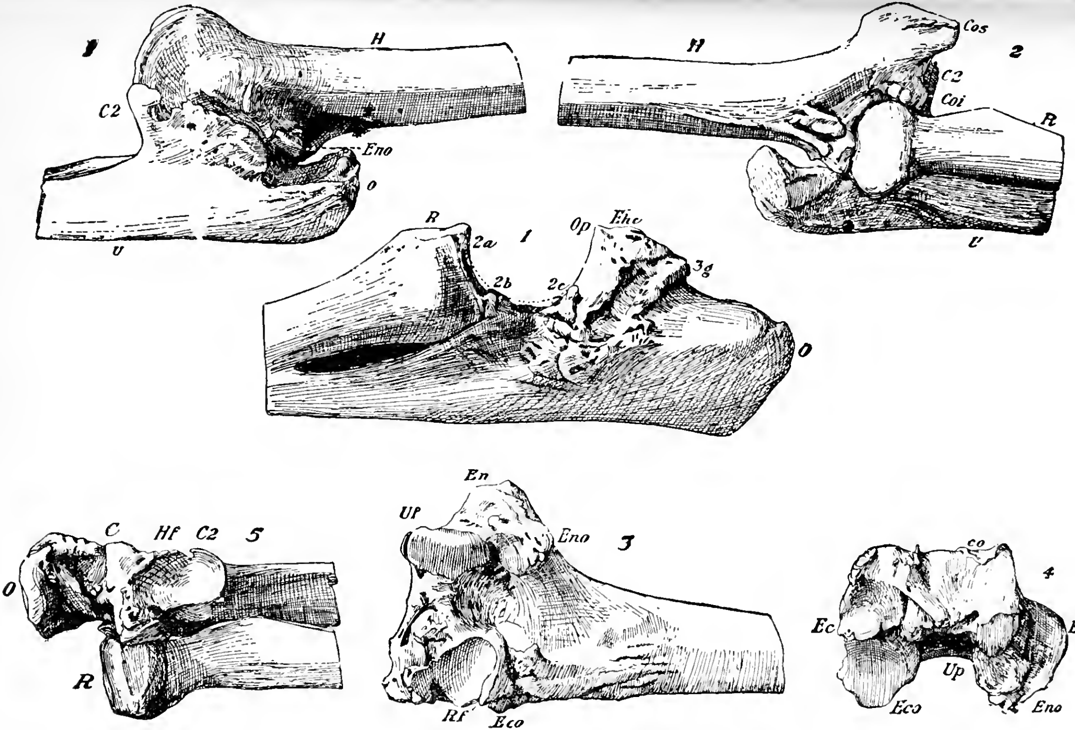

Fig. 66.—Elbows of man and horse.

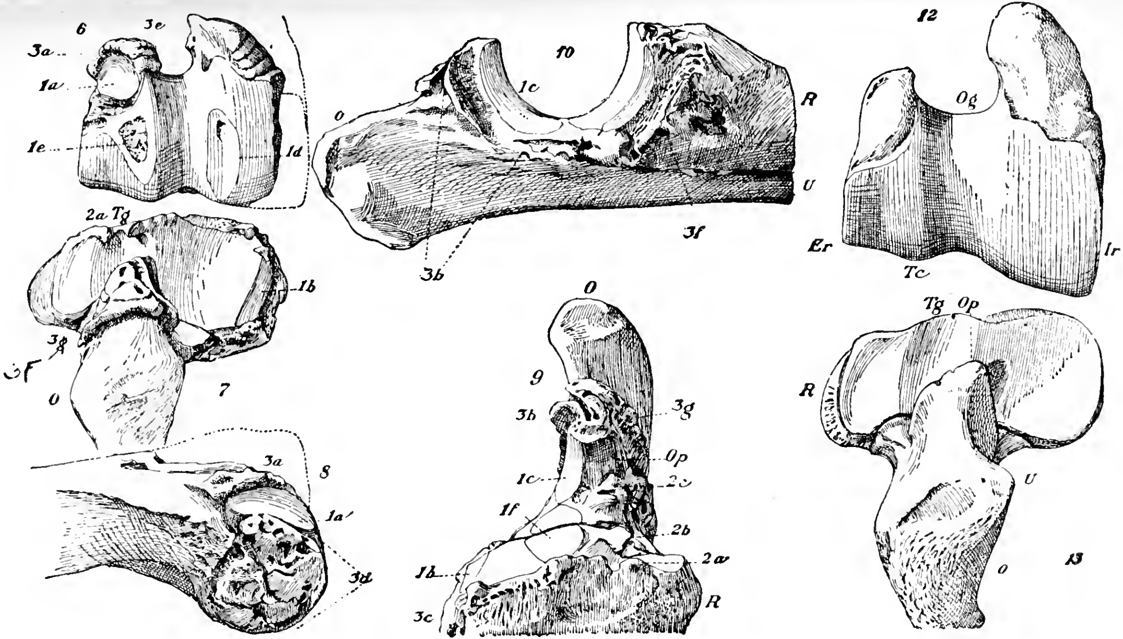

Fig. 67.—Elbow of horse.

adaptation is accomplished and the friction is reduced to a normal minimum. Then a normal articular surface is produced.

Second. Where the normal friction is wanting, and an inflammatory condition is maintained by a pulling stress on the investing synovial membrane, excess of osseous deposit is produced.

Third. Stress on the articular ligaments and tendons stimulates osseous deposit at their insertions, which deposit may be continued into their substance. This is a pulling stress.

These observations therefore show that osseous deposit is produced by different forms of mechanical stimulus.

EXPLANATION OF FIGURES 66 AND 67.

1–5, *Homo sapiens*, luxated elbow joint (one-half natural size); 1, luxated elbow joint, from within; 2, luxated elbow joint, from outer side; 3, humerus, posterior view of distal region; 4, humerus, distal view; 5, ulna and radius, anterior (superior) view; 6–11, bones of abnormal left elbow joint of horse (one-half natural size); 12, 13, normal bones of elbow joint of horse (one-half natural size); 6–12, humerus, distal views; 7–13, cubitus, proximal views; 8, humerus, external view of distal extremity; 9, humeral articulation of cubitus, from above; 10, cubitus, internal view; 11, cubitus, external view. Lettering.—*H*, humerus; *U*, ulna; *R*, radius; *C*, coronoid process; *C2*, second (abnormal) coronoid process; *O*, olecranon; *En*, entepicondyle; *Ec*, ectepicondyle; *Eno*, entepicondylar exostosis; *Eco*, ectepicondylar exostosis; *Co*, condylar exostosis; *Cos*, superior condylar exostosis; *Coi*, inferior condylar exostosis; *Hf*, humeral facet; *Rf*, radial facet; *Uf*, ulnar facet; *Op*, olecranar process of ulna; *Cp*, coronoid process of ulna; *Og*, olecranar groove of humerus; *Tc*, trochlear crest of humerus; *Tg*, trochlear groove of humerus; *Ehc*, external humeral facet of coronoid process; *Ihc*, internal humeral facet of coronoid process; *1a*, abnormal facet for coronoid process of ulna; *1b*, do. for internal roller of humerus; *1c*, do. for abnormal facet of humerus; *1d*, do. for internal border of radius; *1e*, do. for olecranar process of ulna; *1f*, do. for trochlear crest of humerus; *2a*, *2b*, *2c*, exostoses of radius and ulna to fill vacuity between humerus and radius and ulna, *3a*, abnormal crest which serves as a guide to the olecranar process of the humerus; *3b*, abnormal crest which serves as a guide to abnormal crest *3a*; *3c*, exostosis extending head of radius inwards to equalize its width with inward luxation of humerus; *3d*, exostoses of external epicondyle of humerus, to equalize its width with outward luxation of radius; *3e*, abnormal exostosis of insertion of external *flexor metacarpi* muscle; *3f*, *3g*, abnormal crest at insertion of external articular ligament on olecranar process of ulna.

b. Normal Articulations.

The origin of condyles and their corresponding cotyli has been made the subject of investigation by several German anatomists. L. Fick[1] expressed the opinion that the concavo-convex surfaces were produced by a wearing away of the surface which became concave, by the free action on it of the surface which became convex, the former being fixed, and the latter free. He found the conditions of muscular insertions to correspond with the conditions of fixity and freedom required; for the insertions are always nearer to the concave surface than to the convex surface. He constructed plaster models of joints, and by moving one on the other obtained a convex surface on the moving, and a concave surface on the fixed extremities. These observations were confirmed by Henke,[2] but he very properly does not regard the result as due to wearing, but to the stimulation of metabolic action in the required directions. R. Fick[3] has confirmed these positions in an extended memoir, and recently Dr. E. Tornier has devoted a still more thorough research to the same subject.[4] R. Fick applied his observations to the question of the phylogeny of the articulations, but did not see in it proof of the operation of mechanical causes, but ascribed it to "inheritance and natural selection" in accordance with the meaningless formula usual at the time he wrote. W. Roux,[5] however, in reviewing Fick's article saw in the obser-

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[1] *Ueber die Ursachen der Knochenformen, Experimental-Untersuchung*, 1859, Göttingen, G. Wiegand.

[2] *Anatomie und Mechanik der Gelenke*, Leipsic, 1863, p. 57.

[3] *Archiv für Anatomie und Physiologie*, 1890, p. 391.

[4] *Archiv für Entwickelungsmechanik*, I., 1894, p. 157.

[5] *Biologisches Centralblatt*, 1891, p. 188.

vations of Fick proof of a direct mechanical cause of the structure. I have pointed out the phylogeny of the articulations in the Mammalia in various papers from 1877[1] to 1889,[2] and in 1881 I advanced the view that their successive evolution was due to impacts and strains (*American Naturalist*, July, 1881 ; *Origin of the Fittest*, p. 373). The opinion of Roux entirely supports my position, and it is further established by the elaborate memoir of Tornier just cited. This author adopts the view that bone-development is controlled by *Druck und Zug* or impact and strain, and he adds some important considerations to those previously advanced. He asserts that "in all existing Vertebrata true bones may appear as secondary structures, since all of these animals possess bands and threads of connective tissue which possess the latent capacity to be changed wholly or in part into cartilage." Thus is accounted for the development of sesamoid bones in tendons, in which category is included the patella. Tornier also shows that the concave articular face (cotylus) is that to which the flexor and extensor muscular insertions are nearest, while the convex face (condyle) is the one most remote from the muscular insertions.

It must be observed that Tornier adopts the language of the American Neo-Lamarckians in using the expression "impact and strain." Impact and strain are different modes of motion. "Impact" implies pressure, while "strain" implies a pulling stress, either direct or torsional. It is therefore alleged by Tornier, as it has been by myself, that opposite modes of mo-

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[1] *Report U. S. Geol. Survey W. of 100th Meridian*, 1875, Vol. IV., p. 277–279. *Proceeds. Amer. Philosoph. Soc.*, 1884, p. 44.

[2] *Amer. Journal Morphology*, 1889, p. 163.

tion may produce metabolic changes in osseous tissue. For this reason it is possible to account for the lengthening of the limb-bones in heavy animals, as an effect of impact, while the astragalus of bats may have been elongated by a stretching strain.

c. The Physiology of Bone Moulding.

Dr. Koelliker has summarized the results of the observations made by himself and his predecessors on the processes of the growth and absorption of bone, which determine the forms of the elements of the skeleton.[1]

Bone is deposited through the agency of uninuclear cells, or osteoblasts, which may under peculiar conditions become enlarged and multicellular, when they are termed osteoclasts. These osteoclasts produce an absorption or destruction of the bone or dentine with which they are in contact, the bone or dentine being passive under the operation. How this is done is not known. Pieces of ivory which have been used to replace bone removed by surgical methods, have been found to be both corroded by osteoclasts, and overlaid by layers of living bone by osteoblasts.

In explanation of the causes which induce the formation and action of the osteoclasts, Koelliker remarks that: "the totality of changes of the jaws during the development of teeth appears to show that it is pressure by the soft parts which causes the absorption of bone. One can admit in the case of the jaw that the dental sacs in process of growth produce by their enlargement a state of irritation in the layer of osteoblasts which originally border the alveolar edge, and

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[1] "The Normal and Typical Absorption of Bones and Teeth," *Verhandl. der Phys. Med. Ges. von Würzburg*, II., III., 1872.

that in consequence of this irritation the cellules transform themselves into osteoclasts, and acquire a new power, that of absorbing bone. The function will cease as soon as the teeth are formed, by the termination of pressure, and then the formative action of the cellules adjacent to the bone will repair it as a consequence of a retransformation of these elements into osteoblasts.

"I will not push further this first attempt at an explanation of the normal absorption of bone, but I content myself with observing, that in any case, pressure exercised by the soft parts counts for much in this phenomenon. Who does not remember in the face of these facts, numerous cases of pathological absorption of bone due to aneurisms, tumors, and hypertrophied organs? Who will not admit the great effect of the disappearance or arrest of development of organs on the size of their osseous surroundings; as Fick, formerly professor of anatomy at Marburg, has shown to take place in the orbit after the extirpation of the eye? It is possible to go a step further in the proposition, that external pressure has much to do with absorption. Thus the growth of the brain and spinal cord produce the resorption seen in the interior of the skull and of the spinal canal; that of the eye and of the nasal mucosa, and of the cranial vessels and nerves, have resulted in the enlargement of their cavities; and in the case of foramina, in their wider expansion. . . . The medullary cavities of bones are produced in the process of growth by the corrosive activity of osteoclasts."

It is then pressure which produces the excavations which form new cotyli in the construction of new articulations due to dislocations. By such excavations elevated portions remain adjacent to them. Other elevations, as already described, are due to deposit of bone stimulated by the absence of accustomed pressure, as in the filling up of the old ulnar cotylus in the human subject above described. Other elevations or osseous deposits such as occur at muscular and ligamentous insertions appear to follow a pulling stress.

Many other examples of the abnormal production of articulations might be cited, but the above are sufficient to show the plasticity of osseous tissue. It is also evident that if such results follow the stimulus of the parts during a short period of months or years, the continuance of the appropriate mechanical stresses through geologic ages must have been quite sufficient to produce all the characters which we observe in the articulations of the vertebrate skeleton.

I will now present the inferences which may be derived from consideration of the facts hitherto presented in this chapter. We have not been witnesses of the process of evolution, yet we believe that it has been in active operation. We have not been able to observe its *modus operandi*, but we may safely infer what it has been from the facts which are before us. Kinetogenesis having been observed in both the soft sarcode (muscle) and in the hard parts of animals, the law of uniformity obliges us to believe that similar changes have taken place in past ages whenever the necessity arose, and the energy at nature's disposal was sufficient.

ii. MOULDING OF THE ARTICULATIONS.

a. The Limb Articulations.

This part of the subject has the advantage of many facts of paleontology in our possession. We have now discovered the outlines of the phylogeny of many mammalian types, and many detailed histories of special lines of descent are known. Our knowledge is most complete in the unguiculate and ungulate placentals, while it is least as regards the Mutilata, and the implacentals. We have excellent series of skeletal parts, and I have given the successional modifications of some of them on page 139.

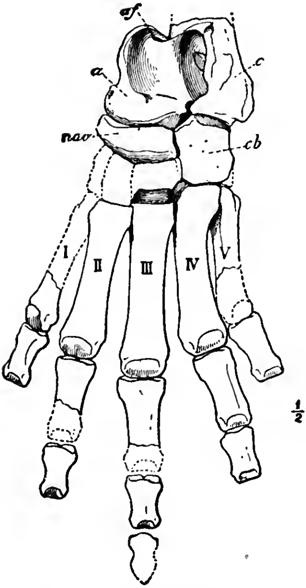

Fig. 68.—*Periptychus rhabdodon* Cope, a condylarthrous genus of the Puerco epoch of New Mexico; posterior foot, one-half natural size, showing pentadactyle plantigrade foot without groove of astragalus, as in the probable ancestor of the Diplarthra. From Scott and Osborn.

In the first place, I will select an illustration of the effects of use on the articulations of the limbs and feet of the Mammalia. I take first the ankle and wrist-joints. In the ruminating animals (ox, deer, camel, etc.) and in the horse, among other living species, the ankle-joint is a very strong one, and yet admits of an extensive bending of the foot on the leg. It is a treble tongue-and-groove joint; that is, two keels of the first bone of the foot, the astragalus, fit into two grooves of the lower bone of the leg, the tibia, while between these grooves a keel of the tibia descends to fill a corresponding groove of the astragalus. Such a joint as this can be broken by force, but it cannot be dislocated.

Now, in all bones the external walls are composed of dense material, while the centers are spongy and comparatively soft. The first bone of the foot (astragalus) is narrower, from side to side, than the tibia which rests upon it. Hence the edges of the dense side-walls of the astragalus fall within the edges of the dense side-walls of the tibia, and they have pressed into the more yielding material that forms the end of the bone, and causing bone absorption, pushed it upward, thus allowing the side-walls of the tibia to embrace the side-walls of the astragalus. Now, this is exactly what would happen if two pieces of plastic dead material, similarly placed, should be subjected to a continual pounding in the direction of their length. And in view of the facts already cited we cannot ascribe any other immediate origin to it in the living material.

The same active cause that produced the two grooves of the lower end of the leg produced the groove of the middle of the upper end of the astragalus. Here we have the yielding lower end of the tibia resting on the equally spongy material of the middle of the astragalus. There is here no question of the hard material cutting into soft, but simply the result of continuous concussion. The consequence of concussion would be to cause the yielding faces of the bones to bend downward in the direction of gravity, or to remain in their primitive position while the edges of the astragalus were pushed into the tibia. If they were flat at first they would begin to hollow downward, and a tongue above and groove below would be the result. And that is exactly what has happened. This inclusion of the astragalus in the tibia does not occur in the reptiles, but appears first in the Mammalia, which descended from them. See Figs. 68–69. I have shown that without exception, every line of Mammalia commenced with types with an astragalus which is flat in the transverse direction, or without median groove.

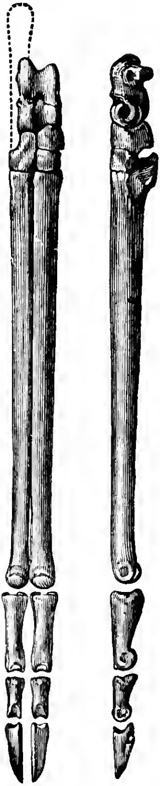

Fig. 69.

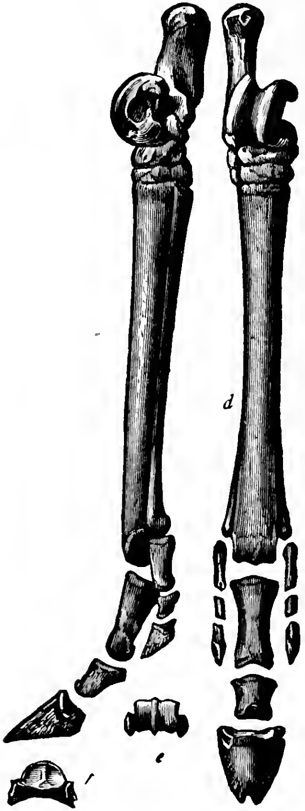

Fig. 70.

Fig. 69.—Hind foot of primitive cameloid *Poëbrotherium labiatum* Cope, showing grooved astragalus and first toe-bones without keel in front at lower end. (From Colorado.)

Fig. 70.—Hind foot of three-toed horse (*Protohippus sejunctus* Cope) (from Colorado), showing grooved astragalus, and trace of keel on front of lower end of first bone of middle toe.

From early Tertiary times to the present day, we can trace the gradual development of this groove in all the lines which have acquired it. The upper surface became first a little concave; the concavity gradually became deeper, and finally formed a well-marked groove.

The history of the wrist-joint is similar. The surface of the fore-arm bones which joins the fore-foot is in the early Tertiary Mammalia uniformly concave. In the ruminating mammals it is divided into three fossæ, which are separated by sharp keels. These fossæ correspond with the three bones which form the first row of the carpus or palm. The keels correspond to the free sutures between them. The process has been evidently similar to that which has been described above as producing the side-grooves in the end of the tibia. The dense walls of the sides of the three bones impinging endwise on the broad yielding surface of the fore-arm (radius) have gradually, under the influence of countless blows, impressed themselves into the latter. On the contrary, the surface above the weaker lines between the bones not having been subject to the impact of the blows, and influenced by

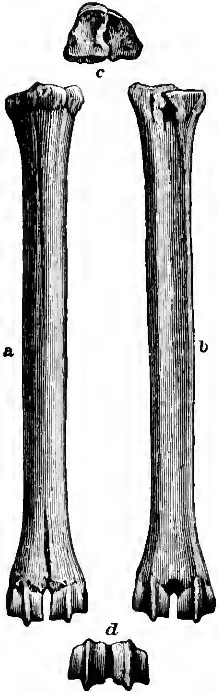

Fig. 71.—United first bones of two middle toes of deer-antelope (*Cosoryx furcatus* Leidy), showing extension of keel on front of lower end. (From Miocene of Nebraska.)

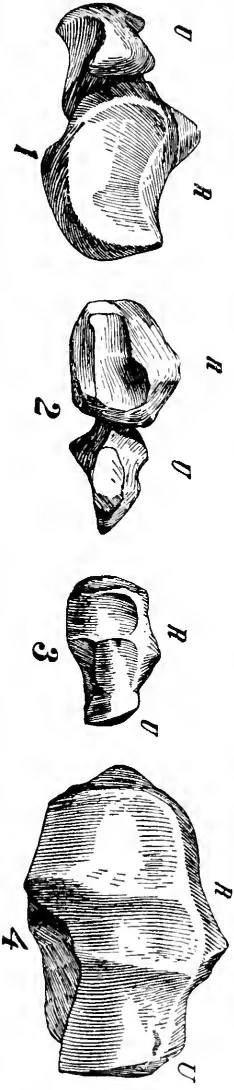

Fig. 72.—Wrist-joint at distal extremity of fore arm. 1, Pachyæna (Creodont Eocene). 2, Phenacodus (Eocene Condylarthron). 3, Prothippus (Upper Neocene three-toed horse). 4, Holomeniscus (Plistocene Camel).

gravity, remains to fill the grooves, and to form the keels which we observe. (See Fig. 72.)

There is another striking instance of the same kind in the feet of Mammalia; that is, in the development of the keels and grooves which appear at the articulation of the first set of bones of the toes (metapodials) with the bones of the second set (phalanges). These keels first appear on the posterior side of the end of the first set of bones, projecting from between two flexor tendons. These tendons, in many mammals, contain two small bones, one on each side, each of which acts like the knee-pan, and resembles it in miniature, which are called sesamoid bones. These tendons and bones exercise a constant pressure on each side of the middle line, when the animal is running or walking, and this pressure, together with the concussion with the ground, appears to have permitted the protrusion of the middle line in the form of a keel, while the lateral parts have been supported and even compressed. The reptilian ancestors of the mammals do not possess these keels.

Now, I have shown that the lines of mammalian descent displayed by paleontology are characterized, among other things, in most instances, by the gradual elevation of the heel above the ground, so that the animal walks on its toes. It is evident that in this case the concussion of running is applied more directly on the ends of the bones of the foot than is the case where the foot is horizontal. As a consequence we find the keel is developed farther forward in such animals. But in many of these, as the Carnivora, hippopotamus, and the camels, there is developed under the toes a soft cushion, which greatly reduces this concussion. In these species the keel makes no further progress. In other lines, as those of the horse, the pig, and of the ruminants, the ends of the toes are applied to the ground, and are covered with larger hoofs, which surround the toe, and the cushion is nearly or quite dispensed with. These animals are especially distinguished by the fact that their metapodial keels extend entirely round the end of the bone, dividing the front, as well as the end and back (Fig. 71); since the front of the metapodial is out of the reach of the sesamoid bones, its keel would seem to be a moulding to the groove of the first phalange, which is itself moulded by the middle and posterior part of the metapodial keel (Wortman.)

A third and similar example is furnished by the elbow-joint of the Quadrumana and Diplarthra. In the lower Mammalia, including the Carnivora (Fig. 73), the distal end of the humerus presents a submedian groove, which receives the ulna, and on the inner side of it, a more or less convex surface, which is applied to the head of the radius. The coronoid process of the ulna is narrow, and its dense bounding walls impinge on the broad face of the humeral condyle in flexion and extension, and transfers to it the force of impact when the foot strikes the ground. In either case strong pressure has been brought to bear on the humeral condyle, and it has yielded to the denser body of the ulna, thus forming the groove in question. In such Mammalia the effect of impact of the limb on the ground has been to impress the head of the radius on the humeral condyle upwards. The dense edges of the former have impressed themselves on the latter, while the unsupported middle portion has yielded in the direction of gravity, and the result is what we find, i. e., a cup-shaped surface of the head of the radius, and a convexity of the humeral condyle adapted to it.

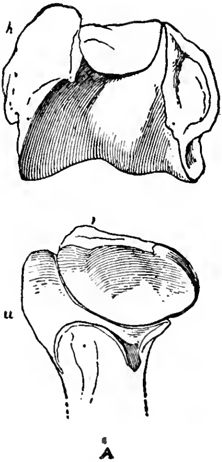

Fig. 73.—Elbow-joint of *Crocuta maculata* L. (spotted hyena) seen from behind; *h*, humerus; *r*, radius; *u*, ulna. Original.

Among specializations of the elbow-joint, I call attention to two. In Quadrumana the head of the radius, probably owing to continued supination of the manus, occupies a position at the external side of the coronoid process of the ulna, and impinges on the outer part of the condyle of the humerus. The concavity of its head, and the convexity of the humeral condyle, are visible as before, but a prominent tongue or keel, which has been called the intertrochlear crest, separates the ulnar and radial surfaces of the humerus (Fig. 74). This keel occupies the groove or interval which separates the head of the radius from the coronoid process of the ulna. It is plain that we have here another tongue and groove-joint, produced by the mutual adaptation of parts under strain, pressure, and impact. The other extreme of elbow-joint is found in that of the diplarthrous Ungulata (Fig. 75). Here the head of the radius, while retaining its normal position on the inner side of the fore-arm, is extended to the external side of the ulna and even beyond it, adapting itself to the entire width of the humeral condyles. The same structure is found in the specialized forms of both series of Diplarthra, the Perissodactyla and Artiodactyla. This expansion of the head of the radius appears to be in direct relation to the duration through long geologic ages of the impacts which have affected the limbs of these, the swiftest of the Mammalia. That the head of the radius should be spread so as to fit the entire surface of the humerus, under all circumstances, seems to be a mechanical necessity. But in addition to this we find a tongue-and-groove adaptation, in which the crest (which I have called the trochlear crest) articulates with a groove in the head of the radius. The internal articulation of the humerus with the radius has the usual form, convex and concave distad. The trochlear crest marks the external border of the olecranar groove of the humerus. But

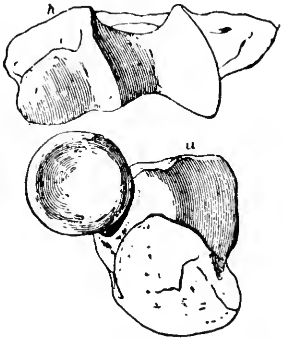

Fig. 74.—Elbow-joint of chimpanzee from behind.

the external part of the humeral condyles is converted into a roller which is set off from the trochlear crest by the abrupt contraction of its diameter; while the corresponding part of the head of the radius projects to fit it exactly.

A probable explanation of the form of this roller may be derived from a consideration of the almost identical structure of the metapodio-phalangeal articulation of the Artiodactyla. The internal and external sides of the distal metapodial condyles are not similar, the external being more strongly impressed than the internal (Fig. 77D). This is simply due to the unequal pressure exerted on the two extremities of the condyle by the phalanges, owing to the divergent direction of the digits when serving as a support. In the distal end of the humerus the same effect is seen, the external part of the condyle nearly resembling the corresponding part of the metapodial bones. This is traceable to the same cause, viz.: the divergent position assumed by the fore arm on the humerus, when the weight is supported on one fore leg only. This brings the line of pressure through the external part of both the head of the radius and the humeral condyle (Fig. 77A). That the higher ungulates are "knock-elbowed" may be readily observed by watching their gaits (Fig. 76).

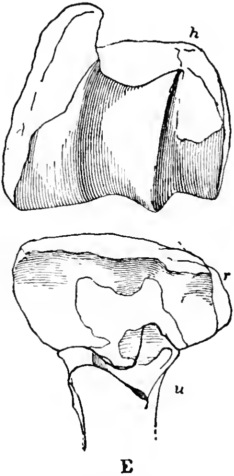

Fig. 75.—Elbow-joint of *Cervus elaphus* (red deer) from behind.

A distinct consequence of combined impact and strain is seen in the evolution of the carpus and tarsus of the Diplarthra. In primitive Mammalia, as in most Unguiculata, the bones of the carpus and tarsus succeed each other in such a way that the principal lines of separation between the elements coincide in the two rows, thus producing a linear relation between the former. In the Diplarthra, on the other hand, the elements of the two rows alternate with each other so as to produce a strong interlocking. I have shown that in the primitive Ungulata, the Taxeopoda, the linear arrangement is observed, while in three orders of ungulates, the Proboscidea, Toxodontia, and Amblypoda, there are various degrees of alternation intermediate between the linear type of the Taxeopoda and the completely interlocked condition of the Diplarthra. It has been already pointed out in the chapter on phylogeny that the taxeopodous type

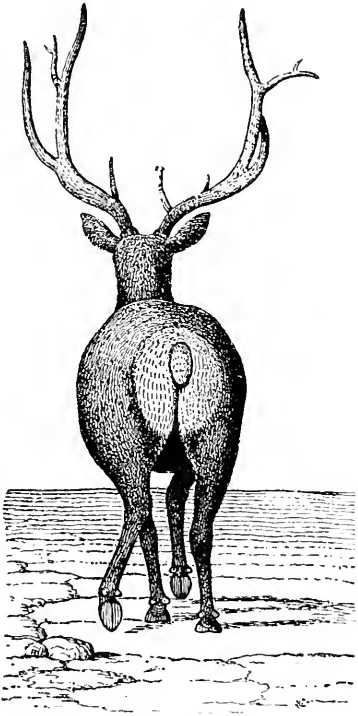

Fig. 76.—*Cervus canadensis* in motion: from Muybridge's *Animal Motion*; showing the "knock-elbow" position of the fore leg, in both plantation and recover.

of foot preceded the diplarthrous in time. Besides the alternation mentioned, it is quite general in both types for the metapodial bones to possess a facet for contact with that element of the carpus and tarsus next exterior to the one to which they have their principal articulation. From these facts it is evident that the bones of the second carpal and tarsal rows have, in the process of evolution, assumed a position interior to their primitive position, with reference to the first row proximad to them, and the metapodials distad to them. The cause of this shifting of position is to be found in the movements of the limbs in progression, and especially in rapid progression (Fig. 78).

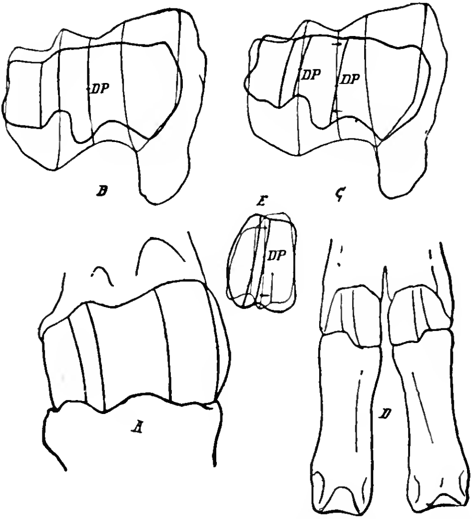

Fig. 77.—*Cervus elaphus*: *A*, *B*, *C*, humero-radial articulation; *A* and *B*, with the radius in position; *C*, with radius twisted; *D*. *E*, metatarsophalangeal articulation; *D*, front; *E*, distal view, twisted.

If we observe the movements of the limbs in a diplarthrous ungulate, we shall see that as the foot is planted on the ground the prominent flexures of the limbs, the elbow and gambril joints, are turned inwards, so that the limb, were it free from the ground, would be twisted or rotated on its long axis from within, forwards and outwards. As the foot rests on the ground, the limb experiences a torsion strain in the directions mentioned. This throws the weight on the interior bones of the lower legs, the radius and the tibia. Thus these bones have acquired a great supe-

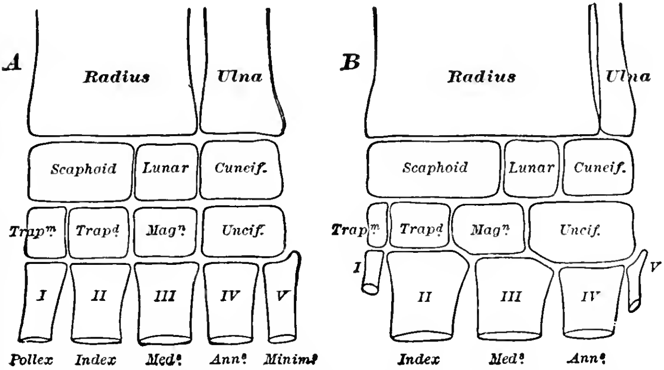

Fig. 78.—Diagram of carpus of a Taxeopod (*A*) and (*B*) of a diplarthrous ungulate. From Osborn.

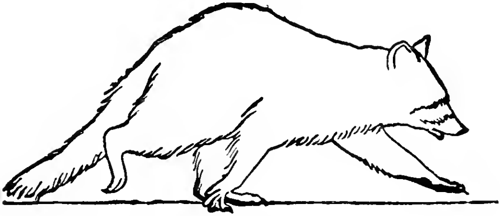

Fig. 79.—Raccoon pacing, showing right fore foot just before recovery. From H. Allen.

riority in dimensions over the external elements (ulna and fibula) in all the Diplarthra. The bones of the inner side of the first carpal and tarsal rows have thus transmitted an ever-increasing share of the impact, as the radius and tibia have developed, and have grown with their growth at the expense of the external elements, the cuneiform in the carpus, and the calcaneum in the tarsus, which have become very narrow elements in the higher Diplarthra. As the pressure has been obliquely from within outwards, the growth of the proximal elements, the scaphoid and lunar in front,

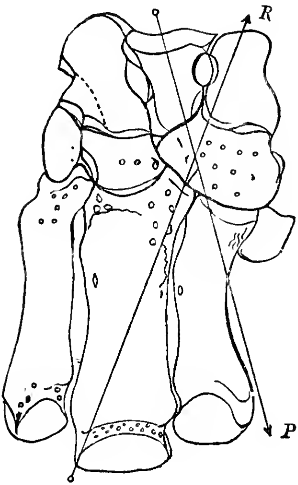

Fig. 80.

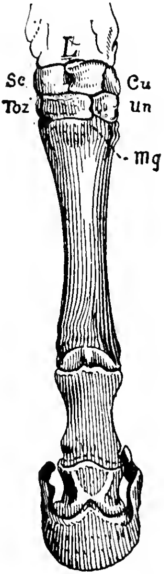

Fig. 81.

Fig. 80.—*Rhinocerus unicornis* carpus. Arrow ending in *P*, line of impact in plantation; *do.* ending in *R*, line of strain in recover.

Fig. 81.—*Equus caballus* fore foot. *Sc*, scaphoid; *L*, lunar; *Cu*, cuneiform; *Toz*, trapezium and trapezoideo; *Un*, unciform; *mg.*, magnum.

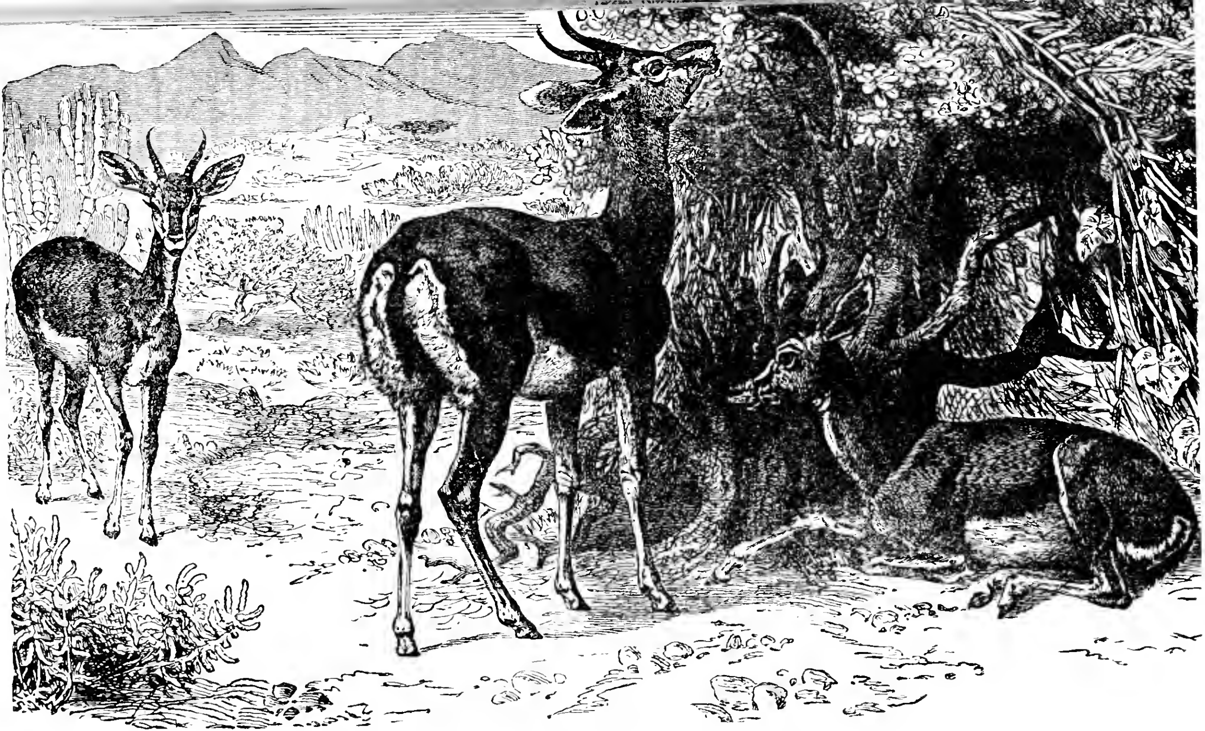

Fig. 82.—*Gazella dorcas*, gazelle. From Brehm.

and the astragalus behind, has been in the same direction. It has been shown by Dr. H. Allen that just before the recover of the foot, the latter is directed outwards from a line parallel with the axis of the body, so that the weight falls on the inner part of the sole of the former. This naturally causes the bones of the foot to press inwards on the heads of the metapodials, so that the latter tend to grow outwards on the second tarsal row. In this way were produced the facets on the external side of the heads of the metapodials. Thus is accounted for, on simple mechanical principles, the phenomenon of carpal and tarsal displacement exhibited in its highest development, by the Diplarthra.

It is significant that diplarthrism has not appeared in mammals which possess an elastic pad of connective tissue on the soles, as in Unguiculata generally, and especially in the Carnivora. Diplarthrism is present in the camels, which have a pad, but I have shown that this pad did not appear until a comparatively late geologic epoch, and long after diplarthrism had become established in the camels' ancestors, the Poëbrotheriïdæ.

The faceting of the head of the astragalus as the result of impacts, is seen on comparison of the astragali of Phenacodus and Hyracotherium in Ungulata (Figs. 33–35), and of Dissacus and Mesonyx among the Creodonta. In this last genus we have the only faceted astragalus among carnivorous mammals, but this genus is at the same time subungulate.

b. The Forms of Vertebral Centra.

The mutual articulations of the vertebral column are those of the centra and of the zygapophyses. Many important modifications in these articulations are to be seen in Vertebrata, the Reptilia presenting the greatest variety, excepting in the zygapophyses, which are tolerably uniform in that class. In the Mammalia, modifications of the central articulations are not more striking than are those of the zygapophyses.

The forms of central articulation are four, viz.: the amphicœlous, the ball-and-socket, the plane, and the saddle-shaped. The first type is only seen in a very imperfect degree in Mammalia and in but very few vertebræ, where it is indeed but a modification of the plane. The ball-and-socket is chiefly found in the neck of the long-necked Mammalia, as the higher Diplarthra, and to a less degree in their lumbar regions, while the dorsal vertebræ present an approach to the same type in the same groups. The saddle-shaped centrum is only found in Mammalia in the necks of certain genera of monkeys. The majority of Mammalia present the plane articulation of all the vertebral centra.

In Mammalia in which movement of the vertebræ on each other has become impossible, the centra coössify, as for instance in the sacrum. In this region the number of vertebræ coösified is directly as the length of the iliac bone, which supports and holds them immovable. Such is their condition throughout the dorsal region in the extinct Edentata of the family Glyptodontidæ, where the carapace is, as in the tortoises, inflexible, and which therefore limits the possibility of motion of the vertebral column. Another illustration is seen in the necks of the balænid Cetacea, and to some degree in the Delphinidæ and Physeteridæ. The lack of present mobility of this part of the column is due to its extreme abbreviation, a character which has been gradually developing during Cenozoic time; since the earliest Cetacea had considerably longer necks than the later ones, and had their vertebral centra distinct. It appears to me probable that the shortening was the result of disuse. This disuse would arise from gradually increasing powers of locomotion through the water, a progress, which, judging from the character of the limbs of the Zeuglodon, was evidently made after the time of the Eocene. The increase of speed would enable the animal to overtake and capture its prey, without the necessity of using a long prehensile neck in seizing it in the pursuit.

The ball-and-socket articulation of the vertebræ is well known to be the predominant condition in the Reptilia, and the fact that it is necessarily associated with the flexibility of the column is equally well understood. The flexibility is directly as the weakness of the limbs, for in the large and long-limbed terrestrial Reptilia of the order Dinosauria, the vertebral articulations of the dorsal region, at least, are plane. That it is chiefly confined to, and best developed in, the most flexible regions, i. e., the cervical and lumbar, of the column of the Mammalia, also shows this necessary connection. There can be no doubt but that the ball-and-socket vertebral articulation has been produced by constant flexures of the column in all directions, as has been suggested by Marsh.

iii. INCREASE OF SIZE THROUGH USE.

Under this head I enumerate examples where the mechanical causes in operation are less self-evident than those included under the preceding section. They are, however, probably due to the same process, viz., impact and strain.

a. The Proportions of the Limbs and of Their Segments.

The length of the legs of terrestrial Mammalia has increased with the passage of time. The inferior types of Mammalia now existing, as Marsupialia, Glires, Insectivora, Edentata, have short legs, with a few cases of extreme specialization as exceptions, such as kangaroos, rabbits, and jerboas (hind legs only), the *Dolichotis patachonica*, the Rhynchocyonidæ, and the sloths. In the orders which stand at the summit of the series, as the Diplarthra, Proboscidia, Carnivora, and Anthropomorpha, the legs are much increased in length, and this is especially marked in certain forms which stand in all respects at the summit of their respective orders. Thus in Diplarthra, the deer, antelope, and horse are distinguished for length of limb; in the Proboscidia, the elephant; in the Carnivora, the large cats and hyænas; in the Anthropomorpha, the fore limbs are long in all, the hind ones especially so in man.

The cause of this elongation is apparently use. It is the hind legs that are elongated in a straight line in animals that walk on them, as man; and both, in those that walk on both, as the elephant. In animals that leap with the hind legs these are still more elongated, and are folded when at rest, and rapidly extended when in motion. In animals that climb with the fore legs, these are elongated, as in the Anthropomorpha, except man. In those that climb with all fours, all are elongate, as in the sloths. It must be remembered that these elongations are the sum of increments added one to the other through long ages of use in geologic time. The mechanical character of that use has not been identical. It is of two principal kinds, viz.: impact and longitudinal strain. These two forms of energy move in directions opposite to each other; the one as compression in the direction of the length of the bone; the other, as a stretching in the direction of the length of the bone. Both processes alike appear to have stimulated growth in the direction of the length of the bone.

The increase in the length of the legs has not been always due to increase in length of the same segment. In a majority of the higher mammals, the increase has been principally in the foot, and especially in the metapodials and digits, producing digitigradism. In the forms which have remained plantigrade, the femur (Proboscidia), or femur and tibia (Quadrumana), or all three segments (Tarsius), have been the seat of the elongation. We can again trace these especial elongations to special uses. In animals which leap, the distal segments of the limbs are elongated; in those which do not leap, but which merely run or walk, it is the proximal segments of the limbs which are elongated.

Animals which run by leaping are divided into those which run and leap with all fours, as Diplarthra; and those which run and leap with the posterior limbs only, as the jerboas and kangaroos. In both types, the distal segments of the hind limb are elongated, and in the Diplarthra, those of the fore limb also.

Animals which do not leap in progression (elephants, Quadrumana, bears) are always plantigrade, and have very short feet, but elongate thighs, and, mostly, tibias.

These facts show that those elements which receive the principal impact in progression are those which increase in length. In digitigrade animals it is the feet which receive the impact of the repeated blows on the

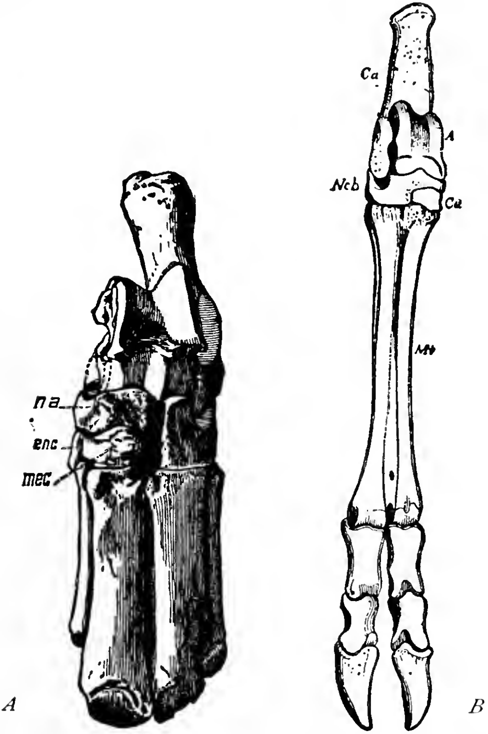

Fig. 83.—Pes of (*A*) *Merychochœrus montanus* from Scott; (*B*) *Bos taurus*, much reduced. *Ca*, Calcaneum; *As*, Astragalus; *Na*, Navicular; *Neb*, Naviculocuboid; *Cu*, *Mec*, Ecto-mesocuneiform; *Mt*, Metatarsals (cannon bone); *Enc*, Entocuneiform.

earth while in progression, while supporting the weight of the body at every stage of the process. In plantigrade animals it is the soles of the feet, and the bones of the leg in line with them. which receive the impact,

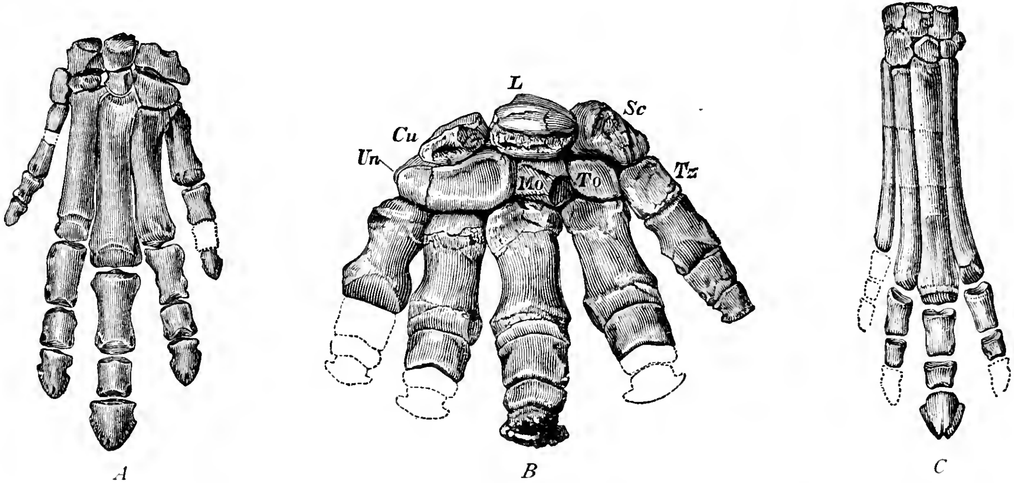

Fig. 84.—Anterior feet of primitive Ungulata, reduced. *A*, *Phenacodus primævus*. *B*, *Coryphodon elephantopus*. *C*, *Hyracotherium venticolum.*

while the feet beyond this point receive none, and do not support the body, except very partially at the moment of leaving the earth.

b. The Number of the Digits.

The reduction in the number of toes is supposed to be due to the elongation of those which receive the greater number of strains and impacts in rapid progression, and the complementary loss of material available for the growth of those not subject to this stimulus. This is rendered probable from the fact that the types with reduced digits are dwellers on dry land, and those that have more numerous digits are inhabitants of swamps and mud, or are more or less aquatic. That this inequality is due to these mechanical causes is still further indicated by the fact that in those forms where the soles are thickly padded (Carnivora, Proboscidia) the reduction has either not taken place, or has made little progress, amounting to the loss of only one digit. (An apparent exception in the case of the camels will be mentioned later.) A still more important body of evidence which shows that the inequality in size and number of digits is due to impacts and strains unequally distributed, has been brought forward by Ryder. He points out that definite results are to be observed in those limbs of a given type of animal which experience correspondingly definite influences; while in the limbs where the strains are equal, the modifications do not appear. Examples of this kind are to be found in the unguiculate Mammalia and in the Marsupialia. Thus in the jerboas which use the hind limbs in leaping, these only display reduced digits, the fore limbs remaining of primitive character. The same is true of the kangaroos. In digging genera, the fore limbs experience the modifications, while the hind limbs are more normal, as in Chrysochloris and various Edentata.

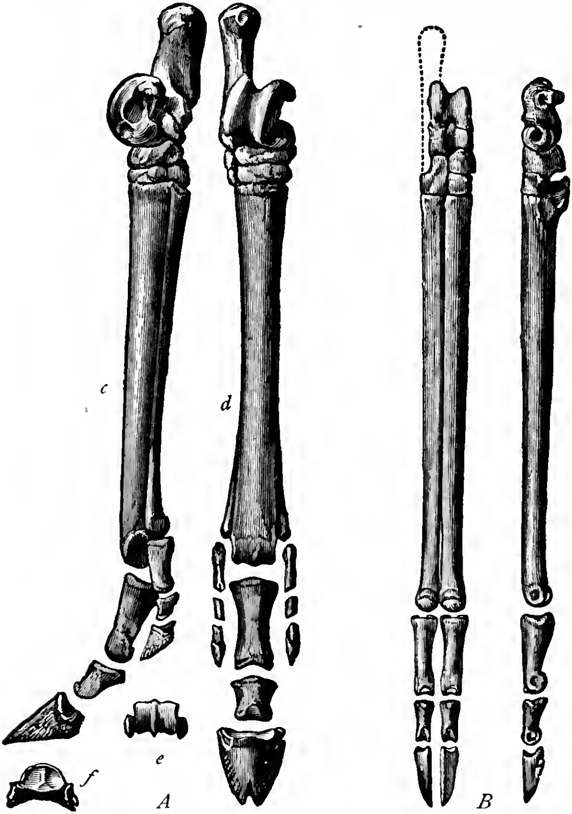

Fig. 85.—*A*, Right posterior foot of *Protohippus sejunctus* Cope, from Colorado, about one-half natural size. From *U. S. Geological Survey of Territories*, F. V. Hayden, IV. *B*, Right posterior foot of *Poëbrotherium labiatum* Cope, from Colorado, three-fifths natural size. From Hayden's Report, IV., Plate CXV.

Ryder sums up the evidence in two propositions, as follows:[1]

"I. The mechanical force used in locomotion during the struggle for existence has determined the digits which are now performing the pedal function in such groups as have undergone digital reduction.

"II. When the distribution of mechanical strains has been alike upon all the digits of the manus or of the pes, or both, they have remained in a state of approximate uniformity of development."

The application of the impact, or strain, or both, in progression, is easily understood. In recover (see p. 299), the leg is bent on the foot as it rests on the ground, and those digits which then leave the ground last, sustain greater strain than those which leave it sooner. In replacing the foot on the ground (plantation), those digits which strike it first experience greater force of impact than those which strike it later. Supposing the five primitive digits to have been of equal length, the distribution of the impact and of the strain will depend on the angle at which the foot is directed with reference to the direction of motion. If the feet are pointed forwards, the middle digits will experience strain and impact; if outwards, the inner digits bear the weight; if inwards, the external digits receive it.

Observation on five-toed plantigrade mammals shows that their feet are turned neither inwards nor outwards in progression, but straight forwards. It is probable that the primitive Mammalia moved in the same manner. This is also to be inferred from the fact that they were plantigrade, so that the leverage transversely in or out which results from the elevated heel of the digitigrade leg was very much less in them.

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[1] *American Naturalist*, 1877, p. 607.

In progression of this type, the middle digits of course leave the ground last and strike it first. Thus the middle toes have been stimulated at the expense of the lateral ones, so that in the Diplarthra, either the middle one (Perissodactyla) alone remains, or the middle two (Artiodactyla). In the kangaroos the external toes have been chiefly used, so that the fourth and fifth digits have been principally developed. In man, who

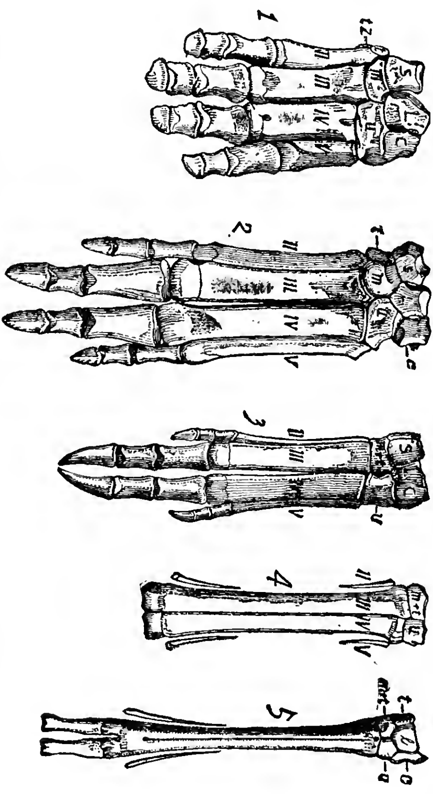

Fig. 86.—Manus of Artiodactyla, much reduced; from Kowalevsky. 1, *Hippopotamus*; 2, *Hyopotamus*; 3, *Sus*; 4, *Gelocus*; 5, *Cervus*.

now turns his feet out when using them as bases of resistance to muscular labor, the inner digit has become most robust. The mechanical history of the human great toe is however yet unknown.

As regards the equal development of the third and fourth digits in the Artiodactyla, as distinguished from the development of the middle digit of the Perissodactyla, I have advanced the following hypothesis. I have supposed that the primitive members of this former division sprung from pentadactyl plantigrades who dwelt in swamps and walked on very soft ground. The effect of progression in mud is to spread the toes equally in all directions and on each side of the median line. Such feet remain in the mud-loving hippopotamus, and to a lesser degree in the true pigs. From such ancestry the cloven-footed Diplarthra derived their characters. The Hyracotheriinæ, the ancestors of all Perissodactyla, display on the other hand evidence of a life on harder ground, especially in the posterior foot, where articulations are already rigidly defined, and the third digit is longer than the others. Some of their descendants love swamps, as one or two species of tapirs and rhinoceroses, but others live on the dryest ground, as the Andean tapir and the African rhinoceros. As to the highest members of both even and odd toed groups, the Bovidæ and the Equidæ, their habitat is in the vast majority of cases the dry land (Figs. 80–81).

Continued and excessive prehensile strain with weight on the longest digits, must be assigned as the cause of the especial elongation; and disuse as the cause of the loss of the external and shorter digits, of the sloths; so that there remain but two and three (Cholœpus and Bradypus), and in the climbing ant-eater (Cycloturus) but one principal toe and two rudiments. The excessive strain and impact experienced by certain digits in leaping, accounts for the digital reduction in the hinder foot of the kangaroos and jerboas, precisely as in the perissodactyle ungulates.

c. The Horns.

Horns are developed in Mammalia and other Vertebrata on similar parts of the skull, principally on the posterior lateral angles, as in various Batrachia, Reptilia, and Mammalia, and on the nose, as in a few Mammalia and several reptiles, recent and extinct. These parts are the ones which are especially brought into contact with resisting bodies; the nose in pushing a path or way for the head and body; the lateral occipital region in defence and assault, when the sensitive nose and eyes are protected by being held near the ground. In the latter position the posterolateral angles, when present, receive more frequent collision with, and vigorous stimulation from, a body attacked or resisted, and in accordance with the observed results of irritation on dermal and osseous tissues, additional matter has been deposited. In Lacertilia and Batrachia Salientia there are distinct posteroexternal cranial angles; in Batrachia Urodela such angles are less prominent. In unguiculate Mammalia and in all others with a sagittal crest there are no such angles; hence this type of skull has never developed posterior horns. The rhinoceros has developed the dermal nasal horn, and the Elasmotherium, a median osseous horn, since posterolateral angles of the skull are wanting or close together. In the Dinocerata and the Artiodactyla, where the temporal crests are lateral, leaving a wide fronto-parietal plane with posterior lateral angles, horns are developed. In members of both groups horns have been developed over the orbits also (Fig. 87), and in the Dinocerata on the extremities of the nasal bones as well. These growths are all on parts which are subject to especial irritation by contact with other bodies, animate and inanimate.

Among Artiodactyla, the deer (Cervidæ) are especially distinguished by the periodical shedding of all but the bases of their horns. Extinct forms found in the Upper Miocene of the United States and France (the Loup Fork series) furnish the explanation of the origin of this remarkable peculiarity. In the genus Cosoryx we find that the horns may or may not possess a burr near the base of the beam, like that of the deer; the same species being indifferently with it or without it. This observation has been made on three species,—the *C. necatus*, *C. furcatus* and *C. ramosus*. The following explanation of these facts has been proposed by myself.[1] "From the facts of the case the following inference may be derived, premising that it is very probable that a genus allied to the present one has given origin to the family of the deer. It is obvious that the horns of (Dicrocerus) Cosoryx did not possess a horny sheath as in the Bovidæ, from the fact of their being branched. As the sheath grows by addition at the base, the presence of branches which necessarily obstruct its forward movement, would be fatal to the process. There is much to be said in favor of the view that the horns were covered with an integument, probably furred, as in the giraffe and young stage in the deer. Thus there are grooves in the surface of the beam for superficial blood-vessels, which

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[1] *U. S. G. G. Survey West of the 100th Mer.*, G. M. Wheeler: IV., *Paleontology*, 1877, p. 348.

must have been protected by skin (I do not observe these grooves on the beam of *C. teres*). The retention of the broken extremity of an antler, so as to be reunited, as described (Fig. 87, *C*), could not have been accomplished without an integument. The presence of the burrs cannot be accounted for on any other supposition, as there are no foramina to give exit to nutrient vessels at the point where they exist; the irregularity of those positions also forbids the latter idea, and adds to the probability that the arteries which furnished the deposit of phosphate of lime were contained in a superficial dermal coating. The supposition is also strengthened by the fact that the only existing ruminants (the giraffes) with permanent horns without horny sheaths have them covered with hairy skin.

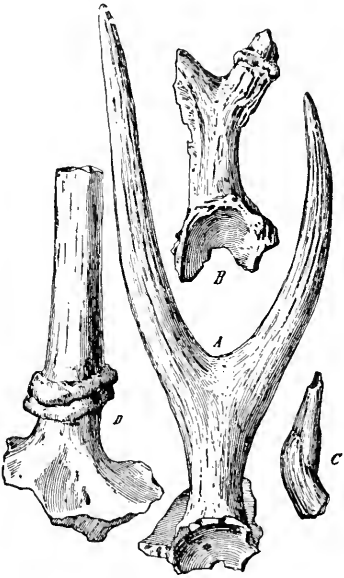

Fig. 87.—*A*, *B*, *Cosoryx necatus* Leidy; *A*, without, *B*, with, burr on antler; *C*, *D*, *Cosoryx ramosus* Cope; *C*, antler broken and reunited; *D*, beam with burr; one-half natural size; original; from *Report U. S. Gov. Geol. Expl. 100th Mer.*, G. M. Wheeler.

"It appears that in the antlers of the Cosoryx the deposit of a burr was immediately associated with the death of the portion of the horn beyond it, so that it disintegrated and disappeared. This was not the case with the beam in the specimens observed. Nevertheless it is probable that the death of the horn would be associated with the deposit of the burr in this case also, were the conditions the same. What those conditions were we can only surmise. It was very probably the death of the integument which invested and nourished the horn that produced that result; and this would more readily occur in the exposed antlers than in the more protected basal portion of the beam. It is very probable that this result would follow blows and laceration of the surface received during combat, or accidental contact with hard substances. The integument would be stripped up to near the junction of the antlers with each other, or of the beam with the cranium, and the arteries would be constricted or closed at those points. It is near these junctions that all of the burrs are found. But as such lesion would be necessarily less complete at the point where the horn has greatest circumference, so the entire death of the horn might be less usual than that of the branches. Should such lesions have occurred for a long period at the breeding season, nature's efforts to repair by redeposit of bony tissue might as readily become periodical as the increase in size and activity of the reproductive organs and other growths which characterize the breeding season in many animals. The subsequent death of the horn would be at some time followed by its shedding by the ordinary process of sloughing."

Cosoryx is not the true ancestor of the Cervidæ, as its teeth have already attained the prismatic type of the higher Bovidæ. But Blastomeryx is most probably the ancestor of the deer. The remains of this genus occur with those of Cosoryx, but the burr has not yet been observed on its horns.

IV. THE MECHANICAL ORIGIN OF DENTAL TYPES.

In investigating the origin of dental types it is necessary to become acquainted with the nature of the mutual movements of the series of the opposing jaws. I have classified them as follows :[1]

I. Inferior molars work within superior molars, but not between them. Psalidodect mastication.
  1. The inferior molars shear on the interior side of the superior : *Triconodontidæ.*

II. Part or all of inferior molars work alternately to and between superior molars. Amœbodect mastication.
  2. The inferior molar shears forwards on the superior molar. Proterotome mastication : *Creodonta; Carnivora.*
  3. The inferior molars shear posteriorly against the superior molars. Opisthotome mastication : *Coryphodontidæ, Uintatheriidæ.*

III. Molar teeth of both jaws oppose each other. Antiodect mastication.
  4. The movement of the lower jaw is vertical. Orthal mastication : *Suoïdea, Tapiridæ.*
  5. The movement of the lower jaw is from without inwards. Ectal mastication : many *Perissodactyla.*
  6. The movement of the lower jaw is from within outwards. Ental mastication : most *Artiodactyla;* some *Perrissodactyla.*
  7. The movement of the lower jaw is from before backwards. Proal : some *Monotremata Multituberculata* and most *Glires.*
  8. The movement of the lower jaw is from behind forwards. Palinal : *Proboscidea* (Ryder).

The distinction of teeth into incisors, canines, and molars appears independently at various points in the line of Vertebrata. Incisors and molars are distin-

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[1] *Mechan. Origin Hard Parts of Mammalia*, 1889, p. 226.

guished in sparoid fishes, and in placodont and diadectid reptiles. Canine-like teeth, or pseudo-canines, appear in clepsydropid and crocodilian reptiles, and in saurodont fishes. Canine-like incisors appear in the Clepsydropidæ. The variety of character in these structures presented by the Mammalia to be considered is great, and the principles deduced from observation of them are applicable to the Vertebrata in general.

As mechanical causes of the origin of dental modifications, I have enumerated the following:

1. Increase of size of a tooth, or a part of a tooth, is due to increased use, within a certain maximum of capacity for increased nutrition.

2. The change of direction and use of a tooth take place away from the direction of greatest, and in the direction of least resistance.

3. It follows, from their greater flexibility, that crests of crowns of teeth yield to strains more readily than do the cusps.

4. The increase in the length of crests and cusps in all directions, and therefore the plications of the same, is directly as the irritation from use to which their apices and edges are subjected, to the limit set by the destructive effects of such use, or by the recuperative energy of nutrition.

5. The direction of growth of the branches of a V, or of the horns of a crescent, will be the direction of movement of the corresponding parts of the opposite jaw.

Before giving a review of the various dental types of Mammalia, I wish to describe some special examples where the effect of mechanical causes is most obvious. I therefore first repeat the observation of Ryder as to the origin of the selenodont molars of the Artiodactyla; and my own as to the origin of a similar structure in the molars of certain multituberculate Prototheria. In the former the mastication is ental; in the latter it is proal, as shown by Osborn.

In the accompanying figure from Ryder the movements of the lower jaw in mastication of lophodonts, are diagrammatically represented. *a* represents the movement in Carnivora, and in the orthal bunodonts, as the pigs. *b* shows a slight lateral movement believed by Ryder to exist in the wart hog (Phacochœrus). *c* represents the movement in kangaroos, phalangers, and tapirs. In *d* a theoretical intermediate movement is represented, such as Ryder supposed to have characterized the Anchitherium. In *e* the usual movement among ruminants is depicted, as is seen in the deer, etc. In *f* the wider excursion of the jaw is that seen in the giraffe, camel, and ox. In these movements from *b* to *f*, the lower jaw is moved transversely across the upper jaw from one side to the other. Some of the Diplarthra masticate on one side of the jaw when performing this movement, and some on the other. That is, in passing the lower jaw across the face of the upper, some masticate the food on the side

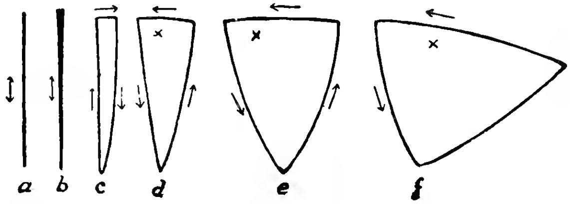

Fig. 88.—Diagram of excursion of lower jaw in mastication; from Ryder; *a*-*b*, orthal; *c*-*f*, ental.

where the external face of the lower jaw crosses the upper jaw from within outwards (ental); while in other types the food is masticated on the side where the lower jaw passes the external edge of the upper jaw from without inwards (ectal). While masticating with one side of the jaws, the opposing dental series of the other side are not in contact. All mutual effect of the teeth of one jaw on the other could therefore appear on the side temporarily used for mastication only. Among recent Ungulata the ruminants present the ental mastication; the rhinoceros and horses, the ectal; and rodents, the proal. Ryder is of the opinion that the mastication of the Proboscidia is palinal, but I have not been able to satisfy myself of this.

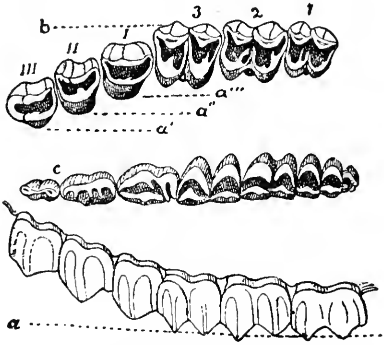

Fig. 89.—Cervus, molars: *a*, superior, external view; *b*, *do*. inferior view; *c*, inferior molars, superior view; from Ryder.

When the crests of the inferior molars were developed, their relation to the crests of the superior molars was always anterior in mastication. That is, the inferior crest, in the closing of the jaw, collides with the crest of the upper molar, with its posterior edge against the anterior edge of the latter. This is because: *first*, as to position, the two anterior cusps of the lower molar are the remains of the anterior triangle which fit originally between two superior molars, and because, in the closing of the jaw, these cusps continue to hold that position; and *second*, as to function, because the canine in the ungulate series diminishes in size, and does not, therefore, draw the inferior molars forwards by wedging on the superior molar, as in the Carnivora, but allows free scope to the posterior traction of the temporal muscle in its exercise on the lower jaw.

In those forms which masticate from the inside outwards (the ental type), the cusps of the inferior molars, passing between those of the superior molars, would tend to flatten the sides on which they exerted friction, and to extend those sides outwards beyond the median apex of the cusp. (Fig. 90.) The result would be, and taking into view the yielding of the tissue to such strain, has been, to modify the shape of the cusp by pushing its side walls, so that a horizontal section of it would become successively more and more crescentic. The effect on the inferior teeth would be to produce the same result in their external cusps, but in the opposite direction. The sides of the cusps would be pushed inwards, past the apex, giving a crescentic section more or less perfect, as the operation of the cause had been of long or short duration. The result of the lateral movement in mastication may be understood by reference to the accompanying cut, Fig. 91. The external crescents of the inferior molars (*b*) are seen to pass between the internal crescents of the

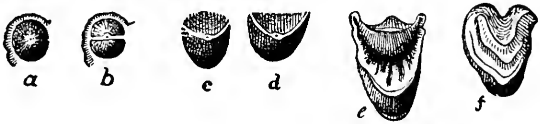

Fig. 90.—Cusps of superior premolars and molars: *a*, external cusps of molar of Sarcothraustes; *b*, of Phenacodus; *c*, of Anthracotherium; *d*, of Oreodon; *e*, half of inferior molar of Cervus; *f*, superior premolar of Coryphodon; from Ryder.

superior molars (*a*). The mutual interaction and effect on the form of the crescents may be readily understood. In Fig. 90 the successive stages of this effect on one or two cusps may be seen, beginning with a cone (*a*) and terminating with crescents (*ef*). Thus is the origin of the selenodont dentition of the highest artiodactyle explained by Ryder, and, I believe, correctly.

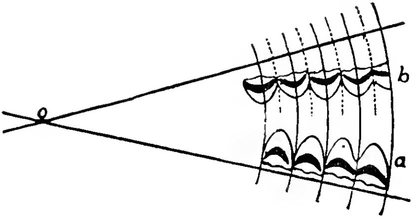

Fig. 91.—Two true molars of both jaws of a ruminant: *a*, superior molars, their inner crescents; *b*, inferior molars, their external crescents; the arcs show directions of motion of jaws in mastication; from Ryder.

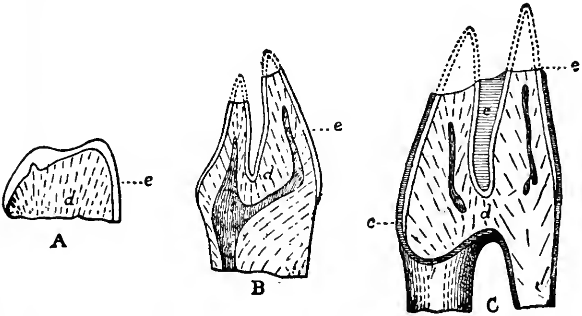

Fig. 92.—Transverse vertical sections of superior molar teeth, showing transition from bunodont (*A*) type to lophodonts (*B*, *C*). *A*, *Sus erymanthius*. *B*, *Ovis amaltheus*. *C*, *Bos taurus*. From Gaudry. Letters: *d*, dentine; *e*, enamel; *c*, cementum.

Kowalevsky and I have shown that the types with selenodont (crescent-bearing) molars, have descended from tubercle-bearing (bunodont) ancestors. This descent has witnessed an increased depth of the infolding of the crown, as represented in the accompanying figure. Now, in the table of masticatory types above given it is shown that in the bunodont type of the Suoidea the mastication is orthal, and a gradual increase in the length of the lateral excursions of the lower jaw has been shown to have resulted in the ental mastication. Thus has structure kept pace with function in the evolution of the selenodont dentition.

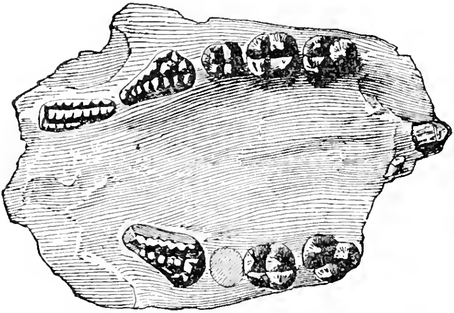

Fig. 93.– *Chirox plicatus* Cope, palate and molar teeth from below, three-halves natural size. From Puerco bed of New Mexico. From *American Naturalist*, 1887, p. 566.

The general structure of the dentition in the Prototheria Multituberculata is similar to that of the Glires. The incisors in the Plagiaulacidæ, Chirogidæ, and Polymastodontidæ have structure and functions generally similar to those of that order. The result in the form and function of the molar dentition has been similar to that observed in the Glires. The postglenoid process is probably absent in these animals; in any case the mandibular condyle is rounded, and is not transverse. Prof. H. F. Osborn has pointed out to me that mastication was performed by a fore-and-aft movement of the inferior molars on the superior in Plagiaulacidæ. This was no doubt the case in the other families named. The molar teeth of the lower types, as Tritylodon from the Trias, present conical tubercles in longitudinal series, two in the lower and three in the upper jaw. The two series of the lower jaw alternate with the three in the upper jaw, moving in the grooves between the latter, while the three series of the upper molars reciprocally embrace the two of the lower molars. This is demonstrated by the mutual wear of the tubercles seen in Ptilodus and Chirox (Fig. 93). The trituration was probably the same in Tritylodon, but in Polymastodon the increased thickening of the tubercles prevented their interlocking action in mastication. In this genus the tubercles slid over each other, and truncated the apices until in old specimens they were entirely worn away. In Meniscoëssus (Fig. 94) and Stereognathus we have an interesting illustration of the effect of the action of cusps on each other when under prolonged mutual lateral thrust. Their external sides have been drawn out into angles in the direction of thrust, converting their transverse sections from circles to crescents. As the thrust is in the Multituberculata longitudinal, the crescents are transverse to the axis of the jaw. In the selenodont Artiodactyla, where the thrust is transverse to the line of the jaw, the crescents are longitudinal. That similar effects should accompany similar move-

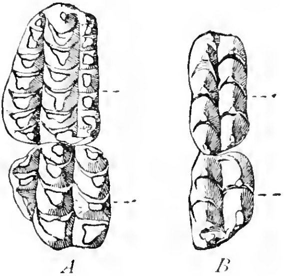

Fig. 94.—*A*, *Meniscoëssus conquistus* Cope, last two superior molars, from the Laramie of Wyoming, twice natural size. *B*, *Meniscoëssus*, second species, from Osborn.

ments in two groups of Mammalia so widely separated as these two is strong evidence in favor of the belief that the two facts stand in the relation of cause and effect.

I now present an example of the effect of strain, as shown by the direction of the inferior incisors of the lemurine Quadrumana. These teeth project horizontally from the extremity of the mandible, so as not to oppose the superior incisors, in consequence of which they are useless as organs of prehension. But they are used by their possessors as a comb for the fur, drawing them from below upwards when thus employing them. The strain is always in one direction, and must have resulted in developing the procumbent position which they now display (Fig. 95). This is a direct deduction from the fact that the incisor teeth are similarly displaced by the pressure of the tongue in cases of the abnormal enlargement of that organ in man.

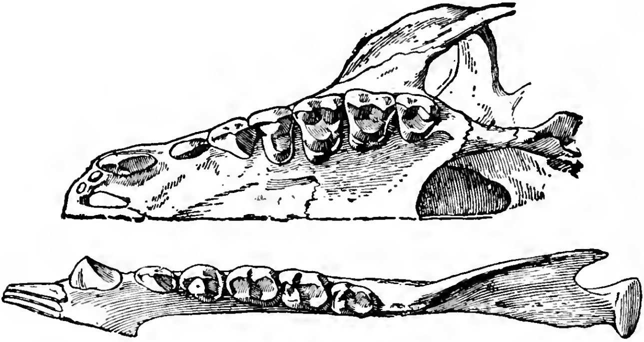

Fig. 95.—*Lemur collaris*, dentition from below and above; natural size; original.

I now describe the general character of mammalian dentition, with the view of pointing out how strong, in the light of the facts already cited, is the evidence of their origin through mechanical strains and impacts.

a. The Origin of Canine Teeth.

The origin of canine, pseudo-canine, and canine-like incisor teeth is due to the strains sustained by them on account of their position in the jaws at points which are naturally utilized in the seizing of prey, or the fighting of enemies. In some reptiles (Dimetrodon) the end of the muzzle has been utilized ; in crocodiles, the side of the jaw ; while the intermediate position has been most used by Mammalia. The reason why the canine instead of the incisor teeth have been selected by carnivorous Mammalia for prehensile purposes is not at present clear to me. In accordance with Rule I., its increased size has been due to the especial and energetic strains to which it has been subjected while in use as a prehensile or offensive weapon, when buried in the body of its prey or enemy. The superior canine would acquire larger size earlier in time than the inferior canine, since it bears the greater part of such strain, as attached to the more fixed head and body of its possessor. The anterior teeth of the lower jaw would be less available for use, since they offer weaker and less fixed resistance to the opposing body. That the first tooth behind the canine was not generally enlarged is (under I.) due to the fact that its posterior position prevents it from having the same amount of use, and experiencing the strain that a tooth more anteriorly placed necessarily receives. It is excluded from considerable use by the projecting muzzle above and in front of it. That it was not drawn out into a horizontal position was due to the presence of teeth anterior to it.

That the increased size of canine teeth is due to strains is strongly indicated by the huge development of these teeth in the walrus. This animal uses its canines for the breaking of ice, and for lifting itself from the water on to the edge of strong ice. The fact that canines and not incisors have been thus developed is a necessary result of the fact that the walrus is a descendant of a line of animals which had already reduced incisors and larger canines.

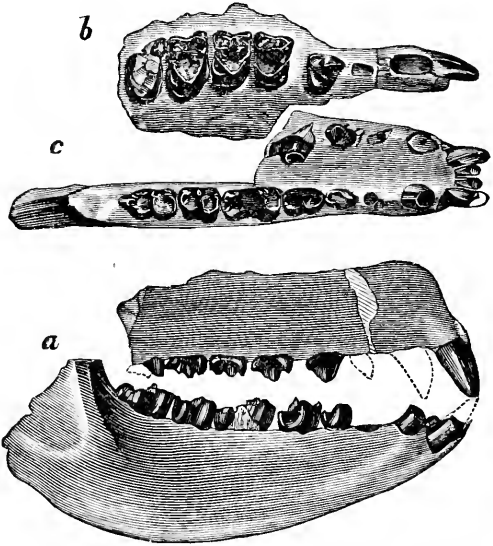

Fig. 96.—*Esthonyx burmeisterii* Cope, dentition: *a*, profile; *b*, superior; *c*, inferior dentition, grinding faces. Reduced.

b. Development of the Incisors.

The history of the incisor teeth of the Mammalia exhibits three processes, viz.: hypertrophy (e. g. Glires), specialization (e. g. Galeopithecus, Lemuridæ), and atrophy (e. g. Boöidea, Phacochœrus, Glossophaga, etc.).

Of hypertrophy we have two types: the first represented by the Glires, Multituberculata, Tillodonta and their ancestors; and second, by the Proboscidia, the narwhal and certain Sirenia. As the uses of the incisors present two types corresponding with their structure, we have ground for believing the uses in question to have been the efficient agent in producing the latter. Esthonyx furnishes us with an example (Fig. 96) where all the incisors are present in the lower jaw, and where the function of one pair of them (the second) has evidently been partially rodent in character; that is, it has served as a scraper and gouger of food substances. Persistent use has apparently developed the size of this pair of teeth, until we find in Psittacotherium (Fig. 97) they have reached a greater efficiency, and that the external incisors of the lower jaw have disappeared. This disappearance can be accounted for on the ground of disuse, a retirement from service due to position, and the increased growth of incisor

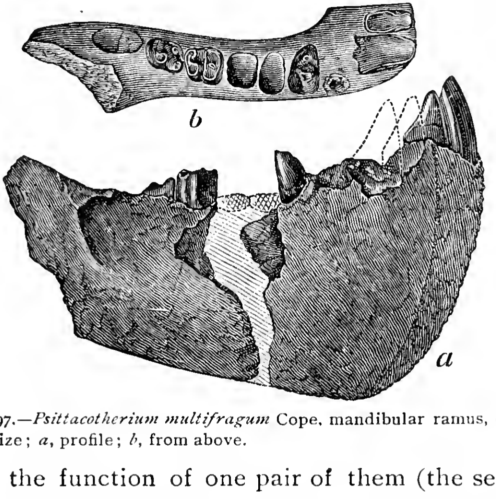

Fig. 97.—*Psittacotherium multifragum* Cope, mandibular ramus, one-half natural size; *a*, profile; *b*, from above.

No. 2. In Calamodon the first incisor has become rudimentary from the same cause, and in Anchippodus it has disappeared altogether, leaving a truly rodent incisor dentition, consisting of the second incisors only, in the lower jaw. Continued use as chisels has developed these teeth to the great proportions seen in such Glires as Castoroides, etc. (Fig. 107).

The use which the Proboscidia and Sirenia (Halicore) give their incisors, is, from a mechanical point of view, like that which the Carnivora give their canines; that is, it consists of impacts in the long axis, and strains transverse to the long axis of the tooth. The elephants use their tusks for prying up the vegetables on which they feed, or for pushing aside the vegetation through which they wish to pass. The ancestors of the Proboscidia are not certainly known, but they possessed incisors of enlarged proportions, such as we find in the Toxodontia and other late representatives of some of the primitive Ungulata. Use of such teeth in the manner referred to, without opposition from the inferior incisors, will account for the tremendous proportions which they ultimately reached in some of the species of Elephas.

The use made by the narwhal of its single huge superior incisor, that of an ice-breaker, indicates the origin of its large dimensions. So with the straight incisors of the hippopotamus; use as diggers has straightened them to a horizontal from their primitive vertical direction, a change which is also partially accomplished in the true pigs (Sus).

In the Sirenian genus Halicore the upper incisors have been used in excavating vegetable growths from the banks and bottom of shallow seas. The transition from three incisors (Prorastomus) to two (Dioplotherium), and to one (Halicore), is identical with what has taken place in the Proboscidia and Glires, and has resulted in the production of an effective digging-tool. In other genera it may be supposed that their habits of browsing on soft growing materials did not necessitate the use of digging incisors, hence these teeth became atrophied, as in the manatee and Rhytina.

c. *Development of Molars.*

In fishes and reptiles where teeth occasionally present very primitive conditions, the theory of the origin of particular types of molar teeth is more simple than in the case of Mammalia. The observations of Hüter on the action of osteoblasts under stimulus show that under moderate irritation osseous tissue is deposited, while under severe pressure osseous tissue is removed. Koelliker has shown that the action of these bodies is the same in dentine as in true bone. Hence modifications of dental structure must stand in close relation to the uses to which they are put. Thus severe pressure on a simple tooth crown would, if long continued, cause it to expand laterally, or in the direction of least resistance, and to grow but little in its vertical axis, i. e., in the direction of greatest resistance. The molar teeth have been subjected to much more severe direct irritation from use than any others in the jaws, and this will account for their increased diameters.

In the case of the eutherian Mammalia, molar teeth are not traceable back to ancestral types of reptilian molars, but to simple conic (haplodont) reptilian teeth. The process of the evolution of the complex mammalian molars from these, forms the subject of a paper in the *American Journal of Morphology* for 1889, from which I quote extensively in the present work.

I have there shown that the greater number of the types of this series have derived the characters of their molar teeth from the stages of the following succession. First a simple cone or reptilian crown, alternating with that of the other jaw (haplodont type). Second, a cone with lateral denticles (the triconodont type). Third, the denticles to the inner or outer side of the crown, forming a three-sided prism, with tritubercular apex, which alternates with that of the opposite jaw (tritubercular type). Fourth, development of a heel projecting from the posterior base of the lower jaw, which meets the crown of the superior, forming a tuberculosectorial inferior molar. From this stage the carnivorous and sectorial dentition is derived, the tritubercular type being retained. Fifth, the development of a posterior inner cusp of the superior molar and the elevation of the heel of the inferior molar, with the loss of the anterior inner cusp. Thus the molars become quadritubercular, and opposite. This is the type of many of the Taxeopoda, including the Quadrumana and Insectivora as well as the inferior Diplarthra. The higher Taxeopoda (Hyracoidea) and Diplarthra, add various complexities. Thus the tubercles become flattened and then concave, so as to form V's in the section produced by wearing; or they are joined by cross-folds, forming various patterns. In the Proboscidia the latter become multiplied so as to produce numerous cross-crests.

d. Origin of the Carnivorous Dentition.

The anterior cusplet of the triconodont crown is (Fig. 98 *A*), in the upper jaw, the paracone, and in the lower jaw the paraconid; and the posterior cusplet is the metacone or metaconid, respectively. As the principal cusps, or protocone and protoconid, alternate with each other, the cusplets stand opposite to them in the closing of the jaws, and a certain amount of interference results. As the lesser cusps are the less resistant to the wedging pressure of such contact, their position would change under its influence, rather than the large central cusps. The lower jaw fitting within the upper, the effect of the collision between the major cusps of the one jaw, and cusplets of the other, would be to emphasize the relation still more; that is, the cusplets of the upper jaw would be wedged outwards, while those of the lower jaw would be pressed inwards, the major cusps retaining at first their original alternate position. With increase of the size of the teeth the cusps would soon assume in each jaw a position more or less transverse to that of the other jaw, producing, as a result of the crowding, a crown with a triangular section in both. The process may be rendered clear by the following diagram:

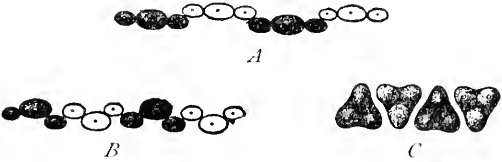

Fig. 98.—Diagrammatic representations of horizontal sections of tricuspidate molars of both jaws in mutual relation; the shaded ones represent those of the upper jaw: *A*, Triconodon; *B*, Menacodon; *C*, ideal tritubercular molars, approached by Menacodon, *B*.

It is supposed on the contrary by Röse and Kükenthal that mammalian molars which support more than one cusp have been formed by the fusion of several simple reptilian cones. So far as regards the higher Mammalia this hypothesis is in opposition to all the facts of paleontology and is not worthy of discussion.

The only question that can arise is with reference to the origin of the multituberculate molar of the Prototheria.

It is further questioned by Forsyth-Major, whether the tritubercular molar has been derived from the triconodont. He believes, on the contrary, that it is derived from the multitubercular type by reduction. There are two objections to this view: (1) the cones of the tritubercular tooth or trigon should be subequal, were they derived from a multitubercular source. On the contrary, the two external cones of the upper, and the two inner cones of the lower series are in the earliest (Jurassic), as well as most of the tritubercular types, smaller than the single opposite cusp or protocone, precisely as are the anterior and posterior cones of the triconodont molar. (2) No paleontologic series from the multitubercular to the tritubercular types has been traced, while the series from the triconodont to the tritubercular is well known. Forsyth-Major's evidence that such a transition exists in the Glires, is better explained by tracing the moderate complexity he describes to a tritubercular origin.

It is also alleged by Allen and Scott that the internal cusps of the premolars, when present, originate by the development of internal cingula, and have no primitive tritubercular ancestry. The evidence at our disposal from paleontological sources is in favor of this view; hence it is reasoned that the history of the molar teeth must have been identical. This however does not follow, especially as the paleontologic evidence points the other way. The history of the two series has been different. In the first place the premolars have been subjected to much less use than the true molars; hence they retained the primitive reptilian simplicity for a much longer period, a simplicity which they retain in the Carnivora, except the $\frac{1}{\ }$, which became the sectorial. Secondly, the premolars, instead of increasing in size, have in many types decreased; the Diplarthra alone presenting an exception to this rule. That the internal cusps of the premolars may have arisen by growth of cingula in this order, is by no means improbable. We seem to have here an excellent illustration of the origin of two identical structures by different evolutionary routes.

The first modification of the tritubercular molar of the lower jaw is the addition of a low cingulum at the posterior base. This is seen in a rudimentary condition in various living species of the Centetidæ and Chrysochloridæ of the insectivorous order (Fig. 100); but in these existing forms the superior molar has added a posterior cingulum also, which widens internally, or towards the palate (Fig. 101). In the evolution of the dentition, the inferior posterior cingulum, or "heel," was developed first, as in the Deltatherium, Centetes, and Stypolophus (Figs. 99, 100, 102), where it is quite large; while the superior cingulum is wanting in Stypolophus and Didelphodus, but is present in a very rudimentary condition in *Deltatherium fundaminis*. In all of these genera the external cusps of the superior series have been pressed inwards, and more or less together, and are therefore removed in this respect from the primitive condition. The more primitive state of the superior cusps is seen in some species of Mioclænus, where, however, a posterior cingulum may be developed. The primitive type of tritubercular superior molar is that of Sarcothraustes, and in the same genus the inferior molar only differs from the primitive type in having a well-developed heel. Among recent Mammalia the carnivorous and insectivorous Marsupialia generally have the tritubercular lower molar with heel. In the Chiroptera and many Insectivora the heel is largely developed, and supports two cusps, as it does in some Creodonta.

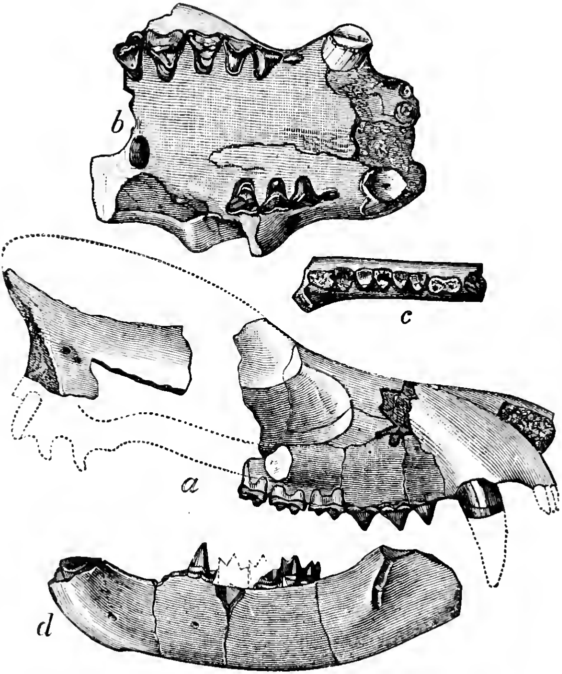

Fig. 99.—*Deltatherium fundaminis* Cope, fragmentary skull, two-thirds natural size; from the Puerco bed of New Mexico. *a*, *b*, *c*, from one individual; *d*, from a second animal; *a*, right side of cranium; *b*, palate from below; *c*, mandible, part from above; *d*, left ramus, outer side; from the *Report of the U. S. Geol. Surv. Terrs.*, Vol. III.

From this point the evolution of the tritubercular molar must be considered from two standpoints. The first is the mechanical cause of the changes of its form; and the second is the mechanical cause of its definite location in a particular part of the jaw. For it has been already stated that in the evolution of the sectorial dentition of the Carnivora, the number of molars and premolars has considerably diminished, while those that remain have become relatively much larger.

In the tritubercular dentition the crowns proper of one jaw alternate with those of the other (Fig. 100); but when heels are added in either jaw, they will oppose such part of the crowns of the teeth in the opposite jaw as comes in contact with them when in use. The development of the heel in the inferior molars produced a type which is known as the tuberculosectorial. This type characterizes the Creodonta and a few Carnivora. In the former there are generally three such teeth, in the latter but one.

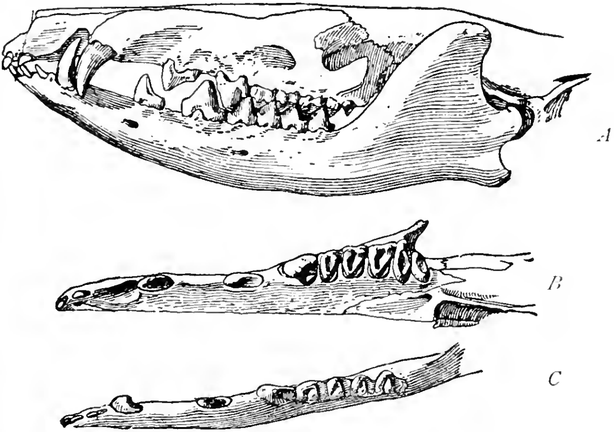

Fig. 100.—*Centetes ecaudatus:* *A*, skull, side seen obliquely from below; *B*, superior molars from below; *C*, inferior molars from above.

In the tuberculosectorial type of inferior molar the primitive tritubercular part of the crown (trigonid of Osborn) stands principally anterior to the posterior root of the tooth. It appears that the posterior root has been extended backwards, so as to occupy a position below the middle of the superior molar, while the tritubercular crown has been confined to the space between the crowns of the superior molars. This would follow of necessity from the alternating action of the crowns of the opposite series, in connection with a general increase in size of the teeth. In the opening of the jaws in a Creodont, the elevated portion of the inferior crown shears by its posterior face against the anterior face of the superior molar, thus restraining its extension posteriorly. The stimulus of use, however, develops a low extension posteriorly, or a heel, which covers the posterior root, and opposes in mastication the internal extremity or tubercle of the crown of the superior molar above it. Thus a molar element in

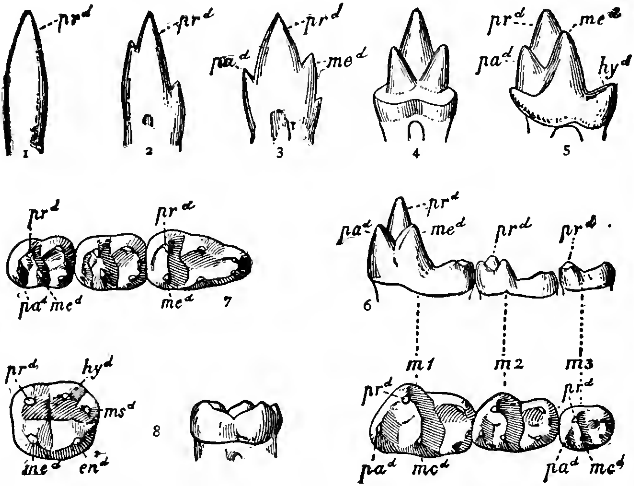

Fig. 101.—Series of inferior molar crowns representing the transition from the simple (haplodont) to the quadritubercular. From Osborn.

mastication is added to the sectorial in some Creodonta, and in Canidæ and Ursidæ, etc., among Carnivora. This function predominates over that of the anterior triangle in the Lemuridæ. (Fig. 95.)

I have already pointed out the successive modifications of form which have resulted in the existing specialized single inferior sectorial tooth of the Felidæ. They consist in the gradual obliteration of the posterior-internal cusp, and of the heel, and the enlargement of the external and anterior internal tubercles of the primitive triangle. The modification in the character of the dentition taken as a whole was shown to consist in the reduction of the number of the teeth, including the sectorials, until in Felis, etc., we have almost the entire function of the molar series confined to a single large sectorial in each jaw.

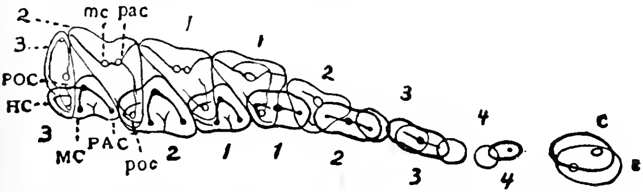

Fig. 102.—*Stypholophus whitiæ* Cope; diagram representing the apposition of the inferior and superior molars. The superior are in light, the inferior in heavy lines. The numbers represent the molars and premolars: *C*, canine; *poc*, protocone; *pac*, paracone; *mc*, metacone; *POC*, protoconid; *PAC*, paraconid; *MC*, metaconid; *hc*, hypocone; *HC*, hypoconid.

The genesis of the superior sectorial tooth has been explained as follows. In consequence of the fact that the lower canine tooth shuts anterior to the superior canine, the result of the enlargement of the diameters of those teeth will be to cause the crowns of the inferior teeth to be drawn from behind forwards against those of the superior teeth when the jaw is closed (Fig. 102). Thus a shearing motion would result between the anterior external edge of the lower triangle and the posterior internal edge of the superior triangle. Now the characters of the true sectorial teeth consist in the enormous extension of these same edges in a fore and aft direction, the inferior shutting inside of the superior. To account for the development of these blades we must understand that the oblique pressure of the front edge of the lower tooth, on the hind edge of the superior tooth, has been continued for a very long time. We must then observe that the internal tubercle of the superior triangle has been pushed continually forwards and been reduced to a very small size. Why should this occur? Why should not the corresponding tubercles of the inner side of the lower crown have been pushed backwards, since action and reaction are equal? The reason is clear: The superior tubercle is on the internal apex of the trigon, and is supported by but one root, while the resistant portion of the inferior crown is the base of the trigonid, and is supported by two, thus offering twice the resistance to the pressure that the superior does. But why should the anterior part of the inferior tooth move forwards? even if it be in the direction of least resistance? This is due to the regular increase in size of the teeth themselves, an increase which can be traced from the beginning to the end of the series. And this increase is the usual result of use (Fig. 102).

The mechanics of the above proposition I believe to be correct, but I have had occasion to modify the statement as to the initiatory cause of the process. In many primitive Ungulata the canines have been as well developed as in the Carnivora, yet the forward pressure of the inferior molars on the superiors has not resulted, or has not been sufficient to produce sectorial molars in those types. In the Amblypoda, the lower molars even shear backwards on the upper ones. It seems then that this growth of the canines is not in all instances sufficient to cause a proterotome mastication. I suspect that the more usual cause is to be found in the voluntary effort of the primitive flesh-eater, to masticate flesh by the manipulation of his lower jaw and the body to be divided. The presence of the inferior canine forbids a posterior shearing movement of the molars, so that the anterior shear is the only one possible to most of the Creodonta. The absence of preglenoid crest in primitive Creodonta will permit a manipulation such as we observe in various ungulates to-day. The formation of a habit of a proterotome mastication would result, and the structural results would succeed as above pointed out.

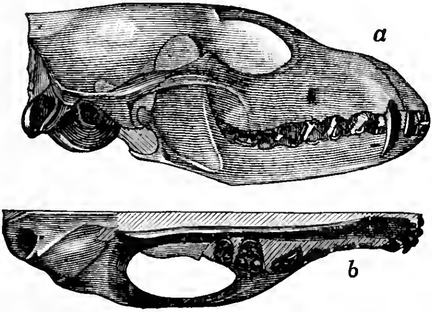

Fig. 103.—*Cynodictis geismarianus* Cope; skull one-half natural size: *a*, right side; *b*, left side from below.

The excess of the forwards pressure of the inferior teeth against the superior over any backwards pressure, has left the posterior internal cusp of the triangle of the inferior molar (metaconid) without contact or consequent functional use. It has, consequently, gradually disappeared, having become small in the highest

Canidæ, and wanting in some Mustelidæ, and all Felidæ. The heel of the same tooth has had a similar history. With the diminution in size of the first superior tubercular, with which it comes in opposition in mastication, its functional stimulus also diminished; and it disappeared sometimes a little sooner (Felidæ) and sometimes a little later (Hyænidæ) than that tooth.

The specialization of one tooth to the exclusion of others as a sectorial, appears to be due to the following causes. It is to be observed in the first place that when a carnivore devours a carcass, it cuts off masses with its sectorials, using them as shears. In so doing it brings the part to be divided to the angle or canthus of the soft walls of the mouth, which is at the front of the masseter muscle. At this point the greatest amount of force is gained, since the weight is thus brought immediately to the power, which would not be the case were the sectorial situated much in front of the masseter. On the other hand, the sectorial could not be situated farther back, since it would then be inaccessible to a carcass or mass too large to be taken into the mouth.

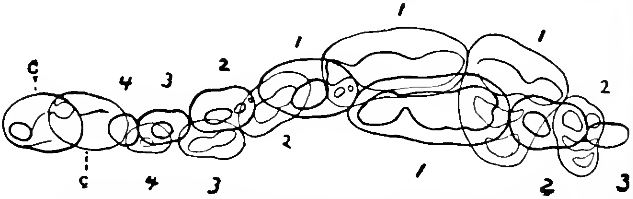

Fig. 104.—*Aelurodon sævus* Leidy; diagram representing coadaptation of crowns of superior and inferior molars in mastication; lines and lettering as in Fig. 102.

The position of the sectorial tooth being thus shown to be dependent on that of the masseter muscle, it remains to ascertain a probable cause for the relation of the latter to the dental series in modern Carnivora. Why, for instance, were not the last molars modified into sectorial teeth in these animals, as in the extinct Hyænodon, and various Creodonta. The answer obviously is to be found in the development of the prehensile character of the canine teeth. It is probable that the gape of the mouth in the Hyænodons was very wide, since the masseter was situated relatively far posteriorly. In such an animal the anterior parts of the jaws with the canines had little prehensile power, as their form and anterior direction also indicates. They doubtless snapped rather than lacerated their enemies. The same habit is seen in the existing dogs, whose long jaws do not permit the lacerating power of the canines of the Felidæ, though more effective in this respect than those of the Hyænodons. The usefulness of a lever of the third kind depends on the approximation of the power to the weight; that is, in the present case, the more anterior the position of the masseter muscle, the more effective the canine teeth. Hence it appears that the relation of this muscle to the inferior dental series depended originally on the use of the canines as prehensile and lacerating organs, and that its relative insertion has advanced from behind forwards in the history of carnivorous types. Thus it is that the only accessible molars, the fourth above and the fifth below, have become specialised as sectorials, while the fifth, sixth, and seventh have, firstly, remained tubercular as in the dogs, or, secondly, have been lost, as in hyænas and cats.

The reduction of the number of molars in relation to the increase in the size of the canines commenced as early as the Jurassic period. It is seen in the genera Triconodon (Owen) and Paurodon (Marsh), where

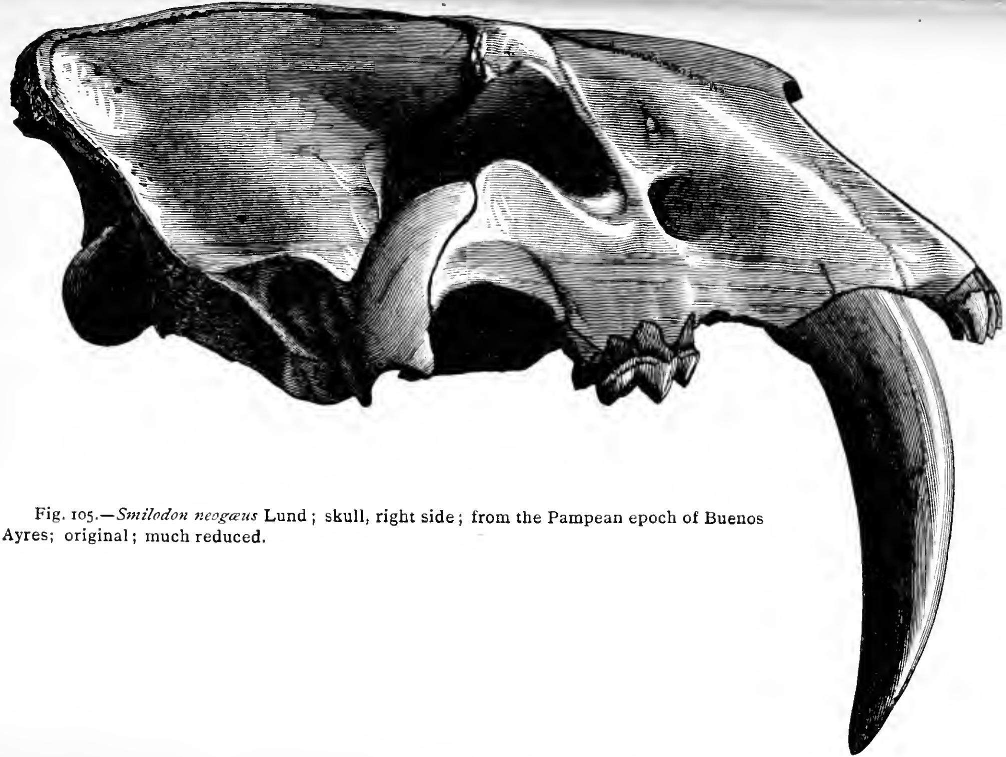

Fig. 105.—*Smilodon neogæus* Lund; skull, right side; from the Pampean epoch of Buenos Ayres; original; much reduced.

the canines are large and the molars few. In the Plagiaulacidæ a similar relation is seen between the development of the incisors and the reduction in number of the molars. This is the modification of relation observed in existing Mammalia of the orders Proboscidia and Glires, which will be mentioned later, under the head of proal dentition.

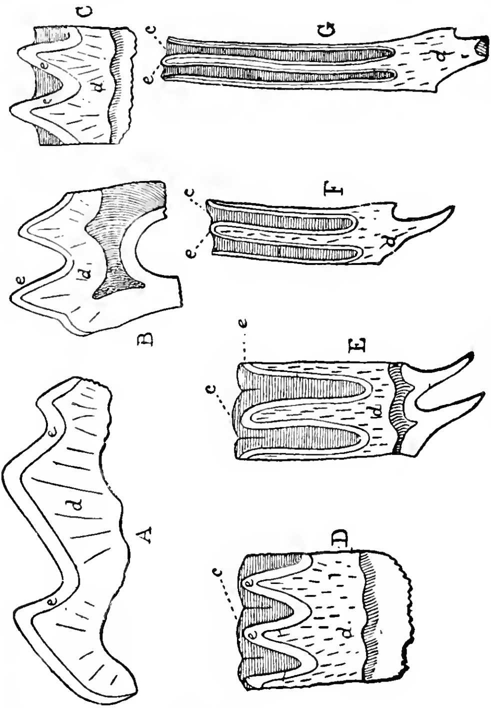

Fig. 106.—Sections of crowns of molars of Ungulata from Dinotherium to *Elephas primigenius*. *A*, *B*, Dinotherium; *C*, *D*, Mastodon; *E*, *F*, *G*, Elephas. From Gaudry.

e. Origin of the Dental Type of the Glires.

The peculiarities of the rodent dentition consist, as is well known, in the great development of the incisors;

the loss of the canine and of all but one, or rarely of two, of the premolars, which leave a wide diastema; and the posterior position of the molar teeth, as relates to the rest of the skull. A peculiarity which belongs to the highest types of the order is the prismatic form of the molars, and the deep inflection of their always transverse enamel folds both laterally and vertically. A peculiarity of the masticating apparatus, which is the basis of distinction from the bunotherian order, is the lack of postglenoid process, and the consequent freedom of the lower jaw to slide backwards and forwards in mastication. Appropriately to this motion the condyle of the mandible is either subglobular, or is extended anteroposteriorly, and the glenoid cavity is a longitudinal instead of a transverse groove.

The mechanical action of the development of the rodent dentition has been as follows. The first factor in the order of time and importance was the increasing length of the incisor teeth. Those of the lower jaw closed behind those of the upper in the progenitors of the Glires (e. g. Psittacotherium) as in other Mammalia. Increase of length of these teeth in both jaws would tend to keep the mouth permanently open, were it not for the possibility of slipping the lower jaw backwards as it closed on the upper. This backward pressure had undoubtedly existed, and has operated from the earliest beginning of the growth of the rodent incisors. The process has been precisely the opposite of that which has occurred to the Carnivora, where the pressure has been ever forwards owing to the development of the canines. The progressive lengthening of the incisors through use has been dwelt on by Professor Ryder (*l. c.*). The posterior pressure on the lower jaw, produced by its closing on the upper, has been increased directly as the increase in the length of the incisors, especially those of the lower jaw.

The first effect of this posterior pressure will have been to slide the condyle of the mandible posteriorly

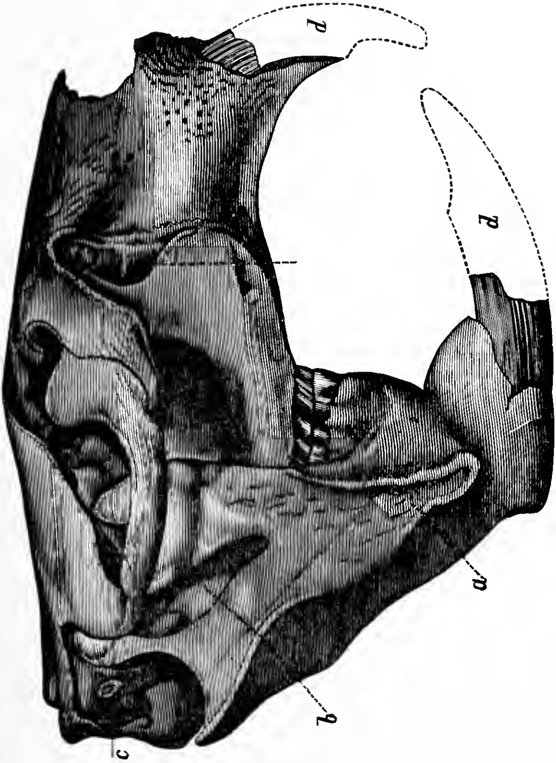

Fig. 107.—*Castoroïdes ohioensis* Foster, skull, right side; two-fifths natural size. *a*, inferior insertion of masseter muscle; *b*, fossa inside of ascending ramus; *c*, external auditory meatus; *d*, incisors; *e*, foramen infraorbitale; from Hall and Wyman.

over the postglenoid surface, if any were present, as is probable, in the bunotherian ancestor of the rodent. Continued repetition of the movement would probably push the process backwards so as to render it ineffective as a line of resistance, and ultimately to flatten it out against the otic bulla, and atrophy it. The lower jaw would thus come to occupy that peculiarly posterior position which it does in all rodents.

The anteroposterior (proal[1]) type of mastication becoming necessary, an appropriate development of the muscles moving the lower jaw, with their insertions, follows, *pari passu*. As a result we see that the insertion of the temporal muscle creeps forward on the ramus, until in the highest rodents (Cavia) it extends along the ramus to opposite the first true molars. The office of this muscle is to draw the ramus backwards and upwards, a movement which is commenced so soon as the inferior incisor strikes the apex of the superior incisor on the posterior side. By this muscle the inferior molars are drawn posteriorly and in close apposition to the superior molars. Connected with this movement, probably as an effect, we find the coronoid process of the mandible to have become gradually reduced in size to complete disappearance in some of the genera, e. g. of Leporidæ. In these genera the groove-like insertion of the temporal muscle develops as the coronoid process disappears.

As third and fourth effects of the posterior position of the lower jaw, we have the development of the internal pterygoid and masseter muscles and their insertions and origins. The angle of the ramus being forced backwards, these muscles are gradually stretched backwards at their insertions, and their contraction becomes more anteroposterior in direction than before. The internal pterygoid becomes especially developed, and its point of origin, the pterygoid fossa, becomes much enlarged. The border of the angle of the mandible becomes more or less inflected. In their effect

[1] Page 318.

on the movements of the ramus they oppose that of the temporal muscle, since they draw the ramus forwards. They are the effective muscles in the use of the incisor teeth; that is, in the opposition of the inferior incisors against the superior from below and posteriorly. Hence the great development of the internal pterygoid, and, in a less degree, of the masseter. Both muscles tend also to close the jaws, but at a different point in the act of mastication from that at which the temporal acts. If we suppose the mouth to be open, the action of the masseter and internal pterygoid muscles draws the mandible forwards and upwards until the incisors have performed their office, or the molars are in contact with each other or with the food. They then relax, and their temporal muscle continues the upward pressure, but draws the ramus backwards to the limit set by the adjacent parts, causing the act of mastication.

A fifth effect of the development of the incisors and of the proal mastication, is seen in the position of the molar teeth. The indefinitely repeated strain and pressure applied to the superior molars from forwards and below has evidently caused a gradual extension of the maxillary bone backwards, so that the last molars occupy a position much posterior to that which they do in other orders of mammals. This is especially the case in such forms as Bathyergus, Arvicola, and Castoroïdes (Figs. 107–108), where the last molars are below the temporal fossa, and posterior to the orbit.

A sixth effect of the causes mentioned has been referred to by Ryder.[1] This is the oblique direction of the axes of the molar teeth. These directions are opposite in the two jaws; upwards and forwards for the

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[1] *Proceedings Philadelphia Academy*, 1877, p. 314.

lower, and downwards and backwards for the upper. The mechanics of this change of direction from vertical in the primitive forms (Sciuridæ) to oblique in the genera with prismatic molars, is simple enough. The inferior crowns when closely appressed to the superior, and drawn posteriorly in the direction of the long axis of the jaw, press and strain the teeth in the two

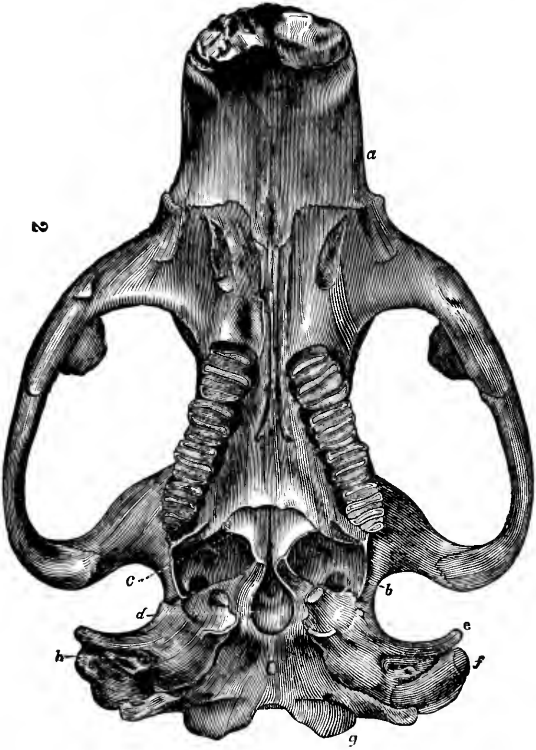

Fig. 108 —*Castoroïdes ohioensis* Foster; two-thirds natural size; skull from below. *a*, incisine foramen; *b*, pterygoid fossa; *c*, internal pterygoid plates; *d*, fossa in basioccipital bone; *e*, external auditory meatus; *f*, mastoid process; *g*, occipital condyles; *h*, tympania bulla, after Hall and Wyman.

directions mentioned. The development of the long prismatic crowns which has proceeded under these circumstances, has been undoubtedly affected by the pressure and strain, and the direction we find has been the result.

The seventh effect is in the detailed structure of the teeth themselves. Beginning with short crowns with simple transverse crests (Psittacotherium and Sciuridæ, Figs. 106, 109), we reach through intermediate forms, crowns with vertical laminæ of enamel, which sometimes divide the crown entirely across (Chinchillidæ, Caviidæ, Castoroïdidæ) or appear only on the side of the crown, through the continued coalescence of the prisms of which each molar crown is composed (Arvicola). In many instances the crowns increase in transverse at the expense of their longitudinal diameter (Castor, Lepus). The vertically laminated structure is evidently due to the crowding together of transverse crests by the same pressure which has given the crowns their oblique direction. In many genera the lengthening of the crown has included the lengthening of the longitudinal connection between the transverse crests, as in Arvicola, Castor, and Hystricidæ generally. In others this connection has not been continued, so that the crown is

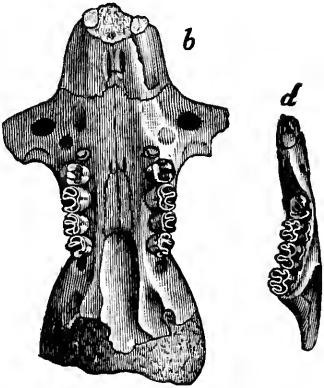

Fig. 109.—*Ischyromys typus* Leidy, from the White River beds of Colorado; original; from the *Report U. S. Geol. Surv Terrs.*: *b*, cranium from below; *d*, mandible from above.

composed of prisms which are separate to near the base, as in Amblyrhiza and Geomyidæ. In others, connection between the prisms has been lost by cænogeny, as in Chinchillidæ and Caviidæ generally. The latter families display also the greatest amount of crowding.

V. DISUSE IN MAMMALIA.

Modifications of structure of the mammalian skeleton accompany the disuse of parts, no less distinctly than in other divisions of animals. That these modifications are the direct consequences of this disuse may be reasonably inferred as the antithesis to the thesis of development of structure through use, maintained in the preceding pages. The evidence is more convincing from the fact that the same structures are observed to be related to similar dynamic conditions in groups of different taxonomic position. I select four illustrations from the Mammalia, from types in which the phylogeny is known, so that there is no question as to the degeneracy of the parts described.

a. Natatory Limbs.

The limbs have undergone great modifications of form in their gradual adaptation to aquatic habits. The stages of this process are to be observed first in the sea-otter (Enhydra), then in the seals, then in the sirenians, and last in the Cetacea. This succession of groups is not given here as a phylogeny, for paleontology does not warrant any such history, but the phylogeny of the limbs has been similar in the order of succession.

The use of a limb as an oar for propulsion in the water requires that it shall be, so far as the blade is concerned, inflexible. Such a structure has existed in all thoroughly aquatic Vertebrata. This implies the immobility of the articulations, which is due to the loss of their condylar surfaces. This may be traced to disuse of such articulations. This disuse would be at first voluntary, the limb being held stiffly while used as an oar in the act of swimming. Loss of power of extension and flexion is well known to result from disuse. It is well known that the flexors and extensors of the manus have become atrophied in the Cetacea. Not so, however, with the flexors and extensors of the humerus, which become those of the entire limb. In the whales the first segment of the fore limb is enclosed within the integument of the body, so that its motion being much restricted, the insertional crests are reduced in size. In the eared seals (Otariidæ) the hind limbs are somewhat free from the body integument, so that they can be turned forward when on land. They are further enclosed in the true seals (Phocidæ) so that their motion is very slight and they cannot be used for progression on land, and are available only for swimming.

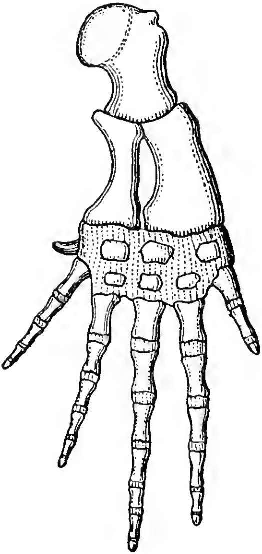

Fig. 110.—*Balæna mysticetus* fore limb: from Cuvier, *Oss. Fossiles.*

b. Abortion of Phalanges in Ungulata.

In the heavy Ungulata the longitudinal diameter of the phalanges is greatly reduced in relation to their transverse. The successive increase in depression in the bones of the feet with the advance of time is to be

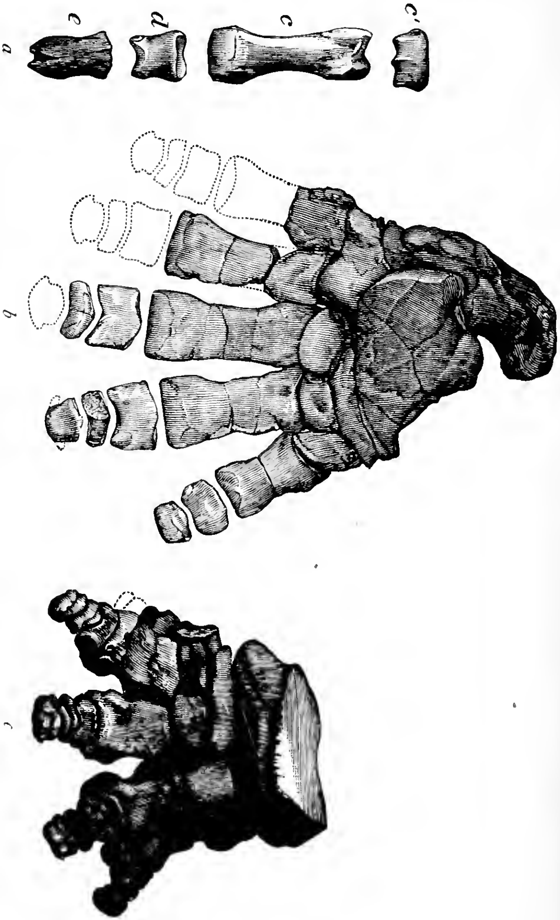

Fig. 111.—*a*, *Pantolambda bathmodon*, digit of posterior foot. *b*, Right posterior foot of a species of Coryphodon from New Mexico, one-half natural size. From Cope, *Report Expl. W. of 100th Mer.*, G. M. Wheeler, IV., Pl. LIX. *c*, *Eobasileus mirabilis*, right posterior foot; from Marsh, Dinocerata.

most readily seen in the order Amblypoda, where we pass from Pantolambda to Coryphodon and Uintatherium (Fig. 111.) A similar successive reduction is to be seen in the lines of the Perrisodactyla, as we pass from the smaller and lighter to the heavier and more bulky types. Such series are those which commence in the Lophiodontidæ, and terminate in the Menodontidæ on the one hand, and the rhinoceroses on the other. The elephants display the end of a similar line, which commences in the Condylarthra. In all of these bulky mammals the weight in progression is borne on the extremities of the metapodial bones, and the phalanges take but little share in it. They are turned forwards and are nearly useless. Their great reduction in dimensions in these forms appears to me to have followed disuse, and this is then the probable cause of it.

c. Atrophy of the Ulna and Fibula.

Successive atrophy of the ulna and fibula has been already referred to (p. 135). This is coextensive with reduction of the number of the digits in the ungulate Mammalia, and with the development of the digital patagium in the bats. This is in broad contrast to the subequal development of the ulna and radius in the Cetacea, where the fore limb functions as the blade of an oar. The cause of the reduction of the two elements in the Ungulata is the restriction of the functions of the fore and hind limb to the radius and tibia respectively. The distal extremities of the ulna and fibula are supported by the external bones of the carpal and tarsal series respectively. The reduction of the external digit deprives the external bones in question of their share in the support of the general weight, and consequently relieves them of the impact which passes through the longer median digits which remain. The median digits, on the other hand, support the radius and tibia through the medium of the carpus and tarsus, and it is these elements therefore which function in the use of the limb. We have here an evident illustration of the effect of disuse in effecting the atrophy of an element, and of use in increasing the size and complexity of an adjacent element, of the same organism. No other explanation seems possible, for the elements which are reduced and those which are enlarged, are subjected in every other respect to the same conditions.

d. Atrophy of Incisor Teeth.

This is complete in both jaws of existing Edentata; the upper jaw of Dinocerata and many Artiodactyla, and is partial in the upper jaw in various Chiroptera and Lemuridæ. We have already seen (p. 326) that the superior incisors of certain Lemuridæ are without utility, owing to the conversion of the inferior incisors into a horizontal comb. I have ascribed the reduction of the superior incisors of bats to disuse consequent on the adoption of a frugivorous diet.[1] Further reason, which is common to the living members of the orders mentioned, is to be found in the disuse which has followed the use of the tongue as an organ for the prehension of food. The fruit-eating bats with most reduced incisors (Glossophaginæ) carry the soft parts of fruits into the mouth with the tongue. The Edentata use the tongue for the collection of both insect and vegetable food, projecting it far exterior to the mouth. The Artiodactyla without superior incisors however, combine the prehensile use of the tongue with a use of the lower incisors, which bite off the grass thus seized,

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[1] *Mechan. Origin, etc., Mammalia*, 1889, p. 224. See also Dr. H. Allen, *Proceeds. Academy, Philadelphia*, 1891, p. 451.

while it is pressed against the pad which replaces the superior incisors. Why the superior incisors should have disappeared in this group is not yet clear to my mind.

In this connection Dr. Allen (*l. c.*) reminds us that in hypertrophy of the tongue in man, the inferior incisors are thrown forward and are widely separated from each other. He considers it reasonable to infer that in lower animals where the tongue is used for prehension, the similar change which takes place in the teeth, from a vertical to a horizontal position, is induced by this cause.

VI. HOMOPLASSY IN MAMMALIA.

The direct evidence in favor of kinetogenesis above adduced is greatly strengthened by corroborative testimony presented by distinct phyla of animals. Restricting myself here to Mammalia, I will enumerate a number of cases where the same structures have appeared in distinct lines of descent under similar mechanical conditions, a phenomenon already referred to on page 72 under the name of Homoplassy.

Before reviewing the subject, I cite what is the most remarkable example of homoplassy in the Mammalia which has yet come to the knowledge of paleontologists. Ameghino has discovered in the Cenozoic formations of Argentina a group of Ungulata which he calls the Litopterna, and which I regard as a suborder of the Taxeopoda, allied to the Condylarthra (p. 128). Ameghino placed the group under the Perissodactyla, but the tarsus and carpus are of a totally different character, and indicate an origin from the Condylarthra quite independently of that division. The carpal and tarsal bones are in linear series, or if they overlap, it is in

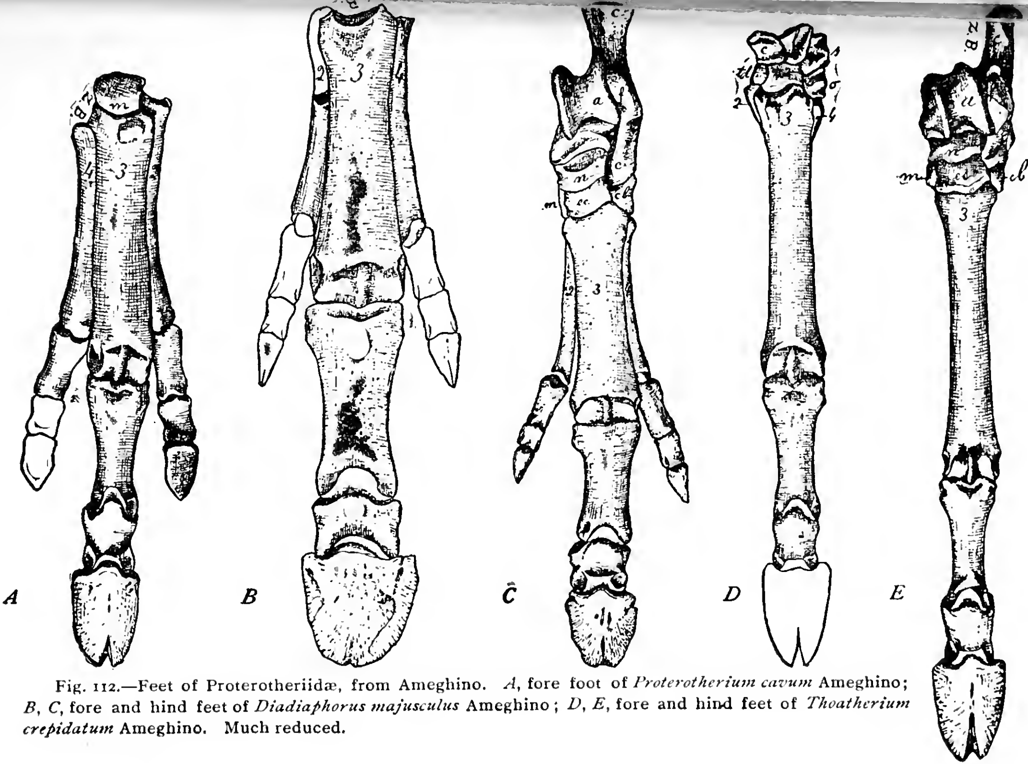

Fig. 112.—Feet of Proterotheriidæ, from Ameghino. *A*, fore foot of *Proterotherium cavum* Ameghino; *B*, *C*, fore and hind feet of *Diadiaphorus majusculus* Ameghino; *D*, *E*, fore and hind feet of *Thoatherium crepidatum* Ameghino. Much reduced.

a direction the opposite of that which characterizes the order Diplarthra (=Perissodactyla and Artiodactyla). But the Litopterna present a most remarkable parallelism to the Perissodactyla in the characters of both the feet and the dentition. No genus is known as yet which possesses more than three toes before and behind, and these are of equal length in Macrauchenia Owen. In this genus the teeth are not primitive but are much modified. The most primitive dentition is seen in the genus Proterotherium (Ameghino) where the superior molars are tritubercular as in many Condylarthra. In this genus (Fig. 112, *A*), there are three toes, but the lateral ones are reduced, about as in the Equine genus Anchitherium (p. 148). In the next genus, Diadiaphorus Ameghino, the superior molars are quadritubercular and crested, while the lateral toes are reduced still more, being quite rudimental (Fig. 112, *B*, *C*), as in the equine genera Hippotherium and Prothippus (p. 149; Fig. 70). The superior molars have not progressed so far as in these genera, but are not very different from those of Anchitherium. In the third and last type (Thoatherium Ameghino), the lateral digits have disappeared from both fore and hind feet (Fig. 112, *C*, *D*), so that the condition is that of the genus Equus (Fig. 81), but the splints in the *Thoatherium crepidatum* Ameghino are even more reduced than in the known species of horse. The superior molars have not assumed the pattern of the genus Equus, but resemble rather those of Macrauchenia, and could have been easily derived from those of Diadiaphorus.

Here we have a serial reduction of the lateral digits and their connections with the leg, and increase in the proportions of the middle digit and corresponding increase in the proximal connections, exactly similar to that which took place in the horse-line, in a different order of Mammalia.

In review I now cite as examples of homoplassy:

First, as regards the development of the tongue-and-groove ankle-joint. This has been developed independently along four distinct phyla, viz., in the leporid Glires, the Carnivora, and the even and odd toed Diplarthra.

Second, the wrist-joint. The faceting of the radial surface has appeared independently in the perissodactyle and artiodactyle lines, but is best developed in the latter. Also it appeared independently in the separate suoid and boöid lines in the latter suborder.

Third, the trochlear crest of the elbow-joint appeared independently in the perissodactyle and artiodactyle Diplarthra, and in the leporid Glires (the rabbit family).

Fourth, the round head of the radius appeared independently in the lines of the Edentata (ant-eater) and Quadrumana, under the stress of supination of the hand.

Fifth, the development of cusps with crescentic section out of cusps with round section has occurred in the widely different groups of the multituberculate Prototheria, and the selenodont Artiodactyla. In the former the crescents are transverse, since the thrust of the teeth in use is longitudinal; in the latter they are longitudinal, since the thrust of the jaws is transverse.

Sixth, the deep plication and hypsodonty of molars appeared independently in the Glires, Tillodonta, Proboscidia, Sirenia, Perissodactyla, and Artiodactyla; and probably in the Edentata and Toxodontia.

Seventh, increase in the length of the legs has ensued in the Marsupialia, Glires (Lepus, Dolichotis, Dipus), Carnivora, Ungulata, Quadrumana.

Eighth, reduction of digits has occurred under similar conditions in Marsupialia, Glires, Insectivora, Carnivora, Ungulata.

Ninth, the atrophy of the ulna and fibula occur in the distinct lines of the Perissodactyla and Artiodactyla, and the atrophy of the fibula in the leporid Glires; all in limbs which function in the most rapid progression.

Further confirmation of the law of kinetogenesis is to be found in those cases where different structures appear in different parts of the skeleton of the same individual animal, in direct correspondence with the different mechanical conditions to which these parts have been subjected. Examples: the diverse modifications of the articulations of the limbs in consequence of the uses to which they have been put, in mammals which excavate the earth with one pair of limbs only; as in the anterior limbs of the fossorial Edentata, Insectivora, and Glires. The reduction of the number of the digits in the posterior limb only when this is extensively used for rapid progression, as in leaping: this is seen in the kangaroo and jerboas, in the orders Marsupialia and Glires.

The development of a dental structure of premolars identical with that of the molars, from a different structural origin, in the Perissodactyla.

From the preceding facts I have inferred that in biologic evolution, as in ordinary mechanics, *identical causes produce identical results.*

vii. A HYPOTHESIS OF THE ORIGIN OF THE DIVISIONS OF THE VERTEBRATA.

In order to estimate the part which has been played by the movements of the Vertebrata in changing their environment in past geologic ages, we have to rely principally on inferences derived from the present physical characteristics of the earth. Formerly, as now, conditions of temperature, humidity, soil, shelter, food, etc., were avoided or appropriated by animals, through their capacity for moving from place to place. What concerns us chiefly here, is the effects on their structure produced by the movements of Vertebrata. In examining this question I will take it up in systematic order, so as to observe whether kinetogenesis has been the principal or only a subordinate agency in the evolution of this branch of the animal kingdom.

The most conspicuous index of the serial succession of the vertebrate classes, is, as has been already remarked, the circulatory system. The modifications of this system have been immediately connected with those of the method of respiration, which the exigencies of the environment induced in vertebrates. The existence of branchial arteries and veins dates from the earliest vertebrate, if not from prevertebrate life. They are already established in the Tunicata, and continued throughout the rising scale in diminished numbers, so long as Vertebrata were exclusively aquatic in their modes of life. When at the close of the Devonian system the land masses assumed great proportions in both the Eastern and Western Hemispheres, it is probable that many fishes were entangled in shallow water, which rapidly freshened, and ultimately were desiccated, and respiration by the swallowing of air into the alimentary canal began to take the place of respiration by gills. It is well known that respiration by this means may be carried on by fishes of various genera, e. g. Cobitis; and Professor Gage has shown that the same habit exists in Batrachia and in certain tortoises (Tronychidæ). In the middle Carboniferous shales tracks of land animals occur, and the bones of Batrachia abound in the coal measures. Already in the Permian these Batrachia are accompanied by numerous Reptilia, and air breathers of terrestrial habits had become numerous on the earth.

The habit of holding in the œsophagus large quantities of air while engaged in seeking food in foul water, or on land, on the part of vertebrates which normally oxygenated the blood by means of gills, was probably the mechanical cause of the development of a pouch, and afterwards of a diverticulum of the œsophagus, which became ultimately a swim-bladder or a lung. In vertebrates in which a return to aquatic life became necessary, it became the former; in those which remained for a shorter or longer period of time on land it became the latter.[1] It is noteworthy that among fresh-water fishes generally, the swim-bladder is more complex than among marine forms, showing that the varying conditions of shore and fresh-water life have been mainly responsible for its development.

The development of a lung at once produced a change in the uses to which the various branchial arches were put. The posterior, which supply the lung, would be subjected to greater pressure owing to the increased blood supply demanded by the lung,

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[1] This view is adopted by C. Morris, *American Naturalist*, 1892, p. 975.

and a correspondingly diminished pressure would be experienced by the now unused branchial portions of the bows. The first would retain the importance of its basal portion, as the source of the carotids, while the middle arches would continue their existence as the bases of the central dorsal aorta. The loss of the right aorta-root in Mammalia was probably due to the fact that the great arteries which supply the digestive system are primitively branches of the left aorta-root, as they are to-day in the crocodiles and in many of the Batrachia. The right aorta-root disappeared through disuse. Probably in the immediate ancestors of the birds, as in the crocodiles, the right aorta-root gave off the carotides and the subclaviæ. As the birds demand an excessive blood-supply for the fore limbs, we have here probably the reason why the right root remained in this subclass.

The next index of successional development in Vertebrata is the brain. Our belief that use under stimulus has been the cause of its successive growth, can only be based on the analogy of our own experiences in the matter of education. No part of the human organism is so susceptible to stimuli as the nervous system, and the marvellous effects on faculty of continued exercise are well known to everybody. Since the changes of mental states are necessarily due to corresponding structural changes no one will find in ignorance of the mechanics of brain-evolution a serious obstacle to believing that it has taken place under the influence of the innumerable stimuli always present to animal life.

It is in the skeleton that we have the actual record and evidence of the effect of movement on structure. It must be remembered in this connection that skeletal and dental tissues exhibit the phenomena of nutrition and waste (metabolism), common to all living organic matter. Hence even the hardest osseous tissues are plastic and are subject to mechanical influences to a degree which is not possible to dead matter of equal density.

Fundamental differences between Vertebrata are displayed by their organs of movement, but before specially considering these I will refer briefly to certain other fundamental characters displayed by the skull. In advancing from the fishes to the Mammalia we observe a successive consolidation of the mandibular arch, and of its mode of connection with the cranium. The mandibular arch in its entirety displays in the fishes a segmented condition, generally comparable to that which characterizes the branchial arches. Among Batrachians and Reptilia various degrees oi fixation of its suspensor (hyomandibular, quadrate) to the cranium exist, and in some of them it is closely united by immovable suture. The complete fusion with the squamosal seen in the Mammalia is its final status. The segmentation of the mandibular portion of the arch seems, from the discoveries of Ameghino, to have continued among some of the Lower Eocene mammals, but that finally disappeared, so that in the modern mammals the movable mandibular arch consists of a single element on each side. In this history we see an instance of the progressive coössification of parts, which results from the constant strain of use, of which many other normal and abnormal examples are known. This use is the act of mastication. Where there is no mastication, and the jaws are used only as prehensile organs, this coössification does not occur, as, for instance, in the snakes. In this most specialized and modern type of Reptilia, the segmentation is complete.

The segmentation of the limbs in the Vertebrata is a simple mechanical problem. Paleontology and embryology concur in proving that the limbs originated in primitive folds in the external integument, and that their connection with the internal skeleton was of later accomplishment, has been shown by Wiedersheim. At first free, they sought points of support on the skeleton, but did not lose their free mobility when this contact was attained. Appropriately to the mechanical conditions of rigidity and flexibility necessary to their use in a fluid medium, they were originally composed of slender rods which were segmented by interruptions at suitable points. The articulations of the fin-rays of fishes have been made the subject of an interesting research by Ryder, who finds them to be fractures, due to flexures during motion in the water medium.[1] The limb of land vertebrates (the chiropterygium) was derived from one of the forms of fins (rhipidopterygium) of water vertebrates. This is the simple type of primitive fin displayed by the Paleozoic Teleostomi of the superorder Rhipidopterygia. Whether the subdivisions of the chiropterygium, the propodial, metapodial, and phalangeal bones, etc., were divided from the primitive branches of the archipterygium, as held by Gegenbaur, or whether they have developed by sprouting from a simple axial series of segments, as held by Baur, or whether, as I have suggested, it is a derivation from the rhipidopterygian type of paired fin, is not yet decided. In either case, the limbs of the first land animals were segmented and flexible at the joints between the segments. The ne-

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[1] *Proceedings of the American Philosophical Society*, 1889, p. 547.

cessities of such limbs are twofold: first, to serve as supports when at rest or in progression; second, to be applied to the body in protection from enemies, or in aiding the functions of feeding, reproduction, etc. The first function requires principally mobility at the point of connection with the body. The second, flexibility at some point on the shaft of the limb. The two kinds of movements in question would conserve two principal points of flexure, and these would be for the fore limb, just what we find, the shoulder and elbow joints; and for the hind limbs, the hip and knee joints. The two median joints are directed in opposite ways, the elbow backwards and the knee forwards. This diversity is clearly due to the diverse positions of the functioning regions. The opposite extremities of the alimentary canal, the posterior including the exits of the urogenital organs, requires that the fore limbs should bend forwards, and the posterior limbs backwards. And the constantly recurring necessity for the exercise of these flexures must necessarily have developed the appropriate articulations in preference to all others. The terminal flexure, that of the wrist or ankle, has been evidently due to a similar mechanical cause, viz., the flexure due to pressure of the weight of the body on the terminal segments when in contact with earth. The distal segments are the most slender in all types, and least able to maintain a linear direction under pressure, hence, they have flexed easily and thus the line of separation between leg and foot had its origin. The ankle and wrist in the Batrachia Urodela is still a mere flexure.

Mr. Herbert Spencer has endeavored to account for the origin of the segmentation of muscles into myotomes, and the division of the sheath of the notochord into vertebræ, by supposing it to be due to the lateral swimming movements of the fishes, which first exhibit these structures.[1] With this view various later authors have agreed, and I have offered some additional evidence of the soundness of this position with respect to the vertebral axis of Batrachia,[2] and the origin of limb articulations.[3] It is true that the origin of segmentation in the vertebral column of the true fishes and the Batrachia turns out to have been less simple in its process than was suggested by Mr. Spencer, but his general principle holds good, now that paleontology has cleared up the subject.

The Echinodermata, Mollusca, Arthropoda, and Vertebrata possess external or internal calcareous or chitinous skeletons for the most part. The lower forms of all these branches, however, are more or less deficient in this kind of protection, and embryology indicates that all of them are the descendants of the Vermes or worms, which are mostly without such hard supports and protections. Whether this be demonstrated or not, we have plenty of evidence to show that the primitive Vertebrata were without hard skeletons, and that their bodies were composed internally and externally of perfectly flexible tissues.

If we now imagine that either the integuments, or an axial rod, of a worm-like animal has become the seat of a calcareous or chitinous deposit, it is evident that the movements of the animal in swimming or creeping must have interrupted the deposit at definite points of its length. The lateral flexure of the body would be restricted to certain points, and the intervening spaces

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[1] *Principles of Biology*, 1873, pp. 198–204.

[2] *Origin of the Fittest*, 1887, p. 305.

[3] *Mechanical Causes of Origin of Hard Parts of Mammalia*, 1889, p. 163.

would become the seat of the deposit. At the lines of interruption joints would be formed, and if the movements were habitually symmetrical, these interruptions would be equidistant. In this way the well-known segmentation of the external skeletons of Arthropoda, and the internal skeletons of Vertebrata would be formed. We have more detailed evidence that this has been the case. Thus the segmentation of the osseous sheath of the chorda dorsalis in both primitive fishes and batrachians has been accomplished in wedge-shaped tracts precisely as may be observed in the folding of a tolerably stiff sleeve of a coat which ensheathes the arm, under the influence of lateral flexures. The wedge-shaped tracts are superior and inferior, the apices directed towards each other. Seen from the side they form two wedges with their apices together, and their bases one up and the other down. Now, if a person who wears a coat of rather thick material will examine the folds of his sleeve as they are produced on the inner side of his arm, he will see a figure nearly like that of the segments of the vertebral column described. The folds will correspond to the sutures, and the interspaces to the bony segments. He will find that the spaces are lens-shaped, or, when viewed in profile, wedge-shaped, with the apices together. This arrangement results from the necessary mechanics of flexure to one side. In flexure of a cylinder like the sleeve, or like a vertebral column, the shortest curve is along the line of the greatest convexity of the cylinder. Here is the closest folding of the sheath, and here, consequently, the lines of fold in soft material, or interruption in hard material, will converge and come together. That is just what they do in both the sleeve and the rhachitomous vertebral column, the only difference being that in the animal it is exhibited on both sides, and on the sleeve on only one side. This difference is, of course, due to the fact that the animal can bend himself in both directions, while the arm only bends in one direction.

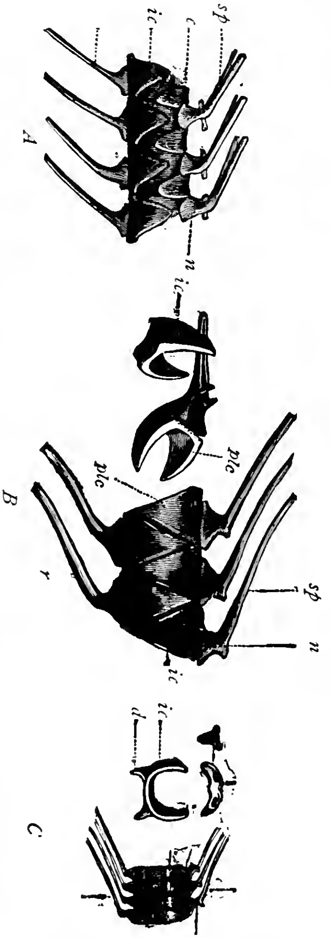

Fig. 113.—Portions of dorsal vertebræ of merospondylous fishes; from Zittel. *A. Caturus furcatus. B Callopterus agasizzi. C. Euthynotus micropodius. Sp*, neural spine; *n*, neurapophysis; *c*, *plc*, centrum; *ic*, intercentrum; *d*, diapophysis; *r*, rib.

It results from the above observations that the structure of the rhachitomous vertebral column *has been produced by the movements of the body from side to side, as in swimming, during the process of the deposit of mineral material* in and around the chorda dorsalis.[1]

See figures 113 to 114*a* where the coat-sleeve is compared with the "rhachitomous" vertebræ of primitive

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[1] See *American Naturalist*, January, 1884.

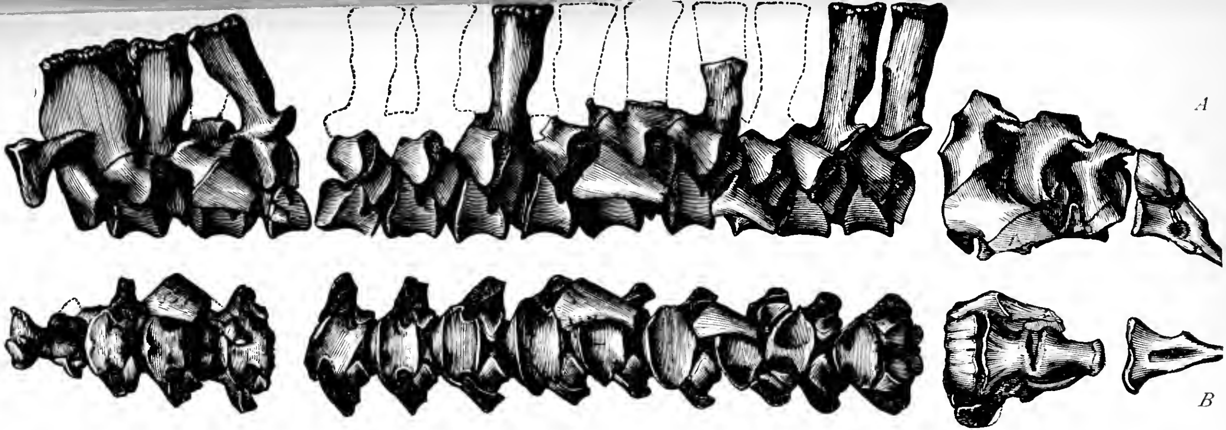

Fig. 114.—Rhachitomous vertebral column of *Eryops megacephalus Cope*, one-fourth natural size. *A*, profile; *B*, from below. From the Permian epoch of Texas.

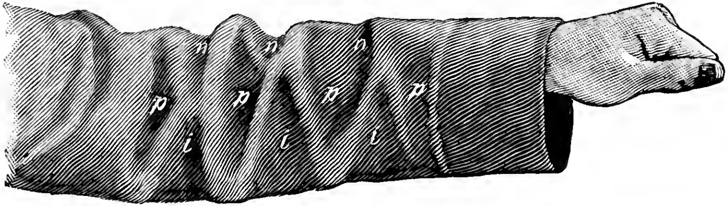

Fig. 114*a*.—Sleeve of a coat, showing folds produced by lateral flexure which leaves interspaces similar to the segments of a rhachitomous vertebra. Thus, *i* represents intercentrum; *p*, centrum or pleurocentrum; and *n*, neurapophysis.

fishes (Merospondyli[1]) and Batrachia (Rhachitomi). Such was the origin of the segmentation in the primitive sharks, Pleuracanthus, whose structure has been pointed out by Sauvage, and Hybodus, whose characters have been demonstrated by Smith Woodward. The segmented (or rhachitomous, as I have termed it,) condition may be then regarded as the primitive one of the osseous column in the Vertebrata. From the rhachitomous column two divergent lines have arisen as already remarked (pp. 89, 209). The inferior segment has been retained in the fish-batrachian line, whence I have termed their vertebræ "intercentral," while these bodies have disappeared or become rudimental in the higher Vertebrata. The pleurocentra (Figs. 113–114*a*, *c*, *pl.*) have, on the other hand, developed downwards, and, meeting below, have formed the effective centrum of the vertebra. Hence, in the Monocondylia and Mammalia the vertebræ are "central."

The Reptilia display a greater variety of vertebral articulation than any of the classes of Vertebrata. After the primitive biconcave (amphicœlous) type was abandoned, the two principal types assumed are the ball and socket (procœlous and opisthocœlous), and the plane (amphiplatyan). In those families in which the body is more or less in contact with the ground, owing to the absence, shortness, or position of the limbs (Lacertilia, Ophidia), the vertebral bodies exhibit the ball-and-socket articulation, while in types with longer limbs which supported the body in progression, so that the latter never reached the ground (Dinosauria), the articulations are plane. The ball-and-socket articulation may be inferred to have been pro-

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[1] Zittel, *Handbuch der Palæontologie*, III., p. 138, 1887, where this character is first clearly pointed out in fishes.

duced by vermiform movements which utilize points of resistance on the earth as aids to progression, while the plane articulation has probably resulted from the persistence of the fixed relation which is appropriate to a body which should be relieved by the legs of all share in movements necessary to progression. That this position is correct is sustained by the fact that the cervical vertebræ of various reptiles and mammals which have plane dorsal vertebræ have the ball-and-socket structure. This is probably due to the constant flexures to which that part of the column has been subjected, as compared with the fixity of the dorsal region.

Owing to the comparatively advanced state of our knowledge of the phylogeny of the Mammalia (Chapter II.), this class furnishes especial opportunities for the study of kinetogenetic evolution. But our knowledge is not yet sufficiently complete to enable us to account on mechanical grounds for the origin of all the characters which distinguish all its subdivisions. This being the case, I have not presented the subject in taxonomic order, but have contented myself with offering it in the order of evidential value. I have first described certain cases where the action of kinetogenesis is self-evident. This has been followed by the presentation of cases where the evidence amounts to a high degree of probability.

Referring now to the table of definitions of the orders of Mammalia on pages 127–128, I will go over the characters *seriatim*, and show how far our knowledge warrants us in giving a kinetogenetic explanation of their origin. No mechanical cause can be at present assigned for the loss of the coracoid and episternal bones in the Eutheria. In the Eutheria the presence of the marsupial bones of the Didelphia is a survival, and it may be that their absence in the Monodelphia is due to disuse, on the withdrawal of strain on the abdominal walls which followed the abandonment of the oviparous habit of the Prototheria, and the young-bearing habit of the Marsupialia. The very considerable weight actually borne by existing forms and probable weight carried by extinct forms will probably account for the development of these bones through strain on the prepubic cartilage. The perforate palate is a reptilian survival, and the closure of the fontanelles may have been due to the increased strain due to the increased energy of mastication which early ensued, owing to the increased size and specialization of the molar teeth. Of the three divisions of the Monodelphia, the Mutilata, Unguiculata, and Ungulata, the Unguiculata possess modifications of a character of ungual phalanges inherited from the Reptilia, while the other two groups have experienced still greater modification. The limbs of the Mutilata display the result of disuse as to the posterior ones, and special use as to the anterior, as I have already pointed out. The Sirenia display a less degree of modification than the Cetacea. The hoofs of the Ungulata may well have assumed their laterally expanded and transverse forms by the extreme pressure and impact on the earth, incident to their function as supports.

The origins of most of the dental characters which characterize the orders of Mammalia have already been referred to mechanical causes, and have been already treated of. The same is true of tarsal and carpal characters, which are of so much importance among the Ungulata.

The characters enumerated on page 139 as indicating progressive modification in time have also been mainly accounted for on mechanical grounds.

5. OBJECTIONS TO THE DOCTRINE OF KINETOGENESIS

It has been objected that Neo-Lamarckians are self-contradictory and illogical in their defense of the doctrine of the development of structures by use, or by motion. It is asserted that they believe that stimuli of different kinds produce similar results, and that stimuli of the same kind may produce different results. The charge that Neo-Lamarckians hold those views is correct, but it is not correct to suppose that they are illogical or self-contradictory. This criticism is one of those generalities which will not bear examination, while the doctrine of kinetogenesis will bear examination.

Thus it has been experimentally shown that bone irritation will produce both bone deposit and bone absorption, according to the degree of irritation. Moderate irritation produces deposit, and greater irritation produces absorption. Hence it is that both impact and strain, or pressure and stretching, will elongate a bone, by stimulating growth, if not excessive. We have the illustrations in the elongation of ligaments and cartilages and their ossification under stretching, and the shortening of both in absence of use, from which we may infer their lengthening under use. The continued lengthening of the limbs and teeth of the higher Mammalia, in the course of geologic time, is an illustration of the effect of continued impact and transverse strain ; while the lengthening of the limb bones of the sloth, and of the tarsal bones of many bats, is a consequence of longitudinal strain.

The differing directions of the elements entering into the articulations of the limbs of Mammalia may be cited in illustration of the supposed inconsistency of supposing them all to be the result of impact and strain. Thus most of the condyles are directed distad, but the heads of the humerus and femur, and the proximal surfaces of the carpus and tarsus are directed proximad (except the trochlear groove of the astragalus when present). So far as regards the distal ends of the radius and tibia (fore arm and leg) I have pointed out that here dense layers disposed longitudinally impinge on a similar layer disposed transversely, with the natural consequence the latter has yielded to the excess of impact so produced. The direct relation of the sculpture of the surfaces concerned, to the lengthening of the foot and increase of speed of the animal, and hence increase of force of impact, leads irresistibly to this conclusion. As regards the convexity of the heads of the humerus and femur, or rather the concavity of the corresponding surfaces of the scapula and acetabulum the explanation has been already given. Henke was apparently the first to call attention to the fact that the concavity and convexity of the articular surfaces is directly related to the positions of the insertions of the muscles which move them. He shows that a concave surface is developed at the extremity which is nearest to the muscular insertion, while the convex surface is developed on the extremity which is most remote from its muscular insertion. Thus is accounted for the apparently contradictory evidence of the limb articulations mentioned. In some cases at least, as those of the glenoid cavities of the scapula, ilium, and phalanges, the muscular insertions are so near to their borders, as to suggest that the growth of the latter is due to a pulling strain on them, as well as to the greater mobility of the element which becomes convex, as supposed by Fick.

It is claimed in the preceding pages, that impacts on the extremities of a bone or tooth, gradually increase its length. It may be hastily supposed that in this assumption I derive elongation of the shaft of a bone from the same stimulus which produces excavation and therefore abbreviation of its extremities. In the gross this charge is correct; but the position I have assumed is defensible, because in detail it is easy to perceive that effect of the use of a limb on an articular surface of a bone is quite distinct from that which it has on the shaft. At the articular faces we have discontinuity; and therefore *friction*; in the shaft we have only the concussions produced by impact, together with some torsion strain. That the former movement stimulates the development and activity of the osteoclasts has been shown by Koelliker; that the latter may stimulate the activity of osteoblasts is rendered highly probable from the facts of pathological anatomy. These show that a very slight modification of stimulus is sufficient to change the building cells into the absorbent cells and back again. For the same reason belief in the elongation of bones under stretching strain may not be inconsistent with belief in an elongation under impacts.

Cary makes specific objections against the kinetogenesis of the articulations of the mammalian skeleton.[1] After a study of the carpus of the Eocene perissodactyle genus Palæosyops he concludes that the trapezoid bone is too small to express properly the direct result of purely mechanical causes. He says that

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[1] *American Journal of Morphology*, 1892, p. 305.

in reaching this result he has applied geometrical methods. "First, the volume of the bones was got at. Next the area of the bearing surfaces and their inclination to the digits were measured. Then giving to the thrust of each metacarpal a value proportional to its volume, the distribution of that thrust can by resolution and composition of forces, be traced through the foot, and the pressure on each surface and bone approximately obtained." Further than this the author does not explain how he reached the result that the trapezoid is too small. It is quite essential that this demonstration should be given if we are expected to accept his conclusion. An essential part of the problem is, however, unnoticed by Mr. Cary; and that is the condition of the trapezoid in the reptilian ancestors of the Mammalia. The phylogeny of an element must be known, since it furnishes the "physical basis" of the problem. The fact is that the trapezium, trapezoides, and the magnum owe their small size to their being the only carpal elements which have not been produced by the fusion of two or more primitive elements of the batrachian and reptilian carpus. The trapezoides moreover occupies a place in a longitudinal series of three elements in the primitive carpus, while the trapezium forms one of a series of only two elements. For similar reasons the cuneiforms are the smallest elements of the tarsus.

Mr. Cary then proceeds to criticize the explanations offered by Professor Osborn and myself, in accounting for the origin of certain structures. He finds our explanations to be self-contradictory, and that we also contradict each other. Osborn has supposed that the conules of the molars are produced by friction of the molars of opposite series on each other. I have expressed the opinion that the shear of the sectorial teeth of Carnivora was produced by lateral friction during vertical movement of the lower tooth on the upper. I have also asserted that the forms of facets of limb articulations are due to pressure. Mr. Cary sees here the attempt to explain the origin of totally different structures through identical mechanical processes, and believes that the attempt is a failure. Were the conditions of the problems alike, as Mr. Cary thinks them to be, he would have good reason for his opinion. But the conditions in the three cases are entirely different, and our author's conclusion is due to neglect of the elementary facts of the proposition.

The development of conules at the points indicated by Professor Osborn, has been supposed by him to be due to friction between existing ridges of enamel which cross each other when in action, at the points in question. In the case of the development of the sectorial shear, the faces between which the shearing motion takes place are smooth, and without ridges or crests. Hence the entire surface receives a homogeneous friction. In the third case, that of the foot articulations, there is no friction, but there is pressure which when abruptly applied in movement becomes impact. There is really no parity between the three cases.

The author of this paper also thinks that the explanation of the elongation of bones through use of different kinds is not a permissible hypothesis. He cites my attempt to account for the elongation of the leg bones of higher mammals through impact-stimulus; and of other limb bones of other mammals through stretching. But he does not prove that similar results may not flow from mechanical stresses applied in different ways. I suppose that any mechanical stress which determines nutritive processes to a part, will increase its size, *cæteris paribus* ; and the stretch as well as the impact has this effect. I have in fact shown, in the observations already cited (pp. 277–279), on the production of artificial elbow joints, that osseous deposit is stimulated by pulling strain as well as by pushing or impact.

In concluding, Mr. Cary admits one of the two contentions of the Neo-Lamarckians in his two closing propositions. He says "Plasticity of bone, using the word *plasticity* not in a physical sense merely, but to include absorption under pressure, will probably account for much structure in the foot and elsewhere, especially the connection with the joints, and in the fields of variation and correlation." In the second proposition he says that facts have been adduced by him which are inconsistent with the theory that the size of bones has been increased by the stimulus they receive, and with the theory that regions of growth are determined by regions of pressure and strain. "The testimony of the literature as to the latter point," he says, "is conflicting." I have shown that the supposed conflict is due to a misunderstanding on the part of the author of this paper. The proposition that pressure does not affect growth is in contradiction to the admission made by the author in his first proposition, where he admits that pressure determines structure ; for in such change of structure there is always growth. Finally Mr. Cary remarks "That race changes follow those produced in the individual life, or that they are directly caused by their mechanical surroundings, I do not think it has been satisfactorily shown." The fact that the characters of bone structure admitted by Mr. Cary to have had a mechanical origin appear in the young before birth, is evidence that race characters are produced, in other words, that they are inherited.

Another objection proposed by Tomes, and quoted by Poulton and Wallace with approval, has reference to the kinetogenesis of teeth of Mammalia as described by Ryder and myself. Tomes asserts that it is quite impossible that the crowns of the teeth could have been altered by mechanical impacts and strains, since their form is determined in the recesses of the dental grooves, entirely removed from all the mechanical influences which affect the external surfaces of the jaws. But the observations of Koelliker and others show that osteoclasts are as active in dental as in ordinary osseous tissue. It is altogether probable that the modifications of dental structure have been produced by strain and friction under use in the adult, precisely as in the skeleton, and that the share that the unerupted crowns have in the process is that of inheritance only, as in the case of the skeleton. That teeth deposit dentine as process of repair in adult mammals is well known, and this repair is in direct relation to use. That the effects of dental wear are inherited is proven by the fact cited by Tomes and Wallace.

Another objection to the doctrine of kinetogenesis which has been made by some of the Neo-Darwinians is, that if growth under stimulus be true, how can it have limits, so long as the stimulus of use exists. In other words, what is to prevent, in the case of the vertebrate skeleton, of an indefinite increase in the length of the legs, of the teeth, and of their cusps, etc. The answer to this objection will vary more or less with the part of the structure considered. In general, however, it may be assumed that stimulus is stress due to a want of harmony between an organism and its environment, and that kinetogenesis is the result of the effort of the organism to adjust itself. So soon as equilibrium is attained, the stress of stimulus ceases or is much reduced, and evolution in this direction ceases. Such equilibrium is attained when the mechanism of an animal is sufficient for the satisfaction of its needs. When this is the case severe exertion is no longer necessary, and a period of easy use follows which is sufficient to maintain the mechanism in working condition. In the case where circumstances should become so favorable for the easy satisfaction of the necessities of life, as to call for little or no exertion, degeneracy of the organism is sure to follow. The well-known phenomena of degeneracy from disuse show that a large part, and in some cases all, of the stimulus of use, is only sufficient for the maintenance of the organism in working condition, and that there is no surplus to be expended in progressive evolution.

It is however true that some organs are stimulated to excessive growth by active use. Such are some of the teeth, which, if not worn at the crown by the opposition of those of the opposite jaw, soon grow to an inconvenient length. This occurs in the hypsodont molars of horses and artiodactyles, and in the prismatic molars and incisors of Glires. Hypsodonty in general is an illustration of continuous growth induced by long-continued stimulus in those orders of Mammalia, and in the Toxodontia and Proboscidia. The excessive growth of the canines in the South American saber-tooth tiger, and of the incisors of the mammoth, are cases where the energy of growth has not subsided in time to prevent excess.

Several years ago Prof. August Müller and I called attention nearly simultaneously to the probability that many of the forms of the reproductive organs of plants, especially the flowers, are due to the strains and other effects produced by their use by insects. Rev. George Henslow has written a book in which this subject is set forth in detail.[1] It is impossible to demonstrate this point with the same certainty as the kinetogenetic origin of the articulations of the vertebrate skeleton and their characters, owing to the absence of paleontologic evidence. Henslow, however, says: "When we find innumerable coincidences all tending in one direction, coupled with an indefinite capacity for varying in response to forces in all parts of plants, I still maintain that [this] theory does not utterly break down," as asserted by Mr. Wallace.[2] Wallace argues that since many regular flowers have been subject to the irritation of insects and have not become irregular, there is no reason to suppose that this is the cause of the irregularity in question. To this Henslow replies:[3] [Mr. Wallace] "will see that existing regular flowers being mostly terminal, have no lower petals at all, but are so situated as to offer access to insects from all points of the compass. Moreover, when a plant with normally irregular flowers (which are always situated close to the axis, so that insects can only enter them in one way) produces a blossom in a terminal position (as foxglove, larkspur, horse-chestnut, etc., often do), it at once becomes quite regular." This change may be brought about artificially, for, says

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[1] *The Origin of the Floral Structures by Insect and Other Agencies.* International Science Series, Vol. LXIV.

[2] *Natural Science*, 1894, p. 178.

[3] *Natural Science*, 1894, p. 262.

Henslow, "flowers normally irregular in nature often revert to their ancestral regular forms under cultivation in the absence of insects, and then come true from seed, as the Gloxinias."

CHAPTER VII.–NATURAL SELECTION.

NATURAL SELECTION is the process of discrimination of variations, by which those which are most in harmony with the environment survive. It is, in short, as expressed by Spencer, "the survival of the fittest." Fitness is of various kinds, and is only determined by the nature of the environment. The success of a variety which appears in aquatic surroundings will depend on characters different from those which bring success in a forest. Variations which favor survival and increase among carnivorous animals differ from those useful to the life of herbivorous forms. So survival in human society depends on characters different from those which secure the same result among the lower animals, etc. It is thus evident that natural selection is of many kinds and that forms survive for various reasons; and it is hence of universal application. The reasons for survival may be divided into those which depend for survival on the relations of a type to the non-living environment, and those which depend on the living. The former may be divided into those which are passive and those which are active. The particular influences may be imperfectly enumerated as follows:

Non-living environment.
  a. Passive.
    Isolation of areas ; continuity of areas ; building material ; food ; place of concealment ; temperature ; humidity.
  aa. Active.
    Pressure of earth, water, and air.
II. Living environment.
    Food ; reproductive potency ; sexual selection ; digestive and other physiological power ; muscular strength ; superior weapons and other special mechanisms ; intelligence.

I have already (page 4) quoted the language of Darwin, where he states that the supposition that natural selection is a cause of the origin of variations is a mistake. From the nature of selection, Darwin's position thus expressed, is self-evidently sound. The attempt has, however, been made to apply the term selection to the efficient cause of all variation, and to divide its exhibitions into two kinds, natural and artificial selection. If the primary assumption involved in this position is illogical, the dual division proposed is absurd. As may be readily seen in the table in the preceding paragraph, in which the factors of natural selection are enumerated, the conditions necessary to selection are mostly identical, whether imposed by nature or by the hand of man ; i. e., whether natural or artificial. The physiological effects of food, temperature, exercise, etc., do not differ, whether due to natural conditions, or to the influence of man. The observation of man's influence is indeed especially instructive in increasing our knowledge of the effects of natural causes, since in the former case we have the process in action within our control, while in the latter case it is not.

The subject of natural selection has been ably treated by Darwin, Wallace, and other writers, and it is one on which much further research may be profitably expended. It is the science of adaptations, and the name Chorology has been framed for it by Haeckel, but the earlier term Œcology is now generally used. It was not overlooked by biologists prior to Darwin and Wallace, and is stated in general terms by Lamarck in his *Philosophie Zoologique*, but it was reserved for the two authors just mentioned to create the science. I shall here only refer to a few aspects of the subject.

Isolation naturally tends to emphasize any peculiarities of structure which may harmonize with the conditions of the environment, by the barrier which it sets up against the entrance and mixture of forms from other localities where the environments are more or less different, and where the characters are correspondingly proportionately diverse. Isolation conversely prevents the emigration of forms, and the consequent mixture with the differing forms of other regions. Breeding in and in is produced on a large scale. Geographical isolation is a result of the formation and population of islands, whether this be accomplished by submergence below or by elevation above sea level. A noteworthy illustration of the former case is seen in the West Indian Islands, which represent the elevated regions of a former continent. Here the faunæ of the respective islands have been separated from each other since late Pliocene time. We find that while most of the genera of land Vertebrata are generally distributed, each island possesses peculiar species. This is even true of the birds, whose powers of migration are quite sufficient to enable them to pass from island to island. The restriction of land mollusca is still greater, several islands having genera peculiar to them.

Isolation is also produced by inequalities of land-surface, resulting from the elevation of mountain ranges, plateaus, etc. This is well seen in Mexico and Central America where the number of species of Vertebrata is large, owing to the fact that many of them are restricted to very narrow areas bounded by impassable barriers. The restriction of species of land Mollusca to each of the numerous valleys of the Hawaiian Islands has been made the subject of an especial study by Dr. Gulick, who treats of them with especial reference to the evolution of their forms.

The assimilation of inorganic matter necessarily preceded that of organic matter, so that this function characterized the first organic beings, whether animal or plant-like in other respects. Among animals we may regard the vegetable feeders as having by a little preceded the carnivorous forms. Omnivorous forms must have come into existence soon after, and from these, both classes of feeders have been from time to time recruited ever since. The primitive Vertebrata were probably carnivorous, and most of the fishes and Batrachia have always been such. Herbivorous forms have arisen from time to time among Reptilia, and of granivorous birds there are many. The early Mammalia were divided between omnivorous (Multituberculata) and insectivorous types (Protodonta, Pantotheria); while the higher Mammalia of all kinds were derived from more or less omnivorous forms (primitive Condylarthra and some Creodonta). We may account primitive insects to have been largely herbivorous, even more than they are at the present time, while Carnivora predominate in marine invertebrate life. It is not difficult to understand that circumstances of the environment would determine the food of animals, and would divert omnivorous forms into carnivorous or herbivorous habits as abundance of food and competition of rivals might dictate.

Sexual selection is of two general classes, that in which the male selects, and that in which the female determines the result. In the former case the most vigorous males, or those in which the mechanisms for seizing the females are most effective, propagate their kind most successfully. It is well known that in many animals, especially the Arthropoda, the males are furnished with especial organs of prehension. In vertebrates similar organs are especially conspicuous in some of the Batrachia Salientia. (See p. 65.)

The species of Arcifera exhibit peculiar structures during the breeding season ; either an extension of the natatory membrane, or the development of corneous plates or spurs, as aids to prehension. There is much variety and efficiency displayed in this point (except in Bufonidæ), in especial contrast to the apparent absence of all but the weakest modifications among the Ranidæ. This is in compensation for the structure of the sternum, whose lateral halves, being movable on each other, offer a slighter basis of resistance for the flexor and extensor muscles of the fore limbs of the male. In the Firmisternia the halves of the shoulder girdle do not overlap below on the middle line, but abut against each other, thus preventing compression (Fig. 51, page 198).

While no appendages of the season have been observed in some Cystignathidæ, in several genera two acute spurs appear on the superior aspect of the thumb and more rarely spur-like tubercles on the breast ; the body is sometimes shielded with hardened points on the rugosities, or the lip surrounded by an arched series of corneous rugæ. In the *Leptodactylus pentadactylus* Laur. a huge acute process of the metacarpal of the thumb, projects inwards. Its apex is covered by a horny cap, and it is a formidable grappling-hook to aid the male in retaining his hold. There is added to this in the same species a horny plate on each side of the thorax of the male, from which project three acute points. With these fixed in her back and the thumb spikes in her breast the females cannot escape. Structures like this do not appear in the Firmisternia. Here the inferior elements of the scapular arch abut against each other, so that the thoracic cavity does not contract on pressure, and the possibility of the male retaining a firm grip on the female is thereby greatly increased. In the *Cystignathus pachypus* the males exhibit a permanent enlargement of the brachium, dependent on largely developed anterior and posterior alæ of the humerus. (*Vide* Günther, *Ann. Mag. N. H.*, 1859.)

Another kind of male selection is accomplished by the combats of males for the possession of the females. This is usual in polygamous birds and Mammalia, and in some promiscuous species of both. Of the birds the Gallinæ form the best known example; and of the mammals, most Ungulata, and the eared seals (Otariidæ), are illustrations. In this way the weak males are eliminated either by death, or by exclusion from the opportunity of reproduction. The males in such species are armed with spurs, horns, or large teeth, except in some of the Perissodactyla, which have neither.

Female selection is seen in another direction. Here the male attracts by the superior brilliancy of his colors or peculiarity of physical appearance, as well as by his notions. The available growth-energy of the male being superior to that of the female in most animals, his structure is more liable to excess of development in useless directions. In many of the Arthropoda, especially the Insecta, the males possess processes of the head and thorax besides the especially useful prehensile peculiarities of the limbs. Among Vertebrata the male generally possesses the more brilliant colors. This is especially noteworthy in fishes and birds. It is also frequently the case in lizards, although in one genus (Liocephalus) the female has the brighter hues. The selection (taking no account of the origin of these characters) acts in the probable preference by the females for the most brilliant colors and most impressive forms, thus propagating both, and in the neglect of those males in which these characters are not so well developed. The plainness of the females aids in their concealment and enables them to perform their maternal functions in safety.

The desire of the males to attract the favor of the females leads to many peculiar performances among birds. The males display their plumage by spreading their wings, tail, tail-coverts, etc., and strut and go through many antics in the presence of the females. Familiar examples are seen in our barnyards in the turkeys, peafowls, and pigeons. In the paradise-bird the most remarkable exhibitions occur, according to Wallace. In song-birds the male is frequently the only or the best songster, and the development of the vocal powers resulting from the sexual impulse is most remarkable. Among Mammalia the female selection is less common than male selection. In the case of some of the old world monkeys (Macacus, e. g.) the female presents the greater physical indication of excitement in the extraordinary development of the nates at the season of heat. Mankind, appropriately to the high development of the mental powers, is selected with reference to qualities of mind as well as with regard to the physical attractions. Mental advantages being equal, beauty is preferred, but beauty is often neglected in favor of superior moral and intellectual characteristics. Both sexes take part in the selection; in the lower races chiefly the male, while in the higher races the choice rests ultimately with the female. It is probable that in future civilized mankind will exercise more care than now in the prevention of marriage of persons affected with serious physical and mental defects, such as chronic diseases, insanity, alcoholism, criminality, etc.; but beyond this, supervisory selection cannot go. The supposition which is sometimes entertained by some persons, that mankind will in a state of higher civilization prefer physical to mental perfection, is certainly ill founded. And among mental qualities, a high value will always be attached to those which render social life easiest and most pleasant; the standards of ease and pleasure being innumerable.

Among the most conspicuous examples of the action of natural selection are to be found those resemblances in color or form between animals and their environment which serve to conceal them from enemies. Animals possessing such protective appearances naturally escape the observation of enemies which prey on them, while those which do not possess them are more readily captured and eaten. Much is to be found of interest on this attractive subject in the writings of Wallace, Poulton, Beddard, and others. The two authors first named ascribe these color and form characters to natural selection *as a cause*. This is, however, impossible; yet natural selection has undoubtedly been the cause of their survival. Professor Poulton has demonstrated (p. 230) that the protective colors in lepidopterous pupæ are produced directly by the influences of light on the nerves of the animal and its reflex action on the pigment depository process.

The first objection to the belief that natural selection is the primary cause of organic evolution has been already stated as follows: "A selection cannot be the cause of those alternatives from which it selects. The alternatives must be presented before the selection can commence." But the supporters of the view that natural selection is the origin of variation allege that it produces this result by the continued survival of minute differences which are useful, thus accumulating variation. That minute advantageous differences will secure survival no one can doubt, but it must be remembered that the variations which constitute evolution have been in a vast number of cases too minute to be useful. But the general question is not affected by the supposition that advantageous variations may be sometimes minute. Minute or great, they have to be assumed in the argument for selection; and whether minute or great, they have a definite cause.

* * *

In conclusion of Part II. of this book, I trust that I have adduced evidence to show that the stimuli of chemical and physical forces, and also molar motion or use or its absence, are abundantly sufficient to produce variations of all kinds in organic beings. The variations may be in color, proportions, or details of structure, according to the conditions which are present.

PART III.

THE INHERITANCE OF VARIATION.

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PRELIMINARY.

IN THE first section of this book I have endeavored to show that variation of character is not promiscuous or multifarious, but that it is limited to certain definite directions. That this rule applies to all kinds of characters, whether they are of the less fundamental kind which distinguish species, or of the more fundamental kind which distinguish the higher divisions.

In the second section I have endeavored to show that many characters, both those of the more superficial and those of the profounder kinds, are the direct result of chemical and physical stimuli, and of molar motion or use, or of the absence of the latter or disuse.

It now remains to ascertain whether the characters or variations so produced are inherited; that is, whether characters so acquired are transmitted to succeeding generations. Unless this proposition is demonstrated, our knowledge of the method of evolution remains incomplete, and we must look for some new explanation of the progressive increments and decrements of structure which constitute the history of organic life. The present part of this book will be devoted to an examination of this question, and to the exposition of such laws as may be derived from such examination.

CHAPTER VIII.—HEREDITY.

I. THE QUESTION STATED.

IT IS the popular belief that characteristics of parents are transmitted to their offspring through the medium of the reproductive cells. This opinion is founded on an infinitude of observations easily made on plants, animals, and men, and in fact it is not denied as a general statement by anybody. It is a fact of ordinary observation that many and apparently most of the structural characteristics of one generation are inherited by its offspring. Not only is this the case, but the functionings of organs which depend on minute histological peculiarities are inherited. Such are points of mental and muscular idiosyncrasy; of weakness and strength of all or any of the viscera, and consequent tendencies to disease or vigor of special organs. Darwin has collected in his work on the Descent of Man numerous instances of the inheritance of various tricks of muscular movement of the face, hands, and other parts of the body. But it is a fact of equally ordinary observation that some peculiarities of parents are not, or may not be inherited, and among these may be enumerated mutilations and injuries, as well as characters which are normal. It is then a question of essential importance to ascertain what kinds of characters are inheritable, and what are not inheritable.

It has been insisted by Weismann and others that characters which are newly acquired by an organism are not inherited, whether they be products of normal or abnormal conditions. In support of this view, he points to the early isolation in embryonic life of the reproductive cells from the remainder of the organism, and their continued isolation during later life, so that they are protected from the stimulating influences which affect the remainder of the body. He also points to the permanence of this isolation of the germ plasma from generation to generation, which insures only the transmission of those characters which it contains, as distinct from those which are found in the remaining cells of the organism, which constitute the body or soma. The characters which are inherited, and which are present at birth are termed congenital, while those which appear in the body under the influence of external stimuli are termed acquired. The theory of Weismann then is, that the acquired characters are not inherited.

Besides the fact that sporadic injuries and mutilations of the soma are not inherited, there have been cited various cases of the non-inheritance of mutilations which have been often repeated and for long periods of time. Thus the rupture of the hymen in human females has not been followed by its abolition. The practice of circumcision by the Jews has not resulted in the disappearance from that race of the portion of the body thus artificially removed. The continued cutting of the hair of men of many races has not made it less abundant. The practice of distorting the feet of a class of their women by the Chinese has not modified the shape of that part of the structure in the race. I have myself cut off the tails of nine successive generations of mice without producing the slightest effect on the length of the tails of the tenth.

Nevertheless such negative evidence only demonstrates that such modifications of the structure *may not* be inherited. A single undoubted example of the inheritance of a mutilation would prove that no insurmountable barrier to such inheritance exists. And well authenticated examples of such cases are known and will be mentioned later on. But it is not with mutilations that the paleontologist has to do. The rupture of the hymen and circumcision, and most mutilations, can only occur once in the life of the individual, and generally they produce no appreciable direct effect on his or her metabolic physiology. Moreover, the mutilations above cited as not inherited are experienced by but one sex, except in the case of the tails of the mice. The question is widely different with regard to the parts of the structure in which we observe the real differences between organic types. The definitions of natural divisions rest to a great extent on the diversities displayed by the organs of motion and nutrition. Now these are in use in animals during most of the hours not spent in sleep. Their movements are perpetual, and their activities only cease with death. It is then quite unreasonable to cite the history of mutilations as evidence against the inheritance of natural characters produced by oft-repeated and long continued natural causes.

It has been shown in Part Second of this book that structural characters are produced by use and other stimuli to growth. It has also been shown in Part First that the characters so produced show a progressive increment or evolution from earlier or later geologic periods. There are two possible explanations of this phenomenon. The one is that the characters of one generation are inherited by the next, which adds to them by the activity of the same stimuli which gave them origin, thus producing progressive increase of growth. The alternative is, that these structural characters are produced by each generation for itself. It is obvious that the latter hypothesis provides for no additional development of a character in one generation above another. There are other objections to the latter view, but letting these pass for the present, it is only necessary to examine the embryonic history of animals to show that it is entirely untenable. For if some or all of these acquired characters can be found present in the early stages of growth, as in the egg, the pupa, the fœtus, etc., it becomes clear that such acquired characters have been inherited. That such is the fact is abundantly demonstrated by embryological researches. This fact alone is sufficient to set at rest by an affirmative answer the question as to the inheritance of acquired characters. And that this answer applies to all time and to all evolution is made evident by the fact, which is disclosed by paleontology, *that all characters now congenital have been at some period or another acquired.*

2. EVIDENCE FROM EMBRYOLOGY.

a. Vertebrata.

I have already (p. 292) pointed out the gradual evolution through mechanical causes of the tongue and groove-joints in the Mammalia as exhibited by the distal ends of the metapodial bones of the feet where they articulate with the phalanges. Mr. Carey having agreed with me that those have been produced by mechanical causes, he alleges that they are not inherited, but are produced by each generation for itself. To this Dr. J. L. Wortman remarks as follows:

"With reference to Mr. Carey's first proposition that the metapodial crests are produced during the life of each individual by the necessary interaction of parts, it appears to me to be a very simple one indeed. If they are produced, by pressure during the lifetime of each individual, and are not inherited, then clearly we should find the crests absent in new born animals that had never walked, and in which the metapodials had not been subjected to any impact or pressure whatever. I have taken the trouble to examine a number of such examples in which the distal ends of the bones were entirely cartilaginous, and I find that the keels and grooves are as well developed as they are in the adult animal. I will cite one case in particular in which I happen to know the history completely. During the past winter, a young hippopotamus was born in the Zoölogical Gardens in Central Park, New York, and it was stated to have been a premature birth; the animal lived but twenty-four hours, and I was informed by the keeper that it never stood upon its feet. An examination of the feet shows that the distal ends of the metapodials are entirely cartilaginous, and in them the keels are as well prefigured in cartilage as they are formed in bone in the adult animal. I have also found the same to be true of new-born rabbits and guinea-pigs. In another case of a young buffalo calf preserved in the American Museum Collection, the distal keels of the metapodials are complete notwithstanding the fact that the epiphyses of all the bones are very imperfectly ossified. This evidence, it appears to me, effectually disposes of the question of the production of these structures during the lifetime of the individual. They are as truly inherited as is the number of digits or any other important organ in the animal economy."

Such observations may be repeated indefinitely. Thus the astragali of the higher Mammalia are already grooved before birth, and are not flat up to that time as in their Puerco ancestry. The reduction of digits appears very early in fœtal life, and the ball and socket articulations of the cervical vertebræ of the Diplarthra are by no means introduced after birth.

The teeth possess the normal structure of their crowns while yet in the alveoli before eruption. In some cases the transition from a primitive to a modern type of tooth has been observed to take place in the embryo.

Dr. A. von Brunn[1] has shown that in the embryos of the rat, the enamel-producing epithelial layer of the molar teeth undergoes a remarkable change at the places where the transverse crests of the crowns are to appear. Before the enamel layer is deposited, the portion of the epithelial layer corresponding to the cross-crests undergoes degeneration, as a result of which it acquires the character of a stratified squamous epithelium. Thus no enamel is laid down on the summits of the cross-crests, which present the exposed dentine when erupted. Now it is a fact that the crowns of the molar teeth of the ancestors of the genus Mus, were covered with enamel at maturity, like all other

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[1] "Notiz über unvollkommene Schmelzentwickelung auf den Mahlzähnen der Ratte, *Mus decumanus*": *Archiv für Mikroskopische Anatomie*, 1880, XVII, pp. 241–243, Pl. XXVII. Ryder, *American Naturalist*, 1888, p. 547.

primitive Glires. The removal of the enamel from the apices of the tubercles and crests of their descendents is due to the abrasion consequent on ordinary use. On this Ryder (*l. c.*) remarks: "The great value which is to be attached to the fact that abrasions of the enamel of the adult, which have reacted upon the functional activity of the enamel organ of the embryo rat, so that such mechanically induced alterations could be inherited, does not consist so much in the proof it affords that mutilations can be inherited, as it does that mutilations incurred in the ordinary struggle for existence, may, under certain conditions in certain practically feral species, be transmitted."

Having shown by these examples that acquired characters can be inherited, I offer some other illustrations which are at hand.

b. Arthropoda.

It has been already rendered probable if not certain (p. 268) that the segments of the body and limbs of the Arthropoda were originally produced by the movements of definite tracts on each other, during the period that the external surfaces were becoming hardened by chitinous or calcareous deposits. It is well known that this segmentation is no longer produced by this mechanical cause during the adolescent or any other post-embryonic stage of the life of the individual, but that it appears during the various stages of embryonic life, and is therefore inherited. Thus segmentation of the body appears in the embryo while still attached to the yolk. During the larval life of many insects the process of segmentation is suspended, but during the repose of pupal life, it goes on with great rapidity. In this stage while protected from external mechanical stimuli, the limbs with their specialized segments are fully developed, so that the individual is mature as it issues from its prison. This illustration of inheritance derives its point in the present connection from the fact that it presents an example of the inheritance of characters which were plainly acquired by mechanical stimuli during post-embryonic life of the primitive ancestors of the Arthropoda.

3. EVIDENCE FROM PALEONTOLOGY.

a. The Impressed Zone of the Nautiloids.

I have already quoted Professor Hyatt on the parallelism which is characteristic of the various series of nautiloid Cephalopoda, as discovered by paleontologic research. (P. 182.) The impressed zone is a character which has been produced by mechanical causes (pressure), and Prof. Hyatt has observed cases where this acquired peculiarity has been inherited in instances where the mechanical cause which produced it no longer existed. He describes these instances as follows:[1]

"The characteristic dealt with in the paper of which this is an abstract, is of essential importance among nautiloids and ammonoids or all of the Cephalopoda having chambered shells and living within their shells. It consists mainly of an impression made on the inner side or dorsum of each outer whorl during the coiling up, as the whorl grows and is moulded over the venter or outer side of the next inner whorl.

"This matter will be better understood, if a short description is given of the following figures. Fig. 115 shows an almost complete fossil cast of a full grown

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[1] *American Naturalist*, 1893. October, p. 865. Professor Hyatt has personally looked over and corrected these quotations.

Metatoceras cavatiformis Hyatt, and some of the lines or sutures made in the external surface of the cast by the intersections of the partitions or septa that cut up the coiled tube of the living shell into air chambers. Fig. 116 shows a broken specimen of the same species, but with the outer and older whorls in large part removed. The innermost septum near the center of the coil was built across the interior after the animal had constructed the hollow apex or point. It then moved along, adding to the external wall of the tube, which has been destroyed and removed from this cast, and built the second septum, and so on until it reached the tenth septum. By some freak of fossilization a number of the septa beyond this have been destroyed, so that if we were to remove the fragment of the external whorl and take out the center which has just been described, this would have the exact aspect of a cast of a young shell with ten air chambers.[1] The

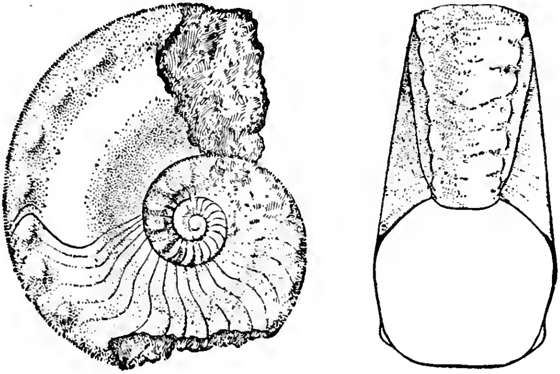

Fig. 115.

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[1] The shaded area in the center, shaped like a large inverted comma, was an open space in the living shell. This is almost invariably filled by the

eleventh air space or chamber being open and without divisions would then appear to be the living chamber which the animal occupied when it built the tenth septum. Normally the shell really continued to progress from the tenth septum by additions to the outer wall and put in new septa behind it, together with the connecting tube until it reached *s*′, and finally the last septum, *ls*. This one, *ls*, was really the last one built

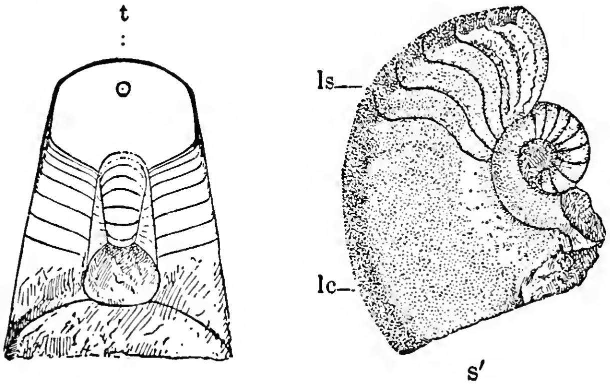

Fig. 116.

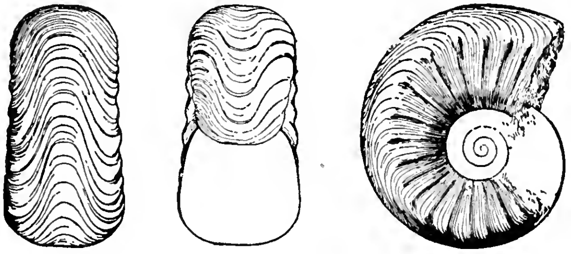

Fig. 117.

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rocky matrix in which the shells occur and is often, as in this specimen, allowed to remain. See also 4, 5, 6, of Fig. 119, which show the comma shaped umbilical perforations or openings left at the center through the crytoceran form of the young.

and it formed the floor of a true living chamber, *lc*, formerly occupied by the animal at the time of its death and burial in the sediment of the carboniferous period. Fig. 115 shows a similar fossil but with a longer, although still incomplete living chamber. If the external wall of shell had been preserved none of these structures could be seen. Fig. 117 shows a fossil *Temnochilus crassus*, a shell of the same family, with this external wall preserved, and all these internal structures covered up. The impressed zone is the reëntrant curve shown in all these figures and especially marked in the lower outline of an outer whorl of another carboniferous species, *Metacoceras dubium* Hyatt, Fig. 118, *im. z.*

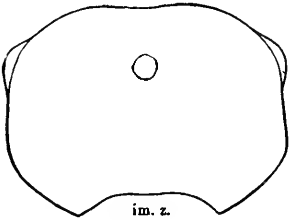

Fig. 118.

"It is not necessary to go into a discussion of the details of internal structures and their relations to the impressed zone in this abstract, but it is essential to give a general description of the morphogeny of the order of nautiloids.

"This group of chambered Cephalopods contains the following classes of forms: first, straight, conical shells, type Orthoceras, Fig. 119, No. 1; second, curved cones, Cyrtoceras, Fig. 119, No. 2; third loosely coiled, open whorled cones, do., No. 3; fourth, coiled cones with the whorls more or less enveloping, do., No. 5. The fourth and fifth forms are usually included in the old genus, Nautilus. Practically, it is better to designate the first class as orthoceran, the second as cyrtoceran, the third as gyroceran, and the fourth and fifth as nautilian. In tracing genetic series through time they are found to diverge in their evolution, starting with the orthoceran and passing through parallel lines of forms, many of the genetic series having in succession cyrtoceran, gyroceran, and even nautilian forms of the fourth and fifth classes. Others are not so perfectly parallel, stopping short with the cyrtoceran class of forms or the gyroceran. Many also begin with cyrtoceran shells, while others diverge from the gyroceran, and still other series have only nautilian shells of different grades of close coiling and involution.

"The application of the law of repetition in heredity to the chambered shell-covered cephalopods, shows that the straight orthoceran shells, Fig. 119, No. 1, were repeated in the young of the curved cyrtoceran forms, Fig. 119, No. 2, and these forms in their turn in the young of the gyroceran forms, Fig. 119, No. 3; and this may be seen by comparing the young or apical part of each shell represented in outline with the full-grown shells of the preceding figures. The apex of No. 2, with the whole of No. 1; the apex of No. 3, with the whole of No. 2. It will be understood, of course, that the figures in outline represent full-grown shells, except when otherwise explained, and that they were built like the shells of Nos. 1–2, by an animal living in their interiors and adding band after band of shelly matter to the exterior, but in these outlines the shell is supposed to be perfect and the internal structures concealed.[1] The young of Fig. 119, No. 4, which represents the fourth class of forms repeats the cyrtoceran form, then curves more closely, and just before it comes in contact there is a short time when

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[1] Except in No. 9, in which a portion of the shell is broken away, showing the cast of the interior and the sutures.

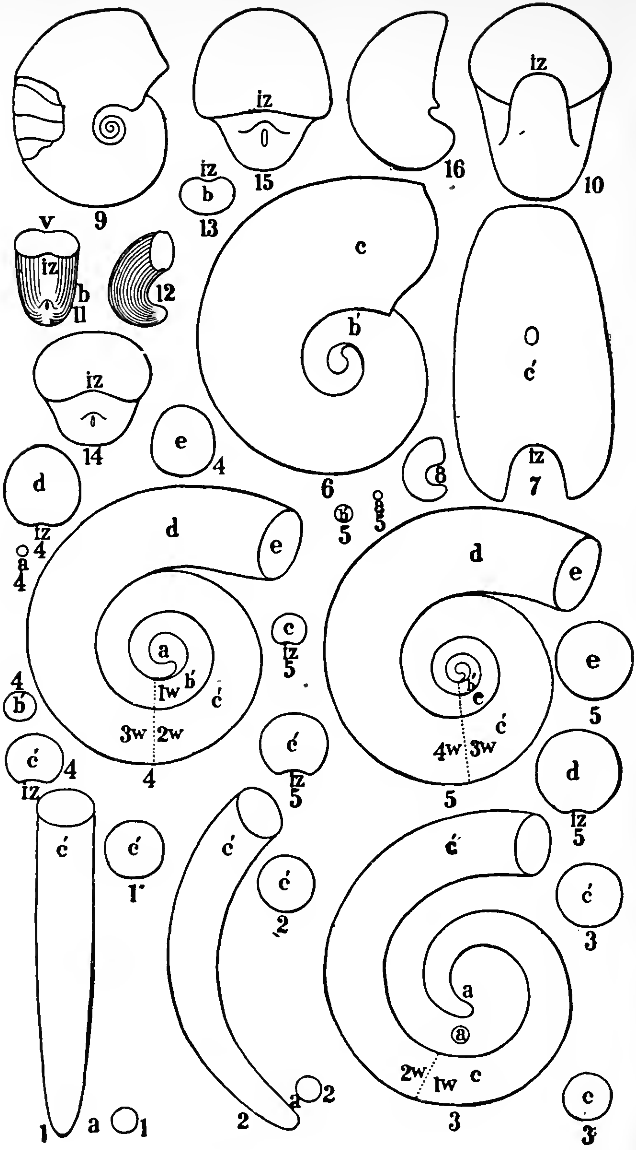

Fig. 119.—Hyatt on Cephalopoda.

EXPLANATION OF FIG. 119.

LETTERING.

a. Apex of shell. This usually bears a scar on the point, as shown in Nos. 14 and 15, but this has no bearing on the question discussed, and has not been described. This also represents the youngest (nepionic) or cyrtoceran stage in the growth of the shell, No. 8 being a young shell with complete living chamber. This letter also indicates the location of the sections correspondingly lettered in the figures.

b is used to indicate the section of the cyrtoceran stage in Nos. 11–13.

b' is used to indicate the place of the sections, Nos. 4–5*b'*, upon the whorls of Nos. 4–5. They were taken through the whorl in the gyroceran stage.

c is used for the adolescent (neanic) stage of growth in the whorl and the corresponding sections.

c' is used for the full-grown (ephebic) stage in the growth of the whorl and the corresponding sections.

d for the first part of the senile (gerontic) stage.

e for the final and most degenerative part of the senile stage.

iz for the impressed zone.

v venter or outer side of the shell, the dorsum being the inner side of the whorl.

w for the whorls, thus 1 *w* in Nos. 3 and 4 means the end of the first whorl, 2 *w* the beginning of the second whorl, 3 *w* that of the third whorl. These letters serve to show the progressive increase in numbers of the whorls in the different classes of forms.

FIGURES.

No. 1. Outline of an orthoceran shell.

No. 2. Outline of cyrtoceran shell.

No. 3. Outline of gyroceran shell.

No. 4. Outline of nautilian shell, having a larger umbilical perforation at (*a*) and fewer whorls at the same age, than in No. 5; in other words, it is less tightly and completely coiled up than the class of shells represented by that figure.

No. 5. A nautilian shell with tighter coils than in No. 4 and the whorls coming in contact and the impressed zone beginning at an earlier stage.

No. 6. *Barrandeoceras bohemicum* (sp. Barrande) Hyatt, showing the most involute of the Silurian shells so far as known; No. 6 is reduced in size, but the section No. 7 is natural size.

No. 8. A young shell of the same, natural size, with complete living chamber.

Nos. 9–10. *Coloceras globatum* (sp. De Koninck) Hyatt, adult. No. 9 has a part of the outer shell broken off, showing the edges of the septal partitions (sutures) as lines on the strong cast of the interior.

Nos. 11–13. Same to show the cyrtoceran stage and section, with its impressed zone.

No. 14. *Cenoceras clausum*, Hyatt.

Nos. 15–16. *Nautilus pompilius*, to show the cyrtoceran stage with its impressed zone.

it overlaps the apex without touching it. At this time it is plainly gyroceran, like the whole of No. 3. After it touches the first whorl just beyond the apex it remains in contact, and the inner side or dorsum of the second or overlapping whorl begins to show a flattening as a result of this collision of the whorls. The sections of the orthoceran, cyrtoceran, and gyroceran whorls show no such flattening in any of the specimens examined, although hundreds of different kinds have been studied. The sections are designated on the plate by the same letters as the supposed lines of the sections made through the tube, and although diagrammatic figures, they give a sufficiently clear general explanation of the facts observed. More specific figures could have been given in abundance and will be given in the paper now in course of preparation.[1]

"Fig. 119, No. 5, shows the same phenomena as No. 4. The young is at first cyrtoceran like the adult whorl of No. 2, and open, then becomes gyroceran in curvature and finally overlaps the apex when it has arrived at the end of the first volution, but does not at first touch it. Then coming into contact it acquires a flattened area or faint impressed zone on the dorsum or inner side of the second volution, as is shown in the section No. 5*c*. This is similar to the section of No. 4 shown in No. 4*c*′, which represents a cut through an adult whorl of the fourth class of forms. It differs only in being smaller, on account of the younger stage of growth at which it occurs.

"The entire series of forms from orthoceran to nautilian is more or less represented, even in the earliest period at which the nautiloids appear, namely, in the

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[1] See "Phylogeny of an Acquired Characteristic," Hyatt, *Proceedings American Philosophical Society*, Philadelphia, XXXII., No. 143.

rocks of the Quebec group. There is, however, this qualification: the fifth class of forms, or the involute nautilian, are relatively rare and become more abundant in successive periods. The young of nautilian shells of the earlier periods are also apt to be less closely coiled, or, in other words, remain open and similar to cyrtoceras for a longer time during their growth. This is shown by the large size of the central hole, or umbilical perforation, left in the center of full-grown shells. This perforation is much larger, as a rule, in Paleozoic than in the Mesozoic forms.

"In each period the genetic series or groups of nautilian forms have peculiarities of structure in the sutures, ornaments, apertures, etc., by which they can be separated from each other, and these peculiarities are the same as those possessed by gyroceran, cyrtoceran, and often orthoceran shells which occurred often earlier in time, so that one can trace each group of nautilian shells back to its ancestors through the parallel stages of evolution above described. The groups, in other words, are parallel in their morphogenesis, like two individuals of the same parents in their development from youth to old age.

"As a general rule the impressed zone originates, as described above, after the whorls come in contact, rarely before this time in the growth of any individuals. Barrandeoceras is one of the most involute shells known in the Silurian, and Fig. 119, No. 6, gives a true sketch of this species; No. 7, shows a section of a full-grown shell with a decided impressed zone, and No. 8 is the young. This last is a purely cyrtoceran form with a compressed elliptical section like that of No. 7, but no impressed zone, the inner side being rounded like the diagram of Cyrtoceras, No. 2. The impressed zone is not present in the young of Ophidioceras, the closest coiled of all these forms, nor in the young of most species of the Silurian before the whorls touch, and all of the species likely to present this peculiarity have been investigated.

"The impressed zone is also, as a rule, lost in the oldest stage of the whorl of every individual when the whorls cease to continue to grow in contact. This condition is represented in the last part of the outermost whorl of Nos. 4 and 5 in sections, Nos. 4*e*, 5*e*, and in the outlines of their apertures, which are elliptical. The sections represent cuts through the whorls when, as is the case in extreme age, these cease to increase in size. As soon as this senile contraction begins to occur, the sides shrink, becoming narrower, the amount of involution becomes less, and the impressed zone shrinks in breadth, as shown in the sections. When the whorl finally parts company in consequence of continued contraction, the already shrunken impressed zone, Nos. 4*d*, 5*d*, rapidly disappears, and the apertures of such shells are frequently as round and free from indentations on the inner as on the outer side, as is shown at the free end of Nos. 4 and 5.

"In normally uncoiled forms, usually named Lituites, when the adult or young is coiled, and the succeeding stages, whether representing adults or old shells, are uncoiled, the phenomena are similar. The impressed zone is lost after the growth ceases to bring the whorls of the shell into contact.

"The young and the adults of many of these forms have now been observed in the earliest periods, and it is, therefore, obvious that during these early times the impressed zone must have been a modification of the whorl which took place in consequence of the mechanical effects produced by close coiling. This characteristic is slight when the coiling is slight and is developed in precise proportion to the increase of coiling or involution of the whorls, and, on the other hand, when through degeneration due to age, or to other causes, the whorls cease growing in contact, the impressed zone gradually disappears.

"Thus it generally appears preceded and accompanied by an observable tendency in the mode of growth toward closer coiling and that this tendency is quite capable of producing the impressed zone can hardly be denied with any show of reason, since the characteristic tends to disappear in proportion as the pressure is relieved through the degeneration of the powers of growth-force to continue the normal rate of progressive increase of bulk in old or young or prematurely degenerate shells and in uncoiled whorls of all kinds and all ages.

"The shells of Devonian series of nautiloids have also been extensively examined, especially in the more involute nautilian forms of the genus Nephriticeras, and so far not one has been found with the slightest indication of the presence of an impressed zone in the cyrtoceran or gyroceran stages of development. In several examples also, the disappearance of this characteristic has been observed in the last stages of old whorls. There is, therefore, every reason for regarding the impressed zone as a ctetic characteristic acquired in the later stages of growth and not hereditary so far as is known in any shells of the earlier Paleozoic periods.[1]

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[1] Certain exceptions have been found since this was written, but their evidence is purely negative, it is impossible to say of them at present whether

"The same statement may also be made with regard to the majority of Carboniferous shells. There is, however, a notable exception in *Coloceras globatum* (sp. De Kon.) Hyatt, and very likely some other species of closely coiled nautilian shells. In *C. globatum* of Visé, Belgium, I found in seven specimens that the impressed zone appeared while the whorl was still in the cyrtoceran (or open) stage. Fig. 119, Nos. 9–10, give outlines of the adult of this species, and Nos. 11–12, of the young and the zone, showing that the impression appeared long before the whorls touched each other and began to assume nautilian characters. Section, No. 13*b*, shows the impressed zone occurring in the cyrtoceran stage while the venter or outer side of the whorl was rounded. Such facts admit of but one explanation, namely, that in this species the impressed zone had become hereditary and was in consequence repeated at an early age, previous to the occurrence of close coiling which usually produced it in the ancestral forms of the same group.

"There are certain correlative characters which lead me to think that this is only a partial statement and perhaps a more complete and better one would be as follows: that the impressed zone, together with a peculiar broadening out of the dorsum and helmet-shaped section of the whorl, and perhaps also certain forms of sutures occurred in the early stages of some Carboniferous species before the nautilian stage, and consequently they must have been introduced by heredity into the development of this species before the tendency to close coiling had completed the first whorl.

the impressed zone appeared as a genetic character or as a mechanical necessity. Either view can be taken, but the positive evidence is that they are very rare, and the impressed zone appears in them as a parallel character of distinct diverging series of forms.—*A. H.*

Thus these characters, although purely ctetic in origin, were repeated before the usual conditions recurred in the ontogeny of this species which had obviously and repeatedly produced them in the nautilian forms of the earlier Paleozoic and the more generalized genetic series of the Carboniferous. That this species, *Col. globatum*, is a highly specialized species is shown by other characteristics, especially the early inheritance of a furrowed abdomen, shown at *v* in Fig. 119, No. 11, and a peculiar aperture.

"The Triassic period is unimportant in this connection since it has but few nautilian species that are deeply involute and also sufficiently well known to throw any light upon this problem. All of the true orthoceran, cyrtoceran, and gyroceran forms diminish in the Carboniferous and disappear with the Trias.

"The Jura contains a considerable number of nautilian shells of different genera of which the cyrtoceran stages are sufficiently well known. *Cenoceros aratum*, of which several specimens have been studied, shows the impressed zone and correlative characters in this stage; *C. lineatum* is the same; *C. clausum*, same; *C. intermedium*, same. Fig. 119, No. 14, shows the cyrtoceran stage in a shell of *C. clausum*, with a well developed impressed zone, *i. z.* Endolobus is a characteristic Paleozoic type and there is a single survivor of this series in the Jura, *End.* (*Naut.*) *excavatum* sp. D'Orb. It is, therefore, very interesting and instructive to note that this species has the impressed zone, according to D'Orbigny's figure, during the cyrtoceran stage. This species has a large umbilical perforation and is slower in coiling up than other Jurassic species. The evidence that the impressed zone and its correlative characteristics are inherited in most species of the

Jura before the habit of close coiling could have acted upon the whorls so as to produce this modification is, therefore very general and convincing.

"The leading characteristic of parallelism in all genetic series of nautiloids is, as may be inferred from the facts cited, a tendency toward closer coiling and greater involution in the more specialized forms of each separate series and a correlative increase in the profundity of the impressed zone. When the impressed zone becomes inheritable in some closely coiled and involute specialized shells of the Carboniferous and in similar shells in all of the genetic series of the Jura this result is also directly connected with the observed fact of the quicker development of the coiling up tendency in the young of these Jurassic shells. This is shown by the small diameter of the umbilical perforation in the centers of the shells of the Carboniferous. It is also connected with the fact that the primitive uncoiled forms, orthoceran, cyrtoceran, and gyroceran shells begin to die out in the Carboniferous and cease with the Trias as mentioned above.

"This demonstration of the characters that accompany progress in close coiling, enables me to fill a gap which occurs in the evidence during the Cretaceous. In this period the existence of the impressed zone during the cyrtoceran stage of individuals has not been clearly established by observation except in two species, a form allied to *Cymatoceras pseudoelegans* D'Orbigny, from Faxoe, and *Cymatoceras elegans* from Rouen. In other shells, although a considerable number have been broken down, the state of preservation has been invariably imperfect. The coiling, however, in the young of all the shells examined is notably more accelerated than in the similar shells of the Jura, and the whorls broader and having more specialized characteristics correlative with closer coiling and the early existence of an impressed zone. It is, therefore, fair to infer that the evidence when accessible will confirm the facts observed in previous periods.[1]

"The same arguments apply also to the tertiary forms as far as known.

"The terminal members of the nautiloids are, of course, the existing species. *Nautilus pompilius* and *umbilicatus* have been examined in a considerable number of specimens, and in all of these the impressed zone and correlative helmet-shaped whorl and broad flattened dorsal side appears during the cyrtoceran stage. Fig. 119, Nos. 15–16, are outlines of the shell of *pompilius* during the cyrtoceran stage exhibiting the helmet-shaped whorl, broad dorsum, or inner side, and its impressed zone, *i z*. Thus, when the whorls touch, as in all the nautilian shells of the Carboniferous, Jura, and Cretaceous, in which the same acceleration of development also occurs, the whorl is already prepared to become involute and to mould itself more readily and rapidly over the surfaces of the apex and the side of the succeeding whorls. In other words, heredity has begun the work before the whorls touch, and before the deepening and enlargement of the impressed zone through the pressure of close coiling is begun. There are quite a number of characteristics of the species of existing Nautili which lead to the inference that they are survivors of Jurassic and generalized Cretaceous and Cenozoic forms; the size of the umbilical perforations, the smoothness of the shells, the simplicity of the sutures, and so on. These facts are

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[1] This inference has been fully sustained by subsequent investigations.—*A. Hyatt.*

of importance only in so far as they show that the existing Nautilus does not represent the acme of progress of its order, but is a descendant of shells with less complicated structures than many of the genera of the Carboniferous, Jura, and Cretaceous."

In these cases it seems that the mechanically acquired impressed zone is inherited from the greater part of the soma where it existed to a part of the soma of the young where it could not be produced by mechanical causes, by reason of the non-contact of the parts. This acquisition appears in a few Carboniferous species, and then it is present in the cyrtoceran or mesozoid stage of all the Jurassic, Cretaceous, and Cenozoic species. Professor Hyatt, in his "Phylogeny of an Acquired Characteristic," thus summarizes his conclusions:

"The facts and arguments brought forward seem to justify the following conclusions:

"1. The impressed zone is primitively a contact furrow, an acquired characteristic of the dorsum of the whorls of nautilian shells having large umbilical perforations, which appeared either in the ananeanic or metaneanic (maturing) substages, and rarely later in their ontogeny. There is abundant positive evidence that in these primitive forms this furrow is a purely mechanical result of the nautilian mode of growth, not appearing in the ontogeny before contact, and either partially or entirely disappearing on the free gerontic (senile) volution.

"2. The impressed zone does occur independently of contact on the free dorsum of the paranepionic (adolescent) substage as a dorsal furrow in some close-coiled, highly tachygenic (accelerated) nautilian shells in the Quebec group and in the Devonian.

"3. While there is no positive proof that the dorsal furrow originated through heredity in the paranepionic substages of these nautiloids of pre-Carboniferous age, there is also no satisfactory evidence that it originated in the young of such species as have this character, through purely mechanical agencies.

"4. There is positive evidence that the similar dorsal furrow which also appears at the same age in the young shells of *Coloceras globatum* and perhaps *Cœlogasteroceras canaliculatum* among Carboniferous nautiloids can be explained only when it is considered as a transmitted, tachygenetic (accelerated) characteristic.

"5. This fourth conclusion is supported by the presence of a similar dorsal furrow in the paranepionic (adolescent) substage of the young shells of all the nautiloids of the Jura, so far observed.

"6. The fourth and fifth conclusions are rendered still more probable by the presence of the dorsal furrow at an earlier age, the metanepionic substage, in all of the nautiloids so far observed, from the beginning of the Cretaceous, through the Tertiaries, to and including the living species of the genus Nautilus. Its presence on this cyrtoceran volution in Cretacic shells can be explained only when it is considered as a transmitted, tachygenetic (accelerated) characteristic derived from ancestral nautilian shells of the Jura, which have the same characteristic at a later age, i. e., in the paranepionic substage.

"7. The first conclusion is also sustained by the parallel phylogeny of the impressed zone in the ancestral forms of the Ammonoidea, the Nautilinidæ, and especially in the Mimoceras, the radical genus of this family.

"8. The fourth, fifth, and sixth conclusions are also supported by the presence of a contact furrow on the dorsum of the earliest age of the conch in the specialized and highly tachygenic forms of the Goniatitinæ of the Devonian and of all the remaining ammonoids to the end of the Cretaceous.

"9. These cumulative results favor the theory of tachygenesis (acceleration) and diplogenesis, and are opposed to the Weismannian hypothesis of the subdivision of the body into two essentially distinct kinds of plasm, the germ-plasm, which receives and transmits acquired characteristics, and the somatoplasm, which, while it is capable of acquiring modifications, either does not or cannot transmit them to descendants." (*Proceedings American Philosophical Society*, Vol. XXXII., p. 615).

4. EVIDENCE FROM BREEDING.

Under this head I cite the results of experience of breeding of the domesticated Vertebrata. It is here that we have had the best opportunity of testing the possibility of the inheritance of acquired characters, since the species in question have been the objects of observation and experiment for a long period of time. I especially avail myself of the writings in this connection of Prof. Wm. H. Brewer, of Yale University, President of the Agricultural Society of Connecticut. The result of his long-continued observations is contained in a series of papers in the journal *Agricultural Science* of the years 1892–1893. He considers the subject under the following heads, viz.: The inheritance of characters which are due to nutrition; of those due to the exercise of function; of those due to disease; of those due to mutilation and injuries; of those due to habit, training, and education; of those due to regional influences and to a combination of causes; and of those of acquired plasticity and adaptation. I commence with an example of the

a. *Inheritance of Characters Due to Nutrition.*

"One class of 'acquired characters,' the transmission of which by heredity is especially denied by Weismann, includes all 'those which are directly due to nutrition.'

"This denial strikes at the very foundation of what has heretofore been considered an essential factor in the practical improvement of breeds as to size. The size attained by adult, healthy domestic animals depends practically upon two causes—heredity and nutrition. Heredity is of course the chief one, for no amount of feeding will make the Shetland pony equal the Norman horse in size; but whatever the heredity, the size of the adult individual as compared with the average of others of the same breed depends usually upon its food. The ultimate weight of the mature animal varies of course with the amount of fat assimilated, which may occur long after maturity; but the size as dependent upon the frame, such as the weight, length, and general proportions, is modified by the quantity and quality of food available during the growing period of early life. This fact no one questions; and if these acquired characters are in no degree whatever transmitted, then certain practices of breeders, which are founded upon the contrary belief are delusive and expensive mistakes.

"Practical breeders have hitherto believed that these characters are to some degree transmitted, and practice accordingly. I have searched extensively the writings of practical breeders to see if I could find a single one who questions it, and I fail to find even so much as an intimation of any such belief. All the recorded observations founded upon actual practice appear to point the other way, and consequently the fact of partial transmission is assumed.

"The practical value given to this factor is now much smaller than formerly given, but that it is a factor of some value is universally assumed.

"During the last century, and early part of this, many graziers had a maxim that in the profitable production of animals for slaughter, 'feed is more than breed,' but now both breeders and graziers know that heredity or 'breed,' is the more important. But no breeder claims that a breed is or can be kept up to extra size by selection alone. This belief is so universal, and is apparently so grounded upon long and extensive experience, that I cannot find there has ever been an attempt to increase the size of any breed without special attention to this factor, and consequently conclusive and direct experiment is entirely wanting. Positive proof either way cannot be deduced from the actual experiments of breeders; their belief that feed as well as selection is necessary, is a deduction from the observation of many facts which bear upon the question.

"In this connection it must be borne in mind that all the best breeders recognize the rule laid down by Darwin, that those characters are transmitted with most persistency which have been handed down through the longest line of ancestry. Breeders do not believe that the characters acquired through the feeding of a single ancestor, or generation of ancestors, can oppose more than a slight resistance to that force of heredity which has been accumulated through many preceding generations, and is concentrated from many lines of ancestry. Yet the belief is universal that the acquired characters due to food during the growing period has *some* force, and that this force is cumulative in successive generations. All the observed facts in the experience with herds and flocks point in this direction. It is the same whether the observations relate to the increase in the size of breeds, which has been brought about by systematic selection and feeding directed with this special aim, or to the local development of breeds under the combined influence of the food supply and unsystematic selection.

"Where both large and small breeds have been in process of improvement in the same region at the same time and with the same kinds of food, liberal feeding along with systematic selection is always practised where an increase of size is aimed at, and underfeeding during growth is practised when it is desired to reduce the size. We have examples of these going on together contemporaneously. Breeding for increase of size is more common than that for reducing, but the latter occurs not only in the small fancy breeds of poultry and dogs, but even of cattle. When small and delicate Alderney cows were a fashionable ornament for parks and lawns, some of the most successful breeders practised starving systematically, and at least one eminently successful breeder of these animals so underfed the growing calves that it led to legal interference by a local Society for the Prevention of Cruelty to Animals.

"So far as I know, all the breeds of especially large horses, cattle, and sheep have originated in districts of abundant food, usually in fertile valleys or on plains, and excepting fancy breeds of poultry and pets, all the smaller breeds have originated in districts of scantier forage. This can hardly be due to accident, for it is as true of local varieties of wild animals under natural selection as of domestic animals under artificial selection."

b. Inheritance of Characters Due to the Exercise of Function.

This class of cases has an especial bearing on the doctrine of kinetogenesis. We have a very conspicuous example of such inheritance in the case of the evolution of the trotting horse, which is described by Professor Brewer as follows:

"We have a copious literature relating to the development of this breed, and the 'records' of speed provide the data for a mathematical history of the rate of progress, and also the measure of amount of cumulative variation that has occurred up to this time. These data give to this breed a special interest for scientific study.

"The facts briefly stated are as follows: Trotters had their uses for ages, but fast trotters were not wanted until the improvement in roads and in wheeled vehicles during the last quarter of the last century caused an increasing demand for faster roadsters for light draft. Trotting is the gait of traction, as running is for riding, and trotting as a sport sprang up in nearly all the countries of Europe as well as in America so soon as faster trotters were needed for the road. Then trotting-horses began to be bred, and long before the close of the century there were trotting-stallions of considerable fame. There were also recorded statements as to the speed attained.

"Lawrence, a lover of trotters, in his *Treatise on*

Horses (London, 1796), considered that 'the utmost speed of the English trotter' (which he believes to excel all others), to be a mile in two minutes and fifty-seven seconds. During the next twenty years there were very many recorded trials of speed, and a few of the best animals, both here and in Europe, trotted a mile in three minutes, but none in less time than that given by Lawrence.

"Considering the number of animals that were tested, the widespread interest in the matter, and that these records were the best of both Europe and America, it is fair to assume that this was the utmost speed actually attained by the best trotting-horses until after 1820, although some specific selection in breeding trotters had been going on for half a century, and possibly much longer.

"By 1810, the taste for trotting as a sport had died out in western Europe, but it increased here, and in 1818 it became a recognized sport under specific rules. This is practically the beginning of technical 'trotting records' as we now know them. It soon became fashionable to drive a single horse for pleasure, a social factor in breeding that was lacking in the Old World. This created a demand for trotters, as well as increased the taste of trotting as a sport. Associations were chartered for the promoting of trotting, and special tracks built for the exercising and training of trotters.

"At the end of 1824, six years after the first accepted three-minute record, the record had fallen to 2:34, a reduction of twenty-six seconds. This great reduction so rapidly effected was, doubtless, due chiefly to better training, but also in part to special exercise of function, in part to heredity, and in part to the larger number of animals trained. It is not probable that mere exercise of training could materially further increase this speed, for the next ten years lowered the record only two and a half seconds, and twenty-one years more passed before the first 2:30 record in harness was made.

"By 1848, the record was lowered to 2:29½, and we have now a 2:30 class, with two or three horses technically in it, and perhaps half a dozen that had actually trotted at that speed. Now we began to have distinctively trotting blood, and heredity began to tell.

"The next decade lowered the record five seconds; and the next (ending in 1868), lowered it seven and a fourth seconds more; there were several horses in the 2:20 class, and nearly one hundred and fifty in the 2:30 list.

"The next decade lowered the record four seconds; and the next (ending in 1888), four and a half seconds, and the number of 2:30 horses had increased to 3,255 animals. At the close of last year, the record had been further lowered half a second, to 2:08¼; there were 5,908 in the 2:30 list, 507 in the 2:20 list, and seven in the 2:10 list. This is the history for seventy-three years of 'records.'

"Parallel with the evolution of this breed has been the development of a breed of pacers. The fast animals are not so numerous, but the speed is greater, and the gait, as a fast gait, is more distinctly artificial. The instincts involved will be discussed in a later paper; here I will notice only the development of speed, because that is the direct and obvious result of functional development, and because we have mathematical data as to the rate and amount of actual evolution.

"That the gain in speed has been cumulative, and that for three-fourths of a century, that it has gone on along with systematic exercise of special function in successive generations of the present fast trotters, is indisputable and very evident. Selection has doubtless determined the proper correlation of the various organs involved in the special evolution, but the increase in speed has only come along with the functional development, which was enhanced by special exercise in the individuals of successive generations. The cumulative value of this, if transmitted, would be vastly more than enough to account for all the increase that has actually occurred, great as that is. Viewed as phenomena, there is every appearance and indication that the changes acquired by individuals through the exercise of function have been to some degree transmitted, and have been cumulative, and that this has been one factor in the evolution of speed. The cumulative variation has been most marked since we have had a 2:30 class, that is, since we have produced animals that are swift by heredity, and whose ancestors, as well as themselves, have been exercised and trained to trot. Studied as phenomena, there is not a particle of evidence that these special changes acquired by the individuals were totally lost to each successive generation, and that all that was 'transmitted by heredity,' was a something that did not exist in either parent or in any ancestor. There is nothing whatever in the actual phenomena observed anywhere along the line of this development of speed that would lead us to even suspect that the changes due to exercise of function had *not* been a factor in the evolution, and there is not a particle of evidence, other than metaphysical deductions, much less proof, that it would or could have gone on just the same by mere selection and adventitious variation."

c. Inheritance of Characters Due to Disease.

Under this head Brewer cites a well-known case. He says: "The most extensive and complete set of experiments yet published on the artificial production of disease by mechanical injuries are those of Dr. Brown-Sequard on the artificial production of epilepsy. This is a disease which is certainly sometimes hereditary and which may also be produced by art in previously sound animals. He experimented with guinea pigs and produced many artificial epileptics, and by breeding these he produced many congenital epileptics. The disease artificially produced in the parents was transmitted to the offspring in numerous cases. The acquired characters in those cases were certainly transmitted to the offspring and became hereditary. These experiments were continued and repeated by his assistant and pupil Depuy, and the results abundantly confirmed. It was shown, moreover, that in many cases it was the *tendency* to become epileptic that was transmitted rather than the disease itself. Just as in a great majority of cases of strictly hereditary disease it is the constitutional tendency rather than the disease itself that is commonly transmitted.

"These experiments have now been before the world some years, during which time ideas have greatly changed as to the causes of disease, and the nature of hereditary tendencies, but as yet there are no published accounts of experiments indicating that those of Brown-Sequard and of Depuy were not carefully performed, or that the conclusions were illusive. Medical literature abounds with alleged instances where nervous diseases acquired by parents through environment have been transmitted in some shape to children, but this evidence is not nearly so conclusive as the experimental proof cited.

"In conclusion we may say that the drift of all the collated observations on both man and brute seem to indicate that certain of the changes produced in the animal body by disease are often to some degree transmitted, that these may be cumulative and lead to degeneration if not indeed to the extinction of families. The experience of breeders as well as the observations of medical men practically establishes the fact that acquired weakness and defects occurring in successive generations may result in truly hereditary unsoundness."

d. Inheritance of Characters Due to Mutilation and Injuries.

While characters of this kind are relatively rarely inherited, there is little doubt that they can be. Dr. Brewer cites a few cases for illustration; "some of them have been already published, others have not. They are not the most striking, but are chosen because they are representative.

"*a.* A mare in foal had an eye seriously injured by burdocks entangled in the forelock. She suffered with violent ophthalmia, and in due time dropped a foal (a filly) which had the corresponding eye aborted. She afterwards bore several normal foals.

"(This case came under the observation of the eminent veterinarian, Professor Law of Cornell University. *Papers American Public Health Association*, 2, p. 254.)

"*b.* A game-cock, in his second year, lost an eye in a fight. Soon after, and while the wound was very malignant (it never entirely healed), he was turned into a flock of game hens of another strain. He was otherwise healthy and vigorous. A very large proportion of his progeny had the corresponding eye defective. The chicks were not blind when hatched, but became so before attaining their full growth; some at the time of acquiring the pin-feathers, others later and before reaching maturity. The hens afterwards produced normal chickens with another cock. Both strains had been purely bred for ten or more years, and none of the fowls had been blind unless from fights.

"(This case was reported to me by an educated and reliable breeder of game-fowls.)

"*c.* A hunting mare had a split pastern and was then used for breeding. Her first, third, and fourth foals were sound, the second one had 'almost an exact reproduction of the mare's unsoundness.'

"(This is on the authority of the celebrated veterinary surgeon, Clement Stevenson, as occurring under his own observation, 'not hearsay.' *Live Stock Journal,* London, November 23, 1888, p. 508.)

"*d.* A female (and very prolific) cat, when about half grown met with an accident. 'Her fine, long tail was trodden on and had a compound fracture, two vertebræ being so displaced that they ever after formed a short offset between the near and far end of the tail, leaving the two out of line. At first I noted that out of every litter of kittens some had a tail with a querl in it.' With successive litters the deformity increased, until 'not a kitten of the old cat had a straight tail, and it grew worse in her progeny until now we have not a cat with a normal tail on the premises,' (in a cat-population of six or eight, exclusive of young kittens). 'The tails are now in part mere stumps, some have a semicircular sweep sideways, and some have the original querl. Perhaps the deformity was somewhat aggravated by in-and-in breeding and by artificial selection practised by my Chinaman, who, with the perversity of his race, preferred the crooked tails, and thus preserved them in preference to the normal kittens. There are no other abnormally-tailed cats in the neighborhood.'

"This is the essential part of an unpublished letter from that keen observer and eminent scientist, Prof. Eugene W. Hilgard of the University of California.

"Numerous cases have been recorded as occurring with mankind. I will give but two, both of which have not before been published.

"*e.* A person, when a boy of ten years, cut the terminal phalange of the little finger of his left hand with a sickle. The joint was not injured, nor was the function of the finger seriously impaired. There was, however, an obvious deformity. The finger was ill-shaped and crooked, and the nail abnormal. He married and had two children, the first a son, with normal fingers, the second a daughter, who had the little finger of the corresponding (the left) hand deformed from birth in the same manner. The function of the finger was not seriously injured, but the deformity was precisely the same in shape, even to the malformation of the finger-nail. She died at thirty, without children, consequently no observation on a succeeding generation could be noted. None of his other kindred had malformed fingers, nor had any ancestor of the child for at least three generations, and there was no knowledge of any such in the more remote ancestry.

"(This case was related to me in full detail by the father with the deformed finger, and with whom I was personally acquainted. He was an eminent physician, the president of a large and reputable medical college, and his name is well known to the profession.)

"*f.* A woman thirty-five years of age had both kneepans broken. Erysipelas and other complications prevented the use of the usual surgical appliances for keeping the severed parts together while healing, so they never united by bony union, but became joined by intervening cartilage. The hurt was peculiarly painful and slow of healing, because of the complications alluded to, but the general health was fully restored. For some years after healing there was a very pronounced groove or furrow along the line of fracture over the connecting cartilage, especially in the right knee. The outer edges of the fractured bone were sharp at first, but ultimately became rounded by absorption. Both fractures were V-shaped. The right knee had the parts wider separated at the time of the accident, and was again partially torn asunder three and a half months later, and the furrow consequently remained very much broader and deeper than in the other knee. About four months (124 days) after the first accident, and while still unable to walk, she gave birth to a son. No abnormal appearance was noticed at the time, and later was not looked for until the child was ten or more years old, when he called attention to the matter himself. There was then a deep and well-defined groove across the surface of the right kneepan, very plainly perceivable through the skin. It corresponded precisely in shape and position with the fracture and the later furrow in the corresponding bone in the mother. It was most pronounced before the age of sixteen. After that the edges became modified by growth or absorption, becoming less sharp, following in this respect the changes that gradually occurred in the shape of the bone in the mother. The son is otherwise normal. Three other children of the same parents, one born before and two after the birth of the one described, are entirely normal. The ancestors of both parents are known for several generations (from three to eight in the several lines) and all were normal, so far as is known."

"(This case has been under my own observation during the whole period.)

"It will be noticed that in the cases *a*, *b*, and *f*, the injury to the parent occurred shortly before or during gestation, and that the healing had not taken place until after the birth of the offspring. Also, that the function of the organ involved, an important organ in the animal economy, was at the time suspended. Also that in all these cases, later offspring were normal."

e. Inheritance of Characters Due to Regional Influences.

Characters of this kind mostly come under the head of Physiogenesis. A case of inheritance is thus recorded by Brewer.

"The texture and certain other characters of wool which are of practical importance to manufacturers, depend in part on the breed and health of the animals, in part on the kind of food and on its uniformity of supply, and in part on local conditions of climate, soil, and forage. The wool grown in some regions is harsher than that grown in others, and this is certainly an acquired character in that it takes place in flocks taken from one region to another. I have specimens of wool alleged to have been taken from the same flock, the same individual animals, when pastured at two stations. The first were shorn when the sheep were pastured in southeastern Ohio, where the sheep were bred, a region noted for certain excellencies of its wool. Taken to a certain portion of Texas, and pastured on an alkaline soil, the wool of those sheep took another character, affecting both its texture and also its behavior with dyes. Treated in the same vats, as to dye, lac and mordant, the difference is very obvious.

"A certain harshness of the wools produced in some regions where the soil is alkaline or salt, the climate dry, and the forage plants characteristic of such regions, is widely known and is considered a defect by manufacturers. It is stated that when a flock is taken from a favorable region to such a less favorable one the change in the character of the wool begins immediately, but is more marked in the succeeding fleeces than in the first. It is also alleged that the harshness increases with succeeding generations, and that the flocks which have inhabited such regions several generations produce naturally a harsher wool than did their ancestors, or do the new-comers.

"Now, in this case, the deterioration in successive generations cannot possibly be due to panmixia, the withdrawal of selection; on the contrary, selection goes on under the new conditions just as carefully as under the old, and often more so, for this is the means used to lessen the evil.

"If this increase in the harshness of the wool of succeeding generations is due in part to the inheritance of an acquired character, it is very understandable. That it is a congenital adventitious variation coincident in all the individuals of immense flocks, is a mathematical absurdity.

"We have an analogous regional character in the hoofs of horses. From early times it has been a known fact that the feet of horses produced in mountainous and hilly regions stand travel on hard roads and on city pavements better than those bred on softer low lands, however rich and fertile the latter may be. European writers of previous centuries are very specific on this point. Jacquet, over two centuries ago, cites it as a fact true alike in Spain, Italy, and other countries of Europe. I have interviewed the livery-stable men in various eastern cities as to the relative character in that particular of the horses bred in the hilly regions of New England, New York, and Pennsylvania, compared with those produced on the prairies, and the testimony is almost unanimous to the same effect. The old Vermont bred horses are still famous.

"This regional character cannot be a matter of selection and adventitious variation. It must be related to the environment alone, and environment can only act on the living individual. If this fact is due to the inheritance of acquired characters, it is very easily understood. The different effects of exercise of the feet of the growing animal in the one case on the hard, stony soil of the hills, in the other, on the softer and fine soil of the prairies, makes a difference in the acquired characters, a difference of the very kind spoken of, and which becomes congenital."

At the close of this series of papers Brewer remarks: "The art of breeding has become in a measure an applied science; the enormous economic interests involved stimulate observation and study, and what is the practical result? This ten years of active promulgation of the new theory has not resulted in the conversion of a single known breeder to the extent of inducing him to conform his methods and practice to the theory. My conclusion is that they are essentially right in their deductions founded on their experience and observations, namely, that acquired characters may be, and sometimes are, transmitted, and that the speculations of the Weismann school of naturalists are unfounded."

5 THE CONDITIONS OF INHERITANCE.

Since the evidence adduced must be regarded as proving that characters acquired by an organism may be transmitted by inheritance, we next endeavor to ascertain what information is within our reach which can throw light on this mysterious process. Although Weismann has demonstrated the isolation and stability of the germ-plasma to exceed that of other tissues, he has not proven that it is entirely inaccessible to external influences. He admits that its continual subdivision by the development from it of the embryonic soma, would have speedily reduced it to an infinitesimal quantity, were it not that it grows by accession of nutritive material like other tissues, which nutritive material is furnished by the soma. The accessibility of the germ-plasma to stimuli which affect the soma is then clearly possible.

The effect of the specialization of tissues on their nutrition and repair after injury, is well known. Nutrition of each tissue produces only that tissue. Repair or restoration of parts is confined to the reproduction of a tissue similar to the part lost, or similar to some unfinished or embryonic stage of it. The lower we descend in the scale of life, the more complete is the reproduction of a lost part. The specialization of the higher organisms deprives the tissue of the capacity for exact reproduction. As an example of the reduction of this capacity, I cite the reproduction of the tail of lizards, where no vertebræ are reproduced, but in its place a notochord; while the squamation presents a simpler character than that of the normal tail. The possibility of reproducing the entire organism is restricted, in the multicellular animals, to the germ-plasma, which therefore may be regarded as retaining the characteristic of the protozoön, which reproduces itself by division. But in the multicellular plants the power of reproduction of the entire organism from any of its parts, is retained to a much greater degree than in multicellular animals. The reproduction of plants by cuttings, buds, tubers, and even by single leaves, is well known; a characteristic which is due to the general distribution of unspecialized protoplasm throughout the organism. Inheritance of characters is in these cases known to be very exact, and there can be here no isolation of the germ-plasma. This isolation is progressively more pronounced as we rise in the scale of specialization of structure, but that it ever becomes absolute, the facts before us forbid us to believe.

Having thus seen that the plasma of the germ-cells is open to the influence of stimuli, let us see how it is possible that such stimuli can be transmitted to it, and how they could affect growth of the embryo.

It has been shown that impressions experienced by an animal during one stage of development may be effective in causing the appearance of new structure in a later stage. I have already quoted (Chap. V.) from Poulton the results of experiments on the colors of

Lepidoptera by several English entomologists. By exposure to different colors, of larvæ which were approaching the period of pupation, corresponding colors were produced in the pupæ. Thus black, dark, green, and yellow larvæ, and larvæ with gilt spots or entirely gilded, were produced at will. In this instance the dynamic effect produced by the exposure was stored for the period which elapsed between the exposure of the larva and the full development of the pupa. In another experiment, larvæ which were in the act of weaving cocoons, on exposure to certain colors, were induced to weave cocoons of corresponding color. This experiment demonstrates that a stimulus may be transmitted to a gland so as to modify the character of its secretion in a new direction. From both experiments we learn the transmissibility of energy from the point of stimulus to a remote region of the body, and its conversion into growth energy (in this case by Physiogenesis). This prepares us to look upon heredity as an allied phenomenon, i. e., the transmission of a special energy from a point of stimulus to the germ-cells, and its composition there with the emphytogenic (inherited) energy into bathmism (or evolutionary energy).

The relation of inherited and acquired characters in a series of generations may be graphically represented as follows: Let S represent the aggregate of character of the body (*soma*) of a given species in process of progressive evolution or acceleration. Let g represent the aggregate of characters potential (or dynamically present) in the germ cells of the same individual. For the sake of simplification of the problem I consider here only one sex, and imagine the reproduction to be parthenogenetic. Let A represent the new character acquired by the *soma* under the appropriate stimulus, and let a represent the same characteristic as it is impressed on the germ-plasma of the same individual at the same time, and in consequence of the same stimulus. The history of the acquisition and incorporation of newly acquired characters by the line of descent originating with the species $S+g$, may be represented as follows, for successive generations, which are numbered 1, 2, 3, etc.

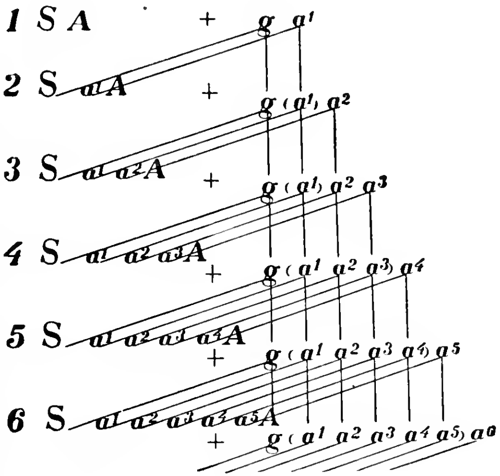

Fig. 120.—Diagram explanatory of Diplogenesis.

Under the appropriate stimulus the soma S acquires A, and the germ plasma g the identical a^1 as the first stage. The character $A\,a^1$ being only inheritable *via* the germ-plasma, it is represented by a^1 in the second stage or generation, where it appears as an addition to the characters of S and g, so that the soma of the second generation is represented by the expression $S a^1$, and the germ-plasma by $g(a^1)$; (on the supposition that $SA + ga^1$ represents the first of a line in which a given character appears). A new character or an additional increment of the same character, appears in the second stage of acceleration "2," and is represented as before, by Aa^2, the A appearing in the soma, and the a^2 being added to the character of the germ-plasma. In the third stage, the new character a^2 appears in the soma, which now becomes Sa^1a^2. The a^2 acquired by the germ-plasma of the second stage, is inherited by that of the third, which is therefore represented by $g(a^1a^2)$. To the third stage is now added the acquisition Aa^3. The a^3 is again incorporated into the soma of the succeeding or fourth stage, which is therefore represented by the expression $Sa^1a^2a^3$; while the germ-plasma of the same (fourth, "4,") stage, is represented by $g(a^1a^2a^3)$, and so on. The lines of immediate inheritance are represented by straight lines. The vertical lines represent the descent of characters from one type of the germ-plasma to a succeeding one; and the oblique lines represent the transmission of the same characters to the soma into which it grows, as the succeeding generation or stage.

The letters a^1, a^2, etc., expressive of characters acquired by the germ-plasma, are numbered for identification only. Should the influences derived from the ancestry of the other sex be added to the diagram its complexity would become inconvenient, and they are therefore omitted. It is to be also observed, that the enumeration of generations as immediately successive, as 1–2–3 etc., is to be understood as indicating succession only, and not any exact number of generations.

In the hypothesis of heredity above outlined, it is insisted that the effects of use and disuse are two-fold; viz.: the effect on the soma, and the effect on the germ-plasma. Those who sustain the view that acquired characters are inherited, must, I believe, understand it as thus stated. The character must be potentially acquired by the germ-plasma as well as actually by the soma. Those who insist that acquired characters are not inherited, forget that the character acquired by the soma is identical with that acquired by the germ-plasma, so that the character acquired by the former is inherited, but not directly. It is acquired contemporaneously by the germ-plasma, and inherited from it. There is then truth in the two apparently opposed positions, and they appear to me to be harmonized by the doctrine above laid down, which I have called the Theory of Diplogenesis, in allusion to the double destination of the effects of use and disuse in inheritance.

From the preceding considerations we learn that a new character is not inherited unless it is acquired by germ-plasma, as well as by the soma. Should it fail of the former it will not be inherited, although it may appear in the soma. It is also evident that the same character appears in the soma of later generations by virtue of its inheritance by their germ-plasma. Hence should it fail to appear in the adult soma of one generation, it might arise in a later one ; and hence the possibility of atavism, and an alternation of generations. Intermittent stimulus might be followed by intermittent activity of growth energy. This would be especially apt to occur during the assumption of sexuality by animals and plants whose reproduction had been performed by cell-division or budding only. And such is the character of most types of alternate generations ; a sexual type alternates with a non-sexual type. The advantages being on the side of sexual reproduction on account of its increased opportunity of variation, it has replaced the more primitive method by the process of natural selection.

The time when the impressions of physical habits are conveyed to the reproductive elements has an important bearing on the question of inheritance. Professor Osborn[1] has thus classified the agencies which lie at the basis of organic evolution. Opposite to each he states the theories which have been proposed to account for them:

A. Ontogenic Variations.

a. Gonagenic, i. e., those arising in the germ-cells, including "blastogenic" in part of Weismann, the "primary variations" of Emery.	Theoretically connected with pathological, nutritive chemico-physical, nervous influences, including the doubtful phenomena of Xenia and Telegony.
b. Gamogenic, i. e., those arising from maturation and fertilization, including the "blastogenic" in part of Weismann, and secondary or Weismannian variations of Emery.	Theoretically connected with influences named above, also with the combination of diverse ancestral characters, Amphimixis of Weismann.
c. Embryogenic, i.e., those occurring during early cell-division, including the blastogenic and somatogenic of Weismann.	Theoretically connected with extensive anomalies due to abnormal segmentation, and other causes observed in the mechanical embryology of Roux, Wilson, Driesch, and others.
d. Somatogenic, i.e., those occurring during larval and later development after the formation of the germ-cells.	Connected with reactions between the hereditary development forces of the individual and the environment.

B. Phylogenic Variations.

Variations from types originating in any of the above stages which become hereditary.

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[1] *American Naturalist*, 1895, p. 426: "On the Hereditary Mechanism and the Search for Unknown Factors of Evolution."

Osborn points out that Buffon appealed to the "direct action of the environment" as a cause of evolution, in so general a way, as to embrace all the conditions above enumerated. St. Hilaire dwelt on the embryogenic influences, while Lamarck laid stress on the somatogenic. Darwin only discussed variation after it came into being.

The distinctions pointed out by Osborn relate to the period of life at which modifying influences are experienced; that is, they are time distinctions. They must all, however, be included under two heads when the sources of influence are considered. That is, they must proceed from the organism itself, or from the environment directly. Those proceeding from the organism may also be divided into two classes, viz., those which are inherent in the physical and chemical characters of protoplasm, and those which have been acquired by generations prior to any given one under consideration. In this work I attend first to the probably efficient or phylogenetic causes, and these may be regarded as having been at some time or another during the history of the phylum as somatogenic. On this view, I have regarded the life of an animal as divided into three periods; those of embryonic life, of adolescence, and of maturity. During embryonic life impressions are exclusively somatic, and can be only obtained through or from parental stimulus and parental environment. Such will reach the embryo through nutrition, and through the direct mechanical contacts and strains of the environment. The environment of unprotected embryos is external to the parent; that of long protected embryos is the walls of the oviduct, uterus, etc., within the parent. Ryder has alleged with much reason that the nature of the contact of the chorion with the walls of the oviducts or uterus has determined the shape of the placenta ; and that the invagination of the embryo which resulted in the development of the amnion is a result of gravitation. While these facts have an important bearing on the study of inheritance, they have but a collateral relation to evolution ; since the embryo, whether in utero or in ovo, has little opportunity of experiencing the external influences which are only possible at later periods of life. It is during adolescence that the normal activities of maturity, except reproduction, are first practised, whether inherited or learned for the first time. The superior capacity of the adolescent stage for acquisition in all directions is well known, and it is reasonable to suppose that since growth is not completed, changes in its details can be most readily introduced. It is to this period of life then that we must look for the effective influence of the factors of evolution in the acquisition of new characters of the soma. And if the nervous, muscular and other tissues react at this period most readily to external stimuli, it is to be supposed that the developing reproductive cells possess the same characteristic, and record in their molecular movements the influences which are experienced by the entire body. Such influences on the reproductive cells, repeated millions of times from generation to generation, must produce a definite effect on them, in spite of the conservatism which their comparative isolation imposes on them.[1]

The transmission of acquired characters is evidently accomplished during the adult period. While the influence on the soma is greatest during adolescence, the influence on the germ-plasma is probably important during maturity, because habits formed

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[1] *American Naturalist*, December, 1889, "On Inheritance in Evolution."

during adolescence are now practised with especial energy and frequency. The influence on the constantly renewed germ-plasma is correspondingly greater, and transmission is of course more certain. Some characters seem to have been mainly acquired during maturity. Such is the permanent dentition of the higher Mammalia, which does not appear until or after maturity. In this case the influence of use on the germ-plasma must be more energetic than that on the soma. It is, however, not unlikely that the fundamental characters of mammalian dentition were laid during adolescence by direct influence on the temporary dentition. The tritubercular molar was established at that time and owes its present existence to inheritance. Only the sectorial and lophodont types have been added since the extensive development of the milk dentition in geologic time.

The chief source from which acquired characters are introduced into the germ-plasma, and hence into the soma of the next generation, is probably the spermatozoöid, since it is endowed with a greater kinetic energy than the ovum. The latter furnishes nutritive material for the supply of the needs of growth. That the male is the chief source of variation is also indicated in the numerous cases when he is more active than the female, and hence more capable of supplying the stimulus of use.

The manner in which influences which have affected the general structure are introduced into the germ-cells remains the most difficult problem of biology. For its explanation we have nothing as yet but hypotheses. The one which has seemed to me to be the most reasonable belongs to the field of molecular physics, and it must be long before it is either proved or disproved. I have termed it a "dynamic theory," and it is in some respects similar to that subsequently proposed by Haeckel under the name of the "perigenesis of the plastidule." I have already referred to the phenomena of the building or growth of the added characters which constitute progressive evolution as evidence of the existence of a peculiar species of energy, which I termed bathmism. This is to be explained as a mode of motion of the molecules of living protoplasm, by which the latter build tissue at particular points, and do not do so at other points. This action is most easily observed in the beginnings of growth, as in the segmentation of the oösperm, the formation of the blastodermic layers, of the gastrula, of the primitive groove, etc. In the meroblastic embryo the energy is evidently in excess at one part of the oösperm, and in defect at another. This is a simple example of the "location of growth force or bathmism." In all folding or invagination there is excess of growth at the region which becomes the convex face of the fold; i. e., a location or especial activity of bathmism at that point. All modifications of form can be thus traced to activity of this energy at particular points. A basis is thus laid for a more or less complex organism, and the channels of nutritive pabulum being once established, the location or distribution of the energy is assured in the directions in which they lead. Thus with the establishment of circulating channels nutrition is definitely guided to particular points. It is evident that on this hypothesis the bases of evolutionary change are laid in the embryonic tissues, where bathmism displays its activity in producing the base forms on which all subsequent structure is moulded.

The building energy being thus understood to be a mode of molecular motion, we are not at liberty to suppose that its existence is dependent on the dimensions of the organic body which exhibits it. It is as characteristic of the organic unit or plastidule as the mode of motion which builds the crystal is of the simplest molecular aggregate from which the crystal arises. Bathmism has, however, no other resemblance to crystalloid cohesion. The latter is a simple energy which acts within geometrically related spaces, without regard to anything else but the present compulsion of superior weight-energy. In bathmism we see the resultant of innumerable antecedent influences, which builds an organism constructed for adaptations to the varied and irregularly occurring contingencies which characterize the life of living beings. As this resultant is distinctive for every species, bathmism must be regarded as a generic term, and the characteristic growth-energy of each species as distinct species of energy, which presents also diversities expressive of the peculiarities of individuals.

The preceding statements do not, of course, constitute an explanation of the exact manner in which a stimulus which effects say the contraction of a muscle, effects molecular movements of the nuclei of the reproductive cells. This is a question of organic molecular physics, a science which has made scarcely a beginning. That the transmission of such influence is through nutritive channels, by the intermediation of a nervous structure where one exists, may be supposed. Poulton's experiments on Lepidoptera, already cited, led him to believe that the effect of color-environment was transmitted to the pigment-cells through the medium of the nervous system. That the *modus operandi* is similar to that which produces reflexes may be also reasonably supposed. How the record of these movements become reflexes, is concentrated in a reproductive cell, is a question to be solved only in a more advanced stage of knowledge of organic physics than we now possess.

Speculation in this direction takes the following forms. According to one view the energy or molecular movement must be transmitted to the germ-plasma through a material or molecular basis. This basis, it may be supposed, must be that which receives the mechanical impression which is to produce a corresponding modification of growth-energy in the ovum or spermatozoöid; that is, in the case of a modified bone-articulation, particles of matter must pass from the latter through the medium of the circulation to the reproductive cells. The alternative hypothesis is, that the energy which causes the active region to make or omit to make a given movement, the result of which is to be structural modification in the young, is impressed through protoplasmic channels on the germ-cells of either sex. In this case the transmission of particles of matter is not necessary, as material connection through the cells, nervous or other, already exists.

To the first of these points of view belong the pangenesis theory of Darwin, and the modified pangenesis of Weismann. These hypotheses present the difficulty that we must conceive of each particle or "gemmule" derived from a given part of the organism finding its way through the circulation to its exact place in the growing embryo; or otherwise, of transmitting its peculiar mode of motion to the correct molecules of the embryo, without error as to locality. The difficulties to be encountered in accomplishing such a feat seem to be insuperable. Hyatt well expresses these in the following language: "Every purely corpuscular throng . . . must not only account for a difficulty as great as that of the camel and the needle's eye, but must also account for putting the numberless characters derived from the entire caravan of its immediate progenitors and remote wild ancestors and their progenitors back to the origin of their phylum, through the same narrow tunnel. This physical difficulty is still further enhanced by the fact that the ova and spermatozoa do not increase in size in proportion to the increasing number of characters transmitted." (*Proc. Boston Soc. N. H.*, 1893, p. 70.)

The transmission of a mode of motion organized in a central nervous system, is less inconceivable. This central system is the seat of a composition of incoming stimuli and of outgoing energies, the resultant of both combined constituting the active agency in the production of automatic adaptive or intelligent adaptive movements of any and all of the organs. It appears to me that we can more readily conceive of the transmission of a resultant form of energy of this kind to the germ-plasma than of material particles or gemmules. Such a theory is sustained by the known cases of the influence of maternal impressions on the growing fœtus. Going into greater detail, we may compare the building of the embryo to the unfolding of a record or memory, which is stored in the central nervous organism of the parent, and impressed in greater or less part on the germ-plasma during its construction, in the order in which it was stored. This record may be supposed to be woven into the texture of every organic cell, and to be destroyed by specialization in modified cells in proportion as they are incapable of repro-

cf. [illegible]
+ [illegible]
([illegible]

ducing anything but themselves. The basis of memory is reasonably supposed to be a molecular (or atomic) arrangement from which can issue only a definite corresponding mode of motion. That such an arrangement exists in the central nervous organism is demonstrated by automatic and reflex movements. It is also demonstrated by the fact that the memory of the position and parts of amputated limbs is retained by the sensory center, so that irritation of the stump is referred to the lost limb. That the entire record is not repeated in automatic and reflex acts, but only that part of it which was last acquired, may be regarded as due to the muscular and other systems concerned in it having performed it most recently, and having for a longer or shorter period omitted to perform the older movement, because the latest structures of the organs would render the performance of the old movements impossible. In other words, the physiological division of labor extends to memory at the basis. In the case of the germ-plasma no other specialization exists, so that the entire record may be repeated stage after stage, thus producing the succession of type-structures which embryology has made familiar to us. In the process of embryonic growth, one mode of motion would generate its successor in obedience to the molecular structural record first laid down in the ovum and spermatozooïd, and then combined and recomposed on the union of the two in the oöspore, or fertilized ovum.

If the doctrine of kinetogenesis be true, this energy has been moulded by the interaction of the living being and its environment. It is the recorded expression of the habitual movements of the organism which have become impressed on, and recorded in, the reproductive elements. It is evident that these and the other organic units of which the organism is composed possess a memory-structure which determines their destiny in the building of the embryo. This is indicated by the recapitulation of the phylogenetic history of its ancestors displayed in embryonic growth. This memory has perhaps the same molecular basis as the conscious memory, but for reasons unknown to us, consciousness does not preside over its activities. The energy which follows its guidance has become automatic, and it builds what it builds with the same regardlessness of immediate surroundings as that which is displayed by the crystallific growth-energy. It is incapable of a new design, except as an addition to its record.

Were all cells identical in characters, every one would retain the structural record, or memory of its past physical history, as do the unicellular organisms. Evolution has, however, so modified most of the structural units of the organic body that none but the nervous and reproductive cells retain this record, in greater or less perfection. The nervous cells have been specialized as the recipients of new impressions, and the excitors of definite corresponding movements in the cells of the remainder of the organism. The somatic cells retain only the record or memory of their special function. On the other hand, the reproductive cells, which most nearly resemble the independent unicellular organisms, retain first the impressions received during their primitive unicellular ancestral condition; and second, those which they have acquired through the organism of which they have been and are only a part. The medium through which they can receive such impression is continuous protoplasm. Whether, in the higher animals, it is effected through that system of cells called the nervous system, which has been specialized through use and natural selection to receive impressions from without, and to transmit them to such parts of the organism as are capable of receiving them, or whether it is transmitted through other media, as in lower animals and in plants which possess no such system, is unknown. The only cells which can retain the entire record in the higher animals are the reproductive cells. In the lower animals and plants it is well known that germ-plasma is not confined to reproductive organs, but is widely disseminated throughout the organism. In some forms it seems that all of the sarcode is capable of reproduction.

This is the logical result of the considerations which have occupied the preceding pages, and is the carrying out of the bathmism theory of heredity, of which I have given hitherto only the bare outline.

Since Darwin, successive contributions have been made to the theory of heredity in its relation to evolution. In 1868 and 1871 the present writer advanced the dynamic hypothesis, but made no attempt to explain the mode of conveyance of dynamic impressions and modifications to the germ-cells. The theory of "perigenesis," proposed by Haeckel in 1873, is of the same character, and is deficient in the same way. The modified pangenesis theory of Brooks, published in 1883,[1] attempts to supply the defect found in the previous conceptions, but does so by assuming with Darwin the intermediation of gemmules, a hypothesis to which sufficient objection has been made by Galton and others. Brooks's theory also fails to admit the origin of variations through mechanical stresses, although he seeks for the origin of gemmules through

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[1] *The Law of Heredity*, Baltimore, 1883, p. 80.

the lack of equilibrium between the organization and its environment, which embraces that proposition without definite specification. To Weismann we are indebted for the exposition of the separate origin and relative isolation of the germ-plasma, but no sufficient explanation of the origin and inheritance of new characters is offered. Ryder[1] has especially dwelt on the physiological division of labor seen in the tissues of the organism, and on the special function of the germ-plasma as the recipient of impressions through the processes of metabolism; but he does not go into greater detail.

What is true of the somatic cells is also true of those which follow immediately the segmentation of the oösperm. Each division contains the entire record, until a point is reached in which specialization of its growth-capacities begins.

Dr. Chalmers Mitchell thus discusses the question as to the location of specialized growth in the oösperm:[2]

"Loeb uses the term heteromorphosis to denote the power of organisms, under the stimulus of outer conditions, to produce organs on parts of the organism where they do not occur normally, or the power to replace lost parts by parts unsimilar to them. Regeneration is the reproduction of like parts. Heteromorphosis is the reproduction of unlike parts.

"If one cuts off part of the stem of almost any plant, on placing the stem in suitable soil, roots will grow out, although roots are not natural to that part of the stem. The prothallus of fern produces the male and female organs on the lower side turned away from the light. If the prothallus be darkened on the upper

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[1] *American Naturalist*, 1890, p. 85.

[2] *Natural Science*, 1894, p. 187.

surface, and illumined by reflected light on the lower surface, then the antheridia and archegonia will be produced on the upper surface. Galls are produced under the stimulus of the insect almost anywhere on the surface of the plant. Yet in most cases these galls, in a sense grown at random on the surface of a plant, when placed in damp earth will give rise to a young plant. In the hydroid, *Tubularia mesembryanthemum*, when the polyp-heads are cut off, new heads arise. But if both head and root be cut off, and the upper end be inserted in the mud, then from the original upper end not head-polyps, but root-filaments, will arise, while from the original lower end, not root-filaments, but head-polyps will grow. In *Ciona intestinalis*, round a slit cut into the body-wall, a tubular process grew out, forming a new mouth, while around the base of this, a series of eye-spots, corresponding to the eye-spots round the real mouth, appeared. In all these cases, it is plain that there were present in parts affected, the determinants, to use Weismann's term, not only of the normal parts, but also of parts, which, under normal conditions, would never have appeared there; and these new parts growing in the unwonted places bore the normal species-stamp as characteristically as similar parts grown in their normal places. It can hardly be supposed that the architecture of the germ-plasm contains special determinants to be ready for occurrences so casual, especially as these are called into existence by circumstances quite foreign to the normal environment of the organisms. On the other hand, the facts are consonant with Hertwig's belief that, as all division is heirs-equal division, all the species-characters that depend upon cells are latent in every cell.

"The experiments of Driesch, Wilson, and Hertwig upon the early stages of developing ova show that heteromorphosis begins with the very earliest divisions of the egg. Thus Driesch, working upon echinoderm embryos, was able to flatten out the stage where there was a sphere of sixteen cells into a flat plate where all the cells were in the same plane. In such a plate, the nuclei of the cells occupied relative positions very different from the normal conditions. Yet from these Driesch obtained normal plutei larvæ. It was, in fact, as if the cells could be pushed about like billiard balls without destroying the future shape and characters of the embryo. Did each cell contain only the determinants that would correspond to the structures that would arise from it under normal conditions then change of its normal position would have arrested development. Each cell must, on the other hand, have contained the determinants for all the animal, and have allowed those to come into operation that were required by the new positions into which the cells were forced. Driesch, by separating the first two and the first four segmentation-spheres of an Echinus ovum, obtained two or four normal plutei, respectively one-half and a quarter of the normal size. Here again each sphere must have contained all the determinants for the whole organism. Heirs-equal division must have occurred. So, also, in the case of Amphioxus, Wilson obtained a normal, but proportionately diminished, embryo with complete nervous system from a separated sphere of a two or four or eight-celled stage.

"Hertwig himself, some years ago, published the results of experiments he made upon the development of frogs' eggs under abnormal conditions. He showed that there could be no question of imperative divisions separating the germ-plasm into right and left halves, and so forth, but that the method of division was determined by pressures and relative gravities. Alteration of these made the ova divide into novel but symmetrical forms. Chabry obtained normal embryos in cases where some of the segmentation-spheres had been artificially destroyed.

"These cases all show that in its possibilities each segmentation-sphere is identical; that as a result of heirs-equal division, each cell contains all the material necessary to cause the development of a complete embryo. Weismann would have to suppose that in all these cases, in addition to its half of the nuclear matter resulting from heirs-equal division, it had also a stock of unaltered germ-plasm ready to be called into activity by unwonted stimuli. But even this hypothesis would not account for cells distorted by compression responding with the production of unwonted symmetries."

6. OBJECTIONS TO THE DOCTRINE OF INHERITANCE OF ACQUIRED CHARACTERS.

I will now mention some objections to the theory of epigenesis, or the inheritance of acquired characters. Some of them appear at first to have considerable force, but the explanations which have been offered seem to me to be sufficient.

Weismann's merit consists in having directed attention to the isolation and continuity of the germplasma, factors which must be taken account of in any theory of inheritance. The continuity of reproductive function which this substance displays is a fact of great interest, and one which has given rise to the statement that it is under normal conditions, immortal.

Isolation of the germ-plasma is however doubtfully complete anywhere, and in the vegetable kingdom it scarcely exists. Most plants may be propagated either by roots, cuttings, bulbs, buds, or even by leaves. The germ-plasma is evidently as widely distributed in these multicellular organisms, as it is in a Protozoön. The greater degree of isolation exhibited by the higher animals is one of their many specializations, but that it is not complete is shown by the facts already cited in the preceding pages. The continuity of protoplasm in the organism is likely to be true of the germ-cells as of other cells; and they are not deprived of nutrition, so that they are evidently accessible to influences from or through the soma. As regards the immortality of the Protozoön there is reason to believe, that like its descendent the germ-cell, it requires renewal from another cell to escape death. According to Maupas, the Protozoa after reproducing by self-division for many generations, require conjugation, or they dwindle and die.

The old formula that variation is due to "natural selection and heredity" has derived new life from the fact that sexual conjugation is necessary for the renewal of the vitality of the ovarian cell. It is supposed by Weismann that variation as well as reproductive energy is introduced in this way, the process being termed by him Amphimixis. But like the old formula this explains nothing, for if the parents are the sources of variation, the question as to the source of the variation is simply relegated to the parents for answer. Moreover, Brooks, who made this suggestion prior to Weismann, points out that it has less force than appears at first sight to belong to it. He shows[1] that the ancestors of the individuals of a given species are in greater or less degree identical persons, and that they are on this account less numerous than has been sometimes assumed. Thus, if the population of a given district had for ten generations married first cousins, the total ancestry of each person for that period would number only thirty-eight persons. If, on the contrary, all the ancestors of each person had been distinct individuals, the total number of ancestors in ten generations would be two thousand and forty-six persons. An investigation into the ancestry of three persons, not nearly related, living on an island on the Atlantic coast where the records are complete for seven and eight generations, shows that the ancestry of each of the three averages only three hundred and eighty-two persons. That this consideration is of even greater importance in estimating the ancestry of the lower animals than in man, is evident from the fact that no consideration of kinship modifies their reproductive habits.

The fact that mutilations are not generally inherited is cited as evidence against the inheritance of acquired characters. A particular mutilation, however, as already remarked, rarely happens more than once or twice in the lifetime of a single individual; in fact its occurrence more than once is, in many cases, as in amputations, impossible. Such sporadic events must necessarily have little influence as stimuli to the organism, in comparison with the habitual movements of animals, or the continued exposure to especial physical conditions, as is experienced by both plants and animals, and are not worth considering in this connection.

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[1] *Science*, 1895, February, p. 121.

One of the cases which is cited in opposition to the view here sustained, is the alleged fact that the artificial contraction of the feet undergone by high-caste Chinese female children, resulting in deformity of the feet of the women, is not inherited. That this abnormality has never been transmitted has not yet been satisfactorily shown; but in any case there are some reasons why it should not be inherited. One of these is, that the deformity is confined to one sex. The male, who is without it, has the advantage of an ancestry possessing normal feet extending backwards indefinitely, while the modification of the female is a very modern interference with the law of the species. Moreover, a positive stimulus to ontogenetic growth, such as is in this instance furnished by the male, is always likely to be prepotent as compared with the negative part played by the female.

Professor Poulton, whose interesting experiments in the production of color changes in lepidopterous larvæ and pupæ have been previously cited, states that none of the color varieties which he has obtained, have been inherited. I cannot regard this result as conclusive until the experiments have been continued for a longer period than has yet been possible to devote to them.

Perhaps the strongest case that can be made out against the theory of use-inheritance as defended in the present book, is that of the variety of structure displayed by the neuter members of the colonies of ants and termites. Mr. W. P. Ball describes these briefly as follows:[1]

"But there happens to be a tolerably clear proof that such changes as the evolution of complicated

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[1] *The Effects of Use and Disuse*, Nature Series, 1890, p. 24.

structures and habits and social instincts *can* take place independently of use-inheritance. The wonderful instincts of the working-bees have apparently been evolved (at least in all their later social complications and developments) without the aid of use-inheritance—nay, in spite of its utmost opposition. Working-bees, being infertile 'neuters,' cannot, as a rule, transmit their own modifications and habits. They are descended from countless generations of queen-bees and drones, whose habits have been widely different from those of the workers, and whose structures are dissimilar in various respects. In many species of ants there are two, and in the leaf-cutting ants of Brazil there are *three*, kinds of neuters which differ from each other and from their male and female ancestors 'to an almost incredible degree.'[1] The soldier caste is distinguished from the workers by enormously large heads, very powerful mandibles, and extraordinarily different instincts. In the driver ant of West Africa one kind of neuter is three times the size of the other, and has jaws nearly five times as long. In another case, 'the workers of one caste alone carry a wonderful sort of shield on their heads.' One of the three neuter classes in the leaf-cutting ants has a single eye in the midst of its forehead. In certain Mexican and Australian ants

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[1] *Origin of Species*, pp. 230–232; Bates's *Naturalist on the Amazons*. Darwin is surprised that no one has hitherto advanced the demonstrative case of neuter insects against the well-known doctrine of inherited habit as advanced by Lamarck. As he justly remarks, "it proves that with animals, as with plants, any amount of modification may be effected by the accumulation of numerous slight, spontaneous variations, which are in any way profitable, without exercise or habit having been brought into play. For peculiar habits confined to workers, however long they might be followed, could not possibly affect the males and fertile females, which alone leave any descendants." Some slight modification of these remarks, however, may possibly be needed to meet the case of "factitious queens," who (probably through eating particles of the royal food) become capable of producing a few male eggs.

some of the neuters have high spherical abdomens, which serve as living reservoirs of honey for the use of the community. In the equally wonderful case of the termites, or so-called 'white ants' (which belong, however, to an entirely different order of insects from the ants and bees), the neuters are blind and wingless, and are divided into soldiers and workers, each class possessing the requisite instincts and structures adapting it for its tasks. Seeing that natural selection can form and maintain the various structures and the exceedingly complicated instincts of ants and bees and wasps and termites in direct defiance of the alleged tendency to use-inheritance, surely we may believe that natural selection, unsupported by use-inheritance, is equally competent for the work of complex or social or mental evolution in the many cases where the strong presumptive evidence cannot be rendered almost indisputable by the exceptional exclusion of the modified animal from the work of reproduction.

"Ants and bees seem to be capable of altering their habits and methods of action much as men do. Bees taken to Australia cease to store honey after a few years' experience of the mild winters. Whole communities of bees sometimes take to theft, and live by plundering hives, first killing the queen to create dismay among the workers. Slave ants attend devotedly to their captors and fight against their own species. Forel reared an artificial ant-colony made up of five different and more or less hostile species. Why cannot a much more intelligent animal modify his habits far more rapidly and comprehensively without the aid of a factor which is clearly unnecessary in the case of the more intelligent of the social insects."

The explanation of this phenomenon will be probably some day found by paleontological discovery. We may suppose, on the basis of discoveries already made in other animals, that the primitive ants and termites presented homogeneous colonies, and that the varied structures which they present to-day have been primarily due to the usual process of specialization through use-inheritance. It is necessary to suppose that the varied functions of the different members of the community have modified the structures of the parts essential to their performance. It is probable that the earliest ants in an early geologic period became soldiers under the usual exigencies of their struggle for existence, and having thus secured a place in the economy of nature, certain members of the communities underwent degenerative changes, appropriate to their respective functions, of a less exacting character. In a second stage of evolution the community would present the character of a family of varied forms all of whose members would produce any or all of the types of form to be found in it, under slight diversities of conditions, just as now, all species produce young of two sexes. The differences between the members of an ant community are considerable in appearance, but not so great essentially as that between sexes.

Finally, in a third stage of the history, the functions of reproduction come to be the special office of a few members of the community. This may have been due to starvation, or to excessive labor on the part of certain individuals aborting the reproductive powers; but whatever may have been the cause, a majority of individuals became sterile. The reproducing members of the community, however, have continued to produce all the forms of the community.

They produce sterile workers and soldiers, sometimes of several forms, although themselves unlike most of their progeny. "This," says Mr. Ball, "is evidence that inheritance can have no share in the process." He believes that each one of the structural types of the community is produced by the treatment accorded to the young by the workers, *each generation for itself.*

As we have seen that the embryonic and paleontologic histories distinctly negative the idea that each generation has been produced by itself without inheritance, let us endeavor to read the riddle in the light of the knowledge we have gained from paleontology. I assume that the most specialized types, the soldiers, represent the type of the species in Mesozoic and possibly earlier time. They are already known from early Cenozoic formations (Scudder). The process of change into workers and breeders has been degenerative. I suppose, however, that in ants, as in the case of many other animals, slight differences in the supply of nutritive energy will prevent or produce these degenerative processes, as it appears to do in the case of the production of the sexes. (Experiments on lepidopterous larvæ have shown that excessive food supply produces females, and deficient supply produces males). In bees the larvæ of the female (queen) receives the largest food supply ; those of the males less ; and those of the neuters the least of all. How the food supply came to be varied so as to produce the several types in accordance with the exigencies of the community, is a question to be solved by future research. Perhaps it was due to variations in the supplies available at particular times of the year ; and perhaps the ants ultimately learned the secret, and now practice it intelligently. It is enough for my present purpose to have shown that the basis of the entire community, the most specialized form, the original fertile soldier, acquired his characters in the usual way, by use, and that all other forms have been derived from him by inheritance modified by disuse, or degeneracy, under the influence of variations in the food supply.

This reply to Mr. Ball's argument was made by me at a meeting of the Philadelphia Academy of Natural Sciences on May 23, 1893. In the latter part of the same year an almost identical answer was published by Herbert Spencer. My remarks were not published until the end of the year.

Mr. A. R. Wallace[1] presents the fact of change of character under external stimulus as evidence of the non-inheritance of acquired characters. Thus he cites the cases of change of species of Artemia, in consequence of increased salinity of water (antea, p. 229); and of the change of color of a Texan Saturnia, when its normal food-plant *Juglans nigra* was replaced by *J. regia*. Under the new conditions the old characters were not continued. In the same way the appearance of all new characters might be assumed to prove non-inheritance of the old ones. The obvious interpretation of these facts is the one generally given them; that is, they demonstrate the superior potency of certain new stimuli over the inherited type of growth-energy. They demonstrate that the energy of inheritance is not unchangeable in its type, which is the condition of the possibility of evolution. They do not demonstrate that acquired characters cannot be inherited.

Objections have been made to the supposition that the simian characters of the lower human races are due to inheritance because it has been shown that

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[1] *Nature*, 1893, p. 267.

some of them are due to mechanical causes acting after birth.

The demonstration of the mechanical origin of a given peculiarity, however, by no means precludes that such peculiarity may not be an inheritance from or reversion to pithecoid ancestors. It has been already pointed out that all of the form characters of the vertebrate skeleton, and for that matter, of the hard parts of all animals, have been produced by muscular pressures and contractions, and the friction, strains, and impacts, due to these. The demonstrations by Virchow and others that such is the origin of the platycnemic human tibia, is directly in the line of Neo-Lamarckian evolutionary doctrine, and shows us that atavistic and reversionary characters are found in the muscular system as well as in the skeleton. Such characters are inheritable as well as those of the skeleton. But the characters of the skeleton can generally be shown to be inherited, because they appear before birth, and are found at some stage or another of fœtal life. The later appearance of the muscular structures in the ontogeny, is simply a case of cænogeny, where the record has been falsified by retardation of the parts in question.

The variations in the characters of the human skeleton are of very various significance and value, and the zoölogist and paleontologist can perceive that they are sometimes misinterpreted by archeologists. Thus the presence of wormian (Inca) bones, and of a perforation of the olecranar fossa, have no zoölogical value; while the prognathous jaws, tritubercular molar, and platycnemic tibia have such a value. The tufted hair of the negro has a human value only, as it does not occur in any of the Quadrumana. But archeologists who are not zoölogists are not careful to point out these distinctions.

If the platycnemic tibia has been produced by muscular pressure in man, it has been probably so produced in the apes, where it is a universal character. If the early fusion of the sagittal suture is produced by the vigorous contractions of the temporal muscle as suggested by Brinton, in the black race, due to prognathous jaws, this is probably why it is a universal character of the apes, where the jaws are still more prognathous. What may be the cause of prognathism is not explained by archeologists, but has been discussed in my book on the *Origin of the Fittest*, and by Dr. C. S. Minot. That the prognathous jaws and platycnemic tibia are not found in the fœtus by no means proves that they are not inherited characters. Besides the fact already mentioned, that we are by this only thrown back on an inherited muscular structure, it is further to be remarked that characters which indicate the evanescence or degeneracy of parts, do not usually appear in the fœtus, but are disclosed at later stages. The prognathous jaws are disappearing from the higher races, and the process of disappearance is in this point accomplished by a retention of the fœtal face, which is excessively orthognathous. Prognathism is characteristic of most of the lower Mammalia, and whenever man displays it, if he be, as evolutionists believe, descended from some other mammal, he is simply continuing to develop the old character in the old manner. The same reasoning applies to the platycnemic tibia and the tritubercular molar.

As regards the lemurine character of the tritubercular molar, the term is a good one, as indicating the nearest of kin to man which present such molars. But this type can with equal propriety be called, as I have shown, the primitive placental molar. The lemur is the highest form next to man which displays it, but it was universal among the placentals at one geological epoch. It is possible that Topinard's suggestion as to the cause of its appearance in man is the correct one, as I made the same many years before, but that does not affect its value as an evidence of reversion, as in the cases already cited. There are various other ways in which molar teeth may degenerate, besides reversion to trituberculy, with which dentists are familiar, and which may be explained as Topinard and I have done ; i. e., by change of food ; but why the regular and normal mode should be trituberculy, and not one of those other modes, requires additional explanation. This explanation is that a regular or normal retrogressive modification of a structure is likely to be a return on the line by which it advanced. This is atavism or reversion.

That the anthropoids have been directly derived by descent from the false lemurs rather than from the Old World monkeys (Cercopithecidæ) is probable for various reasons which I have pointed out on page 157. I mention now that this view is somewhat confirmed by the recent discovery by Forsyth-Major, in Madagascar, in beds of Plistocene age, of a skull of a new genus of Lemuridæ with tritubercular molars, whose single species is nearly as large as a chimpanzee.

In closing these remarks, I call attention to the frequent muscular and occasional cerebral anomalies found in the negro, which are of simian character, and which indicate simian descent. An excellent synopsis of these has been given by Dr. Frank Baker in his address at Cleveland in 1888 as Vice-President of the

American Association for the Advancement of Science, and by Prof. H. F. Osborn in 1891 in the Cartwright lecture before the New York College of Physicians.

It is evident that evolutionists are reaching greater harmony of opinion on the question of inheritance. In fact, the discussion is sometimes a logomachy dependent on the significance which one attaches to the term "acquired characters." Thus Von Rath[1] remarks: "There is nothing in the way of the opinion that by the continued working of such external influences and stimuli the molecular structure of the germ-plasma also experiences a change which can lead to a transmission of transformations. Above all, it ought not to be forgotten in this case that the somatic cells are in no way the first to be modified by the stimulus, and that then by some sort of unexplained process (pangenesis or intracellular pangenesis), this stimulus is transmitted gradually by these cells to the plasma of the germ-cells. The influence on the germplasm is rather a direct one, and if by continued influence a transformation of the structure of this plasm takes place and transmission occurs, we have then simply a transmission of blastogenic, and by no means of somatogenic characters, and therein is not the slightest admission of the transmission of acquired characters."

This paragraph contains an admission of the doctrine of diplogenesis, and does not regard the phenomena as including a transmission of acquired characters. Nevertheless the stimuli traverse the soma in order to reach the germ-plasma. Such an energy is evidently then not of blastogenic origin, although it is

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[1] *Berichte der naturforschenden Gesellschaft zu Freiburg in Baden*, Bd.VI., Heft 3.

such in its effects. Moreover, Von Rath omits to mention the fact that in traversing the soma, the stimulus, frequently, if not always, produces effects on the latter similar to those which it produces on the germ-plasma. I should call this process the inheritance of an acquired character, even in the case where no corresponding modification appears in the soma, since the causative energy is acquired by the soma and is not derived from the existing germ-plasma.

Romanes[1] says, in reviewing the opinions of Weismann: "(1) Germ-plasm ceases to be continuous in the sense of having borne a perpetual record of congenital variations from the first origin of sexual propagation. (2) On the contrary, *as all such variations have been originated by the direct action of external conditions* [italics mine], the continuity of the germ-plasm in this sense has been interrupted at the commencement of every inherited change during the phylogeny of all plants and animals, unicellular as well as multicellular. (3) But germ-plasm remains continuous in the restricted though highly important sense of being the sole repository of hereditary characters of each successive generation, so that acquired characters can never have been transmitted to progeny 'representatively,' even though they have frequently caused those 'specialized' changes in the structure of germ-plasm, which as we have seen, must certainly have been of considerable importance in the history of organic evolution."

Here the inheritance of characters acquired by the soma is admitted, and the process is after the method of diplogenesis. According to Romanes, Galton origin-

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[1] *An Examination of Weismannism*, Chicago, 1893, p. 169.

ally propounded this doctrine. Galton's language[1] is as follows:

"It is said that the structure of an animal changes when he is placed under changed conditions; that his offspring inherit some of his change; and that they vary still further on their own account, in the same direction, and so on through successive generations until a notable change in the congenital characteristics of the race has been effected. Hence, it is concluded that a change in the personal structure has reacted on the sexual elements. For my part, I object to so general a conclusion, for the following reasons. It is universally admitted that the primary agents in the processes of growth, nutrition, and reproduction, are the same, and that a true theory of heredity must so regard them. In other words, they are all due to the development of some germinal matter, variously located. Consequently, when similar germinal matter is everywhere affected by the same conditions, we should expect that it would be everywhere affected in the same way. The particular kind of germ whence the hair sprang, that was induced to throw out a new variety in the cells nearest to the surface of the body under certain changed conditions of climate and food, might be expected to throw out a similar variety in the sexual elements at the same time. The changes in the germs would everywhere be collateral, although the movements where any of the changed germs happen to receive their development might be different."

This is the first statement of the doctrine of diplogenesis with which I have met, and it appears to furnish the most rational basis for the investigation into the dynamics of the process.

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[1] *Contemporary Review*, 1875, pp. 343-344; *Proc. Royal Society*, 1872, No. 136.

CHAPTER IX.—THE ENERGY OF EVOLUTION.

IF we view the phenomena of organic life from the standpoint of the physicist, the first question that naturally arises in the mind is as to the kind of energy of which it is an exhibition. Ordinary observation shows that organic bodies perform molar movements, and that many of them give out heat. A smaller number exhibit emanations of light and electricity. Very little consideration is sufficient to show that they include among their functions chemical reactions, a conviction which is abundantly sustained by researches into the physiology of both animals and plants. The phenomena of growth are also evidently exhibitions of energy. The term energy is used to express the motion of matter, and the building of an embryo to maturity is evidently accomplished by the movement of matter in certain definite directions. The energy which accomplishes this feat is, however, none of those which characterize inorganic matter, some of which have just been mentioned, but, judging from its phenomena, is of a widely different character. If we further take a broad view of the general process of progressive evolution, which is accomplished by successive modifications of this growth-energy, we see further reason for distinguishing it widely from the inorganic energies.

In considering the dynamics of organic evolution, it will be convenient to commence by considering the claims of natural selection to include the energy which underlies the process. That natural selection cannot be the cause of the origin of new characters, or variation, was asserted by Darwin;[1] and this opinion is supported by the following weighty considerations:

1. A selection cannot be the cause of those alternatives from which it selects. The alternatives must be presented before the selection can commence.

2. Since the number of variations possible to organisms is very great, the probability of the admirably adaptive structures which characterize the latter having arisen by chance, is extremely small.

3. In order that a variation of structure shall survive, it is necessary that it shall appear simultaneously in two individuals of opposite sex. But if the chance of its appearing in one individual is very small, the chance of its appearing in two individuals is very much smaller. But even this concurrence of chances would not be sufficient to secure its survival, since it would be immediately bred out by the immensely preponderant number of individuals which should not possess the variation.

4. Finally, the characters which define the organic types, so far as they are disclosed by paleontology, have commenced as minute buds or rudiments, of no value whatever in the struggle for existence. Natural selection can only effect the survival of characters when they have attained some functional value.

In order to secure the survival of a new character, that is, of a new type of organism, it is necessary that

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[1] *Origin of Species*, Ed. 1872, p. 65.

the variation should appear in a large number of individuals coincidentally and successively. It is exceedingly probable that that is what has occurred in past geologic ages. We are thus led to look for a cause which affects equally many individuals at the same time, and continuously. Such causes are found in the changing physical conditions that have succeeded each other in the past history of our planet, and the changes of organic function necessarily produced thereby.

1. ANAGENESIS.

It is customary to distinguish broadly between inorganic and organic energies, as those which are displayed by non-living and living bodies. This classification is inexact, since, as already remarked, nearly all of the inorganic energies are exhibited by living beings. A division which appears to be, with our present knowledge, much more fundamental, is into the energies which tend away from, and those which tend toward, the phenomena of life. In other words, those which are not necessarily phenomena of life, and those which are necessarily such. And the phenomena of life here referred to are the phenomena of growth and evolution, as distinguished from all others. I have termed[1] these classes the Anagenetic, which are exclusively vital, and the Catagenetic, which are physical and chemical. The anagenetic class tends to upward progress in the organic sense; that is, toward the increasing control of its environment by the organism, and toward the progressive development of consciousness and mind. The catagenetic energies tend to the creation of a stable equilibrium of matter, in

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[1] *The Monist*, Chicago, 1893, p. 630.

which molar motion is not produced from within, and sensation is impossible. In popular language the one class of energies tends to life; the other to death.

Herbert Spencer has defined evolution as a process of "integration of matter and dissipation of motion";[1] "the absorption of motion and the diffusion of matter" he terms dissolution. If by evolution Mr. Spencer referred only to that of inorganic bodies and masses, his definition must be accepted; but the evolution of organic bodies, since it has proceeded in a direction the opposite of the inorganic, cannot be so characterized. Organic evolution has passed beyond the domain of the inorganic, and the terms applicable to the latter process cannot be correctly applied to the former. In organic anagenesis there is absorption of energy; dissipation of energy is only known in the functioning of organic structures, which is catagenetic; not in their progressive evolution, which is anagenetic.

Huxley, in a lecture delivered in 1854,[2] remarks: "Tendency to equilibrium of force and permanency of form then are the characters of that portion of the universe which does not live, the domain of the chemist and the physicist. Tendency to disturb existing equilibriums, to take on forms which succeed one another in definite cycles, is the character of the living world." In the letter to Professor Tyndall, prefatory to the volume *Lay Sermons and Addresses*, in which this essay appeared, Huxley says: "The oldest essay of the whole, that on 'The Educational Value of the Natural History Sciences,' contains a view of the differences between living and not-living bodies, which I have long since outgrown." Whatever might have

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[1] *First Principles*, ed. II., 1873, p. 542.

[2] *Lay Sermons and Addresses*, 1880, p. 75.

been the cause of this change of opinion in Huxley's mind, the cause which has produced a similar change in the minds of many men, has been the discovery of means of producing in the laboratory numerous organic compounds, which, it had been previously supposed, could not be produced excepting through the action of living things, vegetable and animal. But it has been shown that all of these substances are the result of the running down of protoplasm, and are, hence, catagenetic, and not anagenetic.

That the catagenetic energies, whether physical or chemical, tend away from life is clear enough. Thus molar motion, unless continuously supplied, or directed by a living source, speedily ceases, being converted by friction into heat, which is dissipated. The same is true of molecular movements, under the same conditions. Chemical reactions, which are fundamental in world-building, result in the production of solids and the radiation of heat. This is the general result, although in the process, as it occurs in nature, irregularities occur, owing to local and temporary elevation of temperature. This arises from the decomposition of organic substances, which liberates heat; the oxydization of carbon, which owes its position as a terrestrial element to vegetable and animal organisms; and the access of heat from the interior of the earth, or from the sun's rays. Finally cosmic creation involves the perpetual radiation of heat into space, and the gradual reduction of all forms of matter to the solid state.

The endothermic chemical reaction, where inorganic matter undergoes a change of molecular aggregation the reverse of that just mentioned, with the absorption of heat, as in the case of several nitrogen compounds, is rare in nature, where free from organic complications, and is necessarily soon reversed by further reactions.

In the anagenetic energies, on the other hand, we have a process of building machines, which not only resist the action of catagenesis, but which press the catagenetic energies into their service. In the assimilation of inorganic substances they elevate them into higher, that is more complex compounds, and raise the types of energy to their own level. In the development of molar movements they enable their organisms to escape many of the destructive effects of catagenetic energy, by enabling them to change their environment; and this is especially true in so far as sensation or consciousness is present to them. The anagenetic energy transforms the face of nature by its power of assimilating and recompounding inorganic matter, and by its capacity for multiplying its individuals. In spite of the mechanical destructibility of its physical basis (protoplasm), and the ease with which its mechanisms are destroyed, it successfully resists, controls, and remodels the catagenetic energies for its purposes.

The anagenetic power of assimilation of the inorganic substances is chiefly seen in the vegetable kingdom. Atmospheric air, water, and inorganic salts furnish it with the materials of its physical basis. Then from its own protoplasm it elaborates by a catagenetic retrograde metamorphosis, the non-nitrogenous substances, as wood (cellulose), waxes, and oils, and the nitrogenous alkaloids, and it may take up inorganic substances and deposit them without alteration in its cells. Many of the compounds elaborated by plants and animals have been manufactured of latter time by chemists. The discovery that the living organism is not necessary for the production of these substances has led to the hasty conclusion that the supposed distinction between "organic" and "inorganic" energy does not exist. But the elaboration of these substances is not accomplished by anagenetic or "vital" energy, but by a process of running down of the higher compound protoplasm, which is catagenesis. No truly anagenetic process has yet been imitated by man.

All forms of functioning of organs, except assimilation, reproduction, and growth, are catagenetic. That is, functioning consists in the retrograde metamorphosis of a nitrogenous organic substance or proteid with the setting free of energy. The proteid is decomposed in the functioning tissue into carbon dioxide, water, urea, etc., and energy appears in the muscle as contraction, in the glands as secretion, and in all parts of the body as heat. The general result of physiologic research is, that the decomposition of the blood is the source of energy, while the tissue of each organ determines the character of that energy. That the tissue itself suffers from wear, and requires repair, is also true, but to a less extent than was once supposed.

In the anagenetic process of the growth of the embryo the case is different. Here the processes of functioning of organs are in complete abeyance, the plasma of the oösperm is not sensibly broken down in chemical decomposition, but it is in great part elaborated into tissues and organs. All the mechanisms necessary to the mature life of the individual are constructed by the activity of the special form of energy known as growth-energy or Bathmism. It is the modifications of this energy which constitute evolution, and it is these to which we will hereafter direct our attention. Its simplest exhibition is the subdivision of a unicellular protoplasmic body into two or more individuals or structural units of a multicellular organism. Further division of the latter does not abolish the individual, but extends it, and we now observe the elaboration of different structural types to become the conspicuous function of this form of energy. In other words, a once simple energy becomes specialized into specific energies, each of which, once established, pursues its mode of motion in opposition to all other modes not more potent than itself. Besides the evident truth of the proposition that a mode of building is a mode of motion, we have another very good reason for believing in the existence of a class of bathmic or growth-energies. This is found in the phenomena of heredity. The most rational conception of this inheritance of structural characters is the transmission of a mode of motion from the soma to the germ-cells. This is a far more conceivable method than that of the transmission of particles of matter, other than the ordinary material of nutrition. The bathmic theory of heredity bears about the same relation to a theory of transmission of the pangenes of Darwin, or the ids of Weismann, as the undulatory theory of light and other forms of radiant energy does to the molecular theory of Newton. I have therefore assumed as a working hypothesis the existence of the bathmic energy, and have inquired how far the facts in our possession sustain it. In doing so it has been necessary to elaborate the theory so as to render clearer its application to specific cases. The fact to be accounted for is its specialization into so many diverse specific forms.

A further indication of the existence of the bathmic energy is the quantitative limitation to which growth is obedient. Thus the successive stages of embryonic growth are limited in number in each species. The dimensions of most species are limited within a definite range. The duration of life, or of the functioning organic machine, has a definite limit in time. All this means that a certain limited quantity of energy is at the disposal of each individual organism.

In the preceding pages I have endeavored to show what causes have been and are efficient in the production of different types of organic life, through the modifications of the bathmic energy. We will now briefly consider the question of the origin of the living substance, protoplasm or sarcode, which exhibits bathmism.

On this subject Professor Manly Miles remarks:[1] "Omitting subordinate details, which represent the separate links in the chain of events, the processes of nutrition may be summarized in general terms as follows: In plants the chemical elements and binary compound on which they feed, are built up by successive steps of increasing complexity and instability into protoplasm, with a storing of the energy made use of in the constructive process, which is derived from the heat and light of the sun. The constructive processes are expressed by the term anabolism, and the products of the different upward steps are called anastatic. Protoplasm, the most complex and unstable of organic substances, is the summit of the ascending steps of anabolism; and katabolism, which represents the succeeding downward steps of metabolism, then follows, and its products or katastates are starch, cellulose, proteids, etc., or what we recognize as the proximate

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[1] *Proceeds. Amer Assoc. Adv. Sci.*, 1892, p. 203.

constituents and tissues of plants." I interject here the remark, that from a chemical point of view, protoplasm is, under certain conditions, not unstable.

If the tendency of the catagenetic energies is away from vital phenomena, it is impossible that they, or any of them, should be the cause of the origin of living matter. This logical inference is confirmed by the failure of all attempts to demonstrate spontaneous generation of living organisms from inorganic matter. Further, the principle of continuity leads us to infer that the energy which produced organic matter must be identical with or allied to that which is the efficient agent in progressive evolution of organisms, and is, therefore, anagenetic. Such a conclusion may seem to lead to a dualism which is itself opposed to the principle of continuity or uniformity, and which is opposed to experience of the phenomena of energy in general. How is uniformity to be harmonized with the hypothesis of two types of energy acting in different directions, apparently in opposition to each other? Since facts and logic do not support the derivation of the anagenetic from the inorganic energies, can the reverse process, the derivation of the catagenetic from the anagenetic be and have been the order of nature? In support of this hypothesis, we have the universal prevalence of the retrograde metamorphosis of energy in both the inorganic and organic kingdoms. Phenomena of structural degeneracy are well known in the organic world, and purely chemical phenomena in both organic and inorganic processes are all degenerate. It appears, then, much more probable that catagenesis succeeds anagenesis as a consequence, and does not precede it as a cause. In other words, it is more probable that death is a consequence of life, rather than that the living is a product of the non-living. I have therefore given to that energy which is displayed by the plant in the elaboration of living from non-living matter the name of antichemism.[1] Thus, while the heat of the sun is necessary to the building of protoplasm, within a certain range of temperature this form of energy has its opportunity.

The actual demonstration of this hypothesis can only come from researches into the thermochemistry of proteids and protoplasm. As these substances have not been made in the laboratory, these researches are not yet possible. We may, however, consider the problem as follows. In the process of making protoplasm, three gases, oxygen, hydrogen, and nitrogen are converted into a semisolid. In this case heat should be dissipated, to an amount reduced by the molecular dissolution of carbon. This is however not the case, for heat is absorbed with an integration of atomic bonds. In other words, it would seem that the manufacture of protoplasm by plants is an endothermic process. This view is strengthened by the discovery by Berthollet[2] that the production of numerous solid organic substances, in which organic bases are used, is also endothermic. These facts confirm the inference above recited, that the phenomena of organic growth involve the absorption of energy and not its dissipation.

Referring to the composition of protoplasm *C O H N*, I have called attention to the fact that each of its elements represents one of the great divisions defined

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[1] *American Naturalist*, 1884, p. 979; *Origin of the Fittest*, 1887, p, 431.

[2] *Annales de Chimie et de Physique*, VI, 1895, p. 232.

by their valency, into which the ultimate substances of nature naturally fall. This combination I have suggested might account for the chemical inertness of protoplasm, through the mutual inhibition which each of these elements might be supposed to exercise over the other, owing to the diversity of their modes of chemical action.

In order to present more clearly the views enunciated in the preceding pages, I give a synoptic table of energies.

I. Anagenetic	Organic	Antichemism Bathmism
II. Catagenetic	Exclusively organic	Neurism Myism
	Inorganic and organic	Radiant Energy Chemism Cohesion Gravitation

2. BATHMOGENESIS.

The innumerable structures which are due to the activity of bathmisms may be supposed to result from the composition of the inherited form with energies which are derived from sources external to the germplasma, whether within the soma or external to it. These interferences produce new and specific types of energy. The inherited bathmism I have termed "simple growth force," and the modified forms I have termed "grade growth force."[1] It appears that these types of energy should be distinguished by special names. Hence I have proposed to restrict the term bathmism

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[1] *Proceedings American Philosophical Society*, 1871, p. 253.

to the modified or "grade" growth force, and to term the inherited or "simple" type of growth force, emphytism.[1] As a matter of fact, pure emphytism can only be observed in the embryos of sexless or parthenogenetic origin, and in the repair of tissues.

Ryder has called the exhibition of growth-energy ergogenesis, and he calls attention to the fact that it appears under two aspects. In the first, ergogenesis is due to mechanical causes resident in the organism exclusively, and consists of the physical tensions inherent in protoplasm under all the conditions of growth. With these the growth-energies have to reckon, as they are the conditions which underlie them. They are not, however, strictly speaking, growth-energies, but would be exhibited by any similar colloid under similar conditions. To the movements due to physical causes under these circumstances, Ryder gives the name of Statogenesis.[2] The second aspect of the energies necessary to growth is present under the two forms already referred to, as emphytism and bathmism. The latter class, or interference energies, are naturally differentiated into those which are due to physical (or chemical) external agencies (molecular movements), and those that are due to molar movements as expressed in tissues, as impact, strain, etc. To the former I have given the name of physiobathmism, to the latter, kinetobathmism.[3]

The relations of these forms of energy may be represented in tabular form as follows:

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[1] I have supposed in a late paper (*American Naturalist*, 1894, p. 212) that this is the statogenic energy of Ryder. This mistake has been corrected.

[2] *Proceedings American Philosophical Society*, 1893, p. 194.

[3] *American Naturalist*, 1894, p. 214. The two types of growth are then physiogenesis and kinetogenesis. (*Origin of the Fittest*, 1887, p. 423.)

Ergogenesis
Catagenetic *Statogenesis*
Anagenetic
- Inherited *Emphytogenesis*
- With interference *Bathmogenesis*
  - Molecular *Physiogenesis*
  - Molar *Kinetogenesis*

Emphytogenesis I shall hereafter endeavor to show is an automatic (catagenetic) product of bathmogenesis, and a stationary factor in evolution.

The above table is designed to be a classification and formulation of the innumerable well-known facts of organic growth and evolution. It does not pretend to be an explanation of the processes involved, but it is the first step to be taken in attempting the explanation, i. e. a discrimination and classification of its factors.

Ryder thus expressed the relation between statogenesis and kinetogenesis.[1]

"So universal is this interference of the statical conditions of the plasma of segmenting ova with the ontogenetic processes, that not a single metazoan organism can be named, the development of which is not thus marred in some way or other. It is often a long time relatively after development has begun that there is any obvious delineation of the embryo. In fact, this cannot take place until the statical energies of surface-tension which have kept the egg globular are overridden. In so far as the ontogeny of any organism is marred by statical conditions of energy-display, its embryonic form is also modified. In so far as such statical interference affects the figure of the organism they are morphogenetic or form-determining. In so far the figure of a developing being is disturbed or

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[1] *Proceeds. Amer. Philos. Society*, 1893, pp. 197–201.

modified by statical agencies its figure may be said to be subject to statogenetic influences. No existing larval form has escaped the influence upon its own shape of a constantly active statical equilibrium of its own substance. There is, therefore, a constant struggle going on during development between the phylogenetic and ontogenetic forces, determining the sequence and relations of the successive cleavages of the egg and the statical equilibria that obtain amongst its several parts. Statogenetic processes are, therefore, as constant and universal as the phylogenetic and ontogenetic. One may even go so far as to say that possibly the relations thus tending to be established by statical conditions may tend to become transmissible as hereditary tendencies. Such indeed is the view upheld by Prof. E. B. Wilson in his remarkable paper on 'The Cell-Lineage of Nereis.' I have myself seen no less than three consecutive recurrences of the same statical conditions in a fish egg, none of which can, for this reason, be definitely proved to be purely ontogenetic.

"While such phenomena as those of the genesis of the heterocercal or upwardly deflected condition of the axis in the tails of fishes, or the downwardly deflected condition of the axis in Ichthyosauri are almost purely kinetogenetic, the multiplicity of factors concerned, statogenetic as well as ontogenetic and phylogenetic, must always be considered and each given its due weight and importance in achieving the morphogenetic result. That there is an absolute conflict between statogeny and kinetogeny on the one hand, and of phylogeny and ontogeny on the other, in the case of the development of the ova of multicellular forms admits of no doubt. All metazoa pass through larval stages in which the statical conditions of equilibrium of the plasma of the egg is gradually, in a great measure, overriden by the hereditary energies represented by phylogeny and ontogeny. That there still remain traces of the effects of kinetogeny and statogeny in the adult organism cannot be denied in view of the facts to be derived from the shapes of tissue elements, and even of organs, as the foregoing paragraphs show."

The first appearance of bathmogenetic action is the first modification of the statogenetic and emphytogenetic energies from whatever source. Changes may be effected in the weight, color, and in functional capacity by temperature, humidity, food, etc., thus exhibiting physiogenesis. Or changes in the size and forms of parts of the body may be produced by movements of the organism, or of its environment, so displaying kinetogenesis. So long as these modifications of structure should be confined to the individuals thus modified, there would be no evolution. A second generation, if not subjected to the same stimuli, would not possess the modifications; and their possession of them would depend entirely on the amount of stimulus. In other words, there would be no accumulation of modification. It has, however, been generally believed that these modifications are inherited, and I think it has been shown that this belief rests on a solid basis. Meanwhile I have called the bathmogenesis which does not extend beyond the generation in which it appears, autobathmogeny.

The quantitative relation which necessarily exists between bathmism and its sources may be expressed as follows, with due recognition of the fact that such expression does not rest upon any experimental tests. Emphytogenesis is work done in the construction of tissues like those of the parent and without interference. Here we have the molecular energy of the parent converted into the molar movements observed to be concomitants of segmentation ; to be represented in the completed tissue by the mutual tensions by virtue of which each structural element maintains its integrity. It is evidently a process of metamorphosis of energy in which there is less waste than in any other known to us. Embryonic growth is accompanied by a very slight dissipation of heat, since a slight rise of temperature is noticeable in the eggs of cold-blooded animals and in flowers, when reproduction is active. The products of breaking down are equally rare in embryonic growth, and both this and the dissipation of heat are perhaps largely due to the changes wrought in non-cleavable nutritive substances with which the yolks are sometimes charged. It is probably to accomplish this process that the oxygen necessary for the embryonic growth is used. How much loss is due to cell-division itself is not known, but it must be very little if any. We have probably here a nearly perfect conversion of energy. Theoretically we have anagenesis wherever the up-building exceeds the downbreaking.

The attempt to realize in the imagination the *modus operandi* of bathmic energy in embryo-building takes the following form. It is to be supposed that movement which has been most frequently repeated, and for the longest period, is prepotent, and takes precedence of all others. This is clearly simple cell-division, which follows the nutrition supplied by the spermatozoön, and which represents the first act of animal life. Hence, segmentation of the oösperm is the first movement of bathmism. Each subsequent movement appears in the order of potency, which is, other things being equal, a time order, or the order of record. The cause of the localization of tissues and structures is much more difficult to understand than the cause of the order of their appearance. The more energetic part of the process naturally requires the greater space for its products. The ectoderm, which becomes the seat of the nervous axis and its muscular adjuncts, occupies the superficial portions of the yolk. Hence, we may regard this expression of the structural record of these functions as more energetic than that of the record-structure of the nutritive functions, which displays itself below the ectoderm. In meroblastic and amphiblastic embryos, the segmentation which develops the nutritive tissues is evidently more sluggish, for the cells are larger and fewer in number than those of the ectoderm.

In evolution external stimuli modify the course of emphytogeny above described, and by producing new structural records, cause a new form of energy, due to composition of the new with the old, and the process of growth then becomes bathmogeny. The external stimuli are molecular or molar, determining physiobathmism or kinetobathmism.

The effect of motion or use on the soma may be conveniently termed autokinetogenesis. Moderate use of a muscle is known to increase its size. Irritation of the periosteum is known to cause deposit of bone. Friction and pressure of the epithelium increases its quantity or changes its form. Increased activity of the functions of nervous tissues increases their relative proportions, as in the enlargement of nerves which replace others which are interrupted by mutilations, etc.

On the other hand, it is equally well known that disuse produces diminution of muscular tissues, and through it, a reduction in the quantity of the harder tissue (bone, chitin, etc.) to which it is attached (as muscular insertions, etc.). It was the observation of such well-known phenomena as these that led Lamarck to advance his doctrine of evolution under use and disuse, and which has led many others to give their adherence to such a view.

Thus much for cell-growth. Another class of modifications of a similar kind may be found in the parts of an organism which consist of a complex of cells, or tissues. Thus the lumen of a small artery is enlarged under the influence of pressure when it is compelled to assume the function of a larger vessel through the interruption of the latter. A part of an internal or external skeleton which is fractured will form an artificial joint at the point of fracture, if the adjacent surfaces are kept in motion. Marey (*Animal Mechanism*, pp. 88–89) says, "After dislocations the old articular cavities will be filled up and disappear, while at the new point where the head of the bone is actually placed, a fresh articulation is formed, to which nothing will be wanting in the course of a few months, neither articular cartilages, synovial fluid, nor the ligaments to retain the bone in place." I have given some illustrations of this fact,[1] which have come under my observation, and which have an important bearing on the origin of the articulations of the vertebrate skeleton as I have traced them throughout geological time. I have, as I think, conclusively shown that these varied structures have been produced by impacts and strains,

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[1] Page 275 and *Proceeds. Amer. Philos. Soc.*, 1892, p. 285.

which are concomitants of the movements of the animals, acting through long periods of time.[1]

The term mnemogenesis is employed by Professor Hyatt[2] to characterize the manner in which kinetogenesis is supposed to produce results in inheritance. I have suggested that the phenomena of recapitulation, characteristic of ontogeny (*American Naturalist*, Dec., 1889), are due to the presence of a record in the germ cells, having a molecular basis similar to that of memory. This view is adopted by Professor Hyatt. I have already referred to it in the preceding pages.

A general statement of this doctrine was made by Mr. Sedgwick in *The British and Foreign Medico-Chirurgical Review* for July 1863 in the following language: "For atavism in disease appears to be but an instance of memory in reproduction, as imitation is expressed in direct descent; and in the same way that memory never, as it were, dies out, but in some state always exists, so the previous existence of some peculiarity in organization may likewise be regarded as never absolutely lost in succeeding generations, except by extinction of race." The next formulation of mnemogenesis is by Hering in 1870.[3]

It is concentrated in the following paragraph:

"The appearance of properties of the parental organism in the full-grown filial organism can be nothing else but the reproduction of such processes of organized matter as the germ when still in the germinal vesicles had taken part in; the filial organism remembers, so to speak, those processes, and as soon as

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[1] "Mechanical Origin of the Hard Parts of the Mammalia," *Amer. Journal of Morphology*, 1889. *Origin of the Fittest*, 1887, pp. 305-373.

[2] *Proceeds. Boston Soc. Nat. History*, 1893, p. 73.

[3] Address before the Imperial Academy of Sciences of Vienna, May 30, 1870, by Ewald Hering; English translation, Chicago, 1895.

an occasion of the same or similar irritations is offered, a reaction takes place as formerly in the parental organism, of which it was then a part and whose destinies influenced it." In explanation of this theory, Hering says: "We notice, further on, that the process of development of the germs which are destined to attain an independent existence, exercises a powerful reaction both on the conscious and unconscious life of the whole organism. And this is a hint that the organ of germination is in closer and more momentous relation to the other parts, especially to the nervous system, than any other organ. In an inverse ratio, the conscious destinies of the whole organism, it is most probable, find a stronger echo in the germinal vesicles than elsewhere."

If heredity is a form of memory, its laws may resemble those of the psychic memory. In the latter, everything depends on what we call the strength of the impression. A single impression is often easily forgotten, and the certainty of recollection is largely dependent on the frequency of repetition of the stimulus. This is the essence of mental education, and it is probably the law of education of the germ-plasma as well. Thus may be understood how stimuli endlessly repeated through long geologic ages, must produce results far more profound and lasting than sporadic impressions of modern and artificial origin.

It must be here remarked for the benefit of the reader who may be unfamiliar with the explanation of the psychic memory, that it is the conscious part of memory which gives it its psychic character. This side is due to a fundamental molecular arrangement caused by stimuli, which may be retained for long periods without expression in consciousness. Thus

Bain regards memory as consisting of an unconscious and a conscious stage, and the latter he terms reminiscence. Other psychologists in common with mankind generally, use the word memory for the conscious expression. I have termed the unconscious condition of the molecular basis of mind, cryptopnoÿ.

CHAPTER X.—THE FUNCTION OF CONSCIOUSNESS.

1. CONSCIOUSNESS AND AUTOMATISM.

CONSCIOUSNESS is a general term, which embraces all forms of self-knowledge. Sentiency is sometimes used with an identical meaning. Consciousness must be distinguished from self-consciousness, which implies introspection. Consciousness may or may not be characterised by attention. There are two widely different types of consciousness, viz., the presentative and the representative. The former includes sense-perception only; the latter includes all the combinations of sense-perception which characterize mental action, from simple memory to the most comprehensive classification and conception. Most, if not all, animals appear to possess sense-perception, and all such possess the representative faculty of memory; but the higher grades of representative mental function are not so general among animals, and the extent of their occurrence is yet in dispute.

In the preceding pages I have endeavored to show that the factors of evolution are bathmogenesis corrected by natural selection. Bathmogenesis embraces the two factors physiogenesis and kinetogenesis, or the products of molecular and molar motion, respectively.

These two forms of motion have been coëxtensive with the existence of life, neither one preceding the other in time. Statogenesis is the expression of a form of energy which characterizes inorganic matter, while bathmogenesis is entirely peculiar to living things. Kinetogenesis is the fundamental principle in organic evolution, since it determines the amount and kind of physiogenesis, because it creates the environment which furnishes the conditions of physiogenesis. Progressive organic evolution may, then, be described as due to kinetogenesis corrected by natural selection. At the basis, however, molar organic motion, i. e., contraction of protoplasm, is probably molecular, but it is distinguished from other forms of molecular motion in the vast aggregate of molecules which move simultaneously in one direction, as in an amœba or a muscle, thus effecting a change in the position of all or a part of an organism. Hence the distinction is a real one.

Molar motion being, then, of such fundamental importance as a factor in evolution, the cause of such motion is also a capital question. Contraction of protoplasm is caused by stimuli, such as currents of electricity and chemical reagents; but such stimuli are not those which ordinarily produce the contractions to which the molar movements of living animals are due. In those animals which possess a nervous system it has been shown that contractions only follow stimuli which are conveyed to the contractile elements by nervous threads, and the internal energy which represents the external stimulus, is called nervous energy or neurism. In animals without a nervous system, and in plants, external stimuli must be justly supposed to be converted into the same form of energy, which in such organisms has a general circulation throughout the contractile protoplasm. The important point about these movements in most animals is, that their direction directly subserves the attainment of some position which is favorable for the procurement of relief from some unpleasant sensation, or the acquisition of some agreeable one, or both. We have the best reasons for believing this to be true of the vast majority of animals, because their structure is fundamentally like our own, and the inference that the same is true of the lowest forms of life is justifiable until it is proven to be mistaken.

Lamarck has attributed the movements of animals to the necessity of satisfying their instincts, without entering into the metaphysical questions which this involves. I have regarded the question as a metaphysical one by asserting that the necessary preliminary to movement is "effort," referring to what are called "voluntary" as distinguished from automatic motions.[1]

Without special organs of movement, a great part of the phenomena of kinetogenesis would have no existence, precisely as natural selection cannot act unless the materials for selection (i. e. variations) are already in existence. In explanation of the origin of organs of movement we have the general ability of the primitive animal, or protozoön, to project portions of its body-substance as pseudopodia, which, in more specialized forms, become persistent and more or less rigid, as flagella, cilia, etc.; which are the first distinct organs which subserve the transportation of the body from place to place. The causes which lead to these changes are as yet obscure, but that the use of these

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[1] *Proceeds. Am. Philos. Soc.*, 1871, p. 18. *Origin of the Fittest*, 1887, p. 194.

organs when once called into existence is due to stimuli similar to those which affect the motions of the limbs of the higher animals, is altogether probable. Whatever be its nature, the preliminary to any animal movement which is not automatic, is an effort. And as no adaptive movement is automatic the first time it is performed, we may regard effort as the immediate source of all movement. Now, effort is a conscious state, and is a sense of resistance to be overcome. When an act is performed without effort, resistance has been overcome, and the mechanism necessary for the performance of the act has been completed. The stage of automatism has been reached. At the inception of a new movement resistance is necessarily experienced. It is generally believed that a mental state, as a sensation or a desire, which may or may not stimulate a rational process as an intervening element in the circuit, is concerned in overcoming this resistance.

A different view is held by certain physiologists and metaphysicians, as e. g. Wundt and Höffding. Huxley thus states his opinion in his Belfast address of 1874,[1] *à propos* of Descartes's doctrine that all animals below man are automata. "The consciousness of brutes would appear to be related to the mechanism of their body simply as a collateral product of its working, and to be as completely without any power of modifying that working as the steam-whistle which accompanies the work of a locomotive-engine is without influence on its machinery. *Their volition, if they have any, is an emotion indicative of physical changes, not a cause of such changes.*" (Italics mine.) In other words, stimulus excites conscious states, but the state thus produced has no influence on the resulting act.

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[1] *Scientific Culture and Other Essays*, p. 243.

That sense-perceptions are stimuli to the immediate appearance of structural changes or movements is admitted. This is shown by the production of color changes in animals through changes in the condition of the organs of sight. Pouchet showed that the extirpation of both eyes of the turbot, and of a Gobius, paralyzed the chromatophorous cells, so that the usual color-adaptations to the color of the surface of the bottom on which they rested, could not be made. He also produced the same effect on one side of a trout by removing the eye of the opposite side. The chromatophoræ were permanently expanded, and the colors dark.

Some experiments which I tried with tree frogs of the species *Hyla gratiosa*, and *Hyla carolinensis*, are as follows : The color is usually green in both species, but it changes to dark brown where the frog rests on a brown surface, as of bark, etc. It appears that the maintenance of the brown color requires a more vigorous nervous stimulus than the green. The frogs are green at death ; and limbs which I ligated remained green when the remainder of the surface became brown. Now in individuals with extirpated eyes, the color was always green, no matter what the surface on which they rested. The power of assuming the brown color was lost.

In these experiments it is difficult to connect the expansion of the chromatophorous cells as any effect of consciousness of color, by direct proof. If, however, muscular cells can be contracted under the influence of mental states, a similar mechanism may be supposed to exist in the case of chromatophoræ. The fact that the process may be now reflex does not exclude the other fact of the influence of consciousness at the inception, and its necessity for the continuance of the habit.

If we examine muscular movements, the evidence of control by consciousness becomes more distinct. New conditions bring forth new acts in animals too frequently to permit us to believe otherwise. Thus Mr. Belt tells of a procession of ants which crossed a railroad in Panama. Many were killed on the rail, so the column excavated a passage beneath the rail, and thus escaped further injury. No one can reasonably deny the intervention of a conscious state of a high order, as directly controlling the muscular movements of those ants. According to Beauchamp, termites in the same region display similar intelligence. A number of them were confined in a deep glass vessel with smooth sides which they could not scale. They thereupon deposited drops of their building secretion, which hardens on drying, on the glass, ascending backwards, and so made a stair out of their prison, by which they escaped.

A *Cebus capucinus* in my possession imitated some carpenters who were working in the room with a drawing-knife. He used a triangular piece of tin, and, holding the corners, drew the edge towards him over the surface of a piece of squared wood on which he sat. He did this rapidly and repeatedly, with many grimaces. A *Cebus apella* in the Philadelphia Zoölogical Garden lights matches whenever he can get them. He always selects the proper end, and holds it at a proper distance, so that the stick is not broken and his fingers are not burned. He strikes them on the rough outside of his drinking-kettle. My *Cebus* came direct from the forests of Venezuela, and he had not been educated among carpenters. The history of the *apella*

I do not know, but he had not probably been brought up among matches, and his act was in any case not reflex.

As an illustration of the simplest of movements, and their physical conditions, I cite those of the Myxomycetes, from Stahl.[1]

"The movement of Myxomycetes is influenced by:

"1. Moisture (Hydrotropism): In their young stages they wander from the parts of the substratum (i. e. of the deposit on which they are creeping), which are gradually drying up, toward those which continue moist longer; 'it is even possible, by bringing moist bodies into the proximity of any ramifications, to cause the production of pseudopodia, which elevate themselves from the substratum, and soon come into contact with the moist object, so as to enable the whole mass of the plasmodium to migrate on to it.' On the entrance of the plasmodia into the fructifying condition, positive hydrotropism gives place to negative; the myxomycete quits the moist substratum and creeps upwards on to the surface of dry objects.

"2. Unequal distribution of warmth in the substratum, and

"3. Unequal supplies of oxygen also cause locomotion in the myxomycete.

"4. Chemical substances soluble in water have a similar action. Contact of the plasmodia on one side with solutions of common salt, saltpetre, or carbonate of potash, cause them to withdraw from the dangerous spot, while infusion of tan, or a dilute solution of sugar, produces a flow of the protoplasm and ulti-

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[1] E. Stahl, "Zur Biologie der Myxomyceten," *Botan. Zeitung*, 1884, No. 10–12. Abstract in *Sitzungsbericht der Jenaischen Gesellschaft für Medizin und Naturwissenschaft*, 1883, Sitzung vom 16. November.

mately translocation of the whole plasmodial mass towards the source of nourishment. Some solutions have an attractive or repulsive effect, according to their degree af concentration.

"5. Finally, they withdraw from light (negative heliotropism).

"With regard to the acceleration or definite direction of movement produced entirely by stimuli, compare the following:

"The knowledge of the remarkably delicate reaction of the plasmodia under external influences enables us to comprehend how these tender structures, destitute of every kind of external protection, are able to carry on their existence. The plasmodia which are not yet ripe for reproduction are kept in the moist substratum by positive hydrotropism, which is assisted by negative heliotropism.

"But within the darkness and moisture of the substratum the plasmodia by no means remain in one place, because the differences in the chemical composition of the substratum cause continual migrations. The plasmodia have the faculty in a wonderful way of avoiding harmful substances, and, traversing their substratum in all directions, of taking up the materials they require.

"When the internal changes have proceeded so far that the plasmodia approach the fructifying condition, they are brought by the negative hydrotropism which now sets in, from the moist parts of the ground in the forest or wood to the surface, where they creep up various upright objects, often only forming rigid reproductive capsules at some height from the ground.

"When in autumn the substratum becomes gradually colder a change which takes place from the surface downwards, the plasmodia migrate into deeper regions still having a higher temperature. When the cooling proceeds very gradually, which especially happens in large tan-heaps, the plasmodia may, in their migration reach somewhat considerable depths, where they then change into sclerotia. To find the sclerotia of Æthalium in winter it is, therefore, not seldom necessary to search through the mass of tan to a depth of several feet. When the temperature again begins to rise, the sclerotia again germinate, and movement in the opposite direction takes place from the deeper and cooler parts to the upper portions already warmed.

"In the locomotion of the Myxomycetes, then, we see extremely interesting cases of movements due to stimulation. Heliotropism, geotropism, hydrotropism, trophotropism, in general, are stimulus-movements, and ultimately all growth depends on stimulus-movement. It is the most primitive kind of protoplasmic movement. Stimuli in fixed directions and constantly repeated, produced, but only secondarily, fixed paths of conduction, and responses of a quite definite kind (reflexes). Thus arose nerves, and finally apparatus for stirring up stimuli, arose sensation and will—as acquired and inherited faculties."

In this lowest type of organic movement it is difficult to discern any cause for it different from those which actuate higher organisms. What form of inorganic energy can be cited as sufficient to cause the organism to change its position with regard to stimuli to self-preservation, and without regard to gravitation, or any known form of attraction or repulsion? In the Fuligo (tan flowers) a most pronounced example of designed movement has been observed. This form, in the amœbula stage, will, according to H. J. Carter, "confine itself to the water of the watch-glass in which it may be placed, when away from the sawdust and chips of wood among which it has been living; but if the watch-glass be placed upon the sawdust it will very soon make its way over the side of the watch-glass and get to it." This act probably depends on a sense-perception of the presence and position of the tan-bark, and of a feeling of desire to reach it. This may have been due to a sense of discomfort due to the surrounding water, or to a recollection of superior comfort associated with the tan-bark.

Ordinary observation of most animals leads to the belief that their movements are provoked by sensations, as of hunger, thirst, temperature, etc.; also of sight, hearing, smell, etc., when they possess those senses. There are physiologists who deny that such is the case, but I must insist on the importance of a psychological rather than a physiological study of animals as a most important source of information in this direction. The students of dead or mutilated animals miss important evidence as to the phenomena of consciousness. The attempt has been made to identify hunger, for instance, with chemical energy, a proposition which is simply irrational. It may be none the less true, however, that hunger is a necessary concomitant of a molecular condition. Observation on living animals shows in the most conclusive manner that by far the greater number of species are capable of the performance of acts in response to new situations and circumstances for the performance of which no automatic mechanism exists. Memory is clearly present in them, and, as a consequence, judgments are formed which determine the succeeding acts. The process, be it ever so simple, is "representative," and thus a mental act, at least one stage beyond sense-impression. The doctrine that conscious states have preceded organisms in time and evolution I have called archæsthetism. It seems to have been first clearly formulated by Erasmus Darwin, who believed that growth has been stimulated by "irritations" (of hunger, thirst, etc.) and by the pleasurable sensations attending those irritations, and by exertions in consequence of painful sensations, similar to those of hunger and suffocation,"[1] etc.

The weakness of the doctrine of archæsthetism consists in our ignorance of the characters of the Protozoa, with respect to the presence or absence of consciousness or sensation. While many of the acts of these low organisms need not be explained by supposing its presence, others seem to be impossible without it. We are, however, led to infer its presence rather on uniformitarian grounds, than by any certainty of explanation of the phenomena. We can trace sensation so far down in the scale of animal life, that it seems unreasonable to deny its presence when the same phenomena are exhibited by the Protozoa. We are confirmed in our belief in the presence of sensation in these low forms, by the knowledge that reflex acts are the product of conscious acts, whereas we have no evidence that conscious acts are the product of the reflex.

Although it is frequently alleged or assumed that designed conscious acts are the product of reflexes, no one has yet shown how this is possible. On the other hand, the development of automatic acts out of conscious ones is of ordinary occurrence, and is known under the name of education.

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[1] *Zoonomia*, XXXIX., 3; Osborn, *From the Greeks to Darwin*, p. 148.

The relation of consciousness to the physical basis is as yet a profound mystery, but that they exercise over each other a definite mutual control is unquestionable. The processes which produce thought, as conception, judgment, etc., are, however, not qualitatively related to the amount of nutritious proteids consumed in the central nervous system, but only quantitatively; yet it is the outcome of these processes that directs animal movements, when they are not automatic. In other words, the forms of thought, which have no weight, direct the movements of muscles, which have weight. This is not in accord with the doctrine of the correlation of energy. But what has the formation of a concept, or the development of a judgment, to do, *per se*, with the correlation of energy? I may give this idea a more definite expression by the following diagram :[1]

1

AFFIRMATIVE.	NEGATIVE.
1	5
2	6
3	
4	

2

AFFIRMATIVE.	NEGATIVE.
1	3
2	4
	5
	6

Let each square represent the grammes of energy necessary for the maintenance in consciousness of six propositions. Judgment issues from the side of the predominating number of propositions. They arrange themselves in consciousness in accordance with their qualities, in two aggregations represented by columns in the squares. Now if they arrange themselves in four affirmative and two negative, as in square 1, the

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[1] This is in explanation of the same proposition as stated by me in the *Proceedings of the American Philosophical Society*, 1889, p. 504.

judgment is affirmative. If, on the other hand, they arrange themselves in two affirmative and four negative, as in square 2, the judgment is negative. The energy expended in the two cases is the same. So also in forming different concepts from the same set of particular sense-impressions or memories. Is there any difference in the energy expended in forming from them the concept of bigness as compared with that of redness? While, therefore, every mental process is expensive as a whole, the mental content is obedient to the forms of thought rather than the correlation of energy. This is what mind is. While it is doubtful whether any animal below man can form a concept (with a very few possible exceptions), the formation of simple judgments is general. Any decision based on experience is a judgment.

In order to render this proposition clearer, I have formulated it in the following language, although it is possible that the definition of energy will not bear the strain of the statement.

"The formal statement of this phenomenon may be found in the thesis, that *energy can be conscious*. If true, this is an ultimate fact, neither more nor less difficult to comprehend than the nature of energy or matter in their ultimate analyses. But how is such a hypothesis to be reconciled with the facts of nature, where consciousness plays a part so infinitesimally small? The explanation lies close at hand, and has been already referred to. *Energy become automatic is no longer conscious*, or is about to become unconscious. That this is the case is matter of every-day observation on ourselves and on other animals. What the molecular conditions of consciousness are, is one of the problems of the future, and for us a very interesting one. One thing is certain, the organization of the mechanism of habits is its enemy. *It is clear that in animals, energy, on the loss of consciousness, undergoes a retrograde metamorphosis.*

"To regard consciousness as the primitive condition of energy, contemplates an order of evolution in large degree the reverse of the one which is ordinarily entertained. The usual view is, that life is a derivative from inorganic energies as a result of high or complex molecular organization, and that consciousness (=sensibility) is the ultimate outcome of the nervous or equivalent energy possessed by living bodies. The failure of the attempts to demonstrate spontaneous generation will prove, if continued, fatal to this theory. With our present evidence it may be affirmed that not only 'has life preceded organization,' but that *consciousness was coincident with the dawn of life.*"

The facts cited, and the doctrines defended in the preceding pages lead to one inference as to the relation of consciousness to its physical basis. The condition of matter necessary to the maintenance of consciousness is, in the language of morphology, *generalized*; in the language of chemistry, *neutral*; in the language of physics, *non-equilibrated.* The materialist and the animist can alike agree as to this generalization. The difference between the two positions is a difference of view as to the mutual relations of the two members of the partnership. Is the permanent absence of equilibrium of living protoplasm due to control by consciousness? or is consciousness a product of an absence of equilibrium, which is due to chemical and physical action? The latter proposition is untenable, because the inevitable tendency of chemical and physical energies is to an equilibrium. Is, therefore, the other alternative true? There seems to be no escape from it, and it accords also with our personal human experience of the agency of conscious states in our various activities, physical and mental.

2. THE EFFECTS OF CONSCIOUSNESS.

From the facts cited it is evident that sensation (consciousness) has preceded in time and in history, the evolution of the greater part of plants and animals, both unicellular and multicellular. It appears also that if kinetogenesis be true, consciousness has been essential to a rising scale of organic evolution.

Animals who do not perform simple acts of self-preservation must necessarily perish sooner or later. In fact it is impossible to understand how the lowest forms of life, utterly dependent as they are on physical conditions of many kinds, should not have been all destroyed, were they not possessed of some degree of consciousness under stimuli at least. And the case is even plainer with the higher forms. We have only to picture to ourselves the condition of a vertebrate without general or special sensation, to perceive how essential consciousness is to its existence. If now, as maintained in Chapter IV., use has modified structure, and so, in coöperation with the environment, has directed evolution, we can understand the origin and development of useful organs. And we can understand how by parasitism or other mode of gaining a livelihood without exertion, the adoption of new and skilful movements would become unnecessary, and consciousness itself would be seldom aroused. Contiued repose would be followed by subconsciousness, and later by unconsciousness. Such appears to be the history of degeneracy everywhere, and such is, perhaps, the history of the entire vegetable kingdom. From their ability to manufacture protoplasm from inorganic substances, plants do not need to move about in search of food, so that they require no consciousness of conditions to guide their movements. They become fixed, and their entire organization becomes monopolized by the functions of nutrition and reproduction. Movements rarely occur, and when present are confined to those of one part of the structure or another. They are mostly rhythmic or rotary, and very seldom exhibit the quality of impromptu design. The satisfactory explanation of those that exhibit general design, as the adaptation for transportation often seen in seeds, may be chance coincidence and natural selection.

The ascending scale of development of intelligence observed among animals is strong evidence in support of the hypothesis here outlined. There can be no doubt that in the long run the most intelligent have survived. They have survived because they were capable of the most successful designed acts, thus directing their movements to the most useful ends. These movements ultimately modified their structure usefully, to the perfecting of mechanisms in every way important to their possessors. This much having been established as to the cause of anagenesis, let us look more closely into the history of catagenesis.

Movements of organic beings on frequent repetition become automatic, reflex, and finally, as it is termed, organic. This means the running down of energy through various grades, beginning with the highest or conscious stage, and ending with the purely reflex, which is as unconscious of changes in the environment as is any one of the physical energies. The conscious stage is evidently the most susceptible to the stimuli of the environment, and the process of catagenesis is one of degeneracy to less and less sensitive and to more and more mechanical conditions. The resemblance of the lowest grade of organic activities to physical mechanical energy is so great that it is almost universally supposed by evolutionists to be of purely mechanical origin, but I have endeavored to show that they are of totally different origin, and that the only explanation of their characteristics is the hypothesis of catagenesis.

In accordance with this view, the automatic "involuntary" movements of the heart, intestines, reproductive systems, etc., were organized in primitive and simple animals in successive states of consciousness, which stimulated "voluntary" movements, which ultimately became rhythmic; whose results varied with the machinery already existing and the material at hand for use. It is not inconceivable that circulation may have been established by the suffering produced by an overloaded stomach demanding distribution of its contents. The structure of the Infusoria offers the structural conditions of such a process. A want of propulsion in a stomach or body-sack occupied with its own functions would lead to a painful clogging of the flow of its products, and the "voluntary" contractility of the body or tube-wall being thus stimulated, would at some point originate the pulsation necessary to relieve the tension. Thus might have originated the "contractile vesicle" or contractile tube of some protozoa; its ultimate product being the mammalian heart. So with reproduction. Perhaps an excess of assimilation in well-fed individuals of the first animals led to the discovery that self-division constituted a relief from the oppression of too great bulk. With the increasing specialization of form, this process would become necessarily localized in the body, and growth would repeat such resulting structure in descent, as readily as any of the other structural peculiarities. No function of the higher animals bears the mark of conscious origin more than this one, as consciousness is still one of the conditions of its performance. While less completely "voluntary" than muscular action, it is more dependent on stimulus for its initial movements, and does not in these display the unconscious automatism characteristic of many other functions.

There remain, however, some phenomena which do not yield so readily to this analysis. First, we have the conversion of inorganic substances into protoplasm by plants. It is also well known that living animal organisms act as producers, by conversion, of various kinds of inorganic energy, as heat, light, sound, electricity, motion, etc. It is the uses to which these forces are put by the animal organism, the evident design in the occasion of their production, that gives them the stamp of organic life. We recognize the specific utility of the secretions of the glands, the appropriate distribution of the products of digestion and adaptation of muscular motion to many uses. The increase of heat to protect against depression of temperature ; the light to direct the sexes to each other ; the electricity as a defence against enemies—display unmistakably the same utility. We must not only believe that these functions of animals were originally used by them under stimulus, for their benefit, but, if life preceded organism, that the mechanism which does the work has developed as the result of the animal's exertions under stimuli. This will especially apply to the mechanism for the production of motion and sound. The production of heat, light, chemism, and electricity doubtless result from molecular aptitudes inherent in the constitution of protoplasm. But the first and last production of even these phenomena is dependent on the motions of the animal in obtaining and assimilating nutrition. For without nutrition all energy would speedily cease. Now the motion required for the obtaining of nutrition has its origin in the sensation of hunger. So, even for the first steps necessary to the production of inorganic forces in animals, we are brought back to a primitive consciousness. This hypothesis I have termed Archæsthetism.

"It maintains that consciousness as well as life preceded organism, and has been the *primum mobile* in the creation of organic structure. This conclusion also flows from a due consideration of the nature of life. I think it possible to show that the true definition of life is, *energy directed by sensibility, or by a mechanism which has originated under the direction of sensibility.* If this be true, the two statements that life has preceded organism, and that consciousness has preceded organism are coëqual expressions.

"Granting the existence of living protoplasm on the earth, there is little doubt that we have some of its earliest forms still with us. From these simplest of living beings both vegetable and animal kingdoms have been derived. But how was the distinction between the two lines of development, now so widely divergent, originally produced? The process is not difficult to imagine. The original plastid dissolved the salts of the earth and appropriated the gases of the atmosphere and built for itself more protoplasm. Its energy was sufficient to overcome the chemism that binds the molecules of nitrogen and hydrogen in ammonia, and of carbon and oxygen in carbonic dioxide. It apparently communicated to these molecules its own method of being, and raised the type of energy from the polar non-vital to the adaptive vital by the process. Thus it transformed the dead inorganic world, perhaps by a process of invasion, as when a fire communicates itself from burning to not burning combustible material. Thus it has been doing ever since, but it has redeposited some of its gathered stores in various non-vital forms. Some of these are in organic forms, as cellulose ; others are crystals imprisoned in its cells ; while others are amorphous, as waxes, resins, and oils. But consciousness apparently early abandoned the vegetable line. Doubtless all the energies of vegetable protoplasm soon became automatic. The plants in general, in the persons of their protist ancestors, soon left a free-swimming life and became sessile. Their lives thus became parasitic, more automatic, and in one sense degenerate.

"The animal line may have originated in this wise. Some individual protists, perhaps accidentally, devoured some of their fellows. The easy nutrition which ensued was probably pleasurable, and once enjoyed was repeated, and soon became a habit. The excess of energy thus saved from the laborious process of making protoplasm was available as the vehicle of consciousness and motion. From that day to this, consciousness has abandoned few if any members of the animal kingdom. In many of them it has specialized into more or less mind. Organization to subserve its needs has achieved a multifarious development. There is abundant evidence to show that the permanent and the successful forms have ever been those in which motion and sensibility have been preserved, and most highly developed.[1]

We must remember, however, that in the matter of the evolution of plant-types we have an especial factor in the influence which insects have exerted on the conditions of almost all of their organs. Insects originated early in geological time, and have closely accompanied plants in their evolution. As the source of the food, and as the dwelling-places of great numbers of insects, they have been subjected to a class of stimuli and strains similar to those which animals have experienced. It is believed that the forms of the organs of fructification and especially of the flowers, have been greatly modified by the influence of insects.[2] The general evolution of plants, however, presents us with a greater predominance of physiogenetic or simple dynamical conditions over the bathmic, than in the case of animals. Thus many peculiarities of the inflorescence directly result from the shortening of the axial growth in complementary relation to the increase of peripheral growth. Such is evidently the origin of flowers themselves ; secondly of the umbel as compared with the spike or panicle and finally of the composite head as compared with the other modes of inflorescence. To the cohesion of the elements of a whorl, possible only in the case of an abbreviated axis, can we ascribe the formation of a seed vessel from discrete carpels, and a gamopetalous from a polypetalous corolla. Degeneracy or specialization is to be seen everywhere, as in the abortion of ovules, carpels, and perianth.

"Catagenesis of living organisms has been epito-

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[1] *Origin of the Fittest*, p. 428, 432.

[2] Henslow.

mized in the following language: 'Evolution of living types is then a succession of elevation of platforms, on which succeeding ones have built. The history of one horizon of life is that its own completion but prepares the way for a higher one, furnishing the latter with conditions of a still further development. Thus the vegetable kingdom died, so to speak, that the animal kingdom might live, having descended from an animal stage to subserve the function of food for animals. The successive types of animals first stimulated the development of the most susceptible to the conflict, in the struggle for existence, and afterwards furnished them with food.' In the occupation of the world's fields, the easiest and nearest at hand have been first occupied, and successively those which were more difficult. The digging animals are generally those which first abandoned the open field to more courageous or stronger rivals; and they remain to this day generally of low type compared with others of their classes (e. g. *Monotremata*, *Glires*, *Insectivora*). All occupations have been filled before that one which requires the greatest expenditure of energy, i. e. mental activity. But all other modes of life have fallen short of this one in giving the supremacy over nature."

We now approach an explanation of the phenomenon of anagenesis. Why should evolution be progressive in the face of universal catagenesis? No other ground seems discoverable but the presence of sensation or consciousness, which is, metaphysically speaking, the protoplasm of mind. The two sensations of hunger and sex, have furnished the stimuli to internal and external activity, and memory, or experience with natural selection, have been the guides. Mind and body have thus developed contemporaneously and have reacted mutually. Without the coöperation of all these factors, anagenesis seems impossible.

From this point of view the study of the evolution of mind and its relation to the organic world assumes a new importance. Circumstances have forbidden my entering on this subject in the present volume, but I hope to be able to devote especial attention to it at a future time. One fundamental postulate of mental evolution may, however, be mentioned here. That is, as Spencer has pointed out, the instinct of hunger is at the basis of the activity which has developed the intelligence, while that of sex is at the basis of the development of the altruistic or social instincts and affections. With this proposition I leave this interesting part of the doctrine of evolution.

CHAPTER XI.—THE OPINIONS OF NEOLAMARCKIANS.

LAMARCK ascribed some of the evolutionary changes of structure to changes in the environment, some to the motions of organic beings, and others to both combined.[1] Spencer in 1865[2] devoted a short chapter to the effect of motion in producing variations, and specified the mechanical effect of flexure in producing segmentation of the vertebral column. The present writer in 1871[3] insisted on the importance of motion as a factor in determining growth, and in 1872[4] I approached the subject more definitely in the following language: "The first physical law is that growth force . . . must develop extent in the direction of least resistance, and density on the side of greatest resistance." In 1877 Ryder further applied the principle of motion to the origin of structural changes, chiefly reduction of digits, in the feet of Mammalia in language[5] which I have quoted on page 311.

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[1] *Philosophie Zoologique*, Chap. VII., 1809; translation in *American Naturalist* for 1888.

[2] *Principles of Biology*, II., pp. 167 and 195.

[3] *Proceeds. Amer. Philosoph. Soc.*, 1871, p. 259. *Origin of the Fittest*, 1887, p. 210.

[4] *Penn Monthly Magazine*, July, 1872. *Origin of the Fittest*, 1887, p. 30.

[5] *American Naturalist*, 1877, p. 607.

In the same year, in discussing the origin of the great development of the incisor teeth in the Rodentia,[1] Professor Ryder, in summing up, ventured "the reflection that the more severe strains to which they were subjected by enforced or intelligently assumed changes of habit, were the initiatory agents in causing them to assume their present forms, such forms as were best adapted to resist the greatest strains without breaking." In 1878 the writer[2] advanced the following proposition: "Change of structure is seen to take place in accordance with the mechanical effect of three kinds of motion, viz., by *friction*, *pressure*, and *strain*." In the same year Professor Ryder went into a discussion of the specific application of strains in the evolution of the dental types of the diplarthrous Ungulata, and prepared the field for work in the Rodentia and Proboscidia.[3] In 1879 the writer gave mechanical reasons for the reduction of the sectorial teeth of Carnivora to one, and for their present position in the jaws.[4] In 1881 the writer[5] described the specific action of impacts and strains in the production of the existing characters of the articulations of the limbs in the higher Mammalia. In 1887 the same subject, together with that of the mechanical origin of the characters of the molar teeth, was more fully investigated in a paper on the Perissodactyla.[6] In 1888 the writer published a paper on the mechanical origin of the sectorial teeth of the Carnivora,[7] one on the mechanical

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[1] *Proceeds. Phila. Acad.*, 1877, p. 318.

[2] *American Naturalist*, January, 1878. *Origin of the Fittest*, p. 354.

[3] *Proceeds. Phila. Acad.*, 1878, p. 45.

[4] *American Naturalist*, March, 1879.

[5] *American Naturalist*, April and June, 1881.

[6] *American Naturalist*, 1887, pp. 985, 1060.

[7] Read before the American Association for the Advancement of Science, New York, 1887, p. 254.

origin of the peculiar dentition of the Glires,[1] and a third on the mechanical origin of the dentition of the Amblypoda.[2] In 1889 I discussed the mechanical causes of the structures of the elbow and other joints in the Artiodactyla and the origin of the peculiar intervertebral articulations in that order.[3] In the same year I published a *résumé* of the work done on this subject with reference to the Mammalia.[4] Since that time important contributions to the subject have been made by Ryder, Osborn, Wortman, Dall, Jackson, and others, to which reference will now be made.

Hyatt says as a result of his exhaustive studies of the phylogeny of the Cephalopoda[5]; "The action of physical changes takes effect upon an irritable, plastic organism which necessarily responds to external stimulants by an internal reaction or effort. This action from within upon the parts of organisms modifies their hereditary forms by the production of new growths or changes, which are therefore adapted or suitable to the conditions of the habitat, and are therefore physiologically and organically equivalent to the physical agents and forces from which they directly or indirectly originated. In so far then, as causes and habits are similar, they probably produce representation or morphological equivalence in different series of the same type in similar habitats: and in so far as they are different, they probably produce the differen-

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[1] *American Naturalist*, January, 1888, p. 3.

[2] *Proceeds. Amer. Philosoph. Soc.*, 1888, p. 80.

[3] *American Naturalist*, March, 1889.

[4] *The American Journal of Morphology*, September, 1889, pp. 137–277, "On the Mechanical Causes of the Development of the Hard Parts of the Mammalia."

[5] *The Genesis of the Arietidæ*, by Alpheus Hyatt; *Smithsonian Contributions to Knowledge*, and *Memoirs of the Museum of Comparative Zoölogy*, Vol. XVI., No. 3, 1889.

tials which distinguish series and groups from each other."

Packard[1] in discussing the causes of the blindness of cave animals, says: "Such a phrase as 'natural selection,' we repeat does not to our mind definitely bring before us the actual working-causes of the evolution of these cave organisms, and no one cause can apparently account for the result. The causes are 'change in the environment,' disuse of certain organs; 'adaptation,' 'isolation,' and 'heredity' operating to secure for the future the permanence of the newly originated forms as long as the physical conditions remain the same."

In 1889, Ryder described the ontogenetic origin of the articulations of the cartilaginous fin-rays of the *Salmo fontinalis*, and used the facts observed as evidence that these articulations are due to the mechanical strain experienced by the rays in use as motors of the body of the fish in the water.[2]

Prof. H. F. Osborn in 1890[3] discussed thoroughly the mechanical causes for the displacement of the elements of the feet of the ungulate Mammalia from linear to alternating relations. (See *antea*, p. 299.) In an article in *Nature*,[4] the same distinguished naturalist remarks: "The following views are adopted from those held by Cope and others, so far as they conform to my own observations and apply to the class of variations which come within the range of paleontological evidence. In the life of the individual, adap-

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[1] "On the Cave Fauna of North America," *Memoirs of the U. S. National Academy of Sciences*, IV, pt., I., p. 137.

[2] *Proceedings of the American Philosophical Society*, 1889, p. 546.

[3] *Transactions of the American Philosophical Society*, XVI., February, 1890, p. 531.

[4] January 9, 1890, p. 277.

tation is increased by local and general metatrophic changes of necessity correlated, which take place most rapidly in the regions of least perfect adaptation, since here the reactions are greatest; the main term of variation is determined by the slow transmission, not of the full increase of adaptation, but of the disposition to adaptive atrophy or hypertrophy at certain points; the variations thus transmitted are accumulated by the selection of the individuals in which they are most marked, and by the extinction of inadaptive varieties or species; selection is thus of the ensemble of new and modified characters. Finally, there is sufficient paleontological and morphological evidence that acquired characters in the above limited sense, are transmitted. . . . Excepting in two or three side-lines the teeth of all the Mammalia have passed through closely parallel early stages of evolution, enabling us to formulate a law: *The new main elements of the crown make their appearance at the first points of contact, and chief points of wear of the teeth in preceding periods.* Whatever may be true of spontaneous variations in other parts of the organism, these new cusps arise in the perfectly definite lines of growth. . . . Now, after observing these principles operating in the teeth, look at the question enlarged by the evolution of parallel species of the horse series in America and Europe, and add to the development of the teeth what is observed in progress in the feet. Here is the problem of correlation in a stronger form even than that presented by Spencer and Romanes. To vary the mode of statement: what must be assumed in the strict application of the selection-theory? (*a*) that variations in the lower molars correlated with coincident variations of reversed patterns in the upper molars, these with metamorphosis in the premolars and pocketing of the incisor-enamel; (*b*) all new elements and forms at first so minute as to be barely visible, immediately selected and accumulated; (*c*) in the same individuals favorable variations in the proportions of the digits involving readjustments in the entire limbs and skeleton, all coincident with those in the teeth; (*d*) finally, all the above new variations, correlations, and readjustments not found in the hereditary germ-plasm of one period, but arising fortuitously by the union of different strains, observed to occur simultaneously and to be selected at the same rate in the species of the Rocky Mountains, the Thames Valley, and Switzerland! These assumptions, if anything, are understated."

I have already referred to the contribution by Dall to the doctrine of kinetogenesis which has resulted from his investigations of the origin of the characters of the lamellibranchiate (or pelecypod) Mollusca.[1] He observes: "In reflecting upon the origin of the complicated mechanical arrangements in bivalves which we call the hinge, I have come to the conclusion that here, as in the cases of the mammalian foot and tooth elaborated so clearly by Cope and Ryder, we have the result of influences of a mechanical nature operating upon an organ or apparatus in the process of development. . . . The shell is in one sense the product of secretion from the mantle, as the mammalian tooth is derived from the ectoderm of the jaw, or the skeleton from the periosteum and cartilages. Both are that and much more. It would be as reasonable to say that a steam boiler in process of construction is the product of the boy inside who holds the rivet-heads, as to claim that the shell has no more significance

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[3] *American Journal of Science and Arts*, December, 1889, p. 447.

than is implied in the term 'secretion of the mantle.' The original theoretic protoconch may have been so, but as soon as it came into being, its development was governed by the physical forces impinging upon it from all sides, and through it influencing the growth and structure of the soft parts beneath. The gastropod shell is the result of the action and reaction between the physical forces of the environment, and the evolutionary tendencies of the organic individual. In the pelecypod we have the mechanical stresses and reactions of one valve upon the other, added to the category of influences. To some extent it is doubtless as true that the animal is moulded by its shell, as it is that the shell is shaped by the soft parts of the animal."

Dr. Dall in an able paper on the "Dynamic Influences in Evolution," read before the Biological Society of Washington, March 8, 1890, writes thus forcibly:

"It is often assumed, in discussing variation, that the possibility of variation is equal in every direction. A consideration of the dynamic conditions of life show that this is not the case, or, at least, if we grant its theoretic truth, in practice it can never be true. Under any conditions which would permit it, the resulting organic forms would have to pass their existence in constant rotation. The moment that any one of them came to rest, it would begin to be subjected to unequal stresses relatively to its different parts. Light, gravity, friction, opportunities for nutrition, would be unequally distributed, with the result of forcing an unequal growth, development, and specialization of its regions. Inequality of form once established, if it were a moving organism, friction and resistance of the circumambient medium, would confirm the inequality, and put individuals of its kind at a disadvantage when they varied towards the original shape."

This is an excellent statement of kinetogenesis in concentrated form.

Prof. A. S. Packard in an important essay "On the Evolution of the Bristles, Spines, and Tubercles of Certain Caterpillars," etc., remarks as follows:[1] "The Lamarckian factors (1) of change (both direct and indirect) in the *milieu*, (2) need, (3) habit, and the now generally adopted principle that a change of function induces change in organs, and in some or many cases actually induces the hypertrophy and specialisation of what otherwise would be indifferent parts or organs. These factors are all important in the evolution in the colors, ornaments, and outgrowths from the cuticle of caterpillars. . . .

"So far as I am aware no one has suggested why these horns and high tubercles and often pencils of hairs are restricted to these particular segments. As a partial explanation of the reason, it may be stated that the presence of these high tubercles, etc., is correlated with the absence of abdominal legs on the segments bearing the former. It will also be noticed that in walking the apodous segments of the caterpillar are more elevated and prominent than those to which the legs are appended. They tend to bend or hump up, particularly the first and the eighth abdominal, the ninth segment being reduced to a minimum, and the tenth simply represented by the suranal and paranal plates, together with the last pair of legs.

"As is well known, the loopers or geometrid worms, while walking elevate or bend up the part of the body

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[1] *Proceedings of the Boston Society of Natural History*, 1890, p. 493, 510–513.

situated between the last thoracic and first pair of abdominal legs, which are appended to the seventh euomere. Now in the larva of *Nematocarpa filamentaria* which bears two pairs of remarkable filamental tubercles rolled up at the end, it is certainly very suggestive that these are situated on top of the loop made by the caterpillar's body during progression, the first pair arising from the second, and the hinder pair from the fourth abdominal segment.

"It seems, therefore, that the humps or horns arise from the most prominent portions of the body, at the point where the body is most exposed to external stimuli; and the force of this is especially seen in the conspicuous position of those tubercles which are voluntarily made to nod or so move as to frighten away other creatures. Perhaps the tendency of these segments to loop or hump up, has had a relation of cause and effect in inducing the hypertrophy of the dermal tissues entering into the composition of the tubercles or horns."

Prof. W. B. Scott[1] says: "To sum up the results of our examination of certain series of fossil mammals, one sees clearly that transformation, whether in the way of the addition of new parts or the reduction of those already present, acts just *as if* the direct action of the environment and the habits of the animal were the efficient cause of the change, and any explanation which excludes the direct action of such agencies is confronted by the difficulty of an immense number of the most striking coincidences. . . . So far as I can see the theory of determinate variations and of use-inheritance, is not antagonistic, but supplementary to natural selection, the latter theory attempting no explana-

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[1] *American Journal of Morphology*, 1891, pp. 395, 398.

tion of the *causes* of variation. Nor is it pretended for a moment that use and disuse are the sole or even the chief factors in variation."

European authors, partly from their less favorable situation for the obtaining of paleontologic evidence, have not contributed as much as Americans to the doctrine of bathmogenesis. Nevertheless, in England Spencer, Cunningham, Henslow, and others have sustained this doctrine, and in France Giard and Edmond Perrier, and in Germany, Semper, Eimer, and others, who lean principally in their writings to its physiogenetic aspect. Says Eimer:[1]

"According to my conception, the physical and chemical changes which organisms experience during life, through light or want of light, air, warmth, cold, moisture, food, etc., and which they transmit by heredity, are the primary elements in the production of the manifold variety of the organic world, and in the origin of species. From the materials thus supplied, the struggle for existence makes its selection. These changes, however, express themselves simply as growth."

Nägeli discards completely the agency of natural selection, and sees an internal "Principle of Improvement" as the active agent in evolution. He apparently includes both statogenesis and bathmogenesis in his conception.[2] He says:

"Such internal causes must necessarily be supposed merely on the ground that modifications or variations of the phyla do actually take place in definite directions, are not irregular. The internal causes effect

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[1] *Organic Evolution*, English Translation, 1890, p. 22.

[2] *Mechanische physiologische Abstammungslehre*, C. V. Nägeli, Munich, 1884.

a constant alteration of the phyla in definite directions, towards greater perfection, that is, towards greater complexity." Accordingly Nägeli describes his theory of internal causes, as the "Principle of Improvement." "Superficial reasoners," he says, "have pretended to discover mysticism in this. But the principle is one of a mechanical nature and constitutes the law of persistence of motion in the field of organic evolution. Once the motion of evolution is started it cannot cease, but must persist in its original direction."

For convenience of reference I give a list of papers by American authors on this subject. European authors, beginning with Lamarck, and including Spencer, have implicitly included in their theses the effects of mechanical strains and impacts in developing the structures of animals. Fick, Henke, Tornier, and others have attempted an exact demonstration of the manner in which these forms of mechanical energy have produced the results. These attempts have great merit as physiological studies, but they have not been used by their authors as illustrations of specific evolution, owing to the fact that they have not carried their researches into the field of paleontology.

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