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THE PALEONTOLOGICAL SOCIETY

CONFERENCE ON THE ASPECTS OF
PALEONTOLOGY

Clark

FIRST ANNUAL MEETING,
CAMBRIDGE, MASS., DECEMBER 29, 1909.

Reprinted from the POPULAR SCIENCE MONTHLY, June to November, 1910.

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THE PALEONTOLOGIC RECORD

THE PALEONTOLOGICAL SOCIETY CONFERENCE PAPERS

BY PROFESSOR JOHN M. CLARKE

STATE MUSEUM, ALBANY, N. Y.

Introductory.—The birth of a new society devoted to special scientific aims counts but little for the advancement of knowledge and culture in these days of multiplex organizations if it fails to come into being and before the world with an adequate excuse and a clean-cut purpose. The Paleontological Society, which was conceived a year ago and born last winter in Boston at the meetings of the American Association, is the outcome of a conviction on the part of workers in this science that there is a common bond of interest among them all, in spite of the peculiar conditions which have stamped paleontology with their diversity and kept its devotees asunder. Students of this science have approached it along different avenues. Some, and chiefly those dealing with the vertebrates, have laid the foundations of their work in the living world; others, and here chiefly the students of invertebrates, have made their entry as geologists and have worked their way from beneath upward to the earth's surface. Among the paleobotanists good men have arrived through both approaches. As an equipment for trustworthy and lasting work, both of these lines of preparation have proved their efficiency and so all arguments bent to demonstrate the superiority of the one over the other schooling resolve themselves to a conclusion that both are essential to the best result.

Diversity in training and in the field of activity has led to diversity of sympathy, and it seemed, even to those who had long hoped for a unification of these interests, that it might hardly be practicable to obliterate these cleavage planes. The governing principles of the science are common, the bearings of paleontologic researches and results are the widest conceivable in their relation to the problems of life, whether past, present or future, and it is not likely that the magnitude of the science can be unduly stated. From some such considerations as these, the writer, chosen as first president of the new society, endeavored to bring into the foreground of the society's first meeting, by a "Conference on the Aspects of Paleontology," an introductory presentment of some of the broader factors and principles of the science, and the articles that follow herewith are the partial outcome of this conference. In every case where practicable, the themes were presented by two

speakers making their approach from different fields of interest. The conference was an effort to define and emphasize the common platform on which the paleontologists must stand together; even more than this, it was a purpose to declare at the outset that the organization, though the patron of detailed researches and patient endeavor, recognizes that the sole impulse which can guarantee its usefulness and maintain its integrity is its devotion to a standard which touches close on human interests.

ADEQUACY OF THE PALEONTOLOGIC RECORD

BY PROFESSOR SAMUEL CALVIN

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WHEN or how life began on our planet no one may be able to tell us; but that life has been present and has been an important factor in the world's geological development since before the beginning of the Cambrian is known to the most callow of embryo geologists taking his first course at the village high school. So far as relates to the skeleton-bearing, marine invertebrates which have lived on floors of epicontinental seas, there are remarkably complete records of this long history of living things, the order of their succession, their migrations, their geographic distribution during any given portion of geologic time, as well as of the progressive and orderly modifications which resulted in the extermination of decadent or unfit types, on the one hand, or resulted, on the other hand, in the advancement of certain types and their adaptation to the conditions prevailing in the living world to-day.

The zoologist, confining attention to living forms, gets a view of the animal creation as it exists, after ages of development and modification, during a fraction of a single faunal stage. The paleontologist, while unable to see the beginnings of life, gets the broader view which comes from a study of the organic world as it has appeared during numberless successive stages. He may trace the origin of forms and note the trend and tendency of variations in ways denied the zoologist. Neither the depth of the water nor the distance from the shore at the points where the objects of his study lived interferes with the thoroughness of his explorations. He is not limited to what he may learn by taking samples of the old sea bottom, here and there, with a dredge; he traces his life zones with practical continuity over areas of continental extent.

The faithfulness with which the paleontological record has been kept since the beginning of the Cambrian is a matter of constant surprise. No organism was too small for preservation, if only its soft

parts were supported or protected by a stony skeleton of some kind; no parts of the skeletal structure were too minute to be kept practically unaltered to the smallest microscopic detail; no period of time has been so long that the records of the large or the small things of life were necessarily obliterated. The shells of such minute and delicate things as radiolaria and foraminifera, on the one hand, and that king of invertebrates, the giant *Camaroceras*, on the other, have all been kept through the ages with equal fidelity. The hinge characters of the brachiopods, their internal arm supports, their spires and loops, the distribution of the ramifying blood channels in the mantle, the surface markings of every rank and grade down to the smallest which can be observed only with the lens, and the microscopic structure of the shell itself, are other examples of the faithfulness with which details, however insignificant in point of magnitude, have been guarded, protected, preserved. Strangely enough, in respect to a very large proportion of the animal remains buried in the ancient sediments it looks as if time had been standing still; it has neither marred nor destroyed. The organic remains from the Ordovician formations are quite as perfectly preserved as those from the Tertiary.

The profusion of the life of the ancient seas is as much a source of surprise as the detailed perfection of the record. In the Mississippi Valley limestones constitute a very large proportion of the sedimentary rocks, and it is unnecessary to say that these limestones record the life and death of countless myriads of organisms. In some cases the waters of the old seas were comparatively quiet, and the shells or other hard parts, undisturbed and unbroken, remain in the positions they occupied when the individuals they represent were alive. There is a bed of marly shale carrying many thin lenses of limestone, lying between the Platteville and the Galena, from 60 to 70 feet above the base of the Mohawkian, and these lenses are made up in large part of unbroken brachiopod shells. On the surface of one of these slabs, in an area measuring 35 square inches, one may count more than 60 perfect specimens of *Dalmanella subæquata* and *Orthis tricenaria*. The rate is about 290 individuals to the square foot. The number on a square mile of such sea bottom runs up into the billions. The number of individuals of the species *Pentamerus oblongus* that swarmed on the bottom of the Niagaran sea is strikingly demonstrated in every paleontological museum. The wide geographic range of this species is well known; its range in time was such as to make possible the accumulation of beds of limestone, 70 feet in thickness, from the detritus of its broken shells. Like other persistent or widely ranging species, it gave rise to a very large number of varietal forms, some of which have been described as specifically distinct.

The Devonian formations furnish similar evidence of the wonder-

ful profusion of the ancient life and help us to appreciate the wealth of material that the paleontologist has at his command. In the quarries at Independence, Iowa, there are beds crowded with beautifully preserved forms, mostly brachiopods, as perfect to-day in every detail of shell structure and ornamentation as when the currents of life pulsed within. A coral reef, no species lost, has been cut into by a small intermittent stream near Littleton, Iowa; and perfect coralla, wagon loads of them, are strewn along the sandy channel a quarter of a mile or more. A successor to the reef just noted, composed of different species, the corals still in place, may be seen and studied on the west side of the river opposite the village of Littleton. The state quarry beds near North Liberty are simply cemented masses of brachiopods; they illustrate the remarkable prodigality of the Devonian life, but the individuals are not in good condition for study. It is a different case that is presented by the fossils in the marly beds of the Lime Creek shales at the exposures between Mason City and Rockford. A very large proportion of the specimens here are as perfect as when the animals lived; and there is a beauty and delicacy and exquisite refinement about most of them that is scarcely matched, certainly not surpassed, anywhere among fossils of any age or time. More than 65 species occur in the Lime Creek fauna, and thousands of individuals of some of the species, illustrating wide ranges of variation, enrich the museums of the world.

Along the Aux Sables River at many points near Thedford and Arkona, Ontario, there are calcareous shales containing a marine fauna, or rather a succession of faunas which once flourished in wonderful profusion and is still preserved in equally wonderful perfection. Statistics and computations would fail to give an adequate conception of the abundance and character of the material here offered for study. No detail of the skeletal parts has been lost; and as for the number of individuals, they are simply uncountable. There lies before me a small fragment of this old sediment having a surface of less than 15 square inches and it shows 51 identifiable individual specimens, not counting stem segments of crinoids. The 51 individuals are distributed among eleven species, and these represent eleven genera—namely, *Phacops*, *Platyceras*, *Tentaculites*, *Spirifer*, *Chonetes*, *Hederella*, *Orthopora*, *Chætetes*, *Arthræacantha*, *Striatopora* and *Aulopora*. Can any bit of modern sea bottom of similar size make a better showing? Above and below the Rocky Glen, near Arkona, from which this specimen came, there are opportunities to study continuous sections approximately 100 feet in thickness, the successive beds crowded with organic remains and revealing the historic sequence of varying organic types as the life responded to slight changes of environment. Here, as at countless other localities, the paleontologist gets a view of

changes, of movements, of trend and tendency among living things ranging over a period of time equal to many millenniums.

Another life record of especial interest, typical of many scattered up and down the land areas of the globe, is furnished by the Osage division of the Mississippian at Burlington and Keokuk. Of one group of crinoids, the Camerata, these Mississippian limestones have yielded about 250 species, and of other groups a number about equally as great. The beauty and perfection of the individual specimens can be appreciated only by those who have had the good fortune to see the superb collections of Wachsmuth and Springer. Crinoids flourished here in such numbers that beds of limestone 150 feet in thickness are built practically of crinoidal remains and nothing else. The time represented was long enough to allow of a series of modifications of such extent that the crinoid fauna of the Upper Burlington is very distinct from that of the lower beds of the same formation, while the fauna of the Keokuk differs from both. Here again the paleontologist is favored, not only with a wealth of material, but with an opportunity to note the trend and tendency of things. This was the time of greatest development, of highest prosperity, among camerate crinoids. But in the midst of this prosperity the trained paleontologist may discover signs of degeneration, the prophecy of speedy extinction. The law enunciated by Beecher and quoted by Professor Woodward in his address before the geological section of the British Association at its meeting in Winnipeg last summer, is well exemplified in the Mississippian history of this particular group of crinoids. The tendency among any division of skeletal-bearing animals to run to extravagant ornamentation in the way of ribs, nodes, spines or other excesses of dead, useless, skeletal matter, is something that precedes and presages the decline and death of the race. Even in the Upper Burlington the skeleton of the crinoids is heavier than in the Lower; stronger nodes on the plates are produced; more arm plates are incorporated in the dorsal cup; the animals are weighted down with useless matter. This tendency is carried to extremes in the Keokuk limestone, a fact well exemplified by the species figured on plate 15 of Hall's "Geology of Iowa," Volume I., part II. In these species the development of massive spines and heavy nodose plates reaches its maximum. The race has come to the end of its career. When the Keokuk closes, only a few of the simpler forms of the Camerata survive, and even these shortly disappear. The paleontologist sees the operation of the same law, the same trend and tendency, among the Cretaceous Ammonoids; in many other groups of animals it is as clearly manifest; but it would not be profitable, before such a body as this, to carry the discussion farther, even if the limits of the paper permitted. Let me close by

quoting from the address of Professor Woodward, to which reference has already been made:

Geology and paleontology in the past have furnished some of the grandest contributions to our knowledge of the world of life; they have revealed hidden meanings which no study of the existing world could even suggest; and they have started lines of inquiry which the student of living plants and animals alone would scarcely have suspected to be profitable.

ADEQUACY OF THE PALEONTOLOGIC RECORD

By R. S. BASSLER

U. S. NATIONAL MUSEUM

THE imperfection or inadequacy, instead of the adequacy of the paleontologic record, has long been a favorite subject of discussion, and it is only within recent years that this heresy of an imperfect record is being abandoned by paleontologists in general. However, as many of our biologic, and even a few of our paleontologic, friends still have doubts regarding the matter, the present conference upon this and allied subjects is very opportune.

I have a vivid recollection of the joy experienced in my school days, when, during an examination in geology, the subject of an impromptu essay was announced as "The Imperfection of the Paleontologic Record." Here was a subject in which I was well grounded from textbook reading, and I remember distinctly the telling points made. The lack of hard parts causing the absence of many classes of animals; the great amount of unrepresented time in the geologic column; the metamorphism and consequent disappearance of fossils, and, when present, the frequent imperfectness of the specimens themselves, were dwelt on in great detail. Since that time, my experience in invertebrate paleontology has compelled me to unlearn every one of these supposed facts, and to come to the conclusion that, considered both biologically and stratigraphically, the paleontologic record is sufficiently adequate for all reasonable purposes.

Professor Calvin's paper tells us (1) of the detailed perfection of the record, (2) of the profusion of the material, and (3) of the broad view as to trend and tendency of biologic characters which the study of paleontology gives. His presentation of the subject is such that we must all agree with him. It therefore seems best for me to confine my remarks to the reasons usually advocated for the imperfection, namely, the lack of hard parts in many animals, metamorphism, the frequent imperfect preservation of fossils, and the unrepresented time in the geologic column.

The lack of hard parts in many animals is a serious, although not fatal, objection to their preservation as fossils. For the best results as

fossils, a stony framework of some kind is desirable, as we all know, but horny, or even the most perishable materials may be preserved under favorable conditions. Mr. Walcott's work on the *Medusæ*, and the researches of Ruedemann on the graptolites, as well as the work of others whom we can call to mind, are examples of excellent results from material of the latter nature, not to mention the hairs of the worm so carefully described by the Cincinnati paleontologist!

The metamorphism and apparently complete obliteration of all fossil remains in the rocks of certain large areas is likewise an apparently serious objection to the adequacy of the record, but here careful searching with the structural relations in mind will reveal the fossils, if present at all. The greatly folded and cleaved slates, schists and volcanic tuffs of the Piedmont area have long been the despair of both paleontologist and geologist, but at this meeting of the Geological Society of America, the State Geologist of Virginia will tell of Cincinnati fossils in the so-called Algonkian and other schists and volcanics of the easternmost Piedmont of that state. In this case the discovery of well-preserved fossils was quite simple. It consisted merely in finding a place where the cleavage and stratification coincided, and then working hard.

Professor Calvin has spoken of the richness and beautiful preservation of certain Paleozoic faunas. While the beauty and occasional richness of such faunas is not to be gainsaid, we must not forget the many horizons and localities affording, in comparison, specimens so poorly preserved that they might readily furnish an argument for the inadequacy of the record. Nor must we forget that in quite a portion of the geologic column organic remains are not only poorly preserved, but are, as known at present, very rare. However, these lean spots can be made most productive of paleontologic results by careful search and by methods of preparation. Several years ago the number of lower Paleozoic fossils found in the Ozarks could almost be counted on one's fingers, but we now have in the National Museum, from this formerly almost barren spot, several hundred drawers of beautiful material.

Fortunately the preparation and methods of study of paleontologic material has progressed to such a point that a poor fossil is no longer a bugbear. A specimen may be considered inadequate for study because it is covered with refractory clay. The application of caustic potash solves this difficulty. Certain limestone bands in the New York Niagaran and Cayugan are crowded with fossils, although often few of the species can be determined because of a hard, clayey covering. In preparing some specimens for exhibition, the treatment with caustic of a single slab, about three inches wide and five inches long, enabled me to bring out over a hundred species on one surface alone, not including the ostracods and other microscopic organisms. How often will the present sea bottom furnish such results?

Nature is very kind in preparing fossils for us. The Onondaga limestone, at the Falls of the Ohio, although only a few feet in thickness, has yielded seven hundred or more species of exquisitely preserved fossils. Examine the freshly quarried limestone and you may be able to crack out perhaps two dozen species of poorly preserved material, but go to the neighboring field where solution of the limestone and silicification of its contained fossils has occurred, and a host of beautiful forms awaits you. Strata, which under ordinary circumstances would yield very poor fossils, can, if silicification has commenced, be made to afford excellent specimens. By exposure to the weather for a year or so, the silicification can be advanced to such a stage that etching with acid will free the fossils. The beautiful etched material from the New Scotland of New York is a familiar example of this style of preparatory work. Most of the Cambrian and Ordovician formations of the Appalachian Valley yield shells which, as they occur in the limestone, are almost impossible as subjects for study, but as silicified pseudomorphs, all the beauty and detail of the original shell are reproduced.

Thin sections are a valuable aid in identifying the merest fragment of certain classes of organisms, and their use here is indispensable. A thin section of an otherwise undeterminable fragment of a Cambrian protremate brachiopod will distinguish the horizon. Other methods of preparation and study might be mentioned, but time forbids, although I can not refrain from speaking of the several whitening processes. The use of a coating of ammonium chloride or anilin chloride on fossils for photographic purposes is well known, but the excellent results obtained from the use of the same process in the study of poor material may not be so apparent to all. A trilobite indistinctly outlined in the rock under ordinary circumstances, flashes into bold relief when covered with the ivory white film of ammonium chloride. Casts and molds of fossils too indistinct to show any structure ordinarily, will reveal many characters when so whitened. Recently occasion arose to study a species of Cambrian phyllopod which had already been described and figured. The specimen was practically nothing but a film upon the rock, and apparently the last word had been said upon it. It was suggested that the specimen be whitened and then photographed with the sun's rays nearly parallel to its surface. The result was most gratifying as structures which could not be proved to exist by the aid of the eye alone, came into plain view in the negative. All these various methods of preparation and study make available a vast amount of material which formerly was thought too imperfect to be fully considered in determining the adequacy of the record, hence the great value of such methods to the paleontologist is obvious.

The real adequacy of the record, if it might be so called, lies in the

imperfections or gaps in the stratigraphic column. Measured according to the sections of twenty-five years ago, the number of these gaps is growing greater and greater, yet with the discovery and intercalation of new formations, the aggregate of which at the present day has almost doubled the thickness of Paleozoic rocks in the last decade, manifestly the great breaks are being reduced. It was not so many years ago that the Potsdam sandstone was supposed to be the oldest fossiliferous sedimentary rock, yet now we know that many thousands of feet of much more highly fossiliferous strata intervene between this formation and the Azoic, and that other thousands occur above the Potsdam and below the Ordovician as then recognized.

With the intercalation of new formations and the consequent diminution in the size of the stratigraphic gaps, it is then probably only a matter of time before the complete faunal succession can be established. The break in stratigraphy at one point will be bridged over in another area, and it is possible that in only a few regions, such as on the borders of the continent, will permanent gaps exist. Faunas are and will be traced from one area to another until in time we shall know their complete geologic history. With these data in hand, the study of their correlation will not only be greatly simplified, but also will not be hampered by time breaks in the record. While imperfect, or possibly irretrievably lost at the dawn, the faunas of succeeding times are ample for all purposes.

INTERDEPENDENCE OF STRATIGRAPHY AND PALEONTOLOGY

BY DR. W. J. SINCLAIR
PRINCETON UNIVERSITY

IN discussing this subject from the view-point of a vertebrate paleontologist, I am disposed to lay stress on what I believe ought to be, rather than what has been, the degree of interdependence of these two branches of geology. Vertebrate paleontology has been studied very largely from the morphological and genealogical side, a study of structure, adaptation and the evolution of phyla. Stratigraphic geology has been invoked only when it became necessary to know the order of superposition of the various horizons, to determine the true evolutionary succession of a phylum or development of an adaptation.

I have purposely presented this extreme view, not because I believe that such studies may not be classed legitimately as paleontological, but because I wish to emphasize, by contrast, the view-point which we should ever keep before us as paleontologists—the use of our materials as *Leitfossilien*. The two correlative conceptions of the faunal unit and the zone, a more or less restricted association of animals and the

rock layer in which it occurs and which it characterizes, long and successfully employed by the invertebrate paleontologist, must be recognized and used by us also.

I need hardly refer to the fact that the determination of the geological age and the successful correlation of many North American formations, ranging from Mesozoic to Pleistocene, depend in large measure, if not entirely, on vertebrate fossils. I need only contrast the American series of Pleistocene glacial and interglacial stages, determinable at present only by the strictly stratigraphic method of superposition, with the carefully worked-out series in Europe, where each epoch of ice advance and retreat is characterized by its particular fauna and flora. That even the beginnings of stratigraphic paleontology, as contrasted with the morphological, will lead to immediate and valuable results, is strikingly shown by Professor Calvin's¹ recent paper in the *Bulletin* of our parent society, the Geological Society, in which he describes the Aftonian mammal fauna from the earliest of American interglacial stages.

While readily admitting that the slow-moving invertebrate, living, it may be, in the very mud which is destined to become the matrix of its fossil remains, enjoys advantages as a prospective horizon-determiner which the agile vertebrate can more readily, and does most willingly, escape, still the short life of vertebrate species, and their comparatively rapid evolution, fit them for use as index fossils quite admirably. The localization of mammalian faunas, their inability to cross barriers such as ocean basins and great mountain ranges, their dependence on temperature, etc., are comparable to similar conditions circumscribing the free migration of invertebrates. We should not expect to find in the distribution of vertebrate faunas the analogues of the cosmopolitan graptolite zones of the Ordovician or the ammonite zones of the Trias, but we can work out our major zones as recognized by the great migrational movements among vertebrates, expressed in changes in the faunas and the rock succession, which will give us a world scale, and then, by interpolation, fill in the minor and local subdivisions which we probably shall not be able to correlate at once, but which there is every reason to believe we may be able to do later.

The attempt will be accompanied by difficulties which are not appreciated by the invertebrate paleontologist, and I speak feelingly and from experience, for there is a difference between collecting, on the one hand, from a layer a few inches thick, crowded with shells, and, on the other, tramping miles up hill and down over beds hundreds of feet thick, to be rewarded by a few teeth, a lot of useless bone fragments or nothing. Horizons based on vertebrates must include larger stratigraphic units

¹ *Bulletin of the Geological Society of America*, Vol. 20, pp. 341-356, Pls. 16-27, October, 1909.

than are recognized for invertebrates, because of the scattered nature of the material and the additional probability that continental deposits, in which alone vertebrates have their chief importance as guide fossils, have accumulated more rapidly than marine beds. Similarly, conditions peculiar to their mode of deposition make it difficult, perhaps impossible, to define lithologically the limits of the zones we are attempting to characterize. And here another trouble confronts us, for the faunas are incompletely known, and we are not yet in a position to dogmatize too freely on the subject of vertebrate index fossils. But that the method of zonal studies is the correct one is very clearly shown in Dr. Matthew's² recent monograph on the Carnivora and Insectivora of the Bridger Eocene, and will be demonstrated with equal force when Professor Osborn's volume on the titanotheres is published.

Various attempts have been made at the correlation of European and American mammal horizons, their measure of success depending entirely on the degree of closeness with which these correspond to true zones. At present, we are attempting to correlate subdivisions, both faunal and stratigraphic, of all orders of magnitude, the majority including many faunules and many zones. Evidently, this tendency must be corrected by careful zonal studies, if vertebrate paleontology is to have any standing as an aid to stratigraphy in the correlation of our non-marine formations.

BIOLOGIC PRINCIPLES OF PALEOGEOGRAPHY

BY PROFESSOR CHARLES SCHUCHERT

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IN deciphering the ancient geography as to the position of the marine waters and the land masses, we as pioneers in this work must be controlled primarily by the known fossilized life and secondarily by the character and place of deposition of the geologic formations. This record is most extensive and best preserved in the deposits of the continental and the littoral region along the continental shelves of the oceanic areas. Back of these two principles, however, there is another that eventually will become the primary guiding factor. It is the principle of diastrophism—one seeking to explain the causes for the periodic movements of the lithosphere.

In our study of the ancient seas with their sediments and entombed life we have safe guidance in the phenomena of the present. Ludwig in 1886 estimated the species of animals then known to naturalists as upwards of 312,000, and in 1905 Stiles thought this great total had increased to about 470,000 forms. Of this sum fully 60 per cent. are insects, and of the remainder, the writer concludes that about 25 per

² *Memoirs American Museum of Natural History*, Vol. IX., Part VI., 1909.

cent., or 115,000 species, live in the sea, and 71,000 have their habitat on the land or in the waters of the land. Of the 115,000 kinds of known animals inhabiting the seas nearly 70 per cent. are Cœlenterata, Echinodermata, Molluscoidea and Mollusca, the types of organisms most often found by the stratigrapher and on which he is largely dependent in deciphering the ancient geography.

Let us now examine into the number of available fossil forms made known by the paleontologists. As early as 1868, Bigsby in his "Thesaurus Siluricus" listed 8,897 species from the strata beneath the Devonian, and in his "Thesaurus Devonico-Carboniferous" of 1878, he further enumerated about 5,600 Devonian and 8,700 Carbonian forms. In 1889 Neumayr concluded that there were then known about 10,000 Jurassic species. We may therefore estimate that the paleontologists of to-day have access to at least 100,000 species of fossils. Their numbers in the geologic scale are about as follows: Cambrian 2,000, Ordovician 8,000, Silurian 8,000, Devonian 9,000, Lower Carbonian 7,000, Upper Carbonian 8,000, Permian 4,000, Triassic 6,000, Jurassic 15,000, Cretaceous 10,000 and Tertiary 25,000. The end of species-making is not at all in sight, and the day will come when paleontologists will deal with ten times as many species as are now known.

Stiles tells us that zoologists know but from 10 to 20 per cent. of the living forms, and there should therefore be from 3,760,000 to 4,700,000 different kinds of animals alive to-day, ranging from the protozoa to man. Now let us compare the abundance of living animals with those of the geologic ages, and especially with the Jurassic period, of which life we have probably a better knowledge than of any time back of the Tertiary. The European Jurassic has long been divided into 33 zones (Buckman hints at a probable 100), and if we hold that each one of these times had only one quarter as many species as in the lowest estimate of the present world, there must have lived during the entire Jurassic something like 31,000,000 kinds of animals. Yet paleontologists have described not more than 15,000 Jurassic forms. The great imperfection of the extinct life record is thus forcibly brought to our attention, and we learn from these estimates that for each kind of animal preserved in the rocks more than 2,000 other kinds are utterly blotted out of the geologic record.

Much of this more apparent than real imperfection, however, is due to the vast number of insect species now living—animals that must have been comparatively few in the Jurassic, due in the main to the absence of flowering plants. From these figures, however, we must not conclude that the geologic record is equally imperfect throughout; for the paleontologist studying marine fossils well knows that he can not, as a rule, hope to study other than those kinds of animals that have hard and calcareous or siliceous external or internal skeletons. Of

such there may be in the present seas about 250,000 kinds, of which about 25,000 have been named. Therefore on this basis we can say that the student of Jurassic faunas knows 1 species in every 54 of shelled animals that lived during this period.

This admittedly great imperfection of the life record needs to be further explained so that the reader will not arrive at the erroneous conclusion that modern stratigraphy rests upon very insecure foundations. The stratigrapher in determining the age of a given deposit, and in the identification of it from place to place and from country to country, and even across the great oceans, deals in his work not with quantity of species, but with comparatively small numbers of constantly recurring hard parts of certain species that are more often of marine than of land origin. Many of these forms have but local value but others have spread thousands of miles, and some of the long enduring species range over the greater part of the earth. Some of the best guide fossils in the Paleozoic are the brachiopods because they are present in nearly all the strata of this era. The writer in 1897 listed 1,859 forms then known from these rocks of North America. Of these about 28 per cent., or 537 species, had great geographic distribution. 117 species are found in the Rocky Mountain area, the Mississippi valley and the Appalachian region, and of these 36 are also known to occur in foreign countries. The number of species common to North America and other continents, however, is 121. It is upon faunal assemblages of this quantity and nature that the stratigrapher relies most in deciphering the former extent of the continental seas.

In the making of paleogeographic maps or in the determination of geologic time, using fossils as the essential basis, we have guidance in those of marine faunas, and the floras and faunas of the land and its fresh waters. Of these widely differing realms or habitats we now know that the fossils of the marine faunas are the more reliable not only because there are so many more of them than of the land dwellers, but more especially because their geologic succession is far more complete. The conditions of preservation, that is, appropriate burial in sediments, are always at hand in marine waters, but on the land entombment occurs only exceptionally, whereas the life of fresh waters is very meager and almost unchanging during geologic time. Then, too, marine life is "less affected by meteorologic factors, and more dependent upon conditions which affect the whole hydrosphere rather than small areas of it. The struggle for life is less intense, the food supply generally more adequate, enemies less vigorous, and dangerous fluctuations of temperature far less frequent, in the sea than on land. The same features make the land fauna more clearly indicative of minor divisions of the scale, and of the progress of organic evolution

in the general region concerned; while less conclusive as to the contemporaneity of widely separated though analogous faunas."¹

In regard to the probable geographic position of the shore lines we rarely have safe guidance in the fossils, and for this depend on the nature of the deposits. Greatest dependence is placed upon the geographic position of sandstones and especially on conglomerates to indicate the probable former shores. Limestones of uniform character and wide distribution are indicative of greater distance from land. Shallowness of the continental seas is proved by a rapid change in the character of the sediments both laterally and vertically, and by the oolite and dolomite deposits. Intraformational conglomerates, coral reefs, ripple marks, and shrinkage cracking furnish further evidence to the same conclusion. Storm waves are known to plough the present sea-bottom to depths of 160 feet. Calcareous muds are now forming in tropical and subtropical waters at sea-level around coral reefs, and elsewhere in these latitudes at depths from 200 to 600 meters. It is probable that all of the ancient great limestone deposits are of warm waters, and, if so, are an additional aid in discerning the geologic times and regions of milder climates.

Phosphatic concretions form in the littoral region where the temperature changes are rapid, as off the coast of the New England states, and periodically cause much destruction of the individual life. The carcasses decompose at the bottom of the sea, making nuclei for the accretion of phosphate of lime, and because of the irregular periodicity of accumulation come to be arranged in definite stratigraphic zones. Old Red sandstone fishes are also usually found in clay nodules but abundantly only in limited zones (Scaumenac, Canada and Wildungen, Germany). Have these also been killed by rapid changes in the temperature of these waters? In any event the fish-bearing beds are always found near the shore lines of Devonian seas.

Scour of sea bottom is met with in the present seas where great streams of water are forced through narrow passages, as the Gulf Stream in the Floridian area; or where such streams impinge against the continental shelf, as north of Cape Hatteras, or flow across submerged barriers "a few miles broad," as the Wyville-Thomson ridge connecting the British and Faeroese plateaus (Johnstone, 1908, 31). Strong currents preventing sedimentation also occur in long and narrow bays, as that of Fundy, where the undertow caused by the very high tides of this region sweeps the bottom clean. These exceptional and, after all is said, rather local occurrences can not be the explanation for the many known breaks in the geological sedimentary record, the disconformities of stratigraphers. These breaks are at times as extensive as the North American continent (post Utica break), and are usually

¹ Dall, *Jour. Geol.*, 1909, 494.

of very wide extent. Scour of the bottom by the currents of the ancient continental seas will not explain away the presence of these truly land times, but it is to be sought in the oscillatory nature of the seas of all time which is probably caused by the periodic unrest of the earth's crust due to earth shrinkage. We agree with Suess that "Every grain of sand which sinks to the bottom of the sea expels, to however trifling a degree, the ocean from its bed," and every movement of the sea-bottoms and the periodic down fracturing of the horsts causes the strand lines to tremble in and out, be they of a positive or transgressive or of a negative or land-making character.

The ancient marine life had similar zoogeographic arrangement to that of the present. It can be grouped into local faunas and these combined into subprovinces, provinces and realms. Their distribution is governed primarily by the presence or absence of land barriers, and secondarily by temperature and latitude. In the present seas temperature is one of the main factors controlling the distribution of the species, but during the geologic ages the climate was, as a rule, far more uniform than now, as we are living under the influence of polar ice caps and a passing glacial period, or possibly even an Interglacial period.

The faunas with which the stratigraphic paleontologist works appear in many instances as suddenly introduced biotas. Our collaborators of half a century ago explained them as Special Creations, but since their time we have learned that the suddenly appearing faunas are not such in reality but only seem to appear rather quickly due to the slowness of sedimentary accumulation. Ulrich estimates that the American Paleozoic has less than 100 mapable units or formations, each with a duration of probably not less than 175,000 years. Accordingly, each foot of average sedimentary rock has taken not less than 833 years to accumulate. Our knowledge regarding the average rate of sedimentary marine accumulation is, however, as yet very insecure, and to make this clear some of the remarks made by Sollas, President of the Geological Society of London (1910), will be quoted. He was led to make these remarks after the reading of a paper by Buckman correlating the Jurassic sections of South Dorset. He said, "The correlation of thin seams with thick deposits was a matter of great importance. . . . It might afford some hints as to the order of magnitude of the scale of time. If we assumed that one foot of sediment might accumulate in a century, in an area of maximum deposition, then in the case of the seam two inches thick, which was represented by 250 feet in the Cottswolds, the rate of formation would be less probably than 1 foot in 150,000 years." What Ulrich's estimate of time necessary for the accumulation of one foot of average sediment means to migratory faunas may be illustrated by the spreading of *Littorina littorea*. In the last

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century this edible European gastropod was introduced at Halifax, Nova Scotia, and in 50 years attained the Delaware Bay and north to Labrador. Taking this dispersion as the basis for calculating faunal migrations, we learn that they may spread 500 miles, while one sixteenth of an inch of average sediment is depositing, or 8,000 miles during the time of one foot of sedimentary accumulation. If, therefore, Paleozoic faunas migrated "only one fiftieth as fast as this living shell, then we may reasonably assert essential contemporaneity for stratigraphic correlations extending entirely across the continent." We have here an explanation for the apparently sudden distribution of the Ordovician brachiopod *Rhynchotrema capax*, that everywhere holds an identical geologic horizon from Anticosti to the Big Horns and from El Paso, Texas, to Arctic Alaska. *Spirifer hungerfordi* spreads during the first half of Upper Devonian time from the Urals to Iowa, and another brachiopod, *Stringocephalus burtoni*, migrates during the last third of Middle Devonian time from western Europe to Manitoba.

The life of the present seas extends from the strand-line to the deepest abyss, but by far the greatest quantity and variety lives in the upper sunlight, photic or diaphanous region. Photographically the light of the sun is detectable in exceptionally clear-water tropical seas to a depth of about 2,000 feet, but Johnstone places the average depth for all waters at 650 feet, beyond which there is more or less of total darkness, the aphotic realm.

Sunlight is the first essential for the existence of life. Where it penetrates, there plant life is possible, and this life is the substratum on which all animal life is ultimately dependent for food. Near the surface of the sea lives the plankton, sometimes referred to as the "pastures of the sea" and compared with the "grass of the fields." Most of this plankton consists of diatoms that at present are by far more prolific in the cooler polar waters. At times of greatest abundance in Kiel Bay as many as 200 of these "jewels of the plant world" are contained in a drop of water, and in the Antarctic seas there is an area of ten and one half million square miles where diatom ooze is accumulating. They are the principal food supply for most of the sessile benthos, or bottom life, among which the mollusca and brachiopods are of the greatest importance in paleogeography.

Geologic deposits rich in diatoms are sometimes regarded as those of the deep sea, at least as of deeper waters than those of continental seas. The English Carboniferous deposits, rich in diatoms, have a fauna whose species are all of the shallow water kinds. The vast Miocene diatom deposits of California, described by Arnold, have living bottom types of foraminifera that, according to Bagg, do not indicate a depth of over 500 fathoms.

From the present distribution of marine life we learn that the

greatest bulk of invertebrates are restricted to the bottom of the shallow seas within the depth to which sunlight readily penetrates, that is, a depth on the average not over 600 feet. The value of this observation to the paleogeographer and the student of fossil marine life lies in the confirmation of paleontologists that continental seas are shallow seas, to the bottom of which in most places sunlight permeates. These seas are to be compared with the littoral regions of the present oceans, and they are the areas that are most exposed to climatic and physical changes, due to their proximity to the atmosphere and the lands. The life of these waters is, therefore, subject to an environment that is more or less changeable, and one of the basic causes underlying organic change. It is the invertebrates of the littoral and shallow seas that the paleontologist studies.

In the tropical and subtropical shallow seas one meets with the greatest variety of life and with the brighter colored and more ornamental shelled animals, but we are much surprised when told that the greatest number of individuals occur in the colder shallow waters of the temperate and polar regions. Johnstone states, "There is little doubt that the distribution of life in the sea is exactly opposite to that on the land. The greatest fisheries are those of the temperate and arctic seas. . . . Nowhere are sea birds so numerous as in polar waters. The benthic fauna and flora are also most luxuriant." The Bay of Naples has a "richly varied, but (in mass) a scanty fauna and flora," and "at the very least the amount of life in polar seas is not less than in the tropics."

Marine life is also more prolific near river mouths of the temperate zones, probably because of the great quantities of dissolved "salts of nitrous and nitric acid and ammonia, and other substances which are the ultimate food-stuffs of the plankton." Just outside of the estuary of the Mersey in Lancashire there were "not less than twenty, and not more than two hundred animals varying in size from an amphipod (one fourth inch long) to a plaice (eight to ten inches long) on every square meter of bottom" (Johnstone, 1909: 149, 176, 195-6). Finally the quantity of life in the shallow waters of the sea is not directly governed by favorable habitat, such as shallow sunlight waters in constant circulation and of equable temperature, but seems to be primarily controlled by the amount of the minimal food elements. Sea-water may be regarded as a dilute food-solution having the essential materials on which life is dependent. Of these nitrogen and the compounds of silica and phosphoric acid are present in the smallest amount. Johnstone tells us that "The density of the marine plants will therefore fluctuate according to the proportions of these indispensable food-stuffs" (234). "It is only the protophyta among the

"Life in the Sea," 1908, 201-205.

plankton which can utilize the CO_2 and the nitric acid compounds, and so we see that upon these rest the greater part of the task of elaborating the dissolved food-stuff of the sea" (239).

Undoubtedly much of the land-derived nitrogen, estimated at 38 million tons per annum, is used up in the shallow areas by the plants. We therefore arrive at the conclusion that shallow seas bordering naked, cold, or arid lands should have the smallest amount of life, and that those of temperate regions adjacent to low lands under pluvial climates should have the greatest number of individuals. This conclusion, however, may be decidedly altered by the oceanic currents in that they distribute far and wide the salts of the sea.

These factors also suggest that during "critical periods" the faunas should be least abundant and varied, and that at the times of extreme base levels and sea transgressions they ought to be at their maximum development. These suggestions are borne out by the small Cambric, Permian and earliest Eocene faunas and the large cosmopolitan biotas of the Silurian, Jurassic and Oligocene times.

Sessile algæ are not common on muddy or sandy grounds, and these areas in the present seas have been compared with the desert areas of the lands. That muddy grounds are now nearly devoid of algal growth has particular significance in stratigraphy, because in the geologic column at many levels and in nearly all regions occur black shale formations that are not only devoid of plant fragments but are also usually very poor in fossils of the sessile benthos. When the latter are present it is seen that they are usually thin-shelled and small forms, or are types of organisms that live in the upper sunlight realm and are either of the swimming plankton or the floating nekton. As examples of such deposits may be cited the widely distributed Utica formation of the Ordovician extending from southern Ohio to Lake Huron and east to Montreal, and the Genesee (Devonian) of New York. In these cases what appears to be of the sessile benthos is thought to belong to the nekton attached to floating seaweeds or other floating objects, and eventually all of the life of the nekton and the plankton sinks to the bottom of the sea. Therefore the carbonaceous matter of the black shales may be of algal origin like that of the New York Genesee, but it is far more probable that it is largely of animal origin, as the crude petroleum of such deposits usually has the optical properties of animal oil and especially those of fish oil.³ Plants may be torn from rocky bottoms of the shallow areas by the action of the storms and then carried by the currents into eddying areas like the present Sargasso Sea, which has among its algæ a very characteristic assemblage of animals. It is probable, however, that black shales having wide distribution were more often the deposits in closed arms of the sea (cul

³ Dalton, *Economic Geology*, 1909, 627.

de sacs), or when of small areal extent, as the result of fillings of holes in the sea bottom. In all such places there is defective circulation and lack of oxygen resulting in foul asphyxiating bottoms.

These are the "halistas" of Walther and the "dead grounds" of Johnstone. To-day such are the Black Sea and the Bay of Kiel, where sulphur bacteria abound in greatest profusion. These decompose the dead organisms that rain from the photic region into such suffocating areas, or the carcasses which are drawn there by the slow undertow from the higher ground. These bacteria in the transforming process deposit in their cells sulphur that ultimately combines with the iron that is present and replaces the calcareous skeletons of invertebrates by iron pyrite or marcasite. In this way are formed the wonderfully interesting pseudomorphs of *Triarthrus becki*, the Utica trilobite preserving the entire ventral limbs, and of the other well preserved but small invertebrates from the Coal Measures black shale of Danville, Illinois.

Brackish-water and especially deep-sea shelled animals tend to have thin shells, while increase of salinity tends towards the thickening and roughening of the calcareous shells. It is a well known fact that in the dolomite-depositing continental seas like that of the Guelph (Siluric), all of the molluscs have ponderous thick shells. These have been interpreted as reef-living species but actual reefs in the Guelph are unknown. The molluscs are often common but corals are represented by but a few species. Similar conditions are known to occur in other dolomite faunas. Further, the Guelph was of a time of decided progressive emergence and restrictional seas under an arid climate, and therefore the waters must have been abnormally salty.

Rivers constantly discharge into the sea great quantities of plant material, but as a rule little of it other than the wood is swept far out to sea. At present the rivers of northern Siberia float into the sea vast numbers of logs that drift with the currents to Spitzbergen, East and West Greenland and Arctic America. This wide dispersal of wood by the sea is met with only in the cold regions, whereas in tropical waters the wood is rapidly decomposed. Single leaves are rarely transported far from their place of origin, and when of good preservation in geologic deposits, give decisive evidence of the nearness of the shore. On the other hand, tough palm leaves have been seen in the sea 70 miles from land and rafts of leaves are often met with 200 or more miles beyond the mouths of the Kongo and the Amazon. Proximity to shore is also indicated by the presence in marine faunas of land molluscs, insects and bones of land vertebrates.

With tillites now known in the Lower Huronian of Canada, in the Lower Cambrian of northern Norway, China, South Africa and Australia, and in the Permian of India, South Africa, Australia and Brazil, we observe the recurrence of glacial climates. The Silurian and Devonian

coral reefs occurring in Arctic regions, the sponge, coral and bryozoa reefs in the Jurassic of northern Europe, the rudistid and other cemented pelecypods in reefs of wide distribution in the Cretaceous, and the almost world-wide distribution of the Nummulitidæ (north of Siberia) in the late Eocene and Oligocene point as clearly to warm waters and mild polar climates. Further the widely distributed Carbonic foraminifers of the family Fusulinidæ that swarmed in temperate and tropical regions are unknown to Arctic and Antarctic regions. In other words, long before we have a fossil record the earth had climatic zones, and for long periods the climate was mild to warm, punctuated by shorter intervals of cold to mild climates.

The volume of sea water to-day is very great, but we must ask ourselves: Has this quantity always been such or was it even greater, as some geologists still hold? We no longer agree with Laplace and Dana that the earth passed through an astral stage, but rather agree with Chamberlin that it always has had a more or less cold exterior. Through volcanic activity much juvenile water from the interior of the earth was extruded in geologic time and was added to the vadose waters of the surface. Suess states that "the body of the earth has given forth its oceans and is in the middle phase of its gas liberations." Accordingly, the Paleozoic oceans must have been quantitatively smaller than those of the present, and the gradual increase in the volume of vadose waters has been accommodated by the periodic increase of oceanic depth.

We also agree with Walther that the oceans of Paleozoic and earlier time did not have the great abyssal depths they now have. The accentuated deepening of the permanent oceanic basins did not begin until the Triassic, for in none of the great depths of the present oceans are found traces of Paleozoic organisms, and all here are of Mesozoic or Tertiary origin. In the shallow regions, however, are still found a few Paleozoic testaceous-bearing genera of brachiopods, tubicular annelids, pelecypods, gastropods, *Nautilus*, and *Limulus*. The deepening of the Pacific, the Indian, and especially the Atlantic oceans has been at the expense of the lands or horsts, for the ancient continents, Gondwana and Laurentia, have each towards the close of the Mesozoic been broken into several masses. We may therefore speak of permanent oceans, and transgressed, fractured, and partially down faulted, continents or horsts.

These are some of the factors that control the making of some of the modern paleogeographic maps.

BIOLOGIC PRINCIPLES OF PALEOGEOGRAPHY

By DR. F. H. KNOWLTON

U. S. GEOLOGICAL SURVEY

CONSIDERING the breadth and intricacy of the subject assigned me, and the limited time that can be given to its consideration, it has seemed best to me to restrict my remarks to two or three of the obviously more important phases of the problem.

Aside from the study of the rock-masses themselves—which are often difficult of interpretation—reliance for an interpretation of paleogeography must be placed in the former life found entombed, and of the two biologic elements, plants undoubtedly hold a very high—probably the highest—place.

In making use of plants in the study of paleogeography we may first consider distribution. If we find two fossil floras identical or similar in all essential or important details, we feel justified in regarding them for all practical geologic purposes as contemporaneous. In order that we may be certain that the two floras are identical, they must be composed of types that are readily identifiable, that is, forms so well characterized that they may be easily and certainly recognized. As examples of such floral elements mention may be made of many ferns and fern allies, most cycads, conifers and peculiar, well-marked or characteristic dicotyledons. Having settled the contemporaneity of the floras, inquiry may next be made as to the probable manner in which the separated or isolated areas were reached by these floras. Here again we must carefully consider the character of the flora and the means for its natural dispersal. The living flora, and for that matter probably the floras from at least the beginning of the Tertiary progressively to the present time, has developed in many ways means for the comparatively rapid and wide-spread dissemination of their reproductive parts (seeds, etc.). For example, a large percentage of the members of the dominant living family of seed-plants—the Compositæ—have developed seeds with an attachment of soft, fluffy hairs which serve to float them in the air, often to great distances. In many other living groups there are similar, or at least as effective, devices for dissemination, but as we go back in time adaptations calculated to be of aid in distribution grow less and less, and soon even seeds of any kind are unknown, or known but imperfectly, and reproduction is normally by means of spores, that is, reproductive bodies in which there is no embryo already formed when they leave the parent plant. It is obvious that plants that are reproduced by seeds, in which there is both an embryo and a supply of food for use during germination, must possess a decided advantage over those reproduced by means of spores.

In the groups of spore-bearing plants ordinarily found fossil, the spores are not known to have developed any particular devices for their wide dissemination, such as flotation in air, attachment to animals, etc. They are produced in vast quantities, and depend upon a few reaching situations favorable for successful germination. Their vitality is also of apparently exceedingly limited duration, and it is doubtful if they could long survive immersion in salt water.

The bearing of the above digression is apparent. Given a fossil flora made up of ferns or fern allies, exclusive of what are known to belong to the cycadofilices, and when such flora is found in two or more separated areas, we are justified, in my opinion, in arguing a practically continuous land connection. They were incapable of crossing very wide reaches of open water, particularly salt water. Fresh-water streams have been to some extent avenues of distribution, but many fossil floras—and living floras as well—are too widely spread to be explained by this means. When, as is usually the case, identical floras occupying different areas are mixed floras, the bearing on the means of reaching the various areas is more complicated. An example may better serve to bring this out. Thus, the Jurassic flora is practically world-wide in its distribution, ranging from Franz Josef Land, 82° N., to Louis Philippe Land, 63° S. It is composed of ferns, fern-allies, cycads and conifers, a large percentage being true ferns. The probability of a close land connection argued on the basis of the true ferns, has already been alluded to. The cycads—the Jurassic is called the age of cycads—were abundant in individuals and numerous in forms. On the basis of our knowledge of living types, it may be stated that cycad seeds germinate immediately on falling from the cone without any necessary resting period. They are not known to retain their vitality for a longer period than three years, and usually but two years. They sink promptly in fresh water and as the stony coat is easily penetrated by water, they either germinate or rot at once. In salt water they will probably sink and decay even more quickly. Therefore, the probability of their being transported for any great distance over open water is reduced to a minimum. The conifers of the Jurassic were reproduced by seeds. They belong to types not known to enjoy any special means for transportation, nor is it probable they could better withstand fresh- or salt-water immersion than the cycads. All classes of vegetation present in the Jurassic, therefore, argue for a practically continuous land connection.

In considering the bearing of any flora on the paleogeographic problem the process is similar to that outlined above. That is, an analysis of the composition of the flora, a study of the means of natural dissemination which includes duration of vitality, and finally a judgment as to its probable means or avenues of transportation, involving a land connection or otherwise.

A word may be said as to the presence of land plants in marine deposits. That the trunks of trees may float for a considerable time and to great distances is undeniably possible, but unfortunately the study of fossil wood has not yet reached that degree of refinement in most cases that will permit of its general use, and reliance in identification must be placed largely in foliar and reproductive organs. The delicate fronds of ferns, leaf-clad branchlets of conifers and the leaves of seed-bearing plants are incapable of long withstanding the immersion and wave action of salt waters. In my judgment, therefore, the presence of fronds, leaves and similar organs in marine deposits argues very near-by land.

The only other point I shall consider is the bearing of plants on the interpretation of *climate*. Since it is generally acknowledged that plants furnish the most reliable data for this phase of the subject, an inquiry as to the kinds of plants that have been found most valuable in this connection may be of interest. Obviously our interpretation of the probable conditions under which the plants of past geological ages grew, must be on a basis of a knowledge of present conditions found to obtain for similar or closely related groups. That we may occasionally err in this is possible, especially if reliance is based on too few forms, but when all the various elements of a flora are considered, the results are thought to be within a close approximation of the truth. Thus, since *Artocarpus*—the bread-fruit tree—only grows at the present day within 20° of the equator, it follows that when *Artocarpus* is found fossil in Greenland, 72° N., the conditions at the time it flourished there must have been tropical or subtropical, and this conclusion is confirmed by the tree ferns and cycads associated with it. Palms can not flourish with a temperature below 40° ; a fossil flora, rich in palms of well-defined types, could hardly have grown under very much cooler conditions. Tree-ferns are practically confined to within 30° of the equator and a temperature of approximately 60° . A fossil flora, such, for example, as the Triassic of Virginia, that contains numbers of tree-ferns, must have grown under tropical or subtropical conditions. A fossil flora rich in types, the living representatives of which can withstand a temperature of -40° to -60° , or even lower, must have been at least cool-temperate. Cycads are now found only within 30° of the tropics; a rich cycad flora argues then for a tropical or at least a subtropical climate.

Examples of this kind could be multiplied almost indefinitely. In interpreting geological climate selection is made so far as possible of the plants or groups of plants, that are confined at the present day within relatively narrow limits of temperature, be this high, medium or low.

PALEONTOLOGIC EVIDENCES OF CLIMATE

By T. W. STANTON

U. S. GEOLOGICAL SURVEY

TO every one climate is an interesting theme. The climates of the past, especially when they can be shown to differ in character or distribution from those of the present, attract the attention of the general public, and they are of importance to the special student of geologic history whether his researches deal with the purely physical aspects of the subject or include some branch of paleontologic study.

The evidence as to former climates comes from many sources. The records of deposition and denudation in themselves sometimes give more or less definite indications concerning variations in temperature or moisture or both; the land floras when compared with those now living by their general characters and by the details of their structure, show more or less clearly the climatic conditions under which they lived; the land animals, especially the higher vertebrates, afford a good basis for inferring their habits and hence indirectly their environment, including climate; marine invertebrates give trustworthy evidence of differences in temperature of oceanic littoral waters at least in the later periods. It is obvious, however that the data furnished by any one of these lines of evidence will make only unconnected fragments of the history of past climates and that the evidence on the climate of any particular epoch, if derived from a single source, is seldom so complete or so convincing that corroborative testimony from other sources is not desirable. The subject is one in which general cooperation is essential.

It should be stated at the outset that the most abundant and most definite evidence comes from paleobotany, and will be outlined in Mr. White's paper. The discussion of the data derived from fossil vertebrates must also be left for some one who is qualified to present it, and the whole Paleozoic era may be passed over with the statement that so far as indications from the animal life are concerned the climate of the whole earth was mild and equable. The proof of local exceptions to this statement comes from other sources.

All inferences from paleontologic evidence as to former climatic conditions rest in the final analysis on a comparison with the present distribution of animals and plants with reference to climate. Such comparisons may be general or specific, direct or indirect, and the con-

clusions that may be drawn from them vary greatly in positiveness. To take a familiar example, the reef-building corals are now restricted to shallow waters in which the mean temperature during the coldest month in the year is not less than 68° F., and such conditions are not found in the northern hemisphere north of latitude 32° . Since late Tertiary corals differ but little from those of the present time it is justifiable to assume that coral reefs in late Tertiary rocks indicate waters of about the temperature stated. But when Jurassic coral reefs are found as far north as latitude 53° it is by no means so certain that they indicate a minimum monthly mean temperature of 68° F., and concerning Devonian and Silurian coral reefs in high latitudes the doubt must be still greater. At the present time large reptiles are mainly confined to hot moist climates, but that fact alone can not be considered proof that the Mesozoic dinosaurs required the same kind of a climate.

The impress of climate on the present fauna is shown in various ways. A tropical fauna contains the greatest number of species and exhibits its luxuriance in other ways. Thus, taking shell-bearing marine mollusks to illustrate the general law, Dall has shown in Bulletin 84, U. S. Geological Survey, that the average tropical fauna in shallow waters consists of over 600 species, while the temperate fauna has less than 500 species, and the boreal fauna only 250. Again, there are certain genera that are characteristic of particular zones, and assemblages of forms that are recognized as belonging only to frigid, or temperate, or tropical waters, and in genera that have a wide range many of the species are restricted to certain limits of temperature.

In the late Tertiary faunas which contain a large proportion of living genera and many living species justifiable inferences as to climate may be made from direct comparison with living faunas. By one or another of the tests just indicated, or by a combination of them, Dall has produced convincing evidence that the Oligocene fauna of the Atlantic states was subtropical and that the Oligocene maintains its subtropical character even as far north as Arctic Siberia. He has also shown that the Miocene fauna of Maryland indicates a temperate climate and that a similar cool-water fauna extended at that time as far south as Florida.¹ The fossils of the raised Pliocene beaches at Nome, Alaska, according to the same investigator, furnish evidence of warmer climate during Pliocene time even at that high latitude. By similar methods, in a paper published in the *Journal of Geology*, Vol. XVII., Arnold has recently argued for a series of climatic changes in the late Tertiary and Pleistocene of California.

When the investigation is carried back to the Mesozoic and earlier

¹ See especially Dall's "Contributions to the Tertiary Fauna of Florida," published as Vol. III. of the *Transactions of the Wagner Free Institute of Science*, Philadelphia, and a chapter in the Miocene volume of the Maryland Geological Survey.

faunas in which few of the genera and none of the species are identical with those now living the problem becomes more difficult and the conclusions are much less definite, as the comparisons must be more general. Proofs of actual temperatures as measured in degrees should not be expected unless the botanists can furnish data. There is, however, great local differentiation of faunas and it is fair to ask the question to what extent this is due to differences in climate. One of the earliest discussions of this question was by Ferdinand Roemer, who more than fifty years ago in "Die Kreidebildungen von Texas" noted the fact that the Cretaceous of the highlands in Texas is lithologically and faunally much like the Cretaceous of southern Europe and the Mediterranean region, that it differs from the Cretaceous of New Jersey in about the same way that the southern European Cretaceous differs from that of England and northwestern Germany, and that in each case the European deposit is approximately 10° farther north than its American analogue. He concluded that the differences between the northern and southern facies were due to climate and that the climatic relations between the two sides of the Atlantic were about the same in Cretaceous time as they are now. Roemer's conclusion that there were climatic zones in the Cretaceous may be true, but his reasoning was based on false premises so far as the American deposits are concerned, for the New Jersey type of marine Cretaceous extends with little change all the way from New Jersey to the Rio Grande, and the "Cretaceous of the highlands" with which he contrasted it, now known as the Comanche series, is not represented by marine beds on the Atlantic coast. This shows the necessity for careful stratigraphic and areal work as well as for good paleontology before such broad conclusions can be safely made.

The more general work of Neumayr² recognized in the Jurassic and Cretaceous of Europe three faunal provinces designated as boreal, central European, and alpine or equatorial, which on account of their zonal distribution he regarded as indicating climatic differences. He believed that these zones are recognizable throughout the northern hemisphere and cited evidence to show that similar zones exist south of the equator. In recent years Neumayr's conclusions have been questioned by many because in so many instances genera supposed to be characteristic of one zone have been found mingled with those of another. For example, the alpine ammonite genera *Lytoceras* and *Phylloceras* occur in Alaska (lat. 60°) associated with the boreal *Aucella*, and *Aucella* itself ranges from the Arctic Ocean to the torrid zone. Still, in spite of such exceptions and anomalies in distribution, there is much evidence for a real distinction between boreal and southern faunas in the Jurassic and in the Cretaceous which may indicate a zonal distribution of temperature in Mesozoic time. It should be

²"Erdgeschichte," Vol. II., p. 330 et seq.

remembered, however, that a boreal climate probably did not then mean a frigid climate, and that the differences in temperature were probably not so great as at the present time.

The conclusions justified by the evidence from fossil invertebrates are:

1. In the Paleozoic there is practically no faunal evidence of climatic zones comparable with those that now exist.

2. In the Mesozoic there is a more or less definite zonal distribution of faunas which may be in part due to differences in climate but this conclusion in each case should be checked by the study of the floras and all other available lines of evidence.

3. From the middle of the Tertiary on through the Pleistocene trustworthy conclusions as to climatic conditions and changes can be made by direct comparisons with the distribution of living faunas.

THE MIGRATION AND SHIFTING OF DEVONIAN FAUNAS

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IN the year 1881 I presented before the American Association for the Advancement of Science the first definite announcement of the theory of recurrent faunas, applying it to the fauna of the Marcellus, Genesee and Ithaca black shales of New York, which I then conceived to be represented by the continuous fauna of the black shales of Ohio, Indiana, Kentucky and Tennessee; and also in the same paper the theory of shifting of faunas was applied to the Hamilton and Chemung faunas of central New York.¹ Since that time a large amount of evidence has been accumulated confirming these hypotheses.

The two hypotheses are correlated. Recurrence, or the departure of a fauna, its replacement by another and its final reappearance in the same section at a higher level, become the facts upon which the hypothesis of shifting of the faunas is based; and only on the assumption of the continuance and shifting of a fauna without losing its characteristics can we satisfactorily explain its recurrence.

The following facts are among the more important which have come to light in the course of my studies:

§ 1. *The Catskill sedimentation* was shown to be thicker and to start lower down in the geological column in eastern New York than in middle and western New York. In eastern New York it began while the Hamilton marine fauna was still present and cut it off, bringing in estuarian conditions with a brackish water and land fauna and flora. In middle New York no Catskill sedimentation is present until after

¹ *Proc. American Association for the Advancement of Science*, Vol. XXX., p. 186, etc.

the arrival of the Chemung fauna; and in western New York no trace of the Catskill type of sediments appears till after the close of the Devonian.

These facts are direct evidence of shifting of the environmental conditions of the edge of the continent westward as the deposits of the middle and upper Devonian were being laid down. With this shifting westward of the off-shore conditions of the sea, there went on a corresponding shifting of several faunas that were adjusted to each phase of those conditions.

These facts were stated in a paper on the classification of the upper Devonian published in 1885.²

§ 2. *The Appearance of Dominant Species of a General Fauna in Reversed Order of Succession at the Close of a Fossiliferous Zone.*—The case of *Spirifer lævis* in the Ithaca Zone and of the frequent appearance of *Leiorhynchus* at the opening and close of a fossiliferous zone were among the earliest observed facts suggesting the actual shifting of the body of the fauna entering the area in one order of succession and its departure in the reverse order. In the Ithaca section there occurs at the base of the fossiliferous zone of the Ithaca member a bed containing abundance of *Spirifer (Reticularia) lævis*. The discovery of the same species at the top of the fossiliferous zone as the normal Ithaca fauna become sparse gave the first suggestion that the faunas were moving or shifting. The *Reticularia* zone marked the first trace of the fauna to enter and the last to leave the area. Confirmatory evidence was also found in the order of succession of the dominant species of the Ithaca fauna. These facts were reported in 1883.³

§ 3. The study of the *mode of occurrence of Leiorhynchus* still further drew attention to the definite order in which series of species came in and went out of any given area. The species of the genus were generally found abundantly at the base or at the top of the fossiliferous zones rich in the brachiopods in the midst of which *Leiorhynchus* was rare.⁴

§ 4. The *reappearance* in a single or few strata of several *representatives of an earlier fauna* long after the formation to which they were normal had ceased.

Slight traces of this fact were observed in the first survey of the Devonian section passing through Ithaca, reported in 1883, Bull. 3, U. S. G. S., and the fauna No. 14 N (p. 15) was called a recurrent Hamilton fauna because of the appearance there of such species as *Spirifer fimbriatus*, *S. augustus*, *Pleurotomaria capillaria* and others;

²Proc. American Association for the Advancement of Science, XXXIV., p. 222.

³Bull. 3, U. S. G. S., p. 20, and 1885 Proc. A. A. A. S., Vol. XXXIV., p. 222, etc.

⁴See Bull. 3, U. S. G. S., pp. 16 and 17, 1883.

and higher up in the midst of the Chemung section at Chemung narrows *Tropidoleptus carinatus* and *Cypricardella bellistriata*, *Phacops bufo* and *Dalmanites calliteles* were found.

The discovery of such traces of an earlier fauna led to further search; and as the evidence accumulated an elaboration and definite formulation of the theory of recurrence of faunas was made which has been set forth in several papers, and is illustrated in detail in the folio of the Watkins Glen-Catatunk quadrangles, which is now in press, for the U. S. Geological Survey (December, 1909).

The facts there brought out are substantially as follows: There are exhibited in the sections mapped for the quadrangles two series of fossiliferous zones; the separate zones of the two series alternate in succession; the zones of one series dominate the western sections of the area and thus thin out or disappear on tracing them eastward; the zones of the second series dominate the eastern sections and particularly the whole eastern New York sections, but thin out westward and in some cases are entirely wanting in sections west of the Watkins Glen quadrangle. The first set of faunal zones includes the faunas of the Genesee shale, the Portage formation and the several divisions of the Chemung formation.

The second set of zones includes the Hamilton fauna proper and recurrent representatives of that fauna which I have named the *Paracyclas lirata* zone, the *Spirifer mesistrialis* zone, the *Leiorhynchus globuliformis* or Kattel Hill zone. These zones are represented by the typical Ithaca group of Hall in its typical sections at Ithaca; and above them appear the first, second and third recurrent *Tropidoleptus* faunas (which I originally named the Van Etten, the Owego and the Swartwood *Tropidoleptus* zones, respectively). All of these several fossiliferous zones of the second set become decidedly thin on passing westward across the region. The Ithaca fauna is, occasionally, detected west of the Watkins Glen quadrangle, but is confined to less than 100 feet thickness at Watkins, is recognized for three hundred feet at Ithaca and ranges through at least 600 feet along Tioughnioga River.

Only a slight trace of the *Paracyclas* zone is seen as far west as Ithaca, but it is well expressed in the section on the east side of the area. The Van Etten, Owego and Swartwood *Tropidoleptus* zones appear in thin tongues of strata as far west as the Waverly quadrangle and are seen in occasional traces as far west as the Elmira quadrangle. When followed eastward they appear to blend together as a modified Hamilton fauna sparsely appearing in the strata up to the income of the Catskill type of sedimentation.

Where the Hamilton recurrent zones are seen in sharpest expression the recurrent species range through only a foot or a few feet of strata, hold in abundance four or five characteristic Hamilton species such as

Tropidoleptus carinatus, *Cypricardella bellistriata*, *Rhipidomella vanuxemi*, *Spirifer marcyi* and *Delthyris mesacostalis* (= *D. consobrinus*) and others; and the Owego and Swartwood zones appear in the midst of a characteristic Chemung fauna both above and below them. In the Owego recurrent zone both *Phacops rana* and *Dalmanites calliteles* occur.

The Van Etten recurrent zone lies entirely below the range of *Spirifer disjunctus* and associated species of the Chemung formation. On following the sections eastward from the Waverly quadrangle the species of the Chemung fauna become scarce, and east of the Chenango River very few species of the typical Chemung fauna have been detected—although they are still abundant in the Chemung rocks to the southeast and southward across Pennsylvania, Maryland and Virginia.

§ 5. These facts have been interpreted as evidence not only of a general *shifting of faunas* coincident with a rising of the land along the eastern edge of the present continent, but of *oscillation of conditions* and *alternate occupation of the area* by two sets of faunas coming from opposite directions and temporarily living in abundance in the area of central New York.

§ 6. The *lithologic changes* in the sediments containing the different faunas are not sufficient to account for the change in fauna. In quite a number of sections there is no appreciable difference in lithologic constitution between the strata which for a hundred feet thickness have been filled with characteristic Chemung species and the immediately following thin zone (of a foot or two) with scarcely a trace of the Chemung species, but holding, in great number, species which if found by themselves would be undisputed evidence of the Hamilton formation.

§ 7. It becomes necessary therefore to suppose that the *controlling cause* determining the presence of one or other fauna is not the character of the bottom on which the sediments which preserved the fauna were laid. We are thus led to conclude that the qualities of the ocean water have determined the shifting or migration of the faunas. The conditions to which the faunas were adjusted were evidently those of depth, salinity or temperature of the waters in which the species lived; and their change of habitation was occasioned by change in the direction, path or extent of flow of oceanic currents.

This leads us to consider the principles of migration as affecting marine organisms.

§ 8. *Migration of Species and Shifting of Faunas.*—Migration as commonly applied in natural history means the movement of large numbers of the same species from one place to another in a general definite direction at more or less regular periodic times. So birds migrate northward with the advance of warm weather; some fish migrate

from sea up rivers in breeding seasons; pigeons fly eastward or westward in great flocks, or grasshoppers invade a rich country devouring the vegetation in their path, or lemmings migrate across country in great quantities.

The term in these cases has to do with movements of one kind of animal in relation to the comparatively stable range of feeding-ground for the remainder of the fauna inhabiting the areas concerned. The term is rarely if ever applied to the slower movement of the whole body of animals of a fauna, coincident with great changes of climate, such as the advance of the glacial cover over the northern parts of Europe or America produced during the glacial age, or the advance of an Asiatic fauna across the Bering Straits and down the west coast of North America at some Pleistocene time when an ice bridge furnished means of communication by land from one continent to the other. Perhaps there is no impropriety in extending the application of the term migration to these latter cases in which the whole fauna and flora of a region is affected instead of single or a few species; and in which the change of position of habitat is slow and spread over a great period of time instead of being coincident with annual change of seasons. The term may equally well be applied to movements in the seas and movements on the lands.

There is, however, one reason for choosing a separate name for the movements of the latter kind to distinguish them from typical migrations.

In the first class of cases the migration is voluntary and is performed by those organisms which have the power of more or less rapid locomotion. They may be said to do the migrating themselves. In the second case the movements are involuntary and the movement is forced upon all the living organisms of the region and the change in position may be supposed to take place by the contracting on one side of the area of the conditions of possible existence for the species and the extension on the other side of favorable conditions of environment. The movements extend over many generations of life so that relatively sedentary species may gradually adjust their *locus habitans* to a given direction of migration. To this latter process of migration I have been accustomed to apply the term "shifting of faunas."

Migration of species is an expression of the ability of some organisms to appreciate slight changes of favorable conditions of environment and to take advantage of the better conditions during the lifetime of an individual. Shifting of faunas is an expression of the necessity for the perpetuation of the race of certain conditions of environment and the dying out of the whole fauna in the areas from which the favorable conditions are removed with corresponding spread of the fauna into new areas into which the favorable conditions have been shifted.

Shifting of faunas is an expression of the inability of the species of the fauna to survive under the changed conditions of environment which have overwhelmed them in the original habitat; but of an ability on the part of all those which migrate to follow the favorable conditions as they shift from one area to another.

In both typical migration of species and shifting of faunas change in the environmental conditions of life constitute the stimulus to change of habitat on the part of the organisms; and the movement of the organisms is a direct response to the stimulus—those organisms in the first case which migrate showing their greater vitality compared with their neighbors who stay at home; while those who stay at home show a greater power of endurance and organic adjustment to wider range of environmental conditions.

In the case of the shifting faunas those which endure without change of characters exhibit an acquired closeness of adjustment to some particular combination of environmental conditions which they are forced to follow or die and suffer annihilation. The evidence of their endurance is indicated by return and reoccupation of the same area at a later geological stage when by their reappearance, the original condition of environment may be assumed to have recurred.

In the case of living organisms evidence of migration is found in the actual presence of the species at one time in a region at a considerable distance from its ordinary *locus habitans*; and in some cases by seeing the species in the process of migration, as for instance the temporary alighting in fatigued condition of flocks of northern land birds on Bermuda Island on their migration southward.

In the case of fossil species the shifting of a fauna is expressed by the presence of a number of species representing an earlier fauna in a stratum in the midst of rocks containing a different and dominantly later set of species.

The fauna is then said to recur and it is the recurrence of the fauna which forms the basis for the inference that the fauna has shifted its *locus habitans* during the period of time represented by the sedimentary deposits separating the formation in which the fauna is dominant from the zone in the higher formation in which the recurrent species are found.

This theory of the shifting of place and the recurrence in time of the same fauna involves certain conceptions as to the nature of species and the laws of evolution which it is important to consider.

§ 9. *Evidence of Continuity.*—To establish evidence of motion in migration as in any other kind of motion it is all important to know that the body or bodies to which the motion is ascribed is continuously the same.

In the Devonian case I have been studying the moving body is a

fauna; not only have I found it necessary to establish identity of the species in the recurrent zones with those of the initial zones, but it is essential to show that the faunas as a whole are the same.

To put this in another form of statement we must establish the fact that not only the individual species have retained their specific characters, but the further fact that the equilibrium of adjustment to each other in the faunal community has not been changed, in order to prove that the recurrent fauna is the direct successor of a fauna represented in the rocks at a lower horizon.

This has led to such distinction as rare and dominant species of the fauna, and only as some such comparative frequency of the species in the faunal combination is apparent can we be sure that we are not considering an accidentally accumulated sample of a general fauna.

The presence of occasional associated species belonging to the normal fauna of the formation in which the recurrent zone appears is not antagonistic to the theory, because the theory proposes an invading of the territory occupied by the normal fauna, and whatever were the causes which brought about the shifting of the fauna they were not so completely different as to annihilate all evidence of the fauna previously occupying the ground. Hence it is only necessary to find an abrupt change of the grand majority of species to make the induction that the faunas have shifted their habitat.

The theory involves the further conception of grand general faunas which have their center of habitat and distribution in permanent oceanic basins, as distinguished from the special and (in geological strata) temporarily expressed faunas such as we are accustomed to associate with individual geologic formations.

In the case before us two such general faunas are in evidence, one of which in its dominant characteristics is traced westward into Iowa, Idaho and Arizona and up the Mackenzie River valley to the north and across the polar regions to Russia and northern Europe. The other is traced eastward and southward into central and southern Europe and also dominantly into South America.

Although, with our present knowledge, it is not possible to determine in any temporary expression of marine faunas those particular species which were derived from one from those derived from the other grand source, it is possible to recognize numerous species which belong to one center of distribution and others that belong normally to the other.

§10. *Interpretation of the Facts.*—It is also important to keep our heads clear in interpreting the facts.

It is only by close examination and comparison of the fossils themselves that identity of species or identity of faunas can be established.

The fixed characters of species are not only the characters by which

one species is distinguished from another, but they are of generic, ordinal and even class value, and they may be of immense age in the race and mark no special, narrow stage of its history.

It is a question of interpretation whether each particular phase of expression of fluctuating characters is a matter of time or of environment.

I have reached the conclusion that it is those species which have the greater degree of normal and persistent fluctuation of character which migrate and follow the shifting conditions of environment, and their life period is correspondingly longer.

On the other hand species whose plasticity of characters is narrow, are more closely adjusted to their environment, are local in their range of habitat, and temporary in their geological life-period.

Interpreting the facts on this basis it is the phases of continuously fluctuating characters in species of wide geographic distribution and long geologic range which furnish the most satisfactory evidence of temporary stages in the life history of faunas.

Another question of interpretation arises when we attempt to reconstruct the physical condition of the environment at successive stages of time.

In a single vertical section we have positive evidence of succession in time. If we were sure that no recurrence of the same fauna could take place we could correlate two vertical sections strictly upon the fauna contained in the strata, on the basis of the supposition that the single fauna appeared but once in the section and that when it ceased in a given section its whole life period was expressed. But the facts show us that this is not the case in nature. In geological times as in the present, we know that many distinct faunas are living on the face of the earth at the same time, even for very similar conditions of environment. It becomes therefore a very complex matter to correlate two sections in which the order of faunas and the character of the sediments differ; which is generally the case for any two sections separated by fifty miles from each other, although on stratigraphic evidence they may be properly interpreted as covering the same interval of time.

PALEONTOLOGIC EVIDENCES OF ADAPTIVE RADIATION

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THE law of adaptive radiation¹ is an application of paleontology of the idea of divergent evolution as conceived and developed successively in the studies of Lamarck, Darwin, Huxley and Cope. It

¹ Osborn, H. F., "The Law of Adaptive Radiation," *Amer. Naturalist*, Vol. XXXVI., No. 425, pp. 353-363.

is more than divergence because it implies evolution in every direction from a central form. The idea of radii, or radiations from a central form greatly assists the imagination, because a distinctive feature of paleontology is that we are constantly dealing with fragments of history. The radiations which have been discovered must be supplemented by those which remain to be discovered, and it is very remarkable how in group after group of animals these missing "radii" have turned up.

Radiation actually begins in certain single organs, and the first principle to be observed, as shown in the accompanying diagram, is

LIMBS AND FEET

TEETH

MAIN LINES OF ADAPTIVE RADIATION OF (a) limbs and feet, (b) teeth among mammals.

that radiation of different parts of the body is not necessarily correlated; that is, that the adaptive divergence of the feet and limbs may take one direction, while that of the teeth and skull may take another direction. Thus great variety in combinations of characters may arise, bringing about the very antithesis of Cuvier's supposed "law of correlation"; for we find that while the end results of adaptation are such that all parts of an animal conspire to make the whole adaptive, there is no fixed correlation either in the form or rate of development of parts, and that it is, therefore, impossible for the paleontologist to predict the anatomy of an unknown animal from one of its parts only, unless the animal happen to belong to a type generally familiar. For example, among the land vertebrates the feet, which are associated with the structure of the limbs and trunk, may take one of many lines of adaptation to different media or habitats, either aquatic, terrestrial, arboreal or aerial; while the teeth, which are associated with the structure of the skull and jaws, also may take one of many lines of adaptation to different kinds of food or modes of feeding, whether herbivorous, insectivorous or carnivorous. Through this independent adaptation of different parts of animals to their specific ends there have arisen among vertebrates almost unlimited numbers of combinations of food and tooth structure.

Alternations of Habitat.—In the long vicissitudes of time and procession of continental changes animals have been subjected to alternations of habitat either through their own migrations or through the "migration of the environment itself," to employ Van den Broeck's epigrammatic description of the profound and sometimes sudden environmental changes which may take place in a single locality. The traces of alternations of anatomical adaptation corresponding with these alternations of habitat are recorded both in paleontology and anatomy. For example, Huxley in 1880 briefly suggested the arboreal origin of all the marsupials, a suggestion which has been confirmed abundantly by the detailed studies of Dollo and Bensley, according to which we may imagine that the marsupials have passed through a series of phases, as follows: (1) a very early "terrestrial or ambulatory" phase, (2) a "primary arboreal" phase as exemplified by the tree phalangers of the present day, (3) a "secondary terrestrial" phase as exemplified by the kangaroos and wallabies, (4) a "secondary arboreal" phase as exemplified by the tree kangaroos.

Each one of these phases has left its anatomical record in the structure of the feet and limbs, although this record is often obscured by adaptation.

Louis Dollo especially has contributed most brilliant discussions of this theory of "alternations of habitat" as applied not only to the interpretation of the anatomy of the marsupials but of many kinds of

fishes, and to such reptiles as the herbivorous dinosaurs of the Upper Cretaceous.

This brief consideration of the external features of adaptation leads us to glance at groups of animals. We here observe the influence of geographic distribution; we observe the *adaptive radiation of groups both continental and local*.

Continental Adaptive Radiation.—Among the Tertiary mammals we can actually trace the giving off of radii in several, sometimes in all, directions for the purpose of taking advantage of every opportunity to secure food, to escape enemies, and to reproduce kind, the three phenomena of the struggle for existence. Among such well-known quadrupeds as the horses, rhinoceroses and titanotheres the modifications involved in these radiations can be clearly traced. Thus the history of the life of continents presents a picture of contemporaneous radiations in different parts of the world. We observe the contemporaneous and largely independent radiations of the hoofed animals in South America, in Africa and in the great continent comprising Europe, Asia and North America.

Through the laws of parallelism and convergence each of these radiations produced a greater or less number of analogous groups.

While originally independent, the animals thus evolved separately as autochthonous types in many cases finally mingled together as migrant or invading types.

We may thus work out gradually the separate contributions of the great land masses of North America, South America, etc., to the mammalian fauna of the world. As a rule the greater the continents the more important and fundamental the orders or larger groups of mammals which have radiated in them; the lesser land masses and continental islands, like Australia, have been less favorable to wide adaptive radiation. One of the most interesting features of adaptive radiation is that it may also occur locally.

Local Adaptive Radiation.—On a smaller scale are the local adaptive radiations which occur through segregation of habit and local isolation in the same general geographic region wherever physiographic and climatic differences are sufficiently great to produce local differences in food supply or other local factors of change. This principle is well known among living animals, and it is now being demonstrated among many of the Tertiary mammals, remains of four or five distinct genetic series having been discovered in the same geologic deposits.

The existence of multiple phyla of related animals, as of the rhinoceroses, horses and titanotheres in the same localities is due partly to the operation of the law of local adaptive radiation.

This is conspicuously the case among the titanotheres, for example, the chief evolution of which can be traced in the Rocky Mountain

region. In the Eocene we discover four or five independent local phyla; again in the Oligocene we discover five or six independent local phyla. The evolution of these animals appears to have been chiefly American.

In other cases, however, the polyphyletic condition appears to have been through the mingling with local phyla of phyla evolved in other countries. This is illustrated in the case of the Middle Miocene rhinoceroses of America, which are invaded by rhinoceroses of Eurasiatic or European origin.

In studying the herbivorous quadrupeds, therefore, we must keep in the imagination constantly the production of local phyla through local radiation and the intermingling of foreign phyla through migration. There are a few very striking and profound differences between quadrupeds which recur so frequently that where we discover one form we may surely anticipate the discovery of the opposite or antithetic form: in other words, there are extremes of structure shown in the proportions of the skull, of the teeth, of the limbs, and groups of quadrupeds are constantly tending through adaptive radiation to reach these extremes. Some of the contrasting extremes are the following: brachyodonty *vs.* hypsodonty, dolichocephaly *vs.* brachycephaly, dolichopody *vs.* brachypody.

For example, a local adaptive radiation observed in the horses is that the forest-living types are brachyodont, or possess short-crowned teeth, while the desert-living horses are hypsodont, typically grazers, with long-crowned teeth.

Extremes of long-headedness and short-headedness, of long-footedness and of short-footedness, comprise a very large part of the mechanism of adaptive radiation; but we have to do also with long-necked and short-necked types, and with many other chances of proportion which are correlated with different feeding habits.

ANATOMY AND PHYSIOLOGY IN INVERTEBRATE EXTINCT ORGANISMS

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THE inquiry into the position of anatomy and physiology in invertebrate paleontology seems very appropriate at present, since paleontology is steadily becoming more closely affiliated to zoology, and the sphere of zoology is at present dominated by comparative anatomy and physiology.

Since, however, invertebrate paleontology has only the hard parts, mostly outer shells, at its disposal, the view still prevailing among zoologists that little is to be expected from it in regard to the solution of the problems of anatomy and physiology of the lower animals seems natural. Nevertheless, the results already attained prove that if paleontologists do not approach their material with a geological knowledge only, as has been done in the past altogether too often, most gratifying results may be obtained, at least in some classes, for it must be conceded that the connection of the hard parts with the fleshy parts is very unlike in different classes; it is very intimate in some, as the crinoids and brachiopods, and again more indifferent, as in the gastropods.

But it is not claiming too much for invertebrate paleontology if we say that where the hard parts are of great structural importance, paleontology has earlier taken cognizance of this fact and consequently gone ahead of zoology. As an instance I may cite Zittel's investigations of the skeleton of the hexactinellid sponges which have taught the fundamental importance of the form of the spicules and the structure of the skeleton in that class and whose results have been readily adopted by zoologists. In classes which, as the brachiopods and crinoids, are to-day mere shadows of their former greatness, paleontology has its greatest chance, and it would fail in its task if it would there not become the instructor of the affiliated science; and it is gratifying to see that this fact is finding recognition, as, for instance, in Ray Lankester's "Treatise of Zoology," where the chapter on the crinoids has been entrusted to Bather, a paleontologist and one of the best authorities on crinoids.

It is apparent that in such classes as those just mentioned, of which only the last ends of the branches are still alive, the origin and nature

of many structures can not be elucidated, even by the embryology and comparative anatomy of the recent forms, but only by paleontology. Such a structure is, for instance, the mystifying stem of the crinoids which, by a study of the primitive ancestors of the crinoids among the cystids, is readily recognized as a dorsal evagination of the body. Likewise, to cite another example, the siphuncle of the recent *Nautilus*, which is obscure as a wholly rudimentary organ, is in such primitive Paleozoic cephalopods as *Nanno* and *Piloceras*, still seen in its original form and thereby recognized in its nature.

Since that which has already been accomplished in fossil anatomy is proof that there are still larger fields to be ploughed and harvested, it is proper to inquire into the best methods of this work before us.

We first need more extensive and more intensive or more detailed purely descriptive anatomical researches of the invertebrate fossils. There are many species that, when investigated in their smallest detail, are bound to give important results. I may cite here, as examples of such accomplishments, Hudson's minute study of the strange *Blas-toidocrinus* of our Chazy rocks with its 90,000 ossicles, or that of the *Eurypterus fischeri* by Holm. Of this archaic fossil marine arachnoid, a relative of the scorpion and of the king crab, it can be fairly said that, as far as its chitinous integument is concerned, it is as well known as any recent species. We know, through Holm, its gills, its complex genital appendages of both sexes, and even its fine hairs and bristles. Dr. Clarke and myself have lately continued these investigations in the American eurypterids, and there observed the structure of the compound eyes, the pore system of the segments, the genital apertures, the mode of moulting, the arrangement of some of the principal muscles and other anatomical facts of interest.

It can be said that this field of detailed descriptive anatomy has been merely touched thus far, as far as our fossil invertebrates are concerned, and altogether too much neglected. This is not only true as to the gross anatomy, but still more so as to the microscopic structure. It must be conceded that owing to the secondary changes in the rocks, this latter line of investigation meets with great obstacles not fully appreciated by the zoologist, and that it is only in its infantile stage in some classes. But the results obtained by the microscopic research of the Paleozoic bryozoans in this country may be considered as a striking example of what persistency and enthusiasm may still accomplish. In microscopic anatomy of the fossils the training of a geologist is as much required as that of a zoologist and the history of these investigations shows that a zoologist without geologic training may be badly misled by the deceptive states of preservation of the fossils.

The main object of anatomical research is to result in comparative anatomy and to determine what parts are fundamental or primary and

what have undergone modifications due to functional changes. It is obvious that here invertebrate paleontology is in a position to answer a host of questions that could not be successfully approached by comparative anatomy of recent forms, by the direct observation of successive changes. Its methods of investigation have already been applied with wonderful success to large parts of our Paleozoic crinoids, brachiopods, bryozoans and cephalopods. And I do not doubt that the time has come when the preliminary stage of mere description of fossils is passed, and a monographic treatment of each class that would fully enter into the comparative anatomy of all structures preserved, could be profitably undertaken.

It is only by this work that paleontology can hope to make those contributions to philosophical anatomy in revealing the causes of the different structures which it is especially fitted and called upon to furnish by its ability to study the gradual development of the structures. Wherever a class of fossils has been thus thoroughly treated, it has given a fruitful crop of new hypotheses and principles, as is instanced by Hyatt's investigation of the fossil cephalopods. Most classes, and especially the corals, echinoids and trilobites, await such treatment by competent investigators.

Since physiology is that branch of biology that treats of the laws of phenomena of living organisms, it might seem hopeless to expect any information from the fossil world. This is apparently the more true in regard to the invertebrates, since a special physiology exists thus far only for men and the higher invertebrates and the recent invertebrates are largely a virgin field. For this reason also, only the most general foundations of comparative physiology have been laid, and an invertebrate fossil physiology would get as yet but little support from that side. Moreover, the main source of exact information in recent physiology is the experimental method, and this is wholly inapplicable to the fossil world.

And yet it seems to us that the empiric method upon which physiology has so long flourished promises also rich fruit in paleontology. I can do no more now than briefly mention the problems that most readily suggest themselves here. Invertebrate paleontology will be especially competent to furnish contributions to the mechanics of physiology by throwing light on the development of the means and modes of locomotion. In connection with this problem invertebrate paleontology also shows most clearly the deep-reaching influence of secondary fixation on the structure of the organism, as in the case of the strange *Richthofenia* among the brachiopods and the Rudistæ among the lamellibranchs. It can not fail that the progress in recent invertebrate physiology will stimulate inquiry into the physiology of the fossils; and further that, as invertebrate fossil anatomy progresses, the data for such inquiry will also come forth.

Another problem closely connected with that of the mode of locomotion is that of the origin of the organs of sense, and also upon this, as far as the organs of seeing at least are concerned, the fossil invertebrates are able to throw some light, as in the trilobites and eurypterids.

Another line of inquiry is that of the mode of nutrition as recognizable by the appendages, and its influence upon the general structure. Under this heading such interesting minor problems as that of the origin of parasitism arise and may be solved, as indicated by a recent publication as to the time of beginning, causes and gradual changes of parasitism, to its very complex present conditions.

Probably also the physiology of respiration will in time receive important additions as far as the echinoderms, crustaceans, scorpions and eurypterids are concerned.

The widest scope, however, will have those problems that are connected with the reactions of the organisms to their physical and chemical surroundings. The invertebrate paleontologist meets forever, in sight of the ever-changing faunules, the question, what exterior influences caused these changes? Often they can be directly recognized, as in the dwarfed faunules of the Devonian pyritiferous Tully limestone or of the bituminous Marcellus and Genesee shales or the eurypterid faunas of the Salina lagoons. The systematic investigation of these reactions through the series of formations is an inviting task.

A special problem of singular interest connected with the reaction of the organisms to the chemical surroundings is that of the composition of the shell of the invertebrates. There is good evidence for the view that the shells were at first chitinous and that but gradually they became calcareous or siliceous. This important question again is intimately connected with that of the original composition of the ocean, and this line of inquiry again leads us to the highly fascinating paleophysiological problem, lately so happily dealt with by Professor Lane, as to the geological evidence on the original composition and origin of the vital liquid, the original body temperature and the physiological origin of the hard parts of the invertebrates in general.

CONTRIBUTIONS TO MORPHOLOGY FROM PALEONTOLOGY

BY PROFESSOR WILLIAM BULLOCK CLARK

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OUR knowledge of the morphology both of the animal and plant kingdoms has been largely extended by the work of the paleontologist. Mention needs only to be made of the many species, genera and families, even orders and classes, established solely for fossil forms

to show how much we owe to paleontology. There is not a single sub-kingdom but has been immensely enriched from this source.

Some of the fossil species possess morphological characters so closely allied, on the one hand to earlier, and on the other to later, forms as to indicate that they occupy a position in the line of descent, and phylogenetic series have been established frequently on this basis. As examples we have the well-known developmental series of the horse and the camel. Other illustrations may be found in the *Paludinas* of the Slavonian Pliocene and in the *Planorbis* types of Steinheim.

Still other fossil forms combine in the same species several morphological features which later become segregated and characterize different types. Such "synthetic types" serve to show the common origin of the forms in question if not their actual ancestors and have greatly enlarged our knowledge of the morphology of the several groups involved. These early forms are, for the most part, highly generalized, while their descendents are variously specialized. Take, for example, the mammalian *Condylartha*, small, generalized Ungulata with an astragalus shaped almost as in the Carnivora; or the reptilian *Anomodontia* with intermediate skeletal characters between the highest labyrinthodonts and the lowest mammals; or again, the early Paleozoic cystoids with generalized characters in their calyx plates which appear in more specialized forms in later crinoids and blastoids. An almost indefinite number of such illustrations might be cited.

Still other fossil forms present morphological characters so different from other fossil or living species that the genetic relationships may not be determined accurately. Some of these are possible of reference to already defined orders, while others present so many diverse morphological characters as to require the establishment of new divisions for their reception.

A survey of the known fossil and living forms shows that not only have old species constantly become extinct during the progress of geological time, but new species have been as frequently appearing. This is equally true of genera, families, orders or even classes. Some forms have appeared and disappeared, as the case may be, suddenly; others slowly. The great group of the Ammonites, for example, disappeared suddenly at the close of the Cretaceous after showing many degenerate characters, while the Trilobites gradually declined during late Paleozoic time before their final extinction. One of the most striking features in the developmental history of plants and animals is found in the great number of fossil types which have left no descendants.

Both the animal and plant kingdoms furnish a wealth of material with which to demonstrate the aid which paleontology has rendered to morphology.

The contributions of invertebrate paleontology are numerous and striking:

The *Protozoa* afford in the Carboniferous Fusulinidæ and in the Tertiary Nummulinidæ forms with very different morphological characters from those living to-day, while the numerous extinct species of the Lituolidæ and Textularidæ in the Cretaceous and of the Miliolidæ and Globigerinidæ in the Tertiary have greatly widened our knowledge of the entire subkingdom.

The *Cœlenterata* in the Paleozoic Tabulata and Graptoloidea show types so different from living forms that the systematist has never been able to satisfactorily assign them to a position within the limits of the phylum. Many external and internal characters appear that are quite unknown in later forms. On the other hand, the paleontological subclass of the Tetracoralla long imperfectly understood is now regarded with a fuller knowledge of the morphology as affording the probable ancestors of the later Hexacoralla.

The *Echinodermata* have furnished two classes, the Cystoidea and the Blastoidea, unknown after the Paleozoic, whose morphology aids very materially in an interpretation of later and more highly differentiated forms among the Pelmatozoa. Thus the cystoids, which have been regarded as the ancestral type from which the crinoids have sprung, afford forms like the Camarocystites, in which the arms are similar to those of the crinoids although the calyx plates are irregularly arranged and thus cystoidean in character. Both the Asterozoa and Echinozoa are represented in the fossil state by many species that greatly widen our knowledge of the morphology of this group. Take for example, the Echinocystites, regarded as belonging to the Palechinodea which has a valvular pyramid of calcareous anal plates so highly characteristic of the cystoids.

The *Molluscoidea*, to which phylum belong the Bryozoa and Brachiopoda, would be but imperfectly understood from a morphological standpoint but for the vast number of fossil forms. The Brachiopoda have been estimated to have less than 150 living species, while probably more than 6,000 fossil species have been described. Of the 31 families only 7 have living representatives. We are dependent, therefore, largely on the fossil forms for our knowledge of the morphology of this class.

The *Mollusca* with their varied forms, although so well represented to-day, have furnished in the fossil state one of the most interesting and important orders in the animal kingdom, the Ammonoidea with its 5,000 and more species ranging from the Devonian to the Cretaceous. Even the allied Nautiloidea, although containing living forms, attained its chief development in the Paleozoic, and it is from these ancient forms that we obtain our chief knowledge of the morphology of this group with their early straight and irregularly coiled types.

The *Arthropoda* afford in the Paleozoic the important groups of the trilobites and euripterids, forms that have aided greatly in the inter-

pretation of the entire phylum. The trilobites from their morphological features have been generally regarded as entomostracous crustaceans with relationships on the one hand to the Phyllopoda and on the other to the Merostomata, while the coalescing of the caudal segments suggests also a relationship to the Isopoda.

Vertebrate paleontology has also furnished much to morphology.

The *Fishes* would be but imperfectly known in their wonderful variety but for the fossil types. The problematical group Agnatha found only in the Silurian and Devonian affords no certain evidence of a lower jaw or paired limbs, and in some of the genera of the Ostracoderma mimic in a curious way the contemporaneous euripterids, which has led some to erroneously ally them with the Merostomata. The dermal armor of most of these forms is also a striking morphological feature.

Woodward divides the fishes proper into Elasmobranchii, Holocephali, Dipnoi and Teleostomi, and considers that the common ancestors of all were Elasmobranchs. Numerous fossil forms among the Elasmobranchs and Dipnoids as well as the Crossopterygians which have been thought by many to bridge the gap between the Teleostomi and Dipnoi have added largely to our knowledge of the phylum.

The *Batrachians* which consist to-day largely of diminutive forms were represented in the later Paleozoic and early Mesozoic by the Stegocephalia which contain the giant labyrinthodonts with their highly complex infolding of the walls of the teeth.

The *Reptilians* which began their existence toward the close of the Paleozoic became so numerous and diversified during the Mesozoic that this division of geological time has been referred to as the age of reptiles. Several orders of Saurians containing many giant types flourished during this time, but became practically extinct before the close of the period. With the adaptation of some for walking on their hind legs, of others for swimming, and still others for flight we have developed a great variety of morphological features that would never have been suspected from a study of living forms.

The *Birds* which are recognized as possessing certain dinosaurian relationships and were doubtless derived from one of the reptilian orders are unknown prior to the Jurassic. The Mesozoic forms are generalized, the tail at first not being atrophied and the pelvis imperfectly developed as in later forms. The vertebræ also had not acquired their saddle-shaped articulation while teeth were present in the jaws of the adults. Such forms certainly add greatly to our knowledge of the morphology of this class.

The *Mammals* which began in the early Mesozoic were represented throughout the Cenozoic time by highly diversified forms, many of which have left no descendants. The gradual evolution of the mam-

malian skeleton has brought about many morphological modifications from those shown in the Batrachia and Reptilia. We find the skull loses the prefrontal and postfrontal bones, the mandible is simplified, the limb bones show a development of terminal epiphyses with ossification to the center of the vertebræ and the bones of the pelvic arch are ossified. From the beginning of the Tertiary time a marvelous variety of morphological characters appears, and without the fossil types we should have but an inadequate conception of this great phylum.

The contributions of paleobotany to morphology are in some respects quite as striking as those of paleozoology.

The fossil *Thallophytes* have not furnished any very striking variations from their present morphological features, while the *Bryophytes* are scarcely represented as fossils except in very recent deposits.

The remaining phyla, the *Pteridospermatophytes*, the *Pteridophytes* and the *Spermatophytes* have their oldest known beginnings as far back as the Devonian and their study has enormously widened the bounds of plant morphology.

The *Pteridospermatophytes*, which are confined to the Paleozoic, are in habit and vegetative morphology ferns—in methods of reproduction and in the morphology of their reproductive organs typical seed plants. They alter our whole conception of ferns and seed plants and in their significance are comparable to archetypal vertebrata, the acquisition of the seed habit in plants and the vertebral column in animals probably marking the culmination of the transfer of vital activity from aquatic to terrestrial conditions.

In the *Pteridophytes* the extinct Paleozoic class, the Sphenophyllales, is significant, since the morphology of the distinct lycopod and *Equisetum* lines seems to merge in this group. The lycopod type, itself represented in the existing flora by six or seven genera of herbaceous plants, monotonously uniform in their morphology, is found in the Paleozoic to constitute one of the chief units in the arborescent flora with numerous species of complex organization, whose stem, foliar and reproductive morphology was quite unknown to botanists (*Lepidodendron*, *Sigillaria*, etc.). The *Equisetum* type furnishes a like case. With few existing species of minor importance and uniform morphology we find in the Paleozoic a host of forms, many of them arborescent and of varied and complex structure (*Calamites*, *Archæocalamites*, etc.). Similar examples could be drawn from the fossil representatives of the true ferns.

In the *Spermatophytes* another wholly extinct class, the Cordaitales, embraces a curiously organized group of conifers extending back to the oldest horizons from which land plants are found, and continuing to the close of the Paleozoic as one of the most abundant as well as the highest type of pre-Mesozoic plant. In the older Mesozoic we find two

groups of plants which have made similar great contributions to morphology. The Cycadales or cycad-like plants, which to-day are an inconspicuous group, were one of the dominant Mesozoic types, and any understanding of the modern forms rests entirely upon a study of their immensely abundant Mesozoic ancestors. The other group, the Ginkgoales, represented in the existing flora by a single species, the ginkgo, is found in the Mesozoic to have been represented by many genera and species of great diversity.

The dominant plants of to-day, the conifers on the one hand, and the angiosperms on the other, have each afforded many extinct genera, the former with more fossil than recent species, and only understandable in the light of their fossil ancestors. Vegetable morphology based only upon existing plants abundantly demonstrated its sterility before the relative recent study of fossil plants placed it upon an altogether new basis.

RELATION OF EMBRYOLOGY AND VERTEBRATE PALEONTOLOGY

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THE problem of recapitulation among vertebrates gives by no means as accurate results as among invertebrate forms, for while a single adult shell, if perfectly preserved, will often display the entire life history or ontogeny of the individual, a bone, or even a complete skeleton, is rarely retrospective and if at all only in some minor detail. The vertebratist, therefore, in his study of ontogeny, for comparison with racial history must needs follow either the entire growth of one animal, a thing manifestly impossible when the embryonic stages are considered, or study a long series of individuals in various stages of development, the securing of which in the great majority of cases is largely the result of a number of happy accidents. When one comes to weigh the evidence offered by the actual embryos of fossil vertebrates he will find a very great dearth of material, for fossil embryos—that is, the stages in the life history before birth or hatching—are extremely rare.

Recent embryology, on the other hand, is more productive of results and the earlier stages of certain organs often suggest those of equivalent development in animals of the past. In his interpretation of a given structure, however, one has to bear in mind whether it may not have been modified to suit some modern need in the life history of the individual, and thus no longer give us a true image of bygone structure. These cœnogenetic organs are not historic, but as Wilder says, “have to do with such immediate environmental problems as nutrition or protection.” Again, if the organ has approximately the same form

and character in the ancestral type at the same stage of its development, it represents an actual repetition of past history and is therefore palinogenetic. Sometimes it is not quite clear, however, under which caption the embryonic structure comes, and its interpretation must be attempted with caution.

Osborn in his lectures to his students speaks of the three-fold evidence for evolution which stands firmly like a tripod, the legs of which are comparative anatomy, embryology and paleontology; and the evidence of each should correspond, provided the interpretation be correct. Of these, however, embryology is manifestly the weakest member, while paleontology is a tower of strength!

The reptiles are so rare as embryos and withal so ancient a group that their ontogeny throws but little light upon paleontology. Among the fossil forms a number of specimens of *Ichthyosaurus* have been found with young contained within the body of the adult. Many of these are in the normal position for foeti-in-utero; others are displaced, with the head directed forward. These latter Branca thinks may be young that have been eaten. There is also, at times, a very great difference in the size of the contained young. Aside from a slight difference in proportions, especially that of head to trunk, and a less degree of hardness of the embryonic bones, as indicated by their being crushed over the parent's ribs, the young teach us nothing as to ancestral structure as they are in every way perfect ichthyosaurs. They do prove, however, when the evidence of viviparity which they offer is taken in connection with the supreme degree of aquatic adaptation indicated, that the ichthyosaurs were high sea-forms, never coming ashore even for egg-laying.

That certain of the dinosaurs were also viviparous may be proved by an embryo contained in the unique specimen of *Compsognathus longipes* from the Jurassic of Bavaria. So far as I am aware this embryo gives no other evidence of ontogenetic value.

The turtles have been made the subject of exhaustive study by Hay and from the embryological point of view by Clark under L. Agassiz. Anatomically they are the most remarkable of reptiles, having undergone during their career an extreme modification in many directions while retaining a number of very primitive characters. The most remarkable feature is the development of the shield or carapace, which contains what are generally considered as the homologues of the ribs of other vertebrates, but, strangely enough, here lying outside of the shoulder girdle, a feature wherein the turtles are utterly unique. The embryology, which is well known, ought to throw some light upon the origin of this important feature. In their earlier stages of development the Chelonia resemble the Lacertilia, the chief peculiarity being caused by the development of this carapace which appears in the form

of two longitudinal folds extending above the line of insertion of the fore- and hind-limbs which have already made their appearance. Hence the carapace grows outward and over the limb-girdles which come to lie within the rib-like osseous supports. This ontogeny shows us clearly how the ancestral carapace may have been formed. Paleontology has not as yet confirmed this, but doubtless will do so.

Among birds one of the most interesting features is the occurrence of vestigial tooth papillæ in the jaws of certain embryo parrots and owls—reminiscent of Mesozoic days when birds were toothed in their adult state.

Mammalian evidence is very striking in many details and much of it has recently been summarized by Hubrecht, who makes much of the character of the placentation and derives from it and other features some remarkable conclusions. Hubrecht abandons the idea of the derivation of the mammalia from the reptilian-insectivorean stem, but on the contrary derives them from amphibia-like animals of the Carboniferous. The character of the placentation, moreover, places man, the *Anthropomorphæ* and the hedgehog among the most archaic of living mammalian types, an idea also borne out by comparative anatomy and one which paleontology may some day confirm.

The most primitive mammals, the *Prototheria*, are still very suggestive of their old reptilian ancestry in many ways, especially in the method of producing the young inclosed within an eggshell. The position of the *Marsupials* is surely low in the scale of mammalian life, although they show in many respects remarkable specializations. Wilder compares them with the *Prototheria* in that they also bring forth their young at a very early state of development, though not protected by an eggshell. The period during which they are permanently attached to the nipples within the pouch is actually post-embryonic and properly larval. Vestiges of placentation have been found in at least one marsupial, a fact which gives color to the belief that in this respect they may be degenerate rather than primitive. Broom has shown that the modern marsupial shoulder girdle passes through a *prototherian* stage implying a relationship which is strongly supported in other ways.

The foetal *Sirenia* and *Cetacea*, so far as known, show no greater development of hind-limbs than do the post-natal individuals. They do show a marked neck construction and the head bent at right angles with the trunk in a normal quadrupedal posture. The head of the foetal manatee is very suggestive of the modern ungulate. Ryder has tried to prove the homology of the caudal flukes in the *Sirenia* and *Cetacea* with the integument of the hind feet, drawing his evidence largely from comparison with the seals. In the embryo the flukes appear as lateral expansions near the end of the tail, giving it a lance-like form when viewed from above. These flaps by transverse expan-

sion develop into the powerful swimming flukes of the adult. They may be compared with lateral flanges on the tail of the sea otter *Enhydris*, but in the latter the flaps are elongate, while in the Cetacea they are short and situated toward the end of the tail. Nevertheless, the homology of the two types of flange structures appears true, the posterior position and concentration in the whale being a mechanical adaptation which has become accelerated in its appearance so as to be embryonic. The presence of hair on the body of the foetal whale and of distinct calcareous tooth germs in both upper and lower jaws of the unborn young of whalebone whales are both reminiscent.

The horses, our knowledge of which is so complete owing to the pioneer work of Marsh and later of Osborn, show some interesting points of comparison between foetus and ancestor. The skulls of pre-natal modern horses resemble those of *Meshippus* or even of *Eohippus* in the proportions of face and cranium, the short-crowned grinding teeth, lesser angle between basi-cranial and basi-facial axes and the fact that the orbit is incompletely ringed with bone. The feet of the unborn foal are also somewhat reminiscent of old-time conditions.

One of the most difficult points to be reconciled in the acceptance of the Cope-Osborn theory of the origin of molar cusps was the apparent non-agreement of cusp ontogeny with the interpreted phylogeny which this theory upheld. The difficulty has been met in two ways: by the supposition that coenogenesis has entered into the embryogeny, or that the paleontological record as shown by the trituberculists is open to a different interpretation. The present great exponent of the idea claims that the matter is still *sub judice* and thus the problem stands.

In conclusion, the paleontological student of the higher vertebrates can hope to find in embryology a host of valuable suggestions, much verification of his work and sundry apparent inconsistencies which must in some way be reconciled. He should ever bear in mind the influence of nature and nurture, the latter often giving rise to perplexing conflicts between the two records. He will on the whole have in embryology a fair mirror of the past wherein, even though the image be somewhat distorted and the more remote reflections dimmed by time, he can view the striking features of the long procession of the ages.

ONTOGENY: A STUDY OF THE VALUE OF YOUNG FEATURES IN DETERMINING PHYLOGENY

BY PROFESSOR F. B. LOOMIS

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IN this paper I want to study what value is to be given to the principle that ontogeny is a brief recapitulation of phylogeny, when it comes to the concrete determination of the ancestry of a given genus. For the purpose three types have been studied carefully and several more for confirmations, the principal study being between the young and adult of the pig, cat and man, the differences being noted to see if they suggested the forms considered ancestral.

First let us consider the skull of a six weeks' pig in comparison with that of the adult, the two having been drawn to the same length. The first and most marked variation is in the brain case, that of the young being relatively vastly larger. The same is especially true of the sense capsules of the ear and eye. The later growth is much greater in those parts of the skull designated as facial, or having to do with the jaws and their supports. Then there is a change in the axis of the skull, this being due to the growth of the maxilla region, and lastly where there is any cellular bone or bone spaces they are developed in later life. This factor is especially well shown in the development of the elephant skull and in ruminants. It is coincident with high crests and marked protuberances.

While most of the features have been indicated in the pig, the same comparison in the cat reveals the same excessive development of the brain case and sense organs, the same weakness of the jaws and change in the axial relations, and this may be further confirmed in looking at the contrast between a three-year-old child's skull and that of an adult.

The conclusions then to be drawn from this hasty comparison of the two skulls are, first, that the shape of the skull in the young shows the excessive development of the brain and sense capsules, so that the appearance is not that of a primitive animal, but exactly the contrary, the appearance which the genus would assume were its mental or nervous development carried to a much higher degree than is the case. The embryonic development of the brain and sense organs is pushed far toward the beginning, and is matured, as far as size is concerned, the earliest of any of the systems. The skull is first an envelope for the brain and sense organs and is therefore profoundly modified by this embryonic peculiarity, and *the younger the individual the less like the adult or ancestor the skull is shaped.*

Secondly, the change of axis is not in the ancestral direction, the excessive weak condition of the jaws being again an embryonic adaptation and not an ancestral one.

Lastly, in the development of cancellous tissue is a condition which more nearly approximates the phylogenetic development, but here even the use of young features is deceptive, for it is seldom that this cellular bone is developed in the immediate ancestor but is rather found in several genera back, being usually an accompaniment of the development of the heavy facial portion of the skull. So much for form.

Turning to the dentition. The milk set of the pig and those of the adult are drawn side by side, and it is seen that while the front teeth of the young approximate those of the adult, the comparison is between the complicated premolar and molar sets. Briefly, of the four premolars, if all present, in the young (and often but three are developed) the two in front resemble the premolars to succeed them in the permanent set, while the two rear milk premolars resemble the permanent molars, the last milk premolar being especially like the last molar. This granted, the interest centers around whether the pattern of the milk teeth is such as to indicate the ancestry. A glance at the pig and its young will show that while the detail is not exactly the same in young and old, yet they are so alike that no one would identify a single milk molar as *Hyotherium* or any other suine genus, but would have to put it in the genus *Sus*. Taking other cases among the Ungulata, the history of the naming of the Miocene genera of horses gives a good example. There are, according to Gidley, four genera, *Hyotherium*, *Parahippus*, *Merychippus* and *Protohippus*; of these, three were founded on young teeth, i. e., the first three named. When it was recognized that they were young teeth, they were by Cope assigned to *Protohippus*, but when the adult teeth were found it was clear that the distinctive features of these young teeth were the distinctive features of the adult. For the genus *Merychippus* there is a difference in that the young teeth are not cemented, while the adult are. That is ancestral. In analyzing the descriptions of several genera of horses usually some feature can be found in the milk tooth which is ancestral.

In the Carnivora there is the carnassial tooth which is specialized; in the upper jaw it is the third milk premolar and the fourth in the adult; in the lower jaw it is the fourth milk premolar, and the first molar of the adult. Thus it is clear that it is a different dental follicle which forms the young and the adult carnassial. In the case of the dog the permanent and milk carnassials are approximately alike, but in the case of the cat the inner lobe or protocone occupies a very different place in the young from that of the adult, a position characteristic of none of the Felidæ and suggests some of the apparently unrelated Creodonts.

In the matter of the succession of teeth the follicles which form the last two—the milk premolars—form teeth in the first set of a totally different and usually more advanced character than the teeth to be formed from the same follicles in the permanent set. As a general thing then the conclusion would be that the milk teeth tend to have the same characters as mark the permanent set, but when they vary they often retain characters of the phylogenetically ancestral form. Weber adds that the later the succession the less the difference between the milk and permanent sets.

Turning to the limbs, there are again several distinctly ontogenetic characters, which are by no means ancestral. First, the formation of epiphyses, so that a bone ossifies from three or more centers. This is purely an ontogenetic adaptation and has no phylogenetic significance. Then the articular ends of all the limb bones are greatly enlarged as compared with adults. This again is not phylogenetic but an adaptation, the joints and their ligaments being early approximated to their permanent conditions. Then the length of limbs seems to be effected as an embryonic adaptation. First take the case of man born with disproportionately short arms and legs. The legs have been interpreted as representing a phylogenetic condition, but the same rule does not apply to the arms which were ancestrally long. This feature of short limbs is also characteristic of carnivora and I feel that it is an embryonic adaptation; certainly the ancestral limb can not be deduced from the young condition. Quite the reverse of conditions obtains among the Ungulata where the young at birth have disproportionately long limbs, which with equal certainty does not represent any ancestral condition recapitulated, for the ancestral limb in ancestral forms is shorter. Again, I believe the anomalous legs are adaptations to either the necessity for speed on the part of the young, or for height to reach the teats, suckling being while the parent is standing.

In the cases of the reduction of digits, greater portions of the reduced digits are usually found in the young animals than in the adults, but in the case of the entire loss of a digit it is also lacking in the young and embryo.

The general conclusion of the whole matter would then be that the young give us very little which is not deceptive in reconstructing ancestral forms. In certain cases, namely in the teeth and in reduction of digits, confirmatory points may be obtained, but these must be used with care, the valuable constructive evidence being rather found in adult skeletons, and in morphological comparisons. While allowing that many stages are recapitulated in the development of an individual, the vast number of adaptations impressed on the young to be used after birth, *make their skeletons specialized even from birth, and such differences as exist are seldom reminiscent.*

PALEONTOLOGY AND ONTOGENY

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ONTOGENY, or the life history of the individual, is commonly interpreted by zoologists as its embryology, the later stages of development, from infancy to old age, being deemed of little or no importance. This was the case fifty years ago; this is largely the case to-day. From the days when Agassiz first called the attention of zoologists to their one-sided attack of the problem of ontogeny, and urged them to pay attention to the important post-embryonic stages, down to our own time, students of recent animals have for the most part been content to follow the beaten path. They have left to the paleozoologist the study of the later stages in the life history of the individual, and the latter's endeavors in this direction have developed the science of zoontogeny as to-day understood. There was, perhaps, a natural cause for this separation, in the fact that the student of soft tissues finds few changes which he deems worthy of attention, between the embryo and the adult; whereas the student of hard structures generally sees an abundance of such changes. This is especially true of invertebrates, more particularly of such as build external hard structures in which successive additions are marked by the lines of growth. Vertebrates, and invertebrates without permanent hard parts, such as the crustacea, require series of individuals showing the successive steps in development. But mollusks, brachiopods and corals show, by their incremental lines, the steps in the life history during the post-embryonic period, so that one perfect individual suffices to present these later stages in development.

It is not infrequently urged that the hard parts of invertebrates, especially the shells of mollusks, are not reliable indices of ontogenetic development, since they represent only the integument, which is subject to ready modification under the influence of the environment. Such an argument is based on a total ignorance of the relation of the shell or other hard structure to the soft parts of the animal. The paleontologist is convinced that the hard parts of animals are the best indices of its development, since they record in a permanent form all the minute modifications which are not even recognizable in the soft parts. More than this, I believe that shells, those of mollusks at any rate, furnish us with a record of changes wholly independent of the environment, and referable entirely to an inherited impulse towards progressive modification, along definitely determinable lines. I am well aware that I am not expressing the opinion of all paleontologists in this statement, and that this view, moreover, is strongly opposed by some of our ablest European conchologists. But here again I contend that this difference

of opinion is due to a difference of method. When the student of shells directs his attention chiefly to adult characters, this definitely directed variation, independent of environment, is not recognized by him. But no one can study the details of shell ontogeny, especially in the earlier stages, without quickly realizing that ontogenetic development is orthogenetic, and that the inherited impulse towards determinate modifications is the most powerful controlling factor of the animal's life history.

So far as invertebrates are concerned, the study of post-embryonic development was first seriously undertaken by the immortal Hyatt, in his work on the ammonites. To be sure, others before him—notably d'Orbigny—noticed that a distinct series of changes was recognizable in the shell of ammonites, but no one before Hyatt actually employed this method. He himself once told me that when, in the early sixties, he first realized the importance of this method of study when actually applied to shelled organisms, and its value as a guide in phylogeny, it seemed so marvelously simple that he felt sure that the method and its application must be fully understood by all working naturalists. "But," he added, "I soon found that I practically stood alone, and I have spent my life since in the endeavor to convert them to my point of view."

This misunderstanding, on the part of many zoologists, of the ontogenetic method has given rise to their false attitude towards the doctrine of the recapitulation of ancestral characters. This subject will be adequately treated by some of my successors, but I can not forbear to anticipate them to the extent of pointing out this fact: When the embryologist seeks for proof or disproof of this concept in the enormously condensed record of the stages between the ovum and birth, he is bound to be grievously disappointed; for this record, necessarily modified by eliminations, can only furnish general resemblances of the embryo to earlier types, and can not be said to actually recapitulate the life history of the entire race. When, however, the student of post-embryonic ontogeny compares the youthful stages of an individual with the adult of immediately preceding species of the same genetic series, the fact of recapitulation becomes at once apparent.

The post-embryonic life history of an individual falls readily into stages, of which four major ones have been recognized and named, chiefly by Hyatt. These are: (1) the infant or nepionic stage; (2) the adolescent or neanic stage; (3) the adult or ephebic stage, and (4) the senile or gerontic stage, followed by death. These *onto-stages*, as they may be called, are further divided into substages, designated by the prefixes *ana*, *meta* and *para*, and they may be observed in the ontogeny of all individuals. Moreover, in closely related members of one genetic group, the duration of these stages and substages is approximately uniform. Change in form, however, may vary greatly, and have

no necessary relation to the onto-stages, even if they coincide with them. We have thus a second group of stages, which we may designate *form stages*, or morphic stages, and there will be required distinct designations in each case. The best method of naming these stages is to refer them to the adult ancestral type which they represent.

Thus, in all species of the gastropod shell *Fusus*, the earliest morphic stages are a close recapitulation of the adult of *Fusus porrectus* of the Eocene. These stages may therefore be called the *F. porrectus* stage. It may be continued for a considerable period of the early life history, covering several onto-stages, or it may be condensed into a short portion of one stage or substage, in accelerated individuals.

It is of considerable importance that onto-stages and morphic stages should be discriminated, so I will introduce another illustration.

In the Miocene of the Atlantic coast we have the gastropod genus *Fulgur* well represented. *Fulgur fusiformis* is normally characterized, in the adult, by the possession of a pronounced flat shoulder, which is separated from the body of the shell by an angulation carrying rounded tubercles. Some of the more specialized individuals lose the angulation and tubercles in the last whorl and become rounded. Thus, while normally the species is tuberculated in the ephebic onto-stages, specialized individuals acquire a new morphic stage through the loss of ornamentation. This morphic stage is prophetic of the normal adult of *Fulgur maximum*, and hence may be called the *F. maximum* stage. *F. maximum* itself has in its nepionic onto-stage the characters of adult *F. fusiformis*; hence it may be designated the *F. fusiformis* stage. Some individuals acquire a new stage, namely, a spinous stage, characteristic of the adult of *F. carica*. In the type designated as *F. tritonis*, the nepionic stage is characterized by a fusiformis morphic stage, the neanic largely by the maximum stage, though some of the later neanic stages may actually acquire the *carica* stage. In less specialized individuals the maximum stage may continue into the early ephebic in more specialized ones it ceases early in the neanic, the *carica* stage taking its place. Finally, *Fulgur carica* is characterized by the elimination of the maximum morphic stage, so that the neanic as well as the ephebic onto-stages are characterized by the spines of the *carica* stage, which may even begin in the late nepionic.

In the foregoing, the different morphic stages are shown to be telescoped with the onto-stages, appearing either earlier and earlier in the ontogeny of successive individuals, through the operation of the law of acceleration or tachygenesis; or later and later, through the operation of the complementary law of retardation or bradygenesis. These laws are, of course, only applicable to an orthogenetic series, but in such a series they are competent to produce, by interaction, all conceivable combinations of characters.

The paleontologist, more than any other naturalist, is concerned with the product of these interactions, and to him, oftener than to others, has come the question, Are these results species? and, if so, what are the criteria for the separation of species? The student of hard structures appreciates the difficulty of drawing sharp lines, and one of his most trying tasks is to satisfy the idiosyncrasies of his colleagues in the making of species, subspecies, varieties, etc. The student of hard parts finds transitional forms the rule, and he dare not grind them to powder under his heel with the remark credited to Stimpson, that "that is the proper way to dispose of those damned transitional forms."

The philosophic paleontologist recognizes more readily than any one else the truth of the dictum that nature knows only individuals, and that species are special creations, called into being by the fiat of the naturalist. He is concerned not so much with the origin of species as with the origin of individuals; and while he makes use of the artificial divisions called species, and sometimes finds his chief joy in multiplying and subdividing them, he still recognizes their non-existence, and turns to individuals. He may, perhaps, prefer to speak of mutations, meaning individuals, nevertheless.

But individuals are complex entities, and the paleontologist can not investigate their genesis before he has thoroughly investigated the origin of the parts composing it. As Professor Osborn has said, the paleozoologist is concerned primarily with the origin of structures. He alone is able to trace their development, for he is present at their birth, he follows their whole history, and will be present also at their extinction, for the paleontologist alone is immortal.

PALEONTOLOGY AND THE RECAPITULATION THEORY

By E. R. CUMINGS
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I

BATHER once said that "If the embryologists had not forestalled them, the paleontologists would have had to invent the theory of recapitulation." This may be considered as a fair sample of the attitude of at least the Hyatt school of paleontologists toward the theory. It is doubtful if any paleontologist could be found who wholly rejects it.

In violent contrast with the more or less complete acceptance of the theory by paleontologists, is the attitude of many embryologists and zoologists. Montgomery and Hurst have perhaps put the case against recapitulation more strongly than any one else. The former says, for example,

The method is wrong in principle, to compare an adult stage of one organism with an immature stage of another.

And again:

Therefore we can only conclude that the embryogeny does not furnish any recapitulation of the phylogeny, not even a recapitulation marred at occasional points by secondary changes.

Hurst is even more emphatic. He says:

The ontogeny is not an epitome of the phylogeny, is not even a modified or "falsified" epitome, is not a record, either perfect or imperfect of past history, is not a recapitulation of evolution.

It would seem as though two statements could scarcely be more flatly contradictory than those of Bather and Hurst, just quoted. Nevertheless, I venture to make the assertion that both parties to the recapitulation controversy are right, for the simple reason that they are not talking about the same thing. Grabau has called attention to this, by implication, in one of his papers on gastropods. He states that the recapitulation theory has been placed in an evil light by the habit of embryologists of comparing *embryonic* stages with the adults of existing representatives of primitive types, and that they have commonly neglected to compare the *epembryonic* stages with the adults of geologically older species. In other words, paleontologists have usually dealt, in their comparisons, with epembryonic stages, and embryologists with embryonic stages.

There arises here a question of definition: does the biogenetic law mean that the *ontogeny* is a recapitulation of the phylogeny, or does it mean that the *embryogeny* is a recapitulation of the phylogeny? If we take the general consensus of opinion, we shall find for the former definition; and if we take the words of Haeckel, whose statement of the law is the one usually quoted, we shall again find for the former definition.

It is certainly true, at any rate, that the epembryonic stages may and do show recapitulation, even when the embryonic stages do not, or when the embryogeny is so obscured by secondary adaptations as to be untrustworthy. There are many reasons why adaptations should occur in intra-uterine or larval life to obscure the ancestral record. These have often been stated and discussed, and I shall pass them with this mere mention. That the record of remote ancestors, contained in the embryogeny, may be lost or obscured, while the record of nearer ancestors, contained in the epembryogeny, is still clear and convincing, is my contention; and I hold that this contention is substantiated by the studies of a host of paleobiologists.

While contrasting the views of biologists and paleobiologists, I do not wish to create the impression that all of the former have turned against the theory of recapitulation. Several recent studies of the development of extant forms seem to afford very satisfactory evidence that the theory is not wholly rejected in the house of its fathers. Of

these I may mention the very interesting papers by Griggs on juvenile kelps, Zeleny on the development and regeneration of serpulids, and Eigenmann on the blind vertebrates of North America.

Griggs especially criticizes the views of such critics of recapitulation as His, who holds that the reason why ontogeny seems to recapitulate phylogeny is because the developing organism must from physiological necessity pass from less to more complex stages, more or less resembling ancestral forms; and the views of Morgan, who holds that only embryonic stages of ancestors are repeated. This is the so-called "Repetition Theory." To both of these critics Griggs objects that they confuse physiology and morphology. "The recapitulation theory," he says, "has nothing to do with physiology; it is purely a matter of morphology."

On the first point, that the developmental stages are merely the physiologically necessary steps in the development of the adult organism, the conclusions of Eigenmann and Zeleny are of especial interest. Eigenmann shows that in the blind fish, *Amblyopsis*, the development of the foundations of the eye is normal, and is phylogenetic, while the stages beyond the foundations are direct. Zeleny concludes that the ontogenesis of the opercula of serpulids is phylogenetic, and recapitulates ancestral characters; but the regeneratory development of the organ is direct, and may be very different from the ontogenetic development. We may ask, therefore, if development takes a certain course only because that is the physiologically necessary way in which the individual or the organ must develop, why should a condition of perfect blindness, with almost total loss of all the eye structures, be attained only by the round-about method of first developing the foundations of a normal eye? Why, again, if there is any physiologically necessary course of development, should the serpulid be able to regenerate the opercula in a manner entirely different from their ontogenesis?

Hatschek, Hurst, Montgomery and others maintain that, if two individuals differ in the adult, they must also differ in the egg, and consequently must be different at all stages between. From this thesis they draw the conclusion that organisms can not recapitulate adult ancestral characters, because any change in the adult stage of an individual, causing it to be different from its parents, involves a change in the entire ontogeny—"the entire row of cells" from the egg to the adult. That there is some sort of change in the entire row of cells we grant; but that this change necessarily affects the *morphology* of the individual or of its organs, up to the adult stage, we do not grant. We have here again a confusion of morphology and physiology. The cell energies may indeed be changed; but unless a change in the cell energies inevitably necessitates a change in the morphology of all the cells or of all the organs which they compose, the argument of Montgomery proves nothing.

If inheritance were perfect, the individual would take exactly the same course in development as its ancestors. That it does not do this in all cases is a more remarkable fact than that in so many cases it follows the ancestral mode of development so closely. This loss of inheritance is due to a progressive condensation of ontogeny, or as it is commonly called, acceleration. Most embryologists misconceive the law of acceleration, limiting it to the omission of characters or stages. With the classic formulation of the law by Hyatt we are all familiar. According to Hyatt, acceleration involves not only omission, but condensation without omission, through the earlier inheritance of characters acquired in the adult or adolescent stages of life. By the unequal acceleration of characters an overlapping, or telescoping, as Grabau calls it, may be introduced. It follows, therefore, that acceleration may be by *elimination*, by *condensation* without change in the order of appearance of characters, and by condensation with change in the order of appearance, or *telescoping*. As conceived by the paleobiologist, the law of acceleration is an explanation of recapitulation, as well as an explanation of the failure to recapitulate.

Another factor in inheritance is retardation, so named by Cope. By the operation of this law, characters that appear late in the ontogeny may disappear in the descendents, because development terminates before the given characters are reached. In this way the ontogeny may be shortened and simplified, and many ancestral characters may be lost entirely. The result of the continued operation of retardation is retrogression, since the loss of the characters of nearer ancestors, with the continued repetition in early ontogeny of the characters of remote ancestors, must eventually cause the species to resemble the remote, rather than the nearer, ancestors.

II

Of the numerous cases adduced by paleontologists, in which there is clear evidence of recapitulation, I shall mention a few only.

Probably the best known examples of recapitulation are those made known by the researches of Hyatt, Branco, Würtenburger, Buckman, Smith and others among the Cephalopoda. It is shown that Ammonites pass through a goniatite stage, and that, as phrased by Zitttel, "The inner whorls of an ammonite constantly resemble in form, ornament and suture line the adult condition of some previously existing genus or other." The nautilus grows at first straight or orthoceraform, then arched or cyrtoceraform, and finally at the close of the first volution of the shell, becomes close coiled. The impressed zone appears in ancient nautiloidea in the neanic stage, where the whorls first come into contact, and is indeed a *result* of contact. In modern nautilus, and in Mesozoic and Tertiary nautilus the impressed zone appears in

the nepionic stage, before the whorls come into contact. It has been carried back in the ontogeny by acceleration. Smith concludes from a study of the development and phylogeny of *Placenticeras*, an Upper Cretaceous ammonoid, that "the development of *Placenticeras* shows that it is possible, in spite of dogmatic assertions to the contrary, to decipher the race history of an animal in its individual ontogeny."

Among the Gastropoda, Grabau and Burnett Smith have pointed out numerous beautiful cases of recapitulation. In *Fusus* and its allies, the higher forms quite constantly resemble in their earlier stages the adults of ancestral forms. Even in profoundly modified gerontic types, the young resemble the ancestors. Smith has brought to light in *Athleta* (*Volutilithes*) of the Eocene, an almost perfect example of even and regular acceleration, with its correlative, the recapitulation in the young of the Upper Eocene forms of the adult characters of the Lower Eocene forms. The stages passed through by this group of shells are, beginning with the earliest, a *smooth, curved rib, cancellated, spiny* and sometimes a *senile* stage. In the ancestral species (*A. limopsis*) the curved rib stage comes in at the close of the fourth whorl, whereas in the Upper Eocene form (*A. petrosa*), this stage comes in at the beginning of the third whorl.

Among the Pelecypoda the classic researches of Jackson are familiar to all. He shows that the modern *Pecten* passes through, in its ontogeny, a series of stages resembling adult *Rhombopteria*, *Pterinopecten* and *Aviculopecten*, and that the geologic order of these genera is the same as the ontogenetic order in *Pecten*. In such monomyarian genera as *Ostrea*, the initial shell, or prodissoconch, is dimyarian, and resembles the primitive *Nucula*. Again, in various more or less widely separated genera, the condition of complete cemented fixation has produced the ostreaform shape. Each one of these genera, however, except where the modification of shape due to fixation appears very early in ontogeny, recapitulates the adult characters of its respective ancestor. The examples of this are *Mulleria*, a member of the Unionidæ—like *Anodon* in the young; *Hinnites*, a member of the Pectinacea—like *Pecten* in the young; *Spondylus*, another member of the Pectinacea—like *Pecten* in the young.

Beecher's various studies of the Brachiopoda not only brought out the fact that the initial shell or protegulum of the brachiopod is remarkably similar to the most primitive known Lower Cambrian brachiopods, but have supplied in addition numerous other remarkable examples of recapitulation. One of the most striking of these is the case of the Terebratulidæ. In both the boreal and austral subfamilies a very complete series of genera correspond to the ontogenetic stages of the terminal or highest genera. Another interesting case is that of *Orbiculoidæ*. This discoid shell has at first a straight hinge like *Iphidea*.

It next resembles *Obolella*, then at a later stage it is like *Schizocrania*, and finally adult growth brings in the characters of *Orbiculoidea*. Raymond has shown the remarkable similarity of the neanic stage of *Spirifer mucronatus* to the adult *S. crispus* of the Niagara. Shimer and Grabau found in the upper Hamilton of Thedford, Ontario, a variety of *Spirifer mucronatus* that is very mucronate in the young and not at all so in the adult. The derivation of this form from *S. mucronatus* is beyond question. I have pointed out a precisely similar case in *Platystrophia acutilirata* var. *senex*. This variety, which occurs in the upper Whitewater beds of Indiana and Ohio, has a hinge angle of nearly 90° in the adult. In the young, however, the outlines of the shell are exactly like the typical *P. acutilirata*, from which it is beyond any question descended. Greene has shown that *Chonetes granulifer* of the Carboniferous is, in the neanic stage, like the Devonian *Chonetes*, and that the hinge-spines come in at a considerably earlier stage in the Carboniferous than in the Devonian and Silurian forms, showing the acceleration of this character.

In the Bryozoa I have pointed out the fact that the colony behaves as an individual, and like an individual recapitulates in its ontogeny (astogeny) ancestral characters. This is beautifully shown in *Fenestella*, in which the earlier zoecia are strikingly like the adult zoecia of the Cyclostomata. The adolescent zoecia of Devonian *Fenestella* are similar to the adult zoecia of Niagara forms. Lang has brought together numerous cases of recapitulation among Jurassic and Cretaceous *Stomatopora* and *Proboscina*. The method of dichotomy in the earlier portions of the colony is constantly more like the normal dichotomy of ancestral species.

In graptolites the remarkable researches of Ruedemann clearly indicate that the graptolite colony recapitulates ancestral characters, the proximal thecae being similar to ancestral adult thecae. He says:

The rhabdosomes in toto and their parts, the branches, seem also to pass through stages which suggest phylogenetically preceding forms.

Among the trilobites the studies of Beecher, Walcott and Matthew are classic. Beecher has shown that there is a common larval form, the protaspis, and that in higher genera characters appear in the protaspis that are known only in the adults of more primitive genera. For example, the "main features of the cephalon in the simple protaspis forms of *Solenopleura*, *Liostracus* and *Ptychoparia* are retained to maturity in such genera as *Carausia* and *Acontheus*." Larval *Sao* has characters that occur in the adult of *Ctenocephalus*. The larval stages of *Dalmanites* and *Proetus* have characters that appear only in the adult of ancient genera.

Among the corals Beecher and Girty show that such genera as *Favosites* have early stages that suggest *Aulopora*. Lang, in a recent

paper, records very interesting cases of recapitulation in the genus *Parasmilia* of the Cretaceous. Bernard concludes that the coral colony, like the graptolite colony and the bryozoan colony, behaves as an individual.

In the echinoderms the likeness of the stem ossicles and the development of the anal plate of *Antedon*, to Paleozoic and Mesozoic forms has become one of the stock illustrations of recapitulation. Jackson has found interesting examples of recapitulation in the development of the ambulacral and inter-ambulacral plates of echinoids. Miss Smith has shown that the young *Pentremites* is exactly similar in form to the adult *Codaster*. This is an extremely interesting case, for Bather has independently, and from quite different data, come to the conclusion that *Pentremites* is derived from *Codaster*.

The idea of recapitulation has been one of the most fertile in the whole realm of biology, and its usefulness to the paleobiologist has been almost incalculable. But while there can be no doubt that recapitulation is a fact, the paleontologist should observe all due care not to assume too much for it. That there are various sorts of adaptations, arising at all stages of life, and that these may greatly obscure the ancestral record, is a fact too well known to require more than mention. There is also always acceleration, sometimes affecting different characters very unequally; and there may be retardation. All of these factors complicate the record of ontogeny. Nevertheless, after all of these have been taken duly into consideration, the parallel between ontogeny and phylogeny remains a powerful aid to investigation for the paleontologist.

VERTEBRATE PALEONTOLOGY AND THE EVIDENCES FOR RECAPITULATION

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AFTER the careful papers of Professors Loomis and Lull in which the doctrine of recapitulation was so fully set forth from the standpoint of vertebrate paleontology, I can perhaps do no better than devote part of the time allotted me to showing how certain leading vertebrate paleontologists have viewed this question. Then I will cite one or two illustrations of this principle drawn from among the lower vertebrates.

Passing over the period of pre-Darwinian paleontology—the paleontology of Cuvier, Owen and Louis Agassiz—we come to the time of Leidy, who, as Professor Osborn has recently shown,¹ was one of the first,

¹In his address on "Darwin and Paleontology" printed in "Fifty Years of Darwinism." Centennial addresses in honor of Charles Darwin, New York, 1909, p. 209.

if not the first, to bring the fruits of paleontology to the support of evolution. But Leidy, as far as a hasty search through his writings could reveal, nowhere expressly advocated the doctrine of recapitulation. Indeed, he gave but little attention to the philosophical bearings of paleontology, generally partly because of temperament and partly because in those pioneer days material to serve as a basis for generalization was still scanty.

Gaudry, one of the first European paleontologists to champion the cause of evolution,² likewise did not specially advocate the doctrine of recapitulation. An examination of his "Philosophie Paleontologique" fails to reveal any definite belief in this doctrine.

Huxley, as far as I can gather from his papers and essays, believed in this doctrine, though with certain implied reservations as to its general applicability. In his presidential address to the Geological Society of London on "Paleontology and the Doctrine of Evolution" delivered in 1870, we find some interesting comment on the significance of the splints of the living horse, which he regards as indicative of the presence of three complete digits in the horse ancestor. But Huxley was never an out-and-out advocate of the biogenetic law.

Cope and Marsh, as we all know, were staunch upholders of evolution; and Cope, at least, was also a staunch upholder of the doctrine of recapitulation. In his "Primary Factors of Organic Evolution," his last contribution to philosophical paleontology, he devotes considerable space to proving this doctrine. He says:³

The representatives of each class passed through the stages which are permanent in the classes below them in the series.

And he backs up this proposition with evidence derived from the ontogeny and phylogeny of batrachia, the antlers of deer and the blood trunks of vertebrates generally. For all that, Cope recognized the justice of certain criticisms which had been brought against the doctrine of recapitulation and urged caution in its application.

An example or two of recapitulation may now be cited from the field of the lower vertebrates.

The mode of development of the teeth in *Neoceratodus* has sometimes been adduced as an illustration of recapitulation. It is well known that the Devonian dipnoans (*e. g.*, *Dipterus*) had teeth composed of rows of denticles, those in each row being more or less fused at their bases. During the history of the dipnoans since the Devonian period, the separate denticles have merged more and more until in *Ceratodus* and the living *Neoceratodus*, the rows of denticles are, in

² According to a letter from Darwin to Gaudry dated January 21, 1868. "The Life and Letters of Charles Darwin," edited by his son Francis Darwin, New York, 1899, Vol. II., p. 269.

³ "Primary Factors of Organic Evolution," Chicago, 1896, p. 195.

the adult, replaced by almost smooth ridges. Now, Semon in his beautiful studies on the development of *Neoceratodus*⁴ has shown that the teeth of this fish at one stage in ontogeny, are represented by rows of denticles even more discrete than the denticles in the Devonian *Dipterus*; then the denticles gradually merge at their bases, the separate cusps, however, still showing—a stage comparable with the Carboniferous *Otenodus*; then they merge still more and assume the ridge-like form seen in the adult *Neoceratodus*.

Another example: In many sharks the alimentary canal is longer in the embryo than in the adult, the anal opening being situated near the posterior end of the trunk. From such cases one is inclined to believe that in the ancestral sharks this must have been the condition in the adult form; that is to say, the anal opening probably was near the posterior termination of the trunk. We may therefore ask: are there any early fossil sharks which show such a condition? Recently Professor Dean has described⁵ a remarkable specimen of *Cladoseleache* from the Upper Devonian of Ohio which seems to indicate such a condition. In this specimen remnants of both kidneys are preserved. They extend in the posterior half of the fish and by their direction indicate that they were drawn together, toward their external opening, not far from the posterior termination of the trunk. This shows that the anal opening in this ancestral shark was very much as in the early shark embryo to-day.

In conclusion perhaps I may venture to make one other point in regard to this question. A vast amount of skepticism concerning the doctrine of recapitulation is to be found in the literature of to-day; and if we study the reasons for this skepticism we find that it is in some measure justified. It is clearly established that among vertebrates as well as among invertebrates there are many examples of structures appearing during embryonic growth which are identical with structures found in the adult of some remote ancestor. But when we reflect on the amount of adaptation which any embryo has undergone in its long evolutionary history; when we remember how paligenetic characters are on every hand overlaid by ceno-genetic ones; who will say that recapitulation is a principle of general application, or that it is safe to draw conclusions from all embryos concerning their long extinct ancestors? Who will believe that a bony fish which runs through its embryonic development in a few days repeats its ancestral history, when we see at every stage of its ontogeny how it has been adaptively modified for this and for that special need? Only when series of related forms have certain onto-

⁴ "Die Zahnentwicklung des *Ceratodus forsteri*," "Zool. Forsch. in Austral. u. Malay. Archipel," 1899, pp. 115-135, pls. xviii-xx.

⁵ *Mem. Amer. Mus. Nat. Hist.*, Vol. IX., p. 232.

genetic stages in common are we justified in inferring that their racial ancestor may have had such characters in the adult state. But it should never be lost sight of that this inference is only a provisional hypothesis which may or may not be verified when the paleontologic record is more complete. It is no surprise that the efforts of some earnest paleontologists have been discredited in some quarters, especially among zoologists. Some of them have invoked recapitulation as a sort of magic spell by which they can conjure up ancestral forms from almost any embryonic series, forgetting the limitations of this doctrine. As far as the attitude of vertebrate paleontologists is concerned, their view has been aptly summarized by Professor Charles Depéret in his book "*Les Transformations du Monde Animal*" and I can do no better than close with a quotation from him:

If we appeal to paleontology, it must be recognized that this hypothesis [recapitulation] is by no means verified. There do exist here and there certain fossil genera, which all their lives have retained certain youthful characteristics apparent in their living descendants; but when it comes to reconstructing whole series chronologically continuous, grave contradictions are met with, and it is only in the groups of the mammals and perhaps of the reptiles [and, we may add, fishes] that it becomes possible to present a few examples sufficiently demonstrative.*

* "*Les Transformations du Monde Animal*," Paris, 1907, p. 117.

THE RELATION OF PALEOBOTANY TO PHYLOGENY

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THE history of plant life has been the central idea in all botanical studies from the very earliest times, whether expressed in the imperfect methods of the early German and Dutch botanists who desired simply to establish natural affinities on the basis of external resemblances, or in the ambitions of Cæsalpino to arrive at a classification of plants which should satisfy the conditions of relationship through the structure of all parts, and especially of the reproductive organs. For nearly four hundred years the external organs have been employed as the chief basis of those numerous systems of classification which have appeared from time to time. The idea that the reproductive organs and the minute interior structure of plants were of primary importance as first advocated by Cæsalpino, was for a long time lost to view, although it reappeared now and then in the works of later writers. Eventually it gained recognition and became a factor of increasing importance, until the most advanced systems now employed involve an acceptance of both the external parts and the internal anatomy as essential factors.

From the time of Malpighi and Grew, to Goeppert and Corda, our knowledge of the interior structure of plants made great and rapid progress, and was later applied successfully by various investigators in the direction of establishing relationships. To no one are we more fully indebted for an elaboration of this idea than to Williamson, whose researches into the structure of fossil plants from the Coal Measures of Great Britain, during the latter part of the last century, laid the real foundation of modern paleobotany.

In so brief a treatment as that which is now employed, it is impossible to more than touch upon some of the salient features in the relations of paleobotany to the course of phylogeny, but it is, nevertheless, worth while to give special emphasis to the now well-recognized fact that a thorough knowledge of the interior structure of the plant, and especially of the stem, leads to a more comprehensive and exact acquaintance with relationships than that of any other part. This arises from the fact that the minute anatomical details have a greater degree of stability than any other portion of the body, doubtless due to the fact that in its adjustment to the land habit, the environmental influences

present the least variable features in those factors which determine relations to mechanical stress and physiological needs.

External organs are notoriously subject to variation, even under slight alterations of surrounding conditions, within the limits of the species or even within various stages of development of the same individual. From this it is clear that organs such as leaves must be very unreliable for phylogenetic purposes. It is, unfortunately, true that much of the paleobotanical work based upon a study of such parts must be of inferior value, and the conclusions drawn will require extensive revision when the more rigid tests to be applied through a knowledge of the stem structure are brought to bear.

The value of paleobotanical evidence consists in its ultimate correlation with known types of plants, and it is obvious that all such studies should be prosecuted with direct reference to the broader requirements of plant biology. This involves a comprehensive knowledge of the history of plant life from its earliest development; that the data derived from a study of living species should be correlated with the evidence obtained from fossilized remains. Existing vegetation shows a very incomplete record of plant life as a whole. Its history as known until very recent times, and even now to a very large extent, is displayed only through the medium of detached groups, and relates chiefly to the most highly organized types. Through the perspective afforded by paleobotany, it becomes possible to not only supply missing facts, but to establish what theory has for so long a time required a satisfactory demonstration of—a more or less continuous series of phenomena from the rudimentary forms to the most advanced organisms.

Until a very recent date the Linnaean division of plant life into two great phyla, the cryptogams and the phanerogams, was the prevailing conception of the constitution of the plant kingdom. This division recognized no connection between the two great groups, but regarded them as wholly distinct in origin as in character. But the rapid advances in a knowledge of plant anatomy, developed toward the middle of the last century, and especially the remarkable and epoch-making observations of Hofmeister respecting the process of reproduction, enabled him to break down the old barriers erected by the doctrine of the constancy of species, and prove a genetic connection between the primary divisions of Linnaeus. With this starting-point, the cryptogams and the phanerogams were subjected to a severe scrutiny from an entirely new point of view, with the result that each underwent a revision which led to such a rearrangement of subdivisions as to present an entirely fresh conception of their relations to one another. The logical result was finally expressed in the subdivision of the plant world into four great phyla, which, in their evolutionary sequence, came to be known as I., Thallophyta; II., Bryophyta; III., Pteridophyta; IV., Spermatophyta.

Admirable as this scheme is, and scientifically acceptable as it has proved to be, it nevertheless presents certain well-recognized defects with respect to the requirements of theory, although at the time of its formulation and as late as 1899 it represented the sum of available knowledge. It was just at this time that paleobotany became available as a means of meeting those deficiencies which a knowledge of living plants could not overcome. For a long time botanists have been familiar with certain Paleozoic remains having a fern-like aspect which were generally accepted as ferns; but because of their want of direct connection with stems or fruit, there remained a serious doubt as to their real character. In the same horizons, detached fragments of stems were also observed with increasing frequency. The study of their anatomy disclosed a structure which, in some respects, was curiously like that of ferns, while in other respects it approximated to the anatomy of the higher plants as presented in some of the gymnosperms. This combination of filicinean and cycadean characters was noted by Potonié, who succeeded in correlating them and expressing their phylogenetic position in the name of a new order which he called the *Cycadofilices*.

There yet remained to be considered certain remarkable fruits for which no relationship has as yet been determined until, through the work of Scott, Oliver, Kidston and others, it was shown that they were of the nature of seed-bearing organs which could be correlated with the *Cycadofilices*. It thus became evident that there was a hitherto unknown group of plants combining the characters of ferns in their foliage and stem structure with those of primitive gymnosperms as presented in their stems and fruits. On the whole, however, these plants approached most nearly to the pteridophytes in their external features. To this new phylum, of which the *Cycadofilices* formed the most conspicuous member, Scott and Oliver in 1904 assigned the most appropriate name, *Pteridospermæ*. This result was based entirely upon paleontological evidence through comparative anatomy, and it compels us to recognize the existence of five, instead of four great phyla. The far-reaching significance of this achievement can not be overestimated. It is not only of the utmost importance as proving the general course of evolution and bringing into the realm of proved facts what had previously been a working hypothesis only, but it offers an entirely new point of departure for the botanist of the future. Attention may also be directed to one other effect. The tendency of this discovery is to co-ordinate, unify and strengthen all branches of botanical knowledge, bringing to us the conviction that the more extended and thorough our knowledge of the earlier forms of vegetation becomes, the more satisfactory will be our knowledge of the science as a whole; for while the example selected is probably the most important for our special purposes, the general utility of paleontological research in relation to the

history of development is enforced upon our consideration in a great many subordinate ways.

Recognizable plant remains first occur in the Silurian in the form of certain highly organized algæ, the ancestral forms of which are unknown. Nevertheless, the history of *Nematophycus* shows that in the Silurian and extending through the Devonian, members of the brown algæ directly comparable with the modern kelps, both in general character and in detailed structure, had attained to a development unknown to any of the marine algæ of to-day. Arborescent forms with stems two feet in diameter and a corresponding height lead to the inference that they not only represent the culmination of the phylum at that time, but that they must have been preceded by a long line of ancestral forms, extending far back into the earlier horizons, possibly into the Eozoic itself.

Parka decipiens from the old Red Sandstone of Scotland affords striking illustration of the very early period at which heterosporry was developed among vascular plants, which, according to the evidence now available, are comparable with the genus *Marsilea* among existing types. In these remains we meet with prostrate stems often one to two inches in diameter, from which slender, upright branches are produced, bearing in turn conceptacles containing both micro- and mega-sporangia. Some of these latter further contain prothalli in various stages of development.

The earliest form of gymnosperm is that which we recognize in the genus *Cordaites* from the Devonian. The highly developed and dicotyledonous character of the stem affords abundant evidence that the ancestral type must be looked for in some remote and earlier horizon, but, taken as an isolated case, it affords no clue whatever to the origin of that particular phylum, although the subsequent course of development may be traced with considerable certainty to comparatively recent times.

The obvious conclusion to be drawn from the geological relations presented by such illustrations as those recited, is, that the evolution of even very simple forms from the most primitive plants must have called for enormously lengthy periods of time. Even the most liberal application of the law of mutation would fail to adequately account for the extensive gaps which are recognized as occurring between the simpler types and those which lie in the same general line of succession, but with greatly advanced organization.

We are now led to ask, how far have paleontological studies carried us in our knowledge of plant life from the earliest times, that is, do they enable us to trace an unbroken series of steps from the first to the last? To this the answer must be that, while paleobotany has been of the greatest service in supplying missing data, in filling great gaps in a supposed sequence and in giving the fullest support to the law of evo-

lution, it is as yet by no means adequate with respect to meeting all that theory demands. For this there is an intelligible explanation based in part upon the fact that the necessary material is available only under conditions of great difficulty; and that the character of the remains upon which research is based is conditioned by the original nature of the structure and its ability to survive in an unaltered form, the remarkable conditions of decay, infiltration, compression, upheaval and often of volcanic influences to which it has been subjected. The earliest type of vegetation was that which we now find in hot springs, continued with the algæ found in cool or cold waters, all of which possessed a delicacy of structure which permitted speedy decay. The great abundance of such organisms probably afford an adequate explanation of the Laurentian and later forms of graphite which is regarded by many as the remains of former vegetation. While this hypothesis may be accepted provisionally, paleobotany is nevertheless wholly unable to furnish any clue to the life history of the individuals, or even to inform us as to the specific types. Such knowledge as we possess in this direction is the result of inference from parallel conditions and structures as now found.

It might be assumed that with an increasing perfection in the preservation of fossil remains, as found especially in the later formations, it should be possible to trace the course of descent with accuracy and completeness. This is, in a measure, true, but although the general requirements of theory may be verified, yet the haphazard conditions involved in the collection of plant remains make it a very difficult matter to secure a complete narrative, and there remain many gaps which it is difficult to fill. The evolutionary position of the Bryophytes demands that the origin of these plants should lie somewhere in the early Silurian or even in the Eozoic age, but we have no certain knowledge of them until the middle Mesozoic, and their remains do not become familiar or abundant until the later Tertiary. So important a deviation from what theory demands should lead us to caution in drawing conclusions from the direct testimony which is thus presented. Unless otherwise disposed of through paleontological evidence, it would be more correct to infer that the delicacy of the plants, and the conditions of their fossilization, have not admitted of their preservation in a recognizable condition; while there is also the further probability that many of their remains have been overlooked through resemblance to certain Pteridophyta for which they might well be mistaken.

In spite of such apparent contradictions, the evidence everywhere points with great force to the idea that each of the lesser phyla had its origin in some ancestral form, followed by growth and culmination. This latter was, in some cases, abrupt, as in many of the Pteridophytes; in other instances there was a gradual decline, as in the lycopods or the horsetails, which attained their highest development in the later Paleo-

zoic, but have since been in a state of degeneracy, their present representatives being few in number and of a depauperate character. The application of this law throughout the enormously lengthy periods required for the evolution of existing species, has led to the survival of some of the most ancient types until the present day; to the absolute obliteration of others which at one time gained great prominence; and to the gradual dying out of yet others, some of which are now found in the last stages of their existence. But through the entire course of change, the evolution of higher and yet higher forms has been the most conspicuous fact. Furthermore, it is undoubtedly true that the general course of evolution is in progress to-day as in the past, since all the potentialities of such evolution exist now as always, though conditioned by the fact that owing to continued changes in the physical character of the earth's atmosphere as well as of its crust, the possibilities of evolution are steadily diminishing and will eventually cease.

There is one direction in which paleobotany gives well-defined assurance that the evidence derived from existing species leads to correct conclusions. In tracing the succession of types, we are led to the belief that there is no direct sequence. Conterminous evolution is in accord with neither theory nor ascertained facts, and it is, therefore, impossible to conceive of a figure which shall in any way represent a single and unbroken line of succession. If paleontology teaches us anything, it is that each great phylum, as well as its various subdivisions, finally reaches its culmination in a terminal member from which no further evolution is possible. But that from some inferior member, possessing high potentialities, a side line of development arises. There is thus, in the early life of each member of the series, a certain recapitulation of ancestral characters. This conception of a continuance of the main line of descent through a succession of lateral members is both logical and fully in accord with the evidence derived from both recent and extinct forms of plant life, as well as with our present theory of evolution.

PALEONTOLOGY AND ISOLATION

BY DR. JOHN M. CLARKE

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THE notion of isolation as a factor in variation, as I am using the term, is that of geographic separation exclusively, the conception expressed most clearly by Wallace, Moritz Wagner and Jordan. I take it that while this influence has been carefully estimated in the geographical distribution of living species, it has not often been expressed in its own terms in the analysis of extinct faunas. With increasing accuracy in the record of ancient continental lines and bar-

riers, we are coming to a point where the efficiency of this factor can be safely taken into account. The outcome of free interbreeding, as Jordan has pointed out, is to unify species and obliterate variations. *Per contra*, isolation checks this process and gives freer play to tendencies arising from other factors in variation. The effect is thus, as a general rule, negative, but expresses itself freely enough in geographic provinces severed by some barrier or condition which has the effect of a barrier. Among existing species the formative effects of segregation have been very largely illustrated from restricted areas such as the subdivisional valleys and forests of Hawaii with its distinctive forms of the Helicidæ and other terrestrial snails—a case that is paralleled in paleontology by the snails of Steinheim. But the effect is to be reckoned with in larger or continental areas between which there has been at one time opportunity of interchange, especially in the case of marine species, with which we chiefly deal, along the epicontinents.

I have particularly in mind phenomena which have been brought to my notice by a somewhat extended study of the Devonian faunas of the southern hemisphere and the broader application of the factor is best enforced and illustrated by this instance. I may say that this broader notion seems to be that entertained by Darwin so far as he specified the conception of geographic segregation as an element in natural selection and it was his work in South America that formed the basis of his conclusions.

With other students we recognize the existence during the Devonian of austral continental lands which have been variously designated and variously outlined. By some this land has been posited as a north and south Atlantis lying in the meridional axis of the present ocean, by others a broken land mass partly crossing the southern Atlantic from east to west. But now we begin to see its continuity and the extent of its strands, with something of its changes in outline during its early history. It was the precursor and the nucleus of Gondwána-land. With it began, so far as we now know, the long history of that continental land and the successive records of life developing under continued conditions of geographic isolation from the northern strands.

From Argentina, Bolivia and northern Brazil we have very lucid evidence, on the basis of paleontology, that in the late Silurian the shore lines were continuous with those of the north. We have no dependable knowledge of these earlier faunas at the east and indeed their entire absence is indicated by stratigraphy; but with the submergence of the Silurian at the west, there entered from the African east upon this south Atlantic field, a positive diastrophism whose axis was well nigh normal to that of the present Atlantis, and along the shores of this growing land bridge entered an invasion of marine life

at the opening of the Devonian time. It seems to have come westward from a dispersion area in Africa and it evidently disseminated itself without interruption of continuity from the strands which now, as the Bokkeveld beds of Cape Colony, constitute the only evidence of marine life in the South African Paleozoic, to those of the Falkland Islands, two far distant regions which have much more of organic content in common than do the Falklands and the nearer regions of Paraná, Argentina and Bolivia.

This fauna with its special and peculiar features is, however, spread through Bolivia, western Argentina, southern Brazil, including Paraná and as far north as Matto Grosso, thence eastward by way of the Falklands to South Africa. From the boreal strands of the period it was separated by a barrier, often narrow and constituted only of deeper water, so that of the boreal Devonian we find no evidence much south of the equator in Brazil nor of the austral Devonian north of that line. This barrier I believe to have been overpassed at times during the early part of the Devonian by species which are of wider distribution south and north but these passages seem to have become rarer as time passed and as more complete geographic isolation was effected.

There are many evidences in this southern fauna that the land bridge was accompanied by insular strands which are evidenced by varying percentages in community of species and by bathymetrical variations. Apart from these possible island masses, there was clearly a Devonian land bridge extending from South Africa to the Falklands, westward into Argentina and northward into Bolivia, embracing also as continental or island lands parts of the states of Paraná, Matto Grosso and even of Pará.

By virtue of the evident derivation of the fauna of this time from the east along newly forming strands which were, throughout the period of the Devonian, kept asunder from the Atlantic-European lands at the north, and by its further development under conditions of isolation, the fauna presents fundamental contrasts to any development of the Devonian elsewhere in the world. It is in itself a unit and a unit also in relation to the sediments in which it is involved. There is no earlier Devonian in this southern region nor is there any later Devonian, for wherever the succession has been determined this austral fauna, bearing no evidence in itself of a later time stamp than early Devonian, is overlain by Carboniferous deposits without demonstrated unconformities between. Deposits and faunas which at the north we are accustomed to regard as of later Devonian age, are absent at the south, either because this austral land was broadly above the sea during these stages and its strands now lie buried or, as seems much more probable, this sedimentation represents the total Devonian sedimentation and this fauna the total Devonian fauna at the south.

I can not in this place analyze the peculiarities which give the austral fauna of these "Falklandia" strands their special impress but I may specially cite the trilobites which are astonishingly developed. I presume any competent student of northern faunas, being shown a series of these without knowledge of their origin, would pronounce them of early Devonian age and yet they are neither northern species nor, in any large degree, northern genera. While they bear the impress of boreal genera and resort to morphologic equivalencies thereto in fugitive epidermal structures which so richly characterize the boreal trilobites at this time, they are on the whole constructed on a series of modified types which hold their fundamental expression while developing minor details with the chronology normal to their succession at the north. The *Phacopes* are seldom true *Phacopes*, the *Dalmanites* seldom true *Dalmanites*, yet the same structural decorations and extravagances we are familiar with at the north, are distributed freely through the group. This is all equally true, in qualifying terms, of the other groups of this fauna, save for the fact that in these we can hardly venture to insist so entirely on generic distinctions south and north. The species differences declare themselves on every hand and taken as a whole the fauna presents fairly conclusive evidence of having derived its distinctiveness through its isolation from the boreal fauna from which it ancestrally took origin. Yet while it has developed this character it has also proceeded to maintain a faunal composition which declares its age, and a morphological stamp which shows that it developed all its parts in the proper time and place in the series.

In predicating geographic isolation as the prime factor in this regional development of the Devonian fauna, its efficiency should not be made to seem qualified by an illustration which is striking by virtue of its contrast with the already well known. There are evidences in plenty that geographic isolation has played a similar rôle with even more diverse effect in the development of the boreal faunas of the same geologic stage. The north Atlantic land bridge was continuous at this time, as evidenced not alone by the presence of the Coblentzian fauna in the Atlantic coast rocks but by an array of additional facts; and it seems very probable that the primary movement of these northern faunas was from the same African dispersion area as that of the south.

THE CONTINUITY OF DEVELOPMENT

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CONTINUITY of development in a broad sense hardly calls for discussion here. The paleontologic evidence in its favor is so extensive and so universal that the perfection of the proof is merely a question of the completeness of the evidence. The question for discussion is rather as to the method of race development and specific change—whether continuous, by the slow accumulation of minute individual variations, definite or indefinite, through the influence of natural selection or of other causes—or discontinuous by the sudden appearance of distinct mutations or sports, usually of subspecific or specific value, sometimes of generic value. This question is much debated nowadays, and it would seem that the evidence from paleontology ought to be of the first importance in deciding it.

It is very commonly asserted that this evidence is strongly in favor of discontinuous development. This would mean that new species and even genera appear, as a rule, suddenly at certain levels, and that the record of a phylum is not usually a slow continuous change from one species into another as we pass upward from stratum to stratum; but that one species has a certain vertical range and is then supplanted by another species, this in turn by a third, and so on, each successive stage being an advance over the preceding, but the species overlapping instead of grading.

I think that there is no question but that in vertebrate paleontology the evidence taken at its face value does appear to be very distinctly in favor of discontinuous development. Where we are able to follow a phylum of Tertiary mammalia through a series of strata in one locality, we find that the successive stages appear, as a rule, full formed at certain levels, supplant and replace the more primitive stages, and are in turn supplanted and replaced by more advanced stages. In former years, when the records of locality and level were less exact, it was possible to arrange a series of gradations from one stage to another among the specimens pertaining to a particular phylum, and to assume that this gradation corresponded to the levels in the formation at which the specimens had been collected, and that the specific change was through continuous gradation. The more exact records of locality and level and the more extensive and complete collections in recent years have in general failed to confirm this arrangement. In the great majority of cases, so far as the record shows, new species appear already

distinct, at first sporadically along with the more primitive ones, then more abundantly, finally replacing the older ones altogether. The intermediate gradations occur along with the more typical individuals, but without much definite relationship to intergradation in the succession of strata.¹

We may illustrate from the evolution of the oreodonts, as these are the most abundant and most completely known of American fossil mammals.

The earliest known representatives of the phylum are *Protoreodon* and *Protagriochærus* from the Upper Eocene Uinta beds of Utah. Both have very short crowned teeth with five crescents on the upper molar, the fifth crescent quite distinct. The fourth premolar is not molariform. For the next stage we have to shift to another formation, 400 miles away, the White River. In the lowest strata of this formation, the Titanotherium beds, we find *Oreodon*, *Bathygenys* and *Agriochærus*, all with decidedly longer crowned teeth, and no trace of the fifth crescent in the molars. In *Oreodon* and *Bathygenys* the fourth premolar is non-molariform, composed of one inner and one outer crescent, as usual among Artiodactyls. In *Agriochærus* it has become imperfectly molariform with two outer crescents and one inner one. Between the Uinta and White River oreodonts a sharp break intervenes and no intermediates are known. From this point we can trace the subphyla of oreodonts up through a considerable succession in the Big Badlands of South Dakota and the adjoining region. *Oreodon culbertsoni*, *O. bullatus*, *Eucrotaphus*, *Eporeodon*, *Mesoreodon* and *Merychys* appear to be approximately successive stages in specialization. The skull is shortened, the teeth become longer crowned, the tympanic bullæ are enlarged, lachrymal vacuities appear, the limbs are lengthened, the feet lengthened and compacted and the thumb is lost. But there is not a continuous intergradation in any of these features as we pass upward in the beds. Oreodonts with small bullæ are abundant in the lower and middle White River, the bullæ varying very little in size. A species with medium-sized bullæ occurs occasionally associated with them. In the Upper White River all the oreodonts that I have seen have bullæ of large size. The size of the bulla, then, does not increase continuously as we go up through the formation. Another and much more specialized genus of oreodonts, *Leptauchenia*, suddenly appears in abundance in the Upper White River. I have seen a single specimen of this genus from the Middle beds, but it shows no more primitive features than those of the Upper beds. In the Lower Rosebud, immediately overlying the White River, species of *Eporeodon* are common, like

¹ The statements of fact herein contained are based partly upon field experience, chiefly upon the records of some 20,000 specimens of fossil mammals and reptiles in the American Museum collections, most of which the writer has had occasion to examine and identify and to post the field records of level and locality, in the course of cataloguing work.

those of the underlying beds except that some of them have well-developed lachrymal vacuities while others have none. Another new race also makes its appearance suddenly, and in great abundance, in the genus *Promerycochærus*—structurally derivable perhaps from some of the older oreodons, but not connected with them by intergradations. *Agriochærus* has disappeared. In the Upper Rosebud the *Oreodon-Merychys* phylum shows a distinct and marked advance in the length of the crowns of the teeth; lachrymal vacuities are always present, the feet are decidedly more compact and elongate. *Promerycochærus* disappears entirely and is replaced by a very distinct and more advanced genus *Merycochærus*. The *Leptauchenia* series has disappeared temporarily, to re-appear in the Middle Miocene in a more specialized genus, *Cyclopidius*, the last known member of this race.

The Middle Miocene (which should follow the Upper Rosebud) is unrepresented at the locality under consideration (Pine Ridge, South Dakota), but elsewhere overlies beds with an equivalent fauna, and contains *Merycochærus* in one locality with *Merychys* (both represented by more specialized species); in another locality it contains instead, *Promerycochærus* with *Ticholeptus* (allied to *Merychys*); in a third is found the most highly specialized member of the *Merycochærus* line, *Pronomotherium*. In the Upper Miocene and Lower Pliocene the oreodonts become much scarcer, and the skulls and skeletons are known only in two or three instances. *Pronomotherium* certainly occurs in Montana; in Nebraska the *Merychyi* are more advanced in dentition, belonging to a distinct subgenus *Metoreodon*; but whether the skulls and skeletons are equally different we do not yet know, nor are we in a position to say whether the change is gradual or saltatory.

But the sum of results in regard to the changes from one stage to another in this best known group of fossil mammals is either that the changes are abrupt, constituting clean-cut faunal divisions marked by the sudden appearance in abundance of a more advanced stage; or else that the new form replaces the older one little by little, but on the whole can not be fairly said to be gradually converted into it by infinitesimal gradations.

This general observation applies, in my opinion, equally well to any abundant group of fossil vertebrates whose phylogeny is sufficiently known to make them worth considering.

If, therefore, we consider that the record is continuous where there is no apparent stratigraphic break, and that the known record really represents what was going on over the entire continent of North America, I do not see that we can fairly escape from the conclusion that new species, new genera and even larger groups have appeared by saltatory evolution, not by continuous development.

But—and here lies the crux of the whole question—we have no

right whatsoever to make either of these assumptions. And without them the argument from paleontology for discontinuous development is almost or quite worthless.

If we consider the general conditions controlling evolution and migration among land mammals, it will be evident, I think, that—

1. The external conditions favoring the evolution and progress of a given phylum will not be uniformly developed all over the world or all over one continent, but will appear first, and be at all times more advanced, in some circumscribed region in one or another continent, or simultaneously in limited areas of two or more continents, similarly situated as to climate, temperature, etc.

2. The animal best able to take advantage of these conditions will be existing at the time (*a*) in one continent or (*b*) in more than one, or (*c*) different animals in different continents may be equally able to adapt themselves to the new conditions.

3. As a result, the new stages of any progressive race will first appear in a limited area and will spread out from that region as the favoring environment spreads, the race at the same time continuing its progress further within that area. This area will be the center of dispersal of the race. Its location will be conditioned by two factors, the early appearance of the new environmental conditions, and the existence of species most able to take advantage of these conditions. Parallelism and convergence in racial evolution will be conditioned by 2*b* and 2*c*.

4. Progressive change from uniformly warm to zonal climates during the Tertiary must needs have been a great factor in controlling the progress and distribution of Tertiary mammals. As the new conditions appeared first at the poles, the chief centers of dispersal of the animals adapted to them must have been in the northern parts of one or another of the great northern continents.² The exact location of the dispersal center for each race would be variously decided by the complex of environmental and faunal relations of each, and might be shifted from time to time by changes in these relations.

5. In the regions distant from the center of dispersal the geological record, if complete, should show the successive appearance of progressively higher types in a phylum, arriving in successive waves of migration, and each new type suddenly or gradually displacing the previous stages. Whether the evolution of a race at its center of diffusion was continuous or discontinuous, the geological record of its progress preserved in any other region would be apparently that of a discontinuous development. It would be not the actual history of its evolution but

² To a minor extent in the southern parts of the southern continents, whose restricted area and isolation prevailed in the writer's opinion throughout the Tertiary. There is some evidence, however, along the lines indicated in paragraphs 5 and 6, that Patagonia was the chief center of dispersal of South American Tertiary mammals.

an approximation to it. The closeness of the approximation would be largely measured by the nearness and accessibility of the region in question to the center of dispersal of the race.

6. If the evolution at the center of dispersal was sharply discontinuous this discontinuity would be merely emphasized elsewhere. If on the other hand it was continuous, we should get a near approach to continuity in a complete evolutionary series from a region not remote from the center of diffusion of the race, while the evolutionary series from the same region, of a race whose center of dispersal was remote, would be sharply discontinuous.

7. Applying these principles to some of our American Tertiary phyla, we find that certain phyla which we can be sure were of North American origin, such as the camels, oreodonts and peccaries, do present a much nearer approach to continuity of development than do other phyla which we can be sure were of old world origin, such as the deer, the antelopes or the proboscideans.

I assume that since the oreodonts and peccaries never reached the old world, and the camels did not reach it till the Pliocene, their centers of dispersal were well to the south of the Bering Sea connection with the old world. I assume that since the horses are represented by a double evolutionary series, one in Europe, a closer one in North America, their center of dispersal lay far enough north to spread into Europe on one hand, North America on the other, but that the latter was nearer or more accessible, *i. e.*, their center of dispersal was north-eastern Asia or Alaska. On similar grounds the center of dispersal of most of the Tertiary ruminants might be located in northwest Asia, of proboscideans in central Asia, of tapirs in northeastern Asia, of rhinoceroses northeast Asia and Alaska, of dogs in northwest Canada, and so on—a series of indefinite guesses which a careful study of the present geographic distribution, with these principles and the imperfect geologic data in mind, might serve to fix more definitely.

The point at present to be considered is that in such series as the camels, oreodonts and peccaries, we do have a sufficiently close approach to a continuous series to warrant our believing that the true process of their evolution in the center of their dispersal was a gradual one as regards the evolution of genera and higher groups, but for aught that paleontology tells to the contrary, it may have been partly, though not wholly, discontinuous and saltatory so far as the evolution of new species is concerned. But the larger and more complete the series of specimens studied, the more perfect the record in successive strata, and the nearer is the hypothetic center of dispersal of the race, the closer do we come to a phyletic series whose intergrading stages are well within the limits of observed individual variation in the race. The known facts in vertebrate paleontology are, in my opinion, utterly inadequate

to prove whether the development of races was or was not wholly continuous. But I think that the evidence, considered in relation to the imperfection of our knowledge, goes to show that the gaps were not normally wide. In exceptional cases I think we have reason to believe that they were wide (*Otocyon*, for instance), but in these instances the evidence is not that of the paleontological record.

THE CONTINUITY OF DEVELOPMENT

BY DR. T. WAYLAND VAUGHAN

U. S. GEOLOGICAL SURVEY

AS nearly every one now admits the validity of the arguments in favor of the derivations of the existing groups of organisms from previous somewhat different organisms through the operation of natural causes, I will not enter upon a discussion of the truth of the theory of organic evolution, nor will I present the results of phylogenetic studies. We will assume evolution to be true, and having made this assumption, the theories of the process and the underlying causes may be discussed.

Only two theories of the process of evolution seem to me possible: (1) Darwin's theory of gradual transformation, or the origin of new species by the gradual augmentation through successive generations of the difference between progeny and ancestors; (2) that brought particularly into prominence by de Vries, the theory of saltation, called by him mutation, according to which the progeny differs definitely, without intergradation, from the parents, and the difference is perpetuated by heredity. There are two theories of the cause of evolution. According to the first, that of Weismann, the cause is within the organisms themselves, new kinds being produced by an inherent tendency to vary, this tendency being due to differences in the germ cells of the two parents; the second theory attributes the cause to the action of the environment on the organisms inhabiting it.

The fundamental problems of evolution can then be resolved into two questions. Is evolution through gradual divergence from the parental type, or by saltation; and is it caused merely by the differences in the parental germ-plasms or is heritable variation produced by the environment acting on the organisms?

As we are all paleontologists, the question may appropriately be put, what light can paleontology throw on these problems? It may perhaps render some assistance in deciding between gradual transformation and saltation, when superimposed conformable beds contain sufficiently abundant faunas, and perhaps the Tertiary marine formations of our southern states will yield important results when studied in

proper detail. Dr. Dall has already traced more or less completely the genealogy of some of the species, and I have noticed certain series of species—the group of *Corbula fossata*, *C. oniscus*, *C. wailesiana*, etc., being one of them—deserving thorough study, but the paleontologic work known to me has not as yet been done with the requisite detail to form the basis of an opinion. The principal contribution to our general knowledge of the evolution of organisms that paleontology can make, however, is, I believe, in tracing out phylogenetic lines, and I believe the discovery of the processes and causes of evolution must rest with the experimental biologist. During the past few years very important experimental investigations have been made by several men, and I venture to refer to their results, as I regard paleontology as only an aspect of biology, and think the students in that field should utilize the information gleaned in others.

In the study of variation it has been shown that the selection of fluctuating variations does not carry the species beyond a certain limit, or the extent of the variation is limited, leading to the conclusion that new species can not be produced by this method. I may here refer to ecological surveys and the unreliability of conclusions reached by such researches. Dr. Merriam several years ago presented a paper "Is Mutation a Factor in the Evolution of the Higher Vertebrates?" in which he announced the conclusion that it was not. A critical examination of Dr. Merriam's data showed he had not sufficient information on which to base such a conclusion. His data possess value for the study of evolution in that they indicate material that may be profitably investigated by the experimental method. Attention should also be called to the probable insufficiency of conclusions reached by studying material from successive geologic horizons. For instance, suppose that two usually distinct forms are connected by intermediates. There are no means of ascertaining whether the intermediates represent transition stages between the two forms or are examples of blended hybridism.

That new species may originate through saltation is rather definitely proved; but that it is the only process is not established.

To consider the causes of the origin of new forms: That new forms should originate from the old without the action of some new influence seems to me impossible. The circle of possible combinations of already existent characters could not be transcended, and there would result by crossing only all the combinations possible within definite limits; this would be especially obvious if the de Vries hypothesis of unit-characters be true. Many experiments to determine the influence of various physical factors on individuals showed only somatic changes not of heritable nature and the data accumulated seem definitely to prove that somatic changes, or acquired characters induced through the soma, are not inherited.

Weismann made a great contribution to the progress of biology by focusing attention on the germ cells, and although many of his speculations may be discarded, he was a great stimulator of thought. The work of MacDougal and Tower seems to show how the environment may act on the individual through the germ-cells and induce permanent changes in the progeny.

MacDougal has experimented with species of evening-primroses, by injecting salt solutions into the seed capsules, and summarizes his conclusions in two paragraphs:¹

The action of reagents having an osmotic and a chemical effect has resulted in the induction of mutants in the progeny of *Raimannia odorata* and *Oenothera biennis*. The mutants thus induced have been tested to the second and third generation and found to come true to their newly assumed characters.

The induction of mutants by the action of reagents is a conclusive demonstration of the fact that hereditary characters may be altered by external forces acting directly upon the reproductive mechanism. The action of the reagents used experimentally is simulated by many conditions occurring in nature.

Tower has conducted a series of experiments on species of beetles belonging to the genus *Leptinotarsa*. He endeavored to influence development by the conditions of moisture and temperature during the germinal stages, and induced changes that were perpetuated in the offspring, the changed offspring at least in some instances mendelizing with the parent species. He presents his conclusions in the following words:²

A careful consideration of the various lines of experimentation recorded and of the pedigree cultures and the data from observations in nature irresistibly forces one to the conclusion that in these beetles the only variations of permanence are germinal, and that evolution is through germinal variations. Those germinal variations which arise in nature are permanent and the same variations, of the same degree of permanence, are produced in experiment. The diverse kinds of evidence produced in this and in preceding chapters all go to show that under varying conditions of their surroundings these beetles vary, and that as they become more and more extreme an increasing percentage of striking, permanent variations is found; and as I have just shown, it is possible in experiment to produce in this same way a variety of permanent modifications. From all this evidence, however, there nowhere appears the least trace of a suggestion of any specific action of the conditions of existence, but everywhere there appears only the action of environment as a stimulus, while the response is entirely determined by the organism. All of these variations of purely temporary and of permanent kinds resolve themselves into responses of the organism to the stimuli of its environment, but the nature of the response is entirely determined within the organisms. It is true that different intensities of the same stimuli call forth different responses, but, as is shown in the chapter on

¹ "Mutations, Variations and Relationships of the *Oenotheras*," Carnegie Institution of Washington, No. 81, p. 90, 1907.

² "An Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*," Carnegie Institution of Washington, Publication No. 48, p. 295, 1906.

coloration, the response is entirely determined within the organism, which is adjusted to different intensities of stimuli and reacts according to its own method and on the basis of its own constitution, there being no specific reaction called forth by a given stimulus.

I conclude in the light of these experiments that the production of heritable variations, slight or extreme, represents in these beetles the response of the germ plasm to stimuli. In my experiments these stimuli were external, but there is no *a priori* reason why they might not also be internal.

I desire also to call your attention to some remarks by Loeb:³

It is obvious that no theory of evolution can be true which disagrees with the fundamental facts of heredity. It is the merit of de Vries to have shown that a mutation of species can be directly observed in certain groups of plants, and he has further shown that the changes occur by jumps, not gradually. This fact harmonizes with the consequence to be drawn from Mendel's experiments that each individual characteristic of a species is represented by an individual determinant in the germ. This determinant may be a definite chemical compound. The transition or mutation from one form into another is therefore only possible through the addition or disappearance of one or more of the characteristics of determinants. If this view can be applied generally, it is just as inconceivable that there should be gradual variation of an individual characteristic and intermediary stages between two elementary mutations, as that there should be gradual transitions between one alcohol and its next neighbor in a chemical series.

To summarize my own opinions on this subject:

1. I think it very doubtful if paleontology can make any especially valuable contribution to our knowledge of the process or causes of the evolution of organisms, and that this field must be surrendered to the experimental biologist.

2. The results of experimental work indicate that the process is not by the gradual transformation of species, but by saltation. However, the former method has not been shown impossible.

3. Experimental investigations also indicate that the cause of evolution is by the environment acting on an organism capable of responding to it.

4. The causes of evolution are chemical in their nature, and the aid of the chemist is necessary for their thorough elucidation.

* "The Dynamics of Living Matter," p. 3, 1906.

THE BIRTHPLACE OF MAN

BY PROFESSOR S. W. WILLISTON

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VARIOUS writers, from Le Conte to Smith Woodward, have spoken of critical or rhythmical periods in evolution, periods when evolutionary forces have acted more vigorously than at others, with intervals of relative quiescence. What these forces are and have been we are not yet sure, whether extrinsic, that is, environmental or Lamarckian, or intrinsic, that is, orthogenetic, teleological or what not. Perhaps we shall sometime be more certain of the basal causes of evolution, for the paleontologist at least is not satisfied with the crass ignorance of our Weismannian friends who impute the beginning of all things to mere chance. Perhaps when we do know these fundamental causes we shall understand better why evolution has been rhythmical, if such was really the case, as some of us believe with Woodward.

But, whether there have been internal forces which have had chiefly to do with the rhythm of evolution, or whether such critical periods in the evolution of organic life have been due solely to the larger cosmic forces, I think we shall all admit that there have been critical places of organic evolution, places upon the earth where evolution has advanced with more rapid pace than in others, places perhaps where environmental conditions have conspired to hasten the development of life, or of particular groups, classes or kingdoms of life.

Such a critical period, at least for the higher organisms, it seems to me, was the early Pliocene; such a critical place was central Asia; and both together resulted in the birth of man.

It is a curious fact that nearly all our domestic animals had their origin in Asia. It is also a curious fact that the domestic animals are, almost without exception, the crowning ends of their respective lines of descent, the most highly specialized of their kinds. The genus *Bos*, the most highly developed of the even-toed ungulates began, to the best of our present knowledge, in the Lower Pliocene of India. And its four distinctive types likewise first appeared there: the *Bubalus* group, including the domestic buffalo of India, and its untamable kin of Africa; the group that is represented by the domesticated humped oxen of India and their wild relatives of Africa; the bison strain which spread in Pleistocene times almost to the remote corners of the earth;

and the true oxen, the most useful of all creatures to man, which spread to Europe as *Bos primigenius*, the ancestor of *Bos taurus*.

The sheep also found their expression point in India, and their home to-day is central Asia. So too the domestic goat yet lives wild in western Asia, a less plastic type, but purely Asiatic in origin. Indeed, of the whole family of Bovidæ, Asia was the origin and dispersal center, and it is a curious fact that it still remains the home of the higher types while others of lower degree have wandered afar to find their homes in Africa, Europe and America. The camelids after long ages of exclusive development in North America migrated to Asia to find their highest evolution in the true camels, the highest and probably final stage in the evolution of the family, while their kin, of lower degree, went southward to terminate in the llama and alpaca, the only mammals among all man's servants which we can say with tolerable certainty have been entirely beyond the influence, direct or indirect, of Asiatic environment. The reindeer, the highest of all the cervid family, doubtless arose in northern Asia; certainly its home is in part there, though some of its early kin migrated to America and have left their descendants in the caribous. And India was the birthplace, as it is the home, of the pig, whence came originally our domesticated swine. Whether or not we give to *Sus* the highest place among the non-ruminant, even-toed ungulate mammals, or to the Babirusa, matters not, for both are of Asiatic origin.

Of the odd-toed ungulates our domestic horse, *Equus caballus*, stands on the very summit; and *Equus caballus* arose in Asia, where its ancestors yet have their wild progeny. And I believe that eventually we must give to Asia the honor of the birthplace of the genus itself. And the next lower type of the Equidæ, the asses, are of Asiatic ancestry, though our domestic species comes from Arabia and Africa, while the most primitive of the horses yet living found their refuge in Africa.

Southern or central Asia was the birthplace in early Pliocene times of the elephants, and was their dispersal center; and, in *Elephas indicus*, the only domesticated species, we have the last and highest stage in the evolution of the Proboscidea, and, as is the case with the cape buffalo, the zebras, wart hogs and others, we find in Africa their only living kin, of more primitive form and untamable.

Of all the great order of Carnivora the genus *Felis* admittedly occupies the highest place. The home of the cats is southern Asia and there doubtless was their birthplace and the center of their dispersal. The known paleontological record of the true cats is very meager indeed, and doubtless always will be till we know more of the Pliocene and Pleistocene faunas of Asia. Two of the domesticated cats, the Siamese and the cheetah, are of immediate Asiatic origin, and our fire-

side pet, while coming from northern Africa, doubtless arose from Asiatic forebears in Pliocene or Pleistocene times. What the origin of the various strains of dogs was we know not, though the wild forms most nearly allied are living in Asia to-day, and the greyhound and mastiff almost surely were domesticated in Africa thousands of years ago. I believe that we may safely give to Asia the honor of the birth-place of most of the domesticated species in Pliocene or Pleistocene times.

Nor does it seem that this remarkable evolutionary acceleration during Pliocene times in central Asia was confined to the mammals alone. The ostrich, the highest type of ratite birds, arose in central Asia. The jungle fowl, the highest of the gallinaceous birds and the ancestral stock of our most valued domestic fowls, arose in India and is still at home there. The peacock is exclusively Asiatic; the gray goose, the parent of our domestic geese, has its home in part at least in Asia; and the same may be said of the ancestors of the domestic doves; while the domestic duck may have originated there for aught we yet know. The guinea fowls only are exclusively African, and the turkey American.

Of the reptiles I will venture to say less. But is it not a significant fact that the highest specialization of the reptilian class appeared during Pliocene times in the gigantic extinct gavials of central Asia? Certainly the cobra is entitled to a high but unenviable distinction among the snakes. And *Megalobatrachus*, the largest of all recent amphibians, lives in Japan and China. Finally, of the domestic plants by far the majority come directly or indirectly from the Asiatic flora.

Have all these and doubtless many other facts of their kind no significance? Has man been an exception among so many branches of vertebrate evolution? The common inference has been that so many of our domesticated animals and plants come from India because man first reached civilization there, but the inference is, I believe, quite unjustifiable. Man was born and attained elemental civilization in Asia because there was the place of all others upon the earth where evolution in general of organic life reached its highest development in late Cenozoic times. No mammals and few other creatures have been domesticated by man in thousands of years, for the simple reason that he had eliminated all but the most advanced and most adaptable long before, and none were left to compete with them.

That man originated in the western continent is quite impossible. There is not a particle of evidence in support of such an hypothesis, for there is no evidence that either man or any of his ancestry ever inhabited the western continent till late in Pleistocene times. Indeed, so far as North America is concerned, there is much to justify the assertion that the Pliocene and Pleistocene were a period of evolutionary depression here, of relative quiescence when the rhinoceroses, tapirs,

and later the camels and horses, found conditions uncongenial and migrated to Asia, a more favored region.

It has often been assumed that man must have originated in a warm or tropical climate, to account for the loss of his hairy covering. But I quite agree with Dr. Matthew, that the loss of hair is almost conclusive evidence of his origin in a temperate or cold climate where he found clothing necessary to protect himself from the inclemencies of the weather. We know of no mammals or birds losing their pelage or plumage because of tropical conditions, though some may have lost their hair because of vermin.

Taking all these facts and conclusions into consideration it seems to me that such evidence as paleontology can at the present time offer points toward central Asia as the birthplace of *Homo*, and that the time of his origin, as a family, was late Miocene or early Pliocene. If *Pithecanthropus* be really a true hominid, then we already have evidence of his origin in the Asiatic region. Be it as it may, I confidently believe that within a very few years the discovery of indubitable links in man's ancestry will be made in central Asia, in China or northern India. Perhaps to no region of the world does the paleontologist look with more eager expectation for the solution of many profound problems in the phylogenies and migrations of the mammals than to central and eastern Asia. That there are remains of many extinct vertebrates awaiting discovery there in the late Tertiary and Pleistocene deposits has been made evident by the many fragments brought to light by explorers and travelers.

A field second to none other in the importance and richness of the results to be expected awaits the paleontologist in Asia.

THE RELATION OF PALEONTOLOGY TO THE HISTORY OF MAN, WITH PARTICULAR REFERENCE TO THE AMERICAN PROBLEM

BY PROFESSOR JOHN C. MERRIAM

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CONSIDERED in its broadest aspect, the most important relation of paleontology to the study of man concerns the support which it gives to the general theory of evolution of the organic world. If it be held that we have reason to believe man, with all his highest qualities, a product of evolution out of so-called lower animal types, then it becomes necessary to have a full knowledge of the history of man and of the forms preceding him, in order to understand the origin and the true nature of man's fundamental characteristics as they exist to-day. On the other hand, if there is reason to believe that man as

represented in his highest attributes is entirely apart from nature, the importance of paleontology, as offering a part of the explanation of the fundamental characteristics of man, is very greatly diminished. The value of paleontology would then lie largely in an interpretation of the setting or environment in which man is developing.

With these considerations in mind, it appears of the greatest importance for us to obtain as full a history of the organic world, and as satisfactory an interpretation of the processes therein concerned, as it is possible to secure. Particularly is it desirable to have before us a clear statement of that portion of the paleontological record which leads from the higher vertebrates through the primate division to man.

One of the important phases of general paleontological work which must receive special attention is the early history of the primate order with particular reference to the development of those characteristics which are most prominent in the human family. We have, as yet, accumulated too little evidence in this field. Among the characters which must be followed would be (1) extraordinary brain development, (2) the tendency to development of an upright position, (3) the freeing of the anterior limbs from the work of locomotion and the development in them of extraordinary adaptability. Whatever other interests one may have, there is certainly no more alluring problem than tracing from the primitive mammalia into the early primate those peculiar characters through which later on primitive man began the process of making nature subservient to himself. We may never know whether the brain actually grew large first and requisitioned the hands, so that the animal became bipedal and therefore finally erect in position, or whether a tendency to erect position was directed by the frequent assuming of a vertical position in a tree-climbing ancestor; but it is not beyond reason to presume that a thoroughly satisfactory paleontological record might give us an explanation of the origin of these characters.

The later primate history, or that which leads directly to the human type, is also unfortunately incomplete, though most remarkable advances have been made in the last few years. More missing links have already been furnished than science was supposed to require a few decades ago, but we can hardly be said to have one tenth of the material that it is desirable to have in order to show the transition from anthropoid to human, or from pithecanthropoid to the type of *Spy* or Neanderthal. European paleontologists are at the present time making rapid strides in filling the gaps of that portion of our ancestral chain which falls in the Quaternary system, and we may look for other important discoveries within the next decade.

It is to be presumed that the greater part of the work on the late Tertiary and Quaternary history of man will be carried on in the old world. The writer sees no reason why in this important work Amer-

ican paleontologists should not interest themselves to some extent in investigations now in progress in Europe and Asia, just as American archeologists have contributed to the success of work on the later history of man. Whether American paleontologists, working in their own field, are to have a part in interpreting the Pleistocene history of man is a burning question at the present time.

Whether we find that man was in North America in Pleistocene time or not, it is certainly true that one of the most important problems in the general history of the human race concerns the date of occupation of the western hemisphere by the human family. Discussion of the numerous finds reported to represent Pleistocene man in North America are too well known to every one to require particular mention. It should only be noted in passing, that as yet no specimens representing either skeletal remains or implements of man found in North America are generally recognized by geologists and paleontologists as of Pleistocene age. A careful search through the literature, and the investigation of many of the actual occurrences, lead the writer to the conclusion that we have, as yet, nothing in North America which can be considered as unquestionably representing Pleistocene man.

Also in South America there has been serious discussion of many interesting finds. The evidence on the whole seems to be more distinctly in favor of Pleistocene occupation there than is the case in North America. The discoveries made in recent years in the cave at Last Hope Inlet, and the numerous remains found in the Pampean formation at levels very far below the surface, seem difficult to interpret excepting on the supposition that man was present in South America before the beginning of the recent epoch.

It is to be presumed that any occupation of South America would necessarily be through migration by way of the northern continent, and proof of the presence of man in South America in Pleistocene time would be tantamount to proof that he was in North America at least as early. This suggestion does not, of course, take into account the theories of Ameghino to the effect that man is possibly derived from some of the South American monkey forms. Another suggestion made by Ameghino would give us an immigration of old world forms, possibly with ancestral man, coming into the southern continent in comparatively late time, by some other route than North America.

In the consideration of man's history in America, it is particularly important to notice the probable relation of migrations of the human family to migrations of other groups of mammals. The presumption is that the migrations of primitive man were caused or occasioned largely by influences of the same sort as have produced the spreading out or migration of many other mammalian types. It becomes then particularly necessary to discover exactly when the more recent migra-

tions of mammals into the North American continent have taken place, and, so far as possible, the exact routes of migration. This problem is in a large part paleontological, requiring for its interpretation a satisfactory account of the paleontology of vertebrates, invertebrates and plants of North America and of Asia, with particular reference to the relations of adjacent areas. We must also have, associated with this information, a full statement of the crustal movements in these regions as interpreted by the stratigraphic geologists and the physiographers.

Through the accumulated efforts of paleontologists in this country particularly, we have already a considerable mass of evidence bearing on the general relationships of the faunas of North America and Asia in comparatively recent geological time, but the detail of the problem is, as yet, scarcely indicated. Particularly for Pleistocene and Pliocene time our knowledge of the faunal succession is exceedingly meager, and we can scarcely expect to know anything satisfactorily until the Pleistocene mammalian paleontology of America has been worked out in detail. This work must be followed or accompanied by similar studies of the mammalian faunas of western and southern Asia. When this is completed we shall know the time of the various migratory movements, the nature of the faunas which migrated, the character of the land areas over which they have passed, and the climatic conditions which obtained along the routes of migration. The presumption is, that when this is done we shall have actual evidence of the time of man's occupation of North America.

Viewed in the large, and without regard to the detail which has just been indicated, it seems possible to present several reasonable conclusions with reference to the probable period of migration of man to America. It is shown by study of a map of linguistic stocks of the western hemisphere that the northern and southern continents taken together may be divided into between one hundred and two hundred provinces, based on the number of stocks represented. These languages vary greatly in their structure, and are not similar to the languages of other parts of the world. There is every reason to believe that a large percentage of them have been developed by linguistic differentiation which occurred since man first occupied this continent, and that measured in years the time required for this differentiation has been long. On the other hand, considering the American continent as a whole, we find that the greatly differing physical environments are not reflected to any extent in different physical types of people occupying this region. That the human family is not exempt from physical differentiation, such as is almost universally indicated in mammals which have for some time been distributed over large areas with varying environments, is clearly shown by the map of the old world. In that region the human race is known to have been spread over a wide

area for a long period, and we find several greatly differing human physical stocks in different geographic regions, just as we find differing stocks of mammals and birds.

With the lack of physical diversity among the people of the western hemisphere, there is also noticeable a resemblance of the whole group to the people of the adjacent region of Asia. Judged by the standards of differentiation which we obtain through a study of the history of geographical distribution of other mammalian groups, we have every reason to think that the people of America are immigrants who came from the Asiatic region and spread themselves over America after the period of the first great physical differentiation of the race, and so recently that a second stage of physical differentiation has not yet had time to develop. On the other hand, the time measured in years has been long enough so that linguistic differentiation could take place.

Inasmuch as a large part of human history falls within the Quaternary period, the question naturally arises as to whether the principal migrations of man to the American continent occurred *before, during* or *after* the Glacial epoch.

As primates are naturally animals of a warm or temperate zone, it is hardly to be presumed that primitive man came to America *during* the ice age, though there is a possibility of immigration in some of the interglacial epochs. Judging from what is suggested through study of physical differentiation, it appears improbable that man came over as early as the epoch preceding the ice age. In other groups of animals spread over large areas, marked physical differentiation has ordinarily taken place in a space of time comparable to the Glacial epoch. Had man been present in America during this long period, widely differing physical types would almost certainly have developed. On the whole it seems most probable that he arrived after the end of the last division of glacial time, or very near the beginning of the present epoch. Whether his arrival is shown to have occurred just before or just after the beginning of this epoch remains to be determined.

In conclusion it seems desirable to call the attention of paleontologists once more to the important part which their work must play in obtaining the information which we need with reference to the history of man and his antecedents. Only a small beginning has been made, and the results which must come are of great importance in the large problem of man's relation to nature. It is necessary that paleontologists keep the subject before them, in order to make certain that all information bearing upon it may be recognized as it becomes available, and be given its proper place in relation to other evidence now at hand.

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