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Produced by Sue Asscher, and David Widger

DARWIN AND MODERN SCIENCE

ESSAYS IN COMMEMORATION OF THE CENTENARY OF THE BIRTH OF CHARLES DARWIN AND OF THE FIFTIETH ANNIVERSARY OF THE PUBLICATION OF "THE ORIGIN OF SPECIES"

By A.C. Seward and Others

"My success as a man of science, whatever this may have amounted to, has been determined, as far as I can judge, by complex and diversified mental qualities and conditions. Of these, the most important have been—the love of science—unbounded patience in long reflecting over any subject—industry in observing and collecting facts—and a fair share of invention as well as of common sense. With such moderate abilities as I possess, it is truly surprising that I should have influenced to a considerable extent the belief of scientific men on some important points."

Autobiography (1881); "The Life and Letters of Charles Darwin", Vol. 1. page 107.

PREFACE

At the suggestion of the Cambridge Philosophical Society, the Syndics of the University Press decided in March, 1908, to arrange for the publication of a series of Essays in commemoration of the Centenary of the birth of Charles Darwin and of the Fiftieth anniversary of the publication of "The Origin of Species". The preliminary arrangements were made by a committee consisting of the following representatives of the Council of the Philosophical Society and of the Press Syndicate: Dr H.K. Anderson, Prof. Bateson, Mr Francis Darwin, Dr Hobson, Dr Marr, Prof. Sedgwick, Mr David Sharp, Mr Shipley, Prof. Sorley, Prof. Seward. In the course of the preparation of the volume, the original scheme and list of authors have been modified: a few of those invited to contribute essays were, for various reasons, unable to do so, and some alterations have been made in the titles of articles. For the selection of authors and for the choice of subjects, the committee are mainly responsible, but for such share of the work in the preparation of the volume as usually falls to the lot of an editor I accept full responsibility.

Authors were asked to address themselves primarily to the educated layman rather than to the expert. It was hoped that the publication of the essays would serve the double purpose of illustrating the far-reaching influence of Darwin's work on the progress of knowledge and the present attitude of original investigators and thinkers towards the views embodied in Darwin's works.

In regard to the interpretation of a passage in "The Origin of Species" quoted by Hugo de Vries, it seemed advisable to add an editorial footnote; but, with this exception, I have not felt it necessary to record any opinion on views stated in the essays.

In reading the essays in proof I have availed myself freely of the willing assistance of several Cambridge friends, among whom I wish more especially to thank Mr Francis Darwin for the active interest he has taken in the preparation of the volume. Mrs J.A. Thomson kindly undertook the translation of the essays by Prof. Weismann and Prof. Schwalbe; Mrs James Ward was good enough to assist me by translating Prof. Bougle's article on Sociology, and to Mr McCabe I am indebted for the translation of the essay by Prof. Haeckel. For the translation of the botanical articles by Prof. Goebel, Prof. Klebs and Prof. Strasburger, I am responsible; in the revision of the translation of Prof. Strasburger's essay Madame Errera of Brussels rendered valuable help. Mr Wright, the Secretary of the Press Syndicate, and Mr Waller, the Assistant Secretary, have cordially cooperated with me in my editorial work; nor can I omit to thank the readers of the University Press for keeping watchful eyes on my shortcomings in the correction of proofs.

The two portraits of Darwin are reproduced by permission of Messrs Maull and Fox and Messrs Elliott and Fry. The photogravure of the study at Down is reproduced from an etching by Mr Axel Haig, lent by Mr Francis Darwin; the coloured plate illustrating Prof. Weismann's essay was originally published by him in his "Vortrage uber Descendenztheorie" which afterwards appeared (1904) in English under the title "The Evolution Theory". Copies of this plate were supplied by Messrs Fischer of Jena.

The Syndics of the University Press have agreed, in the event of this volume being a financial success, to hand over the profits to a University fund for the endowment of biological research.

It is clearly impossible to express adequately in a single volume of Essays the influence of Darwin's contributions to knowledge on the subsequent progress of scientific inquiry. As Huxley said in 1885: "Whatever be the ultimate verdict of posterity upon this or that opinion which Mr Darwin has propounded; whatever adumbrations or anticipations of his doctrines may be found in the writings of his predecessors; the broad fact remains that, since the publication and by reason of the publication of "The Origin of Species" the fundamental conceptions and the aims of the students of living Nature have been completely changed... But the impulse thus given to scientific thought rapidly spread beyond the ordinarily recognised limits of Biology. Psychology, Ethics, Cosmology were stirred to their foundations, and 'The Origin of Species' proved itself to be the fixed point which the general doctrine needed in order to move the world."

In the contributions to this Memorial Volume, some of the authors have more especially concerned themselves with the results achieved by Darwin's own work, while others pass in review the progress of research on lines which, though unknown or but little followed in his day, are the direct outcome of his work.

The divergence of views among biologists in regard to the origin of species and as to the most promising directions in which to seek for truth is illustrated by the different opinions of contributors. Whether Darwin's views on the *modus operandi* of evolutionary forces receive further confirmation in the future, or whether they are materially modified, in no way affects the truth of the statement that, by employing his life "in adding a little to Natural Science," he revolutionised the world of thought. Darwin wrote in 1872 to Alfred Russel Wallace: "How grand is the onward rush of science: it is enough to console us for the many errors which we have committed, and for our efforts being overlaid and forgotten in the mass of new facts and new views which are daily turning up." In the onward rush, it is easy for students convinced of the correctness of their own views and equally convinced of the falsity of those of their fellow-workers to forget the lessons of Darwin's life. In his autobiographical sketch, he tells us, "I have steadily endeavoured to keep my mind free so as to give up any hypothesis, however much beloved...as soon as facts are shown to be opposed to it." Writing to Mr J. Scott, he says, "It is a golden rule, which I try to follow, to put every fact which is opposed to one's preconceived opinion in the strongest light. Absolute accuracy is the hardest merit to attain, and the highest merit. Any deviation is ruin."

He acted strictly in accordance with his determination expressed in a letter to Lyell in 1844, "I shall keep out of controversy, and just give my own facts." As was said of another son of Cambridge, Sir George Stokes, "He would no more have thought of disputing about priority, or the authorship of an idea, than of writing a report for a company promoter." Darwin's life affords a striking confirmation of the truth of Hazlitt's aphorism, "Where the pursuit of truth has been the habitual study of any man's life, the love of truth will be his ruling passion." Great as was the intellect of Darwin, his character, as Huxley wrote, was even nobler than his intellect.

A.C. SEWARD.

Botany School, Cambridge, March 20, 1909.

CONTENTS

[PREFACE](#)

[DATES OF THE PUBLICATION OF CHARLES DARWIN'S BOOKS AND OF THE PRINCIPAL EVENTS IN HIS LIFE](#)

[I. INTRODUCTORY LETTER From Sir Joseph Dalton Hooker, O.M., G.C.S.I., C.B., M.D., D.C.L., LL.D., F.R.S., ETC.](#)

[II. DARWIN'S PREDECESSORS. By J. Arthur Thomson.](#)

[III. THE SELECTION THEORY, By August Weismann.](#)

[IV. VARIATION. By HUGO DE VRIES.](#)

[V. HEREDITY AND VARIATION IN MODERN LIGHTS. By W. Bateson, M.A., F.R.S.](#)

[VI. THE MINUTE STRUCTURE OF CELLS IN RELATION TO HEREDITY. By Eduard Strasburger.](#)

[VII. "THE DESCENT OF MAN". By G. Schwalbe.](#)

[VIII. CHARLES DARWIN AS AN ANTHROPOLOGIST. By Ernst Haeckel.](#)

[X. THE INFLUENCE OF DARWIN ON THE STUDY OF ANIMAL EMBRYOLOGY. By A. Sedgwick, M.A., F.R.S.](#)

[XI. THE PALAEONTOLOGICAL RECORD. By W.B. Scott.](#)

[XII. THE PALAEONTOLOGICAL RECORD. By D.H. Scott, F.R.S.](#)

[XIII. THE INFLUENCE OF ENVIRONMENT ON THE FORMS OF PLANTS. By Georg Klebs, PH.D.](#)

[XIV. EXPERIMENTAL STUDY OF THE INFLUENCE OF ENVIRONMENT ON ANIMALS. By Jacques Loeb, M.D. Professor of Physiology in the University of California.](#)

[XV. THE VALUE OF COLOUR IN THE STRUGGLE FOR LIFE. By E.B. Poulton.](#)

[XVI. GEOGRAPHICAL DISTRIBUTION OF PLANTS. By Sir William Thiselton-Dyer, K.C.M.G., C.I.E. Sc.D., F.R.S.](#)

[XVII. GEOGRAPHICAL DISTRIBUTION OF ANIMALS. By Hans Gadow, M.A., Ph.D., F.R.S.](#)

[XVIII. DARWIN AND GEOLOGY. By J.W. Judd, C.B., LL.D., F.R.S.](#)

[XIX. DARWIN'S WORK ON THE MOVEMENTS OF PLANTS. By Francis Darwin.](#)

[XX. THE BIOLOGY OF FLOWERS. By K. Goebel, Ph.D.](#)

[XXI. MENTAL FACTORS IN EVOLUTION. By C. Lloyd Morgan, LL.D., F.R.S.](#)

[XXII. THE INFLUENCE OF THE CONCEPTION OF EVOLUTION ON MODERN PHILOSOPHY. By H. Hoffding.](#)

[XXIII. DARWINISM AND SOCIOLOGY. By C. Bougle.](#)

[XXIV. THE INFLUENCE OF DARWIN UPON RELIGIOUS THOUGHT.
By P.N. Waggett, M.A., S.S.J.E.](#)

[XXV. THE INFLUENCE OF DARWINISM ON THE STUDY OF
RELIGIONS. By Jane Ellen Harrison.](#)

[XXVI. EVOLUTION AND THE SCIENCE OF LANGUAGE. By P. Giles,
M.A., LL.D. \(Aberdeen\).](#)

[XXVII. DARWINISM AND HISTORY. By J.B. Bury, Litt.D., LL.D.](#)

[XXVIII. THE GENESIS OF DOUBLE STARS. By Sir George Darwin,
K.C.B., F.R.S.](#)

[XXIX. THE EVOLUTION OF MATTER. By W.C.D. Whetham, M.A., F.R.S.](#)

[INDEX.](#)

DATES OF THE PUBLICATION OF CHARLES DARWIN'S BOOKS AND OF THE PRINCIPAL EVENTS IN HIS LIFE

1809:

Charles Darwin born at Shrewsbury, February 12.

1817:

"At 8 1/2 years old I went to Mr Case's school." (A day-school at Shrewsbury kept by the Rev G. Case, Minister of the Unitarian Chapel.)

1818:

"I was at school at Shrewsbury under a great scholar, Dr Butler; I learnt absolutely nothing, except by amusing myself by reading and experimenting in Chemistry."

1825:

"As I was doing no good at school, my father wisely took me away at a rather earlier age than usual, and sent me (Oct. 1825) to Edinburgh University with my brother, where I stayed for two years."

1828:

Began residence at Christ's College, Cambridge.

"I went to Cambridge early in the year 1828, and soon became acquainted with Professor Henslow...Nothing could be more simple, cordial and unpretending than the encouragement which he afforded to all young naturalists."

"During the three years which I spent at Cambridge my time was wasted, as far as the academical studies were concerned, as completely as at Edinburgh and at school."

"In order to pass the B.A. Examination, it was...necessary to get up Paley's 'Evidences of Christianity,' and his 'Moral Philosophy'... The careful study of these works, without attempting to learn

any part by rote, was the only part of the academical course which...was of the least use to me in the education of my mind."

1831:

Passed the examination for the B.A. degree in January and kept the following terms.

"I gained a good place among the oi polloi or crowd of men who do not go in for honours."

"I am very busy,...and see a great deal of Henslow, whom I do not know whether I love or respect most."

Dec. 27. "Sailed from England on our circumnavigation," in H.M.S. "Beagle", a barque of 235 tons carrying 6 guns, under Capt. FitzRoy.

"There is indeed a tide in the affairs of men."

1836:

Oct. 4. "Reached Shrewsbury after absence of 5 years and 2 days."

"You cannot imagine how gloriously delightful my first visit was at home; it was worth the banishment."

Dec. 13. Went to live at Cambridge (Fitzwilliam Street).

"The only evil I found in Cambridge was its being too pleasant."

1837:

"On my return home (in the 'Beagle') in the autumn of 1836 I immediately began to prepare my journal for publication, and then saw how many facts indicated the common descent of species... In July (1837) I opened my first note-book for facts in relation to the Origin of Species, about which I had long reflected, and never ceased working for the next twenty years... Had been greatly struck from about the month of previous March on character of South American fossils, and species on Galapagos Archipelago. These facts (especially latter), origin of all my views."

"On March 7, 1837 I took lodgings in (36) Great Marlborough Street in London, and remained there for nearly two years, until I was married."

1838:

"In October, that is fifteen months after I had begun my systematic enquiry, I happened to read for amusement 'Malthus on Population,' and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species. Here then I had at last got a theory by which to work; but I was so anxious to avoid prejudice, that I determined not for some time to write even the briefest sketch of it."

1839:

Married at Maer (Staffordshire) to his first cousin Emma Wedgwood, daughter of Josiah Wedgwood.

"I marvel at my good fortune that she, so infinitely my superior in every single moral quality, consented to be my wife. She has been my wise adviser and cheerful comforter throughout life, which without her would have been during a very long period a miserable one from ill-health. She has earned the love of every soul near her" (Autobiography).

Dec. 31. "Entered 12 Upper Gower street" (now 110 Gower street, London). "There never was so good a house for me, and I devoutly trust you (his future wife) will approve of it equally. The little garden is worth its weight in gold."

Published "Journal and Researches", being Vol. III. of the "Narrative of the Surveying Voyage of H.M.S. 'Adventure' and 'Beagle'..."

Publication of the "Zoology of the Voyage of H.M.S. 'Beagle'", Part II., "Mammalia", by G.R. Waterhouse, with a "Notice of their habits and ranges", by Charles Darwin.

1840:

Contributed Geological Introduction to Part I. ("Fossil Mammalia") of the "Zoology of the Voyage of H.M.S. 'Beagle'" by Richard Owen.

1842:

"In June 1842 I first allowed myself the satisfaction of writing a very brief abstract of my (species) theory in pencil in 35 pages; and this was enlarged during the summer of 1844 into one of 230 pages, which I had fairly copied out and still (1876) possess." (The first draft of "The Origin of Species", edited by Mr Francis Darwin, will be published this year (1909) by the Syndics of the Cambridge University Press.)

Sept. 14. Settled at the village of Down in Kent.

"I think I was never in a more perfectly quiet country."

Publication of "The Structure and Distribution of Coral Reefs"; being Part I. of the "Geology of the Voyage of the Beagle".

1844:

Publication of "Geological Observations on the Volcanic Islands visited during the Voyage of H.M.S. 'Beagle'; being Part II. of the "Geology of the Voyage of the 'Beagle'".

"I think much more highly of my book on Volcanic Islands since Mr Judd, by far the best judge on the subject in England, has, as I hear, learnt much from it." (Autobiography, 1876.)

1845:

Publication of the "Journal of Researches" as a separate book.

1846:

Publication of "Geological Observations on South America"; being Part III. of the "Geology of the Voyage of the 'Beagle'".

1851:

Publication of a "Monograph of the Fossil Lepadidae" and of a "Monograph of the sub-class Cirripedia".

"I fear the study of the Cirripedia will ever remain 'wholly unapplied,' and yet I feel that such study is better than castle-building."

1854:

Publication of Monographs of the Balanidae and Verrucidae.

"I worked steadily on this subject for...eight years, and ultimately published two thick volumes, describing all the known living species, and two thin quartos on the extinct species... My work was of considerable use to me, when I had to discuss in the "Origin of Species" the principles of a natural classification. Nevertheless, I doubt whether the work was worth the consumption of so much time."

"From September 1854 I devoted my whole time to arranging my huge pile of notes, to observing, and to experimenting in relation to the transmutation of species."

1856:

"Early in 1856 Lyell advised me to write out my views pretty fully, and I began at once to do so on a scale three or four times as extensive as that which was afterwards followed in my 'Origin of Species'."

1858:

Joint paper by Charles Darwin and Alfred Russel Wallace "On the Tendency of Species to form Varieties; and on the perpetuation of Varieties and Species by Natural Means of Selection," communicated to the Linnean Society by Sir Charles Lyell and Sir Joseph Hooker.

"I was at first very unwilling to consent (to the communication of his MS. to the Society) as I thought Mr Wallace might consider my doing so unjustifiable, for I did not then know how generous and noble was his disposition."

"July 20 to Aug. 12 at Sandown (Isle of Wight) began abstract of Species book."

1859:

Nov. 24. Publication of "The Origin of Species" (1250 copies).

"Oh, good heavens, the relief to my head and body to banish the whole subject from my mind!... But, alas, how frequent, how almost universal it is in an author to persuade himself of the truth of his own

dogmas. My only hope is that I certainly see many difficulties of gigantic stature."

1860:

Publication of the second edition of the "Origin" (3000 copies).

Publication of a "Naturalist's Voyage".

1861:

Publication of the third edition of the "Origin" (2000 copies).

"I am going to write a little book... on Orchids, and to-day I hate them worse than everything."

1862:

Publication of the book "On the various contrivances by which Orchids are fertilised by Insects".

1865:

Read paper before the Linnean Society "On the Movements and Habits of Climbing plants".
(Published as a book in 1875.)

1866:

Publication of the fourth edition of the "Origin" (1250 copies).

1868:

"I have sent the MS. of my big book, and horridly, disgustingly big it will be, to the printers."

Publication of the "Variation of Animals and Plants under Domestication".

"About my book, I will give you (Sir Joseph Hooker) a bit of advice. Skip the whole of Vol. I, except the last chapter, (and that need only be skimmed), and skip largely in the 2nd volume; and then you will say it is a very good book."

"Towards the end of the work I give my well-abused hypothesis of Pangenesis. An unverified hypothesis is of little or no value; but if anyone should hereafter be led to make observations by which some such hypothesis could be established, I shall have done good service, as an astonishing number of isolated facts can be thus connected together and rendered intelligible."

1869:

Publication of the fifth edition of the "Origin".

1871:

Publication of "The Descent of Man".

"Although in the 'Origin of Species' the derivation of any particular species is never discussed, yet I thought it best, in order that no honourable man should accuse me of concealing my views, to add that by the work 'light would be thrown on the origin of man and his history'."

1872:

Publication of the sixth edition of the "Origin".

Publication of "The Expression of the Emotions in Man and Animals".

1874:

Publication of the second edition of "The Descent of Man".

"The new edition of the "Descent" has turned out an awful job. It took me ten days merely to glance over letters and reviews with criticisms and new facts. It is a devil of a job."

Publication of the second edition of "The Structure and Distribution of Coral Reefs".

1875:

Publication of "Insectivorous Plants".

"I begin to think that every one who publishes a book is a fool."

Publication of the second edition of "Variation in Animals and Plants".

Publication of "The Movements and Habits of Climbing Plants" as a separate book.

1876:

Wrote Autobiographical Sketch ("Life and Letters", Vol. I., Chap II.).

Publication of "The Effects of Cross and Self fertilisation".

"I now (1881) believe, however,...that I ought to have insisted more strongly than I did on the many adaptations for self-fertilisation."

Publication of the second edition of "Observations on Volcanic Islands".

1877:

Publication of "The Different Forms of Flowers on Plants of the same species".

"I do not suppose that I shall publish any more books... I cannot endure being idle, but heaven knows whether I am capable of any more good work."

Publication of the second edition of the Orchid book.

1878:

Publication of the second edition of "The Effects of Cross and Self fertilisation".

1879:

Publication of an English translation of Ernst Krause's "Erasmus Darwin", with a notice by Charles Darwin. "I am EXTREMELY glad that you approve of the little 'Life' of our Grandfather, for I have been repenting that I ever undertook it, as the work was quite beyond my tether." (To Mr Francis Galton, Nov. 14, 1879.)

1880:

Publication of "The Power of Movement in Plants".

"It has always pleased me to exalt plants in the scale of organised beings."

Publication of the second edition of "The Different Forms of Flowers".

1881:

Wrote a continuation of the Autobiography.

Publication of "The Formation of Vegetable Mould, through the Action of Worms".

"It is the completion of a short paper read before the Geological Society more than forty years ago, and has revived old geological thoughts... As far as I can judge it will be a curious little book."

1882:

Charles Darwin died at Down, April 19, and was buried in Westminster Abbey, April 26, in the north aisle of the Nave a few feet from the grave of Sir Isaac Newton.

"As for myself, I believe that I have acted rightly in steadily following and devoting my life to Science. I feel no remorse from having committed any great sin, but have often and often regretted that I have not done more direct good to my fellow creatures."

The quotations in the above Epitome are taken from the Autobiography and published Letters:—

"The Life and Letters of Charles Darwin", including an Autobiographical Chapter. Edited by his son, Francis Darwin, 3 Vols., London, 1887.

"Charles Darwin": His life told in an Autobiographical Chapter, and in a selected series of his published Letters. Edited by his son, Francis Darwin, London, 1902.

"More Letters of Charles Darwin". A record of his work in a series of hitherto unpublished Letters. Edited by Francis Darwin and A.C. Seward, 2 Vols., London, 1903.

I. INTRODUCTORY LETTER From Sir Joseph Dalton Hooker, O.M., G.C.S.I., C.B., M.D., D.C.L., LL.D., F.R.S., ETC.

The Camp,
near Sunningdale,
January 15, 1909.

Dear Professor Seward,

The publication of a Series of Essays in Commemoration of the century of the birth of Charles Darwin and of the fiftieth anniversary of the publication of "The Origin of Species" is assuredly welcome and is a subject of congratulation to all students of Science.

These Essays on the progress of Science and Philosophy as affected by Darwin's labours have been written by men known for their ability to discuss the problems which he so successfully worked to solve. They cannot but prove to be of enduring value, whether for the information of the general reader or as guides to investigators occupied with problems similar to those which engaged the attention of Darwin.

The essayists have been fortunate in having for reference the five published volumes of Charles Darwin's Life and Correspondence. For there is set forth in his own words the inception in his mind of the problems, geological, zoological and botanical, hypothetical and theoretical, which he set himself to solve and the steps by which he proceeded to investigate them with the view of correlating the phenomena of life with the evolution of living things. In his letters he expressed himself in language so lucid and so little burthened with technical terms that they may be regarded as models for those who were asked to address themselves primarily to the educated reader rather than to the expert.

I may add that by no one can the perusal of the Essays be more vividly appreciated than by the writer of these lines. It was my privilege for forty years to possess the intimate friendship of Charles Darwin and to be his companion during many of his working hours in Study, Laboratory, and Garden. I was the recipient of letters from him, relating mainly to the progress of his researches, the copies of which (the originals are now in the possession of his family) cover upwards of a thousand pages of foolscap, each page containing, on an average, three hundred words.

That the editorship of these Essays has been entrusted to a Cambridge Professor of Botany must be gratifying to all concerned in their production and in their perusal, recalling as it does the fact that Charles Darwin's instructor in scientific methods was his lifelong friend the late Rev. J.S. Henslow at that time Professor of Botany in the University. It was owing to his recommendation that his pupil was appointed Naturalist to H.M.S. "Beagle", a service which Darwin himself regarded as marking the dawn of his scientific career.

Very sincerely yours,
J.D. HOOKER.

II. DARWIN'S PREDECESSORS. By J. Arthur Thomson.

**Professor of Natural History in the University of
Aberdeen.**

In seeking to discover Darwin's relation to his predecessors it is useful to distinguish the various services which he rendered to the theory of organic evolution.

(I) As everyone knows, the general idea of the Doctrine of Descent is that the plants and animals of the present-day are the lineal descendants of ancestors on the whole somewhat simpler, that these again are descended from yet simpler forms, and so on backwards towards the literal "Protozoa" and "Protophyta" about which we unfortunately know nothing. Now no one supposes that Darwin

originated this idea, which in rudiment at least is as old as Aristotle. What Darwin did was to make it current intellectual coin. He gave it a form that commended itself to the scientific and public intelligence of the day, and he won wide-spread conviction by showing with consummate skill that it was an effective formula to work with, a key which no lock refused. In a scholarly, critical, and pre-eminently fair-minded way, admitting difficulties and removing them, foreseeing objections and forestalling them, he showed that the doctrine of descent supplied a modal interpretation of how our present-day fauna and flora have come to be.

(II) In the second place, Darwin applied the evolution-idea to particular problems, such as the descent of man, and showed what a powerful organon it is, introducing order into masses of uncorrelated facts, interpreting enigmas both of structure and function, both bodily and mental, and, best of all, stimulating and guiding further investigation. But here again it cannot be claimed that Darwin was original. The problem of the descent or ascent of man, and other particular cases of evolution, had attracted not a few naturalists before Darwin's day, though no one (except Herbert Spencer in the psychological domain (1855)) had come near him in precision and thoroughness of inquiry.

(III) In the third place, Darwin contributed largely to a knowledge of the factors in the evolution-process, especially by his analysis of what occurs in the case of domestic animals and cultivated plants, and by his elaboration of the theory of Natural Selection, which Alfred Russel Wallace independently stated at the same time, and of which there had been a few previous suggestions of a more or less vague description. It was here that Darwin's originality was greatest, for he revealed to naturalists the many different forms—often very subtle—which natural selection takes, and with the insight of a disciplined scientific imagination he realised what a mighty engine of progress it has been and is.

(IV) As an epoch-marking contribution, not only to Aetiology but to Natural History in the widest sense, we rank the picture which Darwin gave to the world of the web of life, that is to say, of the inter-relations and linkages in Nature. For the Biology of the individual—if that be not a contradiction in terms—no idea is more fundamental than that of the correlation of organs, but Darwin's most characteristic contribution was not less fundamental,—it was the idea of the correlation of organisms. This, again, was not novel; we find it in the works of naturalist like Christian Conrad Sprengel, Gilbert White, and Alexander von Humboldt, but the realisation of its full import was distinctively Darwinian.

AS REGARDS THE GENERAL IDEA OF ORGANIC EVOLUTION.

While it is true, as Prof. H.F. Osborn puts it, that "'Before and after Darwin' will always be the ante et post urbem conditam of biological history," it is also true that the general idea of organic evolution is very ancient. In his admirable sketch "From the Greeks to Darwin" ("Columbia University Biological Series", Vol. I. New York and London, 1894. We must acknowledge our great indebtedness to this fine piece of work.), Prof. Osborn has shown that several of the ancient philosophers looked upon Nature as a gradual development and as still in process of change. In the suggestions of Empedocles, to take the best instance, there were "four sparks of truth,—first, that the development of life was a gradual process; second, that plants were evolved before animals; third, that imperfect forms were gradually replaced (not succeeded) by perfect forms; fourth, that the natural cause of the production of perfect forms was the extinction of the imperfect." (Op. cit. page 41.) But the fundamental idea of one stage giving origin to another was absent. As the blue Aegean teemed with treasures of beauty and threw many upon its shores, so did Nature produce like a fertile artist what had to be rejected as well as what was able to survive, but the idea of one species emerging out of another was not yet conceived.

Aristotle's views of Nature (See G.J. Romanes, "Aristotle as a Naturalist", "Contemporary Review", Vol. LIX. page 275, 1891; G. Pouchet "La Biologie Aristotelique", Paris, 1885; E. Zeller, "A History of Greek Philosophy", London, 1881, and "Ueber die griechischen Vorgänger Darwin's", "Abhandl. Berlin Akad." 1878, pages 111-124.) seem to have been more definitely evolutionist than those of his predecessors, in this sense, at least, that he recognised not only an ascending scale, but a genetic series from polyp to man and an age-long movement towards perfection. "It is due to the resistance of matter to form that Nature can only rise by degrees from lower to higher types." "Nature produces those things which, being continually moved by a certain principle contained in themselves, arrive at a certain end."

To discern the outcrop of evolution-doctrine in the long interval between Aristotle and Bacon seems to be very difficult, and some of the instances that have been cited strike one as forced. Epicurus and Lucretius, often called poets of evolution, both pictured animals as arising directly out of the earth, very much as Milton's lion long afterwards pawed its way out. Even when we come to Bruno who wrote that "to the sound of the harp of the Universal Apollo (the World Spirit), the lower organisms are called by stages to higher, and the lower stages are connected by intermediate forms with the higher," there is great room, as Prof. Osborn points out (op. cit. page 81.), for difference of opinion as to how far he was an evolutionist in our sense of the term.

The awakening of natural science in the sixteenth century brought the possibility of a concrete evolution theory nearer, and in the early seventeenth century we find evidences of a new spirit—in the embryology of Harvey and the classifications of Ray. Besides sober naturalists there were speculative dreamers in the sixteenth and seventeenth centuries who had at least got beyond static formulae, but, as Professor Osborn points out (op. cit. page 87.), "it is a very striking fact, that the basis of our modern methods of studying the Evolution problem was established not by the early naturalists nor by the speculative writers, but by the Philosophers." He refers to Bacon, Descartes, Leibnitz, Hume, Kant, Lessing, Herder, and Schelling. "They alone were upon the main track of modern thought. It is evident that they were groping in the dark for a working theory of the Evolution of life, and it is remarkable that they clearly perceived from the outset that the point to which observation should be directed was not the past but the present mutability of species, and further, that this mutability was simply the variation of individuals on an extended scale."

Bacon seems to have been one of the first to think definitely about the mutability of species, and he was far ahead of his age in his suggestion of what we now call a Station of Experimental Evolution. Leibnitz discusses in so many words how the species of animals may be changed and how intermediate species may once have linked those that now seem discontinuous. "All natural orders of beings present but a single chain"... "All advances by degrees in Nature, and nothing by leaps." Similar evolutionist statements are to be found in the works of the other "philosophers," to whom Prof. Osborn refers, who were, indeed, more scientific than the naturalists of their day. It must be borne in mind that the general idea of organic evolution—that the present is the child of the past—is in great part just the idea of human history projected upon the natural world, differentiated by the qualification that the continuous "Becoming" has been wrought out by forces inherent in the organisms themselves and in their environment.

A reference to Kant (See Brock, "Die Stellung Kant's zur Deszendenztheorie," "Biol. Centralbl." VIII. 1889, pages 641-648. Fritz Schultze, "Kant und Darwin", Jena, 1875.) should come in historical order after Buffon, with whose writings he was acquainted, but he seems, along with Herder and Schelling, to be best regarded as the culmination of the evolutionist philosophers—of those at least who interested themselves in scientific problems. In a famous passage he speaks of "the agreement of so many kinds of animals in a certain common plan of structure"... an "analogy of forms" which "strengthens the supposition that they have an actual blood-relationship, due to derivation from a common parent." He speaks of "the great Family of creatures, for as a Family we must conceive it, if the above-mentioned continuous and connected relationship has a real foundation." Prof. Osborn alludes to the scientific caution which led Kant, biology being what it was, to refuse to entertain the hope "that a Newton may one day arise even to make the production of a blade of grass comprehensible, according to natural laws ordained by no intention." As Prof. Haeckel finely observes, Darwin rose up as Kant's Newton. (Mr Alfred Russel Wallace writes: "We claim for Darwin that he is the Newton of natural history, and that, just so surely as that the discovery and demonstration by Newton of the law of gravitation established order in place of chaos and laid a sure foundation for all future study of the starry heavens, so surely has Darwin, by his discovery of the law of natural selection and his demonstration of the great principle of the preservation of useful variations in the struggle for life, not only thrown a flood of light on the process of development of the whole organic world, but also established a firm foundation for all future study of nature." ("Darwinism", London, 1889, page 9). See also Prof. Karl Pearson's "Grammar of Science" (2nd edition), London, 1900, page 32. See Osborn, op. cit. Page 100.))

The scientific renaissance brought a wealth of fresh impressions and some freedom from the tyranny of tradition, and the twofold stimulus stirred the speculative activity of a great variety of men from old Claude Duret of Moulins, of whose weird transformism (1609) Dr Henry de Varigny ("Experimental Evolution". London, 1892. Chap. 1. page 14.) gives us a glimpse, to Lorenz Oken (1799-1851) whose writings are such mixtures of sense and nonsense that some regard him as a far-seeing prophet and others as a fatuous follower of intellectual will-o'-the-wisps. Similarly, for De Maillet, Maupertuis, Diderot, Bonnet, and others, we must agree with Professor Osborn that they were not actually in the main Evolution movement. Some have been included in the roll of honour on very slender evidence, Robinet for instance, whose evolutionism seems to us extremely dubious. (See J. Arthur Thomson, "The Science of Life". London, 1899. Chap. XVI. "Evolution of Evolution Theory".)

The first naturalist to give a broad and concrete expression to the evolutionist doctrine of descent was Buffon (1707-1788), but it is interesting to recall the fact that his contemporary Linnaeus (1707-1778), protagonist of the counter-doctrine of the fixity of species (See Carus Sterne (Ernest Krause), "Die allgemeine Weltanschauung in ihrer historischen Entwicklung". Stuttgart, 1889. Chapter entitled "Beständigkeit oder Veränderlichkeit der Naturwesen".), went the length of admitting (in 1762) that new species might arise by intercrossing. Buffon's position among the pioneers of the evolution-doctrine is weakened by his habit of vacillating between his own conclusions and the orthodoxy of the Sorbonne, but there is no doubt that he had a firm grasp of the general idea of "l'enchainement des etres."

Erasmus Darwin (1731-1802), probably influenced by Buffon, was another firm evolutionist, and the outline of his argument in the "Zoonomia" ("Zoonomia, or the Laws of Organic Life", 2 vols. London, 1794; Osborn op. cit. page 145.) might serve in part at least to-day. "When we revolve in our minds the metamorphoses of animals, as from the tadpole to the frog; secondly, the changes produced by artificial cultivation, as in the breeds of horses, dogs, and sheep; thirdly, the changes produced by conditions of climate and of season, as in the sheep of warm climates being covered with hair instead of wool, and the hares and partridges of northern climates becoming white in winter: when, further, we observe the changes of structure produced by habit, as seen especially in men of different occupations; or the changes produced by artificial mutilation and prenatal influences, as in the crossing of species and production of monsters; fourth, when we observe the essential unity of plan in all warm-blooded animals,—we are led to conclude that they have been alike produced from a similar living filament"... "From thus meditating upon the minute portion of time in which many of the above changes have been produced, would it be too bold to imagine, in the great length of time since the earth began to exist, perhaps millions of years before the commencement of the history of mankind, that all warm-blooded animals have arisen from one living filament?"... "This idea of the gradual generation of all things seems to have been as familiar to the ancient philosophers as to the modern ones, and to have given rise to the beautiful hieroglyphic figure of the proton oon, or first great egg, produced by night, that is, whose origin is involved in obscurity, and animated by Eros, that is, by Divine Love; from whence proceeded all things which exist."

Lamarck (1744-1829) seems to have become an evolutionist independently of Erasmus Darwin's influence, though the parallelism between them is striking. He probably owed something to Buffon, but he developed his theory along a different line. Whatever view be held in regard to that theory there is no doubt that Lamarck was a thorough-going evolutionist. Professor Haeckel speaks of the "Philosophie Zoologique" as "the first connected and thoroughly logical exposition of the theory of descent." (See Alpheus S. Packard, "Lamarck, the Founder of Evolution, His Life and Work, with Translations of his writings on Organic Evolution". London, 1901.)

Besides the three old masters, as we may call them, Buffon, Erasmus Darwin, and Lamarck, there were other quite convinced pre-Darwinian evolutionists. The historian of the theory of descent must take account of Treviranus whose "Biology or Philosophy of Animate Nature" is full of evolutionary suggestions; of Etienne Geoffroy St Hilaire, who in 1830, before the French Academy of Sciences, fought with Cuvier, the fellow-worker of his youth, an intellectual duel on the question of descent; of Goethe, one of the founders of morphology and the greatest poet of Evolution—who, in his eighty-first year, heard the tidings of Geoffroy St Hilaire's defeat with an interest which transcended the political anxieties of the time; and of many others who had gained with more or less confidence and clearness a

new outlook on Nature. It will be remembered that Darwin refers to thirty-four more or less evolutionist authors in his Historical Sketch, and the list might be added to. Especially when we come near to 1858 do the numbers increase, and one of the most remarkable, as also most independent champions of the evolution-idea before that date was Herbert Spencer, who not only marshalled the arguments in a very forcible way in 1852, but applied the formula in detail in his "Principles of Psychology" in 1855. (See Edward Clodd, "Pioneers of Evolution", London, page 161, 1897.)

It is right and proper that we should shake ourselves free from all creationist appreciations of Darwin, and that we should recognise the services of pre-Darwinian evolutionists who helped to make the time ripe, yet one cannot help feeling that the citation of them is apt to suggest two fallacies. It may suggest that Darwin simply entered into the labours of his predecessors, whereas, as a matter of fact, he knew very little about them till after he had been for years at work. To write, as Samuel Butler did, "Buffon planted, Erasmus Darwin and Lamarck watered, but it was Mr Darwin who said 'That fruit is ripe,' and shook it into his lap"... seems to us a quite misleading version of the facts of the case. The second fallacy which the historical citation is a little apt to suggest is that the filiation of ideas is a simple problem. On the contrary, the history of an idea, like the pedigree of an organism, is often very intricate, and the evolution of the evolution-idea is bound up with the whole progress of the world. Thus in order to interpret Darwin's clear formulation of the idea of organic evolution and his convincing presentation of it, we have to do more than go back to his immediate predecessors, such as Buffon, Erasmus Darwin, and Lamarck; we have to inquire into the acceptance of evolutionary conceptions in regard to other orders of facts, such as the earth and the solar system (See Chapter IX. "The Genetic View of Nature" in J.T. Merz's "History of European Thought in the Nineteenth Century", Vol. 2, Edinburgh and London, 1903.); we have to realise how the growing success of scientific interpretation along other lines gave confidence to those who refused to admit that there was any domain from which science could be excluded as a trespasser; we have to take account of the development of philosophical thought, and even of theological and religious movements; we should also, if we are wise enough, consider social changes. In short, we must abandon the idea that we can understand the history of any science as such, without reference to contemporary evolution in other departments of activity.

While there were many evolutionists before Darwin, few of them were expert naturalists and few were known outside a small circle; what was of much more importance was that the genetic view of nature was insinuating itself in regard to other than biological orders of facts, here a little and there a little, and that the scientific spirit had ripened since the days when Cuvier laughed Lamarck out of court. How was it that Darwin succeeded where others had failed? Because, in the first place, he had clear visions—"pensees de la jeunesse, executees par l'age mur"—which a University curriculum had not made impossible, which the "Beagle" voyage made vivid, which an unrivalled British doggedness made real—visions of the web of life, of the fountain of change within the organism, of the struggle for existence and its winnowing, and of the spreading genealogical tree. Because, in the second place, he put so much grit into the verification of his visions, putting them to the proof in an argument which is of its kind—direct demonstration being out of the question—quite unequalled. Because, in the third place, he broke down the opposition which the most scientific had felt to the seductive modal formula of evolution by bringing forward a more plausible theory of the process than had been previously suggested. Nor can one forget, since questions of this magnitude are human and not merely academic, that he wrote so that all men could understand.

AS REGARDS THE FACTORS OF EVOLUTION.

It is admitted by all who are acquainted with the history of biology that the general idea of organic evolution as expressed in the Doctrine of Descent was quite familiar to Darwin's grandfather, and to others before and after him, as we have briefly indicated. It must also be admitted that some of these pioneers of evolutionism did more than apply the evolution-idea as a modal formula of becoming, they began to inquire into the factors in the process. Thus there were pre-Darwinian theories of evolution, and to these we must now briefly refer. (See Prof. W.A. Locy's "Biology and its Makers". New York, 1908. Part II. "The Doctrine of Organic Evolution".)

In all biological thinking we have to work with the categories Organism—Function—Environment, and theories of evolution may be classified in relation to these. To some it has always seemed that the

fundamental fact is the living organism,—a creative agent, a striving will, a changeful Proteus, selecting its environment, adjusting itself to it, self-differentiating and self-adaptive. The necessity of recognising the importance of the organism is admitted by all Darwinians who start with inborn variations, but it is open to question whether the whole truth of what we might call the Goethian position is exhausted in the postulate of inherent variability.

To others it has always seemed that the emphasis should be laid on Function,—on use and disuse, on doing and not doing. Practice makes perfect; *c'est a force de forger qu'on devient forgeron*. This is one of the fundamental ideas of Lamarckism; to some extent it met with Darwin's approval; and it finds many supporters to-day. One of the ablest of these—Mr Francis Darwin—has recently given strong reasons for combining a modernised Lamarckism with what we usually regard as sound Darwinism. (Presidential Address to the British Association meeting at Dublin in 1908.)

To others it has always seemed that the emphasis should be laid on the Environment, which wakes the organism to action, prompts it to change, makes dints upon it, moulds it, prunes it, and finally, perhaps, kills it. It is again impossible to doubt that there is truth in this view, for even if environmentally induced "modifications" be not transmissible, environmentally induced "variations" are; and even if the direct influence of the environment be less important than many enthusiastic supporters of this view—may we call them Buffonians—think, there remains the indirect influence which Darwinians in part rely on,—the eliminative process. Even if the extreme view be held that the only form of discriminate elimination that counts is inter-organismal competition, this might be included under the rubric of the animate environment.

In many passages Buffon (See in particular Samuel Butler, "Evolution Old and New", London, 1879; J.L. de Lanessan, "Buffon et Darwin", "Revue Scientifique", XLIII. pages 385-391, 425-432, 1889.) definitely suggested that environmental influences—especially of climate and food—were directly productive of changes in organisms, but he did not discuss the question of the transmissibility of the modifications so induced, and it is difficult to gather from his inconsistent writings what extent of transformation he really believed in. Prof. Osborn says of Buffon: "The struggle for existence, the elimination of the least-perfected species, the contest between the fecundity of certain species and their constant destruction, are all clearly expressed in various passages." He quotes two of these (op. cit. page 136.):

"Le cours ordinaire de la nature vivante, est en general toujours constant, toujours le meme; son mouvement, toujours regulier, roule sur deux points inebanlables: l'un, la fecondite sans bornes donnee a toutes les especes; l'autre, les obstacles sans nombre qui reduisent cette fecondite a une mesure determinee et ne laissent en tout temps qu'a peu pres la meme quantite d'individus de chaque espece"... "Les especes les moins parfaites, les plus delicates, les plus pesantes, les moins agissantes, les moins armees, etc., ont deja disparu ou disparaîtront."

Erasmus Darwin (See Ernst Krause and Charles Darwin, "Erasmus Darwin", London, 1879.) had a firm grip of the "idea of the gradual formation and improvement of the Animal world," and he had his theory of the process. No sentence is more characteristic than this: "All animals undergo transformations which are in part produced by their own exertions, in response to pleasures and pains, and many of these acquired forms or propensities are transmitted to their posterity." This is Lamarckism before Lamarck, as his grandson pointed out. His central idea is that wants stimulate efforts and that these result in improvements, which subsequent generations make better still. He realised something of the struggle for existence and even pointed out that this advantageously checks the rapid multiplication. "As Dr Krause points out, Darwin just misses the connection between this struggle and the Survival of the Fittest." (Osborn op. cit. page 142.)

Lamarck (1744-1829) (See E. Perrier "La Philosophie Zoologique avant Darwin", Paris, 1884; A. de Quatrefages, "Darwin et ses Precurseurs Francais", Paris, 1870; Packard op. cit.; also Claus, "Lamarck als Begrunder der Descendenzlehre", Wien, 1888; Haeckel, "Natural History of Creation", English translation London, 1879; Lang "Zur Charakteristik der Forschungswege von Lamarck und Darwin", Jena, 1889.) seems to have thought out his theory of evolution without any knowledge of Erasmus Darwin's which it closely resembled. The central idea of his theory was the cumulative inheritance of functional modifications. "Changes in environment bring about changes in the habits of animals. Changes in their wants necessarily bring about parallel changes in their habits. If new wants become

constant or very lasting, they form new habits, the new habits involve the use of new parts, or a different use of old parts, which results finally in the production of new organs and the modification of old ones." He differed from Buffon in not attaching importance, as far as animals are concerned, to the direct influence of the environment, "for environment can effect no direct change whatever upon the organisation of animals," but in regard to plants he agreed with Buffon that external conditions directly moulded them.

Treviranus (1776-1837) (See Huxley's article "Evolution in Biology", "Encyclopaedia Britannica" (9th edit.), 1878, pages 744-751, and Sully's article, "Evolution in Philosophy", *ibid.* pages 751-772.), whom Huxley ranked beside Lamarck, was on the whole Buffonian, attaching chief importance to the influence of a changeful environment both in modifying and in eliminating, but he was also Goethian, for instance in his idea that species like individuals pass through periods of growth, full bloom, and decline. "Thus, it is not only the great catastrophes of Nature which have caused extinction, but the completion of cycles of existence, out of which new cycles have begun." A characteristic sentence is quoted by Prof. Osborn: "In every living being there exists a capability of an endless variety of form-assumption; each possesses the power to adapt its organisation to the changes of the outer world, and it is this power, put into action by the change of the universe, that has raised the simple zoophytes of the primitive world to continually higher stages of organisation, and has introduced a countless variety of species into animate Nature."

Goethe (1749-1832) (See Haeckel, "Die Naturanschauung von Darwin, Goethe und Lamarck", Jena, 1882.), who knew Buffon's work but not Lamarck's, is peculiarly interesting as one of the first to use the evolution-idea as a guiding hypothesis, e.g. in the interpretation of vestigial structures in man, and to realise that organisms express an attempt to make a compromise between specific inertia and individual change. He gave the finest expression that science has yet known—if it has known it—of the kernel-idea of what is called "bathmism," the idea of an "inherent growth-force"—and at the same time he held that "the way of life powerfully reacts upon all form" and that the orderly growth of form "yields to change from externally acting causes."

Besides Buffon, Erasmus Darwin, Lamarck, Treviranus, and Goethe, there were other "pioneers of evolution," whose views have been often discussed and appraised. Etienne Geoffroy Saint-Hilaire (1772-1844), whose work Goethe so much admired, was on the whole Buffonian, emphasising the direct action of the changeful milieu. "Species vary with their environment, and existing species have descended by modification from earlier and somewhat simpler species." He had a glimpse of the selection idea, and believed in mutations or sudden leaps—induced in the embryonic condition by external influences. The complete history of evolution-theories will include many instances of guesses at truth which were afterwards substantiated, thus the geographer von Buch (1773-1853) detected the importance of the Isolation factor on which Wagner, Romanes, Gulick and others have laid great stress, but we must content ourselves with recalling one other pioneer, the author of the "Vestiges of Creation" (1844), a work which passed through ten editions in nine years and certainly helped to harrow the soil for Darwin's sowing. As Darwin said, "it did excellent service in this country in calling attention to the subject, in removing prejudice, and in thus preparing the ground for the reception of analogous views." ("Origin of Species" (6th edition), page xvii.) Its author, Robert Chambers (1802-1871) was in part a Buffonian—maintaining that environment moulded organisms adaptively, and in part a Goethian—believing in an inherent progressive impulse which lifted organisms from one grade of organisation to another.

AS REGARDS NATURAL SELECTION.

The only thinker to whom Darwin was directly indebted, so far as the theory of Natural Selection is concerned, was Malthus, and we may once more quote the well-known passage in the Autobiography: "In October, 1838, that is, fifteen months after I had begun my systematic enquiry, I happened to read for amusement 'Malthus on Population', and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species." ("The Life and Letters of Charles Darwin", Vol. 1. page 83. London, 1887.)

Although Malthus gives no adumbration of the idea of Natural Selection in his exposition of the eliminative processes which go on in mankind, the suggestive value of his essay is undeniable, as is strikingly borne out by the fact that it gave to Alfred Russel Wallace also "the long-sought clue to the effective agent in the evolution of organic species." (A.R. Wallace, "My Life, A Record of Events and Opinions", London, 1905, Vol. 1. page 232.) One day in Ternate when he was resting between fits of fever, something brought to his recollection the work of Malthus which he had read twelve years before. "I thought of his clear exposition of 'the positive checks to increase'—disease, accidents, war, and famine—which keep down the population of savage races to so much lower an average than that of more civilized peoples. It then occurred to me that these causes or their equivalents are continually acting in the case of animals also; and as animals usually breed much more rapidly than does mankind, the destruction every year from these causes must be enormous in order to keep down the numbers of each species, since they evidently do not increase regularly from year to year, as otherwise the world would long ago have been densely crowded with those that breed most quickly. Vaguely thinking over the enormous and constant destruction which this implied, it occurred to me to ask the question, Why do some die and some live? And the answer was clearly, that on the whole the best fitted live. From the effects of disease the most healthy escaped; from enemies the strongest, the swiftest, or the most cunning; from famine the best hunters or those with the best digestion; and so on. Then it suddenly flashed upon me that this self-acting process would necessarily IMPROVE THE RACE, because in every generation the inferior would inevitably be killed off and the superior would remain—that is, THE FITTEST WOULD SURVIVE." (Ibid. Vol. 1. page 361.) We need not apologise for this long quotation, it is a tribute to Darwin's magnanimous colleague, the Nestor of the evolutionist camp,—and it probably indicates the line of thought which Darwin himself followed. It is interesting also to recall the fact that in 1852, when Herbert Spencer wrote his famous "Leader" article on "The Development Hypothesis" in which he argued powerfully for the thesis that the whole animate world is the result of an age-long process of natural transformation, he wrote for "The Westminster Review" another important essay, "A Theory of Population deduced from the General Law of Animal Fertility", towards the close of which he came within an ace of recognising that the struggle for existence was a factor in organic evolution. At a time when pressure of population was practically interesting men's minds, Darwin, Wallace, and Spencer were being independently led from a social problem to a biological theory. There could be no better illustration, as Prof. Patrick Geddes has pointed out, of the Comtian thesis that science is a "social phenomenon."

Therefore, as far more important than any further ferreting out of vague hints of Natural Selection in books which Darwin never read, we would indicate by a quotation the view that the central idea in Darwinism is correlated with contemporary social evolution. "The substitution of Darwin for Paley as the chief interpreter of the order of nature is currently regarded as the displacement of an anthropomorphic view by a purely scientific one: a little reflection, however, will show that what has actually happened has been merely the replacement of the anthropomorphism of the eighteenth century by that of the nineteenth. For the place vacated by Paley's theological and metaphysical explanation has simply been occupied by that suggested to Darwin and Wallace by Malthus in terms of the prevalent severity of industrial competition, and those phenomena of the struggle for existence which the light of contemporary economic theory has enabled us to discern, have thus come to be temporarily exalted into a complete explanation of organic progress." (P. Geddes, article "Biology", "Chambers's Encyclopaedia".) It goes without saying that the idea suggested by Malthus was developed by Darwin into a biological theory which was then painstakingly verified by being used as an interpretative formula, and that the validity of a theory so established is not affected by what suggested it, but the practical question which this line of thought raises in the mind is this: if Biology did thus borrow with such splendid results from social theory, why should we not more deliberately repeat the experiment?

Darwin was characteristically frank and generous in admitting that the principle of Natural Selection had been independently recognised by Dr W.C. Wells in 1813 and by Mr Patrick Matthew in 1831, but he had no knowledge of these anticipations when he published the first edition of "The Origin of Species". Wells, whose "Essay on Dew" is still remembered, read in 1813 before the Royal Society a short paper entitled "An account of a White Female, part of whose skin resembles that of a Negro" (published in 1818). In this communication, as Darwin said, "he observes, firstly, that all animals tend to vary in some degree, and, secondly, that agriculturists improve their domesticated animals by

selection; and then, he adds, but what is done in this latter case 'by art, seems to be done with equal efficacy, though more slowly, by nature, in the formation of varieties of mankind, fitted for the country which they inhabit.'" ("Origin of Species" (6th edition) page xv.) Thus Wells had the clear idea of survival dependent upon a favourable variation, but he makes no more use of the idea and applies it only to man. There is not in the paper the least hint that the author ever thought of generalising the remarkable sentence quoted above.

Of Mr Patrick Matthew, who buried his treasure in an appendix to a work on "Naval Timber and Arboriculture", Darwin said that "he clearly saw the full force of the principle of natural selection." In 1860 Darwin wrote—very characteristically—about this to Lyell: "Mr Patrick Matthew publishes a long extract from his work on "Naval Timber and Arboriculture", published in 1831, in which he briefly but completely anticipates the theory of Natural Selection. I have ordered the book, as some passages are rather obscure, but it is certainly, I think, a complete but not developed anticipation. Erasmus always said that surely this would be shown to be the case some day. Anyhow, one may be excused in not having discovered the fact in a work on Naval Timber." ("Life and Letters" II. page 301.)

De Quatrefages and De Varigny have maintained that the botanist Naudin stated the theory of evolution by natural selection in 1852. He explains very clearly the process of artificial selection, and says that in the garden we are following Nature's method. "We do not think that Nature has made her species in a different fashion from that in which we proceed ourselves in order to make our variations." But, as Darwin said, "he does not show how selection acts under nature." Similarly it must be noted in regard to several pre-Darwinian pictures of the struggle for existence (such as Herder's, who wrote in 1790 "All is in struggle... each one for himself" and so on), that a recognition of this is only the first step in Darwinism.

Profs. E. Perrier and H.F. Osborn have called attention to a remarkable anticipation of the selection-idea which is to be found in the speculations of Etienne Geoffroy St Hilaire (1825-1828) on the evolution of modern Crocodilians from the ancient Teleosaurs. Changing environment induced changes in the respiratory system and far-reaching consequences followed. The atmosphere, acting upon the pulmonary cells, brings about "modifications which are favourable or destructive ('funestes'); these are inherited, and they influence all the rest of the organisation of the animal because if these modifications lead to injurious effects, the animals which exhibit them perish and are replaced by others of a somewhat different form, a form changed so as to be adapted to (a la convenance) the new environment."

Prof. E.B. Poulton ("Science Progress", New Series, Vol. I. 1897. "A Remarkable Anticipation of Modern Views on Evolution". See also Chap. VI. in "Essays on Evolution", Oxford, 1908.) has shown that the anthropologist James Cowles Prichard (1786-1848) must be included, even in spite of himself, among the precursors of Darwin. In some passages of the second edition of his "Researches into the Physical History of Mankind" (1826), he certainly talks evolution and anticipates Prof. Weismann in denying the transmission of acquired characters. He is, however, sadly self-contradictory and his evolutionism weakens in subsequent editions—the only ones that Darwin saw. Prof. Poulton finds in Prichard's work a recognition of the operation of Natural Selection. "After enquiring how it is that 'these varieties' are developed and preserved in connection with particular climates and differences of local situation,' he gives the following very significant answer: 'One cause which tends to maintain this relation is obvious. Individuals and families, and even whole colonies, perish and disappear in climates for which they are, by peculiarity of constitution, not adapted. Of this fact proofs have been already mentioned.'" Mr Francis Darwin and Prof. A.C. Seward discuss Prichard's "anticipations" in "More Letters of Charles Darwin", Vol. I. page 43, and come to the conclusion that the evolutionary passages are entirely neutralised by others of an opposite trend. There is the same difficulty with Buffon.

Hints of the idea of Natural Selection have been detected elsewhere. James Watt (See Prof. Patrick Geddes's article "Variation and Selection", "Encyclopaedia Britannica" (9th edition) 1888.), for instance, has been reported as one of the anticipators (1851). But we need not prolong the inquiry further, since Darwin did not know of any anticipations until after he had published the immortal work of 1859, and since none of those who got hold of the idea made any use of it. What Darwin did was to follow the clue which Malthus gave him, to realise, first by genius and afterwards by patience, how the complex

and subtle struggle for existence works out a natural selection of those organisms which vary in the direction of fitter adaptation to the conditions of their life. So much success attended his application of the Selection-formula that for a time he regarded Natural Selection as almost the sole factor in evolution, variations being pre-supposed; gradually, however, he came to recognise that there was some validity in the factors which had been emphasized by Lamarck and by Buffon, and in his well-known summing up in the sixth edition of the "Origin" he says of the transformation of species: "This has been effected chiefly through the natural selection of numerous successive, slight, favourable variations; aided in an important manner by the inherited effects of the use and disuse of parts; and in an unimportant manner, that is, in relation to adaptive structures, whether past or present, by the direct action of external conditions, and by variations which seem to us in our ignorance to arise spontaneously."

To sum up: the idea of organic evolution, older than Aristotle, slowly developed from the stage of suggestion to the stage of verification, and the first convincing verification was Darwin's; from being an a priori anticipation it has become an interpretation of nature, and Darwin is still the chief interpreter; from being a modal interpretation it has advanced to the rank of a causal theory, the most convincing part of which men will never cease to call Darwinism.

III. THE SELECTION THEORY, By August Weismann.

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I. THE IDEA OF SELECTION.

Many and diverse were the discoveries made by Charles Darwin in the course of a long and strenuous life, but none of them has had so far-reaching an influence on the science and thought of his time as the theory of selection. I do not believe that the theory of evolution would have made its way so easily and so quickly after Darwin took up the cudgels in favour of it, if he had not been able to support it by a principle which was capable of solving, in a simple manner, the greatest riddle that living nature presents to us,—I mean the purposiveness of every living form relative to the conditions of its life and its marvellously exact adaptation to these.

Everyone knows that Darwin was not alone in discovering the principle of selection, and that the same idea occurred simultaneously and independently to Alfred Russel Wallace. At the memorable meeting of the Linnean Society on 1st July, 1858, two papers were read (communicated by Lyell and Hooker) both setting forth the same idea of selection. One was written by Charles Darwin in Kent, the other by Alfred Wallace in Ternate, in the Malay Archipelago. It was a splendid proof of the magnanimity of these two investigators, that they thus, in all friendliness and without envy, united in laying their ideas before a scientific tribunal: their names will always shine side by side as two of the brightest stars in the scientific sky.

But it is with Charles Darwin that I am here chiefly concerned, since this paper is intended to aid in the commemoration of the hundredth anniversary of his birth.

The idea of selection set forth by the two naturalists was at the time absolutely new, but it was also so simple that Huxley could say of it later, "How extremely stupid not to have thought of that." As Darwin was led to the general doctrine of descent, not through the labours of his predecessors in the early years of the century, but by his own observations, so it was in regard to the principle of selection. He was struck by the innumerable cases of adaptation, as, for instance, that of the woodpeckers and tree-frogs to climbing, or the hooks and feather-like appendages of seeds, which aid in the distribution of plants,

and he said to himself that an explanation of adaptations was the first thing to be sought for in attempting to formulate a theory of evolution.

But since adaptations point to CHANGES which have been undergone by the ancestral forms of existing species, it is necessary, first of all, to inquire how far species in general are VARIABLE. Thus Darwin's attention was directed in the first place to the phenomenon of variability, and the use man has made of this, from very early times, in the breeding of his domesticated animals and cultivated plants. He inquired carefully how breeders set to work, when they wished to modify the structure and appearance of a species to their own ends, and it was soon clear to him that SELECTION FOR BREEDING PURPOSES played the chief part.

But how was it possible that such processes should occur in free nature? Who is here the breeder, making the selection, choosing out one individual to bring forth offspring and rejecting others? That was the problem that for a long time remained a riddle to him.

Darwin himself relates how illumination suddenly came to him. He had been reading, for his own pleasure, Malthus' book on Population, and, as he had long known from numerous observations, that every species gives rise to many more descendants than ever attain to maturity, and that, therefore, the greater number of the descendants of a species perish without reproducing, the idea came to him that the decision as to which member of a species was to perish, and which was to attain to maturity and reproduction might not be a matter of chance, but might be determined by the constitution of the individuals themselves, according as they were more or less fitted for survival. With this idea the foundation of the theory of selection was laid.

In ARTIFICIAL SELECTION the breeder chooses out for pairing only such individuals as possess the character desired by him in a somewhat higher degree than the rest of the race. Some of the descendants inherit this character, often in a still higher degree, and if this method be pursued throughout several generations, the race is transformed in respect of that particular character.

NATURAL SELECTION depends on the same three factors as ARTIFICIAL SELECTION: on VARIABILITY, INHERITANCE, and SELECTION FOR BREEDING, but this last is here carried out not by a breeder but by what Darwin called the "struggle for existence." This last factor is one of the special features of the Darwinian conception of nature. That there are carnivorous animals which take heavy toll in every generation of the progeny of the animals on which they prey, and that there are herbivores which decimate the plants in every generation had long been known, but it is only since Darwin's time that sufficient attention has been paid to the facts that, in addition to this regular destruction, there exists between the members of a species a keen competition for space and food, which limits multiplication, and that numerous individuals of each species perish because of unfavourable climatic conditions. The "struggle for existence," which Darwin regarded as taking the place of the human breeder in free nature, is not a direct struggle between carnivores and their prey, but is the assumed competition for survival between individuals OF THE SAME species, of which, on an average, only those survive to reproduce which have the greatest power of resistance, while the others, less favourably constituted, perish early. This struggle is so keen, that, within a limited area, where the conditions of life have long remained unchanged, of every species, whatever be the degree of fertility, only two, ON AN AVERAGE, of the descendants of each pair survive; the others succumb either to enemies, or to disadvantages of climate, or to accident. A high degree of fertility is thus not an indication of the special success of a species, but of the numerous dangers that have attended its evolution. Of the six young brought forth by a pair of elephants in the course of their lives only two survive in a given area; similarly, of the millions of eggs which two thread-worms leave behind them only two survive. It is thus possible to estimate the dangers which threaten a species by its ratio of elimination, or, since this cannot be done directly, by its fertility.

Although a great number of the descendants of each generation fall victims to accident, among those that remain it is still the greater or lesser fitness of the organism that determines the "selection for breeding purposes," and it would be incomprehensible if, in this competition, it were not ultimately, that is, on an average, the best equipped which survive, in the sense of living long enough to reproduce.

Thus the principle of natural selection is THE SELECTION OF THE BEST FOR REPRODUCTION, whether the "best" refers to the whole constitution, to one or more parts of the

organism, or to one or more stages of development. Every organ, every part, every character of an animal, fertility and intelligence included, must be improved in this manner, and be gradually brought up in the course of generations to its highest attainable state of perfection. And not only may improvement of parts be brought about in this way, but new parts and organs may arise, since, through the slow and minute steps of individual or "fluctuating" variations, a part may be added here or dropped out there, and thus something new is produced.

The principle of selection solved the riddle as to how what was purposive could conceivably be brought about without the intervention of a directing power, the riddle which animate nature presents to our intelligence at every turn, and in face of which the mind of a Kant could find no way out, for he regarded a solution of it as not to be hoped for. For, even if we were to assume an evolutionary force that is continually transforming the most primitive and the simplest forms of life into ever higher forms, and the homogeneity of primitive times into the infinite variety of the present, we should still be unable to infer from this alone how each of the numberless forms adapted to particular conditions of life should have appeared **PRECISELY AT THE RIGHT MOMENT IN THE HISTORY OF THE EARTH** to which their adaptations were appropriate, and precisely at the proper place in which all the conditions of life to which they were adapted occurred: the humming-birds at the same time as the flowers; the trichina at the same time as the pig; the bark-coloured moth at the same time as the oak, and the wasp-like moth at the same time as the wasp which protects it. Without processes of selection we should be obliged to assume a "pre-established harmony" after the famous Leibnitzian model, by means of which the clock of the evolution of organisms is so regulated as to strike in exact synchronism with that of the history of the earth! All forms of life are strictly adapted to the conditions of their life, and can persist under these conditions alone.

There must therefore be an intrinsic connection between the conditions and the structural adaptations of the organism, and, **SINCE THE CONDITIONS OF LIFE CANNOT BE DETERMINED BY THE ANIMAL ITSELF, THE ADAPTATIONS MUST BE CALLED FORTH BY THE CONDITIONS.**

The selection theory teaches us how this is conceivable, since it enables us to understand that there is a continual production of what is non-purposive as well as of what is purposive, but the purposive alone survives, while the non-purposive perishes in the very act of arising. This is the old wisdom taught long ago by Empedocles.

II. THE LAMARCKIAN PRINCIPLE.

Lamarck, as is well known, formulated a definite theory of evolution at the beginning of the nineteenth century, exactly fifty years before the Darwin-Wallace principle of selection was given to the world. This brilliant investigator also endeavoured to support his theory by demonstrating forces which might have brought about the transformations of the organic world in the course of the ages. In addition to other factors, he laid special emphasis on the increased or diminished use of the parts of the body, assuming that the strengthening or weakening which takes place from this cause during the individual life, could be handed on to the offspring, and thus intensified and raised to the rank of a specific character. Darwin also regarded this **LAMARCKIAN PRINCIPLE**, as it is now generally called, as a factor in evolution, but he was not fully convinced of the transmissibility of acquired characters.

As I have here to deal only with the theory of selection, I need not discuss the Lamarckian hypothesis, but I must express my opinion that there is room for much doubt as to the cooperation of this principle in evolution. Not only is it difficult to imagine how the transmission of functional modifications could take place, but, up to the present time, notwithstanding the endeavours of many excellent investigators, not a single actual proof of such inheritance has been brought forward. Semon's experiments on plants are, according to the botanist Pfeffer, not to be relied on, and even the recent, beautiful experiments made by Dr Kammerer on salamanders, cannot, as I hope to show elsewhere, be regarded as proof, if only because they do not deal at all with functional modifications, that is, with modifications brought about by use, and it is to these **ALONE** that the Lamarckian principle refers.

III. OBJECTIONS TO THE THEORY OF SELECTION.

(a) Saltatory evolution.

The Darwinian doctrine of evolution depends essentially on **THE CUMULATIVE AUGMENTATION** of minute variations in the direction of utility. But can such minute variations,

which are undoubtedly continually appearing among the individuals of the same species, possess any selection-value; can they determine which individuals are to survive, and which are to succumb; can they be increased by natural selection till they attain to the highest development of a purposive variation?

To many this seems so improbable that they have urged a theory of evolution by leaps from species to species. Kolliker, in 1872, compared the evolution of species with the processes which we can observe in the individual life in cases of alternation of generations. But a polyp only gives rise to a medusa because it has itself arisen from one, and there can be no question of a medusa ever having arisen suddenly and de novo from a polyp-bud, if only because both forms are adapted in their structure as a whole, and in every detail to the conditions of their life. A sudden origin, in a natural way, of numerous adaptations is inconceivable. Even the degeneration of a medusoid from a free-swimming animal to a mere brood-sac (gonophore) is not sudden and saltatory, but occurs by imperceptible modifications throughout hundreds of years, as we can learn from the numerous stages of the process of degeneration persisting at the same time in different species.

If, then, the degeneration to a simple brood-sac takes place only by very slow transitions, each stage of which may last for centuries, how could the much more complex ASCENDING evolution possibly have taken place by sudden leaps? I regard this argument as capable of further extension, for wherever in nature we come upon degeneration, it is taking place by minute steps and with a slowness that makes it not directly perceptible, and I believe that this in itself justifies us in concluding that THE SAME MUST BE TRUE OF ASCENDING evolution. But in the latter case the goal can seldom be distinctly recognised while in cases of degeneration the starting-point of the process can often be inferred, because several nearly related species may represent different stages.

In recent years Bateson in particular has championed the idea of saltatory, or so-called discontinuous evolution, and has collected a number of cases in which more or less marked variations have suddenly appeared. These are taken for the most part from among domesticated animals which have been bred and crossed for a long time, and it is hardly to be wondered at that their much mixed and much influenced germ-plasm should, under certain conditions, give rise to remarkable phenomena, often indeed producing forms which are strongly suggestive of monstrosities, and which would undoubtedly not survive in free nature, unprotected by man. I should regard such cases as due to an intensified germinal selection—though this is to anticipate a little—and from this point of view it cannot be denied that they have a special interest. But they seem to me to have no significance as far as the transformation of species is concerned, if only because of the extreme rarity of their occurrence.

There are, however, many variations which have appeared in a sudden and saltatory manner, and some of these Darwin pointed out and discussed in detail: the copper beech, the weeping trees, the oak with "fern-like leaves," certain garden-flowers, etc. But none of them have persisted in free nature, or evolved into permanent types.

On the other hand, wherever enduring types have arisen, we find traces of a gradual origin by successive stages, even if, at first sight, their origin may appear to have been sudden. This is the case with SEASONAL DIMORPHISM, the first known cases of which exhibited marked differences between the two generations, the winter and the summer brood. Take for instance the much discussed and studied form Vanessa (Araschnia) levana-prorsa. Here the differences between the two forms are so great and so apparently disconnected, that one might almost believe it to be a sudden mutation, were it not that old transition-stages can be called forth by particular temperatures, and we know other butterflies, as for instance our Garden Whites, in which the differences between the two generations are not nearly so marked; indeed, they are so little apparent that they are scarcely likely to be noticed except by experts. Thus here again there are small initial steps, some of which, indeed, must be regarded as adaptations, such as the green-sprinkled or lightly tinted under-surface which gives them a deceptive resemblance to parsley or to Cardamine leaves.

Even if saltatory variations do occur, we cannot assume that these HAVE EVER LED TO FORMS WHICH ARE CAPABLE OF SURVIVAL UNDER THE CONDITIONS OF WILD LIFE. Experience has shown that in plants which have suddenly varied the power of persistence is diminished. Korschinsky attributes to them weaknesses of organisation in general; "they bloom late, ripen few of

their seeds, and show great sensitiveness to cold." These are not the characters which make for success in the struggle for existence.

We must briefly refer here to the views—much discussed in the last decade—of H. de Vries, who believes that the roots of transformation must be sought for in SALTATORY VARIATIONS ARISING FROM INTERNAL CAUSES, and distinguishes such MUTATIONS, as he has called them, from ordinary individual variations, in that they breed true, that is, with strict inbreeding they are handed on pure to the next generation. I have elsewhere endeavoured to point out the weaknesses of this theory ("Vortrage uber Descendenztheorie", Jena, 1904, II. 269. English Translation London, 1904, II. page 317.), and I am the less inclined to return to it here that it now appears (See Poulton, "Essays on Evolution", Oxford, 1908, pages xix-xxii.) that the far-reaching conclusions drawn by de Vries from his observations on the Evening Primrose, *Oenothera lamarckiana*, rest upon a very insecure foundation. The plant from which de Vries saw numerous "species"—his "mutations"—arise was not, as he assumed, a WILD SPECIES that had been introduced to Europe from America, but was probably a hybrid form which was first discovered in the Jardin des Plantes in Paris, and which does not appear to exist anywhere in America as a wild species.

This gives a severe shock to the "Mutation theory," for the other ACTUALLY WILD species with which de Vries experimented showed no "mutations" but yielded only negative results.

Thus we come to the conclusion that Darwin ("Origin of Species" (6th edition), pages 176 et seq.) was right in regarding transformations as taking place by minute steps, which, if useful, are augmented in the course of innumerable generations, because their possessors more frequently survive in the struggle for existence.

(b) SELECTION-VALUE OF THE INITIAL STEPS.

Is it possible that the significant deviations which we know as "individual variations" can form the beginning of a process of selection? Can they decide which is to perish and which to survive? To use a phrase of Romanes, can they have SELECTION-VALUE?

Darwin himself answered this question, and brought together many excellent examples to show that differences, apparently insignificant because very small, might be of decisive importance for the life of the possessor. But it is by no means enough to bring forward cases of this kind, for the question is not merely whether finished adaptations have selection-value, but whether the first beginnings of these, and whether the small, I might almost say minimal increments, which have led up from these beginnings to the perfect adaptation, have also had selection-value. To this question even one who, like myself, has been for many years a convinced adherent of the theory of selection, can only reply: WE MUST ASSUME SO, BUT WE CANNOT PROVE IT IN ANY CASE. It is not upon demonstrative evidence that we rely when we champion the doctrine of selection as a scientific truth; we base our argument on quite other grounds. Undoubtedly there are many apparently insignificant features, which can nevertheless be shown to be adaptations—for instance, the thickness of the basin-shaped shell of the limpets that live among the breakers on the shore. There can be no doubt that the thickness of these shells, combined with their flat form, protects the animals from the force of the waves breaking upon them,—but how have they become so thick? What proportion of thickness was sufficient to decide that of two variants of a limpet one should survive, the other be eliminated? We can say nothing more than that we infer from the present state of the shell, that it must have varied in regard to differences in shell-thickness, and that these differences must have had selection-value,—no proof therefore, but an assumption which we must show to be convincing.

For a long time the marvellously complex RADIATE and LATTICE-WORK skeletons of Radiolarians were regarded as a mere outflow of "Nature's infinite wealth of form," as an instance of a purely morphological character with no biological significance. But recent investigations have shown that these, too, have an adaptive significance (Hacker). The same thing has been shown by Schutt in regard to the lowly unicellular plants, the Peridineae, which abound alike on the surface of the ocean and in its depths. It has been shown that the long skeletal processes which grow out from these organisms have significance not merely as a supporting skeleton, but also as an extension of the superficial area, which increases the contact with the water-particles, and prevents the floating organisms from sinking. It has been established that the processes are considerably shorter in the colder

layers of the ocean, and that they may be twelve times as long (Chun, "Reise der Valdivia", Leipzig, 1904.) in the warmer layers, thus corresponding to the greater or smaller amount of friction which takes place in the denser and less dense layers of the water.

The Peridineae of the warmer ocean layers have thus become long-rayed, those of the colder layers short-rayed, not through the direct effect of friction on the protoplasm, but through processes of selection, which favoured the longer rays in warm water, since they kept the organism afloat, while those with short rays sank and were eliminated. If we put the question as to selection-value in this case, and ask how great the variations in the length of processes must be in order to possess selection-value; what can we answer except that these variations must have been minimal, and yet sufficient to prevent too rapid sinking and consequent elimination? Yet this very case would give the ideal opportunity for a mathematical calculation of the minimal selection-value, although of course it is not feasible from lack of data to carry out the actual calculation.

But even in organisms of more than microscopic size there must frequently be minute, even microscopic differences which set going the process of selection, and regulate its progress to the highest possible perfection.

Many tropical trees possess thick, leathery leaves, as a protection against the force of the tropical rain drops. The DIRECT influence of the rain cannot be the cause of this power of resistance, for the leaves, while they were still thin, would simply have been torn to pieces. Their toughness must therefore be referred to selection, which would favour the trees with slightly thicker leaves, though we cannot calculate with any exactness how great the first stages of increase in thickness must have been. Our hypothesis receives further support from the fact that, in many such trees, the leaves are drawn out into a beak-like prolongation (Stahl and Haberlandt) which facilitates the rapid falling off of the rain water, and also from the fact that the leaves, while they are still young, hang limply down in bunches which offer the least possible resistance to the rain. Thus there are here three adaptations which can only be interpreted as due to selection. The initial stages of these adaptations must undoubtedly have had selection-value.

But even in regard to this case we are reasoning in a circle, not giving "proofs," and no one who does not wish to believe in the selection-value of the initial stages can be forced to do so. Among the many pieces of presumptive evidence a particularly weighty one seems to me to be THE SMALLNESS OF THE STEPS OF PROGRESS which we can observe in certain cases, as for instance in leaf-imitation among butterflies, and in mimicry generally. The resemblance to a leaf, for instance of a particular Kallima, seems to us so close as to be deceptive, and yet we find in another individual, or it may be in many others, a spot added which increases the resemblance, and which could not have become fixed unless the increased deceptiveness so produced had frequently led to the overlooking of its much persecuted possessor. But if we take the selection-value of the initial stages for granted, we are confronted with the further question which I myself formulated many years ago: How does it happen THAT THE NECESSARY BEGINNINGS OF A USEFUL VARIATION ARE ALWAYS PRESENT? How could insects which live upon or among green leaves become all green, while those that live on bark become brown? How have the desert animals become yellow and the Arctic animals white? Why were the necessary variations always present? How could the green locust lay brown eggs, or the privet caterpillar develop white and lilac-coloured lines on its green skin?

It is of no use answering to this that the question is wrongly formulated (Plate, "Selektionsprinzip u. Probleme der Artbildung" (3rd edition), Leipzig, 1908.) and that it is the converse that is true; that the process of selection takes place in accordance with the variations that present themselves. This proposition is undeniably true, but so also is another, which apparently negatives it: the variation required has in the majority of cases actually presented itself. Selection cannot solve this contradiction; it does not call forth the useful variation, but simply works upon it. The ultimate reason why one and the same insect should occur in green and in brown, as often happens in caterpillars and locusts, lies in the fact that variations towards brown presented themselves, and so also did variations towards green: THE KERNEL OF THE RIDDLE LIES IN THE VARYING, and for the present we can only say, that small variations in different directions present themselves in every species. Otherwise so many different kinds of variations could not have arisen. I have endeavoured to explain this remarkable fact by means

of the intimate processes that must take place within the germ-plasm, and I shall return to the problem when dealing with "germinal selection."

We have, however, to make still greater demands on variation, for it is not enough that the necessary variation should occur in isolated individuals, because in that case there would be small prospect of its being preserved, notwithstanding its utility. Darwin at first believed, that even single variations might lead to transformation of the species, but later he became convinced that this was impossible, at least without the cooperation of other factors, such as isolation and sexual selection.

In the case of the GREEN CATERPILLARS WITH BRIGHT LONGITUDINAL STRIPES, numerous individuals exhibiting this useful variation must have been produced to start with. In all higher, that is, multicellular organisms, the germ-substance is the source of all transmissible variations, and this germ-plasm is not a simple substance but is made up of many primary constituents. The question can therefore be more precisely stated thus: How does it come about that in so many cases the useful variations present themselves in numbers just where they are required, the white oblique lines in the leaf-caterpillar on the under surface of the body, the accompanying coloured stripes just above them? And, further, how has it come about that in grass caterpillars, not oblique but longitudinal stripes, which are more effective for concealment among grass and plants, have been evolved? And finally, how is it that the same Hawk-moth caterpillars, which to-day show oblique stripes, possessed longitudinal stripes in Tertiary times? We can read this fact from the history of their development, and I have before attempted to show the biological significance of this change of colour. ("Studien zur Descendenz-Theorie" II., "Die Entstehung der Zeichnung bei den Schmetterlings-raupen," Leipzig, 1876.)

For the present I need only draw the conclusion that one and the same caterpillar may exhibit the initial stages of both, and that it depends on the manner in which these marking elements are INTENSIFIED and COMBINED by natural selection whether whitish longitudinal or oblique stripes should result. In this case then the "useful variations" were actually "always there," and we see that in the same group of Lepidoptera, e.g. species of Sphingidae, evolution has occurred in both directions according to whether the form lived among grass or on broad leaves with oblique lateral veins, and we can observe even now that the species with oblique stripes have longitudinal stripes when young, that is to say, while the stripes have no biological significance. The white places in the skin which gave rise, probably first as small spots, to this protective marking could be combined in one way or another according to the requirements of the species. They must therefore either have possessed selection-value from the first, or, if this was not the case at their earliest occurrence, there must have been SOME OTHER FACTORS which raised them to the point of selection-value. I shall return to this in discussing germinal selection. But the case may be followed still farther, and leads us to the same alternative on a still more secure basis.

Many years ago I observed in caterpillars of *Smerinthus populi* (the poplar hawk-moth), which also possess white oblique stripes, that certain individuals showed RED SPOTS above these stripes; these spots occurred only on certain segments, and never flowed together to form continuous stripes. In another species (*Smerinthus tiliae*) similar blood-red spots unite to form a line-like coloured seam in the last stage of larval life, while in *S. ocellata* rust-red spots appear in individual caterpillars, but more rarely than in *S. Populi*, and they show no tendency to flow together.

Thus we have here the origin of a new character, arising from small beginnings, at least in *S. tiliae*, in which species the coloured stripes are a normal specific character. In the other species, *S. populi* and *S. ocellata*, we find the beginnings of the same variation, in one more rarely than in the other, and we can imagine that, in the course of time, in these two species, coloured lines over the oblique stripes will arise. In any case these spots are the elements of variation, out of which coloured lines MAY be evolved, if they are combined in this direction through the agency of natural selection. In *S. populi* the spots are often small, but sometimes it seems as though several had united to form large spots. Whether a process of selection in this direction will arise in *S. populi* and *S. ocellata*, or whether it is now going on cannot be determined, since we cannot tell in advance what biological value the marking might have for these two species. It is conceivable that the spots may have no selection-value as far as these species are concerned, and may therefore disappear again in the course of phylogeny, or, on the other hand, that they may be changed in another direction, for instance towards imitation of the rust-red fungoid patches

on poplar and willow leaves. In any case we may regard the smallest spots as the initial stages of variation, the larger as a cumulative summation of these. Therefore either these initial stages must already possess selection-value, or, as I said before: THERE MUST BE SOME OTHER REASON FOR THEIR CUMULATIVE SUMMATION. I should like to give one more example, in which we can infer, though we cannot directly observe, the initial stages.

All the Holothurians or sea-cucumbers have in the skin calcareous bodies of different forms, usually thick and irregular, which make the skin tough and resistant. In a small group of them—the species of *Synapta*—the calcareous bodies occur in the form of delicate anchors of microscopic size. Up till 1897 these anchors, like many other delicate microscopic structures, were regarded as curiosities, as natural marvels. But a Swedish observer, Oestergren, has recently shown that they have a biological significance: they serve the footless *Synapta* as auxiliary organs of locomotion, since, when the body swells up in the act of creeping, they press firmly with their tips, which are embedded in the skin, against the substratum on which the animal creeps, and thus prevent slipping backwards. In other Holothurians this slipping is made impossible by the fixing of the tube-feet. The anchors act automatically, sinking their tips towards the ground when the corresponding part of the body thickens, and returning to the original position at an angle of 45 degrees to the upper surface when the part becomes thin again. The arms of the anchor do not lie in the same plane as the shaft, and thus the curve of the arms forms the outermost part of the anchor, and offers no further resistance to the gliding of the animal. Every detail of the anchor, the curved portion, the little teeth at the head, the arms, etc., can be interpreted in the most beautiful way, above all the form of the anchor itself, for the two arms prevent it from swaying round to the side. The position of the anchors, too, is definite and significant; they lie obliquely to the longitudinal axis of the animal, and therefore they act alike whether the animal is creeping backwards or forwards. Moreover, the tips would pierce through the skin if the anchors lay in the longitudinal direction. *Synapta* burrows in the sand; it first pushes in the thin anterior end, and thickens this again, thus enlarging the hole, then the anterior tentacles displace more sand, the body is worked in a little farther, and the process begins anew. In the first act the anchors are passive, but they begin to take an active share in the forward movement when the body is contracted again. Frequently the animal retains only the posterior end buried in the sand, and then the anchors keep it in position, and make rapid withdrawal possible.

Thus we have in these apparently random forms of the calcareous bodies, complex adaptations in which every little detail as to direction, curve, and pointing is exactly determined. That they have selection-value in their present perfected form is beyond all doubt, since the animals are enabled by means of them to bore rapidly into the ground and so to escape from enemies. We do not know what the initial stages were, but we cannot doubt that the little improvements, which occurred as variations of the originally simple slimy bodies of the Holothurians, were preserved because they already possessed selection-value for the *Synaptidae*. For such minute microscopic structures whose form is so delicately adapted to the role they have to play in the life of the animal, cannot have arisen suddenly and as a whole, and every new variation of the anchor, that is, in the direction of the development of the two arms, and every curving of the shaft which prevented the tips from projecting at the wrong time, in short, every little adaptation in the modelling of the anchor must have possessed selection-value. And that such minute changes of form fall within the sphere of fluctuating variations, that is to say, THAT THEY OCCUR is beyond all doubt.

In many of the *Synaptidae* the anchors are replaced by calcareous rods bent in the form of an S, which are said to act in the same way. Others, such as those of the genus *Ankyroderma*, have anchors which project considerably beyond the skin, and, according to Oestergren, serve "to catch plant-particles and other substances" and so mask the animal. Thus we see that in the *Synaptidae* the thick and irregular calcareous bodies of the Holothurians have been modified and transformed in various ways in adaptation to the footlessness of these animals, and to the peculiar conditions of their life, and we must conclude that the earlier stages of these changes presented themselves to the processes of selection in the form of microscopic variations. For it is as impossible to think of any origin other than through selection in this case as in the case of the toughness, and the "drip-tips" of tropical leaves. And as these last could not have been produced directly by the beating of the heavy rain-drops upon them, so the calcareous anchors of *Synapta* cannot have been produced directly by the friction of the sand and

mud at the bottom of the sea, and, since they are parts whose function is PASSIVE the Lamarckian factor of use and disuse does not come into question. The conclusion is unavoidable, that the microscopically small variations of the calcareous bodies in the ancestral forms have been intensified and accumulated in a particular direction, till they have led to the formation of the anchor. Whether this has taken place by the action of natural selection alone, or whether the laws of variation and the intimate processes within the germ-plasm have cooperated will become clear in the discussion of germinal selection. This whole process of adaptation has obviously taken place within the time that has elapsed since this group of sea-cucumbers lost their tube-feet, those characteristic organs of locomotion which occur in no group except the Echinoderms, and yet have totally disappeared in the Synaptidae. And after all what would animals that live in sand and mud do with tube-feet?

(c) COADAPTATION.

Darwin pointed out that one of the essential differences between artificial and natural selection lies in the fact that the former can modify only a few characters, usually only one at a time, while Nature preserves in the struggle for existence all the variations of a species, at the same time and in a purely mechanical way, if they possess selection-value.

Herbert Spencer, though himself an adherent of the theory of selection, declared in the beginning of the nineties that in his opinion the range of this principle was greatly over-estimated, if the great changes which have taken place in so many organisms in the course of ages are to be interpreted as due to this process of selection alone, since no transformation of any importance can be evolved by itself; it is always accompanied by a host of secondary changes. He gives the familiar example of the Giant Stag of the Irish peat, the enormous antlers of which required not only a much stronger skull cap, but also greater strength of the sinews, muscles, nerves and bones of the whole anterior half of the animal, if their mass was not to weigh down the animal altogether. It is inconceivable, he says, that so many processes of selection should take place SIMULTANEOUSLY, and we are therefore forced to fall back on the Lamarckian factor of the use and disuse of functional parts. And how, he asks, could natural selection follow two opposite directions of evolution in different parts of the body at the same time, as for instance in the case of the kangaroo, in which the forelegs must have become shorter, while the hind legs and the tail were becoming longer and stronger?

Spencer's main object was to substantiate the validity of the Lamarckian principle, the cooperation of which with selection had been doubted by many. And it does seem as though this principle, if it operates in nature at all, offers a ready and simple explanation of all such secondary variations. Not only muscles, but nerves, bones, sinews, in short all tissues which function actively, increase in strength in proportion as they are used, and conversely they decrease when the claims on them diminish. All the parts, therefore, which depend on the part that varied first, as for instance the enlarged antlers of the Irish Elk, must have been increased or decreased in strength, in exact proportion to the claims made upon them,—just as is actually the case.

But beautiful as this explanation would be, I regard it as untenable, because it assumes the TRANSMISSIBILITY OF FUNCTIONAL MODIFICATIONS (so-called "acquired" characters), and this is not only undemonstrable, but is scarcely theoretically conceivable, for the secondary variations which accompany or follow the first as correlative variations, occur also in cases in which the animals concerned are sterile and THEREFORE CANNOT TRANSMIT ANYTHING TO THEIR DESCENDANTS. This is true of WORKER BEES, and particularly of ANTS, and I shall here give a brief survey of the present state of the problem as it appears to me.

Much has been written on both sides of this question since the published controversy on the subject in the nineties between Herbert Spencer and myself. I should like to return to the matter in detail, if the space at my disposal permitted, because it seems to me that the arguments I advanced at that time are equally cogent to-day, notwithstanding all the objections that have since been urged against them. Moreover, the matter is by no means one of subordinate interest; it is the very kernel of the whole question of the reality and value of the principle of selection. For if selection alone does not suffice to explain "HARMONIOUS ADAPTATION" as I have called Spencer's COADAPTATION, and if we require to call in the aid of the Lamarckian factor it would be questionable whether selection could explain any adaptations whatever. In this particular case—of worker bees—the Lamarckian factor may

be excluded altogether, for it can be demonstrated that here at any rate the effects of use and disuse cannot be transmitted.

But if it be asked why we are unwilling to admit the cooperation of the Darwinian factor of selection and the Lamarckian factor, since this would afford us an easy and satisfactory explanation of the phenomena, I answer: BECAUSE THE LAMARCKIAN PRINCIPLE IS FALLACIOUS, AND BECAUSE BY ACCEPTING IT WE CLOSE THE WAY TOWARDS DEEPER INSIGHT. It is not a spirit of combativeness or a desire for self-vindication that induces me to take the field once more against the Lamarckian principle, it is the conviction that the progress of our knowledge is being obstructed by the acceptance of this fallacious principle, since the facile explanation it apparently affords prevents our seeking after a truer explanation and a deeper analysis.

The workers in the various species of ants are sterile, that is to say, they take no regular part in the reproduction of the species, although individuals among them may occasionally lay eggs. In addition to this they have lost the wings, and the receptaculum seminis, and their compound eyes have degenerated to a few facets. How could this last change have come about through disuse, since the eyes of workers are exposed to light in the same way as are those of the sexual insects and thus in this particular case are not liable to "disuse" at all? The same is true of the receptaculum seminis, which can only have been disused as far as its glandular portion and its stalk are concerned, and also of the wings, the nerves tracheae and epidermal cells of which could not cease to function until the whole wing had degenerated, for the chitinous skeleton of the wing does not function at all in the active sense.

But, on the other hand, the workers in all species have undergone modifications in a positive direction, as, for instance, the greater development of brain. In many species large workers have evolved,—the so-called SOLDIERS, with enormous jaws and teeth, which defend the colony,—and in others there are SMALL workers which have taken over other special functions, such as the rearing of the young Aphides. This kind of division of the workers into two castes occurs among several tropical species of ants, but it is also present in the Italian species, *Colobopsis truncata*. Beautifully as the size of the jaws could be explained as due to the increased use made of them by the "soldiers," or the enlarged brain as due to the mental activities of the workers, the fact of the infertility of these forms is an insurmountable obstacle to accepting such an explanation. Neither jaws nor brain can have been evolved on the Lamarckian principle.

The problem of coadaptation is no easier in the case of the ant than in the case of the Giant Stag. Darwin himself gave a pretty illustration to show how imposing the difference between the two kinds of workers in one species would seem if we translated it into human terms. In regard to the Driver ants (*Anomma*) we must picture to ourselves a piece of work, "for instance the building of a house, being carried on by two kinds of workers, of which one group was five feet four inches high, the other sixteen feet high." ("Origin of Species" (6th edition), page 232.)

Although the ant is a small animal as compared with man or with the Irish Elk, the "soldier" with its relatively enormous jaws is hardly less heavily burdened than the Elk with its antlers, and in the ant's case, too, a strengthening of the skeleton, of the muscles, the nerves of the head, and of the legs must have taken place parallel with the enlargement of the jaws. HARMONIOUS ADAPTATION (coadaptation) has here been active in a high degree, and yet these "soldiers" are sterile! There thus remains nothing for it but to refer all their adaptations, positive and negative alike, to processes of selection which have taken place in the rudiments of the workers within the egg and sperm-cells of their parents. There is no way out of the difficulty except the one Darwin pointed out. He himself did not find the solution of the riddle at once. At first he believed that the case of the workers among social insects presented "the most serious special difficulty" in the way of his theory of natural selection; and it was only after it had become clear to him, that it was not the sterile insects themselves but their parents that were selected, according as they produced more or less well adapted workers, that he was able to refer to this very case of the conditions among ants "IN ORDER TO SHOW THE POWER OF NATURAL SELECTION" ("Origin of Species", page 233; see also edition 1, page 242.). He explains his view by a simple but interesting illustration. Gardeners have produced, by means of long continued artificial selection, a variety of Stock, which bears entirely double, and therefore infertile flowers (Ibid. page 230.). Nevertheless the variety continues to be reproduced from seed, because in addition to the double and infertile flowers, the seeds always produce a certain number of single, fertile blossoms, and

these are used to reproduce the double variety. These single and fertile plants correspond "to the males and females of an ant-colony, the infertile plants, which are regularly produced in large numbers, to the neuter workers of the colony."

This illustration is entirely apt, the only difference between the two cases consisting in the fact that the variation in the flower is not a useful, but a disadvantageous one, which can only be preserved by artificial selection on the part of the gardener, while the transformations that have taken place parallel with the sterility of the ants are useful, since they procure for the colony an advantage in the struggle for existence, and they are therefore preserved by natural selection. Even the sterility itself in this case is not disadvantageous, since the fertility of the true females has at the same time considerably increased. We may therefore regard the sterile forms of ants, which have gradually been adapted in several directions to varying functions, AS A CERTAIN PROOF that selection really takes place in the germ-cells of the fathers and mothers of the workers, and that SPECIAL COMPLEXES OF PRIMORDIA (IDS) are present in the workers and in the males and females, and these complexes contain the primordia of the individual parts (DETERMINANTS). But since all living entities vary, the determinants must also vary, now in a favourable, now in an unfavourable direction. If a female produces eggs, which contain favourably varying determinants in the worker-ids, then these eggs will give rise to workers modified in the favourable direction, and if this happens with many females, the colony concerned will contain a better kind of worker than other colonies.

I digress here in order to give an account of the intimate processes, which, according to my view, take place within the germ-plasm, and which I have called "GERMINAL SELECTION." These processes are of importance since they form the roots of variation, which in its turn is the root of natural selection. I cannot here do more than give a brief outline of the theory in order to show how the Darwin-Wallace theory of selection has gained support from it.

With others, I regard the minimal amount of substance which is contained within the nucleus of the germ-cells, in the form of rods, bands, or granules, as the GERM-SUBSTANCE or GERM-PLASM, and I call the individual granules IDS. There is always a multiplicity of such ids present in the nucleus, either occurring individually, or united in the form of rods or bands (chromosomes). Each id contains the primary constituents of a WHOLE individual, so that several ids are concerned in the development of a new individual.

In every being of complex structure thousands of primary constituents must go to make up a single id; these I call DETERMINANTS, and I mean by this name very small individual particles, far below the limits of microscopic visibility, vital units which feed, grow, and multiply by division. These determinants control the parts of the developing embryo,—in what manner need not here concern us. The determinants differ among themselves, those of a muscle are differently constituted from those of a nerve-cell or a glandular cell, etc., and every determinant is in its turn made up of minute vital units, which I call BIOPHORS, or the bearers of life. According to my view, these determinants not only assimilate, like every other living unit, but they VARY in the course of their growth, as every living unit does; they may vary qualitatively if the elements of which they are composed vary, they may grow and divide more or less rapidly, and their variations give rise to CORRESPONDING variations of the organ, cell, or cell-group which they determine. That they are undergoing ceaseless fluctuations in regard to size and quality seems to me the inevitable consequence of their unequal nutrition; for although the germ-cell as a whole usually receives sufficient nutriment, minute fluctuations in the amount carried to different parts within the germ-plasm cannot fail to occur.

Now, if a determinant, for instance of a sensory cell, receives for a considerable time more abundant nutriment than before, it will grow more rapidly—become bigger, and divide more quickly, and, later, when the id concerned develops into an embryo, this sensory cell will become stronger than in the parents, possibly even twice as strong. This is an instance of a HEREDITARY INDIVIDUAL VARIATION, arising from the germ.

The nutritive stream which, according to our hypothesis, favours the determinant N by chance, that is, for reasons unknown to us, may remain strong for a considerable time, or may decrease again; but even in the latter case it is conceivable that the ascending movement of the determinant may continue, because the strengthened determinant now ACTIVELY nourishes itself more abundantly,—that is to say, it attracts the nutriment to itself, and to a certain extent withdraws it from its fellow-determinants.

In this way, it may—as it seems to me—get into PERMANENT UPWARD MOVEMENT, AND ATTAIN A DEGREE OF STRENGTH FROM WHICH THERE IS NO FALLING BACK. Then positive or negative selection sets in, favouring the variations which are advantageous, setting aside those which are disadvantageous.

In a similar manner a DOWNWARD variation of the determinants may take place, if its progress be started by a diminished flow of nutriment. The determinants which are weakened by this diminished flow will have less affinity for attracting nutriment because of their diminished strength, and they will assimilate more feebly and grow more slowly, unless chance streams of nutriment help them to recover themselves. But, as will presently be shown, a change of direction cannot take place at EVERY stage of the degenerative process. If a certain critical stage of downward progress be passed, even favourable conditions of food-supply will no longer suffice permanently to change the direction of the variation. Only two cases are conceivable; if the determinant corresponds to a USEFUL organ, only its removal can bring back the germ-plasm to its former level; therefore personal selection removes the id in question, with its determinants, from the germ-plasm, by causing the elimination of the individual in the struggle for existence. But there is another conceivable case; the determinants concerned may be those of an organ which has become USELESS, and they will then continue unobstructed, but with exceeding slowness, along the downward path, until the organ becomes vestigial, and finally disappears altogether.

The fluctuations of the determinants hither and thither may thus be transformed into a lasting ascending or descending movement; and THIS IS THE CRUCIAL POINT OF THESE GERMINAL PROCESSES.

This is not a fantastic assumption; we can read it in the fact of the degeneration of disused parts. USELESS ORGANS ARE THE ONLY ONES WHICH ARE NOT HELPED TO ASCEND AGAIN BY PERSONAL SELECTION, AND THEREFORE IN THEIR CASE ALONE CAN WE FORM ANY IDEA OF HOW THE PRIMARY CONSTITUENTS BEHAVE, WHEN THEY ARE SUBJECT SOLELY TO INTRA-GERMINAL FORCES.

The whole determinant system of an id, as I conceive it, is in a state of continual fluctuation upwards and downwards. In most cases the fluctuations will counteract one another, because the passive streams of nutriment soon change, but in many cases the limit from which a return is possible will be passed, and then the determinants concerned will continue to vary in the same direction, till they attain positive or negative selection-value. At this stage personal selection intervenes and sets aside the variation if it is disadvantageous, or favours—that is to say, preserves—it if it is advantageous. Only THE DETERMINANT OF A USELESS ORGAN IS UNINFLUENCED BY PERSONAL SELECTION, and, as experience shows, it sinks downwards; that is, the organ that corresponds to it degenerates very slowly but uninterruptedly till, after what must obviously be an immense stretch of time, it disappears from the germ-plasm altogether.

Thus we find in the fact of the degeneration of disused parts the proof that not all the fluctuations of a determinant return to equilibrium again, but that, when the movement has attained to a certain strength, it continues IN THE SAME DIRECTION. We have entire certainty in regard to this as far as the downward progress is concerned, and we must assume it also in regard to ascending variations, as the phenomena of artificial selection certainly justify us in doing. If the Japanese breeders were able to lengthen the tail feathers of the cock to six feet, it can only have been because the determinants of the tail-feathers in the germ-plasm had already struck out a path of ascending variation, and this movement was taken advantage of by the breeder, who continually selected for reproduction the individuals in which the ascending variation was most marked. For all breeding depends upon the unconscious selection of germinal variations.

Of course these germinal processes cannot be proved mathematically, since we cannot actually see the play of forces of the passive fluctuations and their causes. We cannot say how great these fluctuations are, and how quickly or slowly, how regularly or irregularly they change. Nor do we know how far a determinant must be strengthened by the passive flow of the nutritive stream if it is to be beyond the danger of unfavourable variations, or how far it must be weakened passively before it loses the power of recovering itself by its own strength. It is no more possible to bring forward actual proofs in this case than it was in regard to the selection-value of the initial stages of an adaptation. But if we

consider that all heritable variations must have their roots in the germ-plasm, and further, that when personal selection does not intervene, that is to say, in the case of parts which have become useless, a degeneration of the part, and therefore also of its determinant must inevitably take place; then we must conclude that processes such as I have assumed are running their course within the germ-plasm, and we can do this with as much certainty as we were able to infer, from the phenomena of adaptation, the selection-value of their initial stages. The fact of the degeneration of disused parts seems to me to afford irrefutable proof that the fluctuations within the germ-plasm ARE THE REAL ROOT OF ALL HEREDITARY VARIATION, and the preliminary condition for the occurrence of the Darwin-Wallace factor of selection. Germinal selection supplies the stones out of which personal selection builds her temples and palaces: ADAPTATIONS. The importance for the theory of the process of degeneration of disused parts cannot be over-estimated, especially when it occurs in sterile animal forms, where we are free from the doubt as to the alleged LAMARCKIAN FACTOR which is apt to confuse our ideas in regard to other cases.

If we regard the variation of the many determinants concerned in the transformation of the female into the sterile worker as having come about through the gradual transformation of the ids into worker-ids, we shall see that the germ-plasm of the sexual ants must contain three kinds of ids, male, female, and worker ids, or if the workers have diverged into soldiers and nest-builders, then four kinds. We understand that the worker-ids arose because their determinants struck out a useful path of variation, whether upward or downward, and that they continued in this path until the highest attainable degree of utility of the parts determined was reached. But in addition to the organs of positive or negative selection-value, there were some which were indifferent as far as the success and especially the functional capacity of the workers was concerned: wings, ovarian tubes, receptaculum seminis, a number of the facets of the eye, perhaps even the whole eye. As to the ovarian tubes it is possible that their degeneration was an advantage for the workers, in saving energy, and if so selection would favour the degeneration; but how could the presence of eyes diminish the usefulness of the workers to the colony? or the minute receptaculum seminis, or even the wings? These parts have therefore degenerated BECAUSE THEY WERE OF NO FURTHER VALUE TO THE INSECT. But if selection did not influence the setting aside of these parts because they were neither of advantage nor of disadvantage to the species, then the Darwinian factor of selection is here confronted with a puzzle which it cannot solve alone, but which at once becomes clear when germinal selection is added. For the determinants of organs that have no further value for the organism, must, as we have already explained, embark on a gradual course of retrograde development.

In ants the degeneration has gone so far that there are no wing-rudiments present in ANY species, as is the case with so many butterflies, flies, and locusts, but in the larvae the imaginal discs of the wings are still laid down. With regard to the ovaries, degeneration has reached different levels in different species of ants, as has been shown by the researches of my former pupil, Elizabeth Bickford. In many species there are twelve ovarian tubes, and they decrease from that number to one; indeed, in one species no ovarian tube at all is present. So much at least is certain from what has been said, that in this case EVERYTHING depends on the fluctuations of the elements of the germ-plasm. Germinal selection, here as elsewhere, presents the variations of the determinants, and personal selection favours or rejects these, or,—if it be a question of organs which have become useless,—it does not come into play at all, and allows the descending variation free course.

It is obvious that even the problem of COADAPTATION IN STERILE ANIMALS can thus be satisfactorily explained. If the determinants are oscillating upwards and downwards in continual fluctuation, and varying more pronouncedly now in one direction now in the other, useful variations of every determinant will continually present themselves anew, and may, in the course of generations, be combined with one another in various ways. But there is one character of the determinants that greatly facilitates this complex process of selection, that, after a certain limit has been reached, they go on varying in the same direction. From this it follows that development along a path once struck out may proceed without the continual intervention of personal selection. This factor only operates, so to speak, at the beginning, when it selects the determinants which are varying in the right direction, and again at the end, when it is necessary to put a check upon further variation. In addition to this, enormously long periods have been available for all these adaptations, as the very gradual transition stages between

females and workers in many species plainly show, and thus this process of transformation loses the marvellous and mysterious character that seemed at the first glance to invest it, and takes rank, without any straining, among the other processes of selection. It seems to me that, from the facts that sterile animal forms can adapt themselves to new vital functions, their superfluous parts degenerate, and the parts more used adapt themselves in an ascending direction, those less used in a descending direction, we must draw the conclusion that harmonious adaptation here comes about WITHOUT THE COOPERATION OF THE LAMARCKIAN PRINCIPLE. This conclusion once established, however, we have no reason to refer the thousands of cases of harmonious adaptation, which occur in exactly the same way among other animals or plants, to a principle, the ACTIVE INTERVENTION OF WHICH IN THE TRANSFORMATION OF SPECIES IS NOWHERE PROVED. WE DO NOT REQUIRE IT TO EXPLAIN THE FACTS, AND THEREFORE WE MUST NOT ASSUME IT.

The fact of coadaptation, which was supposed to furnish the strongest argument against the principle of selection, in reality yields the clearest evidence in favour of it. We MUST assume it, BECAUSE NO OTHER POSSIBILITY OF EXPLANATION IS OPEN TO US, AND BECAUSE THESE ADAPTATIONS ACTUALLY EXIST, THAT IS TO SAY, HAVE REALLY TAKEN PLACE. With this conviction I attempted, as far back as 1894, when the idea of germinal selection had not yet occurred to me, to make "harmonious adaptation" (coadaptation) more easily intelligible in some way or other, and so I was led to the idea, which was subsequently expounded in detail by Baldwin, and Lloyd Morgan, and also by Osborn, and Gulick as ORGANIC SELECTION. It seemed to me that it was not necessary that all the germinal variations required for secondary variations should have occurred SIMULTANEOUSLY, since, for instance, in the case of the stag, the bones, muscles, sinews, and nerves would be incited by the increasing heaviness of the antlers to greater activity in THE INDIVIDUAL LIFE, and so would be strengthened. The antlers can only have increased in size by very slow degrees, so that the muscles and bones may have been able to keep pace with their growth in the individual life, until the requisite germinal variations presented themselves. In this way a disharmony between the increasing weight of the antlers and the parts which support and move them would be avoided, since time would be given for the appropriate germinal variations to occur, and so to set agoing the HEREDITARY variation of the muscles, sinews, and bones. ("The Effect of External Influences upon Development", Romanes Lecture, Oxford, 1894.)

I still regard this idea as correct, but I attribute less importance to "organic selection" than I did at that time, in so far that I do not believe that it ALONE could effect complex harmonious adaptations. Germinal selection now seems to me to play the chief part in bringing about such adaptations. Something the same is true of the principle I have called "Panmixia". As I became more and more convinced, in the course of years, that the LAMARCKIAN PRINCIPLE ought not to be called in to explain the dwindling of disused parts, I believed that this process might be simply explained as due to the cessation of the conservative effect of natural selection. I said to myself that, from the moment in which a part ceases to be of use, natural selection withdraws its hand from it, and then it must inevitably fall from the height of its adaptiveness, because inferior variants would have as good a chance of persisting as better ones, since all grades of fitness of the part in question would be mingled with one another indiscriminately. This is undoubtedly true, as Romanes pointed out ten years before I did, and this mingling of the bad with the good probably does bring about a deterioration of the part concerned. But it cannot account for the steady diminution, which always occurs when a part is in process of becoming rudimentary, and which goes on until it ultimately disappears altogether. The process of dwindling cannot therefore be explained as due to panmixia alone; we can only find a sufficient explanation in germinal selection.

IV. DERIVATIVES OF THE THEORY OF SELECTION.

The impetus in all directions given by Darwin through his theory of selection has been an immeasurable one, and its influence is still felt. It falls within the province of the historian of science to enumerate all the ideas which, in the last quarter of the nineteenth century, grew out of Darwin's theories, in the endeavour to penetrate more deeply into the problem of the evolution of the organic world. Within the narrow limits to which this paper is restricted, I cannot attempt to discuss any of these.

V. ARGUMENTS FOR THE REALITY OF THE PROCESSES OF SELECTION.

(a) SEXUAL SELECTION.

Sexual selection goes hand in hand with natural selection. From the very first I have regarded sexual selection as affording an extremely important and interesting corroboration of natural selection, but, singularly enough, it is precisely against this theory that an adverse judgment has been pronounced in so many quarters, and it is only quite recently, and probably in proportion as the wealth of facts in proof of it penetrates into a wider circle, that we seem to be approaching a more general recognition of this side of the problem of adaptation. Thus Darwin's words in his preface to the second edition (1874) of his book, "The Descent of Man and Sexual Selection", are being justified: "My conviction as to the operation of natural selection remains unshaken," and further, "If naturalists were to become more familiar with the idea of sexual selection, it would, I think, be accepted to a much greater extent, and already it is fully and favourably accepted by many competent judges." Darwin was able to speak thus because he was already acquainted with an immense mass of facts, which, taken together, yield overwhelming evidence of the validity of the principle of sexual selection.

NATURAL SELECTION chooses out for reproduction the individuals that are best equipped for the struggle for existence, and it does so at every stage of development; it thus improves the species in all its stages and forms. SEXUAL SELECTION operates only on individuals that are already capable of reproduction, and does so only in relation to the attainment of reproduction. It arises from the rivalry of one sex, usually the male, for the possession of the other, usually the female. Its influence can therefore only DIRECTLY affect one sex, in that it equips it better for attaining possession of the other. But the effect may extend indirectly to the female sex, and thus the whole species may be modified, without, however, becoming any more capable of resistance in the struggle for existence, for sexual selection only gives rise to adaptations which are likely to give their possessor the victory over rivals in the struggle for possession of the female, and which are therefore peculiar to the wooing sex: the manifold "secondary sexual characters." The diversity of these characters is so great that I cannot here attempt to give anything approaching a complete treatment of them, but I should like to give a sufficient number of examples to make the principle itself, in its various modes of expression, quite clear.

One of the chief preliminary postulates of sexual selection is the unequal number of individuals in the two sexes, for if every male immediately finds his mate there can be no competition for the possession of the female. Darwin has shown that, for the most part, the inequality between the sexes is due simply to the fact that there are more males than females, and therefore the males must take some pains to secure a mate. But the inequality does not always depend on the numerical preponderance of the males, it is often due to polygamy; for, if one male claims several females, the number of females in proportion to the rest of the males will be reduced. Since it is almost always the males that are the wooers, we must expect to find the occurrence of secondary sexual characters chiefly among them, and to find it especially frequent in polygamous species. And this is actually the case.

If we were to try to guess—without knowing the facts—what means the male animals make use of to overcome their rivals in the struggle for the possession of the female, we might name many kinds of means, but it would be difficult to suggest any which is not actually employed in some animal group or other. I begin with the mere difference in strength, through which the male of many animals is so sharply distinguished from the female, as, for instance, the lion, walrus, "sea-elephant," and others. Among these the males fight violently for the possession of the female, who falls to the victor in the combat. In this simple case no one can doubt the operation of selection, and there is just as little room for doubt as to the selection-value of the initial stages of the variation. Differences in bodily strength are apparent even among human beings, although in their case the struggle for the possession of the female is no longer decided by bodily strength alone.

Combats between male animals are often violent and obstinate, and the employment of the natural weapons of the species in this way has led to perfecting of these, e.g. the tusks of the boar, the antlers of the stag, and the enormous, antler-like jaws of the stag-beetle. Here again it is impossible to doubt that variations in these organs presented themselves, and that these were considerable enough to be decisive in combat, and so to lead to the improvement of the weapon.

Among many animals, however, the females at first withdraw from the males; they are coy, and have to be sought out, and sometimes held by force. This tracking and grasping of the females by the males has given rise to many different characters in the latter, as, for instance, the larger eyes of the male bee,

and especially of the males of the Ephemerids (May-flies), some species of which show, in addition to the usual compound eyes, large, so-called turban-eyes, so that the whole head is covered with seeing surfaces. In these species the females are very greatly in the minority (1-100), and it is easy to understand that a keen competition for them must take place, and that, when the insects of both sexes are floating freely in the air, an unusually wide range of vision will carry with it a decided advantage. Here again the actual adaptations are in accordance with the preliminary postulates of the theory. We do not know the stages through which the eye has passed to its present perfected state, but, since the number of simple eyes (facets) has become very much greater in the male than in the female, we may assume that their increase is due to a gradual duplication of the determinants of the ommatidium in the germ-plasm, as I have already indicated in regard to sense-organs in general. In this case, again, the selection-value of the initial stages hardly admits of doubt; better vision DIRECTLY secures reproduction.

In many cases THE ORGAN OF SMELL shows a similar improvement. Many lower Crustaceans (Daphnidae) have better developed organs of smell in the male sex. The difference is often slight and amounts only to one or two olfactory filaments, but certain species show a difference of nearly a hundred of these filaments (Leptodora). The same thing occurs among insects.

We must briefly consider the clasping or grasping organs which have developed in the males among many lower Crustaceans, but here natural selection plays its part along with sexual selection, for the union of the sexes is an indispensable condition for the maintenance of the species, and as Darwin himself pointed out, in many cases the two forms of selection merge into each other. This fact has always seemed to me to be a proof of natural selection, for, in regard to sexual selection, it is quite obvious that the victory of the best-equipped could have brought about the improvement only of the organs concerned, the factors in the struggle, such as the eye and the olfactory organ.

We come now to the EXCITANTS; that is, to the group of sexual characters whose origin through processes of selection has been most frequently called in question. We may cite the LOVE-CALLS produced by many male insects, such as crickets and cicadas. These could only have arisen in animal groups in which the female did not rapidly flee from the male, but was inclined to accept his wooing from the first. Thus, notes like the chirping of the male cricket serve to entice the females. At first they were merely the signal which showed the presence of a male in the neighbourhood, and the female was gradually enticed nearer and nearer by the continued chirping. The male that could make himself heard to the greatest distance would obtain the largest following, and would transmit the beginnings, and, later, the improvement of his voice to the greatest number of descendants. But sexual excitement in the female became associated with the hearing of the love-call, and then the sound-producing organ of the male began to improve, until it attained to the emission of the long-drawn-out soft notes of the mole-cricket or the maenad-like cry of the cicadas. I cannot here follow the process of development in detail, but will call attention to the fact that the original purpose of the voice, the announcing of the male's presence, became subsidiary, and the exciting of the female became the chief goal to be aimed at. The loudest singers awakened the strongest excitement, and the improvement resulted as a matter of course. I conceive of the origin of bird-song in a somewhat similar manner, first as a means of enticing, then of exciting the female.

One more kind of secondary sexual character must here be mentioned: the odour which emanates from so many animals at the breeding season. It is possible that this odour also served at first merely to give notice of the presence of individuals of the other sex, but it soon became an excitant, and as the individuals which caused the greatest degree of excitement were preferred, it reached as high a pitch of perfection as was possible to it. I shall confine myself here to the comparatively recently discovered fragrance of butterflies. Since Fritz Muller found out that certain Brazilian butterflies gave off fragrance "like a flower," we have become acquainted with many such cases, and we now know that in all lands, not only many diurnal Lepidoptera but nocturnal ones also give off a delicate odour, which is agreeable even to man. The ethereal oil to which this fragrance is due is secreted by the skin-cells, usually of the wing, as I showed soon after the discovery of the SCENT-SCALES. This is the case in the males; the females have no SPECIAL scent-scales recognisable as such by their form, but they must, nevertheless, give off an extremely delicate fragrance, although our imperfect organ of smell cannot perceive it, for the males become aware of the presence of a female, even at night, from a long distance off, and gather

round her. We may therefore conclude, that both sexes have long given forth a very delicate perfume, which announced their presence to others of the same species, and that in many species (NOT IN ALL) these small beginnings became, in the males, particularly strong scent-scales of characteristic form (lute, brush, or lyre-shaped). At first these scales were scattered over the surface of the wing, but gradually they concentrated themselves, and formed broad, velvety bands, or strong, prominent brushes, and they attained their highest pitch of evolution when they became enclosed within pits or folds of the skin, which could be opened to let the delicious fragrance stream forth suddenly towards the female. Thus in this case also we see that characters, the original use of which was to bring the sexes together, and so to maintain the species, have been evolved in the males into means for exciting the female. And we can hardly doubt, that the females are most readily enticed to yield to the butterfly that sends out the strongest fragrance,—that is to say, that excites them to the highest degree. It is a pity that our organs of smell are not fine enough to examine the fragrance of male Lepidoptera in general, and to compare it with other perfumes which attract these insects. (See Poulton, "Essays on Evolution", 1908, pages 316, 317.) As far as we can perceive them they resemble the fragrance of flowers, but there are Lepidoptera whose scent suggests musk. A smell of musk is also given off by several plants: it is a sexual excitant in the musk-deer, the musk-sheep, and the crocodile.

As far as we know, then, it is perfumes similar to those of flowers that the male Lepidoptera give off in order to entice their mates, and this is a further indication that animals, like plants, can to a large extent meet the claims made upon them by life, and produce the adaptations which are most purposive, —a further proof, too, of my proposition that the useful variations, so to speak, are ALWAYS THERE. The flowers developed the perfumes which entice their visitors, and the male Lepidoptera developed the perfumes which entice and excite their mates.

There are many pretty little problems to be solved in this connection, for there are insects, such as some flies, that are attracted by smells which are unpleasant to us, like those from decaying flesh and carrion. But there are also certain flowers, some orchids for instance, which give forth no very agreeable odour, but one which is to us repulsive and disgusting; and we should therefore expect that the males of such insects would give off a smell unpleasant to us, but there is no case known to me in which this has been demonstrated.

In cases such as we have discussed, it is obvious that there is no possible explanation except through selection. This brings us to the last kind of secondary sexual characters, and the one in regard to which doubt has been most frequently expressed,—decorative colours and decorative forms, the brilliant plumage of the male pheasant, the humming-birds, and the bird of Paradise, as well as the bright colours of many species of butterfly, from the beautiful blue of our little *Lycaenidae* to the magnificent azure of the large *Morphinae* of Brazil. In a great many cases, though not by any means in all, the male butterflies are "more beautiful" than the females, and in the Tropics in particular they shine and glow in the most superb colours. I really see no reason why we should doubt the power of sexual selection, and I myself stand wholly on Darwin's side. Even though we certainly cannot assume that the females exercise a conscious choice of the "handsomest" mate, and deliberate like the judges in a court of justice over the perfections of their wooers, we have no reason to doubt that distinctive forms (decorative feathers) and colours have a particularly exciting effect upon the female, just as certain odours have among animals of so many different groups, including the butterflies. The doubts which existed for a considerable time, as a result of fallacious experiments, as to whether the colours of flowers really had any influence in attracting butterflies have now been set at rest through a series of more careful investigations; we now know that the colours of flowers are there on account of the butterflies, as Sprengel first showed, and that the blossoms of *Phanerogams* are selected in relation to them, as Darwin pointed out.

Certainly it is not possible to bring forward any convincing proof of the origin of decorative colours through sexual selection, but there are many weighty arguments in favour of it, and these form a body of presumptive evidence so strong that it almost amounts to certainty.

In the first place, there is the analogy with other secondary sexual characters. If the song of birds and the chirping of the cricket have been evolved through sexual selection, if the penetrating odours of male animals,—the crocodile, the musk-deer, the beaver, the carnivores, and, finally, the flower-like fragrances of the butterflies have been evolved to their present pitch in this way, why should decorative

colours have arisen in some other way? Why should the eye be less sensitive to SPECIFICALLY MALE colours and other VISIBLE signs ENTICING TO THE FEMALE, than the olfactory sense to specifically male odours, or the sense of hearing to specifically male sounds? Moreover, the decorative feathers of birds are almost always spread out and displayed before the female during courtship. I have elsewhere ("The Evolution Theory", London, 1904, I. page 219.) pointed out that decorative colouring and sweet-scentedness may replace one another in Lepidoptera as well as in flowers, for just as some modestly coloured flowers (mignonette and violet) have often a strong perfume, while strikingly coloured ones are sometimes quite devoid of fragrance, so we find that the most beautiful and gaily-coloured of our native Lepidoptera, the species of Vanessa, have no scent-scales, while these are often markedly developed in grey nocturnal Lepidoptera. Both attractions may, however, be combined in butterflies, just as in flowers. Of course, we cannot explain why both means of attraction should exist in one genus, and only one of them in another, since we do not know the minutest details of the conditions of life of the genera concerned. But from the sporadic distribution of scent-scales in Lepidoptera, and from their occurrence or absence in nearly related species, we may conclude that fragrance is a relatively MODERN acquirement, more recent than brilliant colouring.

One thing in particular that stamps decorative colouring as a product of selection is ITS GRADUAL INTENSIFICATION by the addition of new spots, which we can quite well observe, because in many cases the colours have been first acquired by the males, and later transmitted to the females by inheritance. The scent-scales are never thus transmitted, probably for the same reason that the decorative colours of many birds are often not transmitted to the females: because with these they would be exposed to too great elimination by enemies. Wallace was the first to point out that in species with concealed nests the beautiful feathers of the male occurred in the female also, as in the parrots, for instance, but this is not the case in species which brood on an exposed nest. In the parrots one can often observe that the general brilliant colouring of the male is found in the female, but that certain spots of colour are absent, and these have probably been acquired comparatively recently by the male and have not yet been transmitted to the female.

Isolation of the group of individuals which is in process of varying is undoubtedly of great value in sexual selection, for even a solitary conspicuous variation will become dominant much sooner in a small isolated colony, than among a large number of members of a species.

Anyone who agrees with me in deriving variations from germinal selection will regard that process as an essential aid towards explaining the selection of distinctive courtship-characters, such as coloured spots, decorative feathers, horny outgrowths in birds and reptiles, combs, feather-tufts, and the like, since the beginnings of these would be presented with relative frequency in the struggle between the determinants within the germ-plasm. The process of transmission of decorative feathers to the female results, as Darwin pointed out and illustrated by interesting examples, in the COLOUR-TRANSFORMATION OF A WHOLE SPECIES, and this process, as the phyletically older colouring of young birds shows, must, in the course of thousands of years, have repeated itself several times in a line of descent.

If we survey the wealth of phenomena presented to us by secondary sexual characters, we can hardly fail to be convinced of the truth of the principle of sexual selection. And certainly no one who has accepted natural selection should reject sexual selection, for, not only do the two processes rest upon the same basis, but they merge into one another, so that it is often impossible to say how much of a particular character depends on one and how much on the other form of selection.

(b) NATURAL SELECTION.

An actual proof of the theory of sexual selection is out of the question, if only because we cannot tell when a variation attains to selection-value. It is certain that a delicate sense of smell is of value to the male moth in his search for the female, but whether the possession of one additional olfactory hair, or of ten, or of twenty additional hairs leads to the success of its possessor we are unable to tell. And we are groping even more in the dark when we discuss the excitement caused in the female by agreeable perfumes, or by striking and beautiful colours. That these do make an impression is beyond doubt; but we can only assume that slight intensifications of them give any advantage, and we MUST assume this SINCE OTHERWISE SECONDARY SEXUAL CHARACTERS REMAIN INEXPLICABLE.

The same thing is true in regard to natural selection. It is not possible to bring forward any actual proof of the selection-value of the initial stages, and the stages in the increase of variations, as has been already shown. But the selection-value of a finished adaptation can in many cases be statistically determined. Cesnola and Poulton have made valuable experiments in this direction. The former attached forty-five individuals of the green, and sixty-five of the brown variety of the praying mantis (*Mantis religiosa*), by a silk thread to plants, and watched them for seventeen days. The insects which were on a surface of a colour similar to their own remained uneaten, while twenty-five green insects on brown parts of plants had all disappeared in eleven days.

The experiments of Poulton and Sanders ("Report of the British Association" (Bristol, 1898), London, 1899, pages 906-909.) were made with 600 pupae of *Vanessa urticae*, the "tortoise-shell butterfly." The pupae were artificially attached to nettles, tree-trunks, fences, walls, and to the ground, some at Oxford, some at St Helens in the Isle of Wight. In the course of a month 93 per cent of the pupae at Oxford were killed, chiefly by small birds, while at St Helens 68 per cent perished. The experiments showed very clearly that the colour and character of the surface on which the pupa rests—and thus its own conspicuousness—are of the greatest importance. At Oxford only the four pupae which were fastened to nettles emerged; all the rest—on bark, stones and the like—perished. At St Helens the elimination was as follows: on fences where the pupae were conspicuous, 92 per cent; on bark, 66 per cent; on walls, 54 per cent; and among nettles, 57 per cent. These interesting experiments confirm our views as to protective coloration, and show further, THAT THE RATIO OF ELIMINATION IN THE SPECIES IS A VERY HIGH ONE, AND THAT THEREFORE SELECTION MUST BE VERY KEEN.

We may say that the process of selection follows as a logical necessity from the fulfilment of the three preliminary postulates of the theory: variability, heredity, and the struggle for existence, with its enormous ratio of elimination in all species. To this we must add a fourth factor, the INTENSIFICATION of variations which Darwin established as a fact, and which we are now able to account for theoretically on the basis of germinal selection. It may be objected that there is considerable uncertainty about this LOGICAL proof, because of our inability to demonstrate the selection-value of the initial stages and the individual stages of increase. We have therefore to fall back on PRESUMPTIVE EVIDENCE. This is to be found in THE INTERPRETATIVE VALUE OF THE THEORY. Let us consider this point in greater detail.

In the first place, it is necessary to emphasise what is often overlooked, namely, that the theory not only explains the TRANSFORMATIONS of species, it also explains THEIR REMAINING THE SAME; in addition to the principle of varying, it contains within itself that of PERSISTING. It is part of the essence of selection, that it not only causes a part to VARY till it has reached its highest pitch of adaptation, but that it MAINTAINS IT AT THIS PITCH. THIS CONSERVING INFLUENCE OF NATURAL SELECTION is of great importance, and was early recognised by Darwin; it follows naturally from the principle of the survival of the fittest.

We understand from this how it is that a species which has become fully adapted to certain conditions of life ceases to vary, but remains "constant," as long as the conditions of life FOR IT remain unchanged, whether this be for thousands of years, or for whole geological epochs. But the most convincing proof of the power of the principle of selection lies in the innumerable multitude of phenomena which cannot be explained in any other way. To this category belong all structures which are only PASSIVELY of advantage to the organism, because none of these can have arisen by the alleged LAMARCKIAN PRINCIPLE. These have been so often discussed that we need do no more than indicate them here. Until quite recently the sympathetic coloration of animals—for instance, the whiteness of Arctic animals—was referred, at least in part, to the DIRECT influence of external factors, but the facts can best be explained by referring them to the processes of selection, for then it is unnecessary to make the gratuitous assumption that many species are sensitive to the stimulus of cold and that others are not. The great majority of Arctic land-animals, mammals and birds, are white, and this proves that they were all able to present the variation which was most useful for them. The sable is brown, but it lives in trees, where the brown colouring protects and conceals it more effectively. The musk-sheep (*Ovibos moschatus*) is also brown, and contrasts sharply with the ice and snow, but it is protected from beasts of prey by its gregarious habit, and therefore it is of advantage to be visible from

as great a distance as possible. That so many species have been able to give rise to white varieties does not depend on a special sensitiveness of the skin to the influence of cold, but to the fact that Mammals and Birds have a general tendency to vary towards white. Even with us, many birds—starlings, blackbirds, swallows, etc.—occasionally produce white individuals, but the white variety does not persist, because it readily falls a victim to the carnivores. This is true of white fawns, foxes, deer, etc. The whiteness, therefore, arises from internal causes, and only persists when it is useful. A great many animals living in a GREEN ENVIRONMENT have become clothed in green, especially insects, caterpillars, and Mantidae, both persecuted and persecutors.

That it is not the direct effect of the environment which calls forth the green colour is shown by the many kinds of caterpillar which rest on leaves and feed on them, but are nevertheless brown. These feed by night and betake themselves through the day to the trunk of the tree, and hide in the furrows of the bark. We cannot, however, conclude from this that they were UNABLE to vary towards green, for there are Arctic animals which are white only in winter and brown in summer (Alpine hare, and the ptarmigan of the Alps), and there are also green leaf-insects which remain green only while they are young and difficult to see on the leaf, but which become brown again in the last stage of larval life, when they have outgrown the leaf. They then conceal themselves by day, sometimes only among withered leaves on the ground, sometimes in the earth itself. It is interesting that in one genus, *Chaerocampa*, one species is brown in the last stage of larval life, another becomes brown earlier, and in many species the last stage is not wholly brown, a part remaining green. Whether this is a case of a double adaptation, or whether the green is being gradually crowded out by the brown, the fact remains that the same species, even the same individual, can exhibit both variations. The case is the same with many of the leaf-like Orthoptera, as, for instance, the praying mantis (*Mantis religiosa*) which we have already mentioned.

But the best proofs are furnished by those often-cited cases in which the insect bears a deceptive resemblance to another object. We now know many such cases, such as the numerous imitations of green or withered leaves, which are brought about in the most diverse ways, sometimes by mere variations in the form of the insect and in its colour, sometimes by an elaborate marking, like that which occurs in the Indian leaf-butterflies, *Kallima inachis*. In the single butterfly-genus *Anaea*, in the woods of South America, there are about a hundred species which are all gaily coloured on the upper surface, and on the reverse side exhibit the most delicate imitation of the colouring and pattern of a leaf, generally without any indication of the leaf-ribs, but extremely deceptive nevertheless. Anyone who has seen only one such butterfly may doubt whether many of the insignificant details of the marking can really be of advantage to the insect. Such details are for instance the apparent holes and splits in the apparently dry or half-rotten leaf, which are usually due to the fact that the scales are absent on a circular or oval patch so that the colourless wing-membrane lies bare, and one can look through the spot as through a window. Whether the bird which is seeking or pursuing the butterflies takes these holes for dewdrops, or for the work of a devouring insect, does not affect the question; the mirror-like spot undoubtedly increases the general deceptiveness, for the same thing occurs in many leaf-butterflies, though not in all, and in some cases it is replaced in quite a peculiar manner. In one species of *Anaea* (*A. divina*), the resting butterfly looks exactly like a leaf out of the outer edge of which a large semicircular piece has been eaten, possibly by a caterpillar; but if we look more closely it is obvious that there is no part of the wing absent, and that the semicircular piece is of a clear, pale yellow colour, while the rest of the wing is of a strongly contrasted dark brown.

But the deceptive resemblance may be caused in quite a different manner. I have often speculated as to what advantage the brilliant white C could give to the otherwise dusky-coloured "Comma butterfly" (*Grapta C. album*). Poulton's recent observations ("Proc. Ent. Soc"., London, May 6, 1903.) have shown that this represents the imitation of a crack such as is often seen in dry leaves, and is very conspicuous because the light shines through it.

The utility obviously lies in presenting to the bird the very familiar picture of a broken leaf with a clear shining slit, and we may conclude, from the imitation of such small details, that the birds are very sharp observers and that the smallest deviation from the usual arrests their attention and incites them to closer investigation. It is obvious that such detailed—we might almost say such subtle—deceptive

resemblances could only have come about in the course of long ages through the acquirement from time to time of something new which heightened the already existing resemblance.

In face of facts like these there can be no question of chance, and no one has succeeded so far in finding any other explanation to replace that by selection. For the rest, the apparent leaves are by no means perfect copies of a leaf; many of them only represent the torn or broken piece, or the half or two-thirds of a leaf, but then the leaves themselves frequently do not present themselves to the eye as a whole, but partially concealed among other leaves. Even those butterflies which, like the species of *Kallima* and *Anaea*, represent the whole of a leaf with stalk, ribs, apex, and the whole breadth, are not actual copies which would satisfy a botanist; there is often much wanting. In *Kallima* the lateral ribs of the leaf are never all included in the markings; there are only two or three on the left side and at most four or five on the right, and in many individuals these are rather obscure, while in others they are comparatively distinct. This furnishes us with fresh evidence in favour of their origin through processes of selection, for a botanically perfect picture could not arise in this way; there could only be a fixing of such details as heightened the deceptive resemblance.

Our postulate of origin through selection also enables us to understand why the leaf-imitation is on the lower surface of the wing in the diurnal *Lepidoptera*, and on the upper surface in the nocturnal forms, corresponding to the attitude of the wings in the resting position of the two groups.

The strongest of all proofs of the theory, however, is afforded by cases of true "mimicry," those adaptations discovered by Bates in 1861, consisting in the imitation of one species by another, which becomes more and more like its model. The model is always a species that enjoys some special protection from enemies, whether because it is unpleasant to taste, or because it is in some way dangerous.

It is chiefly among insects and especially among butterflies that we find the greatest number of such cases. Several of these have been minutely studied, and every detail has been investigated, so that it is difficult to understand how there can still be disbelief in regard to them. If the many and exact observations which have been carefully collected and critically discussed, for instance by Poulton ("*Essays on Evolution*", 1889-1907, Oxford, 1908, *passim*, e.g. page 269.) were thoroughly studied, the arguments which are still frequently urged against mimicry would be found untenable; we can hardly hope to find more convincing proof of the actuality of the processes of selection than these cases put into our hands. The preliminary postulates of the theory of mimicry have been disputed, for instance, that diurnal butterflies are persecuted and eaten by birds, but observations specially directed towards this point in India, Africa, America and Europe have placed it beyond all doubt. If it were necessary I could myself furnish an account of my own observations on this point.

In the same way it has been established by experiment and observation in the field that in all the great regions of distribution there are butterflies which are rejected by birds and lizards, their chief enemies, on account of their unpleasant smell or taste. These butterflies are usually gaily and conspicuously coloured and thus—as Wallace first interpreted it—are furnished with an easily recognisable sign: a sign of unpalatableness or WARNING COLOURS. If they were not thus recognisable easily and from a distance, they would frequently be pecked at by birds, and then rejected because of their unpleasant taste; but as it is, the insect-eaters recognise them at once as unpalatable booty and ignore them. Such IMMUNE (The expression does not refer to all the enemies of this butterfly; against ichneumon-flies, for instance, their unpleasant smell usually gives no protection.) species, wherever they occur, are imitated by other palatable species, which thus acquire a certain degree of protection.

It is true that this explanation of the bright, conspicuous colours is only a hypothesis, but its foundations,—unpalatableness, and the liability of other butterflies to be eaten,—are certain, and its consequences—the existence of mimetic palatable forms—confirm it in the most convincing manner. Of the many cases now known I select one, which is especially remarkable, and which has been thoroughly investigated, *Papilio dardanus* (merope), a large, beautiful, diurnal butterfly which ranges from Abyssinia throughout the whole of Africa to the south coast of Cape Colony.

The males of this form are everywhere ALMOST the same in colour and in form of wings, save for a few variations in the sparse black markings on the pale yellow ground. But the females occur in several

quite different forms and colourings, and one of these only, the Abyssinian form, is like the male, while the other three or four are MIMETIC, that is to say, they copy a butterfly of quite a different family the Danaids, which are among the IMMUNE forms. In each region the females have thus copied two or three different immune species. There is much that is interesting to be said in regard to these species, but it would be out of keeping with the general tenor of this paper to give details of this very complicated case of polymorphism in *P. dardanus*. Anyone who is interested in the matter will find a full and exact statement of the case in as far as we know it, in Poulton's "Essays on Evolution" (pages 373-375). (Professor Poulton has corrected some wrong descriptions which I had unfortunately overlooked in the Plates of my book "Vortrage uber Descendenztheorie", and which refer to *Papilio dardanus* (merope). These mistakes are of no importance as far as and understanding of the mimicry-theory is concerned, but I hope shortly to be able to correct them in a later edition.) I need only add that three different mimetic female forms have been reared from the eggs of a single female in South Africa. The resemblance of these forms to their immune models goes so far that even the details of the LOCAL forms of the models are copied by the mimetic species.

It remains to be said that in Madagascar a butterfly, *Papilio meriones*, occurs, of which both sexes are very similar in form and markings to the non-mimetic male of *P. dardanus*, so that it probably represents the ancestor of this latter species.

In face of such facts as these every attempt at another explanation must fail. Similarly all the other details of the case fulfil the preliminary postulates of selection, and leave no room for any other interpretation. That the males do not take on the protective colouring is easily explained, because they are in general more numerous, and the females are more important for the preservation of the species, and must also live longer in order to deposit their eggs. We find the same state of things in many other species, and in one case (*Elymnias undularis*) in which the male is also mimetically coloured, it copies quite a differently coloured immune species from the model followed by the female. This is quite intelligible when we consider that if there were TOO MANY false immune types, the birds would soon discover that there were palatable individuals among those with unpalatable warning colours. Hence the imitation of different immune species by *Papilio dardanus*!

I regret that lack of space prevents my bringing forward more examples of mimicry and discussing them fully. But from the case of *Papilio dardanus* alone there is much to be learnt which is of the highest importance for our understanding of transformations. It shows us chiefly what I once called, somewhat strongly perhaps, THE OMNIPOTENCE OF NATURAL SELECTION in answer to an opponent who had spoken of its "inadequacy." We here see that one and the same species is capable of producing four or five different patterns of colouring and marking; thus the colouring and marking are not, as has often been supposed, a necessary outcome of the specific nature of the species, but a true adaptation, which cannot arise as a direct effect of climatic conditions, but solely through what I may call the sorting out of the variations produced by the species, according to their utility. That caterpillars may be either green or brown is already something more than could have been expected according to the old conception of species, but that one and the same butterfly should be now pale yellow, with black; now red with black and pure white; now deep black with large, pure white spots; and again black with a large ochreous-yellow spot, and many small white and yellow spots; that in one sub-species it may be tailed like the ancestral form, and in another tailless like its Danaid model,—all this shows a far-reaching capacity for variation and adaptation that wide never have expected if we did not see the facts before us. How it is possible that the primary colour-variations should thus be intensified and combined remains a puzzle even now; we are reminded of the modern three-colour printing,—perhaps similar combinations of the primary colours take place in this case; in any case the direction of these primary variations is determined by the artist whom we know as natural selection, for there is no other conceivable way in which the model could affect the butterfly that is becoming more and more like it. The same climate surrounds all four forms of female; they are subject to the same conditions of nutrition. Moreover, *Papilio dardanus* is by no means the only species of butterfly which exhibits different kinds of colour-pattern on its wings. Many species of the Asiatic genus *Elymnias* have on the upper surface a very good imitation of an immune Euploeine (Danainae), often with a steel-blue ground-colour, while the under surface is well concealed when the butterfly is at rest,—thus there are two kinds of protective coloration each with a different meaning! The same thing may be observed in

many non-mimetic butterflies, for instance in all our species of *Vanessa*, in which the under side shows a grey-brown or brownish-black protective coloration, but we do not yet know with certainty what may be the biological significance of the gaily coloured upper surface.

In general it may be said that mimetic butterflies are comparatively rare species, but there are exceptions, for instance *Limenitis archippus* in North America, of which the immune model (*Danaida plexippus*) also occurs in enormous numbers.

In another mimicry-category the imitators are often more numerous than the models, namely in the case of the imitation of DANGEROUS INSECTS by harmless species. Bees and wasps are dreaded for their sting, and they are copied by harmless flies of the genera *Eristalis* and *Syrphus*, and these mimics often occur in swarms about flowering plants without damage to themselves or to their models; they are feared and are therefore left unmolested.

In regard also to the FAITHFULNESS OF THE COPY the facts are quite in harmony with the theory, according to which the resemblance must have arisen and increased BY DEGREES. We can recognise this in many cases, for even now the mimetic species show very VARYING DEGREES OF RESEMBLANCE to their immune model. If we compare, for instance, the many different imitators of *Danaida chrysippus* we find that, with their brownish-yellow ground-colour, and the position and size, and more or less sharp limitation of their clear marginal spots, they have reached very different degrees of nearness to their model. Or compare the female of *Elymnias undularis* with its model *Danaida genutia*; there is a general resemblance, but the marking of the *Danaida* is very roughly imitated in *Elymnias*.

Another fact that bears out the theory of mimicry is, that even when the resemblance in colour-pattern is very great, the WING-VENATION, which is so constant, and so important in determining the systematic position of butterflies, is never affected by the variation. The pursuers of the butterfly have no time to trouble about entomological intricacies.

I must not pass over a discovery of Poulton's which is of great theoretical importance—that mimetic butterflies may reach the same effect by very different means. ("Journ. Linn. Soc. London (Zool.)", Vol. XXVI. 1898, pages 598-602.) Thus the glass-like transparency of the wing of a certain *Ithomiine* (*Methona*) and its Pierine mimic (*Dismorphia orise*) depends on a diminution in the size of the scales; in the Danaine genus *Ituna* it is due to the fewness of the scales, and in a third imitator, a moth (*Castnia linus* var. *heliconoides*) the glass-like appearance of the wing is due neither to diminution nor to absence of scales, but to their absolute colourlessness and transparency, and to the fact that they stand upright. In another moth mimic (*Anthomyza*) the arrangement of the transparent scales is normal. Thus it is not some unknown external influence that has brought about the transparency of the wing in these five forms, as has sometimes been supposed. Nor is it a hypothetical INTERNAL evolutionary tendency, for all three vary in a different manner. The cause of this agreement can only lie in selection, which preserves and intensifies in each species the favourable variations that present themselves. The great faithfulness of the copy is astonishing in these cases, for it is not THE WHOLE wing which is transparent; certain markings are black in colour, and these contrast sharply with the glass-like ground. It is obvious that the pursuers of these butterflies must be very sharp-sighted, for otherwise the agreement between the species could never have been pushed so far. The less the enemies see and observe, the more defective must the imitation be, and if they had been blind, no visible resemblance between the species which required protection could ever have arisen.

A seemingly irreconcilable contradiction to the mimicry theory is presented in the following cases, which were known to Bates, who, however, never succeeded in bringing them into line with the principle of mimicry.

In South America there are, as we have already said, many mimics of the immune *Ithomiinae* (or as Bates called them *Heliconidae*). Among these there occur not merely species which are edible, and thus require the protection of a disguise, but others which are rejected on account of their unpalatableness. How could the *Ithomiine* dress have developed in their case, and of what use is it, since the species would in any case be immune? In Eastern Brazil, for instance, there are four butterflies, which bear a most confusing resemblance to one another in colour, marking, and form of wing, and all four are unpalatable to birds. They belong to four different genera and three sub-families, and we have to

inquire: Whence came this resemblance and what end does it serve? For a long time no satisfactory answer could be found, but Fritz Muller (In "Kosmos", 1879, page 100.), seventeen years after Bates, offered a solution to the riddle, when he pointed out that young birds could not have an instinctive knowledge of the unpalatableness of the Ithomiines, but must learn by experience which species were edible and which inedible. Thus each young bird must have tasted at least one individual of each inedible species and discovered its unpalatability, before it learnt to avoid, and thus to spare the species. But if the four species resemble each other very closely the bird will regard them all as of the same kind, and avoid them all. Thus there developed a process of selection which resulted in the survival of the Ithomiine-like individuals, and in so great an increase of resemblance between the four species, that they are difficult to distinguish one from another even in a collection. The advantage for the four species, living side by side as they do e.g. in Bahia, lies in the fact that only one individual from the MIMICRY-RING ("inedible association") need be tasted by a young bird, instead of at least four individuals, as would otherwise be the case. As the number of young birds is great, this makes a considerable difference in the ratio of elimination.

These interesting mimicry-rings (trusts), which have much significance for the theory, have been the subject of numerous and careful investigations, and at least their essential features are now fully established. Muller took for granted, without making any investigations, that young birds only learn by experience to distinguish between different kinds of victims. But Lloyd Morgan's ("Habit and Instinct", London, 1896.) experiments with young birds proved that this is really the case, and at the same time furnished an additional argument against the LAMARCKIAN PRINCIPLE.

In addition to the mimicry-rings first observed in South America, others have been described from Tropical India by Moore, and by Poulton and Dixey from Africa, and we may expect to learn many more interesting facts in this connection. Here again the preliminary postulates of the theory are satisfied. And how much more that would lead to the same conclusion might be added!

As in the case of mimicry many species have come to resemble one another through processes of selection, so we know whole classes of phenomena in which plants and animals have become adapted to one another, and have thus been modified to a considerable degree. I refer particularly to the relation between flowers and insects; but as there is an article on "The Biology of Flowers" in this volume, I need not discuss the subject, but will confine myself to pointing out the significance of these remarkable cases for the theory of selection. Darwin has shown that the originally inconspicuous blossoms of the phanerogams were transformed into flowers through the visits of insects, and that, conversely, several large orders of insects have been gradually modified by their association with flowers, especially as regards the parts of their body actively concerned. Bees and butterflies in particular have become what they are through their relation to flowers. In this case again all that is apparently contradictory to the theory can, on closer investigation, be beautifully interpreted in corroboration of it. Selection can give rise only to what is of use to the organism actually concerned, never to what is of use to some other organism, and we must therefore expect to find that in flowers only characters of use to THEMSELVES have arisen, never characters which are of use to insects only, and conversely that in the insects characters useful to them and not merely to the plants would have originated. For a long time it seemed as if an exception to this rule existed in the case of the fertilisation of the yucca blossoms by a little moth, *Pronuba yuccasella*. This little moth has a sickle-shaped appendage to its mouth-parts which occurs in no other Lepidopteron, and which is used for pushing the yellow pollen into the opening of the pistil, thus fertilising the flower. Thus it appears as if a new structure, which is useful only to the plant, has arisen in the insect. But the difficulty is solved as soon as we learn that the moth lays its eggs in the fruit-buds of the Yucca, and that the larvae, when they emerge, feed on the developing seeds. In effecting the fertilisation of the flower the moth is at the same time making provision for its own offspring, since it is only after fertilisation that the seeds begin to develop. There is thus nothing to prevent our referring this structural adaptation in *Pronuba yuccasella* to processes of selection, which have gradually transformed the maxillary palps of the female into the sickle-shaped instrument for collecting the pollen, and which have at the same time developed in the insect the instinct to press the pollen into the pistil.

In this domain, then, the theory of selection finds nothing but corroboration, and it would be impossible to substitute for it any other explanation, which, now that the facts are so well known, could

be regarded as a serious rival to it. That selection is a factor, and a very powerful factor in the evolution of organisms, can no longer be doubted. Even although we cannot bring forward formal proofs of it IN DETAIL, cannot calculate definitely the size of the variations which present themselves, and their selection-value, cannot, in short, reduce the whole process to a mathematical formula, yet we must assume selection, because it is the only possible explanation applicable to whole classes of phenomena, and because, on the other hand, it is made up of factors which we know can be proved actually to exist, and which, IF they exist, must of logical necessity cooperate in the manner required by the theory. WE MUST ACCEPT IT BECAUSE THE PHENOMENA OF EVOLUTION AND ADAPTATION MUST HAVE A NATURAL BASIS, AND BECAUSE IT IS THE ONLY POSSIBLE EXPLANATION OF THEM. (This has been discussed in many of my earlier works. See for instance "The All-Sufficiency of Natural Selection, a reply to Herbert Spencer", London, 1893.)

Many people are willing to admit that selection explains adaptations, but they maintain that only a part of the phenomena are thus explained, because everything does not depend upon adaptation. They regard adaptation as, so to speak, a special effort on the part of Nature, which she keeps in readiness to meet particularly difficult claims of the external world on organisms. But if we look at the matter more carefully we shall find that adaptations are by no means exceptional, but that they are present everywhere in such enormous numbers, that it would be difficult in regard to any structure whatever, to prove that adaptation had NOT played a part in its evolution.

How often has the senseless objection been urged against selection that it can create nothing, it can only reject. It is true that it cannot create either the living substance or the variations of it; both must be given. But in rejecting one thing it preserves another, intensifies it, combines it, and in this way CREATES what is new. EVERYTHING in organisms depends on adaptation; that is to say, everything must be admitted through the narrow door of selection, otherwise it can take no part in the building up of the whole. But, it is asked, what of the direct effect of external conditions, temperature, nutrition, climate and the like? Undoubtedly these can give rise to variations, but they too must pass through the door of selection, and if they cannot do this they are rejected, eliminated from the constitution of the species.

It may, perhaps, be objected that such external influences are often of a compelling power, and that every animal MUST submit to them, and that thus selection has no choice and can neither select nor reject. There may be such cases; let us assume for instance that the effect of the cold of the Arctic regions was to make all the mammals become black; the result would be that they would all be eliminated by selection, and that no mammals would be able to live there at all. But in most cases a certain percentage of animals resists these strong influences, and thus selection secures a foothold on which to work, eliminating the unfavourable variation, and establishing a useful colouring, consistent with what is required for the maintenance of the species.

Everything depends upon adaptation! We have spoken much of adaptation in colouring, in connection with the examples brought into prominence by Darwin, because these are conspicuous, easily verified, and at the same time convincing for the theory of selection. But is it only desert and polar animals whose colouring is determined through adaptation? Or the leaf-butterflies, and the mimetic species, or the terrifying markings, and "warning-colours" and a thousand other kinds of sympathetic colouring? It is, indeed, never the colouring alone which makes up the adaptation; the structure of the animal plays a part, often a very essential part, in the protective disguise, and thus MANY variations may cooperate towards ONE common end. And it is to be noted that it is by no means only external parts that are changed; internal parts are ALWAYS modified at the same time—for instance, the delicate elements of the nervous system on which depend the INSTINCT of the insect to hold its wings, when at rest, in a perfectly definite position, which, in the leaf-butterfly, has the effect of bringing the two pieces on which the marking occurs on the anterior and posterior wing into the same direction, and thus displaying as a whole the fine curve of the midrib on the seeming leaf. But the wing-holding instinct is not regulated in the same way in all leaf-butterflies; even our indigenous species of Vanessa, with their protective ground-colouring, have quite a distinctive way of holding their wings so that the greater part of the anterior wing is covered by the posterior when the butterfly is at rest. But the protective colouring appears on the posterior wing and on the tip of the anterior, TO PRECISELY THE DISTANCE TO WHICH IT IS LEFT UNCOVERED. This occurs, as Standfuss has shown, in different

degree in our two most nearly allied species, the uncovered portion being smaller in *V. urticae* than in *V. polychloros*. In this case, as in most leaf-butterflies, the holding of the wing was probably the primary character; only after that was thoroughly established did the protective marking develop. In any case, the instinctive manner of holding the wings is associated with the protective colouring, and must remain as it is if the latter is to be effective. How greatly instincts may change, that is to say, may be adapted, is shown by the case of the Noctuid "shark" moth, *Xylina vetusta*. This form bears a most deceptive resemblance to a piece of rotten wood, and the appearance is greatly increased by the modification of the innate impulse to flight common to so many animals, which has here been transformed into an almost contrary instinct. This moth does not fly away from danger, but "feigns death," that is, it draws antennae, legs and wings close to the body, and remains perfectly motionless. It may be touched, picked up, and thrown down again, and still it does not move. This remarkable instinct must surely have developed simultaneously with the wood-colouring; at all events, both cooperating variations are now present, and prove that both the external and the most minute internal structure have undergone a process of adaptation.

The case is the same with all structural variations of animal parts, which are not absolutely insignificant. When the insects acquired wings they must also have acquired the mechanism with which to move them—the musculature, and the nervous apparatus necessary for its automatic regulation. All instincts depend upon compound reflex mechanisms and are just as indispensable as the parts they have to set in motion, and all may have arisen through processes of selection if the reasons which I have elsewhere given for this view are correct. ("The Evolution Theory", London, 1904, page 144.)

Thus there is no lack of adaptations within the organism, and particularly in its most important and complicated parts, so that we may say that there is no actively functional organ that has not undergone a process of adaptation relative to its function and the requirements of the organism. Not only is every gland structurally adapted, down to the very minutest histological details, to its function, but the function is equally minutely adapted to the needs of the body. Every cell in the mucous lining of the intestine is exactly regulated in its relation to the different nutritive substances, and behaves in quite a different way towards the fats, and towards nitrogenous substances, or peptones.

I have elsewhere called attention to the many adaptations of the whale to the surrounding medium, and have pointed out—what has long been known, but is not universally admitted, even now—that in it a great number of important organs have been transformed in adaptation to the peculiar conditions of aquatic life, although the ancestors of the whale must have lived, like other hair-covered mammals, on land. I cited a number of these transformations—the fish-like form of the body, the hairlessness of the skin, the transformation of the fore-limbs to fins, the disappearance of the hind-limbs and the development of a tail fin, the layer of blubber under the skin, which affords the protection from cold necessary to a warm-blooded animal, the disappearance of the ear-muscles and the auditory passages, the displacement of the external nares to the forehead for the greater security of the breathing-hole during the brief appearance at the surface, and certain remarkable changes in the respiratory and circulatory organs which enable the animal to remain for a long time under water. I might have added many more, for the list of adaptations in the whale to aquatic life is by no means exhausted; they are found in the histological structure and in the minutest combinations in the nervous system. For it is obvious that a tail-fin must be used in quite a different way from a tail, which serves as a fly-brush in hoofed animals, or as an aid to springing in the kangaroo or as a climbing organ; it will require quite different reflex-mechanisms and nerve-combinations in the motor centres.

I used this example in order to show how unnecessary it is to assume a special internal evolutionary power for the phylogenesis of species, for this whole order of whales is, so to speak, MADE UP OF ADAPTATIONS; it deviates in many essential respects from the usual mammalian type, and all the deviations are adaptations to aquatic life. But if precisely the most essential features of the organisation thus depend upon adaptation, what is left for a phyletic force to do, since it is these essential features of the structure it would have to determine? There are few people now who believe in a phyletic evolutionary power, which is not made up of the forces known to us—adaptation and heredity—but the conviction that EVERY part of an organism depends upon adaptation has not yet gained a firm footing. Nevertheless, I must continue to regard this conception as the correct one, as I have long done.

I may be permitted one more example. The feather of a bird is a marvellous structure, and no one will deny that as a whole it depends upon adaptation. But what part of it DOES NOT depend upon adaptation? The hollow quill, the shaft with its hard, thin, light cortex, and the spongy substance within it, its square section compared with the round section of the quill, the flat barbs, their short, hooked barbules which, in the flight-feathers, hook into one another with just sufficient firmness to resist the pressure of the air at each wing-beat, the lightness and firmness of the whole apparatus, the elasticity of the vane, and so on. And yet all this belongs to an organ which is only passively functional, and therefore can have nothing to do with the LAMARCKIAN PRINCIPLE. Nor can the feather have arisen through some magical effect of temperature, moisture, electricity, or specific nutrition, and thus selection is again our only anchor of safety.

But—it will be objected—the substance of which the feather consists, this peculiar kind of horny substance, did not first arise through selection in the course of the evolution of the birds, for it formed the covering of the scales of their reptilian ancestors. It is quite true that a similar substance covered the scales of the Reptiles, but why should it not have arisen among them through selection? Or in what other way could it have arisen, since scales are also passively useful parts? It is true that if we are only to call adaptation what has been acquired by the species we happen to be considering, there would remain a great deal that could not be referred to selection; but we are postulating an evolution which has stretched back through aeons, and in the course of which innumerable adaptations took place, which had not merely ephemeral persistence in a genus, a family or a class, but which was continued into whole Phyla of animals, with continual fresh adaptations to the special conditions of each species, family, or class, yet with persistence of the fundamental elements. Thus the feather, once acquired, persisted in all birds, and the vertebral column, once gained by adaptation in the lowest forms, has persisted in all the Vertebrates, from *Amphioxus* upwards, although with constant readaptation to the conditions of each particular group. Thus everything we can see in animals is adaptation, whether of to-day, or of yesterday, or of ages long gone by; every kind of cell, whether glandular, muscular, nervous, epidermic, or skeletal, is adapted to absolutely definite and specific functions, and every organ which is composed of these different kinds of cells contains them in the proper proportions, and in the particular arrangement which best serves the function of the organ; it is thus adapted to its function.

All parts of the organism are tuned to one another, that is, THEY ARE ADAPTED TO ONE ANOTHER, and in the same way THE ORGANISM AS A WHOLE IS ADAPTED TO THE CONDITIONS OF ITS LIFE, AND IT IS SO AT EVERY STAGE OF ITS EVOLUTION.

But all adaptations CAN be referred to selection; the only point that remains doubtful is whether they all MUST be referred to it.

However that may be, whether the LAMARCKIAN PRINCIPLE is a factor that has cooperated with selection in evolution, or whether it is altogether fallacious, the fact remains, that selection is the cause of a great part of the phyletic evolution of organisms on our earth. Those who agree with me in rejecting the LAMARCKIAN PRINCIPLE will regard selection as the only GUIDING factor in evolution, which creates what is new out of the transmissible variations, by ordering and arranging these, selecting them in relation to their number and size, as the architect does his building-stones so that a particular style must result. ("Variation under Domestication", 1875 II. pages 426, 427.) But the building-stones themselves, the variations, have their basis in the influences which cause variation in those vital units which are handed on from one generation to another, whether, taken together they form the WHOLE organism, as in Bacteria and other low forms of life, or only a germ-substance, as in unicellular and multicellular organisms. (The Author and Editor are indebted to Professor Poulton for kindly assisting in the revision of the proof of this Essay.)

IV. VARIATION. By HUGO DE VRIES.

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I. DIFFERENT KINDS OF VARIABILITY.

Before Darwin, little was known concerning the phenomena of variability. The fact, that hardly two leaves on a tree were exactly the same, could not escape observation: small deviations of the same kind were met with everywhere, among individuals as well as among the organs of the same plant. Larger aberrations, spoken of as monstrosities, were for a long time regarded as lying outside the range of ordinary phenomena. A special branch of inquiry, that of Teratology, was devoted to them, but it constituted a science by itself, sometimes connected with morphology, but having scarcely any bearing on the processes of evolution and heredity.

Darwin was the first to take a broad survey of the whole range of variations in the animal and vegetable kingdoms. His theory of Natural Selection is based on the fact of variability. In order that this foundation should be as strong as possible he collected all the facts, scattered in the literature of his time, and tried to arrange them in a scientific way. He succeeded in showing that variations may be grouped along a line of almost continuous gradations, beginning with simple differences in size and ending with monstrosities. He was struck by the fact that, as a rule, the smaller the deviations, the more frequently they appear, very abrupt breaks in characters being of rare occurrence.

Among these numerous degrees of variability Darwin was always on the look out for those which might, with the greatest probability, be considered as affording material for natural selection to act upon in the development of new species. Neither of the extremes complied with his conceptions. He often pointed out, that there are a good many small fluctuations, which in this respect must be absolutely useless. On the other hand, he strongly combated the belief, that great changes would be necessary to explain the origin of species. Some authors had propounded the idea that highly adapted organs, e.g. the wings of a bird, could not have been developed in any other way than by a comparatively sudden modification of a well defined and important kind. Such a conception would allow of great breaks or discontinuity in the evolution of highly differentiated animals and plants, shortening the time for the evolution of the whole organic kingdom and getting over numerous difficulties inherent in the theory of slow and gradual progress. It would, moreover, account for the genetic relation of the larger groups of both animals and plants. It would, in a word, undoubtedly afford an easy means of simplifying the problem of descent with modification.

Darwin, however, considered such hypotheses as hardly belonging to the domain of science; they belong, he said, to the realm of miracles. That species have a capacity for change is admitted by all evolutionists; but there is no need to invoke modifications other than those represented by ordinary variability. It is well known that in artificial selection this tendency to vary has given rise to numerous distinct races, and there is no reason for denying that it can do the same in nature, by the aid of natural selection. On both lines an advance may be expected with equal probability.

His main argument, however, is that the most striking and most highly adapted modifications may be acquired by successive variations. Each of these may be slight, and they may affect different organs, gradually adapting them to the same purpose. The direction of the adaptations will be determined by the needs in the struggle for life, and natural selection will simply exclude all such changes as occur on opposite or deviating lines. In this way, it is not variability itself which is called upon to explain beautiful adaptations, but it is quite sufficient to suppose that natural selection has operated during long periods in the same way. Eventually, all the acquired characters, being transmitted together, would appear to us, as if they had all been simultaneously developed.

Correlations must play a large part in such special evolutions: when one part is modified, so will be other parts. The distribution of nourishment will come in as one of the causes, the reactions of different organs to the same external influences as another. But no doubt the more effective cause is that of the internal correlations, which, however, are still but dimly understood. Darwin repeatedly laid great stress on this view, although a definite proof of its correctness could not be given in his time. Such proof requires the direct observation of a mutation, and it should be stated here that even the first observations made in this direction have clearly confirmed Darwin's ideas. The new evening primroses which have sprung in my garden from the old form of *Oenothera Lamarckiana*, and which have

evidently been derived from it, in each case, by a single mutation, do not differ from their parent species in one character only, but in almost all their organs and qualities. *Oenothera gigas*, for example, has stouter stems and denser foliage; the leaves are larger and broader; its thick flower-buds produce gigantic flowers, but only small fruits with large seeds. Correlative changes of this kind are seen in all my new forms, and they lend support to the view that in the gradual development of highly adapted structures, analogous correlations may have played a large part. They easily explain large deviations from an original type, without requiring the assumption of too many steps.

Monstrosities, as their name implies, are widely different in character from natural species; they cannot, therefore, be adduced as evidence in the investigation of the origin of species. There is no doubt that they may have much in common as regards their manner of origin, and that the origin of species, once understood, may lead to a better understanding of the monstrosities. But the reverse is not true, at least not as regards the main lines of development. Here, it is clear, monstrosities cannot have played a part of any significance.

Reversions, or atavistic changes, would seem to give a better support to the theory of descent through modifications. These have been of paramount importance on many lines of evolution of the animal as well as of the vegetable kingdom. It is often assumed that monocotyledons are descended from some lower group of dicotyledons, probably allied to that which includes the buttercup family. On this view the monocotyledons must be assumed to have lost the cambium and all its influence on secondary growth, the differentiation of the flower into calyx and corolla, the second cotyledon or seed-leaf and several other characters. Losses of characters such as these may have been the result of abrupt changes, but this does not prove that the characters themselves have been produced with equal suddenness. On the contrary, Darwin shows very convincingly that a modification may well be developed by a series of steps, and afterwards suddenly disappear. Many monstrosities, such as those represented by twisted stems, furnish direct proofs in support of this view, since they are produced by the loss of one character and this loss implies secondary changes in a large number of other organs and qualities.

Darwin criticises in detail the hypothesis of great and abrupt changes and comes to the conclusion that it does not give even a shadow of an explanation of the origin of species. It is as improbable as it is unnecessary.

Sports and spontaneous variations must now be considered. It is well known that they have produced a large number of fine horticultural varieties. The cut-leaved maple and many other trees and shrubs with split leaves are known to have been produced at a single step; this is true in the case of the single-leaf strawberry plant and of the lacinate variety of the greater celandine: many white flowers, white or yellow berries and numerous other forms had a similar origin. But changes such as these do not come under the head of adaptations, as they consist for the most part in the loss of some quality or organ belonging to the species from which they were derived. Darwin thinks it impossible to attribute to this cause the innumerable structures, which are so well adapted to the habits of life of each species. At the present time we should say that such adaptations require progressive modifications, which are additions to the stock of qualities already possessed by the ancestors, and cannot, therefore, be explained on the ground of a supposed analogy with sports, which are for the most part of a retrogressive nature.

Excluding all these more or less sudden changes, there remains a long series of gradations of variability, but all of these are not assumed by Darwin to be equally fit for the production of new species. In the first place, he disregards all mere temporary variations, such as size, albinism, etc.; further, he points out that very many species have almost certainly been produced by steps, not greater, and probably not very much smaller, than those separating closely related varieties. For varieties are only small species. Next comes the question of polymorphic species: their occurrence seems to have been a source of much doubt and difficulty in Darwin's mind, although at present it forms one of the main supports of the prevailing explanation of the origin of new species. Darwin simply states that this kind of variability seems to be of a peculiar nature; since polymorphic species are now in a stable condition their occurrence gives no clue as to the mode of origin of new species. Polymorphic species are the expression of the result of previous variability acting on a large scale; but they now simply consist of more or less numerous elementary species, which, as far as we know, do not at present exhibit a larger degree of variability than any other more uniform species. The vernal whitlow-grass (*Draba verna*) and the wild pansy are the best known examples; both have spread over almost the whole

of Europe and are split up into hundreds of elementary forms. These sub-species show no signs of any extraordinary degree of variability, when cultivated under conditions necessary for the exclusion of inter-crossing. Hooker has shown, in the case of some ferns distributed over still wider areas, that the extinction of some of the intermediate forms in such groups would suffice to justify the elevation of the remaining types to the rank of distinct species. Polymorphic species may now be regarded as the link which unites ordinary variability with the historical production of species. But it does not appear that they had this significance for Darwin; and, in fact, they exhibit no phenomena which could explain the processes by which one species has been derived from another. By thus narrowing the limits of the species-producing variability Darwin was led to regard small deviations as the source from which natural selection derives material upon which to act. But even these are not all of the same type, and Darwin was well aware of the fact.

It should here be pointed out that in order to be selected, a change must first have been produced. This proposition, which now seems self-evident, has, however, been a source of much difference of opinion among Darwin's followers. The opinion that natural selection produces changes in useful directions has prevailed for a long time. In other words, it was assumed that natural selection, by the simple means of singling out, could induce small and useful changes to increase and to reach any desired degree of deviation from the original type. In my opinion this view was never actually held by Darwin. It is in contradiction with the acknowledged aim of all his work,—the explanation of the origin of species by means of natural forces and phenomena only. Natural selection acts as a sieve; it does not single out the best variations, but it simply destroys the larger number of those which are, from some cause or another, unfit for their present environment. In this way it keeps the strains up to the required standard, and, in special circumstances, may even improve them.

Returning to the variations which afford the material for the sieving-action of natural selection, we may distinguish two main kinds. It is true that the distinction between these was not clear at the time of Darwin, and that he was unable to draw a sharp line between them. Nevertheless, in many cases, he was able to separate them, and he often discussed the question which of the two would be the real source of the differentiation of species. Certain variations constantly occur, especially such as are connected with size, weight, colour, etc. They are usually too small for natural selection to act upon, having hardly any influence in the struggle for life: others are more rare, occurring only from time to time, perhaps once or twice in a century, perhaps even only once in a thousand years. Moreover, these are of another type, not simply affecting size, number or weight, but bringing about something new, which may be useful or not. Whenever the variation is useful natural selection will take hold of it and preserve it; in other cases the variation may either persist or disappear.

In his criticism of miscellaneous objections brought forward against the theory of natural selection after the publication of the first edition of "The Origin of Species", Darwin stated his view on this point very clearly:—"The doctrine of natural selection or the survival of the fittest, which implies that when variations or individual differences of a beneficial nature happen to arise, these will be preserved." ("Origin of Species" (6th edition), page 169, 1882.) In this sentence the words "HAPPEN TO ARISE" appear to me of prominent significance. They are evidently due to the same general conception which prevailed in Darwin's Pangenesis hypothesis. (Cf. de Vries, "Intracellulare Pangenesis", page 73, Jena, 1889, and "Die Mutationstheorie", I. page 63. Leipzig, 1901.)

A distinction is indicated between ordinary fluctuations which are always present, and such variations as "happen to arise" from time to time. ((I think it right to point out that the interpretation of this passage from the "Origin" by Professor de Vries is not accepted as correct either by Mr Francis Darwin or by myself. We do not believe that Darwin intended to draw any distinction between TWO TYPES of variation; the words "when variations or individual differences of a beneficial nature happen to arise" are not in our opinion meant to imply a distinction between ordinary fluctuations and variations which "happen to arise," but we believe that "or" is here used in the sense of ALIAS. With the permission of Professor de Vries, the following extract is quoted from a letter in which he replied to the objection raised to his reading of the passage in question:

"As to your remarks on the passage on page 6, I agree that it is now impossible to see clearly how far Darwin went in his distinction of the different kinds of variability. Distinctions were only dimly guessed at by him. But in our endeavour to arrive at a true conception of his view I think that the

chapter on Pangenesis should be our leading guide, and that we should try to interpret the more difficult passages by that chapter. A careful and often repeated study of the Pangenesis hypothesis has convinced me that Darwin, when he wrote that chapter, was well aware that ordinary variability has nothing to do with evolution, but that other kinds of variation were necessary. In some chapters he comes nearer to a clear distinction than in others. To my mind the expression 'happen to arise' is the sharpest indication of his inclining in this direction. I am quite convinced that numerous expressions in his book become much clearer when looked at in this way."

The statement in this passage that "Darwin was well aware that ordinary variability has nothing to do with evolution, but that other kinds of variation were necessary" is contradicted by many passages in the "Origin". A.C.S.)) The latter afford the material for natural selection to act upon on the broad lines of organic development, but the first do not. Fortuitous variations are the species-producing kind, which the theory requires; continuous fluctuations constitute, in this respect, a useless type.

Of late, the study of variability has returned to the recognition of this distinction. Darwin's variations, which from time to time happen to arise, are MUTATIONS, the opposite type being commonly designed fluctuations. A large mass of facts, collected during the last few decades, has confirmed this view, which in Darwin's time could only be expressed with much reserve, and everyone knows that Darwin was always very careful in statements of this kind.

From the same chapter I may here cite the following paragraph: "Thus as I am inclined to believe, morphological differences,... such as the arrangement of the leaves, the divisions of the flower or of the ovarium, the position of the ovules, etc.—first appeared in many cases as fluctuating variations, which sooner or later became constant through the nature of the organism and of the surrounding conditions... but NOT THROUGH NATURAL SELECTION (The italics are mine (H. de V.)); for as these morphological characters do not affect the welfare of the species, any slight deviation in them could not have been governed or accumulated through this latter agency." ("Origin of Species" (6th edition), page 176.) We thus see that in Darwin's opinion, all small variations had not the same importance. In favourable circumstances some could become constant, but others could not.

Since the appearance of the first edition of "The Origin of Species" fluctuating variability has been thoroughly studied by Quetelet. He discovered the law, which governs all phenomena of organic life falling under this head. It is a very simple law, and states that individual variations follow the laws of probability. He proved it, in the first place, for the size of the human body, using the measurements published for Belgian recruits; he then extended it to various other measurements of parts of the body, and finally concluded that it must be of universal validity for all organic beings. It must hold true for all characters in man, physical as well as intellectual and moral qualities; it must hold true for the plant kingdom as well as for the animal kingdom; in short, it must include the whole living world.

Quetelet's law may be most easily studied in those cases where the variability relates to measure, number and weight, and a vast number of facts have since confirmed its exactness and its validity for all kinds of organisms, organs and qualities. But if we examine it more closely, we find that it includes just those minute variations, which, as Darwin repeatedly pointed out, have often no significance for the origin of species. In the phenomena, described by Quetelet's law nothing "happens to arise"; all is governed by the common law, which states that small deviations from the mean type are frequent, but that larger aberrations are rare, the rarer as they are larger. Any degree of variation will be found to occur, if only the number of individuals studied is large enough: it is even possible to calculate before hand, how many specimens must be compared in order to find a previously fixed degree of deviation.

The variations, which from time to time happen to appear, are evidently not governed by this law. They cannot, as yet, be produced at will: no sowings of thousands or even of millions of plants will induce them, although by such means the chance of their occurring will obviously be increased. But they are known to occur, and to occur suddenly and abruptly. They have been observed especially in horticulture, where they are ranged in the large and ill-defined group called sports. Korschinsky has collected all the evidence which horticultural literature affords on this point. (S. Korschinsky, "Heterogenesis und Evolution", "Flora", Vol. LXXXIX. pages 240-363, 1901.) Several cases of the first appearance of a horticultural novelty have been recorded: this has always happened in the same way; it appeared suddenly and unexpectedly without any definite relation to previously existing variability. Dwarf types are one of the commonest and most favourite varieties of flowering plants; they are not

originated by a repeated selection of the smallest specimens, but appear at once, without intermediates and without any previous indication. In many instances they are only about half the height of the original type, thus constituting obvious novelties. So it is in other cases described by Korschinsky: these sports or mutations are now recognised to be the main source of varieties of horticultural plants.

As already stated, I do not pretend that the production of horticultural novelties is the prototype of the origin of new species in nature. I assume that they are, as a rule, derived from the parent species by the loss of some organ or quality, whereas the main lines of the evolution of the animal and vegetable kingdom are of course determined by progressive changes. Darwin himself has often pointed out this difference. But the saltatory origin of horticultural novelties is as yet the simplest parallel for natural mutations, since it relates to forms and phenomena, best known to the general student of evolution.

The point which I wish to insist upon is this. The difference between small and ever present fluctuations and rare and more sudden variations was clear to Darwin, although the facts known at his time were too meagre to enable a sharp line to be drawn between these two great classes of variability. Since Darwin's time evidence, which proves the correctness of his view, has accumulated with increasing rapidity. Fluctuations constitute one type; they are never absent and follow the law of chance, but they do not afford the material from which to build new species. Mutations, on the other hand, only happen to occur from time to time. They do not necessarily produce greater changes than fluctuations, but such as may become, or rather are from their very nature, constant. It is this constancy which is the mark of specific characters, and on this basis every new specific character may be assumed to have arisen by mutation.

Some authors have tried to show that the theory of mutation is opposed to Darwin's views. But this is erroneous. On the contrary, it is in fullest harmony with the great principle laid down by Darwin. In order to be acted upon by that complex of environmental forces, which Darwin has called natural selection, the changes must obviously first be there. The manner in which they are produced is of secondary importance and has hardly any bearing on the theory of descent with modification. ("Life and Letters" II. 125.)

A critical survey of all the facts of variability of plants in nature as well as under cultivation has led me to the conviction, that Darwin was right in stating that those rare beneficial variations, which from time to time happen to arise,—the now so-called mutations—are the real source of progress in the whole realm of the organic world.

II. EXTERNAL AND INTERNAL CAUSES OF VARIABILITY.

All phenomena of animal and plant life are governed by two sets of causes; one of these is external, the other internal. As a rule the internal causes determine the nature of a phenomenon—what an organism can do and what it cannot do. The external causes, on the other hand, decide when a certain variation will occur, and to what extent its features may be developed.

As a very clear and wholly typical instance I cite the cocks-combs (*Celosia*). This race is distinguished from allied forms by its faculty of producing the well-known broad and much twisted combs. Every single individual possesses this power, but all individuals do not exhibit it in its most complete form. In some cases this faculty may not be exhibited at the top of the main stem, although developed in lateral branches: in others it begins too late for full development. Much depends upon nourishment and cultivation, but almost always the horticulturist has to single out the best individuals and to reject those which do not come up to the standard.

The internal causes are of a historical nature. The external ones may be defined as nourishment and environment. In some cases nutrition is the main factor, as, for instance, in fluctuating variability, but in natural selection environment usually plays the larger part.

The internal or historical causes are constant during the life-time of a species, using the term species in its most limited sense, as designating the so-called elementary species or the units out of which the ordinary species are built up. These historical causes are simply the specific characters, since in the origin of a species one or more of these must have been changed, thus producing the characters of the new type. These changes must, of course, also be due partly to internal and partly to external causes.

In contrast to these changes of the internal causes, the ordinary variability which is exhibited during the life-time of a species is called fluctuating variability. The name mutations or mutating variability is

then given to the changes in the specific characters. It is desirable to consider these two main divisions of variability separately.

In the case of fluctuations the internal causes, as well as the external ones, are often apparent. The specific characters may be designated as the mean about which the observed forms vary. Almost every character may be developed to a greater or a less degree, but the variations of the single characters producing a small deviation from the mean are usually the commonest. The limits of these fluctuations may be called wide or narrow, according to the way we look at them, but in numerous cases the extreme on the favoured side hardly surpasses double the value of that on the other side. The degree of this development, for every individual and for every organ, is dependent mainly on nutrition. Better nourishment or an increased supply of food produces a higher development; only it is not always easy to determine which direction is the fuller and which is the poorer one. The differences among individuals grown from different seeds are described as examples of individual variability, but those which may be observed on the same plant, or on cuttings, bulbs or roots derived from one individual are referred to as cases of partial variability. Partial variability, therefore, determines the differences among the flowers, fruits, leaves or branches of one individual: in the main, it follows the same laws as individual variability, but the position of a branch on a plant also determines its strength, and the part it may take in the nourishment of the whole. Composite flowers and umbels therefore have, as a rule, fewer rays on weak branches than on the strong main ones. The number of carpels in the fruits of poppies becomes very small on the weak lateral branches, which are produced towards the autumn, as well as on crowded, and therefore on weakened individuals. Double flowers follow the same rule, and numerous other instances could easily be adduced.

Mutating variability occurs along three main lines. Either a character may disappear, or, as we now say, become latent; or a latent character may reappear, reproducing thereby a character which was once prominent in more or less remote ancestors. The third and most interesting case is that of the production of quite new characters which never existed in the ancestors. Upon this progressive mutability the main development of the animal and vegetable kingdom evidently depends. In contrast to this, the two other cases are called retrogressive and degressive mutability. In nature retrogressive mutability plays a large part; in agriculture and in horticulture it gives rise to numerous varieties, which have in the past been preserved, either on account of their usefulness or beauty, or simply as fancy-types. In fact the possession of numbers of varieties may be considered as the main character of domesticated animals and cultivated plants.

In the case of retrogressive and degressive mutability the internal cause is at once apparent, for it is this which causes the disappearance or reappearance of some character. With progressive mutations the case is not so simple, since the new character must first be produced and then displayed. These two processes are theoretically different, but they may occur together or after long intervals. The production of the new character I call premutation, and the displaying mutation. Both of course must have their external as well as their internal causes, as I have repeatedly pointed out in my work on the Mutation Theory. ("Die Mutationstheorie", 2 vols., Leipzig, 1901.)

It is probable that nutrition plays as important a part among the external causes of mutability as it does among those of fluctuating variability. Observations in support of this view, however, are too scanty to allow of a definite judgment. Darwin assumed an accumulative influence of external causes in the case of the production of new varieties or species. The accumulation might be limited to the life-time of a single individual, or embrace that of two or more generations. In the end a degree of instability in the equilibrium of one or more characters might be attained, great enough for a character to give way under a small shock produced by changed conditions of life. The character would then be thrown over from the old state of equilibrium into a new one.

Characters which happen to be in this state of unstable equilibrium are called mutable. They may be either latent or active, being in the former case derived from old active ones or produced as new ones (by the process, designated premutation). They may be inherited in this mutable condition during a long series of generations. I have shown that in the case of the evening primrose of Lamarck this state of mutability must have existed for at least half a century, for this species was introduced from Texas into England about the year 1860, and since then all the strains derived from its first distribution over the several countries of Europe show the same phenomena in producing new forms. The production of the

dwarf evening primrose, or *Oenothera nanella*, is assumed to be due to one of the factors, which determines the tall stature of the parent form, becoming latent; this would, therefore, afford an example of retrogressive mutation. Most of the other types of my new mutants, on the other hand, seem to be due to progressive mutability.

The external causes of this curious period of mutability are as yet wholly unknown and can hardly be guessed at, since the origin of the *Oenothera Lamarckiana* is veiled in mystery. The seeds, introduced into England about 1860, were said to have come from Texas, but whether from wild or from cultivated plants we do not know. Nor has the species been recorded as having been observed in the wild condition. This, however, is nothing peculiar. The European types of *Oenothera biennis* and *O. muricata* are in the same condition. The first is said to have been introduced from Virginia, and the second from Canada, but both probably from plants cultivated in the gardens of these countries. Whether the same elementary species are still growing on those spots is unknown, mainly because the different sub-species of the species mentioned have not been systematically studied and distinguished.

The origin of new species, which is in part the effect of mutability, is, however, due mainly to natural selection. Mutability provides the new characters and new elementary species. Natural selection, on the other hand, decides what is to live and what to die. Mutability seems to be free, and not restricted to previously determined lines. Selection, however, may take place along the same main lines in the course of long geological epochs, thus directing the development of large branches of the animal and vegetable kingdom. In natural selection it is evident that nutrition and environment are the main factors. But it is probable that, while nutrition may be one of the main causes of mutability, environment may play the chief part in the decisions ascribed to natural selection. Relations to neighbouring plants and to injurious or useful animals, have been considered the most important determining factors ever since the time when Darwin pointed out their prevailing influence.

From this discussion of the main causes of variability we may derive the proposition that the study of every phenomenon in the field of heredity, of variability, and of the origin of new species will have to be considered from two standpoints; on one hand we have the internal causes, on the other the external ones. Sometimes the first are more easily detected, in other cases the latter are more accessible to investigation. But the complete elucidation of any phenomenon of life must always combine the study of the influence of internal with that of external causes.

III. POLYMORPHIC VARIABILITY IN CEREALS.

One of the propositions of Darwin's theory of the struggle for life maintains that the largest amount of life can be supported on any area, by great diversification or divergence in the structure and constitution of its inhabitants. Every meadow and every forest affords a proof of this thesis. The numerical proportion of the different species of the flora is always changing according to external influences. Thus, in a given meadow, some species will flower abundantly in one year and then almost disappear, until, after a series of years, circumstances allow them again to multiply rapidly. Other species, which have taken their places, will then become rare. It follows from this principle, that notwithstanding the constantly changing conditions, a suitable selection from the constituents of a meadow will ensure a continued high production. But, although the principle is quite clear, artificial selection has, as yet, done very little towards reaching a really high standard.

The same holds good for cereals. In ordinary circumstances a field will give a greater yield, if the crop grown consists of a number of sufficiently differing types. Hence it happens that almost all older varieties of wheat are mixtures of more or less diverging forms. In the same variety the numerical composition will vary from year to year, and in oats this may, in bad years, go so far as to destroy more than half of the harvest, the wind-oats (*Avena fatua*), which scatter their grain to the winds as soon as it ripens, increasing so rapidly that they assume the dominant place. A severe winter, a cold spring and other extreme conditions of life will destroy one form more completely than another, and it is evident that great changes in the numerical composition of the mixture may thus be brought about.

This mixed condition of the common varieties of cereals was well known to Darwin. For him it constituted one of the many types of variability. It is of that peculiar nature to which, in describing other groups, he applies the term polymorphy. It does not imply that the single constituents of the varieties are at present really changing their characters. On the other hand, it does not exclude the

possibility of such changes. It simply states that observation shows the existence of different forms; how these have originated is a question which it does not deal with. In his well-known discussion of the variability of cereals, Darwin is mainly concerned with the question, whether under cultivation they have undergone great changes or only small ones. The decision ultimately depends on the question, how many forms have originally been taken into cultivation. Assuming five or six initial species, the variability must be assumed to have been very large, but on the assumption that there were between ten and fifteen types, the necessary range of variability is obviously much smaller. But in regard to this point, we are of course entirely without historical data.

Few of the varieties of wheat show conspicuous differences, although their number is great. If we compare the differentiating characters of the smaller types of cereals with those of ordinary wild species, even within the same genus or family, they are obviously much less marked. All these small characters, however, are strictly inherited, and this fact makes it very probable that the less obvious constituents of the mixtures in ordinary fields must be constant and pure as long as they do not intercross. Natural crossing is in most cereals a phenomenon of rare occurrence, common enough to admit of the production of all possible hybrid combinations, but requiring the lapse of a long series of years to reach its full effect.

Darwin laid great stress on this high amount of variability in the plants of the same variety, and illustrated it by the experience of Colonel Le Couteur ("On the Varieties, Properties, and Classification of Wheat", Jersey, 1837.) on his farm on the isle of Jersey, who cultivated upwards of 150 varieties of wheat, which he claimed were as pure as those of any other agriculturalist. But Professor La Gasca of Madrid, who visited him, drew attention to aberrant ears, and pointed out, that some of them might be better yielders than the majority of plants in the crop, whilst others might be poor types. Thence he concluded that the isolation of the better ones might be a means of increasing his crops. Le Couteur seems to have considered the constancy of such smaller types after isolation as absolutely probable, since he did not even discuss the possibility of their being variable or of their yielding a changeable or mixed progeny. This curious fact proves that he considered the types, discovered in his fields by La Gasca to be of the same kind as his other varieties, which until that time he had relied upon as being pure and uniform. Thus we see, that for him, the variability of cereals was what we now call polymorphy. He looked through his fields for useful aberrations, and collected twenty-three new types of wheat. He was, moreover, clear about one point, which, on being rediscovered after half a century, has become the starting-point for the new Swedish principle of selecting agricultural plants. It was the principle of single-ear sowing, instead of mixing the grains of all the selected ears together. By sowing each ear on a separate plot he intended not only to multiply them, but also to compare their value. This comparison ultimately led him to the choice of some few valuable sorts, one of which, the "Bellevue de Talavera," still holds its place among the prominent sorts of wheat cultivated in France. This variety seems to be really a uniform type, a quality very useful under favourable conditions of cultivation, but which seems to have destroyed its capacity for further improvement by selection.

The principle of single-ear sowing, with a view to obtain pure and uniform strains without further selection, has, until a few years ago, been almost entirely lost sight of. Only a very few agriculturists have applied it: among these are Patrick Shirreff ("Die Verbesserung der Getreide-Arten", translated by R. Hesse, Halle, 1880.) in Scotland and Willet M. Hays ("Wheat, varieties, breeding, cultivation", Univ. Minnesota, Agricultural Experimental Station, Bull. no. 62, 1899.) in Minnesota. Patrick Shirreff observed the fact, that in large fields of cereals, single plants may from time to time be found with larger ears, which justify the expectation of a far greater yield. In the course of about twenty-five years he isolated in this way two varieties of wheat and two of oats. He simply multiplied them as fast as possible, without any selection, and put them on the market.

Hays was struck by the fact that the yield of wheat in Minnesota was far beneath that in the neighbouring States. The local varieties were Fife and Blue Stem. They gave him, on inspection, some better specimens, "phenomenal yielders" as he called them. These were simply isolated and propagated, and, after comparison with the parent-variety and with some other selected strains of less value, were judged to be of sufficient importance to be tested by cultivation all over the State of Minnesota. They have since almost supplanted the original types, at least in most parts of the State, with the result that the total yield of wheat in Minnesota is said to have been increased by about a million dollars yearly.

Definite progress in the method of single-ear sowing has, however, been made only recently. It had been foreshadowed by Patrick Shirreff, who after the production of the four varieties already mentioned, tried to carry out his work on a larger scale, by including numerous minor deviations from the main type. He found by doing so that the chances of obtaining a better form were sufficiently increased to justify the trial. But it was Nilsson who discovered the almost inexhaustible polymorphy of cereals and other agricultural crops and made it the starting-point for a new and entirely trustworthy method of the highest utility. By this means he has produced during the last fifteen years a number of new and valuable races, which have already supplanted the old types on numerous farms in Sweden and which are now being introduced on a large scale into Germany and other European countries.

It is now twenty years since the station at Svalof was founded. During the first period of its work, embracing about five years, selection was practised on the principle which was then generally used in Germany. In order to improve a race a sample of the best ears was carefully selected from the best fields of the variety. These ears were considered as representatives of the type under cultivation, and it was assumed that by sowing their grains on a small plot a family could be obtained, which could afterwards be improved by a continuous selection. Differences between the collected ears were either not observed or disregarded. At Svalof this method of selection was practised on a far larger scale than on any German farm, and the result was, broadly speaking, the same. This may be stated in the following words: improvement in a few cases, failure in all the others. Some few varieties could be improved and yielded excellent new types, some of which have since been introduced into Swedish agriculture and are now prominent races in the southern and middle parts of the country. But the station had definite aims, and among them was the improvement of the Chevalier barley. This, in Middle Sweden, is a fine brewer's barley, but liable to failure during unfavourable summers on account of its slender stems. It was selected with a view of giving it stiffer stems, but in spite of all the care and work bestowed upon it no satisfactory result was obtained.

This experience, combined with a number of analogous failures, could not fail to throw doubt upon the whole method. It was evident that good results were only exceptions, and that in most cases the principle was not one that could be relied upon. The exceptions might be due to unknown causes, and not to the validity of the method; it became therefore of much more interest to search for the causes than to continue the work along these lines.

In the year 1892 a number of different varieties of cereals were cultivated on a large scale and a selection was again made from them. About two hundred samples of ears were chosen, each apparently constituting a different type. Their seeds were sown on separate plots and manured and treated as much as possible in the same manner. The plots were small and arranged in rows so as to facilitate the comparison of allied types. During the whole period of growth and during the ripening of the ears the plots were carefully studied and compared: they were harvested separately; ears and kernels were counted and weighed, and notes were made concerning layering, rust and other cereal pests.

The result of this experiment was, in the main, no distinct improvement. Nilsson was especially struck by the fact that the plots, which should represent distinct types, were far from uniform. Many of them were as multiform as the fields from which the parent-ears were taken. Others showed variability in a less degree, but in almost all of them it was clear that a pure race had not been obtained. The experiment was a fair one, inasmuch as it demonstrated the polymorphic variability of cereals beyond all doubt and in a degree hitherto unsuspected; but from the standpoint of the selectionist it was a failure. Fortunately there were, however, one or two exceptions. A few lots showed a perfect uniformity in regard to all the stalks and ears: these were small families. This fact suggested the idea that each might have been derived from a single ear. During the selection in the previous summer, Nilsson had tried to find as many ears as possible of each new type which he recognised in his fields. But the variability of his crops was so great, that he was rarely able to include more than two or three ears in the same group, and, in a few cases, he found only one representative of the supposed type. It might, therefore, be possible that those small uniform plots were the direct progeny of ears, the grains of which had not been mixed with those from other ears before sowing. Exact records had, of course, been kept of the chosen samples, and the number of ears had been noted in each case. It was, therefore, possible to answer the question and it was found that those plots alone were uniform on which the kernels of one single ear only had been sown. Nilsson concluded that the mixture of two or more ears in a single

sowing might be the cause of the lack of uniformity in the progeny. Apparently similar ears might be different in their progeny.

Once discovered, this fact was elevated to the rank of a leading principle and tested on as large a scale as possible. The fields were again carefully investigated and every single ear, which showed a distinct divergence from the main type in one character or another, was selected. A thousand samples were chosen, but this time each sample consisted of one ear only. Next year, the result corresponded to the expectation. Uniformity prevailed almost everywhere; only a few lots showed a discrepancy, which might be ascribed to the accidental selection of hybrid ears. It was now clear that the progeny of single ears was, as a rule, pure, whereas that of mixed ears was impure. The single-ear selection or single-ear sowing, which had fallen into discredit in Germany and elsewhere in Europe, was rediscovered. It proved to be the only trustworthy principle of selection. Once isolated, such single-parent races are constant from seed and remain true to their type. No further selection is needed; they have simply to be multiplied and their real value tested.

Patrick Shirreff, in his early experiments, Le Couteur, Hays and others had observed the rare occurrence of exceptionally good yielders and the value of their isolation to the agriculturist. The possibility of error in the choice of such striking specimens and the necessity of judging their value by their progeny were also known to these investigators, but they had not the slightest idea of all the possibilities suggested by their principle. Nilsson, who is a botanist as well as an agriculturist, discovered that, besides these exceptionably good yielders, every variety of a cereal consists of hundreds of different types, which find the best conditions for success when grown together, but which, after isolation, prove to be constant. Their preference for mixed growth is so definite, that once isolated, their claims on manure and treatment are found to be much higher than those of the original mixed variety. Moreover, the greatest care is necessary to enable them to retain their purity, and as soon as they are left to themselves they begin to deteriorate through accidental crosses and admixtures and rapidly return to the mixed condition.

Reverting now to Darwin's discussion of the variability of cereals, we may conclude that subsequent investigation has proved it to be exactly of the kind which he describes. The only difference is that in reality it reaches a degree, quite unexpected by Darwin and his contemporaries. But it is polymorphic variability in the strictest sense of the word. How the single constituents of a variety originate we do not see. We may assume, and there can hardly be a doubt about the truth of the assumption, that a new character, once produced, will slowly but surely be combined through accidental crosses with a large number of previously existing types, and so will tend to double the number of the constituents of the variety. But whether it first appears suddenly or whether it is only slowly evolved we cannot determine. It would, of course, be impossible to observe either process in such a mixture. Only cultures of pure races, of single-parent races as we have called them, can afford an opportunity for this kind of observation. In the fields of Svalof new and unexpected qualities have recently been seen, from time to time, to appear suddenly. These characters are as distinct as the older ones and appear to be constant from the moment of their origin.

Darwin has repeatedly insisted that man does not cause variability. He simply selects the variations given to him by the hand of nature. He may repeat this process in order to accumulate different new characters in the same family, thus producing varieties of a higher order. This process of accumulation would, if continued for a longer time, lead to the augmentation of the slight differences characteristic of varieties into the greater differences characteristic of species and genera. It is in this way that horticultural and agricultural experience contribute to the problem of the conversion of varieties into species, and to the explanation of the admirable adaptations of each organism to its complex conditions of life. In the long run new forms, distinguished from their allies by quite a number of new characters, would, by the extermination of the older intermediates, become distinct species.

Thus we see that the theory of the origin of species by means of natural selection is quite independent of the question, how the variations to be selected arise. They may arise slowly, from simple fluctuations, or suddenly, by mutations; in both cases natural selection will take hold of them, will multiply them if they are beneficial, and in the course of time accumulate them, so as to produce that great diversity of organic life, which we so highly admire.

Darwin has left the decision of this difficult and obviously subordinate point to his followers. But in his Pangenesis hypothesis he has given us the clue for a close study and ultimate elucidation of the subject under discussion.

V. HEREDITY AND VARIATION IN MODERN LIGHTS. By W. Bateson, M.A., F.R.S.

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Darwin's work has the property of greatness in that it may be admired from more aspects than one. For some the perception of the principle of Natural Selection stands out as his most wonderful achievement to which all the rest is subordinate. Others, among whom I would range myself, look up to him rather as the first who plainly distinguished, collected, and comprehensively studied that new class of evidence from which hereafter a true understanding of the process of Evolution may be developed. We each prefer our own standpoint of admiration; but I think that it will be in their wider aspect that his labours will most command the veneration of posterity.

A treatise written to advance knowledge may be read in two moods. The reader may keep his mind passive, willing merely to receive the impress of the writer's thought; or he may read with his attention strained and alert, asking at every instant how the new knowledge can be used in a further advance, watching continually for fresh footholds by which to climb higher still. Of Shelley it has been said that he was a poet for poets: so Darwin was a naturalist for naturalists. It is when his writings are used in the critical and more exacting spirit with which we test the outfit for our own enterprise that we learn their full value and strength. Whether we glance back and compare his performance with the efforts of his predecessors, or look forward along the course which modern research is disclosing, we shall honour most in him not the rounded merit of finite accomplishment, but the creative power by which he inaugurated a line of discovery endless in variety and extension. Let us attempt thus to see his work in true perspective between the past from which it grew, and the present which is its consequence. Darwin attacked the problem of Evolution by reference to facts of three classes: Variation; Heredity; Natural Selection. His work was not as the laity suppose, a sudden and unheralded revelation, but the first fruit of a long and hitherto barren controversy. The occurrence of variation from type, and the hereditary transmission of such variation had of course been long familiar to practical men, and inferences as to the possible bearing of those phenomena on the nature of specific difference had been from time to time drawn by naturalists. Maupertuis, for example, wrote "Ce qui nous reste a examiner, c'est comment d'un seul individu, il a pu naitre tant d'especes si differentes." And again "La Nature contient le fonds de toutes ces varietes: mais le hasard ou l'art les mettent en oeuvre. C'est ainsi que ceux dont l'industrie s'applique a satisfaire le gout des curieux, sont, pour ainsi dire, creatures d'especes nouvelles." ("Venus Physique, contenant deux Dissertations, l'une sur l'origine des Hommes et des Animaux: Et l'autre sur l'origine des Noirs" La Haye, 1746, pages 124 and 129. For an introduction to the writings of Maupertuis I am indebted to an article by Professor Lovejoy in "Popular Sci. Monthly", 1902.)

Such passages, of which many (though few so emphatic) can be found in eighteenth century writers, indicate a true perception of the mode of Evolution. The speculations hinted at by Buffon (For the fullest account of the views of these pioneers of Evolution, see the works of Samuel Butler, especially "Evolution, Old and New" (2nd edition) 1882. Butler's claims on behalf of Buffon have met with some acceptance; but after reading what Butler has said, and a considerable part of Buffon's own works, the word "hinted" seems to me a sufficiently correct description of the part he played. It is interesting to note that in the chapter on the Ass, which contains some of his evolutionary passages, there is a reference to "plusieurs idees tres-elevees sur la generation" contained in the Letters of Maupertuis.),

developed by Erasmus Darwin, and independently proclaimed above all by Lamarck, gave to the doctrine of descent a wide renown. The uniformitarian teaching which Lyell deduced from geological observation had gained acceptance. The facts of geographical distribution (See especially W. Lawrence, "Lectures on Physiology", London, 1823, pages 213 f.) had been shown to be obviously inconsistent with the Mosaic legend. Prichard, and Lawrence, following the example of Blumenbach, had successfully demonstrated that the races of Man could be regarded as different forms of one species, contrary to the opinion up till then received. These treatises all begin, it is true, with a profound obeisance to the sons of Noah, but that performed, they continue on strictly modern lines. The question of the mutability of species was thus prominently raised.

Those who rate Lamarck no higher than did Huxley in his contemptuous phrase "buccinator tantum," will scarcely deny that the sound of the trumpet had carried far, or that its note was clear. If then there were few who had already turned to evolution with positive conviction, all scientific men must at least have known that such views had been promulgated; and many must, as Huxley says, have taken up his own position of "critical expectancy." (See the chapter contributed to the "Life and Letters of Charles Darwin" II. page 195. I do not clearly understand the sense in which Darwin wrote (Autobiography, *ibid.* I. page 87): "It has sometimes been said that the success of the "Origin" proved 'that the subject was in the air,' or 'that men's minds were prepared for it.' I do not think that this is strictly true, for I occasionally sounded not a few naturalists, and never happened to come across a single one who seemed to doubt about the permanence of species." This experience may perhaps have been an accident due to Darwin's isolation. The literature of the period abounds with indications of "critical expectancy." A most interesting expression of that feeling is given in the charming account of the "Early Days of Darwinism" by Alfred Newton, "Macmillan's Magazine", LVII. 1888, page 241. He tells how in 1858 when spending a dreary summer in Iceland, he and his friend, the ornithologist John Wolley, in default of active occupation, spent their days in discussion. "Both of us taking a keen interest in Natural History, it was but reasonable that a question, which in those days was always coming up wherever two or more naturalists were gathered together, should be continually recurring. That question was, 'What is a species?' and connected therewith was the other question, 'How did a species begin?'... Now we were of course fairly well acquainted with what had been published on these subjects." He then enumerates some of these publications, mentioning among others T. Vernon Wollaston's "Variation of Species"—a work which has in my opinion never been adequately appreciated. He proceeds: "Of course we never arrived at anything like a solution of these problems, general or special, but we felt very strongly that a solution ought to be found, and that quickly, if the study of Botany and Zoology was to make any great advance." He then describes how on his return home he received the famous number of the "Linnean Journal" on a certain evening. "I sat up late that night to read it; and never shall I forget the impression it made upon me. Herein was contained a perfectly simple solution of all the difficulties which had been troubling me for months past... I went to bed satisfied that a solution had been found.")

Why, then, was it, that Darwin succeeded where the rest had failed? The cause of that success was two-fold. First, and obviously, in the principle of Natural Selection he had a suggestion which would work. It might not go the whole way, but it was true as far as it went. Evolution could thus in great measure be fairly represented as a consequence of demonstrable processes. Darwin seldom endangers the mechanism he devised by putting on it strains much greater than it can bear. He at least was under no illusion as to the omnipotence of Selection; and he introduces none of the forced pleading which in recent years has threatened to discredit that principle.

For example, in the latest text of the "Origin" ("Origin", (6th edition (1882), page 421.)) we find him saying:

"But as my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position—namely, at the close of the Introduction—the following words: 'I am convinced that natural selection has been the main but not the exclusive means of modification.'"

But apart from the invention of this reasonable hypothesis, which may well, as Huxley estimated, "be the guide of biological and psychological speculation for the next three or four generations," Darwin made a more significant and imperishable contribution. Not for a few generations, but through all ages

he should be remembered as the first who showed clearly that the problems of Heredity and Variation are soluble by observation, and laid down the course by which we must proceed to their solution. (Whatever be our estimate of the importance of Natural Selection, in this we all agree. Samuel Butler, the most brilliant, and by far the most interesting of Darwin's opponents—whose works are at length emerging from oblivion—in his Preface (1882) to the 2nd edition of "Evolution, Old and New", repeats his earlier expression of homage to one whom he had come to regard as an enemy: "To the end of time, if the question be asked, 'Who taught people to believe in Evolution?' the answer must be that it was Mr. Darwin. This is true, and it is hard to see what palm of higher praise can be awarded to any philosopher.") The moment of inspiration did not come with the reading of Malthus, but with the opening of the "first note-book on Transmutation of Species." ("Life and Letters", I. pages 276 and 83.) Evolution is a process of Variation and Heredity. The older writers, though they had some vague idea that it must be so, did not study Variation and Heredity. Darwin did, and so begat not a theory, but a science.

The extent to which this is true, the scientific world is only beginning to realise. So little was the fact appreciated in Darwin's own time that the success of his writings was followed by an almost total cessation of work in that special field. Of the causes which led to this remarkable consequence I have spoken elsewhere. They proceeded from circumstances peculiar to the time; but whatever the causes there is no doubt that this statement of the result is historically exact, and those who make it their business to collect facts elucidating the physiology of Heredity and Variation are well aware that they will find little to reward their quest in the leading scientific Journals of the Darwinian epoch.

In those thirty years the original stock of evidence current and in circulation even underwent a process of attrition. As in the story of the Eastern sage who first wrote the collected learning of the universe for his sons in a thousand volumes, and by successive compression and burning reduced them to one, and from this by further burning distilled the single ejaculation of the Faith, "There is no god but God and Mohamed is the Prophet of God," which was all his maturer wisdom deemed essential:—so in the books of that period do we find the corpus of genetic knowledge dwindle to a few prerogative instances, and these at last to the brief formula of an unquestioned creed.

And yet in all else that concerns biological science this period was, in very truth, our Golden Age, when the natural history of the earth was explored as never before; morphology and embryology were exhaustively ransacked; the physiology of plants and animals began to rival chemistry and physics in precision of method and in the rapidity of its advances; and the foundations of pathology were laid.

In contrast with this immense activity elsewhere the neglect which befel the special physiology of Descent, or Genetics as we now call it, is astonishing. This may of course be interpreted as meaning that the favoured studies seemed to promise a quicker return for effort, but it would be more true to say that those who chose these other pursuits did so without making any such comparison; for the idea that the physiology of Heredity and Variation was a coherent science, offering possibilities of extraordinary discovery, was not present to their minds at all. In a word, the existence of such a science was well nigh forgotten. It is true that in ancillary periodicals, as for example those that treat of entomology or horticulture, or in the writings of the already isolated systematists (This isolation of the systematists is the one most melancholy sequela of Darwinism. It seems an irony that we should read in the peroration to the "Origin" that when the Darwinian view is accepted "Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be a true species. This, I feel sure, and I speak after experience, will be no slight relief. The endless disputes whether or not some fifty species of British brambles are good species will cease." "Origin", 6th edition (1882), page 425. True they have ceased to attract the attention of those who lead opinion, but anyone who will turn to the literature of systematics will find that they have not ceased in any other sense. Should there not be something disquieting in the fact that among the workers who come most into contact with specific differences, are to be found the only men who have failed to be persuaded of the unreality of those differences?), observations with this special bearing were from time to time related, but the class of fact on which Darwin built his conceptions of Heredity and Variation was not seen in the highways of biology. It formed no part of the official curriculum of biological students, and found no place among the subjects which their teachers were investigating.

During this period nevertheless one distinct advance was made, that with which Weismann's name is prominently connected. In Darwin's genetic scheme the hereditary transmission of parental experience and its consequences played a considerable role. Exactly how great that role was supposed to be, he with his habitual caution refrained from specifying, for the sufficient reason that he did not know. Nevertheless much of the process of Evolution, especially that by which organs have become degenerate and rudimentary, was certainly attributed by Darwin to such inheritance, though since belief in the inheritance of acquired characters fell into disrepute, the fact has been a good deal overlooked. The "Origin" without "use and disuse" would be a materially different book. A certain vacillation is discernible in Darwin's utterances on this question, and the fact gave to the astute Butler an opportunity for his most telling attack. The discussion which best illustrates the genetic views of the period arose in regard to the production of the rudimentary condition of the wings of many beetles in the Madeira group of islands, and by comparing passages from the "Origin" (6th edition pages 109 and 401. See Butler, "Essays on Life, Art, and Science", page 265, reprinted 1908, and "Evolution, Old and New", chapter XXII. (2nd edition), 1882.) Butler convicts Darwin of saying first that this condition was in the main the result of Selection, with disuse aiding, and in another place that the main cause of degeneration was disuse, but that Selection had aided. To Darwin however I think the point would have seemed one of dialectics merely. To him the one paramount purpose was to show that somehow an Evolution by means of Variation and Heredity might have brought about the facts observed, and whether they had come to pass in the one way or the other was a matter of subordinate concern.

To us moderns the question at issue has a diminished significance. For over all such debates a change has been brought by Weismann's challenge for evidence that use and disuse have any transmitted effects at all. Hitherto the transmission of many acquired characteristics had seemed to most naturalists so obvious as not to call for demonstration. (W. Lawrence was one of the few who consistently maintained the contrary opinion. Prichard, who previously had expressed himself in the same sense, does not, I believe repeat these views in his later writings, and there are signs that he came to believe in the transmission of acquired habits. See Lawrence, "Lect. Physiol." 1823, pages 436-437, 447 Prichard, Edin. Inaug. Disp. 1808 (not seen by me), quoted *ibid.* and "Nat. Hist. Man", 1843, pages 34 f.) Weismann's demand for facts in support of the main proposition revealed at once that none having real cogency could be produced. The time-honoured examples were easily shown to be capable of different explanations. A few certainly remain which cannot be so summarily dismissed, but—though it is manifestly impossible here to do justice to such a subject—I think no one will dispute that these residual and doubtful phenomena, whatever be their true nature, are not of a kind to help us much in the interpretation of any of those complex cases of adaptation which on the hypothesis of unguided Natural Selection are especially difficult to understand. Use and disuse were invoked expressly to help us over these hard places; but whatever changes can be induced in offspring by direct treatment of the parents, they are not of a kind to encourage hope of real assistance from that quarter. It is not to be denied that through the collapse of this second line of argument the Selection hypothesis has had to take an increased and perilous burden. Various ways of meeting the difficulty have been proposed, but these mostly resolve themselves into improbable attempts to expand or magnify the powers of Natural Selection.

Weismann's interpellation, though negative in purpose, has had a lasting and beneficial effect, for through his thorough demolition of the old loose and distracting notions of inherited experience, the ground has been cleared for the construction of a true knowledge of heredity based on experimental fact.

In another way he made a contribution of a more positive character, for his elaborate speculations as to the genetic meaning of cytological appearances have led to a minute investigation of the visible phenomena occurring in those divisions by which germ-cells arise. Though the particular views he advocated have very largely proved incompatible with the observed facts of heredity, yet we must acknowledge that it was chiefly through the stimulus of Weismann's ideas that those advances in cytology were made; and though the doctrine of the continuity of germ-plasm cannot be maintained in the form originally propounded, it is in the main true and illuminating. (It is interesting to see how nearly Butler was led by natural penetration, and from absolutely opposite conclusions, back to this underlying truth: "So that each ovum when impregnate should be considered not as descended from its

ancestors, but as being a continuation of the personality of every ovum in the chain of its ancestry, which every ovum IT ACTUALLY IS quite as truly as the octogenarian IS the same identity with the ovum from which he has been developed. This process cannot stop short of the primordial cell, which again will probably turn out to be but a brief resting-place. We therefore prove each one of us to BE ACTUALLY the primordial cell which never died nor dies, but has differentiated itself into the life of the world, all living beings whatever, being one with it and members one of another," "Life and Habit", 1878, page 86.) Nevertheless in the present state of knowledge we are still as a rule quite unable to connect cytological appearances with any genetic consequence and save in one respect (obviously of extreme importance—to be spoken of later) the two sets of phenomena might, for all we can see, be entirely distinct.

I cannot avoid attaching importance to this want of connection between the nuclear phenomena and the features of bodily organisation. All attempts to investigate Heredity by cytological means lie under the disadvantage that it is the nuclear changes which can alone be effectively observed. Important as they must surely be, I have never been persuaded that the rest of the cell counts for nothing. What we know of the behaviour and variability of chromosomes seems in my opinion quite incompatible with the belief that they alone govern form, and are the sole agents responsible in heredity. (This view is no doubt contrary to the received opinion. I am however interested to see it lately maintained by Driesch ("Science and Philosophy of the Organism", London, 1907, page 233), and from the recent observations of Godlewski it has received distinct experimental support.)

If, then, progress was to be made in Genetics, work of a different kind was required. To learn the laws of Heredity and Variation there is no other way than that which Darwin himself followed, the direct examination of the phenomena. A beginning could be made by collecting fortuitous observations of this class, which have often thrown a suggestive light, but such evidence can be at best but superficial and some more penetrating instrument of research is required. This can only be provided by actual experiments in breeding.

The truth of these general considerations was becoming gradually clear to many of us when in 1900 Mendel's work was rediscovered. Segregation, a phenomenon of the utmost novelty, was thus revealed. From that moment not only in the problem of the origin of species, but in all the great problems of biology a new era began. So unexpected was the discovery that many naturalists were convinced it was untrue, and at once proclaimed Mendel's conclusions as either altogether mistaken, or if true, of very limited application. Many fantastic notions about the workings of Heredity had been asserted as general principles before: this was probably only another fancy of the same class.

Nevertheless those who had a preliminary acquaintance with the facts of Variation were not wholly unprepared for some such revelation. The essential deduction from the discovery of segregation was that the characters of living things are dependent on the presence of definite elements or factors, which are treated as units in the processes of Heredity. These factors can thus be recombined in various ways. They act sometimes separately, and sometimes they interact in conjunction with each other, producing their various effects. All this indicates a definiteness and specific order in heredity, and therefore in variation. This order cannot by the nature of the case be dependent on Natural Selection for its existence, but must be a consequence of the fundamental chemical and physical nature of living things. The study of Variation had from the first shown that an orderliness of this kind was present. The bodies and the properties of living things are cosmic, not chaotic. No matter how low in the scale we go, never do we find the slightest hint of a diminution in that all-pervading orderliness, nor can we conceive an organism existing for a moment in any other state. Moreover not only does this order prevail in normal forms, but again and again it is to be seen in newly-sprung varieties, which by general consent cannot have been subjected to a prolonged Selection. The discovery of Mendelian elements admirably coincided with and at once gave a rationale of these facts. Genetic Variation is then primarily the consequence of additions to, or omissions from, the stock of elements which the species contains. The further investigation of the species-problem must thus proceed by the analytical method which breeding experiments provide.

In the nine years which have elapsed since Mendel's clue became generally known, progress has been rapid. We now understand the process by which a polymorphic race maintains its polymorphism. When a family consists of dissimilar members, given the numerical proportions in which these

members are occurring, we can represent their composition symbolically and state what types can be transmitted by the various members. The difficulty of the "swamping effects of intercrossing" is practically at an end. Even the famous puzzle of sex-limited inheritance is solved, at all events in its more regular manifestations, and we know now how it is brought about that the normal sisters of a colour-blind man can transmit the colour-blindness while his normal brothers cannot transmit it.

We are still only on the fringe of the inquiry. It can be seen extending and ramifying in many directions. To enumerate these here would be impossible. A whole new range of possibilities is being brought into view by study of the interrelations between the simple factors. By following up the evidence as to segregation, indications have been obtained which can only be interpreted as meaning that when many factors are being simultaneously redistributed among the germ-cells, certain of them exert what must be described as a repulsion upon other factors. We cannot surmise whither this discovery may lead.

In the new light all the old problems wear a fresh aspect. Upon the question of the nature of Sex, for example, the bearing of Mendelian evidence is close. Elsewhere I have shown that from several sets of parallel experiments the conclusion is almost forced upon us that, in the types investigated, of the two sexes the female is to be regarded as heterozygous in sex, containing one unpaired dominant element, while the male is similarly homozygous in the absence of that element. (In other words, the ova are each EITHER female, OR male (i.e. non-female), but the sperms are all non-female.) It is not a little remarkable that on this point—which is the only one where observations of the nuclear processes of gameto-genesis have yet been brought into relation with the visible characteristics of the organisms themselves—there should be diametrical opposition between the results of breeding experiments and those derived from cytology.

Those who have followed the researches of the American school will be aware that, after it had been found in certain insects that the spermatozoa were of two kinds according as they contained or did not contain the accessory chromosome, E.B. Wilson succeeded in proving that the sperms possessing this accessory body were destined to form FEMALES on fertilisation, while sperms without it form males, the eggs being apparently indifferent. Perhaps the most striking of all this series of observations is that lately made by T.H. Morgan (Morgan, "Proc. Soc. Exp. Biol. Med." V. 1908, and von Baehr, "Zool. Anz." XXXII. page 507, 1908.), since confirmed by von Baehr, that in a Phylloxera two kinds of spermatids are formed, respectively with and without an accessory (in this case, DOUBLE) chromosome. Of these, only those possessing the accessory body become functional spermatozoa, the others degenerating. We have thus an elucidation of the puzzling fact that in these forms fertilisation results in the formation of FEMALES only. How the males are formed—for of course males are eventually produced by the parthenogenetic females—we do not know.

If the accessory body is really to be regarded as bearing the factor for femaleness, then in Mendelian terms female is DD and male is DR. The eggs are indifferent and the spermatozoa are each male, OR female. But according to the evidence derived from a study of the sex-limited descent of certain features in other animals the conclusion seems equally clear that in them female must be regarded as DR and male as RR. The eggs are thus each either male or female and the spermatozoa are indifferent. How this contradictory evidence is to be reconciled we do not yet know. The breeding work concerns fowls, canaries, and the Currant moth (*Abraxas grossulariata*). The accessory chromosome has been now observed in most of the great divisions of insects (As Wilson has proved, the unpaired body is not a universal feature even in those orders in which it has been observed. Nearly allied types may differ. In some it is altogether unpaired. In others it is paired with a body of much smaller size, and by selection of various types all gradations can be demonstrated ranging to the condition in which the members of the pair are indistinguishable from each other.), except, as it happens, Lepidoptera. At first sight it seems difficult to suppose that a feature apparently so fundamental as sex should be differently constituted in different animals, but that seems at present the least improbable inference. I mention these two groups of facts as illustrating the nature and methods of modern genetic work. We must proceed by minute and specific analytical investigation. Wherever we look we find traces of the operation of precise and specific rules.

In the light of present knowledge it is evident that before we can attack the Species-problem with any hope of success there are vast arrears to be made up. He would be a bold man who would now assert

that there was no sense in which the term Species might not have a strict and concrete meaning in contradistinction to the term Variety. We have been taught to regard the difference between species and variety as one of degree. I think it unlikely that this conclusion will bear the test of further research. To Darwin the question, What is a variation? presented no difficulties. Any difference between parent and offspring was a variation. Now we have to be more precise. First we must, as de Vries has shown, distinguish real, genetic, variation from FLUCTUATIONAL variations, due to environmental and other accidents, which cannot be transmitted. Having excluded these sources of error the variations observed must be expressed in terms of the factors to which they are due before their significance can be understood. For example, numbers of the variations seen under domestication, and not a few witnessed in nature, are simply the consequence of some ingredient being in an unknown way omitted from the composition of the varying individual. The variation may on the contrary be due to the addition of some new element, but to prove that it is so is by no means an easy matter. Casual observation is useless, for though these latter variations will always be dominants, yet many dominant characteristics may arise from another cause, namely the meeting of complementary factors, and special study of each case in two generations at least is needed before these two phenomena can be distinguished.

When such considerations are fully appreciated it will be realised that medleys of most dissimilar occurrences are all confused together under the term Variation. One of the first objects of genetic analysis is to disentangle this mass of confusion.

To those who have made no study of heredity it sometimes appears that the question of the effect of conditions in causing variation is one which we should immediately investigate, but a little thought will show that before any critical inquiry into such possibilities can be attempted, a knowledge of the working of heredity under conditions as far as possible uniform must be obtained. At the time when Darwin was writing, if a plant brought into cultivation gave off an albino variety, such an event was without hesitation ascribed to the change of life. Now we see that albino GAMETES, germs, that is to say, which are destitute of the pigment-forming factor, may have been originally produced by individuals standing an indefinite number of generations back in the ancestry of the actual albino, and it is indeed almost certain that the variation to which the appearance of the albino is due cannot have taken place in a generation later than that of the grandparents. It is true that when a new DOMINANT appears we should feel greater confidence that we were witnessing the original variation, but such events are of extreme rarity, and no such case has come under the notice of an experimenter in modern times, as far as I am aware. That they must have appeared is clear enough. Nothing corresponding to the Brown-breasted Game fowl is known wild, yet that colour is a most definite dominant, and at some moment since *Gallus bankiva* was domesticated, the element on which that special colour depends must have at least once been formed in the germ-cell of a fowl; but we need harder evidence than any which has yet been produced before we can declare that this novelty came through over-feeding, or change of climate, or any other disturbance consequent on domestication. When we reflect on the intricacies of genetic problems as we must now conceive them there come moments when we feel almost thankful that the Mendelian principles were unknown to Darwin. The time called for a bold pronouncement, and he made it, to our lasting profit and delight. With fuller knowledge we pass once more into a period of cautious expectation and reserve.

In every arduous enterprise it is pleasanter to look back at difficulties overcome than forward to those which still seem insurmountable, but in the next stage there is nothing to be gained by disguising the fact that the attributes of living things are not what we used to suppose. If they are more complex in the sense that the properties they display are throughout so regular (I have in view, for example, the marvellous and specific phenomena of regeneration, and those discovered by the students of "Entwicklungsmechanik". The circumstances of its occurrence here preclude any suggestion that this regularity has been brought about by the workings of Selection. The attempts thus to represent the phenomena have resulted in mere parodies of scientific reasoning.) that the Selection of minute random variations is an unacceptable account of the origin of their diversity, yet by virtue of that very regularity the problem is limited in scope and thus simplified.

To begin with, we must relegate Selection to its proper place. Selection permits the viable to continue and decides that the non-viable shall perish; just as the temperature of our atmosphere decides that no liquid carbon shall be found on the face of the earth: but we do not suppose that the form of the

diamond has been gradually achieved by a process of Selection. So again, as the course of descent branches in the successive generations, Selection determines along which branch Evolution shall proceed, but it does not decide what novelties that branch shall bring forth. "La Nature contient le fonds de toutes ces varietes, mais le hazard ou l'art les mettent en oeuvre," as Maupertuis most truly said.

Not till knowledge of the genetic properties of organisms has attained to far greater completeness can evolutionary speculations have more than a suggestive value. By genetic experiment, cytology and physiological chemistry aiding, we may hope to acquire such knowledge. In 1872 Nathusius wrote ("Vortrage uber Viehzucht und Rassenerkenntniss", page 120, Berlin, 1872.): "Das Gesetz der Vererbung ist noch nicht erkannt; der Apfel ist noch nicht vom Baum der Erkenntniss gefallen, welcher, der Sage nach, Newton auf den rechten Weg zur Ergrundung der Gravitationsgesetze fuhrte." We cannot pretend that the words are not still true, but in Mendelian analysis the seeds of that apple-tree at last are sown.

If we were asked what discovery would do most to forward our inquiry, what one bit of knowledge would more than any other illuminate the problem, I think we may give the answer without hesitation. The greatest advance that we can foresee will be made when it is found possible to connect the geometrical phenomena of development with the chemical. The geometrical symmetry of living things is the key to a knowledge of their regularity, and the forces which cause it. In the symmetry of the dividing cell the basis of that resemblance we call Heredity is contained. To imitate the morphological phenomena of life we have to devise a system which can divide. It must be able to divide, and to segment as—grossly—a vibrating plate or rod does, or as an icicle can do as it becomes ribbed in a continuous stream of water; but with this distinction, that the distribution of chemical differences and properties must simultaneously be decided and disposed in orderly relation to the pattern of the segmentation. Even if a model which would do this could be constructed it might prove to be a useful beginning.

This may be looking too far ahead. If we had to choose some one piece of more proximate knowledge which we would more especially like to acquire, I suppose we should ask for the secret of interracial sterility. Nothing has yet been discovered to remove the grave difficulty, by which Huxley in particular was so much oppressed, that among the many varieties produced under domestication—which we all regard as analogous to the species seen in nature—no clear case of interracial sterility has been demonstrated. The phenomenon is probably the only one to which the domesticated products seem to afford no parallel. No solution of the difficulty can be offered which has positive value, but it is perhaps worth considering the facts in the light of modern ideas. It should be observed that we are not discussing incompatibility of two species to produce offspring (a totally distinct phenomenon), but the sterility of the offspring which many of them do produce.

When two species, both perfectly fertile severally, produce on crossing a sterile progeny, there is a presumption that the sterility is due to the development in the hybrid of some substance which can only be formed by the meeting of two complementary factors. That some such account is correct in essence may be inferred from the well-known observation that if the hybrid is not totally sterile but only partially so, and thus is able to form some good germ-cells which develop into new individuals, the sterility of these daughter-individuals is sensibly reduced or may be entirely absent. The fertility once re-established, the sterility does not return in the later progeny, a fact strongly suggestive of segregation. Now if the sterility of the cross-bred be really the consequence of the meeting of two complementary factors, we see that the phenomenon could only be produced among the divergent offspring of one species by the acquisition of at least TWO new factors; for if the acquisition of a single factor caused sterility the line would then end. Moreover each factor must be separately acquired by distinct individuals, for if both were present together, the possessors would by hypothesis be sterile. And in order to imitate the case of species each of these factors must be acquired by distinct breeds. The factors need not, and probably would not, produce any other perceptible effects; they might, like the colour-factors present in white flowers, make no difference in the form or other characters. Not till the cross was actually made between the two complementary individuals would either factor come into play, and the effects even then might be unobserved until an attempt was made to breed from the cross-bred.

Next, if the factors responsible for sterility were acquired, they would in all probability be peculiar to certain individuals and would not readily be distributed to the whole breed. Any member of the breed also into which BOTH the factors were introduced would drop out of the pedigree by virtue of its sterility. Hence the evidence that the various domesticated breeds say of dogs or fowls can when mated together produce fertile offspring, is beside the mark. The real question is, Do they ever produce sterile offspring? I think the evidence is clearly that sometimes they do, oftener perhaps than is commonly supposed. These suggestions are quite amenable to experimental tests. The most obvious way to begin is to get a pair of parents which are known to have had any sterile offspring, and to find the proportions in which these steriles were produced. If, as I anticipate, these proportions are found to be definite, the rest is simple.

In passing, certain other considerations may be referred to. First, that there are observations favouring the view that the production of totally sterile cross-breeds is seldom a universal property of two species, and that it may be a matter of individuals, which is just what on the view here proposed would be expected. Moreover, as we all know now, though incompatibility may be dependent to some extent on the degree to which the species are dissimilar, no such principle can be demonstrated to determine sterility or fertility in general. For example, though all our Finches can breed together, the hybrids are all sterile. Of Ducks some species can breed together without producing the slightest sterility; others have totally sterile offspring, and so on. The hybrids between several genera of Orchids are perfectly fertile on the female side, and some on the male side also, but the hybrids produced between the Turnip (*Brassica napus*) and the Swede (*Brassica campestris*), which, according to our estimates of affinity should be nearly allied forms, are totally sterile. (See Sutton, A.W., "Journ. Linn. Soc." XXXVIII. page 341, 1908.) Lastly, it may be recalled that in sterility we are almost certainly considering a meristic phenomenon. FAILURE TO DIVIDE is, we may feel fairly sure, the immediate "cause" of the sterility. Now, though we know very little about the heredity of meristic differences, all that we do know points to the conclusion that the less-divided is dominant to the more-divided, and we are thus justified in supposing that there are factors which can arrest or prevent cell-division. My conjecture therefore is that in the case of sterility of cross-breeds we see the effect produced by a complementary pair of such factors. This and many similar problems are now open to our analysis.

The question is sometimes asked, Do the new lights on Variation and Heredity make the process of Evolution easier to understand? On the whole the answer may be given that they do. There is some appearance of loss of simplicity, but the gain is real. As was said above, the time is not ripe for the discussion of the origin of species. With faith in Evolution unshaken—if indeed the word faith can be used in application to that which is certain—we look on the manner and causation of adapted differentiation as still wholly mysterious. As Samuel Butler so truly said: "To me it seems that the 'Origin of Variation,' whatever it is, is the only true 'Origin of Species'" ("Life and Habit", London, page 263, 1878.), and of that Origin not one of us knows anything. But given Variation—and it is given: assuming further that the variations are not guided into paths of adaptation—and both to the Darwinian and to the modern school this hypothesis appears to be sound if unproven—an evolution of species proceeding by definite steps is more, rather than less, easy to imagine than an evolution proceeding by the accumulation of indefinite and insensible steps. Those who have lost themselves in contemplating the miracles of Adaptation (whether real or spurious) have not unnaturally fixed their hopes rather on the indefinite than on the definite changes. The reasons are obvious. By suggesting that the steps through which an adaptative mechanism arose were indefinite and insensible, all further trouble is spared. While it could be said that species arise by an insensible and imperceptible process of variation, there was clearly no use in tiring ourselves by trying to perceive that process. This labour-saving counsel found great favour. All that had to be done to develop evolution-theory was to discover the good in everything, a task which, in the complete absence of any control or test whereby to check the truth of the discovery, is not very onerous. The doctrine "*que tout est au mieux*" was therefore preached with fresh vigour, and examples of that illuminating principle were discovered with a facility that Pangloss himself might have envied, till at last even the spectators wearied of such dazzling performances.

But in all seriousness, why should indefinite and unlimited variation have been regarded as a more probable account of the origin of Adaptation? Only, I think, because the obstacle was shifted one plane

back, and so looked rather less prominent. The abundance of Adaptation, we all grant, is an immense, almost an unsurpassable difficulty in all non-Lamarckian views of Evolution; but if the steps by which that adaptation arose were fortuitous, to imagine them insensible is assuredly no help. In one most important respect indeed, as has often been observed, it is a multiplication of troubles. For the smaller the steps, the less could Natural Selection act upon them. Definite variations—and of the occurrence of definite variations in abundance we have now the most convincing proof—have at least the obvious merit that they can make and often do make a real difference in the chances of life.

There is another aspect of the Adaptation problem to which I can only allude very briefly. May not our present ideas of the universality and precision of Adaptation be greatly exaggerated? The fit of organism to its environment is not after all so very close—a proposition unwelcome perhaps, but one which could be illustrated by very copious evidence. Natural Selection is stern, but she has her tolerant moods.

We have now most certain and irrefragable proof that much definiteness exists in living things apart from Selection, and also much that may very well have been preserved and so in a sense constituted by Selection. Here the matter is likely to rest. There is a passage in the sixth edition of the "Origin" which has I think been overlooked. On page 70 Darwin says "The tuft of hair on the breast of the wild turkey-cock cannot be of any use, and it is doubtful whether it can be ornamental in the eyes of the female bird." This tuft of hair is a most definite and unusual structure, and I am afraid that the remark that it "cannot be of any use" may have been made inadvertently; but it may have been intended, for in the first edition the usual qualification was given and must therefore have been deliberately excised. Anyhow I should like to think that Darwin did throw over that tuft of hair, and that he felt relief when he had done so. Whether however we have his great authority for such a course or not, I feel quite sure that we shall be rightly interpreting the facts of nature if we cease to expect to find purposefulness wherever we meet with definite structures or patterns. Such things are, as often as not, I suspect rather of the nature of tool-marks, mere incidents of manufacture, benefiting their possessor not more than the wire-marks in a sheet of paper, or the ribbing on the bottom of an oriental plate renders those objects more attractive in our eyes.

If Variation may be in any way definite, the question once more arises, may it not be definite in direction? The belief that it is has had many supporters, from Lamarck onwards, who held that it was guided by need, and others who, like Nageli, while laying no emphasis on need, yet were convinced that there was guidance of some kind. The latter view under the name of "Orthogenesis," devised I believe by Eimer, at the present day commends itself to some naturalists. The objection to such a suggestion is of course that no fragment of real evidence can be produced in its support. On the other hand, with the experimental proof that variation consists largely in the unpacking and repacking of an original complexity, it is not so certain as we might like to think that the order of these events is not pre-determined. For instance the original "pack" may have been made in such a way that at the n th division of the germ-cells of a Sweet Pea a colour-factor might be dropped, and that at the n plus n prime division the hooded variety be given off, and so on. I see no ground whatever for holding such a view, but in fairness the possibility should not be forgotten, and in the light of modern research it scarcely looks so absurdly improbable as before.

No one can survey the work of recent years without perceiving that evolutionary orthodoxy developed too fast, and that a great deal has got to come down; but this satisfaction at least remains, that in the experimental methods which Mendel inaugurated, we have means of reaching certainty in regard to the physiology of Heredity and Variation upon which a more lasting structure may be built.

VI. THE MINUTE STRUCTURE OF CELLS IN RELATION TO HEREDITY. By Eduard Strasburger.

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Since 1875 an unexpected insight has been gained into the internal structure of cells. Those who are familiar with the results of investigations in this branch of Science are convinced that any modern theory of heredity must rest on a basis of cytology and cannot be at variance with cytological facts. Many histological discoveries, both such as have been proved correct and others which may be accepted as probably well founded, have acquired a fundamental importance from the point of view of the problems of heredity.

My aim is to describe the present position of our knowledge of Cytology. The account must be confined to essentials and cannot deal with far-reaching and controversial questions. In cases where difference of opinion exists, I adopt my own view for which I hold myself responsible. I hope to succeed in making myself intelligible even without the aid of illustrations: in order to convey to the uninitiated an adequate idea of the phenomena connected with the life of a cell, a greater number of figures would be required than could be included within the scope of this article.

So long as the most eminent investigators (As for example the illustrious Wilhelm Hofmeister in his "Lehre von der Pflanzenzelle" (1867).) believed that the nucleus of a cell was destroyed in the course of each division and that the nuclei of the daughter-cells were produced *de novo*, theories of heredity were able to dispense with the nucleus. If they sought, as did Charles Darwin, who showed a correct grasp of the problem in the enunciation of his Pangenesis hypothesis, for histological connecting links, their hypotheses, or at least the best of them, had reference to the cell as a whole. It was known to Darwin that the cell multiplied by division and was derived from a similar pre-existing cell. Towards 1870 it was first demonstrated that cell-nuclei do not arise *de novo*, but are invariably the result of division of pre-existing nuclei. Better methods of investigation rendered possible a deeper insight into the phenomena accompanying cell and nuclear divisions and at the same time disclosed the existence of remarkable structures. The work of O. Butschli, O. Hertwig, W. Flemming H. Fol and of the author of this article (For further reference to literature, see my article on "Die Ontogenie der Zelle seit 1875", in the "Progressus Rei Botanicae", Vol. I. page 1, Jena, 1907.), have furnished conclusive evidence in favour of these facts. It was found that when the reticular framework of a nucleus prepares to divide, it separates into single segments. These then become thicker and denser, taking up with avidity certain stains, which are used as aids to investigation, and finally form longer or shorter, variously bent, rodlets of uniform thickness. In these organs which, on account of their special property of absorbing certain stains, were styled Chromosomes (By W. Waldeyer in 1888.), there may usually be recognised a separation into thicker and thinner discs; the former are often termed Chromomeres. (Discovered by W. Pfitzner in 1880.) In the course of division of the nucleus, the single rows of chromomeres in the chromosomes are doubled and this produces a band-like flattening and leads to the longitudinal splitting by which each chromosome is divided into two exactly equal halves. The nuclear membrane then disappears and fibrillar cell-plasma or cytoplasm invades the nuclear area. In animal cells these fibrillae in the cytoplasm centre on definite bodies (Their existence and their multiplication by fission were demonstrated by E. van Beneden and Th. Boveri in 1887.), which it is customary to speak of as Centrosomes. Radiating lines in the adjacent cell-plasma suggest that these bodies constitute centres of force. The cells of the higher plants do not possess such individualised centres; they have probably disappeared in the course of phylogenetic development: in spite of this, however, in the nuclear division-figures the fibrillae of the cell-plasma are seen to radiate from two opposite poles. In both animal and plant cells a fibrillar bipolar spindle is formed, the fibrillae of which grasp the longitudinally divided chromosomes from two opposite sides and arrange them on the equatorial plane of the spindle as the so-called nuclear or equatorial plate. Each half-chromosome is connected with one of the spindle poles only and is then drawn towards that pole. (These important facts, suspected by W. Flemming in 1882, were demonstrated by E. Heuser, L. Guignard, E. van Beneden, M. Nussbaum, and C. Rabl.)

The formation of the daughter-nuclei is then effected. The changes which the daughter-chromosomes undergo in the process of producing the daughter-nuclei repeat in the reverse order the changes which they went through in the course of their progressive differentiation from the mother-nucleus. The division of the cell-body is completed midway between the two daughter-nuclei. In animal cells, which

possess no chemically differentiated membrane, separation is effected by simple constriction, while in the case of plant cells provided with a definite wall, the process begins with the formation of a cytoplasmic separating layer.

The phenomena observed in the course of the division of the nucleus show beyond doubt that an exact halving of its substance is of the greatest importance. (First shown by W. Roux in 1883.) Compared with the method of division of the nucleus, that of the cytoplasm appears to be very simple. This led to the conception that the cell-nucleus must be the chief if not the sole carrier of hereditary characters in the organism. It is for this reason that the detailed investigation of fertilisation phenomena immediately followed researches into the nucleus. The fundamental discovery of the union of two nuclei in the sexual act was then made (By O. Hertwig in 1875.) and this afforded a new support for the correct conception of the nuclear functions. The minute study of the behaviour of the other constituents of sexual cells during fertilisation led to the result, that the nucleus alone is concerned with handing on hereditary characters (This was done by O. Hertwig and the author of this essay simultaneously in 1884.) from one generation to another. Especially important, from the point of view of this conclusion, is the study of fertilisation in Angiosperms (Flowering plants); in these plants the male sexual cells lose their cell-body in the pollen-tube and the nucleus only—the sperm-nucleus—reaches the egg. The cytoplasm of the male sexual cell is therefore not necessary to ensure a transference of hereditary characters from parents to offspring. I lay stress on the case of the Angiosperms because researches recently repeated with the help of the latest methods failed to obtain different results. As regards the descendants of angiospermous plants, the same laws of heredity hold good as for other sexually differentiated organisms; we may, therefore, extend to the latter what the Angiosperms so clearly teach us.

The next advance in the hitherto rapid progress in our knowledge of nuclear division was delayed, because it was not at once recognised that there are two absolutely different methods of nuclear division. All such nuclear divisions were united under the head of indirect or mitotic divisions; these were also spoken of as karyo-kineses, and were distinguished from the direct or amitotic divisions which are characterised by a simple constriction of the nuclear body. So long as the two kinds of indirect nuclear division were not clearly distinguished, their correct interpretation was impossible. This was accomplished after long and laborious research, which has recently been carried out and with results which should, perhaps, be regarded as provisional.

Soon after the new study of the nucleus began, investigators were struck by the fact that the course of nuclear division in the mother-cells, or more correctly in the grandmother-cells, of spores, pollen-grains, and embryo-sacs of the more highly organised plants and in the spermatozoids and eggs of the higher animals, exhibits similar phenomena, distinct from those which occur in the somatic cells.

In the nuclei of all those cells which we may group together as gonotokonts (At the suggestion of J.P. Lotsy in 1904.) (i.e. cells concerned in reproduction) there are fewer chromosomes than in the adjacent body-cells (somatic cells). It was noticed also that there is a peculiarity characteristic of the gonotokonts, namely the occurrence of two nuclear divisions rapidly succeeding one another. It was afterwards recognised that in the first stage of nuclear division in the gonotokonts the chromosomes unite in pairs: it is these chromosome-pairs, and not the two longitudinal halves of single chromosomes, which form the nuclear plate in the equatorial plane of the nuclear spindle. It has been proposed to call these pairs *gemi*. (J.E.S. Moore and A.L. Embleton, "Proc. Roy. Soc." London, Vol. LXXVII. page 555, 1906; V. Gregoire, 1907.) In the course of this division the spindle-fibrillae attach themselves to the *gemi*, i.e. to entire chromosomes and direct them to the points where the new daughter-nuclei are formed, that is to those positions towards which the longitudinal halves of the chromosomes travel in ordinary nuclear divisions. It is clear that in this way the number of chromosomes which the daughter-nuclei contain, as the result of the first stage in division in the gonotokonts, will be reduced by one half, while in ordinary divisions the number of chromosomes always remains the same. The first stage in the division of the nucleus in the gonotokonts has therefore been termed the reduction division. (In 1887 W. Flemming termed this the heterotypic form of nuclear division.) This stage in division determines the conditions for the second division which rapidly ensues. Each of the paired chromosomes of the mother-nucleus has already, as in an ordinary nuclear division, completed the longitudinal fission, but in this case it is not succeeded by the immediate separation of the longitudinal halves and their

allotment to different nuclei. Each chromosome, therefore, takes its two longitudinal halves into the same daughter-nucleus. Thus, in each daughter-nucleus the longitudinal halves of the chromosomes are present ready for the next stage in the division; they only require to be arranged in the nuclear plate and then distributed among the granddaughter-nuclei. This method of division, which takes place with chromosomes already split, and which have only to provide for the distribution of their longitudinal halves to the next nuclear generation, has been called homotypic nuclear division. (The name was proposed by W. Flemming in 1887; the nature of this type of division was, however, not explained until later.)

Reduction division and homotypic nuclear division are included together under the term allotypic nuclear division and are distinguished from the ordinary or typical nuclear division. The name Meiosis (By J. Bretland Farmer and J.E.S. Moore in 1905.) has also been proposed for these two allotypic nuclear divisions. The typical divisions are often spoken of as somatic.

Observers who were actively engaged in this branch of recent histological research soon noticed that the chromosomes of a given organism are differentiated in definite numbers from the nuclear network in the course of division. This is especially striking in the gonotokonts, but it applies also to the somatic tissues. In the latter, one usually finds twice as many chromosomes as in the gonotokonts. Thus the conclusion was gradually reached that the doubling of chromosomes, which necessarily accompanies fertilisation, is maintained in the product of fertilisation, to be again reduced to one half in the gonotokonts at the stage of reduction-division. This enabled us to form a conception as to the essence of true alternation of generations, in which generations containing single and double chromosomes alternate with one another.

The single-chromosome generation, which I will call the HAPLOID, must have been the primitive generation in all organisms; it might also persist as the only generation. Every sexual differentiation in organisms, which occurred in the course of phylogenetic development, was followed by fertilisation and therefore by the creation of a diploid or double-chromosome product. So long as the germination of the product of fertilisation, the zygote, began with a reducing process, a special DIPLOID generation was not represented. This, however, appeared later as a product of the further evolution of the zygote, and the reduction division was correspondingly postponed. In animals, as in plants, the diploid generation attained the higher development and gradually assumed the dominant position. The haploid generation suffered a proportional reduction, until it finally ceased to have an independent existence and became restricted to the role of producing the sexual products within the body of the diploid generation. Those who do not possess the necessary special knowledge are unable to realise what remains of the first haploid generation in a phanerogamic plant or in a vertebrate animal. In Angiosperms this is actually represented only by the short developmental stages which extend from the pollen mother-cells to the sperm-nucleus of the pollen-tube, and from the embryo-sac mother-cell to the egg and the endosperm tissue. The embryo-sac remains enclosed in the diploid ovule, and within this from the fertilised egg is formed the embryo which introduces the new diploid generation. On the full development of the diploid embryo of the next generation, the diploid ovule of the preceding diploid generation is separated from the latter as a ripe seed. The uninitiated sees in the more highly organised plants only a succession of diploid generations. Similarly all the higher animals appear to us as independent organisms with diploid nuclei only. The haploid generation is confined in them to the cells produced as the result of the reduction division of the gonotokonts; the development of these is completed with the homotypic stage of division which succeeds the reduction division and produces the sexual products.

The constancy of the numbers in which the chromosomes separate themselves from the nuclear network during division gave rise to the conception that, in a certain degree, chromosomes possess individuality. Indeed the most careful investigations (Particularly those of V. Gregoire and his pupils.) have shown that the segments of the nuclear network, which separate from one another and condense so as to produce chromosomes for a new division, correspond to the segments produced from the chromosomes of the preceding division. The behaviour of such nuclei as possess chromosomes of unequal size affords confirmatory evidence of the permanence of individual chromosomes in corresponding sections of an apparently uniform nuclear network. Moreover at each stage in division chromosomes with the same differences in size reappear. Other cases are known in which thicker

portions occur in the substance of the resting nucleus, and these agree in number with the chromosomes. In this network, therefore, the individual chromosomes must have retained their original position. But the chromosomes cannot be regarded as the ultimate hereditary units in the nuclei, as their number is too small. Moreover, related species not infrequently show a difference in the number of their chromosomes, whereas the number of hereditary units must approximately agree. We thus picture to ourselves the carriers of hereditary characters as enclosed in the chromosomes; the transmitted fixed number of chromosomes is for us only the visible expression of the conception that the number of hereditary units which the chromosomes carry must be also constant. The ultimate hereditary units may, like the chromosomes themselves, retain a definite position in the resting nucleus. Further, it may be assumed that during the separation of the chromosomes from one another and during their assumption of the rod-like form, the hereditary units become aggregated in the chromomeres and that these are characterised by a constant order of succession. The hereditary units then grow, divide into two and are uniformly distributed by the fission of the chromosomes between their longitudinal halves.

As the contraction and rod-like separation of the chromosomes serve to insure the transmission of all hereditary units in the products of division of a nucleus, so, on the other hand, the reticular distension of each chromosome in the so-called resting nucleus may effect a separation of the carriers of hereditary units from each other and facilitate the specific activity of each of them.

In the stages preliminary to their division, the chromosomes become denser and take up a substance which increases their staining capacity; this is called chromatin. This substance collects in the chromomeres and may form the nutritive material for the carriers of hereditary units which we now believe to be enclosed in them. The chromatin cannot itself be the hereditary substance, as it afterwards leaves the chromosomes, and the amount of it is subject to considerable variation in the nucleus, according to its stage of development. Conjointly with the materials which take part in the formation of the nuclear spindle and other processes in the cell, the chromatin accumulates in the resting nucleus to form the nucleoli.

Naturally connected with the conclusion that the nuclei are the carriers of hereditary characters in the organism, is the question whether enucleate organisms can also exist. Phylogenetic considerations give an affirmative answer to this question. The differentiation into nucleus and cytoplasm represents a division of labour in the protoplast. A study of organisms which belong to the lowest class of the organic world teaches us how this was accomplished. Instead of well-defined nuclei, scattered granules have been described in the protoplasm of several of these organisms (Bacteria, Cyanophyceae, Protozoa.), characterised by the same reactions as nuclear material, provided also with a nuclear network, but without a limiting membrane. (This is the result of the work of R. Hertwig and of the most recently published investigations.) Thus the carriers of hereditary characters may originally have been distributed in the common protoplasm, afterwards coming together and eventually assuming a definite form as special organs of the cell. It may be also assumed that in the protoplasm and in the primitive types of nucleus, the carriers of the same hereditary unit were represented in considerable quantity; they became gradually differentiated to an extent commensurate with newly acquired characters. It was also necessary that, in proportion as this happened, the mechanism of nuclear division must be refined. At first processes resembling a simple constriction would suffice to provide for the distribution of all hereditary units to each of the products of division, but eventually in both organic kingdoms nuclear division, which alone insured the qualitative identity of the products of division, became a more marked feature in the course of cell-multiplication.

Where direct nuclear division occurs by constriction in the higher organisms, it does not result in the halving of hereditary units. So far as my observations go, direct nuclear division occurs in the more highly organised plants only in cells which have lost their specific functions. Such cells are no longer capable of specific reproduction. An interesting case in this connection is afforded by the internodal cells of the Characeae, which possess only vegetative functions. These cells grow vigorously and their cytoplasm increases, their growth being accompanied by a correspondingly direct multiplication of the nuclei. They serve chiefly to nourish the plant, but, unlike the other cells, they are incapable of producing any offspring. This is a very instructive case, because it clearly shows that the nuclei are not only carriers of hereditary characters, but that they also play a definite part in the metabolism of the protoplasts.

Attention was drawn to the fact that during the reducing division of nuclei which contain chromosomes of unequal size, gemini are constantly produced by the pairing of chromosomes of the same size. This led to the conclusion that the pairing chromosomes are homologous, and that one comes from the father, the other from the mother. (First stated by T.H. Montgomery in 1901 and by W.S. Sutton in 1902.) This evidently applies also to the pairing of chromosomes in those reduction-divisions in which differences in size do not enable us to distinguish the individual chromosomes. In this case also each pair would be formed by two homologous chromosomes, the one of paternal, the other of maternal origin. When the separation of these chromosomes and their distribution to both daughter-nuclei occur a chromosome of each kind is provided for each of these nuclei. It would seem that the components of each pair might pass to either pole of the nuclear spindle, so that the paternal and maternal chromosomes would be distributed in varying proportion between the daughter-nuclei; and it is not impossible that one daughter-nucleus might occasionally contain paternal chromosomes only and its sister-nucleus exclusively maternal chromosomes.

The fact that in nuclei containing chromosomes of various sizes, the chromosomes which pair together in reduction-division are always of equal size, constitutes a further and more important proof of their qualitative difference. This is supported also by ingenious experiments which led to an unequal distribution of chromosomes in the products of division of a sea-urchin's egg, with the result that a difference was induced in their further development. (Demonstrated by Th. Boveri in 1902.)

The recently discovered fact that in diploid nuclei the chromosomes are arranged in pairs affords additional evidence in favour of the unequal value of the chromosomes. This is still more striking in the case of chromosomes of different sizes. It has been shown that in the first division-figure in the nucleus of the fertilised egg the chromosomes of corresponding size form pairs. They appear with this arrangement in all subsequent nuclear divisions in the diploid generation. The longitudinal fissions of the chromosomes provide for the unaltered preservation of this condition. In the reduction nucleus of the gonotokonts the homologous chromosomes being near together need not seek out one another; they are ready to form gemini. The next stage is their separation to the haploid daughter-nuclei, which have resulted from the reduction process.

Peculiar phenomena in the reduction nucleus accompany the formation of gemini in both organic kingdoms. (This has been shown more particularly by the work of L. Guignard, M. Mottier, J.B. Farmer, C.B. Wilson, V. Hacker and more recently by V. Gregoire and his pupil C.A. Allen, by the researches conducted in the Bonn Botanical Institute, and by A. and K.E. Schreiner.) Probably for the purpose of entering into most intimate relation, the pairs are stretched to long threads in which the chromomeres come to lie opposite one another. (C.A. Allen, A. and K.E. Schreiner, and Strasburger.) It seems probable that these are homologous chromomeres, and that the pairs afterwards unite for a short time, so that an exchange of hereditary units is rendered possible. (H. de Vries and Strasburger.) This cannot be actually seen, but certain facts of heredity point to the conclusion that this occurs. It follows from these phenomena that any exchange which may be effected must be one of homologous carriers of hereditary units only. These units continue to form exchangeable segments after they have undergone unequal changes; they then constitute allelotropic pairs. We may thus calculate what sum of possible combinations the exchange of homologous hereditary units between the pairing chromosomes provides for before the reduction division and the subsequent distribution of paternal and maternal chromosomes in the haploid daughter-nuclei. These nuclei then transmit their characters to the sexual cells, the conjugation of which in fertilization again produces the most varied combinations. (A. Weismann gave the impulse to these ideas in his theory on "Amphimixis".) In this way all the cooperations which the carriers of hereditary characters are capable of in a species are produced; this must give it an appreciable advantage in the struggle for life.

The admirers of Charles Darwin must deeply regret that he did not live to see the results achieved by the new Cytology. What service would they have been to him in the presentation of his hypothesis of Pangenesis; what an outlook into the future would they have given to his active mind!

The Darwinian hypothesis of Pangenesis rests on the conception that all inheritable properties are represented in the cells by small invisible particles or gemmules and that these gemmules increase by division. Cytology began to develop on new lines some years after the publication in 1868 of Charles Darwin's "Provisional hypothesis of Pangenesis" ("Animals and Plants under Domestication", London,

1868, Chapter XXVII.), and when he died in 1882 it was still in its infancy. Darwin would have soon suggested the substitution of the nuclei for his gemmules. At least the great majority of present-day investigators in the domain of cytology have been led to the conclusion that the nucleus is the carrier of hereditary characters, and they also believe that hereditary characters are represented in the nucleus as distinct units. Such would be Darwin's gemmules, which in conformity with the name of his hypothesis may be called pangens (So called by H. de Vries in 1889.): these pangens multiply by division. All recently adopted views may be thus linked on to this part of Darwin's hypothesis. It is otherwise with Darwin's conception to which Pangenesis owes its name, namely the view that all cells continually give off gemmules, which migrate to other places in the organism, where they unite to form reproductive cells. When Darwin foresaw this possibility, the continuity of the germinal substance was still unknown (Demonstrated by Nussbaum in 1880, by Sachs in 1882, and by Weismann in 1885.), a fact which excludes a transference of gemmules.

But even Charles Darwin's genius was confined within finite boundaries by the state of science in his day.

It is not my province to deal with other theories of development which followed from Darwin's Pangenesis, or to discuss their histological probabilities. We can, however, affirm that Charles Darwin's idea that invisible gemmules are the carriers of hereditary characters and that they multiply by division has been removed from the position of a provisional hypothesis to that of a well-founded theory. It is supported by histology, and the results of experimental work in heredity, which are now assuming extraordinary prominence, are in close agreement with it.

VII. "THE DESCENT OF MAN". By G. Schwalbe.

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The problem of the origin of the human race, of the descent of man, is ranked by Huxley in his epoch-making book "Man's Place in Nature", as the deepest with which biology has to concern itself, "the question of questions,"—the problem which underlies all others. In the same brilliant and lucid exposition, which appeared in 1863, soon after the publication of Darwin's "Origin of Species", Huxley stated his own views in regard to this great problem. He tells us how the idea of a natural descent of man gradually grew up in his mind, it was especially the assertions of Owen in regard to the total difference between the human and the simian brain that called forth strong dissent from the great anatomist Huxley, and he easily succeeded in showing that Owen's supposed differences had no real existence; he even established, on the basis of his own anatomical investigations, the proposition that the anatomical differences between the Marmoset and the Chimpanzee are much greater than those between the Chimpanzee and Man.

But why do we thus introduce the study of Darwin's "Descent of Man", which is to occupy us here, by insisting on the fact that Huxley had taken the field in defence of the descent of man in 1863, while Darwin's book on the subject did not appear till 1871? It is in order that we may clearly understand how it happened that from this time onwards Darwin and Huxley followed the same great aim in the most intimate association.

Huxley and Darwin working at the same *Problema maximum*! Huxley fiery, impetuous, eager for battle, contemptuous of the resistance of a dull world, or energetically triumphing over it. Darwin calm, weighing every problem slowly, letting it mature thoroughly,—not a fighter, yet having the greater and more lasting influence by virtue of his immense mass of critically sifted proofs. Darwin's friend, Huxley, was the first to do him justice, to understand his nature, and to find in it the reason why the detailed and carefully considered book on the descent of man made its appearance so late. Huxley,

always generous, never thought of claiming priority for himself. In enthusiastic language he tells how Darwin's immortal work, "The Origin of Species", first shed light for him on the problem of the descent of man; the recognition of a vera causa in the transformation of species illuminated his thoughts as with a flash. He was now content to leave what perplexed him, what he could not yet solve, as he says himself, "in the mighty hands of Darwin." Happy in the bustle of strife against old and deep-rooted prejudices, against intolerance and superstition, he wielded his sharp weapons on Darwin's behalf; wearing Darwin's armour he joyously overthrew adversary after adversary. Darwin spoke of Huxley as his "general agent." ("Life and Letters of Thomas Henry Huxley", Vol. I. page 171, London, 1900.) Huxley says of himself "I am Darwin's bulldog." (Ibid. page 363.)

Thus Huxley openly acknowledged that it was Darwin's "Origin of Species" that first set the problem of the descent of man in its true light, that made the question of the origin of the human race a pressing one. That this was the logical consequence of his book Darwin himself had long felt. He had been reproached with intentionally shirking the application of his theory to Man. Let us hear what he says on this point in his autobiography: "As soon as I had become, in the year 1837 or 1838, convinced that species were mutable productions, I could not avoid the belief that man must come under the same law. Accordingly I collected notes on the subject for my own satisfaction, and not for a long time with any intention of publishing. Although in the 'Origin of Species' the derivation of any particular species is never discussed, yet I thought it best, in order THAT NO HONOURABLE MAN SHOULD ACCUSE ME OF CONCEALING MY VIEWS (No italics in original.), to add that by the work 'light would be thrown on the origin of man and his history.' It would have been useless and injurious to the success of the book to have paraded, without giving any evidence, my conviction with respect to his origin." ("Life and Letters of Charles Darwin", Vol. I. page 93.)

In a letter written in January, 1860, to the Rev. L. Blomefield, Darwin expresses himself in similar terms. "With respect to man, I am very far from wishing to obtrude my belief; but I thought it dishonest to quite conceal my opinion." (Ibid. Vol. II. page 263.)

The brief allusion in the "Origin of Species" is so far from prominent and so incidental that it was excusable to assume that Darwin had not touched upon the descent of man in this work. It was solely the desire to have his mass of evidence sufficiently complete, solely Darwin's great characteristic of never publishing till he had carefully weighed all aspects of his subject for years, solely, in short, his most fastidious scientific conscience that restrained him from challenging the world in 1859 with a book in which the theory of the descent of man was fully set forth. Three years, frequently interrupted by ill-health, were needed for the actual writing of the book ("Life and Letters", Vol. I. page 94.): the first edition, which appeared in 1871, was followed in 1874 by a much improved second edition, the preparation of which he very reluctantly undertook. (Ibid. Vol. III. page 175.)

This, briefly, is the history of the work, which, with the "Origin of Species", marks an epoch in the history of biological sciences—the work with which the cautious, peace-loving investigator ventured forth from his contemplative life into the arena of strife and unrest, and laid himself open to all the annoyances that deep-rooted belief and prejudice, and the prevailing tendency of scientific thought at the time could devise.

Darwin did not take this step lightly. Of great interest in this connection is a letter written to Wallace on Dec. 22, 1857 (Ibid. Vol. II. page 109.), in which he says "You ask whether I shall discuss 'man.' I think I shall avoid the whole subject, as so surrounded with prejudices; though I fully admit that it is the highest and most interesting problem for the naturalist." But his conscientiousness compelled him to state briefly his opinion on the subject in the "Origin of Species" in 1859. Nevertheless he did not escape reproaches for having been so reticent. This is unmistakably apparent from a letter to Fritz Muller dated February 22 (1869?), in which he says: "I am thinking of writing a little essay on the Origin of Mankind, as I have been taunted with concealing my opinions." (Ibid. Vol. III. page 112.)

It might be thought that Darwin behaved thus hesitatingly, and was so slow in deciding on the full publication of his collected material in regard to the descent of man, because he had religious difficulties to overcome.

But this was not the case, as we can see from his admirable confession of faith, the publication of which we owe to his son Francis. (Ibid. Vol. I. pages 304-317.) Whoever wishes really to understand

the lofty character of this great man should read these immortal lines in which he unfolds to us in simple and straightforward words the development of his conception of the universe. He describes how, though he was still quite orthodox during his voyage round the world on board the "Beagle", he came gradually to see, shortly afterwards (1836-1839) that the Old Testament was no more to be trusted than the Sacred Books of the Hindoos; the miracles by which Christianity is supported, the discrepancies between the accounts in the different Gospels, gradually led him to disbelieve in Christianity as a divine revelation. "Thus," he writes ("Life and Letters", Vol. 1. page 309.), "disbelief crept over me at a very slow rate, but was at last complete. The rate was so slow that I felt no distress." But Darwin was too modest to presume to go beyond the limits laid down by science. He wanted nothing more than to be able to go, freely and unhampered by belief in authority or in the Bible, as far as human knowledge could lead him. We learn this from the concluding words of his chapter on religion: "The mystery of the beginning of all things is insoluble by us; and I for one must be content to remain an Agnostic." (Loc. cit. page 313.)

Darwin was always very unwilling to give publicity to his views in regard to religion. In a letter to Asa Gray on May 22, 1860 (Ibid. Vol. II. page 310.), he declares that it is always painful to him to have to enter into discussion of religious problems. He had, he said, no intention of writing atheistically.

Finally, let us cite one characteristic sentence from a letter from Darwin to C. Ridley (Ibid. Vol. III. page. 236. ("C. Ridley," Mr Francis Darwin points out to me, should be H.N. Ridley. A.C.S.)) (Nov. 28, 1878.) A clergyman, Dr Pusey, had asserted that Darwin had written the "Origin of Species" with some relation to theology. Darwin writes emphatically, "Many years ago, when I was collecting facts for the 'Origin', my belief in what is called a personal God was as firm as that of Dr Pusey himself, and as to the eternity of matter I never troubled myself about such insoluble questions." The expression "many years ago" refers to the time of his voyage round the world, as has already been pointed out. Darwin means by this utterance that the views which had gradually developed in his mind in regard to the origin of species were quite compatible with the faith of the Church.

If we consider all these utterances of Darwin in regard to religion and to his outlook on life (Weltanschauung), we shall see at least so much, that religious reflection could in no way have influenced him in regard to the writing and publishing of his book on "The Descent of Man". Darwin had early won for himself freedom of thought, and to this freedom he remained true to the end of his life, uninfluenced by the customs and opinions of the world around him.

Darwin was thus inwardly fortified and armed against the host of calumnies, accusations, and attacks called forth by the publication of the "Origin of Species", and to an even greater extent by the appearance of the "Descent of Man". But in his defence he could rely on the aid of a band of distinguished auxiliaries of the rarest ability. His faithful confederate, Huxley, was joined by the botanist Hooker, and, after longer resistance, by the famous geologist Lyell, whose "conversion" afforded Darwin peculiar satisfaction. All three took the field with enthusiasm in defence of the natural descent of man. From Wallace, on the other hand, though he shared with him the idea of natural selection, Darwin got no support in this matter. Wallace expressed himself in a strange manner. He admitted everything in regard to the morphological descent of man, but maintained, in a mystic way, that something else, something of a spiritual nature must have been added to what man inherited from his animal ancestors. Darwin, whose esteem for Wallace was extraordinarily high, could not understand how he could give utterance to such a mystical view in regard to man; the idea seemed to him so "incredibly strange" that he thought some one else must have added these sentences to Wallace's paper.

Even now there are thinkers who, like Wallace, shrink from applying to man the ultimate consequences of the theory of descent. The idea that man is derived from ape-like forms is to them unpleasant and humiliating.

So far I have been depicting the development of Darwin's work on the descent of man. In what follows I shall endeavour to give a condensed survey of the contents of the book.

It must at once be said that the contents of Darwin's work fall into two parts, dealing with entirely different subjects. "The Descent of Man" includes a very detailed investigation in regard to secondary sexual characters in the animal series, and on this investigation Darwin founded a new theory, that of sexual selection. With astonishing patience he gathered together an immense mass of material, and

showed, in regard to Arthropods and Vertebrates, the wide distribution of secondary characters, which develop almost exclusively in the male, and which enable him, on the one hand, to get the better of his rivals in the struggle for the female by the greater perfection of his weapons, and on the other hand, to offer greater allurements to the female through the higher development of decorative characters, of song, or of scent-producing glands. The best equipped males will thus crowd out the less well-equipped in the matter of reproduction, and thus the relevant characters will be increased and perfected through sexual selection. It is, of course, a necessary assumption that these secondary sexual characters may be transmitted to the female, although perhaps in rudimentary form.

As we have said, this theory of sexual selection takes up a great deal of space in Darwin's book, and it need only be considered here in so far as Darwin applied it to the descent of man. To this latter problem the whole of Part I is devoted, while Part III contains a discussion of sexual selection in relation to man, and a general summary. Part II treats of sexual selection in general, and may be disregarded in our present study. Moreover, many interesting details must necessarily be passed over in what follows, for want of space.

The first part of the "Descent of Man" begins with an enumeration of the proofs of the animal descent of man taken from the structure of the human body. Darwin chiefly emphasises the fact that the human body consists of the same organs and of the same tissues as those of the other mammals; he shows also that man is subject to the same diseases and tormented by the same parasites as the apes. He further dwells on the general agreement exhibited by young, embryonic forms, and he illustrates this by two figures placed one above the other, one representing a human embryo, after Eaker, the other a dog embryo, after Bischoff. ("Descent of Man" (Popular Edition, 1901), fig. 1, page 14.)

Darwin finds further proofs of the animal origin of man in the reduced structures, in themselves extremely variable, which are either absolutely useless to their possessors, or of so little use that they could never have developed under existing conditions. Of such vestiges he enumerates: the defective development of the panniculus carnosus (muscle of the skin) so widely distributed among mammals, the ear-muscles, the occasional persistence of the animal ear-point in man, the rudimentary nictitating membrane (plica semilunaris) in the human eye, the slight development of the organ of smell, the general hairiness of the human body, the frequently defective development or entire absence of the third molar (the wisdom tooth), the vermiform appendix, the occasional reappearance of a bony canal (foramen supracondyloideum) at the lower end of the humerus, the rudimentary tail of man (the so-called taillessness), and so on. Of these rudimentary structures the occasional occurrence of the animal ear-point in man is most fully discussed. Darwin's attention was called to this interesting structure by the sculptor Woolner. He figures such a case observed in man, and also the head of an alleged orang-foetus, the photograph of which he received from Nitsche.

Darwin's interpretation of Woolner's case as having arisen through a folding over of the free edge of a pointed ear has been fully borne out by my investigations on the external ear. (G. Schwalbe, "Das Darwin'sche Spitzohr beim menschlichen Embryo", "Anatom. Anzeiger", 1889, pages 176-189, and other papers.) In particular, it was established by these investigations that the human foetus, about the middle of its embryonic life, possesses a pointed ear somewhat similar to that of the monkey genus *Macacus*. One of Darwin's statements in regard to the head of the orang-foetus must be corrected. A LARGE ear with a point is shown in the photograph ("Descent of Man", fig.3, page 24.), but it can easily be demonstrated—and Deniker has already pointed this out—that the figure is not that of an orang-foetus at all, for that form has much smaller ears with no point; nor can it be a gibbon-foetus, as Deniker supposes, for the gibbon ear is also without a point. I myself regard it as that of a *Macacus*-embryo. But this mistake, which is due to Nitsche, in no way affects the fact recognised by Darwin, that ear-forms showing the point characteristic of the animal ear occur in man with extraordinary frequency.

Finally, there is a discussion of those rudimentary structures which occur only in ONE sex, such as the rudimentary mammary glands in the male, the vesicula prostatica, which corresponds to the uterus of the female, and others. All these facts tell in favour of the common descent of man and all other vertebrates. The conclusion of this section is characteristic: "IT IS ONLY OUR NATURAL PREJUDICE, AND THAT ARROGANCE WHICH MADE OUR FOREFATHERS DECLARE THAT THEY WERE DESCENDED FROM DEMI-GODS, WHICH LEADS US TO DEMUR TO THIS CONCLUSION. BUT THE TIME WILL BEFORE LONG COME, WHEN IT WILL BE THOUGHT

WONDERFUL THAT NATURALISTS, WHO WERE WELL ACQUAINTED WITH THE COMPARATIVE STRUCTURE AND DEVELOPMENT OF MAN, AND OTHER MAMMALS, SHOULD HAVE BELIEVED THAT EACH WAS THE WORK OF A SEPARATE ACT OF CREATION." (Ibid. page 36.)

In the second chapter there is a more detailed discussion, again based upon an extraordinary wealth of facts, of the problem as to the manner in which, and the causes through which, man evolved from a lower form. Precisely the same causes are here suggested for the origin of man, as for the origin of species in general. Variability, which is a necessary assumption in regard to all transformations, occurs in man to a high degree. Moreover, the rapid multiplication of the human race creates conditions which necessitate an energetic struggle for existence, and thus afford scope for the intervention of natural selection. Of the exercise of ARTIFICIAL selection in the human race, there is nothing to be said, unless we cite such cases as the grenadiers of Frederick William I, or the population of ancient Sparta. In the passages already referred to and in those which follow, the transmission of acquired characters, upon which Darwin does not dwell, is taken for granted. In man, direct effects of changed conditions can be demonstrated (for instance in regard to bodily size), and there are also proofs of the influence exerted on his physical constitution by increased use or disuse. Reference is here made to the fact, established by Forbes, that the Quechua-Indians of the high plateaus of Peru show a striking development of lungs and thorax, as a result of living constantly at high altitudes.

Such special forms of variation as arrests of development (microcephalism) and reversion to lower forms are next discussed. Darwin himself felt ("Descent of Man", page 54.) that these subjects are so nearly related to the cases mentioned in the first chapter, that many of them might as well have been dealt with there. It seems to me that it would have been better so, for the citation of additional instances of reversion at this place rather disturbs the logical sequence of his ideas as to the conditions which have brought about the evolution of man from lower forms. The instances of reversion here discussed are microcephalism, which Darwin wrongly interpreted as atavistic, supernumerary mammae, supernumerary digits, bicornuate uterus, the development of abnormal muscles, and so on. Brief mention is also made of correlative variations observed in man.

Darwin next discusses the question as to the manner in which man attained to the erect position from the state of a climbing quadruped. Here again he puts the influence of Natural Selection in the first rank. The immediate progenitors of man had to maintain a struggle for existence in which success was to the more intelligent, and to those with social instincts. The hand of these climbing ancestors, which had little skill and served mainly for locomotion, could only undergo further development when some early member of the Primate series came to live more on the ground and less among trees.

A bipedal existence thus became possible, and with it the liberation of the hand from locomotion, and the one-sided development of the human foot. The upright position brought about correlated variations in the bodily structure; with the free use of the hand it became possible to manufacture weapons and to use them; and this again resulted in a degeneration of the powerful canine teeth and the jaws, which were then no longer necessary for defence. Above all, however, the intelligence immediately increased, and with it skull and brain. The nakedness of man, and the absence of a tail (rudimentariness of the tail vertebrae) are next discussed. Darwin is inclined to attribute the nakedness of man, not to the action of natural selection on ancestors who originally inhabited a tropical land, but to sexual selection, which, for aesthetic reasons, brought about the loss of the hairy covering in man, or primarily in woman. An interesting discussion of the loss of the tail, which, however, man shares with the anthropoid apes, some other monkeys and lemurs, forms the conclusion of the almost superabundant material which Darwin worked up in the second chapter. His object was to show that some of the most distinctive human characters are in all probability directly or indirectly due to natural selection. With characteristic modesty he adds ("Descent of Man", page 92.): "Hence, if I have erred in giving to natural selection great power, which I am very far from admitting, or in having exaggerated its power, which is in itself probable, I have at least, as I hope, done good service in aiding to overthrow the dogma of separate creations." At the end of the chapter he touches upon the objection as to man's helpless and defenceless condition. Against this he urges his intelligence and social instincts.

The two following chapters contain a detailed discussion of the objections drawn from the supposed great differences between the mental powers of men and animals. Darwin at once admits that the

differences are enormous, but not that any fundamental difference between the two can be found. Very characteristic of him is the following passage: "In what manner the mental powers were first developed in the lowest organisms, is as hopeless an enquiry as how life itself first originated. These are problems for the distant future, if they are ever to be solved by man." (Ibid. page 100.)

After some brief observations on instinct and intelligence, Darwin brings forward evidence to show that the greater number of the emotional states, such as pleasure and pain, happiness and misery, love and hate are common to man and the higher animals. He goes on to give various examples showing that wonder and curiosity, imitation, attention, memory and imagination (dreams of animals), can also be observed in the higher mammals, especially in apes. In regard even to reason there are no sharply defined limits. A certain faculty of deliberation is characteristic of some animals, and the more thoroughly we know an animal the more intelligence we are inclined to credit it with. Examples are brought forward of the intelligent and deliberate actions of apes, dogs and elephants. But although no sharply defined differences exist between man and animals, there is, nevertheless, a series of other mental powers which are characteristics usually regarded as absolutely peculiar to man. Some of these characteristics are examined in detail, and it is shown that the arguments drawn from them are not conclusive. Man alone is said to be capable of progressive improvement; but against this must be placed as something analogous in animals, the fact that they learn cunning and caution through long continued persecution. Even the use of tools is not in itself peculiar to man (monkeys use sticks, stones and twigs), but man alone fashions and uses implements **DESIGNED FOR A SPECIAL PURPOSE**. In this connection the remarks taken from Lubbock in regard to the origin and gradual development of the earliest flint implements will be read with interest; these are similar to the observations on modern eoliths, and their bearing on the development of the stone-industry. It is interesting to learn from a letter to Hooker ("Life and Letters", Vol. II. page 161, June 22, 1859.), that Darwin himself at first doubted whether the stone implements discovered by Boucher de Perthes were really of the nature of tools. With the relentless candour as to himself which characterised him, he writes four years later in a letter to Lyell in regard to this view of Boucher de Perthes' discoveries: "I know something about his errors, and looked at his book many years ago, and am ashamed to think that I concluded the whole was rubbish! Yet he has done for man something like what Agassiz did for glaciers." (Ibid. Vol. III. page 15, March 17, 1863.)

To return to Darwin's further comparisons between the higher mental powers of man and animals. He takes much of the force from the argument that man alone is capable of abstraction and self-consciousness by his own observations on dogs. One of the main differences between man and animals, speech, receives detailed treatment. He points out that various animals (birds, monkeys, dogs) have a large number of different sounds for different emotions, that, further, man produces in common with animals a whole series of inarticulate cries combined with gestures, and that dogs learn to understand whole sentences of human speech. In regard to human language, Darwin expresses a view contrary to that held by Max Muller ("Descent of Man", page 132.): "I cannot doubt that language owes its origin to the imitation and modification of various natural sounds, the voices of other animals, and man's own instinctive cries, aided by signs and gestures." The development of actual language presupposes a higher degree of intelligence than is found in any kind of ape. Darwin remarks on this point (Ibid. pages 136, 137.): "The fact of the higher apes not using their vocal organs for speech no doubt depends on their intelligence not having been sufficiently advanced."

The sense of beauty, too, has been alleged to be peculiar to man. In refutation of this assertion Darwin points to the decorative colours of birds, which are used for display. And to the last objection, that man alone has religion, that he alone has a belief in God, it is answered "that numerous races have existed, and still exist, who have no idea of one or more gods, and who have no words in their languages to express such an idea." (Ibid. page 143.)

The result of the investigations recorded in this chapter is to show that, great as the difference in mental powers between man and the higher animals may be, it is undoubtedly only a difference "of degree and not of kind." ("Descent of Man", page 193.)

In the fourth chapter Darwin deals with the **MORAL SENSE** or **CONSCIENCE**, which is the most important of all differences between man and animals. It is a result of social instincts, which lead to sympathy for other members of the same society, to non-egoistic actions for the good of others. Darwin

shows that social tendencies are found among many animals, and that among these love and kin-sympathy exist, and he gives examples of animals (especially dogs) which may exhibit characters that we should call moral in man (e.g. disinterested self-sacrifice for the sake of others). The early ape-like progenitors of the human race were undoubtedly social. With the increase of intelligence the moral sense develops farther; with the acquisition of speech public opinion arises, and finally, moral sense becomes habit. The rest of Darwin's detailed discussions on moral philosophy may be passed over.

The fifth chapter may be very briefly summarised. In it Darwin shows that the intellectual and moral faculties are perfected through natural selection. He inquires how it can come about that a tribe at a low level of evolution attains to a higher, although the best and bravest among them often pay for their fidelity and courage with their lives without leaving any descendants. In this case it is the sentiment of glory, praise and blame, the admiration of others, which bring about the increase of the better members of the tribe. Property, fixed dwellings, and the association of families into a community are also indispensable requirements for civilisation. In the longer second section of the fifth chapter Darwin acts mainly as recorder. On the basis of numerous investigations, especially those of Greg, Wallace, and Galton, he inquires how far the influence of natural selection can be demonstrated in regard to civilised nations. In the final section, which deals with the proofs that all civilised nations were once barbarians, Darwin again uses the results gained by other investigators, such as Lubbock and Tylor. There are two sets of facts which prove the proposition in question. In the first place, we find traces of a former lower state in the customs and beliefs of all civilised nations, and in the second place, there are proofs to show that savage races are independently able to raise themselves a few steps in the scale of civilisation, and that they have thus raised themselves.

In the sixth chapter of the work, Morphology comes into the foreground once more. Darwin first goes back, however, to the argument based on the great difference between the mental powers of the highest animals and those of man. That this is only quantitative, not qualitative, he has already shown. Very instructive in this connection is the reference to the enormous difference in mental powers in another class. No one would draw from the fact that the cochineal insect (*Coccus*) and the ant exhibit enormous differences in their mental powers, the conclusion that the ant should therefore be regarded as something quite distinct, and withdrawn from the class of insects altogether.

Darwin next attempts to establish the SPECIFIC genealogical tree of man, and carefully weighs the differences and resemblances between the different families of the Primates. The erect position of man is an adaptive character, just as are the various characters referable to aquatic life in the seals, which, notwithstanding these, are ranked as a mere family of the Carnivores. The following utterance is very characteristic of Darwin ("Descent of Man", page 231.): "If man had not been his own classifier, he would never have thought of founding a separate order for his own reception." In numerous characters not mentioned in systematic works, in the features of the face, in the form of the nose, in the structure of the external ear, man resembles the apes. The arrangement of the hair in man has also much in common with the apes; as also the occurrence of hair on the forehead of the human embryo, the beard, the convergence of the hair of the upper and under arm towards the elbow, which occurs not only in the anthropoid apes, but also in some American monkeys. Darwin here adopts Wallace's explanation of the origin of the ascending direction of the hair in the forearm of the orang,—that it has arisen through the habit of holding the hands over the head in rain. But this explanation cannot be maintained when we consider that this disposition of the hair is widely distributed among the most different mammals, being found in the dog, in the sloth, and in many of the lower monkeys.

After further careful analysis of the anatomical characters Darwin reaches the conclusion that the New World monkeys (Platyrrhine) may be excluded from the genealogical tree altogether, but that man is an offshoot from the Old World monkeys (Catarrhine) whose progenitors existed as far back as the Miocene period. Among these Old World monkeys the forms to which man shows the greatest resemblance are the anthropoid apes, which, like him, possess neither tail nor ischial callosities. The platyrrhine and catarrhine monkeys have their primitive ancestor among extinct forms of the Lemnidae. Darwin also touches on the question of the original home of the human race and supposes that it may have been in Africa, because it is there that man's nearest relatives, the gorilla and the chimpanzee, are found. But he regards speculation on this point as useless. It is remarkable that, in this connection, Darwin regards the loss of the hair-covering in man as having some relation to a warm

climate, while elsewhere he is inclined to make sexual selection responsible for it. Darwin recognises the great gap between man and his nearest relatives, but similar gaps exist at other parts of the mammalian genealogical tree: the allied forms have become extinct. After the extermination of the lower races of mankind, on the one hand, and of the anthropoid apes on the other, which will undoubtedly take place, the gulf will be greater than ever, since the baboons will then bound it on the one side, and the white races on the other. Little weight need be attached to the lack of fossil remains to fill up this gap, since the discovery of these depends upon chance. The last part of the chapter is devoted to a discussion of the earlier stages in the genealogy of man. Here Darwin accepts in the main the genealogical tree, which had meantime been published by Haeckel, who traces the pedigree back through Monotremes, Reptiles, Amphibians, and Fishes, to Amphioxus.

Then follows an attempt to reconstruct, from the atavistic characters, a picture of our primitive ancestor who was undoubtedly an arboreal animal. The occurrence of rudiments of parts in one sex which only come to full development in the other is next discussed. This state of things Darwin regards as derived from an original hermaphroditism. In regard to the mammary glands of the male he does not accept the theory that they are vestigial, but considers them rather as not fully developed.

The last chapter of Part I deals with the question whether the different races of man are to be regarded as different species, or as sub-species of a race of monophyletic origin. The striking differences between the races are first emphasised, and the question of the fertility or infertility of hybrids is discussed. That fertility is the more usual is shown by the excessive fertility of the hybrid population of Brazil. This, and the great variability of the distinguishing characters of the different races, as well as the fact that all grades of transition stages are found between these, while considerable general agreement exists, tell in favour of the unity of the races and lead to the conclusion that they all had a common primitive ancestor.

Darwin therefore classifies all the different races as sub-species of ONE AND THE SAME SPECIES. Then follows an interesting inquiry into the reasons for the extinction of human races. He recognises as the ultimate reason the injurious effects of a change of the conditions of life, which may bring about an increase in infantile mortality, and a diminished fertility. It is precisely the reproductive system, among animals also, which is most susceptible to changes in the environment.

The final section of this chapter deals with the formation of the races of mankind. Darwin discusses the question how far the direct effect of different conditions of life, or the inherited effects of increased use or disuse may have brought about the characteristic differences between the different races. Even in regard to the origin of the colour of the skin he rejects the transmitted effects of an original difference of climate as an explanation. In so doing he is following his tendency to exclude Lamarckian explanations as far as possible. But here he makes gratuitous difficulties from which, since natural selection fails, there is no escape except by bringing in the principle of sexual selection, to which, he regarded it as possible, skin-colouring, arrangement of hair, and form of features might be traced. But with his characteristic conscientiousness he guards himself thus: "I do not intend to assert that sexual selection will account for all the differences between the races." ("Descent of Man", page 308.)

I may be permitted a remark as to Darwin's attitude towards Lamarck. While, at an earlier stage, when he was engaged in the preliminary labours for his immortal work, "The Origin of Species", Darwin expresses himself very forcibly against the views of Lamarck, speaking of Lamarckian "nonsense," ("Life and Letters", Vol. II. page 23.), and of Lamarck's "absurd, though clever work" (Loc. cit. page 39.) and expressly declaring, "I attribute very little to the direct action of climate, etc." (Loc. cit. (1856), page 82.) yet in later life he became more and more convinced of the influence of external conditions. In 1876, that is, two years after the appearance of the second edition of "The Descent of Man", he writes with his usual candid honesty: "In my opinion the greatest error which I have committed, has been not allowing sufficient weight to the direct action of the environment, i.e. food, climate, etc. independently of natural selection." (Ibid. Vol. III. page 159.) It is certain from this change of opinion that, if he had been able to make up his mind to issue a third edition of "The Descent of Man", he would have ascribed a much greater influence to the effect of external conditions in explaining the different characters of the races of man than he did in the second edition. He would also undoubtedly have attributed less influence to sexual selection as a factor in the origin of the different bodily characteristics, if indeed he would not have excluded it altogether.

In Part III of the "Descent" two additional chapters are devoted to the discussion of sexual selection in relation to man. These may be very briefly referred to. Darwin here seeks to show that sexual selection has been operative on man and his primitive progenitor. Space fails me to follow out his interesting arguments. I can only mention that he is inclined to trace back hairlessness, the development of the beard in man, and the characteristic colour of the different human races to sexual selection. Since bareness of the skin could be no advantage, but rather a disadvantage, this character cannot have been brought about by natural selection. Darwin also rejected a direct influence of climate as a cause of the origin of the skin-colour. I have already expressed the opinion, based on the development of his views as shown in his letters, that in a third edition Darwin would probably have laid more stress on the influence of external environment. He himself feels that there are gaps in his proofs here, and says in self-criticism: "The views here advanced, on the part which sexual selection has played in the history of man, want scientific precision." ("Descent of Man", page 924.) I need here only point out that it is impossible to explain the graduated stages of skin-colour by sexual selection, since it would have produced races sharply defined by their colour and not united to other races by transition stages, and this, it is well known, is not the case. Moreover, the fact established by me ("Die Hautfarbe des Menschen", "Mitteilungen der Anthropologischen Gesellschaft in Wien", Vol. XXXIV. pages 331-352.), that in all races the ventral side of the trunk is paler than the dorsal side, and the inner surface of the extremities paler than the outer side, cannot be explained by sexual selection in the Darwinian sense.

With this I conclude my brief survey of the rich contents of Darwin's book. I may be permitted to conclude by quoting the magnificent final words of "The Descent of Man": "We must, however, acknowledge, as it seems to me, that man, with all his noble qualities, with sympathy which feels for the most debased, with benevolence which extends not only to other men but to the humblest living creature, with his god-like intellect which has penetrated into the movements and constitution of the solar system—with all these exalted powers—Man still bears in his bodily frame the indelible stamp of his lowly origin." (Ibid. page 947.)

What has been the fate of Darwin's doctrines since his great achievement? How have they been received and followed up by the scientific and lay world? And what do the successors of the mighty hero and genius think now in regard to the origin of the human race?

At the present time we are incomparably more favourably placed than Darwin was for answering this question of all questions. We have at our command an incomparably greater wealth of material than he had at his disposal. And we are more fortunate than he in this respect, that we now know transition-forms which help to fill up the gap, still great, between the lowest human races and the highest apes. Let us consider for a little the more essential additions to our knowledge since the publication of "The Descent of Man".

Since that time our knowledge of animal embryos has increased enormously. While Darwin was obliged to content himself with comparing a human embryo with that of a dog, there are now available the youngest embryos of monkeys of all possible groups (Orang, Gibbon, Semnopithecus, Macacus), thanks to Selenka's most successful tour in the East Indies in search of such material. We can now compare corresponding stages of the lower monkeys and of the Anthropoid apes with human embryos, and convince ourselves of their great resemblance to one another, thus strengthening enormously the armour prepared by Darwin in defence of his view on man's nearest relatives. It may be said that Selenka's material fills up the blanks in Darwin's array of proofs in the most satisfactory manner.

The deepening of our knowledge of comparative anatomy also gives us much surer foundations than those on which Darwin was obliged to build. Just of late there have been many workers in the domain of the anatomy of apes and lemurs, and their investigations extend to the most different organs. Our knowledge of fossil apes and lemurs has also become much wider and more exact since Darwin's time: the fossil lemurs have been especially worked up by Cope, Forsyth Major, Ameghino, and others. Darwin knew very little about fossil monkeys. He mentions two or three anthropoid apes as occurring in the Miocene of Europe ("Descent of Man", page 240.), but only names *Dryopithecus*, the largest form from the Miocene of France. It was erroneously supposed that this form was related to *Hylobates*. We now know not only a form that actually stands near to the gibbon (*Pliopithecus*), and remains of other anthropoids (*Pliohylobates* and the fossil chimpanzee, *Palaeopithecus*), but also several lower

catarrhine monkeys, of which *Mesopithecus*, a form nearly related to the modern Sacred Monkeys (a species of *Semnopithecus*) and found in strata of the Miocene period in Greece, is the most important. Quite recently, too, Ameghino's investigations have made us acquainted with fossil monkeys from South America (*Anthropops*, *Homunculus*), which, according to their discoverer, are to be regarded as in the line of human descent.

What Darwin missed most of all—intermediate forms between apes and man—has been recently furnished. (E. Dubois, as is well known, discovered in 1893, near Trinil in Java, in the alluvial deposits of the river Bengawan, an important form represented by a skull-cap, some molars, and a femur. His opinion—much disputed as it has been—that in this form, which he named *Pithecanthropus*, he has found a long-desired transition-form is shared by the present writer. And although the geological age of these fossils, which, according to Dubois, belong to the uppermost Tertiary series, the Pliocene, has recently been fixed at a later date (the older Diluvium)), the MORPHOLOGICAL VALUE of these interesting remains, that is, the intermediate position of *Pithecanthropus*, still holds good. Volz says with justice ("Das geologische Alter der *Pithecanthropus*-Schichten bei Trinil, Ost-Java". "Neues Jahrb. f. Mineralogie". Festband, 1907.), that even if *Pithecanthropus* is not THE missing link, it is undoubtedly *A* missing link.

As on the one hand there has been found in *Pithecanthropus* a form which, though intermediate between apes and man, is nevertheless more closely allied to the apes, so on the other hand, much progress has been made since Darwin's day in the discovery and description of the older human remains. Since the famous roof of a skull and the bones of the extremities belonging to it were found in 1856 in the Neandertal near Dusseldorf, the most varied judgments have been expressed in regard to the significance of the remains and of the skull in particular. In Darwin's "Descent of Man" there is only a passing allusion to them ("Descent of Man", page 82.) in connection with the discussion of the skull-capacity, although the investigations of Schaaffhausen, King, and Huxley were then known. I believe I have shown, in a series of papers, that the skull in question belongs to a form different from any of the races of man now living, and, with King and Cope, I regard it as at least a different species from living man, and have therefore designated it *Homo primigenius*. The form unquestionably belongs to the older Diluvium, and in the later Diluvium human forms already appear, which agree in all essential points with existing human races.

As far back as 1886 the value of the Neandertal skull was greatly enhanced by Fraipont's discovery of two skulls and skeletons from Spy in Belgium. These are excellently described by their discoverer ("La race humaine de Neanderthal ou de Canstatt en Belgique". "Arch. de Biologie", VII. 1887.), and are regarded as belonging to the same group of forms as the Neandertal remains. In 1899 and the following years came the discovery by Gorjanovic-Kramberger of different skeletal parts of at least ten individuals in a cave near Krapina in Croatia. (Gorjanovic-Kramberger "Der diluviale Mensch von Krapina in Kroatien", 1906.) It is in particular the form of the lower jaw which is different from that of all recent races of man, and which clearly indicates the lowly position of *Homo primigenius*, while, on the other hand, the long-known skull from Gibraltar, which I ("Studien zur Vorgeschichte des Menschen", 1906, pages 154 ff.) have referred to *Homo primigenius*, and which has lately been examined in detail by Sollas ("On the cranial and facial characters of the Neandertal Race". "Trans. R. Soc." London, vol. 199, 1908, page 281.), has made us acquainted with the surprising shape of the eye-orbit, of the nose, and of the whole upper part of the face. Isolated lower jaws found at La Naulette in Belgium, and at Malarnaud in France, increase our material which is now as abundant as could be desired. The most recent discovery of all is that of a skull dug up in August of this year (1908) by Klaatsch and Hauser in the lower grotto of the Le Moustier in Southern France, but this skull has not yet been fully described. Thus *Homo primigenius* must also be regarded as occupying a position in the gap existing between the highest apes and the lowest human races, *Pithecanthropus*, standing in the lower part of it, and *Homo primigenius* in the higher, near man. In order to prevent misunderstanding, I should like here to emphasise that in arranging this structural series—anthropoid apes, *Pithecanthropus*, *Homo primigenius*, *Homo sapiens*—I have no intention of establishing it as a direct genealogical series. I shall have something to say in regard to the genetic relations of these forms, one to another, when discussing the different theories of descent current at the present day. ((Since this essay was written Schoetensack has discovered near Heidelberg and briefly described an exceedingly interesting lower

jaw from rocks between the Pliocene and Diluvial beds. This exhibits interesting differences from the forms of lower jaw of *Homo primigenius*. (Schoetensack "*Der Unterkiefer des Homo heidelbergensis*". Leipzig, 1908.) G.S.))

In quite a different domain from that of morphological relationship, namely in the physiological study of the blood, results have recently been gained which are of the highest importance to the doctrine of descent. Uhlenhuth, Nuttall, and others have established the fact that the blood-serum of a rabbit which has previously had human blood injected into it, forms a precipitate with human blood. This biological reaction was tried with a great variety of mammalian species, and it was found that those far removed from man gave no precipitate under these conditions. But as in other cases among mammals all nearly related forms yield an almost equally marked precipitate, so the serum of a rabbit treated with human blood and then added to the blood of an anthropoid ape gives ALMOST as marked a precipitate as in human blood; the reaction to the blood of the lower Eastern monkeys is weaker, that to the Western monkeys weaker still; indeed in this last case there is only a slight clouding after a considerable time and no actual precipitate. The blood of the Lemuridae (Nuttall) gives no reaction or an extremely weak one, that of the other mammals none whatever. We have in this not only a proof of the literal blood-relationship between man and apes, but the degree of relationship with the different main groups of apes can be determined beyond possibility of mistake.

Finally, it must be briefly mentioned that in regard to remains of human handicraft also, the material at our disposal has greatly increased of late years, that, as a result of this, the opinions of archaeologists have undergone many changes, and that, in particular, their views in regard to the age of the human race have been greatly influenced. There is a tendency at the present time to refer the origin of man back to Tertiary times. It is true that no remains of Tertiary man have been found, but flints have been discovered which, according to the opinion of most investigators, bear traces either of use, or of very primitive workmanship. Since Rutot's time, following Mortillet's example, investigators have called these "eoliths," and they have been traced back by Verworn to the Miocene of the Auvergne, and by Rutot even to the upper Oligocene. Although these eoliths are even nowadays the subject of many different views, the preoccupation with them has kept the problem of the age of the human race continually before us.

Geology, too, has made great progress since the days of Darwin and Lyell, and has endeavoured with satisfactory results to arrange the human remains of the Diluvial period in chronological order (Penck). I do not intend to enter upon the question of the primitive home of the human race; since the space at my disposal will not allow of my touching even very briefly upon all the departments of science which are concerned in the problem of the descent of man. How Darwin would have rejoiced over each of the discoveries here briefly outlined! What use he would have made of the new and precious material, which would have prevented the discouragement from which he suffered when preparing the second edition of "*The Descent of Man*"! But it was not granted to him to see this progress towards filling up the gaps in his edifice of which he was so painfully conscious.

He did, however, have the satisfaction of seeing his ideas steadily gaining ground, notwithstanding much hostility and deep-rooted prejudice. Even in the years between the appearance of "*The Origin of Species*" and of the first edition of the "*Descent*", the idea of a natural descent of man, which was only briefly indicated in the work of 1859, had been eagerly welcomed in some quarters. It has been already pointed out how brilliantly Huxley contributed to the defence and diffusion of Darwin's doctrines, and how in "*Man's Place in Nature*" he has given us a classic work as a foundation for the doctrine of the descent of man. As Huxley was Darwin's champion in England, so in Germany Carl Vogt, in particular, made himself master of the Darwinian ideas. But above all it was Haeckel who, in energy, eagerness for battle, and knowledge may be placed side by side with Huxley, who took over the leadership in the controversy over the new conception of the universe. As far back as 1866, in his "*Generelle Morphologie*", he had inquired minutely into the question of the descent of man, and not content with urging merely the general theory of descent from lower animal forms, he drew up for the first time genealogical trees showing the close relationships of the different animal groups; the last of these illustrated the relationships of Mammals, and among them of all groups of the Primates, including man. It was Haeckel's genealogical trees that formed the basis of the special discussion of the relationships of man, in the sixth chapter of Darwin's "*Descent of Man*".

In the last section of this essay I shall return to Haeckel's conception of the special descent of man, the main features of which he still upholds, and rightly so. Haeckel has contributed more than any one else to the spread of the Darwinian doctrine.

I can only allow myself a few words as to the spread of the theory of the natural descent of man in other countries. The Parisian anthropological school, founded and guided by the genius of Broca, took up the idea of the descent of man, and made many notable contributions to it (Broca, Manouvrier, Mahoudeau, Deniker and others). In England itself Darwin's work did not die. Huxley took care of that, for he, with his lofty and unprejudiced mind, dominated and inspired English biology until his death on June 29, 1895. He had the satisfaction shortly before his death of learning of Dubois' discovery, which he illustrated by a humorous sketch. ("Life and Letters of Thomas Henry Huxley", Vol. II. page 394.) But there are still many followers in Darwin's footsteps in England. Keane has worked at the special genealogical tree of the Primates; Keith has inquired which of the anthropoid apes has the greatest number of characters in common with man; Morris concerns himself with the evolution of man in general, especially with his acquisition of the erect position. The recent discoveries of *Pithecanthropus* and *Homo primigenius* are being vigorously discussed; but the present writer is not in a position to form an opinion of the extent to which the idea of descent has penetrated throughout England generally.

In Italy independent work in the domain of the descent of man is being produced, especially by Morselli; with him are associated, in the investigation of related problems, Sergi and Giuffrida-Ruggeri. From the ranks of American investigators we may single out in particular the eminent geologist Cope, who championed with much decision the idea of the specific difference of *Homo neandertalensis* (*primigenius*) and maintained a more direct descent of man from the fossil *Lemuridae*. In South America too, in Argentina, new life is stirring in this department of science. Ameghino in Buenos Ayres has awakened the fossil primates of the Pampas formation to new life; he even believes that in *Tetraprothomo*, represented by a femur, he has discovered a direct ancestor of man. Lehmann-Nitsche is working at the other side of the gulf between apes and men, and he describes a remarkable first cervical vertebra (atlas) from Monte Hermoso as belonging to a form which may bear the same relation to *Homo sapiens* in South America as *Homo primigenius* does in the Old World. After a minute investigation he establishes a human species *Homo neogaeus*, while Ameghino ascribes this atlas vertebra to his *Tetraprothomo*.

Thus throughout the whole scientific world there is arising a new life, an eager endeavour to get nearer to Huxley's *problema maximum*, to penetrate more deeply into the origin of the human race. There are to-day very few experts in anatomy and zoology who deny the animal descent of man in general. Religious considerations, old prejudices, the reluctance to accept man, who so far surpasses mentally all other creatures, as descended from "soulless" animals, prevent a few investigators from giving full adherence to the doctrine. But there are very few of these who still postulate a special act of creation for man. Although the majority of experts in anatomy and zoology accept unconditionally the descent of man from lower forms, there is much diversity of opinion among them in regard to the special line of descent.

In trying to establish any special hypothesis of descent, whether by the graphic method of drawing up genealogical trees or otherwise, let us always bear in mind Darwin's words ("Descent of Man", page 229.) and use them as a critical guiding line: "As we have no record of the lines of descent, the pedigree can be discovered only by observing the degrees of resemblance between the beings which are to be classed." Darwin carries this further by stating "that resemblances in several unimportant structures, in useless and rudimentary organs, or not now functionally active, or in an embryological condition, are by far the most serviceable for classification." (Loc. cit.) It has also to be remembered that NUMEROUS separate points of agreement are of much greater importance than the amount of similarity or dissimilarity in a few points.

The hypotheses as to descent current at the present day may be divided into two main groups. The first group seeks for the roots of the human race not among any of the families of the apes—the anatomically nearest forms—nor among their very similar but less specialised ancestral forms, the fossil representatives of which we can know only in part, but, setting the monkeys on one side, it seeks for them lower down among the fossil Eocene *Pseudo-lemuridae* or *Lemuridae* (Cope), or even among the primitive pentadactylous Eocene forms, which may either have led directly to the evolution of man

(Adloff), or have given rise to an ancestral form common to apes and men (Klaatsch (Klaatsch in his last publications speaks in the main only of an ancestral form common to men and anthropoid apes.), Giuffrida-Ruggeri). The common ancestral form, from which man and apes are thus supposed to have arisen independently, may explain the numerous resemblances which actually exist between them. That is to say, all the characters upon which the great structural resemblance between apes and man depends must have been present in their common ancestor. Let us take an example of such a common character. The bony external ear-passage is in general as highly developed in the lower Eastern monkeys and the anthropoid apes as in man. This character must, therefore, have already been present in the common primitive form. In that case it is not easy to understand why the Western monkeys have not also inherited the character, instead of possessing only a tympanic ring. But it becomes more intelligible if we assume that forms with a primitive tympanic ring were the original type, and that from these were evolved, on the one hand, the existing New World monkeys with persistent tympanic ring, and on the other an ancestral form common to the lower Old World monkeys, the anthropoid apes and man. For man shares with these the character in question, and it is also one of the "unimportant" characters required by Darwin. Thus we have two divergent lines arising from the ancestral form, the Western monkeys (Platyrrhine) on the one hand, and an ancestral form common to the lower Eastern monkeys, the anthropoid apes, and man, on the other. But considerations similar to those which showed it to be impossible that man should have developed from an ancestor common to him and the monkeys, yet outside of and parallel with these, may be urged also against the likelihood of a parallel evolution of the lower Eastern monkeys, the anthropoid apes, and man. The anthropoid apes have in common with man many characters which are not present in the lower Old World monkeys. These characters must therefore have been present in the ancestral form common to the three groups. But here, again, it is difficult to understand why the lower Eastern monkeys should not also have inherited these characters. As this is not the case, there remains no alternative but to assume divergent evolution from an indifferent form. The lower Eastern monkeys are carrying on the evolution in one direction—I might almost say towards a blind alley—while anthropoids and men have struck out a progressive path, at first in common, which explains the many points of resemblance between them, without regarding man as derived directly from the anthropoids. Their many striking points of agreement indicate a common descent, and cannot be explained as phenomena of convergence.

I believe I have shown in the above sketch that a theory which derives man directly from lower forms without regarding apes as transition-types leads ad absurdum. The close structural relationship between man and monkeys can only be understood if both are brought into the same line of evolution. To trace man's line of descent directly back to the old Eocene mammals, alongside of, but with no relation to these very similar forms, is to abandon the method of exact comparison, which, as Darwin rightly recognised, alone justifies us in drawing up genealogical trees on the basis of resemblances and differences. The farther down we go the more does the ground slip from beneath our feet. Even the Lemuridae show very numerous divergent conditions, much more so the Eocene mammals (Creodonta, Condylarthra), the chief resemblance of which to man consists in the possession of pentadactylous hands and feet! Thus the farther course of the line of descent disappears in the darkness of the ancestry of the mammals. With just as much reason we might pass by the Vertebrates altogether, and go back to the lower Invertebrates, but in that case it would be much easier to say that man has arisen independently, and has evolved, without relation to any animals, from the lowest primitive form to his present isolated and dominant position. But this would be to deny all value to classification, which must after all be the ultimate basis of a genealogical tree. We can, as Darwin rightly observed, only infer the line of descent from the degree of resemblance between single forms. If we regard man as directly derived from primitive forms very far back, we have no way of explaining the many points of agreement between him and the monkeys in general, and the anthropoid apes in particular. These must remain an inexplicable marvel.

I have thus, I trust, shown that the first class of special theories of descent, which assumes that man has developed, parallel with the monkeys, but without relation to them, from very low primitive forms cannot be upheld, because it fails to take into account the close structural affinity of man and monkeys. I cannot but regard this hypothesis as lamentably retrograde, for it makes impossible any application of the facts that have been discovered in the course of the anatomical and embryological study of man and monkeys, and indeed prejudices investigations of that class as pointless. The whole method is perverted;

an unjustifiable theory of descent is first formulated with the aid of the imagination, and then we are asked to declare that all structural relations between man and monkeys, and between the different groups of the latter, are valueless,—the fact being that they are the only true basis on which a genealogical tree can be constructed.

So much for this most modern method of classification, which has probably found adherents because it would deliver us from the relationship to apes which many people so much dislike. In contrast to it we have the second class of special hypotheses of descent, which keeps strictly to the nearest structural relationships. This is the only basis that justifies the drawing up of a special hypothesis of descent. If this fundamental proposition be recognised, it will be admitted that the doctrine of special descent upheld by Haeckel, and set forth in Darwin's "Descent of Man", is still valid to-day. In the genealogical tree, man's place is quite close to the anthropoid apes; these again have as their nearest relatives the lower Old World monkeys, and their progenitors must be sought among the less differentiated Platyrrhine monkeys, whose most important characters have been handed on to the present day New World monkeys. How the different genera are to be arranged within the general scheme indicated depends in the main on the classificatory value attributed to individual characters. This is particularly true in regard to *Pithecanthropus*, which I consider as the root of a branch which has sprung from the anthropoid ape root and has led up to man; the latter I have designated the family of the *Hominidae*.

For the rest, there are, as we have said, various possible ways of constructing the narrower genealogy within the limits of this branch including men and apes, and these methods will probably continue to change with the accumulation of new facts. Haeckel himself has modified his genealogical tree of the Primates in certain details since the publication of his "Generelle Morphologie" in 1866, but its general basis remains the same. (Haeckel's latest genealogical tree is to be found in his most recent work, "Unsere Ahnenreihe". Jena, 1908.) All the special genealogical trees drawn up on the lines laid down by Haeckel and Darwin—and that of Dubois may be specially mentioned—are based, in general, on the close relationship of monkeys and men, although they may vary in detail. Various hypotheses have been formulated on these lines, with special reference to the evolution of man. "*Pithecanthropus*" is regarded by some authorities as the direct ancestor of man, by others as a side-track failure in the attempt at the evolution of man. The problem of the monophyletic or polyphyletic origin of the human race has also been much discussed. Sergi (Sergi G. "Europa", 1908.) inclines towards the assumption of a polyphyletic origin of the three main races of man, the African primitive form of which has given rise also to the gorilla and chimpanzee, the Asiatic to the Orang, the Gibbon, and *Pithecanthropus*. Kollmann regards existing human races as derived from small primitive races (pigmies), and considers that *Homo primigenius* must have arisen in a secondary and degenerative manner.

But this is not the place, nor have I the space to criticise the various special theories of descent. One, however, must receive particular notice. According to Ameghino, the South American monkeys (*Pitheculites*) from the oldest Tertiary of the Pampas are the forms from which have arisen the existing American monkeys on the one hand, and on the other, the extinct South American *Homunculidae*, which are also small forms. From these last, anthropoid apes and man have, he believes, been evolved. Among the progenitors of man, Ameghino reckons the form discovered by him (*Tetraprothomo*), from which a South American primitive man, *Homo pampaeus*, might be directly evolved, while on the other hand all the lower Old World monkeys may have arisen from older fossil South American forms (*Clenialitidae*), the distribution of which may be explained by the bridge formerly existing between South America and Africa, as may be the derivation of all existing human races from *Homo pampaeus*. (See Ameghino's latest paper, "Notas preliminares sobre el *Tetraprothomo argentinus*", etc. "Anales del Museo nacional de Buenos Aires", XVI. pages 107-242, 1907.) The fossil forms discovered by Ameghino deserve the most minute investigation, as does also the fossil man from South America of which Lehmann-Nitsche ("Nouvelles recherches sur la formation pampeenne et l'homme fossile de la Republique Argentine". "Revista del Museo de la Plata", T. XIV. pages 193-488.) has made a thorough study.

It is obvious that, notwithstanding the necessity for fitting man's line of descent into the genealogical tree of the Primates, especially the apes, opinions in regard to it differ greatly in detail. This could not be otherwise, since the different Primate forms, especially the fossil forms, are still far from being exhaustively known. But one thing remains certain,—the idea of the close relationship between man

and monkeys set forth in Darwin's "Descent of Man". Only those who deny the many points of agreement, the sole basis of classification, and thus of a natural genealogical tree, can look upon the position of Darwin and Haeckel as antiquated, or as standing on an insufficient foundation. For such a genealogical tree is nothing more than a summarised representation of what is known in regard to the degree of resemblance between the different forms.

Darwin's work in regard to the descent of man has not been surpassed; the more we immerse ourselves in the study of the structural relationships between apes and man, the more is our path illumined by the clear light radiating from him, and through his calm and deliberate investigation, based on a mass of material in the accumulation of which he has never had an equal. Darwin's fame will be bound up for all time with the unprejudiced investigation of the question of all questions, the descent of the human race.

VIII. CHARLES DARWIN AS AN ANTHROPOLOGIST. By Ernst Haeckel.

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The great advance that anthropology has made in the second half of the nineteenth century is due in the first place, to Darwin's discovery of the origin of man. No other problem in the whole field of research is so momentous as that of "Man's place in nature," which was justly described by Huxley (1863) as the most fundamental of all questions. Yet the scientific solution of this problem was impossible until the theory of descent had been established.

It is now a hundred years since the great French biologist Jean Lamarck published his "Philosophie Zoologique". By a remarkable coincidence the year in which that work was issued, 1809, was the year of the birth of his most distinguished successor, Charles Darwin. Lamarck had already recognised that the descent of man from a series of other Vertebrates—that is, from a series of Ape-like Primates—was essentially involved in the general theory of transformation which he had erected on a broad inductive basis; and he had sufficient penetration to detect the agencies that had been at work in the evolution of the erect bimanous man from the arboreal and quadrumanous ape. He had, however, few empirical arguments to advance in support of his hypothesis, and it could not be established until the further development of the biological sciences—the founding of comparative embryology by Baer (1828) and of the cell-theory by Schleiden and Schwann (1838), the advance of physiology under Johannes Muller (1833), and the enormous progress of palaeontology and comparative anatomy between 1820 and 1860—provided this necessary foundation. Darwin was the first to coordinate the ample results of these lines of research. With no less comprehensiveness than discrimination he consolidated them as a basis of a modified theory of descent, and associated with them his own theory of natural selection, which we take to be distinctive of "Darwinism" in the stricter sense. The illuminating truth of these cumulative arguments was so great in every branch of biology that, in spite of the most vehement opposition, the battle was won within a single decade, and Darwin secured the general admiration and recognition that had been denied to his forerunner, Lamarck, up to the hour of his death (1829).

Before, however, we consider the momentous influence that Darwinism has had in anthropology, we shall find it useful to glance at its history in the course of the last half century, and notice the various theories that have contributed to its advance. The first attempt to give extensive expression to the reform of biology by Darwin's work will be found in my "Generelle Morphologie" (1866) ("Generelle Morphologie der Organismen", 2 vols., Berlin, 1866.) which was followed by a more popular treatment of the subject in my "Naturliche Schopfungsgeschichte" (1868) (English translation; "The History of Creation", London, 1876.), a compilation from the earlier work. In the first volume of the "Generelle Morphologie" I endeavoured to show the great importance of evolution in settling the fundamental

questions of biological philosophy, especially in regard to comparative anatomy. In the second volume I dealt broadly with the principle of evolution, distinguishing ontogeny and phylogeny as its two coordinate main branches, and associating the two in the Biogenetic Law. The Law may be formulated thus: "Ontogeny (embryology or the development of the individual) is a concise and compressed recapitulation of phylogeny (the palaeontological or genealogical series) conditioned by laws of heredity and adaptation." The "Systematic introduction to general evolution," with which the second volume of the "Generelle Morphologie" opens, was the first attempt to draw up a natural system of organisms (in harmony with the principles of Lamarck and Darwin) in the form of a hypothetical pedigree, and was provisionally set forth in eight genealogical tables.

In the nineteenth chapter of the "Generelle Morphologie"—a part of which has been republished, without any alteration, after a lapse of forty years—I made a critical study of Lamarck's theory of descent and of Darwin's theory of selection, and endeavoured to bring the complex phenomena of heredity and adaptation under definite laws for the first time. Heredity I divided into conservative and progressive: adaptation into indirect (or potential) and direct (or actual). I then found it possible to give some explanation of the correlation of the two physiological functions in the struggle for life (selection), and to indicate the important laws of divergence (or differentiation) and complexity (or division of labour), which are the direct and inevitable outcome of selection. Finally, I marked off dysteleology as the science of the aimless (vestigial, abortive, atrophied, and useless) organs and parts of the body. In all this I worked from a strictly monistic standpoint, and sought to explain all biological phenomena on the mechanical and naturalistic lines that had long been recognised in the study of inorganic nature. Then (1866), as now, being convinced of the unity of nature, the fundamental identity of the agencies at work in the inorganic and the organic worlds, I discarded vitalism, teleology, and all hypotheses of a mystic character.

It was clear from the first that it was essential, in the monistic conception of evolution, to distinguish between the laws of conservative and progressive heredity. Conservative heredity maintains from generation to generation the enduring characters of the species. Each organism transmits to its descendants a part of the morphological and physiological qualities that it has received from its parents and ancestors. On the other hand, progressive heredity brings new characters to the species—characters that were not found in preceding generations. Each organism may transmit to its offspring a part of the morphological and physiological features that it has itself acquired, by adaptation, in the course of its individual career, through the use or disuse of particular organs, the influence of environment, climate, nutrition, etc. At that time I gave the name of "progressive heredity" to this inheritance of acquired characters, as a short and convenient expression, but have since changed the term to "transformative heredity" (as distinguished from conservative). This term is preferable, as inherited regressive modifications (degeneration, retrograde metamorphosis, etc.) come under the same head.

Transformative heredity—or the transmission of acquired characters—is one of the most important principles in evolutionary science. Unless we admit it most of the facts of comparative anatomy and physiology are inexplicable. That was the conviction of Darwin no less than of Lamarck, of Spencer as well as Virchow, of Huxley as well as Gegenbaur, indeed of the great majority of speculative biologists. This fundamental principle was for the first time called in question and assailed in 1885 by August Weismann of Freiburg, the eminent zoologist to whom the theory of evolution owes a great deal of valuable support, and who has attained distinction by his extension of the theory of selection. In explanation of the phenomena of heredity he introduced a new theory, the "theory of the continuity of the germ-plasm." According to him the living substance in all organisms consists of two quite distinct kinds of plasm, somatic and germinal. The permanent germ-plasm, or the active substance of the two germ-cells (egg-cell and sperm-cell), passes unchanged through a series of generations, and is not affected by environmental influences. The environment modifies only the soma-plasm, the organs and tissues of the body. The modifications that these parts undergo through the influence of the environment or their own activity (use and habit), do not affect the germ-plasm, and cannot therefore be transmitted.

This theory of the continuity of the germ-plasm has been expounded by Weismann during the last twenty-four years in a number of able volumes, and is regarded by many biologists, such as Mr Francis Galton, Sir E. Ray Lankester, and Professor J. Arthur Thomson (who has recently made a

thoroughgoing defence of it in his important work "Heredity" (London, 1908.)), as the most striking advance in evolutionary science. On the other hand, the theory has been rejected by Herbert Spencer, Sir W. Turner, Gegenbaur, Kolliker, Hertwig, and many others. For my part I have, with all respect for the distinguished Darwinian, contested the theory from the first, because its whole foundation seems to me erroneous, and its deductions do not seem to be in accord with the main facts of comparative morphology and physiology. Weismann's theory in its entirety is a finely conceived molecular hypothesis, but it is devoid of empirical basis. The notion of the absolute and permanent independence of the germ-plasm, as distinguished from the soma-plasm, is purely speculative; as is also the theory of germinal selection. The determinants, ids, and idants, are purely hypothetical elements. The experiments that have been devised to demonstrate their existence really prove nothing.

It seems to me quite improper to describe this hypothetical structure as "Neodarwinism." Darwin was just as convinced as Lamarck of the transmission of acquired characters and its great importance in the scheme of evolution. I had the good fortune to visit Darwin at Down three times and discuss with him the main principles of his system, and on each occasion we were fully agreed as to the incalculable importance of what I call transformative inheritance. It is only proper to point out that Weismann's theory of the germ-plasm is in express contradiction to the fundamental principles of Darwin and Lamarck. Nor is it more acceptable in what one may call its "ultradarwinism"—the idea that the theory of selection explains everything in the evolution of the organic world. This belief in the "omnipotence of natural selection" was not shared by Darwin himself. Assuredly, I regard it as of the utmost value, as the process of natural selection through the struggle for life affords an explanation of the mechanical origin of the adapted organisation. It solves the great problem: how could the finely adapted structure of the animal or plant body be formed unless it was built on a preconceived plan? It thus enables us to dispense with the teleology of the metaphysician and the dualist, and to set aside the old mythological and poetic legends of creation. The idea had occurred in vague form to the great Empedocles 2000 years before the time of Darwin, but it was reserved for modern research to give it ample expression. Nevertheless, natural selection does not of itself give the solution of all our evolutionary problems. It has to be taken in conjunction with the transformism of Lamarck, with which it is in complete harmony.

The monumental greatness of Charles Darwin, who surpasses every other student of science in the nineteenth century by the loftiness of his monistic conception of nature and the progressive influence of his ideas, is perhaps best seen in the fact that not one of his many successors has succeeded in modifying his theory of descent in any essential point or in discovering an entirely new standpoint in the interpretation of the organic world. Neither Nageli nor Weismann, neither De Vries nor Roux, has done this. Nageli, in his "Mechanisch-Physiologische Theorie der Abstammungslehre" (Munich, 1884.), which is to a great extent in agreement with Weismann, constructed a theory of the idioplasm, that represents it (like the germ-plasm) as developing continuously in a definite direction from internal causes. But his internal "principle of progress" is at the bottom just as teleological as the vital force of the Vitalists, and the micellar structure of the idioplasm is just as hypothetical as the "dominant" structure of the germ-plasm. In 1889 Moritz Wagner sought to explain the origin of species by migration and isolation, and on that basis constructed a special "migration-theory." This, however, is not out of harmony with the theory of selection. It merely elevates one single factor in the theory to a predominant position. Isolation is only a special case of selection, as I had pointed out in the fifteenth chapter of my "Natural history of creation". The "mutation-theory" of De Vries ("Die Mutationstheorie", Leipzig, 1903.), that would explain the origin of species by sudden and saltatory variations rather than by gradual modification, is regarded by many botanists as a great step in advance, but it is generally rejected by zoologists. It affords no explanation of the facts of adaptation, and has no causal value.

Much more important than these theories is that of Wilhelm Roux ("Der Kampf der Theile im Organismus", Leipzig, 1881.) of "the struggle of parts within the organism, a supplementation of the theory of mechanical adaptation." He explains the functional autoformation of the purposive structure by a combination of Darwin's principle of selection with Lamarck's idea of transformative heredity, and applies the two in conjunction to the facts of histology. He lays stress on the significance of functional adaptation, which I had described in 1866, under the head of cumulative adaptation, as the most important factor in evolution. Pointing out its influence in the cell-life of the tissues, he puts "cellular

selection" above "personal selection," and shows how the finest conceivable adaptations in the structure of the tissue may be brought about quite mechanically, without preconceived plan. This "mechanical teleology" is a valuable extension of Darwin's monistic principle of selection to the whole field of cellular physiology and histology, and is wholly destructive of dualistic vitalism.

The most important advance that evolution has made since Darwin and the most valuable amplification of his theory of selection is, in my opinion, the work of Richard Semon: "Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens" (Leipzig, 1904.). He offers a psychological explanation of the facts of heredity by reducing them to a process of (unconscious) memory. The physiologist Ewald Hering had shown in 1870 that memory must be regarded as a general function of organic matter, and that we are quite unable to explain the chief vital phenomena, especially those of reproduction and inheritance, unless we admit this unconscious memory. In my essay "Die Perigenesis der Plastidule" (Berlin, 1876.) I elaborated this far-reaching idea, and applied the physical principle of transmitted motion to the plastidules, or active molecules of plasm. I concluded that "heredity is the memory of the plastidules, and variability their power of comprehension." This "provisional attempt to give a mechanical explanation of the elementary processes of evolution" I afterwards extended by showing that sensitiveness is (as Carl Nageli, Ernst Mach, and Albrecht Rau express it) a general quality of matter. This form of panpsychism finds its simplest expression in the "trinity of substance."

To the two fundamental attributes that Spinoza ascribed to substance—Extension (matter as occupying space) and Cogitation (energy, force)—we now add the third fundamental quality of Psychoma (sensitiveness, soul). I further elaborated this trinitarian conception of substance in the nineteenth chapter of my "Die Lebenswunder" (1904) ("Wonders of Life", London, 1904.), and it seems to me well calculated to afford a monistic solution of many of the antitheses of philosophy.

This important Mneme-theory of Semon and the luminous physiological experiments and observations associated with it not only throw considerable light on transformative inheritance, but provide a sound physiological foundation for the biogenetic law. I had endeavoured to show in 1874, in the first chapter of my "Anthropogenie" (English translation; "The Evolution of Man", 2 volumes, London, 1879 and 1905.), that this fundamental law of organic evolution holds good generally, and that there is everywhere a direct causal connection between ontogeny and phylogeny. "Phylogenesis is the mechanical cause of ontogenesis"; in other words, "The evolution of the stem or race is—in accordance with the laws of heredity and adaptation—the real cause of all the changes that appear, in a condensed form, in the development of the individual organism from the ovum, in either the embryo or the larva."

It is now fifty years since Charles Darwin pointed out, in the thirteenth chapter of his epoch-making "Origin of Species", the fundamental importance of embryology in connection with his theory of descent:

"The leading facts in embryology, which are second to none in importance, are explained on the principle of variations in the many descendants from some one ancient progenitor, having appeared at a not very early period of life, and having been inherited at a corresponding period." ("Origin of Species" (6th edition), page 396.)

He then shows that the striking resemblance of the embryos and larvae of closely related animals, which in the mature stage belong to widely different species and genera, can only be explained by their descent from a common progenitor. Fritz Muller made a closer study of these important phenomena in the instructive instance of the Crustacean larva, as given in his able work "Fur Darwin" (1864). (English translation; "Facts and Arguments for Darwin", London, 1869.) I then, in 1872, extended the range so as to include all animals (with the exception of the unicellular Protozoa) and showed, by means of the theory of the Gastraea, that all multicellular, tissue-forming animals—all the Metazoa—develop in essentially the same way from the primary germ-layers. I conceived the embryonic form, in which the whole structure consists of only two layers of cells, and is known as the gastrula, to be the ontogenetic recapitulation, maintained by tenacious heredity, of a primitive common progenitor of all the Metazoa, the Gastraea. At a later date (1895) Monticelli discovered that this conjectural ancestral form is still preserved in certain primitive Coelenterata—Pemmatodiscus, Kunstleria, and the nearly-related Orthonectida.

The general application of the biogenetic law to all classes of animals and plants has been proved in my "Systematische Phylogenie". (3 volumes, Berlin, 1894-96.) It has, however, been frequently challenged, both by botanists and zoologists, chiefly owing to the fact that many have failed to distinguish its two essential elements, palingenesis and cenogenesis. As early as 1874 I had emphasised, in the first chapter of my "Evolution of Man", the importance of discriminating carefully between these two sets of phenomena:

"In the evolutionary appreciation of the facts of embryology we must take particular care to distinguish sharply and clearly between the primary, palingenetic evolutionary processes and the secondary, cenogenetic processes. The palingenetic phenomena, or embryonic RECAPITULATIONS, are due to heredity, to the transmission of characters from one generation to another. They enable us to draw direct inferences in regard to corresponding structures in the development of the species (e.g. the chorda or the branchial arches in all vertebrate embryos). The cenogenetic phenomena, on the other hand, or the embryonic VARIATIONS, cannot be traced to inheritance from a mature ancestor, but are due to the adaptation of the embryo or the larva to certain conditions of its individual development (e.g. the amnion, the allantois, and the vitelline arteries in the embryos of the higher vertebrates). These cenogenetic phenomena are later additions; we must not infer from them that there were corresponding processes in the ancestral history, and hence they are apt to mislead."

The fundamental importance of these facts of comparative anatomy, atavism, and the rudimentary organs, was pointed out by Darwin in the first part of his classic work, "The Descent of Man and Selection in Relation to Sex" (1871). ("Descent of Man" (Popular Edition), page 927.) In the "General summary and conclusion" (chapter XXI.) he was able to say, with perfect justice: "He who is not content to look, like a savage, at the phenomena of nature as disconnected, cannot any longer believe that man is the work of a separate act of creation. He will be forced to admit that the close resemblance of the embryo of man to that, for instance, of a dog—the construction of his skull, limbs, and whole frame on the same plan with that of other mammals, independently of the uses to which the parts may be put—the occasional reappearance of various structures, for instance of several muscles, which man does not normally possess, but which are common to the Quadrumana—and a crowd of analogous facts—all point in the plainest manner to the conclusion that man is the co-descendant with other mammals of a common progenitor."

These few lines of Darwin's have a greater scientific value than hundreds of those so-called "anthropological treatises," which give detailed descriptions of single organs, or mathematical tables with series of numbers and what are claimed to be "exact analyses," but are devoid of synoptic conclusions and a philosophical spirit.

Charles Darwin is not generally recognised as a great anthropologist, nor does the school of modern anthropologists regard him as a leading authority. In Germany, especially, the great majority of the members of the anthropological societies took up an attitude of hostility to him from the very beginning of the controversy in 1860. "The Descent of Man" was not merely rejected, but even the discussion of it was forbidden on the ground that it was "unscientific."

The centre of this inveterate hostility for thirty years—especially after 1877—was Rudolph Virchow of Berlin, the leading investigator in pathological anatomy, who did so much for the reform of medicine by his establishment of cellular pathology in 1858. As a prominent representative of "exact" or "descriptive" anthropology, and lacking a broad equipment in comparative anatomy and ontogeny, he was unable to accept the theory of descent. In earlier years, and especially during his splendid period of activity at Wurzburg (1848-1856), he had been a consistent free-thinker, and had in a number of able articles (collected in his "Gesammelte Abhandlungen") ("Gesammelte Abhandlungen zur wissenschaftlichen Medizin", Berlin, 1856.) upheld the unity of human nature, the inseparability of body and spirit. In later years at Berlin, where he was more occupied with political work and sociology (especially after 1866), he abandoned the positive monistic position for one of agnosticism and scepticism, and made concessions to the dualistic dogma of a spiritual world apart from the material frame.

In the course of a Scientific Congress at Munich in 1877 the conflict of these antithetic views of nature came into sharp relief. At this memorable Congress I had undertaken to deliver the first address (September 18th) on the subject of "Modern evolution in relation to the whole of science." I maintained

that Darwin's theory not only solved the great problem of the origin of species, but that its implications, especially in regard to the nature of man, threw considerable light on the whole of science, and on anthropology in particular. The discovery of the real origin of man by evolution from a long series of mammal ancestors threw light on his place in nature in every aspect, as Huxley had already shown in his excellent lectures of 1863. Just as all the organs and tissues of the human body had originated from those of the nearest related mammals, certain ape-like forms, so we were bound to conclude that his mental qualities also had been derived from those of his extinct primate ancestor.

This monistic view of the origin and nature of man, which is now admitted by nearly all who have the requisite acquaintance with biology, and approach the subject without prejudice, encountered a sharp opposition at that time. The opposition found its strongest expression in an address that Virchow delivered at Munich four days afterwards (September 22nd), on "The freedom of science in the modern State." He spoke of the theory of evolution as an unproved hypothesis, and declared that it ought not to be taught in the schools, because it was dangerous to the State. "We must not," he said, "teach that man has descended from the ape or any other animal." When Darwin, usually so lenient in his judgment, read the English translation of Virchow's speech, he expressed his disapproval in strong terms. But the great authority that Virchow had—an authority well founded in pathology and sociology—and his prestige as President of the German Anthropological Society, had the effect of preventing any member of the Society from raising serious opposition to him for thirty years. Numbers of journals and treatises repeated his dogmatic statement: "It is quite certain that man has descended neither from the ape nor from any other animal." In this he persisted till his death in 1902. Since that time the whole position of German anthropology has changed. The question is no longer whether man was created by a distinct supernatural act or evolved from other mammals, but to which line of the animal hierarchy we must look for the actual series of ancestors. The interested reader will find an account of this "battle of Munich" (1877) in my three Berlin lectures (April, 1905) ("Der Kampf um die Entwicklungs-Gedanken". (English translation; "Last Words on Evolution", London, 1906.))

The main points in our genealogical tree were clearly recognised by Darwin in the sixth chapter of the "Descent of Man". Lowly organised fishes, like the lancelet (*Amphioxus*), are descended from lower invertebrates resembling the larvae of an existing Tunicate (*Appendicularia*). From these primitive fishes were evolved higher fishes of the ganoid type and others of the type of *Lepidosiren* (*Dipneusta*). It is a very small step from these to the *Amphibia*:

"In the class of mammals the steps are not difficult to conceive which led from the ancient *Monotremata* to the ancient *Marsupials*; and from these to the early progenitors of the placental mammals. We may thus ascend to the *Lemuridae*; and the interval is not very wide from these to the *Simiadae*. The *Simiadae* then branched off into two great stems, the New World and Old World monkeys; and from the latter, at a remote period, Man, the wonder and glory of the Universe, proceeded." ("Descent of Man" (Popular Edition), page 255.)

In these few lines Darwin clearly indicated the way in which we were to conceive our ancestral series within the vertebrates. It is fully confirmed by all the arguments of comparative anatomy and embryology, of palaeontology and physiology; and all the research of the subsequent forty years has gone to establish it. The deep interest in geology which Darwin maintained throughout his life and his complete knowledge of palaeontology enabled him to grasp the fundamental importance of the palaeontological record more clearly than anthropologists and zoologists usually do.

There has been much debate in subsequent decades whether Darwin himself maintained that man was descended from the ape, and many writers have sought to deny it. But the lines I have quoted verbatim from the conclusion of the sixth chapter of the "Descent of Man" (1871) leave no doubt that he was as firmly convinced of it as was his great precursor Jean Lamarck in 1809. Moreover, Darwin adds, with particular explicitness, in the "general summary and conclusion" (chapter XXI.) of that standard work ("Descent of Man", page 930.):

"By considering the embryological structure of man—the homologies which he presents with the lower animals,—the rudiments which he retains,—and the reversions to which he is liable, we can partly recall in imagination the former condition of our early progenitors; and can approximately place them in their proper place in the zoological series. We thus learn that man is descended from a hairy, tailed quadruped, probably arboreal in its habits, and an inhabitant of the Old World. This creature, if its

whole structure had been examined by a naturalist, would have been classed amongst the Quadrumana, as surely as the still more ancient progenitor of the Old and New World monkeys."

These clear and definite lines leave no doubt that Darwin—so critical and cautious in regard to important conclusions—was quite as firmly convinced of the descent of man from the apes (the Catarrhinae, in particular) as Lamarck was in 1809 and Huxley in 1863.

It is to be noted particularly that, in these and other observations on the subject, Darwin decidedly assumes the monophyletic origin of the mammals, including man. It is my own conviction that this is of the greatest importance. A number of difficult questions in regard to the development of man, in respect of anatomy, physiology, psychology, and embryology, are easily settled if we do not merely extend our progenotaxis to our nearest relatives, the anthropoid apes and the tailed monkeys from which these have descended, but go further back and find an ancestor in the group of the Lemuridae, and still further back to the Marsupials and Monotremata. The essential identity of all the Mammals in point of anatomical structure and embryonic development—in spite of their astonishing differences in external appearance and habits of life—is so palpably significant that modern zoologists are agreed in the hypothesis that they have all sprung from a common root, and that this root may be sought in the earlier Palaeozoic Amphibia.

The fundamental importance of this comparative morphology of the Mammals, as a sound basis of scientific anthropology, was recognised just before the beginning of the nineteenth century, when Lamarck first emphasised (1794) the division of the animal kingdom into Vertebrates and Invertebrates. Even thirteen years earlier (1781), when Goethe made a close study of the mammal skeleton in the Anatomical Institute at Jena, he was intensely interested to find that the composition of the skull was the same in man as in the other mammals. His discovery of the os intermaxillare in man (1784), which was contradicted by most of the anatomists of the time, and his ingenious "vertebral theory of the skull," were the splendid fruit of his morphological studies. They remind us how Germany's greatest philosopher and poet was for many years ardently absorbed in the comparative anatomy of man and the mammals, and how he divined that their wonderful identity in structure was no mere superficial resemblance, but pointed to a deep internal connection. In my "*Generelle Morphologie*" (1866), in which I published the first attempts to construct phylogenetic trees, I have given a number of remarkable theses of Goethe, which may be called "phyletic prophecies." They justify us in regarding him as a precursor of Darwin.

In the ensuing forty years I have made many conscientious efforts to penetrate further along that line of anthropological research that was opened up by Goethe, Lamarck, and Darwin. I have brought together the many valuable results that have constantly been reached in comparative anatomy, physiology, ontogeny, and palaeontology, and maintained the effort to reform the classification of animals and plants in an evolutionary sense. The first rough drafts of pedigrees that were published in the "*Generelle Morphologie*" have been improved time after time in the ten editions of my "*Naturalische Schöpfungsgeschichte*" (1868-1902). (English translation; "*The History of Creation*", London, 1876.) A sounder basis for my phyletic hypotheses, derived from a discriminating combination of the three great records—morphology, ontogeny, and palaeontology—was provided in the three volumes of my "*Systematische Phylogenie*" (Berlin, 1894-96.) (1894 Protists and Plants, 1895 Vertebrates, 1896 Invertebrates). In my "*Anthropogenie*" (Leipzig, 1874, 5th edition 1905. English translation; "*The Evolution of Man*", London, 1905.) I endeavoured to employ all the known facts of comparative ontogeny (embryology) for the purpose of completing my scheme of human phylogeny (evolution). I attempted to sketch the historical development of each organ of the body, beginning with the most elementary structures in the germ-layers of the *Gastrea*. At the same time I drew up a corrected statement of the most important steps in the line of our ancestral series.

At the fourth International Congress of Zoology at Cambridge (August 26th, 1898) I delivered an address on "Our present knowledge of the Descent of Man." It was translated into English, enriched with many valuable notes and additions, by my friend and pupil in earlier days Dr Hans Gadow (Cambridge), and published under the title: "*The Last Link; our present knowledge of the Descent of Man*". (London, 1898.) The determination of the chief animal forms that occur in the line of our ancestry is there restricted to thirty types, and these are distributed in six main groups.

The first half of this "Progonotaxis hominis," which has no support from fossil evidence, comprises three groups: (i) Protista (unicellular organisms, 1-5: (ii) Invertebrate Metazoa (Coelenteria 6-8, Vermalia 9-11): (iii) Monorrhine Vertebrates (Acrania 12-13, Cyclostoma 14-15). The second half, which is based on fossil records, also comprises three groups: (iv) Palaeozoic cold-blooded Craniota (Fishes 16-18, Amphibia 19, Reptiles 20: (v) Mesozoic Mammals (Monotrema 21, Marsupialia 22, Mallotheria 23): (vi) Cenozoic Primates (Lemuridae 24-25, Tailed Apes 26-27, Anthropomorpha 28-30). An improved and enlarged edition of this hypothetic "Progonotaxis hominis" was published in 1908, in my essay "Unsere Ahnenreihe". ("Festschrift zur 350-jährigen Jubelfeier der Thüringer Universität Jena". Jena, 1908.)

If I have succeeded in furthering, in some degree, by these anthropological works, the solution of the great problem of Man's place in nature, and particularly in helping to trace the definite stages in our ancestral series, I owe the success, not merely to the vast progress that biology has made in the last half century, but largely to the luminous example of the great investigators who have applied themselves to the problem, with so much assiduity and genius, for a century and a quarter—I mean Goethe and Lamarck, Gegenbaur and Huxley, but, above all, Charles Darwin. It was the great genius of Darwin that first brought together the scattered material of biology and shaped it into that symmetrical temple of scientific knowledge, the theory of descent. It was Darwin who put the crown on the edifice by his theory of natural selection. Not until this broad inductive law was firmly established was it possible to vindicate the special conclusion, the descent of man from a series of other Vertebrates. By his illuminating discovery Darwin did more for anthropology than thousands of those writers, who are more specifically titled anthropologists, have done by their technical treatises. We may, indeed, say that it is not merely as an exact observer and ingenious experimenter, but as a distinguished anthropologist and far-seeing thinker, that Darwin takes his place among the greatest men of science of the nineteenth century.

To appreciate fully the immortal merit of Darwin in connection with anthropology, we must remember that not only did his chief work, "The Origin of Species", which opened up a new era in natural history in 1859, sustain the most virulent and widespread opposition for a lengthy period, but even thirty years later, when its principles were generally recognised and adopted, the application of them to man was energetically contested by many high scientific authorities. Even Alfred Russel Wallace, who discovered the principle of natural selection independently in 1858, did not concede that it was applicable to the higher mental and moral qualities of man. Dr Wallace still holds a spiritualist and dualist view of the nature of man, contending that he is composed of a material frame (descended from the apes) and an immortal immaterial soul (infused by a higher power). This dual conception, moreover, is still predominant in the wide circles of modern theology and metaphysics, and has the general and influential adherence of the more conservative classes of society.

In strict contradiction to this mystical dualism, which is generally connected with teleology and vitalism, Darwin always maintained the complete unity of human nature, and showed convincingly that the psychological side of man was developed, in the same way as the body, from the less advanced soul of the anthropoid ape, and, at a still more remote period, from the cerebral functions of the older vertebrates. The eighth chapter of the "Origin of Species", which is devoted to instinct, contains weighty evidence that the instincts of animals are subject, like all other vital processes, to the general laws of historic development. The special instincts of particular species were formed by adaptation, and the modifications thus acquired were handed on to posterity by heredity; in their formation and preservation natural selection plays the same part as in the transformation of every other physiological function. The higher moral qualities of civilised man have been derived from the lower mental functions of the uncultivated barbarians and savages, and these in turn from the social instincts of the mammals. This natural and monistic psychology of Darwin's was afterwards more fully developed by his friend George Romanes in his excellent works "Mental Evolution in Animals" and "Mental Evolution in Man". (London, 1885; 1888.)

Many valuable and most interesting contributions to this monistic psychology of man were made by Darwin in his fine work on "The Descent of Man and Selection in Relation to Sex", and again in his supplementary work, "The Expression of the Emotions in Man and Animals". To understand the historical development of Darwin's anthropology one must read his life and the introduction to "The

Descent of Man". From the moment that he was convinced of the truth of the principle of descent—that is to say, from his thirtieth year, in 1838—he recognised clearly that man could not be excluded from its range. He recognised as a logical necessity the important conclusion that "man is the co-descendant with other species of some ancient, lower, and extinct form." For many years he gathered notes and arguments in support of this thesis, and for the purpose of showing the probable line of man's ancestry. But in the first edition of "The Origin of Species" (1859) he restricted himself to the single line, that by this work "light would be thrown on the origin of man and his history." In the fifty years that have elapsed since that time the science of the origin and nature of man has made astonishing progress, and we are now fairly agreed in a monistic conception of nature that regards the whole universe, including man, as a wonderful unity, governed by unalterable and eternal laws. In my philosophical book "Die Weltratsel" (1899) ("The Riddle of the Universe", London, 1900.) and in the supplementary volume "Die Lebenswunder" (1904) "The Wonders of Life", London, (1904.), I have endeavoured to show that this pure monism is securely established, and that the admission of the all-powerful rule of the same principle of evolution throughout the universe compels us to formulate a single supreme law—the all-embracing "Law of Substance," or the united laws of the constancy of matter and the conservation of energy. We should never have reached this supreme general conception if Charles Darwin—a "monistic philosopher" in the true sense of the word—had not prepared the way by his theory of descent by natural selection, and crowned the great work of his life by the association of this theory with a naturalistic anthropology.

IX. SOME PRIMITIVE THEORIES OF THE ORIGIN OF MAN.

By J.G. FRAZER. Fellow of Trinity College, Cambridge.

On a bright day in late autumn a good many years ago I had ascended the hill of Panopeus in Phocis to examine the ancient Greek fortifications which crest its brow. It was the first of November, but the weather was very hot; and when my work among the ruins was done, I was glad to rest under the shade of a clump of fine holly-oaks, to inhale the sweet refreshing perfume of the wild thyme which scented all the air, and to enjoy the distant prospects, rich in natural beauty, rich too in memories of the legendary and historic past. To the south the finely-cut peak of Helicon peered over the low intervening hills. In the west loomed the mighty mass of Parnassus, its middle slopes darkened by pine-woods like shadows of clouds brooding on the mountain-side; while at its skirts nestled the ivy-mantled walls of Daulis overhanging the deep glen, whose romantic beauty accords so well with the loves and sorrows of Procne and Philomela, which Greek tradition associated with the spot. Northwards, across the broad plain to which the hill of Panopeus descends, steep and bare, the eye rested on the gap in the hills through which the Cephissus winds his tortuous way to flow under grey willows, at the foot of barren stony hills, till his turbid waters lose themselves, no longer in the vast reedy swamps of the now vanished Copaic Lake, but in the darkness of a cavern in the limestone rock. Eastward, clinging to the slopes of the bleak range of which the hill of Panopeus forms part, were the ruins of Chaeronea, the birthplace of Plutarch; and out there in the plain was fought the disastrous battle which laid Greece at the feet of Macedonia. There, too, in a later age East and West met in deadly conflict, when the Roman armies under Sulla defeated the Asiatic hosts of Mithridates. Such was the landscape spread out before me on one of those farewell autumn days of almost pathetic splendour, when the departing summer seems to linger fondly, as if loth to resign to winter the enchanted mountains of Greece. Next day the scene had changed: summer was gone. A grey November mist hung low on the hills which only yesterday had shone resplendent in the sun, and under its melancholy curtain the dead flat of the Chaeronean plain, a wide treeless expanse shut in by desolate slopes, wore an aspect of chilly sadness befitting the battlefield where a nation's freedom was lost.

But crowded as the prospect from Panopeus is with memories of the past, the place itself, now so still and deserted, was once the scene of an event even more ancient and memorable, if Greek story-tellers can be trusted. For here, they say, the sage Prometheus created our first parents by fashioning them, like a potter, out of clay. (Pausanias X. 4.4. Compare Apollodorus, "Bibliotheca", I. 7. 1; Ovid, "Metamorph." I. 82 sq.; Juvenal, "Sat". XIV. 35. According to another version of the tale, this creation of mankind took place not at Panopeus, but at Iconium in Lycaonia. After the original race of mankind had been destroyed in the great flood of Deucalion, the Greek Noah, Zeus commanded Prometheus and Athena to create men afresh by moulding images out of clay, breathing the winds into them, and

making them live. See "Etymologicum Magnum", s.v. "Ikonion", pages 470 sq. It is said that Prometheus fashioned the animals as well as men, giving to each kind of beast its proper nature. See Philemon, quoted by Stobaeus, "Florilegium" II. 27. The creation of man by Prometheus is figured on ancient works of art. See J. Toutain, "Etudes de Mythologie et d'Histoire des Religions Antiques" (Paris, 1909), page 190. According to Hesiod ("Works and Days", 60 sqq.) it was Hephaestus who at the bidding of Zeus moulded the first woman out of moist earth.) The very spot where he did so can still be seen. It is a forlorn little glen or rather hollow behind the hill of Panopeus, below the ruined but still stately walls and towers which crown the grey rocks of the summit. The glen, when I visited it that hot day after the long drought of summer, was quite dry; no water trickled down its bushy sides, but in the bottom I found a reddish crumbling earth, a relic perhaps of the clay out of which the potter Prometheus moulded the Greek Adam and Eve. In a volume dedicated to the honour of one who has done more than any other in modern times to shape the ideas of mankind as to their origin it may not be out of place to recall this crude Greek notion of the creation of the human race, and to compare or contrast it with other rudimentary speculations of primitive peoples on the same subject, if only for the sake of marking the interval which divides the childhood from the maturity of science.

The simple notion that the first man and woman were modelled out of clay by a god or other superhuman being is found in the traditions of many peoples. This is the Hebrew belief recorded in Genesis: "The Lord God formed man of the dust of the ground, and breathed into his nostrils the breath of life; and man became a living soul." (Genesis ii.7.) To the Hebrews this derivation of our species suggested itself all the more naturally because in their language the word for "ground" (adamah) is in form the feminine of the word for man (adam). (S.R. Driver and W.H. Bennett, in their commentaries on Genesis ii. 7.) From various allusions in Babylonian literature it would seem that the Babylonians also conceived man to have been moulded out of clay. (H. Zimmern, in E. Schrader's "Die Keilinschriften und das Alte Testament" 3 (Berlin, 1902), page 506.) According to Berosus, the Babylonian priest whose account of creation has been preserved in a Greek version, the god Bel cut off his own head, and the other gods caught the flowing blood, mixed it with earth, and fashioned men out of the bloody paste; and that, they said, is why men are so wise, because their mortal clay is tempered with divine blood. (Eusebius, "Chronicon", ed. A. Schoene, Vol. I. (Berlin, 1875), col. 16.) In Egyptian mythology Khnoumou, the Father of the gods, is said to have moulded men out of clay. (G. Maspero, "Histoire Ancienne des Peuples de l'Orient Classique", I. (Paris, 1895), page 128.) We cannot doubt that such crude conceptions of the origin of our race were handed down to the civilised peoples of antiquity by their savage or barbarous forefathers. Certainly stories of the same sort are known to be current among savages and barbarians.

Thus the Australian blacks in the neighbourhood of Melbourne said that Pund-jel, the creator, cut three large sheets of bark with his big knife. On one of these he placed some clay and worked it up with his knife into a proper consistence. He then laid a portion of the clay on one of the other pieces of bark and shaped it into a human form; first he made the feet, then the legs, then the trunk, the arms, and the head. Thus he made a clay man on each of the two pieces of bark; and being well pleased with them he danced round them for joy. Next he took stringy bark from the Eucalyptus tree, made hair of it, and stuck it on the heads of his clay men. Then he looked at them again, was pleased with his work, and again danced round them for joy. He then lay down on them, blew his breath hard into their mouths, their noses, and their navels; and presently they stirred, spoke, and rose up as full-grown men. (R. Brough Smyth, "The Aborigines of Victoria" (Melbourne, 1878), I. 424. This and many of the following legends of creation have been already cited by me in a note on Pausanias X. 4. 4 ("Pausanias's Description of Greece, translated with a Commentary" (London, 1898), Vol V. pages 220 sq.)) The Maoris of New Zealand say that Tiki made man after his own image. He took red clay, kneaded it, like the Babylonian Bel, with his own blood, fashioned it in human form, and gave the image breath. As he had made man in his own likeness he called him Tiki-ahua or Tiki's likeness. (R. Taylor "Te Ika A Maui, or New Zealand and its Inhabitants", Second Edition (London, 1870), page 117. Compare E. Shortland, "Maori Religion and Mythology" (London, 1882), pages 21 sq.) A very generally received tradition in Tahiti was that the first human pair was made by Taaroa, the chief god. They say that after he had formed the world he created man out of red earth, which was also the food of mankind until bread-fruit was produced. Further, some say that one day Taaroa called for the man by name, and when he came he made him fall asleep. As he slept, the creator took out one of his bones

(ivi) and made a woman of it, whom he gave to the man to be his wife, and the pair became the progenitors of mankind. This narrative was taken down from the lips of the natives in the early years of the mission to Tahiti. The missionary who records it observes: "This always appeared to me a mere recital of the Mosaic account of creation, which they had heard from some European, and I never placed any reliance on it, although they have repeatedly told me it was a tradition among them before any foreigner arrived. Some have also stated that the woman's name was Ivi, which would be by them pronounced as if written "Eve". "Ivi" is an aboriginal word, and not only signifies a bone, but also a widow, and a victim slain in war. Notwithstanding the assertion of the natives, I am disposed to think that "Ivi", or Eve, is the only aboriginal part of the story, as far as it respects the mother of the human race. (W. Ellis, "Polynesian Researches", Second Edition (London, 1832), I. 110 sq. "Ivi" or "iwi" is the regular word for "bone" in the various Polynesian languages. See E. Tregear, "The Maori-Polynesian Comparative Dictionary" (Wellington, New Zealand, 1891), page 109.) However, the same tradition has been recorded in other parts of Polynesia besides Tahiti. Thus the natives of Fakaofu or Bowditch Island say that the first man was produced out of a stone. After a time he bethought him of making a woman. So he gathered earth and moulded the figure of a woman out of it, and having done so he took a rib out of his left side and thrust it into the earthen figure, which thereupon started up a live woman. He called her Ivi (Eevee) or "rib" and took her to wife, and the whole human race sprang from this pair. (G. Turner, "Samoa" (London, 1884), pages 267 sq.) The Maoris also are reported to believe that the first woman was made out of the first man's ribs. (J.L. Nicholas, "Narrative of a Voyage to New Zealand" (London, 1817), I. 59, who writes "and to add still more to this strange coincidence, the general term for bone is 'Hevee'.") This wide diffusion of the story in Polynesia raises a doubt whether it is merely, as Ellis thought, a repetition of the Biblical narrative learned from Europeans. In Nui, or Netherland Island, it was the god Aulialia who made earthen models of a man and woman, raised them up, and made them live. He called the man Tepapa and the woman Tetata. (G. Turner, "Samoa", pages 300 sq.)

In the Pelew Islands they say that a brother and sister made men out of clay kneaded with the blood of various animals, and that the characters of these first men and of their descendants were determined by the characters of the animals whose blood had been kneaded with the primordial clay; for instance, men who have rat's blood in them are thieves, men who have serpent's blood in them are sneaks, and men who have cock's blood in them are brave. (J. Kubary, "Die Religion der Pelauer", in A. Bastian's "Allerlei aus Volks- und Menschenkunde" (Berlin, 1888), I. 3, 56.) According to a Melanesian legend, told in Mota, one of the Banks Islands, the hero Qat moulded men of clay, the red clay from the marshy river-side at Vanua Lava. At first he made men and pigs just alike, but his brothers remonstrated with him, so he beat down the pigs to go on all fours and made men walk upright. Qat fashioned the first woman out of supple twigs, and when she smiled he knew she was a living woman. (R.H. Codrington, "The Melanesians" (Oxford, 1891), page 158.) A somewhat different version of the Melanesian story is told at Lakona, in Santa Maria. There they say that Qat and another spirit ("vui") called Marawa both made men. Qat made them out of the wood of dracaena-trees. Six days he worked at them, carving their limbs and fitting them together. Then he allowed them six days to come to life. Three days he hid them away, and three days more he worked to make them live. He set them up and danced to them and beat his drum, and little by little they stirred, till at last they could stand all by themselves. Then Qat divided them into pairs and called each pair husband and wife. Marawa also made men out of a tree, but it was a different tree, the tavisoviso. He likewise worked at them six days, beat his drum, and made them live, just as Qat did. But when he saw them move, he dug a pit and buried them in it for six days, and then, when he scraped away the earth to see what they were doing, he found them all rotten and stinking. That was the origin of death. (R.H. Codrington op. cit., pages 157 sq.)

The inhabitants of Noo-Hoo-roa, in the Kei Islands say that their ancestors were fashioned out of clay by the supreme god, Doodlera, who breathed life into the clay figures. (C.M. Pleyte, "Ethnographische Beschrijving der Kei-Eilanden", "Tijdschrift van het Nederlandsch Aardrijkskundig Genootschap", Tweede Serie X. (1893), page 564.) The aborigines of Minahassa, in the north of Celebes, say that two beings called Wailan Wangko and Wangi were alone on an island, on which grew a cocoa-nut tree. Said Wailan Wangko to Wangi, "Remain on earth while I climb up the tree." Said Wangi to Wailan Wangko, "Good." But then a thought occurred to Wangi and he climbed up the tree to ask Wailan Wangko why he, Wangi, should remain down there all alone. Said Wailan Wangko to

Wangi, "Return and take earth and make two images, a man and a woman." Wangi did so, and both images were men who could move but could not speak. So Wangi climbed up the tree to ask Wailan Wangko, "How now? The two images are made, but they cannot speak." Said Wailan Wangko to Wangi, "Take this ginger and go and blow it on the skulls and the ears of these two images, that they may be able to speak; call the man Adam and the woman Ewa." (N. Graafland "De Minahassa" (Rotterdam, 1869), I. pages 96 sq.) In this narrative the names of the man and woman betray European influence, but the rest of the story may be aboriginal. The Dyaks of Sakarran in British Borneo say that the first man was made by two large birds. At first they tried to make men out of trees, but in vain. Then they hewed them out of rocks, but the figures could not speak. Then they moulded a man out of damp earth and infused into his veins the red gum of the kumpang-tree. After that they called to him and he answered; they cut him and blood flowed from his wounds. (Horsburgh, quoted by H. Ling Roth, "The Natives of Sarawak and of British North Borneo" (London, 1896), I. pages 299 sq. Compare The Lord Bishop of Labuan, "On the Wild Tribes of the North-West Coast of Borneo," "Transactions of the Ethnological Society of London", New Series, II. (1863), page 27.)

The Kumis of South-Eastern India related to Captain Lewin, the Deputy Commissioner of Hill Tracts, the following tradition of the creation of man. "God made the world and the trees and the creeping things first, and after that he set to work to make one man and one woman, forming their bodies of clay; but each night, on the completion of his work, there came a great snake, which, while God was sleeping, devoured the two images. This happened twice or thrice, and God was at his wit's end, for he had to work all day, and could not finish the pair in less than twelve hours; besides, if he did not sleep, he would be no good," said Captain Lewin's informant. "If he were not obliged to sleep, there would be no death, nor would mankind be afflicted with illness. It is when he rests that the snake carries us off to this day. Well, he was at his wit's end, so at last he got up early one morning and first made a dog and put life into it, and that night, when he had finished the images, he set the dog to watch them, and when the snake came, the dog barked and frightened it away. This is the reason at this day that when a man is dying the dogs begin to howl; but I suppose God sleeps heavily now-a-days, or the snake is bolder, for men die all the same." (Capt. T.H. Lewin, "Wild Races of South-Eastern India" (London, 1870), pages 224-26.) The Khasis of Assam tell a similar tale. (A. Bastian, "Volkerstamme am Brahmaputra und verwandtschaftliche Nachbarn" (Berlin, 1883), page 8; Major P.R.T. Gurdon, "The Khasis" (London, 1907), page 106.)

The Ewe-speaking tribes of Togo-land, in West Africa, think that God still makes men out of clay. When a little of the water with which he moistens the clay remains over, he pours it on the ground and out of that he makes the bad and disobedient people. When he wishes to make a good man he makes him out of good clay; but when he wishes to make a bad man, he employs only bad clay for the purpose. In the beginning God fashioned a man and set him on the earth; after that he fashioned a woman. The two looked at each other and began to laugh, whereupon God sent them into the world. (J. Spieth, "Die Ewe-Stämme, Material zur Kunde des Ewe-Volkes in Deutsch-Togo" (Berlin, 1906), pages 828, 840.) The Innuits or Esquimaux of Point Barrow, in Alaska, tell of a time when there was no man in the land, till a spirit named "a se lu", who resided at Point Barrow, made a clay man, set him up on the shore to dry, breathed into him and gave him life. ("Report of the International Expedition to Point Barrow" (Washington, 1885), page 47.) Other Esquimaux of Alaska relate how the Raven made the first woman out of clay to be a companion to the first man; he fastened water-grass to the back of the head to be hair, flapped his wings over the clay figure, and it arose, a beautiful young woman. (E.W. Nelson, "The Eskimo about Bering Strait", "Eighteenth Annual Report of the Bureau of American Ethnology", Part I. (Washington, 1899), page 454.) The Acagchemem Indians of California said that a powerful being called Chinigchinich created man out of clay which he found on the banks of a lake; male and female created he them, and the Indians of the present day are their descendants. (Friar Geronimo Boscana, "Chinigchinich", appended to (A. Robinson's) "Life in California" (New York, 1846), page 247.) A priest of the Natchez Indians in Louisiana told Du Pratz "that God had kneaded some clay, such as that which potters use and had made it into a little man; and that after examining it, and finding it well formed, he blew up his work, and forthwith that little man had life, grew, acted, walked, and found himself a man perfectly well shaped." As to the mode in which the first woman was created, the priest had no information, but thought she was probably made in the same way as the first man; so Du Pratz corrected his imperfect notions by reference to Scripture. (M. Le Page Du Pratz, "The

History of Louisiana" (London, 1774), page 330.) The Michoacans of Mexico said that the great god Tzacapacha first made man and woman out of clay, but that when the couple went to bathe in a river they absorbed so much water that the clay of which they were composed all fell to pieces. Then the creator went to work again and moulded them afresh out of ashes, and after that he essayed a third time and made them of metal. This last attempt succeeded. The metal man and woman bathed in the river without falling to pieces, and by their union they became the progenitors of mankind. (A. de Herrera, "General History of the vast Continent and Islands of America", translated into English by Capt. J. Stevens (London, 1725, 1726), III. 254; Brasseur de Bourbourg, "Histoire des Nations Civilisees du Mexique et de l'Amerique-Centrale" (Paris, 1857—1859), III. 80 sq; compare id. I. 54 sq.)

According to a legend of the Peruvian Indians, which was told to a Spanish priest in Cuzco about half a century after the conquest, it was in Tiahuanaco that man was first created, or at least was created afresh after the deluge. "There (in Tiahuanaco)," so runs the legend, "the Creator began to raise up the people and nations that are in that region, making one of each nation of clay, and painting the dresses that each one was to wear; those that were to wear their hair, with hair, and those that were to be shorn, with hair cut. And to each nation was given the language, that was to be spoken, and the songs to be sung, and the seeds and food that they were to sow. When the Creator had finished painting and making the said nations and figures of clay, he gave life and soul to each one, as well men as women, and ordered that they should pass under the earth. Thence each nation came up in the places to which he ordered them to go." (E.J. Payne, "History of the New World called America", I. (Oxford, 1892), page 462.)

These examples suffice to prove that the theory of the creation of man out of dust or clay has been current among savages in many parts of the world. But it is by no means the only explanation which the savage philosopher has given of the beginnings of human life on earth. Struck by the resemblances which may be traced between himself and the beasts, he has often supposed, like Darwin himself, that mankind has been developed out of lower forms of animal life. For the simple savage has none of that high notion of the transcendent dignity of man which makes so many superior persons shrink with horror from the suggestion that they are distant cousins of the brutes. He on the contrary is not too proud to own his humble relations; indeed his difficulty often is to perceive the distinction between him and them. Questioned by a missionary, a Bushman of more than average intelligence "could not state any difference between a man and a brute—he did not know but a buffalo might shoot with bows and arrows as well as man, if it had them." (Reverend John Campbell, "Travels in South Africa" (London, 1822, II. page 34.) When the Russians first landed on one of the Alaskan islands, the natives took them for cuttle-fish "on account of the buttons on their clothes." (I. Petroff, "Report on the Population, Industries, and Resources of Alaska", page 145.) The Giliaks of the Amoor think that the outward form and size of an animal are only apparent; in substance every beast is a real man, just like a Giliak himself, only endowed with an intelligence and strength, which often surpass those of mere ordinary human beings. (L. Sternberg, "Die Religion der Giljaken", "Archiv fur Religionswissenschaft", VIII. (1905), page 248.) The Borororos, an Indian tribe of Brazil, will have it that they are parrots of a gorgeous red plumage which live in their native forests. Accordingly they treat the birds as their fellow-tribesmen, keeping them in captivity, refusing to eat their flesh, and mourning for them when they die. (K. von den Steinen, "Unter den Naturvolkern Zentral-Brasiliens" (Berlin, 1894), pages 352 sq., 512.)

This sense of the close relationship of man to the lower creation is the essence of totemism, that curious system of superstition which unites by a mystic bond a group of human kinsfolk to a species of animals or plants. Where that system exists in full force, the members of a totem clan identify themselves with their totem animals in a way and to an extent which we find it hard even to imagine. For example, men of the Cassowary clan in Mabuiag think that cassowaries are men or nearly so. "Cassowary, he all same as relation, he belong same family," is the account they give of their relationship with the long-legged bird. Conversely they hold that they themselves are cassowaries for all practical purposes. They pride themselves on having long thin legs like a cassowary. This reflection affords them peculiar satisfaction when they go out to fight, or to run away, as the case may be; for at such times a Cassowary man will say to himself, "My leg is long and thin, I can run and not feel tired; my legs will go quickly and the grass will not entangle them." Members of the Cassowary clan are reputed to be pugnacious, because the cassowary is a bird of very uncertain temper and can kick with

extreme violence. (A.C. Haddon, "The Ethnography of the Western Tribe of Torres Straits", "Journal of the Anthropological Institute", XIX. (1890), page 393; "Reports of the Cambridge Anthropological Expedition to Torres Straits", V. (Cambridge, 1904), pages 166, 184.) So among the Ojibways men of the Bear clan are reputed to be surly and pugnacious like bears, and men of the Crane clan to have clear ringing voices like cranes. (W.W. Warren, "History of the Ojibways", "Collections of the Minnesota Historical Society", V. (Saint Paul, Minn. 1885), pages 47, 49.) Hence the savage will often speak of his totem animal as his father or his brother, and will neither kill it himself nor allow others to do so, if he can help it. For example, if somebody were to kill a bird in the presence of a native Australian who had the bird for his totem, the black might say, "What for you kill that fellow? that my father!" or "That brother belonging to me you have killed; why did you do it?" (E. Palmer, "Notes on some Australian Tribes", "Journal of the Anthropological Institute", XIII. (1884), page 300.) Bechuanas of the Porcupine clan are greatly afflicted if anybody hurts or kills a porcupine in their presence. They say, "They have killed our brother, our master, one of ourselves, him whom we sing of"; and so saying they piously gather the quills of their murdered brother, spit on them, and rub their eyebrows with them. They think they would die if they touched its flesh. In like manner Bechuanas of the Crocodile clan call the crocodile one of themselves, their master, their brother; and they mark the ears of their cattle with a long slit like a crocodile's mouth by way of a family crest. Similarly Bechuanas of the Lion clan would not, like the members of other clans, partake of lion's flesh; for how, say they, could they eat their grandfather? If they are forced in self-defence to kill a lion, they do so with great regret and rub their eyes carefully with its skin, fearing to lose their sight if they neglected this precaution. (T. Arbousset et F. Daumas, "Relation d'un Voyage d'Exploration au Nord-Est de la Colonie du Cap de Bonne-Esperance" (Paris, 1842), pages 349 sq., 422-24.) A Mandingo porter has been known to offer the whole of his month's pay to save the life of a python, because the python was his totem and he therefore regarded the reptile as his relation; he thought that if he allowed the creature to be killed, the whole of his own family would perish, probably through the vengeance to be taken by the reptile kinsfolk of the murdered serpent. (M. le Docteur Tautain, "Notes sur les Croyances et Pratiques Religieuses des Banmanas", "Revue d'Ethnographie", III. (1885), pages 396 sq.; A. Rancon, "Dans la Haute-Gambie, Voyage d'Exploration Scientifique" (Paris, 1894), page 445.)

Sometimes, indeed, the savage goes further and identifies the revered animal not merely with a kinsman but with himself; he imagines that one of his own more or less numerous souls, or at all events that a vital part of himself, is in the beast, so that if it is killed he must die. Thus, the Balong tribe of the Cameroons, in West Africa, think that every man has several souls, of which one is lodged in an elephant, a wild boar, a leopard, or what not. When any one comes home, feels ill, and says, "I shall soon die," and is as good as his word, his friends are of opinion that one of his souls has been shot by a hunter in a wild boar or a leopard, for example, and that that is the real cause of his death. (J. Keller, "Ueber das Land und Volk der Balong", "Deutsches Kolonialblatt", 1 October, 1895, page 484.) A Catholic missionary, sleeping in the hut of a chief of the Fan negroes, awoke in the middle of the night to see a huge black serpent of the most dangerous sort in the act of darting at him. He was about to shoot it when the chief stopped him, saying, "In killing that serpent, it is me that you would have killed. Fear nothing, the serpent is my elangela." (Father Trilles, "Chez les Fang, leurs Moeurs, leur Langue, leur Religion", "Les Missions Catholiques", XXX. (1898), page 322.) At Calabar there used to be some years ago a huge old crocodile which was well known to contain the spirit of a chief who resided in the flesh at Duke Town. Sporting Vice-Consuls, with a reckless disregard of human life, from time to time made determined attempts to injure the animal, and once a peculiarly active officer succeeded in hitting it. The chief was immediately laid up with a wound in his leg. He SAID that a dog had bitten him, but few people perhaps were deceived by so flimsy a pretext. (Miss Mary H. Kingsley, "Travels in West Africa" (London, 1897), pages 538 sq. As to the external or bush souls of human beings, which in this part of Africa are supposed to be lodged in the bodies of animals, see Miss Mary H. Kingsley op. cit. pages 459-461; R. Henshaw, "Notes on the Efik belief in 'bush soul'", "Man", VI. (1906), pages 121 sq.; J. Parkinson, "Notes on the Asaba people (Ibos) of the Niger", "Journal of the Anthropological Institute", XXXVI. (1906), pages 314 sq.) Once when Mr Partridge's canoe-men were about to catch fish near an Assiga town in Southern Nigeria, the natives of the town objected, saying, "Our souls live in those fish, and if you kill them we shall die." (Charles Partridge, "Cross River Natives" (London, 1905), pages 225 sq.) On another occasion, in the same region, an Englishman shot a hippopotamus

near a native village. The same night a woman died in the village, and her friends demanded and obtained from the marksman five pounds as compensation for the murder of the woman, whose soul or second self had been in that hippopotamus. (C.H. Robinson, "Hausaland" (London, 1896), pages 36 sq.) Similarly at Ndolo, in the Congo region, we hear of a chief whose life was bound up with a hippopotamus, but he prudently suffered no one to fire at the animal. ("Notes Analytiques sur les Collections Ethnographiques du Musee du Congo", I. (Brussels, 1902-06), page 150.)

Amongst people who thus fail to perceive any sharp line of distinction between beasts and men it is not surprising to meet with the belief that human beings are directly descended from animals. Such a belief is often found among totemic tribes who imagine that their ancestors sprang from their totemic animals or plants; but it is by no means confined to them. Thus, to take instances, some of the Californian Indians, in whose mythology the coyote or prairie-wolf is a leading personage, think that they are descended from coyotes. At first they walked on all fours; then they began to have some members of the human body, one finger, one toe, one eye, one ear, and so on; then they got two fingers, two toes, two eyes, two ears, and so forth; till at last, progressing from period to period, they became perfect human beings. The loss of their tails, which they still deplore, was produced by the habit of sitting upright. (H.R. Schoolcraft, "Indian Tribes of the United States", IV. (Philadelphia, 1856), pages 224 sq.; compare id. V. page 217. The descent of some, not all, Indians from coyotes is mentioned also by Friar Boscana, in (A. Robinson's) "Life in California" (New York, 1846), page 299.) Similarly Darwin thought that "the tail has disappeared in man and the anthropomorphous apes, owing to the terminal portion having been injured by friction during a long lapse of time; the basal and embedded portion having been reduced and modified, so as to become suitable to the erect or semi-erect position." (Charles Darwin, "The Descent of Man", Second Edition (London, 1879), page 60.) The Turtle clan of the Iroquois think that they are descended from real mud turtles which used to live in a pool. One hot summer the pool dried up, and the mud turtles set out to find another. A very fat turtle, waddling after the rest in the heat, was much incommoded by the weight of his shell, till by a great effort he heaved it off altogether. After that he gradually developed into a man and became the progenitor of the Turtle clan. (E.A. Smith, "Myths of the Iroquois", "Second Annual Report of the Bureau of Ethnology" (Washington, 1883), page 77.) The Crawfish band of the Choctaws are in like manner descended from real crawfish, which used to live under ground, only coming up occasionally through the mud to the surface. Once a party of Choctaws smoked them out, taught them the Choctaw language, taught them to walk on two legs, made them cut off their toe nails and pluck the hair from their bodies, after which they adopted them into the tribe. But the rest of their kindred, the crawfish, are crawfish under ground to this day. (Geo. Catlin, "North American Indians" 4 (London, 1844), II. page 128.) The Osage Indians universally believed that they were descended from a male snail and a female beaver. A flood swept the snail down to the Missouri and left him high and dry on the bank, where the sun ripened him into a man. He met and married a beaver maid, and from the pair the tribe of the Osages is descended. For a long time these Indians retained a pious reverence for their animal ancestors and refrained from hunting beavers, because in killing a beaver they killed a brother of the Osages. But when white men came among them and offered high prices for beaver skins, the Osages yielded to the temptation and took the lives of their furry brethren. (Lewis and Clarke, "Travels to the Source of the Missouri River" (London, 1815), I. 12 (Vol. I. pages 44 sq. of the London reprint, 1905).) The Carp clan of the Ootawak Indians are descended from the eggs of a carp which had been deposited by the fish on the banks of a stream and warmed by the sun. ("Lettres Edifiantes et Curieuses", Nouvelle Edition, VI. (Paris, 1781), page 171.) The Crane clan of the Ojibways are sprung originally from a pair of cranes, which after long wanderings settled on the rapids at the outlet of Lake Superior, where they were changed by the Great Spirit into a man and woman. (L.H. Morgan, "Ancient Society" (London, 1877), page 180.) The members of two Omaha clans were originally buffaloes and lived, oddly enough, under water, which they splashed about, making it muddy. And at death all the members of these clans went back to their ancestors the buffaloes. So when one of them lay adying, his friends used to wrap him up in a buffalo skin with the hair outside and say to him, "You came hither from the animals and you are going back thither. Do not face this way again. When you go, continue walking. (J. Owen Dorsey, "Omaha Sociology", "Third Annual Report of the Bureau of Ethnology" (Washington, 1884), pages 229, 233.) The Haida Indians of Queen Charlotte Islands believe that long ago the raven, who is the chief figure in the mythology of North-West America, took a cockle from the beach and married it; the cockle gave

birth to a female child, whom the raven took to wife, and from their union the Indians were produced. (G.M. Dawson, "Report on the Queen Charlotte Islands" (Montreal, 1880), pages 149B sq. ("Geological Survey of Canada"); F. Poole, "Queen Charlotte Islands", page 136.) The Delaware Indians called the rattle-snake their grandfather and would on no account destroy one of these reptiles, believing that were they to do so the whole race of rattle-snakes would rise up and bite them. Under the influence of the white man, however, their respect for their grandfather the rattle-snake gradually died away, till at last they killed him without compunction or ceremony whenever they met him. The writer who records the old custom observes that he had often reflected on the curious connection which appears to subsist in the mind of an Indian between man and the brute creation; "all animated nature," says he, "in whatever degree, is in their eyes a great whole, from which they have not yet ventured to separate themselves." (Rev. John Heckewelder, "An Account of the History, Manners, and Customs, of the Indian Nations, who once inhabited Pennsylvania and the Neighbouring States", "Transactions of the Historical and Literary Committee of the American Philosophical Society", I. (Philadelphia, 1819), pages 245, 247, 248.)

Some of the Indians of Peru boasted of being descended from the puma or American lion; hence they adored the lion as a god and appeared at festivals like Hercules dressed in the skins of lions with the heads of the beasts fixed over their own. Others claimed to be sprung from condors and attired themselves in great black and white wings, like that enormous bird. (Garcilasso de la Vega, "First Part of the Royal Commentaries of the Yncas", Vol. I. page 323, Vol. II. page 156 (Markham's translation).) The Wanika of East Africa look upon the hyaena as one of their ancestors or as associated in some way with their origin and destiny. The death of a hyaena is mourned by the whole people, and the greatest funeral ceremonies which they perform are performed for this brute. The wake held over a chief is as nothing compared to the wake held over a hyaena; one tribe only mourns the death of its chief, but all the tribes unite to celebrate the obsequies of a hyaena. (Charles New, "Life, Wanderings, and Labours in Eastern Africa" (London, 1873) page 122.) Some Malagasy families claim to be descended from the babacoote (*Lichanotus brevicaudatus*), a large lemur of grave appearance and staid demeanour, which lives in the depth of the forest. When they find one of these creatures dead, his human descendants bury it solemnly, digging a grave for it, wrapping it in a shroud, and weeping and lamenting over its carcase. A doctor who had shot a babacoote was accused by the inhabitants of a Betsimisaraka village of having killed "one of their grandfathers in the forest," and to appease their indignation he had to promise not to skin the animal in the village but in a solitary place where nobody could see him. (Father Abinal, "Croyances fabuleuses des Malgaches", "Les Missions Catholiques", XII. (1880), page 526; G.H. Smith, "Some Betsimisaraka superstitions", "The Antananarivo Annual and Madagascar Magazine", No. 10 (Antananarivo, 1886), page 239; H.W. Little, "Madagascar, its History and People" (London, 1884), pages 321 sq; A. van Gennep, "Tabou et Totemisme a Madagascar" (Paris, 1904), pages 214 sqq.) Many of the Betsimisaraka believe that the curious nocturnal animal called the aye-aye (*Cheiromys madagascariensis*) "is the embodiment of their forefathers, and hence will not touch it, much less do it an injury. It is said that when one is discovered dead in the forest, these people make a tomb for it and bury it with all the forms of a funeral. They think that if they attempt to entrap it, they will surely die in consequence." (G.A. Shaw, "The Aye-aye", "Antananarivo Annual and Madagascar Magazine", Vol. II. (Antananarivo, 1896), pages 201, 203 (Reprint of the Second four Numbers). Compare A. van Gennep, "Tabou et Totemisme a Madagascar", pages 223 sq.) Some Malagasy tribes believe themselves descended from crocodiles and accordingly they deem the formidable reptiles their brothers. If one of these scaly brothers so far forgets the ties of kinship as to devour a man, the chief of the tribe, or in his absence an old man familiar with the tribal customs, repairs at the head of the people to the edge of the water, and summons the family of the culprit to deliver him up to the arm of justice. A hook is then baited and cast into the river or lake. Next day the guilty brother or one of his family is dragged ashore, formally tried, sentenced to death, and executed. The claims of justice being thus satisfied, the dead animal is lamented and buried like a kinsman; a mound is raised over his grave and a stone marks the place of his head. (Father Abinal, "Croyances fabuleuses des Malgaches", "Les Missions Catholiques", XII. (1880), page 527; A. van Gennep, "Tabou et Totemisme a Madagascar", pages 281 sq.)

Amongst the Tshi-speaking tribes of the Gold Coast in West Africa the Horse-mackerel family traces its descent from a real horse-mackerel whom an ancestor of theirs once took to wife. She lived with him

happily in human shape on shore till one day a second wife, whom the man had married, cruelly taunted her with being nothing but a fish. That hurt her so much that bidding her husband farewell she returned to her old home in the sea, with her youngest child in her arms, and never came back again. But ever since the Horse-mackerel people have refrained from eating horse-mackerels, because the lost wife and mother was a fish of that sort. (A.B. Ellis, "The Tshi-speaking Peoples of the Gold Coast of West Africa" (London, 1887), pages 208-11. A similar tale is told by another fish family who abstain from eating the fish (appei) from which they take their name (A.B. Ellis op. cit. pages 211 sq.).) Some of the Land Dyaks of Borneo tell a similar tale to explain a similar custom. "There is a fish which is taken in their rivers called a puttin, which they would on no account touch, under the idea that if they did they would be eating their relations. The tradition respecting it is, that a solitary old man went out fishing and caught a puttin, which he dragged out of the water and laid down in his boat. On turning round, he found it had changed into a very pretty little girl. Conceiving the idea she would make, what he had long wished for, a charming wife for his son, he took her home and educated her until she was fit to be married. She consented to be the son's wife cautioning her husband to use her well. Some time after their marriage, however, being out of temper, he struck her, when she screamed, and rushed away into the water; but not without leaving behind her a beautiful daughter, who became afterwards the mother of the race." (The Lord Bishop of Labuan, "On the Wild Tribes of the North-West Coast of Borneo", "Transactions of the Ethnological Society of London", New Series II. (London, 1863), pages 26 sq. Such stories conform to a well-known type which may be called the Swan-Maiden type of story, or Beauty and the Beast, or Cupid and Psyche. The occurrence of stories of this type among totemic peoples, such as the Tshi-speaking negroes of the Gold Coast, who tell them to explain their totemic taboos, suggests that all such tales may have originated in totemism. I shall deal with this question elsewhere.)

Members of a clan in Mandailing, on the west coast of Sumatra, assert that they are descended from a tiger, and at the present day, when a tiger is shot, the women of the clan are bound to offer betel to the dead beast. When members of this clan come upon the tracks of a tiger, they must, as a mark of homage, enclose them with three little sticks. Further, it is believed that the tiger will not attack or lacerate his kinsmen, the members of the clan. (H. Ris, "De Onderafdeeling Klein Mandailing Oeloe en Pahantan en hare Bevolking met uitzondering van de Oeloes", "Bijdragen tot de Tall- Land- en Volkenkunde van Nederlandsch-Indie, XLVI." (1896), page 473.) The Battas of Central Sumatra are divided into a number of clans which have for their totems white buffaloes, goats, wild turtle-doves, dogs, cats, apes, tigers, and so forth; and one of the explanations which they give of their totems is that these creatures were their ancestors, and that their own souls after death can transmigrate into the animals. (J.B. Neumann, "Het Pane en Bila-stroomgebied op het eiland Sumatra", "Tijdschrift van het Nederlandsch Aardrijkskundig Genootschap", Tweede Serie, III. Afdeeling, Meer uitgebreide Artikelen, No. 2 (Amsterdam, 1886), pages 311 sq.; id. ib. Tweede Serie, IV. Afdeeling, Meer uitgebreide Artikelen, No. 1 (Amsterdam, 1887), pages 8 sq.) In Amboyna and the neighbouring islands the inhabitants of some villages aver that they are descended from trees, such as the *Capellenia moluccana*, which had been fertilised by the *Pandion Haliaetus*. Others claim to be sprung from pigs, octopuses, crocodiles, sharks, and eels. People will not burn the wood of the trees from which they trace their descent, nor eat the flesh of the animals which they regard as their ancestors. Sickneses of all sorts are believed to result from disregarding these taboos. (J.G.F. Riedel, "De sluk- en kroesharige rassen tusschen Selebes en Papua" (The Hague, 1886), pages 32, 61; G.W.W.C. Baron van Hoevell, "Ambon en meer bepaaldelijk de Oeliasers" (Dordrecht, 1875), page 152.) Similarly in Ceram persons who think they are descended from crocodiles, serpents, iguanas, and sharks will not eat the flesh of these animals. (J.G.F. Riedel op. cit. page 122.) Many other peoples of the Molucca Islands entertain similar beliefs and observe similar taboos. (J.G.F. Riedel "De sluk- en kroesharige rassen tusschen Selebes en Papua" (The Hague, 1886), pages 253, 334, 341, 348, 412, 414, 432.) Again, in Ponape, one of the Caroline Islands, "The different families suppose themselves to stand in a certain relation to animals, and especially to fishes, and believe in their descent from them. They actually name these animals 'mothers'; the creatures are sacred to the family and may not be injured. Great dances, accompanied with the offering of prayers, are performed in their honour. Any person who killed such an animal would expose himself to contempt and punishment, certainly also to the vengeance of the insulted deity." Blindness is commonly supposed to be the consequence of such a sacrilege. (Dr Hahl,

"Mittheilungen uber Sitten und rechtliche Verhaltnisse auf Ponape", "Ethnologisches Notizblatt", Vol. II. Heft 2 (Berlin, 1901), page 10.)

Some of the aborigines of Western Australia believe that their ancestors were swans, ducks, or various other species of water-fowl before they were transformed into men. (Captain G. Grey, "A Vocabulary of the Dialects of South Western Australia", Second Edition (London, 1840), pages 29, 37, 61, 63, 66, 71.) The Dieri tribe of Central Australia, who are divided into totemic clans, explain their origin by the following legend. They say that in the beginning the earth opened in the midst of Perigundi Lake, and the totems (murdus or madas) came trooping out one after the other. Out came the crow, and the shell parakeet, and the emu, and all the rest. Being as yet imperfectly formed and without members or organs of sense, they laid themselves down on the sandhills which surrounded the lake then just as they do now. It was a bright day and the totems lay basking in the sunshine, till at last, refreshed and invigorated by it, they stood up as human beings and dispersed in all directions. That is why people of the same totem are now scattered all over the country. You may still see the island in the lake out of which the totems came trooping long ago. (A.W. Howitt, "Native Tribes of South-East Australia" (London, 1904), pages 476, 779 sq.) Another Dieri legend relates how Paralina, one of the Mura-Muras or mythical predecessors of the Dieri, perfected mankind. He was out hunting kangaroos, when he saw four incomplete beings cowering together. So he went up to them, smoothed their bodies, stretched out their limbs, slit up their fingers and toes, formed their mouths, noses, and eyes, stuck ears on them, and blew into their ears in order that they might hear. Having perfected their organs and so produced mankind out of these rudimentary beings, he went about making men everywhere. (A.W. Howitt op. cit., pages 476, 780 sq.) Yet another Dieri tradition sets forth how the Mura-Mura produced the race of man out of a species of small black lizards, which may still be met with under dry bark. To do this he divided the feet of the lizards into fingers and toes, and, applying his forefinger to the middle of their faces, created a nose; likewise he gave them human eyes, mouths and ears. He next set one of them upright, but it fell down again because of its tail; so he cut off its tail and the lizard then walked on its hind legs. That is the origin of mankind. (S. Gason, "The Manners and Customs of the Dieyerie tribe of Australian Aborigines", "Native Tribes of South Australia" (Adelaide, 1879), page 260. This writer fell into the mistake of regarding the Mura-Mura (Mooramoorra) as a Good-Spirit instead of as one of the mythical but more or less human predecessors of the Dieri in the country. See A.W. Howitt, "Native Tribes of South-East Australia", pages 475 sqq.)

The Arunta tribe of Central Australia similarly tell how in the beginning mankind was developed out of various rudimentary forms of animal life. They say that in those days two beings called Ungambikula, that is, "out of nothing," or "self-existing," dwelt in the western sky. From their lofty abode they could see, far away to the east, a number of inapertwa creatures, that is, rudimentary human beings or incomplete men, whom it was their mission to make into real men and women. For at that time there were no real men and women; the rudimentary creatures (inapertwa) were of various shapes and dwelt in groups along the shore of the salt water which covered the country. These embryos, as we may call them, had no distinct limbs or organs of sight, hearing, and smell; they did not eat food, and they presented the appearance of human beings all doubled up into a rounded mass, in which only the outline of the different parts of the body could be vaguely perceived. Coming down from their home in the western sky, armed with great stone knives, the Ungambikula took hold of the embryos, one after the other. First of all they released the arms from the bodies, then making four clefts at the end of each arm they fashioned hands and fingers; afterwards legs, feet, and toes were added in the same way. The figure could now stand; a nose was then moulded and the nostrils bored with the fingers. A cut with the knife made the mouth, which was pulled open several times to render it flexible. A slit on each side of the face separated the upper and lower eye-lids, disclosing the eyes, which already existed behind them; and a few strokes more completed the body. Thus out of the rudimentary creatures were formed men and women. These rudimentary creatures or embryos, we are told, "were in reality stages in the transformation of various animals and plants into human beings, and thus they were naturally, when made into human beings, intimately associated with the particular animal or plant, as the case may be, of which they were the transformations—in other words, each individual of necessity belonged to a totem, the name of which was of course that of the animal or plant of which he or she was a transformation." However, it is not said that all the totemic clans of the Arunta were thus developed; no such tradition, for example, is told to explain the origin of the important Witchetty Grub clan. The clans

which are positively known, or at least said, to have originated out of embryos in the way described are the Plum Tree, the Grass Seed, the Large Lizard, the Small Lizard, the Alexandra Parakeet, and the Small Rat clans. When the Ungambikula had thus fashioned people of these totems, they circumcised them all, except the Plum Tree men, by means of a fire-stick. After that, having done the work of creation or evolution, the Ungambikula turned themselves into little lizards which bear a name meaning "snappers-up of flies." (Baldwin Spencer and F.J. Gillen, "Native Tribes of Central Australia" (London, 1899), pages 388 sq.; compare id., "Northern Tribes of Central Australia" (London, 1904), page 150.)

This Arunta tradition of the origin of man, as Messrs Spencer and Gillen, who have recorded it, justly observe, "is of considerable interest; it is in the first place evidently a crude attempt to describe the origin of human beings out of non-human creatures who were of various forms; some of them were representatives of animals, others of plants, but in all cases they are to be regarded as intermediate stages in the transition of an animal or plant ancestor into a human individual who bore its name as that of his or her totem." (Baldwin Spencer and F.J. Gillen, "Native Tribes of Central Australia", pages 391 sq.) In a sense these speculations of the Arunta on their own origin may be said to combine the theory of creation with the theory of evolution; for while they represent men as developed out of much simpler forms of life, they at the same time assume that this development was effected by the agency of two powerful beings, whom so far we may call creators. It is well known that at a far higher stage of culture a crude form of the evolutionary hypothesis was propounded by the Greek philosopher Empedocles. He imagined that shapeless lumps of earth and water, thrown up by the subterranean fires, developed into monstrous animals, bulls with the heads of men, men with the heads of bulls, and so forth; till at last, these hybrid forms being gradually eliminated, the various existing species of animals and men were evolved. (E. Zeller, "Die Philosophie der Griechen", I.4 (Leipsic, 1876), pages 718 sq.; H. Ritter et L. Preller, "Historia Philosophiae Graecae et Romanae ex fontium locis contexta" 5, pages 102 sq. H. Diels, "Die Fragmente der Vorsokratiker" 2, I. (Berlin, 1906), pages 190 sqq. Compare Lucretius "De rerum natura", V. 837 sqq.) The theory of the civilised Greek of Sicily may be set beside the similar theory of the savage Arunta of Central Australia. Both represent gropings of the human mind in the dark abyss of the past; both were in a measure grotesque anticipations of the modern theory of evolution.

In this essay I have made no attempt to illustrate all the many various and divergent views which primitive man has taken of his own origin. I have confined myself to collecting examples of two radically different views, which may be distinguished as the theory of creation and the theory of evolution. According to the one, man was fashioned in his existing shape by a god or other powerful being; according to the other he was evolved by a natural process out of lower forms of animal life. Roughly speaking, these two theories still divide the civilised world between them. The partisans of each can appeal in support of their view to a large consensus of opinion; and if truth were to be decided by weighing the one consensus against the other, with "Genesis" in the one scale and "The Origin of Species" in the other, it might perhaps be found, when the scales were finally trimmed, that the balance hung very even between creation and evolution.

X. THE INFLUENCE OF DARWIN ON THE STUDY OF ANIMAL EMBRYOLOGY. By A. Sedgwick, M.A., F.R.S.

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The publication of "The Origin of Species" ushered in a new era in the study of Embryology. Whereas, before the year 1859 the facts of anatomy and development were loosely held together by the theory of types, which owed its origin to the great anatomists of the preceding generation, to Cuvier, L. Agassiz, J. Muller, and R. Owen, they were now combined together into one organic whole by the theory of descent and by the hypothesis of recapitulation which was deduced from that theory. The view (First clearly enunciated by Fritz Muller in his well-known work, "Fur Darwin", Leipzig, 1864; (English Edition, "Facts for Darwin", 1869).) that a knowledge of embryonic and larval histories would lay bare the secrets of race-history and enable the course of evolution to be traced, and so lead to the discovery of the natural system of classification, gave a powerful stimulus to morphological study in general and to embryological investigation in particular. In Darwin's words: "Embryology rises greatly in interest, when we look at the embryo as a picture, more or less obscured, of the progenitor, either in its adult or larval state, of all the members of the same great class." ("Origin" (6th edition), page 396.) In the period under consideration the output of embryological work has been enormous. No group of the animal kingdom has escaped exhaustive examination and no effort has been spared to obtain the embryos of isolated and out of the way forms, the development of which might have an important bearing upon questions of phylogeny and classification. Marine zoological stations have been established, expeditions have been sent to distant countries, and the methods of investigation have been greatly improved. The result of this activity has been that the main features of the developmental history of all the most important animals are now known and the curiosity as to developmental processes, so greatly excited by the promulgation of the Darwinian theory, has to a considerable extent been satisfied.

To what extent have the results of this vast activity fulfilled the expectations of the workers who have achieved them? The Darwin centenary is a fitting moment at which to take stock of our position. In this inquiry we shall leave out of consideration the immense and intensely interesting additions to our knowledge of Natural History. These may be said to constitute a capital fund upon which philosophers, poets and men of science will draw for many generations. The interest of Natural History existed long before Darwinian evolution was thought of and will endure without any reference to philosophic speculations. She is a mistress in whose face are beauties and in whose arms are delights elsewhere unattainable. She is and always has been pursued for her own sake without any reference to philosophy, science, or utility.

Darwin's own views of the bearing of the facts of embryology upon questions of wide scientific interest are perfectly clear. He writes ("Origin" (6th edition), page 395.):

"On the other hand it is highly probable that with many animals the embryonic or larval stages show us, more or less completely, the condition of the progenitor of the whole group in its adult state. In the great class of the Crustacea, forms wonderfully distinct from each other, namely, suctorial parasites, cirripedes, entomostraca, and even the malacostraca, appear at first as larvae under the nauplius-form; and as these larvae live and feed in the open sea, and are not adapted for any peculiar habits of life, and from other reasons assigned by Fritz Muller, it is probable that at some very remote period an independent adult animal, resembling the Nauplius, existed, and subsequently produced, along several divergent lines of descent, the above-named great Crustacean groups. So again it is probable, from what we know of the embryos of mammals, birds, fishes, and reptiles, that these animals are the modified descendants of some ancient progenitor, which was furnished in its adult state with branchiae, a swim-bladder, four fin-like limbs, and a long tail, all fitted for an aquatic life.

"As all the organic beings, extinct and recent, which have ever lived, can be arranged within a few great classes; and as all within each class have, according to our theory, been connected together by fine gradations, the best, and, if our collections were nearly perfect, the only possible arrangement, would be genealogical; descent being the hidden bond of connexion which naturalists have been seeking under the term of the Natural System. On this view we can understand how it is that, in the eyes of most naturalists, the structure of the embryo is even more important for classification than that of the adult. In two or more groups of animals, however much they may differ from each other in structure and habits in their adult condition, if they pass through closely similar embryonic stages, we may feel assured that they all are descended from one parent-form, and are therefore closely related. Thus, community in embryonic structure reveals community of descent; but dissimilarity in embryonic

development does not prove discommunity of descent, for in one of two groups the developmental stages may have been suppressed, or may have been so greatly modified through adaptation to new habits of life, as to be no longer recognisable. Even in groups, in which the adults have been modified to an extreme degree, community of origin is often revealed by the structure of the larvae; we have seen, for instance, that cirripedes, though externally so like shell-fish, are at once known by their larvae to belong to the great class of crustaceans. As the embryo often shows us more or less plainly the structure of the less modified and ancient progenitor of the group, we can see why ancient and extinct forms so often resemble in their adult state the embryos of existing species of the same class. Agassiz believes this to be a universal law of nature; and we may hope hereafter to see the law proved true. It can, however, be proved true only in those cases in which the ancient state of the progenitor of the group has not been wholly obliterated, either by successive variations having supervened at a very early period of growth, or by such variations having been inherited at an earlier stage than that at which they first appeared. It should also be borne in mind, that the law may be true, but yet, owing to the geological record not extending far enough back in time, may remain for a long period, or for ever, incapable of demonstration. The law will not strictly hold good in those cases in which an ancient form became adapted in its larval state to some special line of life, and transmitted the same larval state to a whole group of descendants; for such larvae will not resemble any still more ancient form in its adult state."

As this passage shows, Darwin held that embryology was of interest because of the light it seems to throw upon ancestral history (phylogeny) and because of the help it would give in enabling us to arrive at a natural system of classification. With regard to the latter point, he quotes with approval the opinion that "the structure of the embryo is even more important for classification than that of the adult." What justification is there for this view? The phase of life chosen for the ordinary anatomical and physiological studies, namely, the adult phase, is merely one of the large number of stages of structure through which the organism passes. By far the greater number of these are included in what is specially called the developmental or (if we include larvae with embryos) embryonic period, for the developmental changes are more numerous and take place with greater rapidity at the beginning of life than in its later periods. As each of these stages is equal in value, for our present purpose, to the adult phase, it clearly follows that if there is anything in the view that the anatomical study of organisms is of importance in determining their mutual relations, the study of the organism in its various embryonic (and larval) stages must have a greater importance than the study of the single and arbitrarily selected stage of life called the adult.

But a deeper reason than this has been assigned for the importance of embryology in classification. It has been asserted, and is implied by Darwin in the passage quoted, that the ancestral history is repeated in a condensed form in the embryonic, and that a study of the latter enables us to form a picture of the stages of structure through which the organism has passed in its evolution. It enables us on this view to reconstruct the pedigrees of animals and so to form a genealogical tree which shall be the true expression of their natural relations.

The real question which we have to consider is to what extent the embryological studies of the last 50 years have confirmed or rendered probable this "theory of recapitulation." In the first place it must be noted that the recapitulation theory is itself a deduction from the theory of evolution. The facts of embryology, particularly of vertebrate embryology, and of larval history receive, it is argued, an explanation on the view that the successive stages of development are, on the whole, records of adult stages of structure which the species has passed through in its evolution. Whether this statement will bear a critical verbal examination I will not now pause to inquire, for it is more important to determine whether any independent facts can be alleged in favour of the theory. If it could be shown, as was stated to be the case by L. Agassiz, that ancient and extinct forms of life present features of structure now only found in embryos, we should have a body of facts of the greatest importance in the present discussion. But as Huxley (See Huxley's "Scientific Memoirs", London, 1898, Vol. I. page 303: "There is no real parallel between the successive forms assumed in the development of the life of the individual at present, and those which have appeared at different epochs in the past." See also his Address to the Geological Society of London (1862) 'On the Palaeontological Evidence of Evolution', *ibid.* Vol. II. page 512.) has shown and as the whole course of palaeontological and embryological investigation has

demonstrated, no such statement can be made. The extinct forms of life are very similar to those now existing and there is nothing specially embryonic about them. So that the facts, as we know them, lend no support to theory.

But there is another class of facts which have been alleged in favour of the theory, viz. the facts which have been included in the generalisation known as the Law of v. Baer. The law asserts that embryos of different species of animals of the same group are more alike than the adults and that, the younger the embryo, the greater are the resemblances. If this law could be established it would undoubtedly be a strong argument in favour of the "recapitulation" explanation of the facts of embryology. But its truth has been seriously disputed. If it were true we should expect to find that the embryos of closely similar species would be indistinguishable from one another, but this is notoriously not the case. It is more difficult to meet the assertion when it is made in the form given above, for here we are dealing with matters of opinion. For instance, no one would deny that the embryo of a dogfish is different from the embryo of a rabbit, but there is room for difference of opinion when it is asserted that the difference is less than the difference between an adult dogfish and an adult rabbit. It would be perfectly true to say that the differences between the embryos concern other organs more than do the differences between the adults, but who is prepared to affirm that the presence of a cephalic coelom and of cranial segments, of external gills, of six gill slits, of the kidney tubes opening into the muscle-plate coelom, of an enormous yolk-sac, of a neurenteric canal, and the absence of any trace of an amnion, of an allantois and of a primitive streak are not morphological facts of as high an import as those implied by the differences between the adults? The generalisation undoubtedly had its origin in the fact that there is what may be called a family resemblance between embryos and larvae, but this resemblance, which is by no means exact, is largely superficial and does not extend to anatomical detail.

It is useless to say, as Weismann has stated ("The Evolution Theory", by A. Weismann, English Translation, Vol. II. page 176, London, 1904.), that "it cannot be disputed that the rudiments [vestiges his translator means] of gill-arches and gill-clefts, which are peculiar to one stage of human ontogeny, give us every ground for concluding that we possessed fish-like ancestors." The question at issue is: did the pharyngeal arches and clefts of mammalian embryos ever discharge a branchial function in an adult ancestor of the mammalia? We cannot therefore, without begging the question at issue in the grossest manner, apply to them the terms "gill-arches" and "gill-clefts". That they are homologous with the "gill-arches" and "gill-clefts" of fishes is true; but there is no evidence to show that they ever discharged a branchial function. Until such evidence is forthcoming, it is beside the point to say that it "cannot be disputed" that they are evidence of a piscine ancestry.

It must, therefore, be admitted that one outcome of the progress of embryological and palaeontological research for the last 50 years is negative. The recapitulation theory originated as a deduction from the evolution theory and as a deduction it still remains.

Let us before leaving the subject apply another test. If the evolution theory and the recapitulation theory are both true, how is it that living birds are not only without teeth but have no rudiments of teeth at any stage of their existence? How is it that the missing digits in birds and mammals, the missing or reduced limb of snakes and whales, the reduced mandibulo-hyoid cleft of elasmobranch fishes are not present or relatively more highly developed in the embryo than in the adult? How is it that when a marked variation, such as an extra digit, or a reduced limb, or an extra segment, makes its appearance, it is not confined to the adult but can be seen all through the development? All the clear evidence we can get tends to show that marked variations, whether of reduction or increase, of organs are manifest during the whole of the development of the organ and do not merely affect the adult. And on reflection we see that it could hardly be otherwise. All such evidence is distinctly at variance with the theory of recapitulation, at least as applied to embryos. In the case of larvae of course the case will be different, for in them the organs are functional, and reduction in the adult will not be accompanied by reduction in the larva unless a change in the conditions of life of the larva enables it to occur.

If after 50 years of research and close examination of the facts of embryology the recapitulation theory is still without satisfactory proof, it seems desirable to take a wider sweep and to inquire whether the facts of embryology cannot be included in a larger category.

As has been pointed out by Huxley, development and life are co-extensive, and it is impossible to point to any period in the life of an organism when the developmental changes cease. It is true that

these changes take place more rapidly at the commencement of life, but they are never wholly absent, and those which occur in the later or so-called adult stages of life do not differ in their essence, however much they may differ in their degree, from those which occur during the embryonic and larval periods. This consideration at once brings the changes of the embryonic period into the same category as those of the adult and suggests that an explanation which will account for the one will account for the other. What then is the problem we are dealing with? Surely it is this: Why does an organism as soon as it is established at the fertilisation of the ovum enter upon a cycle of transformations which never cease until death puts an end to them? In other w