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HABIT AND HERITAGE

Frederic Wood Jones
D.Sc., F.R.S., F.R.C.S.

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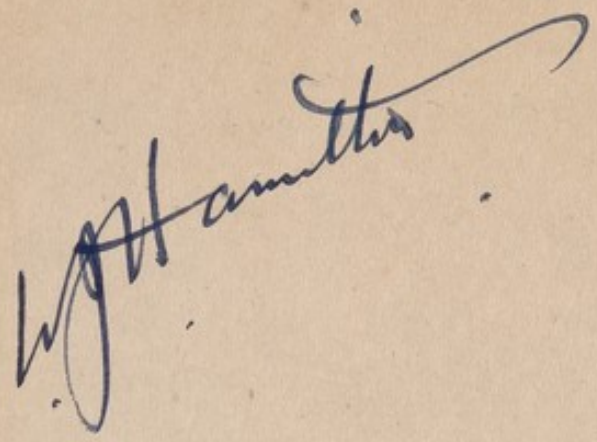

HABIT AND HERITAGE

By the Same Author

LIFE AND LIVING
DESIGN AND PURPOSE

HABIT AND HERITAGE

BY

FREDERIC WOOD JONES
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To my wife.

THIS BOOK IS PRODUCED IN COMPLETE
CONFORMITY WITH THE AUTHORIZED
ECONOMY STANDARDS

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ILLUSTRATIONS

PREFACE

THE writing of this little book has been a wartime recreation : the circumstance of war has largely determined the decision to seek its publication. But although the form in which it is presented and the time at which it is issued have been influenced by present world conditions, the writer's defence of the thesis of the inheritance of acquired characters is no reaction to modern theories of genetics, nor is it in any way the outcome of recent thought.

It does not necessarily imply any validity for a particular opinion to urge that it has been long held by the person who advocates it. We would not expect a geographer to be greatly impressed by a believer in the flatness of the earth who merely urged in support of his thesis that it had remained his sincere belief throughout his thinking life. No one would anticipate sympathy for his belief in the inheritance of acquired characters by reason of the fact that such an inheritance had always seemed to him to be a necessary factor in effecting such evolutionary changes as are well known to have occurred. It is possible that a method, which appears uniquely adequate to produce certain admitted results, is not in fact the one that has been involved in the processes of organic evolution. How, then, are we to put the matter to the test ? In the first place we may try to find out if there are any incontrovertible facts that prohibit a belief in the possibility of this method being utilized by Nature. Should we determine, to the satisfaction of what we honestly believe to be our unbiased judgment, that there is no inherent impossibility in the action of this factor, we may seek for instances in which its action seems clearly to be demonstrated. Even then one thing remains to be done. It is still necessary to weigh against the potency of our elected agency, the virtues of any alternative methods that have been suggested.

In the following chapters there is considered the evidence that has been produced to prove, by reason of certain hypotheses assumed to be incontrovertible facts, that the inheritance of acquired characters is an impossibility. We have come to the conclusion that the validity of this evidence is not absolute and that no truly incontrovertible facts have ever been brought forward to substantiate it. We are, in fact, forced to assume that there is no valid reason that prohibits us from believing that acquired characters may be inherited. More than that, we may even find good evidence in support of the belief in their inheritance. Next, there are detailed some simple happenings in the story of animal structure and function in which the inheritance of acquired characters seems, in the light of ordinary reason, to be clearly demonstrated as a reality. The last task has not been undertaken here. No attempt has been made to demonstrate the relative inadequacy of the selectionist doctrine, whereby "natural selection", acting upon fortuitous variations in genetic constitution, is invoked as the sole agency in producing the conditions dealt with. The final stage has not been embarked upon, not because it is by any means the most difficult part of the journey, but because it is the one least profitable to undertake. Evolution is no simple business, there is room and to spare for many factors in effecting change in matter both living and non-living. The only thing for which there is no room is that type of theory that poses as being the only true doctrine of the only true cause of evolutionary change.

In this little book some attempt has been made at construction : it is an attempt to enlarge our views as to the possibility of evolutionary change. No destructive enterprises have been undertaken, for nothing has done more harm to the cause of evolution than the promulgation of mutually exclusive creeds by certain of its rival high priests.

The subject matter of Chapter IX formed the basis of the Inaugural Lecture at the Medical School of the

University of Leeds, delivered on September 9th, 1942. That of Chapters I–VII was delivered as the Inaugural Lecture of the Manchester Museum series of lectures on October 31st, 1942. Under the title " Human Progress and Biological Theory " the more sociological aspects of the questions involved constituted the subject of the Lloyd Roberts Lecture delivered to the Medical Society of London on December 7th, 1942.

I

The question as to the transmissibility of characters acquired during life by the body of the parent as the result of changes in environment or functional influences is much more than a technical problem for biologists. Our decision in regard to it affects not only our whole theory of organic evolution, but even our every-day conduct. The question should be of interest to the parent, the physician, the teacher, the moralist, and the social reformer—in short, to us all.

J. Arthur Thomson. *Heredity*, London, 1908, p. 165.

TO all thinking people, who contemplate the state of human affairs that confronts us today, there must come a suspicion that it is not enough to blame individuals or political parties for the pass in which humanity finds itself in 1942. Satisfying though it may be to apportion the guilt to this or that wicked or stupid politician, such satisfaction must be short lived, for it is apparent that it is not the times that have produced the wicked and the stupid—they have always been with us—but rather that humanity has been content to permit wickedness and stupidity to work its will in a world that either lacks standards of moral criticism, or fails to give effect to its criticism and take active steps to maintain its ideals in practice. Some there are who hold that nothing is amiss with the standards or ideals of the bulk of ordinary men ; and these would ascribe the present breakdown to the inability of the ordinary man to make his voice heard in the political systems prevailing in many parts of the world. It is not necessary that one should be deeply versed in political affairs to realize the truth of this, and such realization should go far towards counteracting the influence of certain modern racial doctrines. On the other hand, there are those who fancy that the moral and ethical standards of the bulk of ordinary men have gone awry : that the failure to appreciate high standards, and not the failure to enforce them on others, is at the root of the matter.

The ordinary man, so some would maintain, has rather passively acquiesced in the ways and means that have wrought so much evil, because his ethical standards were not greatly outraged in the process. On looking round the world today there would seem to be much evidence to support such a thesis. The business of pointing out the innumerable ways in which high ethical standards have been departed from by all sections of the community during the years of war is so simple a matter that it is devoid of any merit. Nor would an easy analysis be of any real value, since it is a patent fact that there has been a lowering of standards and a shrinkage of human spiritual ideals and it is necessary to look deeper for a cause for this state of affairs. Causes are easily found : indeed, as many causes may be found as there are those who find that the ideals they cherish most dearly are neglected or despised by others. Every one of the ten commandments and religion itself may, in its modern neglect by some section of the community, serve as a text around which to weave a satisfying theory to account for the breakdown of ethical standards.

But I fancy that, apart from all this failure to act up to what we are accustomed to accept as ethical standards, there may be some things that it is worth while examining in the teaching of subjects remote from ethics. I have long had a belief that the light-hearted acceptance, on behalf of the more or less unthinking bulk of mankind, of some of the most widely disseminated, but least firmly established, teachings of science has played its part in world affairs. I have many times called attention to the part that appears to have been played by the wide and unthinking acceptance of all the worst connotations of Charles Darwin's phrase ' the struggle for existence ' and Herbert Spencer's ' survival of the fittest '. For those who think that such deductions are fanciful or exaggerated, there can be no better corrective than the reading of Benedict's latest work, " Race and Racism " (1942). That the grafting of Gobineau's original ridiculous claims for the application of the term ' fittest '

to a certain section of the community on to the Darwinian survival thesis has gone far towards producing the sinister theories that have let loose the present demons of bloodshed and destruction, is not to be doubted. No one who is informed upon these matters can have any doubt whatever that these terms, employed in the first place as purely scientific expressions, have become perverted into the slogans of propaganda for human acts of unthinkable brutality carried out on a scale of unparalleled magnitude. Even the apparently harmless phrases of the poet may be abused and Tennyson's 'Nature red in tooth and claw' cannot escape its burden of responsibility. But I fancy that science has another charge that may be brought against it.

Has not science—even in the most considered and orthodox pronouncements of its most distinguished exponents—possibly led humanity astray in the matter of responsibility in heredity? There was a time when people believed that the sins of the fathers were visited on the children. This belief was incorporated into the teaching that the parents need have some care in their ways of life, lest their acquired shortcomings and moral lapses might be perpetuated in their descendants. It led also to a general belief in the possible ultimate betterment of mankind by a raising of the standard of parental mode of life and well-being. Such hopes have been dashed to the ground. Loud-voiced Science has told the people that characters acquired by individuals can under no circumstances be transmitted to their descendants. It matters not if we live good lives or bad, for, apart from direct disease or social degradation, we cannot hand on to our descendants any virtues or vices, any talents or degeneracies that we may have acquired during our lifetime.

It is not so long ago that scientific circles debated these subjects around a slogan claim for the relative importance of 'Nature or Nurture'. There were some who thought that, in the ultimate betterment of a racial stock, the nurture of the stock was likely to play a master

part. There were others who believed that the nature (or germinal constitution) of the stock was all-important and that nurture (or environment) played little or no part in its ultimate improvement or degradation. Some were prepared to admit that both factors were of importance and that they acted in a reciprocal manner. In the days in which the terms ' nature ' and ' nurture ' were bandied about in scientific discussion, the question was merely a pleasing intellectual exercise. It is true that the ultimate solution of the question might become a practical consideration in the business of the cultivation of domestic plants and animals and so become a guiding principle in the growing science of genetics. Today, the battle has been won for nature (or genetic constitution) and nurture has ceased to be regarded as being of any importance whatever in the ultimate development of a stock. It is only the germinal constitution—the type and disposition of the hypothetical genes—that counts. If all is well with these, the environment in which the stock happens to find itself makes little or no difference. Conversely, no matter how ideal the environment may be for betterment, it is wasted if the stock that enjoys it happens to be of ' inferior ' genetic constitution. It is here that the whole thesis has become interwoven with all the mischief wrought by the blind acceptance of the ' Survival of the fittest ' slogan and all that is worst in the modern pseudo-science of race theories. This modern perversion of the science of genetics teaches that a human stock, which, for some reason, is assumed by some people to be fittest, should be bred from as we breed from stud animals in husbandry ; and that human stocks adjudged to be less fit should be eliminated. The term ' stock ' is then translated as ' race ' and the most dangerous thesis to which real science has ever given countenance, and to which pseudo-science has given absolute assurance and practical effect, is begot. The ' race ' or the section of society that has an assumed inferior genetic constitution is for ever doomed. " Nothing out of all that a human

being acquires during his lifetime through practice and experience can be transmitted by inheritance." "Consequently there is absolutely no prospect that we shall ever be able to bring about a permanent elevation of the human race by means of education and practice." And finally, "If a nation or a particular stratum in a nation has an inferior hereditary equipment (the Negroes, for instance, in the United States of America), education and cultural influences may improve individual members of the nation or stratum, but they cannot alter the stock." These quotations are taken from a standard book that finds its place on the shelves devoted to the accepted textbooks used for the guidance of our medical students in the subject of "Human Heredity." Such statements may appear to be innocuous enough, even though they are somewhat depressing. To some they may seem to be over-dogmatic in their expression of the assumed impossibility of the inheritance of acquired characters, and so to be perhaps vulnerable as scientific pronouncements, but harmless enough in themselves. But to appreciate their real importance one must consider them in the perspective of the whole setting in which they are placed by their authors. This setting is revealed by a further quotation from another section of the book: "Least of all human beings is the Nordic the slave of the moment, for he excels the members of all other races in constancy of will and in foresight. Owing to his Promethean character, he inclines to subordinate his sensual impulses to a remote aim. Self-control is, perhaps, the most distinctive among the characteristics of the Nordic race, and upon this depends in large measure the Nordic gift for civilization." This quotation is taken from the section dealing with "The Inheritance of Intellectual Gifts" by Dr. Fritz Lenz.

Science has broadcast the doctrine of the survival of the fittest: pseudo-science has grafted to this pronouncement the implication that the fittest are those most red in tooth and claw. Science has broadcast the

doctrine of the non-inheritance of acquired characters : pseudo-science would translate this doctrine into a thesis of racialism more cruel, more destructive of hopes of human betterment and of the attainment of international amenities, than any of the other bastard slogan teachings of our time.

It may, therefore, not be inappropriate to examine the foundations of the orthodox scientific creed as to the non-inheritance of acquired characters. Such an examination must, in the first place, involve an inquiry into the origin and the validity of the doctrines of August Weismann and, in the second, the presentation of certain definite happenings in the story of structure and function as seen in some of their more simple manifestations. The field is one that has been traversed again and again in controversies all over the world. At the risk of being charged with evading the issue, these old controversies will not be reviewed here, nor will the experimental evidence that has been brought forward in favour of the inheritance of acquired characters be discussed. These things have become so far enmeshed in verbal tangles as to be somewhat unprofitable subjects for presentation in small compass.

More important than all this, no attempt is here made to assess the recent work of the Russian geneticists. The outstanding work of Lysenko and Michurin, among others, is, in its English presentation, too incomplete to warrant even those rather premature conclusions that have already been arrived at by certain authorities here. Of first-rate importance though it undoubtedly is, it were better to refrain from claiming its support than to arrive at a hasty judgment on necessarily incomplete presentation of the facts. We will, therefore, refrain from relying on man-made experiments and be content to review a few instances in which nature itself, with plenty of time at its disposal, seems to have taken the business in hand.

II

> Much time and energy have been wasted on the discussion as to the transmissibility or non-transmissibility of 'acquired characters' or somatic modifications, through lack of precise definition of the terms. Usually, though not always, the fault has been with the supporters of the affirmative position, who have failed to observe the rules of the game by ignoring the definitions of those who find themselves forced to a negative conclusion.
>
> J. ARTHUR THOMSON. *Heredity*, 1908, p. 172.

IT needs no prolonged study of the literature of this much-debated subject to realize that some of the obscurity and confusion that still envelops the real issue is a direct outcome of the loose employment of certain terms and the lack of very precise definition of the factors involved in the problem. At the outset of any further discussion it is essential to define exactly what is meant by an 'acquired character', and what is implied in the question of the inheritance of such a character.

What do we mean by the term 'acquired character'? It is best that we should seek our definition from the writings of orthodox geneticists and there will be no possibility of ambiguity or confusion if we adopt that which defines an acquired character as "a feature developed during the life of the individual possessing it, in response to the action of use or environment". (1)

The first point to note in this definition is that the feature is '*developed*' and that it comes into being '*in response to the action of use or environment*'. It is obvious that, if we abide by this definition, we rule out the major part of the stupidities that have become intruded into the classical discussions of the subject, for no inflicted mutilation can be considered as being *developed* and still less as being developed in response to the action of use or environment. It is almost incredible that, in the past, the discussion of mutilations inflicted by acci-

dent or design has played so large a part and has been considered so important and conclusive a factor. Man has cut off the tails and ears of his domesticated animals, he has removed the prepuces, pierced the ears and noses of his fellows ; but the fact that these mutilations do not become perpetuated by heredity has nothing whatever to do with the question of the inheritance of *acquired* characters as these things are properly defined.

Having ruled out these irrelevancies that have caused so much confusion in past discussions, our main task is to inquire if acquired characters, as we have agreed to define them, are capable of being inherited. How should we set about the business of proving or disproving the possibility of such a happening ?

It is obvious that, in the spirit of modern science, some attempt should be made to provide evidence by the experimental method. Those who have resorted to direct experiment have, for the most part, failed to realize the dominating influence of time in all the processes of natural evolution. Save in the production of freaks, sports or mutations, nature appears to work extremely slowly in bringing about permanent modifications in living things. This is a factor that is of necessity far more vividly realized by the paleontologist than by the geneticist. In the case of such paleontological series as are sufficiently well known to afford reliable criteria, the immensity of the time involved in the production of any very profound and permanent change is a conspicuous factor. Moreover, the almost completely unaltered uniformity that has prevailed in certain types over vast geological periods, is a warning to the individual experimenter with the necessarily limited span of time available for experiment. We may, therefore, sound the first note of caution by stating that there is every reason to believe that, if acquired characters are inherited, their incorporation into the hereditable make-up of an animal is likely to be a slow process and, unless by reason of some unusual chance of circumstances, we would hardly look to see it accom-

plished in the necessarily short time available to laboratory experiments. The second note of caution is this. The definition we have chosen to adhere to states that the feature is developed during the life of the individual possessing it. Under experimental conditions we might be tempted to look for results in the immediate progeny of the individual submitted to some experimental change in use or environment. Against such an expectation, Charles Darwin himself gave a precise warning. Of the action of use and disuse of parts of the body by individuals he says : " In many cases there is reason to believe that the lessened use of various organs has affected the corresponding parts in the offspring. *But there is no good evidence that this ever follows in the course of a single generation.*" (2) This consideration naturally involves the final caution that is necessary in the acceptance of our agreed definition, for we must realize that, in nature, the circumstances of use or of environment, that call forth the development of the particular character in the individual, are like to be repeated in the case of a long succession of individuals. This note of caution was also sounded by Charles Darwin when he said : " It appears, as in the case of general or indefinitive variability, that *several generations must be subjected to changed habits for any appreciable results.*" (3) So much would seem obvious. The more often a feature is developed in response to the action of use or environment in a succession of individuals, the more likely, we might suppose, it would be to impress itself on the heritage of the species.

We may therefore sum up the connotations of the definition, and thereby introduce reality and order into the discussion of acquired characters, by conceiving the scope of the inquiry to be an attempt to provide an answer to the following very definite question : May a feature developed repeatedly during the successive lives of a long series of generations be ultimately incorporated into the heritage of the species so that in time it will be developed in the offspring not ' as a response to the

action of use or environment' but as a permanent feature of the animal's intrinsic characteristics?

(1) DONCASTER, L. 1911. "Heredity in the light of recent research." Camb. Univ. Press. p. 138.
(2) DARWIN, C. 1868. "The variations of animals and plants under domestication." London. Vol. 2, p. 297.
(3) —— loc. cit. supra (2).

III

Are acquired characters inherited? In fairness we must admit that the verdict of the *practical* man, whether physician or breeder, gardener or farmer, is still in many cases an unhesitatingly affirmative answer.

J. Arthur Thomson. *Heredity*, 1908, p. 193.

Close contemplation of the facts impresses me more strongly than ever with the two alternatives—*either there has been inheritance of acquired characters, or there has been no evolution.*

Herbert Spencer. *Principles of Biology*, 1893. Vol. 1, p. 621.

STATED in that way, the proposition appears to be one that most people would be inclined to accept as being probably true. This acceptance would for the most part be supported by an appeal to common sense. Indeed, a common-sense acceptance of the possibility of the inheritance of acquired characters was practically universal a century ago among both the general run of mankind and those whose preoccupation was with the natural sciences. Today the belief is confined to the non-scientific, for by orthodox science it is completely, or almost completely, discarded. All the early evolutionists accepted the inheritance of acquired characters as axiomatic and their particular conceptions of the processes by which evolution had come about depended upon the recognition of this form of inheritance as a dominant factor in the business. The genius of the pioneers of evolution, such as Lamarck, Buffon and Erasmus Darwin, lay in their recognition of the fact of evolution, not in their suggestion of the means by which it came about. Once the reality of evolution was appreciated there was no difficulty in accounting for the method by which it was effected, since that was obviously the handing on to the offspring of changes that had been wrought by use or environment in the

parents. " The older students of heredity never doubted that these acquired characters were inherited as strongly as inborn characters." (4) Such a belief is implicit in the whole of Lamarck's ' Philosophie Zoologique '. Erasmus Darwin makes clear his position when he writes : " From their first rudiment, or primordium, to the termination of their lives, all animals undergo perpetual transformations, which are in part produced by their own exertions in consequence of their desires and aversions, of their pleasures and their pains, or of irritations, or of associations ; and many of these acquired forms or propensities are transmitted to their progeny." (5) As for his grandson—Charles Darwin —it is easy to follow the way in which his mind was turning towards the question of the transmission of modification after his return from the voyage of the *Beagle*. On February 24th, 1834, when Darwin was at Woollaston Island, he wrote in his diary : " Nature, by making habit omnipotent, has fitted the Fuegian to the climate and productions of his country." (6) Three years later, when he published his edited journal, the passage was altered and in its final form it appears as : " Nature, by making habit omnipotent, *and its effects hereditary*, has fitted the Fuegian to the climate and productions of his miserable country." (7) It was the consideration of the transmissibility of such habits or, as his grandfather would have put it, " these acquired forms or propensities ", that determined Charles Darwin's attitude towards the question. Under the title ' Effects of Use and Disuse ', he states his belief as follows : " In many cases there is reason to believe that the lessened use of various organs has affected the corresponding parts in the offspring." (8) Later, in another publication he says : " I think there can be no doubt that use in our domestic animals has strengthened and enlarged certain parts, and disuse diminished them, and that such modifications are inherited." (9) This was Charles Darwin's last pronouncement on the subject and to it he added the sane proviso : " But

there is no good evidence that this ever follows in the course of a single generation."

Since all the great pioneers in the study of evolution believed in the inheritance of acquired characters in the form in which we have stated the proposition, it must be asked why such a belief is at present held to be absurd. The answer is, of course, that given by Doncaster : " Since the publication of Weismann's theory of heredity with the great body of evidence which has been collected on the other side, opinion has turned increasingly towards the belief that acquired variations are not transmitted." (10)

At first sight it seems a strange thing that Weismannism should have become the accepted creed of British zoologists, but in the flux of opinion during the immediate post-Darwinian period many strange things happened to the cherished faiths of most of those who entered into the prevailing controversies. It is easy in looking back upon those interminable discussions to discern one or two outstanding factors that, first potent nearly a century ago, still exert their influence today. We are probably far enough removed from those times to run but little risk of being charged with misrepresentation (as was Samuel Butler) when it is pointed out that from 1837, when he first began to form his ideas, until his death in 1882, Charles Darwin never decided how much of the change produced in the progress of evolution had been brought about by the inherited effects of use and disuse and how much by the occurrence of chance germinal variations. It is easy to select passages from his works to show that he believed in both methods : it is not difficult to find passages that seem to show that at various times he appeared to rely almost entirely on the one or on the other. Even in his ultimate pronouncement, in the concluding chapter of the last edition of the ' Origin of Species ', his expression appears to lack such clarity as would be expected if the question had been at length resolved in his mind : " I have now recapitulated the facts and considerations which have

thoroughly convinced me that species have been modified, during a long course of descent. 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. It appears that I formerly underrated the frequency and value of these latter forms of variation, as leading to permanent modifications of structure independently of natural selection. 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 have 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.'" (11)

To the end, Charles Darwin remained with one foot at sea in the inheritance of acquired characters and one on shore in the action of natural selection on fortuitous variations. The unfortunate feature in this method of statement lay in the fact that, for most people, Darwin's thesis was the first hint that they had ever received of there being even a possibility of the occurrence of such a thing as evolution. It therefore became a commonly accepted belief that Charles Darwin had originated the thesis of evolution, and many who should have known better broadcast such an idea in popular writings. Regrettably, there are many people even today who still regard 'Darwinism' and 'evolution' as being synonymous terms. Charles Darwin had what nowadays would be called a remarkably good Press. Soon the cry of 'For Darwin or against him' was interpreted as 'For Darwin or against evolution'. Those who,

though not being professional naturalists, had a far sounder knowledge of literature than Darwin's immediate supporters, and who tried to correct this point of view, were silenced in the popular acclaim of the man who, though he did not originate the thesis of evolution, certainly made the world believe in it. But little by little even Darwin's most ardent supporters were forced to realize that many men, among them most conspicuously Buffon, Lamarck and Darwin's own grandfather, Erasmus, had been before him in the business.

It must ever be to the credit of Samuel Butler that, though abused and misrepresented by Darwin's supporters, he forced them to recognize the work of these great pioneers to which Darwin had himself paid so little tribute. Those who had a more impartial outlook realized that the thesis of evolution was no new thing ; that Charles Darwin had not originated the creed and that ' Darwinism ' and ' evolution ' were by no means synonymous. But here arose a dilemma, for if Darwin had not originated Evolution, in what was he original ? Certainly not in supposing it to have come about by the " inherited effects of the use or disuse of parts ", for this had been far more wholeheartedly advocated by his own grandfather and by Lamarck. That which was left that alone could be justly claimed as ' Darwinism ' (or Wallacism) was the action of natural selection on the rather meagre material provided by fortuitous germinal variations. If, therefore, the advocacy for the pre-eminent claims of Charles Darwin as the originator of the true theory of evolution was to be maintained, it was on this last factor that emphasis must be placed. But rather unfortunately Darwin had finally summed up his position by saying that he did not think this " the exclusive means of modification ", for it was " aided in an important manner by the inherited effects of the use and disuse of parts ".

It was in this dilemma that the doctrine of Weismann came to the support of the Darwinian school and Alfred Russell Wallace was one of the first to embrace it.

Evolution could only have come about by natural selection acting on true germinal variations. Clearly, Lamarck had been stupidly misguided and Erasmus Darwin in no better case. In using the terms Lamarckism, teleology and the like as stigmata (as they are used even to this day), the immediate post-Darwinians hardly seem to have realized how little they actually left of Charles Darwin's 'Darwinism'. Anyhow, Weismann had cleared Charles Darwin's rival claimants from the field and no very precise inventory was ever made of what remained of his work once the Lamarckian elements had been taken from it. Weismannism was a very desperate remedy; it may have put an end to the malady that threatened the health of Darwinism but it nearly killed the patient and at the best left it reduced to a mere shadow of its former robust self.

It remains, therefore, to consider Weismann's theory of heredity and to inquire if it is of such assured validity as to cause us to abandon the beliefs of the pioneers.

(4) DONCASTER, L. op. cit. (1). p. 20.
(5) DARWIN, ERASMUS. 1794. "Zoonomia or the laws of organic life." Vol. 1, Sect. 39.4, pp. 502–3.
(6) BARLOW, N. 1933. "Charles Darwin's diary of the voyage of H.M.S. *Beagle*." Edited from the MS. Camb. Univ. Press. p. 213.
(7) DARWIN, C. 1839. "Journal of Researches into the natural history and geology of the countries visited during the voyage round the world of H.M.S. *Beagle*, under the command of Captain FitzRoy, R.N." First edition 1839, quoted from the Edition of 1901, Murray.
(8) —— 1868. loc. cit. supra (2).
(9) —— 1900. "The Origin of Species." Reprinted edition with additions and corrections to the sixth edition of 1872. p. 167.
(10) DONCASTER, L. op. cit. supra (1). p. 20.
(11) DARWIN, C. 1900. op. cit. (9). p. 657.

IV

This denial of the heredity of acquired characters became one of the corner-stones of Weismann's biological theory and he sought in many and various ways to procure proofs for his argument. He bred large quantities of rats whose tails he cut off at birth, but he never succeeded in finding a rat born tailless, nor did other malformations brought about by outward interference ever reproduce themselves. He therefore felt fully justified in maintaining his standpoint that all changes in the outward appearance of the individual compared with other individuals are due to changes in the germinal plasm.

ERIK NORDENSKIOLD. *The History of Biology : a survey.* 1928, p. 564.

When we see a person ' ostrichising ' the evidence which he has to meet, as clearly as I believe Professor Weismann to be doing, we shall in nine cases out of ten be right in supposing that he knows the evidence to be too strong for him.

SAMUEL BUTLER. *Essays on Life, Art and Science.* Edited by R. A. Streatfield. London. 1904.

Essay on " The Deadlock in Darwinism ". Part 2, p. 306. Originally published in the *Universal Review*, 1890.

AUGUST WEISMANN outlined his theory in 1885, three years after the death of Charles Darwin. The full title of the thesis is : ' The Theory of the Continuity of the Germ-plasm '. The theory may be briefly described in Weismann's own words by saying that it postulates " The splitting up of the substance of the ovum into a somatic half, which directs the development of the individual, and a propagative half, which reaches the germ-cells and there remains inactive, and later gives rise to the succeeding generation." (12) In language somewhat simpler, we may say that the fertilized cell which gives rise to the individual splits into two parts. The one part (somatic part) will form the body of the individual and the other will give rise to the sex cells contained in the gonad or sex gland within the body of the individual. The sex cells remain dormant within the gonad until such time

as reproduction takes place and then they continue the race by developing into individuals of the next generation. The somatic cells constitute the body of the individual that possesses the gonad. The germ-plasm is continuous from generation to generation and is immortal. The somatic cells merely form a temporary nidus for the sex cells and, when their allotted span is reached, they die. Moreover, the life of the sex cells and their germ-plasm is strangely aloof from that of the body cells that constitute their temporary resting-place. This aloofness is so complete that no changes produced in the body cells may influence them and their ' determinants ' of heredity. It is therefore clear that, if the theory is indeed true, no modifications that are acquired during the lifetime of the individual, in response to the action of use or environment, can possibly be transmitted to the offspring.

The essential factor in Weismann's theory is the *continuity* of the germ-plasm. Germ-plasm arises from germ-plasm and continues in succeeding generations as germ-plasm—a thing apart from the multitude of somatic cells constituting the body of the transient individual. It is essential to the theory that germ-plasm is derived in continuity with previous germ-plasm, it cannot originate from that portion of the original ovum that is destined to form the somatic cells of the body of the individual. In Weismann's own words : " The familiar fact that the excision of the reproductive organs in all animals produces sterility proves that no other cells of the body are able to give rise to germ cells ; germ-plasm cannot be produced *de novo*." (13)

Such, then, are the premises of the theory that caused the abandonment of the beliefs of the ordinary man, the stock breeder, the student of sociology and the great pioneers of the doctrine of evolution. It is necessary to examine the validity of these premises in the light of modern knowledge and, where proof fails us, in the light of probability.

In the first place, we have adopted what seems to be

a satisfactory and which certainly is an orthodox definition of an acquired character. We have followed Doncaster in defining it as " a feature developed during the life of the individual possessing it, in response to the action of use or environment ". For ' feature ' we might have substituted ' character ' or ' modification ' or some other such word : it would have made no difference to the clarity of the definition. But the more rigid followers of Weismann have been forced to enlarge the definition and, if we follow Thomson, we must say : " An acquired character, or a somatic modification, may be defined as a structural change in the body of a *multicellular* organism, involving a deviation from the normal, directly induced during the individual's lifetime by a change in environment or in function and such that it transcends the limits of organic elasticity, and therefore persists after the factors inducing it have ceased to operate." (14) At the moment we are not concerned with the final clause in the definition ; the important point is to note that the word ' *multicellular* ' has been intruded as a limiting term in the definition of organism.

The reason for such limitation is obvious. Since Weismann's theory demanded a duality of cell individuality in the form of germinal cell and somatic cell, it is clear that it could have no application to organisms that consist of only one cell. In the single cell of a unicellular organism the germinal and the somatic must be assumed to be combined. Any influence, therefore, that is brought to bear on a unicellular animal must be supposed to react both upon the germ-plasm and the somatic plasm that constitute the individual. " It is not to the point to cite cases where unicellular organisms, such as bacteria or monads, have been profoundly and heritably modified by artificial culture, so that, for instance, the descendants of a virulent microbe have been made to lose their evil potency. It is irrelevant because in unicellular organisms we cannot draw the distinction between body and germinal matter,

apart from which the concept of modifications is of no value." (15) It is a simple matter to rule the whole vast host of unicellular organisms outside the application of Weismannism, but it cannot be said that faith in the validity of the thesis is strengthened by this renunciation. To limit the scope of what is held to be a general principle to only one portion of what is clearly recognizable as a continuum is rather to imperil faith in the validity of the principle than to find added support for it in its limited sphere of application. If we pursue the argument to its ultimate implications we are forced to admit that acquired characters may be inherited by unicellular organisms but that the moment evolution has proceeded to the stage of the production of multicellular organisms such inheritance is prohibited. Such a finding brings us face to face with the postulation of a change in hereditary possibilities so abrupt as to appear out of harmony with the general findings of evolutionary inquiries. The follower of Weismann is nevertheless forced to admit that the theory does not apply to all living organisms, for unicellular plants and animals remain without its province.

Weismann's original dictum postulates that in development the substance of the fertilized ovum splits into two halves—a somatic half and a propagative half. The picture is that of a very early, if not an initial, cleavage of the ovum into two moieties, the one moiety being destined to form the present generation, the other being reserved for the formation of future generations. Such a picture involves the conception of the early segregation of the sex cells in the development of the fertilized ovum. It is true that such an early segregation and differentiation of the sex cells appears to take place in the development of certain types ; but it is equally true that in others no evidence of early segregation is obtainable. On such a question we would not expect to obtain any very definite direct evidence, for the primitive characters of the cells bearing the germ-plasm are not sufficiently differentiated from those of the

general body (somatic) cells as to make their identification at different stages a matter of any high degree of certainty.

Even if the orthodox followers of Weismann are forced to admit that in some cases the early segregation of the sex cells and the isolation of the germ-plasm does not in fact occur, they are still free to maintain that this is a matter of little moment since the germ-plasm and the sex cells, even if not recognizable as isolated entities in early stages of development, are nevertheless aloof from the processes and the influences that affect the body cells. This aloofness is maintained throughout the whole of their lives within the nidus provided by the body cells. It would seem that the modern followers of Weismann regard this aloofness or 'apartness' as absolute. In this matter they go further than the originator of the theory, for in his lecture on 'The continuity of the germ-plasm as the foundation of a theory of heredity', Weismann says: "I am also far from asserting that the germ-plasm—which, as I hold, is transmitted as the basis of heredity from one generation to another—is absolutely unchangeable or totally uninfluenced by forces residing in the organism within which it is transformed into germ cells. I am also compelled to admit that it is conceivable that organisms may exert a modifying influence upon their germ cells and even that such a process is to a certain extent inevitable." (16) In making this admission, however, Weismann was merely conceding that such gross factors as changes in nutrition or gross intoxications of the parent might increase or decrease the well-being of the germ cells. He was not contemplating the more subtile influences that must be invoked if the mechanism of adding acquired features to the hereditary characters of the race is ever to be realized. There was in fact a complete inability to realize that, apart from nutritional or toxic agencies, there was any influence that could be invoked in a process so subtile as that involved in a change in the somatic constitution producing an alter-

ation in germinal constitution. The nervous system, the blood stream, the body fluids all appeared to fail when called upon as agents that could possibly produce such changes.

Many theories were made to meet the case. Charles Darwin's ' gemmules ', the ' pangens ' of de Vries, the ' constitutional units ' of Herbert Spencer, were all tried and found wanting. Yet though it appeared incredible that body cells could exert a subtile influence on sex cells, it was a common-place of everyday knowledge that sex cells could and did exert such an influence on body cells. Every disputant who joined in the barren discussions on this subject must have known that alterations in the developing sex cells of the adolescent male inevitably produced changes in the larynx and the vocal cords : that changes in the sex cells of the adolescent female produced enlargement of the breasts. These and a thousand other changes of somatic structure consequent on the action of the sex cells were familiar to everyone. It is true that the precise nature of the agency that effected these changes was not known as it is today, but that some agent was involved was obvious. It seems strange nowadays that since no agent that could produce the reverse action—influence of body cells on sex cells—was forthcoming, the possibility of such a happening was considered unthinkable. Charles Darwin was, however, aware that such a possibility could not be overlooked. His statements upon this question are unambiguous and are best quoted at length : " Variability . . . results from special causes, generally from changed conditions acting during successive generations. Part of the fluctuating variability thus induced is apparently due to the sexual system being easily affected by changed conditions. . . . But variability is not necessarily connected with the sexual system . . . and *although we may not be able to trace the nature of the connection*, it is probable that many deviations of structure which appear in sexual offspring result from changed conditions acting directly on the organism, independently

of the reproductive organs." (17) Two other and later biologists clearly expressed the same caution. Lloyd Morgan warned the disputants that "although we cannot imagine how a modification might, as such, saturate from body to germ-cells, this does not exclude the possibility that it may actually do so." (18) Oscar Hertwig also claimed that "our ignorance of any mechanism which could secure the transmission of an acquired character is not a good argument against the possibility of its occurrence." (19) In 1908, Thomson said in his 'Treatise on Heredity': "It must be noted, however, that, so far as we can understand, *a very complex and special mechanism* would be necessary." (20) But Starling had already isolated and named the first of the hormones three years before he wrote these words. It may be that the mechanism is rightly termed a complex one but nevertheless it is one that is now very well understood.

It is, however, Weismann's ultimate argument in support of his claims, "that the excision of the reproductive organs in all animals produces sterility *proves* that no other cells of the body are able to give rise to germ-cells", that is actually one of the most vulnerable aspects of his whole thesis. Doubtless in this statement Weismann substituted the word 'animal' for his more usual term 'organism', because had he not done so the fallacy would have been immediately detected. The familiar fact that plants may be propagated by slips or cuttings or even, as in the case of the begonia, from small portions of a single vegetative leaf, was too patent to be disregarded. The cells in the vegetative leaf of a begonia must be supposed to be ordinary somatic cells, yet from these cells a new plant will arise and in this new plant sex cells will be produced. Presumably these sex cells *are* derived *de novo* from somatic cells. This difficulty of accounting for the development of sex cells in vegetative cuttings or propagated leaves has had to be faced by all Weismann's followers, and an apologist literature has grown up around the question. Walker,

in 1910, adopted arguments that have by now become incorporated into the literature of modern Weismannism. He says : " The period at which the germ-plasm emerges is not of vital importance, nor is it essential to assume that it is always limited to a particular group of cells in all organisms. Weismann's main points are not seriously affected. It still remains quite possible, and even probable, that the germ-plasm continues independently, that inborn variations arise only in germ-plasm itself, that there is no transmission of any character from parent to offspring except those existing in germ-plasm, and that there is no necessity to believe that acquired characters may be transmitted because Weismann's original theory is thus modified with regard to some details." (21) To this it is only necessary to add that the details that have been thus ' modified ' are such as are essential to the whole structure of the theory.

We have seen that Weismann's theory cannot be stretched so as to embrace unicellular organisms ; it would seem that breaking-point is reached when attempts are made to stretch it so as to embrace the mechanism of heredity in plants. But Herbert Spencer pointed out that plants were not altogether alone in this matter of propagation by cuttings for much the same thing could be done with several lowly multicellular animals. Hydras may be cut into small pieces, consisting entirely of somatic cells, and yet from these small pieces new animals may develop and produce sex cells. To overcome this dilemma, Weismann was forced to make three new postulates : (1) that even in the lowest multicellular animals the differentiation between germ cells and somatic cells remains incomplete ; but that the differentiation increases with the progress of evolution, (2) that it is possible that somatic cells, though differentiated as such, may retain some residual germ-plasm that has not become incorporated in the sex cells, and lastly (3) that there may be in the body such things as " germ tracks ", composed of germ-

plasm, but not demonstrable in a continuous series of germ cells.

Obviously all these postulates are the merest suppositions for the support of which there is not a trace of real evidence. They cannot be said to add strength to any theory that demands their invocation, nor can they justify Thomson's claim, made as comparatively recently as 1908, that "it seems accurate to say that the reproductive cells which have the potentiality of becoming offspring never arise from differentiated body cells". (22)

In the end it must be agreed by everyone that Weismann's theory cannot be applied to unicellular organisms since in them somato-plasm and germ-plasm are presumably combined in the single cell. It must also be conceded that only by being stretched to breaking-point and by the invocation of certain unverified and unverifiable suppositions can it be applied to the whole of the vegetable kingdom. Finally, even its most ardent supporters must agree that, without the same unsatisfactory reservations, it fails in its application to the case of lowly multicellular animals.

It therefore only remains to inquire if its last desperate hope is realized in the supposition that, since differentiation becomes more complete with the progress of evolution, it may be applied without any reservations in the case of animals of mammalian rank.

The experimental investigation of this problem has now extended over a rather long period, but the results have not yet been incorporated into the general literature of the subject of heredity. Experiments upon mammals were apparently first conducted in Russia. It is said that in 1901 Mattisen published in Kief his work on the regeneration of the ovaries of rabbits. The paper was written in Russian and appears to have had but little influence on the literature of Western Europe. It is, however, over thirty years ago that Castle and Phillips in America (23) reported that after complete removal of the ovaries in guinea-pigs and rabbits there

was occasional regeneration of ovarian tissue and that in some cases normal pregnancies followed when the animals with regenerated ovaries were mated. In 1925 Davenport published the results of his own independent experiments carried out on mice. He came to the conclusion : " That ovaries of mice can regenerate is proved by the fact that in nearly two-thirds of the cases ovaries of smaller or larger size are found after the lapse of a few weeks or months after their removal." (24) More recently a far more elaborate piece of research has been undertaken by Parkes, Fielding and Brambell at University College, London. In these newer experiments the utmost precaution was taken lest the results should be invalidated by the possibility that any shred of ovarian tissue was left behind at operation. " Since the operation of ovariotomy consisted of removing the ovaries, capsules and portions of the Fallopian tubes, it seems evident that the regeneration of ovarian tissue took place from non-ovarian structures." (25)

There would seem to be no doubt whatever that such rodents as mice and rabbits and guinea-pigs are in much the same case as the hydra and even the begonia, since they may produce real germ cells from the ordinary somatic cells composing their general body structure.

Weismann's last line of defence, that the complete differentiation of germ cells from body cells attains its absolute expression in the higher animals, has to be abandoned in the face of these very definite experimental findings.

Only one last hope for Weismannism remains, and it is that in the case of Homo, these things cannot possibly hold true, since the inheritance of acquired characters in man has been claimed so repeatedly to be utterly impossible. On this last point, Parkes, Fielding and Bramwell say : " An appreciable number of cases have been reported where the removal of the ovaries in women, and even of part of the tubes as well, has been followed by pregnancy." (26) In operations conducted upon human beings for the relief of pathological con-

ditions it is admittedly not always possible to maintain all the safeguards that would be adopted in laboratory experiments. It is a simple escape from accepting the possibility of ovarian regeneration in women to suggest that, in all probability, some ovarian tissue was left behind at the operation. This criticism cannot, however, be applied to all the recorded cases operated on by skilful and reputable surgeons. Alban Doran has recorded his own case and reviewed the literature of the subject. (27) Other cases have been recorded by Schatz, Stansbury Sutton, S. C. Gordon, J. Anderson Robertson, Kossmann, M. M. Morris and J. E. Englemann. Meredith reported a later case which, as he said, " admitted of no doubt as to the complete extirpation of both ovaries." (28)

It would therefore appear that in man, just as in the mouse and the hydra, germ cells may arise *de novo* from the somatic cells of the body. This being so it would seem that we are permitted to criticize the findings of Weismann to the extent of declaring :

(1) That germ cells do not possess that developmental, anatomical and physiological isolation from body cells demanded by the theory.
(2) That apparently in all forms of life, from plants to man, germ cells may be begot *de novo* from differentiated body cells.
(3) That the agencies by which germ cells influence body cells are now well known and, therefore, there is nothing illogical in supposing that reciprocal action of body cells on germ cells is a possibility.

These things being so, it would seem that we need no longer be under the thraldom of Weismannism and that we are free to consider with an open mind any cases in which acquired characters appear to be inherited.

(12) WEISMANN, A. 1904. " The Evolution Theory." Translated by J. Arthur and M. R. Thomson. Vol. 1, p. 411.
(13) —— loc. cit. supra.

(14) THOMSON, J. ARTHUR. 1908. "Heredity." Progressive Science Series. p. 173.
(15) —— op. cit. supra (14). pp. 185–6.
(16) WEISMANN, A. 1889. "Essays on Heredity and kindred biological problems." Translated by E. B. Poulton *et al.* Lecture IV, p. 170.
(17) DARWIN, C. 1868. op. cit. Vol. 2, p. 371.
(18) Quoted from Thomson (1908). op. cit. p. 200.
(19) HERTWIG, O. 1906. Allgemeine Biologie. p. 621.
(20) THOMSON, J. A. 1908. op. cit. p. 201.
(21) WALKER, C. E. 1910. "Hereditary characters and their modes of transmission." London. p. 57.
(22) THOMSON, J. A. 1908. op. cit. p. 197.
(23) CASTLE, W. E., and PHILLIPS, J. C. 1911. "On germinal transplantation in Vertebrates." Carnegie Institute of Washington. Publication No. 144.
(24) DAVENPORT, C. B. 1925. "Regeneration of ovaries in mice." Jour. Exper. Zool., Vol. 42, p. 11.
(25) PARKES, A. S., FIELDING, U. and BRAMBELL, F. W. R. 1927. "Ovarian regeneration in the mouse after complete double ovariotomy." Proc. Roy. Soc. Series B. Vol. 101, No. 710, p. 328.
(26) —— —— —— op. cit. supra. p. 352.
(27) ALBAN DORAN. 1902. "Pregnancy after removal of both ovaries for cystic tumour." Jour. Obstetrics and Gynæcology of the British Empire. Vol. 2, No. 1, pp. 1–10.
—— 1904. Brit. Med. Jour. p. 730.
(28) MEREDITH, W. A. 1904. "Pregnancy after removal of both ovaries." Brit. Med. Jour. p. 1360.
(29) BOND, C. J. 1914. "Some points of genetic interest in regeneration of the testis after experimental removal in Birds." Jour. Genetics. Vol. 3, p. 131.

In this work there is demonstrated the fact that, in animals in which the male sexual glands remain at the site of their formation, regeneration of the sex cells is complete after removal and that normal breeding is resumed with the regenerated glands.

V

It must be remembered that, however many experiments fail, it is always possible that the effects of use and disuse may be impressed on a species at a rate not susceptible of experimental verification, yet rapid enough to be of importance in geological time.

J. B. S. HALDANE in *Possible Worlds*, 1940.
"Darwinism Today," p. 39.

The true science of experimental embryology did not come into being until the time of Wilhelm Roux.

JOSEPH NEEDHAM. *A History of Embryology*,
Cambridge, 1934, p. 212.

NEITHER Weismann and his followers nor his opponents, who resorted to experimental methods intended to prove or disprove the possibility of the transmission of acquired characters, succeeded in obtaining unequivocal evidence in either direction. The mutilation experiments can only be held as providing negative evidence by those who entertain a complete misconception of the nature of acquired characters.

The experiments that have been conducted by McDougal, Krammer, Harrison, Garrett, Durken, Brecher and others, which have been claimed to prove the transmission of acquired characters, will not be discussed here. Such discussion is like to be wearying and unprofitable, since it has become so repetitive and involved in verbal passages during the past decade.

We have seen that experimental methods devised to prove or disprove the actual transmission have no great probability of attaining success: but experimental methods, such as those of Parkes, Fielding and Brambell, have gone far to show that the very foundations of the thesis that claims to prove the impossibility of transmission are by no means securely established. It is therefore possible that other experimental methods

may throw some light on the problem. Experimental embryology is a comparatively young science, but some of its findings have already given us more insight into these matters.

In making first appeal to the work of Wilhelm Roux (1850–1924)—the acknowledged father of the science—two things must be remembered. The first is that Roux was a pupil both of Haeckel and of Goette and therefore was steeped in the mechanistic dogmatism prevailing at the time in Strassburg and Berlin. The second is that "Roux also has points of contact with Weismann, whose theory of the continuity of the germinal plasm he embraces: he consequently rejects the theory of the heredity of acquired characters". (29) These facts are guarantee that Roux cannot, by training or by natural bent, be suspected of having any Lamarckian or functional leanings in his interpretation of the findings of experimental embryology.

Fortunately, Roux's main conclusions are capable of comparatively brief summary. He became convinced that the embryonic development of any organism was capable of subdivision into two stages. Every embryo and every part and organ of the embryo passes through two phases of development and these two developmental periods he defined as follows: "The first period I call the embryonic period or the period of organ rudiments. It includes the 'directly inherited' structures, i.e. structures which are directly predetermined in the structure of the germ-plasm as, for instance, the first differentiation of the germ, segmentation, the formation of the germ-layers and organ-rudiments, as well as the next stage of 'further differentiation' and of *independent* growth and maintenance, that is, of growth and maintenance which take place without the functioning of organs. This is accordingly the period of direct fashioning through the activity of the formative mechanism implicit in the germ-plasm, also the period of the self-conservation of the formed parts without active functioning." So much for the first

period. " The second period is the period of ' functional development '. It includes the further differentiation and the maintenance in their typical form of the organs laid down in the first period, and this is brought about by the exercise of the specific functions of the organs. This period adds the finishing touches to the finer functional differentiation of the organs, and so brings to pass the ' finer functional harmony ' of all organs with the whole. The formative activity displayed during this period depends upon the circumstance that the functional stimulus, or rather the exercise by the organs of their specific functions, is accompanied by a subsidiary formative activity, which acts partly by producing new form and partly by maintaining that which is already formed. Between the two periods lies presumably a transition period, an intermediary stage of varying duration in the different organs, in which both classes of causes are concerned in the further building-up of the already formed, those of the first period in gradually decreasing measure, those of the second in an increasing degree." (30)

This is Roux's original, and not ambiguous, statement concerning the two phases of embryonic development. As E. S. Russell has summarized the matter : " In the first period, the organ forms or determines the function, in the second period the function forms the organ or at least completes its differentiation. It is characteristic that in the first period functionally adapted structures appear in the complete absence of functional stimulus." (31)

Obviously the existence of two stages in development is, as Roux postulates it, no more than a theoretical supposition. He provided no direct experimental evidence in support of his thesis.

Since 1905, when Roux completed the formulation of his theory of two-stage development, the science of experimental embryology has made vast strides. Thanks to the work of Hans Spemann (32) and his school in Freiburg, we now understand the nature of " the

formative mechanism implicit in the germ-plasm" that produces the first stage of development. This mechanism is the now-familiar organizer that determines the axis, the orientation and the disposition of the earliest rudiments of the form of the embryo. This formative mechanism is now known to be a definite chemical substance and for our present purpose it may be dismissed by saying that it is one of the phenanthrene ring compounds, of which the sterols are the best known examples. There would seem therefore to be no further doubts about the "formative mechanism inherent in the germ-plasm": it has ceased to be the nebulous *vis formatrix* and has now no more mystery attaching to it than that which is implicit in any of its related hormonal compounds.

We must grant, then, that Roux's thesis gains reality in so far as the initiation and regulation of the first stage of development is concerned. Is there any experimental confirmation of the reality of his second stage, separated from the first by a presumable "transition period"? It is from the school of Ross Harrison in Harvard that evidence has come in support of this aspect of the question. The evidence has been derived from the experimental grafting of limb rudiments from one amphibian embryo to another. In brief, it has been found that if a limb rudiment in an early stage of development is grafted into another embryo, the host embryo can organize (by virtue of the formative mechanism inherent in its germ-plasm) the limb in accordance with the dictates of its own body. The host embryo can compel a grafted limb rudiment rotated 180 degrees, to develop into a limb of normal disposition in its new site. It can compel a grafted right-limb rudiment to develop into a normal left limb when made to grow on the left side of the body. It can even determine that a grafted fore-limb rudiment shall develop into a normal hind limb when the site of its grafting demands it. But these conditions are only fulfilled provided the grafted

material is in a sufficiently rudimentary state ; when, as we might suppose, it is in the first stage of development and so still under the influence of the organizer of the host. As the limb employed as a graft becomes more mature it grows refractory to the demands of the host. There dawns what Ross Harrison terms a " critical period " and, " if grafted after the critical period, the transplanted material develops in accordance with its origin ". Translated into the terminology of the doctrine of the organizer or " morphogenic hormone ", the case would be stated thus : The organizer is at first inherent in the mass of the developing embryo, and the site of its initial development is now well known. Later, this organizing property passes to the developing parts and organs, so that their further development is no longer carried out by the central organizer but, owing to the growing perfection and importance of the parts, they are competent to conduct their own organization. In terms of Roux's hypothesis, the development of the early limb bud is first carried out by the " formative mechanism inherent in the germ-plasm " during the first stage of development. Then comes the " transition period " (Ross Harrison's ' critical period '), and after that the development of the limb bud passes into the stage of " functional form-development " of the second period of development. There is therefore no conflict, but rather a very substantial basis of agreement, between the developmental doctrines of Roux and the modern findings of the school of experimental embryologists.

But there is a further implication in these findings. We have seen that Roux was, by training and by association, a confirmed adherent to the mechanistic school of biology, yet strangely enough he was responsible for some of the best work that demonstrates the overwhelming importance of function as the determinant of structure. It was he who pronounced the dictum that " living beings can at present be defined with any approach to completeness only functionally ".

We have seen that Roux was a follower of Weismann, nevertheless, in its final form, Roux's theory of functional development is completely destructive of Weismann's main thesis. As E. S. Russell has pointed out: "First period characters are *inherited* characters and taken together constitute the historical basis of the organism's form and activity: second period characters are those of *later acquirement* which have not yet become incorporated in the racial heritage. Inherited characters appear in development in the absence of the stimulus that originally called them forth; acquired characters are those that have not yet freed themselves from this dependence upon the functional stimulus." (33) The question therefore remains: Are second period characters always destined to remain as such in development or may they ultimately "become incorporated in the racial heritage" as first stage characters? To this question Roux himself has given the answer, for when discussing the formative stimuli that are acting during the second period he says: "These stimuli can also produce new structure, which if it is constantly formed throughout many generations finally becomes hereditary, i.e. develops in the descendants in the absence of the stimuli and becomes in our sense embryonic." Again there is his definite dictum that "form-characteristics which were originally acquired in post-embryonic life through functional adaptation may be developed in the embryo without the functional stimulus, and may in later development become more or less completely differentiated and retain this differentiation without functional activity, or with a minimum of it. But in the continued absence of functional activity they become atrophied and in the end disappear." (34) This sounds strangely like an embryological restatement of the older doctrines of use and disuse.

We are now in a position to reiterate the question previously proposed: May a feature developed repeatedly during the successive lives of a long series of

generations be ultimately incorporated into the heritage of the species so that in time it will be developed in the offspring not "as a response to the action of use or environment" but as a permanent feature of the animal's intrinsic characteristics? To this question we may now, I think, give a very definite answer. The findings of the experimental embryologists have, during the past two decades, so far confirmed the original thesis of Wilhelm Roux that the matter is no longer in doubt. We have every scientific sanction that acquired characters, as we have defined them, will certainly be inherited under the conditions that we have presumed.

(29) NORDENSKIOLD, E. 1928. "History of Biology; a survey." p. 579.
(30) ROUX, W. 1905. "Vortrage u. Aufsatze uber Entwicklungsmechanik der Organismen." Leipzig. Translated by E. S. Russell. Heft 1, pp. 94–6.
(31) RUSSELL, E. S. 1916. "Form and Function; a contribution to the history of animal morphology." pp. 321–2.
(32) SPEMANN, H. See especially Croonian Lecture, 1927. Proc. Roy. Soc., Series B. Vol. 102, No. 716, p. 177.
(33) RUSSELL, E. S. loc. cit. (31).
(34) ROUX, W. 1881. "Der Kampf der Teile im Organismus." Translated by E. S. Russell. pp. 180 and 201.

VI

It is obvious that the necessary surrender of the theory of the hereditary transmissibility of acquired characters greatly weakens the older explanations of evolution, but this does not mean that new and sounder theories will not some day be brought forth.

JAMES HARVEY ROBINSON. *The Human Comedy as devised and directed by mankind itself*, London, 1937, p. 34.

IT may seem strange that so recent a dictum of a zoologist, who is also a zoological philosopher, should claim that we must await a new theory to account for the well-known facts of evolution rather than to examine the basis of the assumption that there is in fact any need to surrender a belief in the transmissibility of acquired characters. Such a dictum merely shows the great influences that the thesis of Weismann has exerted upon all the best minds in zoological research during the past half-century.

The road that we have so far travelled seems to permit us to entertain a well-founded belief in the possibility of the inheritance of acquired characters and to give us the freedom to call in support of this belief certain well-established scientific facts. We may therefore consider ourselves free to go further and to seek for evidence in nature of its actual happening.

We will not turn aside to consider the results of short-time, man-made experiments, for nature has had the great advantage that time unlimited has been at its disposal. If we approach the problem with no bias against the possibility of the occurrence I fancy we shall see, as the older evolutionists saw, evidences of its happening wherever we look for it. It is admitted by one of the most insistent opponents of the doctrine of the inheritance of acquired characters that : " it is easy to find structural features which *may be interpreted* as entailed acquired characters, *if* acquired characters can be entailed ". (35)

With this dictum I am in wholehearted agreement, for it is only if we blind ourselves to the possibility of such things that we fail to see them everywhere in nature. We will, therefore, consider ourselves free—to use Samuel Butler's expression—to refrain from 'ostrichizing' such evidence as may appear to be relevant.

The mode of thought that prevails in the consideration of these problems may be made more clear by quotation. "The African Wart-Hog (*Phacochoerus*) has the peculiar habit of kneeling down on its fore-limbs as it routs with its huge tusks in the ground and pushes itself forward with its hind-limbs. It has strong horny callosities protecting the surfaces on which it kneels, and these are seen even in the embryos. This seems to some naturalists to be a satisfactory proof of the inheritance of an acquired character. It is to others *simply an instance of an adaptive peculiarity of germinal origin wrought out by natural selection.*" (36) We will pass over here the major contradiction involved in speaking of an '*adaptive* peculiarity of *germinal origin*', since by their very definition germinal variations are essentially non-adaptive.

Again: "It has been stated that the Punjabis of India show certain peculiarities of musculature and skeleton which are associated with the frequency with which these people assume on all possible occasions the squatting posture. It is asserted that the peculiarities of structure are due to the peculiarities of function, but this requires definite proof. They may be adaptations originating in germinal variations. It is necessary to know whether the peculiarities are in any degree represented in new-born Punjabi babies, *but even then it would be simpler to regard them as variations than as transmitted modifications.*" (37) Here it is to be noted that the germinal variations are not postulated as being 'adaptive', but rather that the characters may be 'adaptations' originating in germinal variations.

Two observations must be made on these quotations

from an authoritative work upon the subject of heredity. The first is that the callosities of the Wart-Hog are admitted to be present in the embryo, whereas it is said that " it is necessary to know " if the squatting facet is present in the Punjabi baby. This is the more in need of explanation since the work of Havelock Charles, from which Thomson must have gleaned his information, lays particular stress on the fact that the squatting facets are present in the Punjabi fœtus by at least the 8th month of intrauterine life. (38) Why it should be necessary to know if the squatting facet is present at birth, when the fact that the Wart-Hog's callosities are present in the embryo appears to make no difference to the verdict, is very difficult to understand. The verdict is the same in both cases. It is that these things are not really acquired modifications but are in fact true germinal variations and, by definition, such " variations cannot be causally related to peculiarities in habit or surroundings ". Surely this is to land us in a dilemma of complete intellectual absurdity ! The total lack of logic in this attitude is more clearly shown when, later on, discussing Arbuthnot Lane's work (39) on the structural peculiarities produced in tailors sitting cross-legged and in cobblers working at the last, Thomson says : " These are indubitable modifications : what of their transmission ? " The Wart-Hog's callosities and the Punjabi's squatting facets are, according to Thomson, not modifications but are germinal variations—a very different thing. But it is a little difficult for one not biased by zoological theories to see why a structural change produced by the habit of squatting must be regarded as a ' germinal variation ', when those produced by working at a last, or sitting tailor-fashion, are ' indubitable modifications ', i.e. acquired characters. If the reason for this attitude consists in the knowledge that the one structural change is definitely inherited, whereas no evidence is forthcoming that the other is—since cobblers and tailors do not as a rule beget generations of cobblers

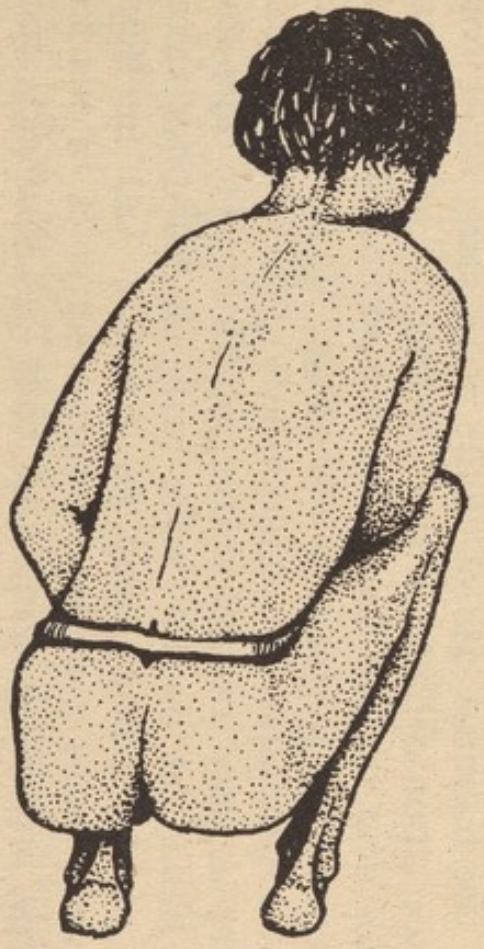

FIG. 1.—The posture of squatting adopted by most oriental races.

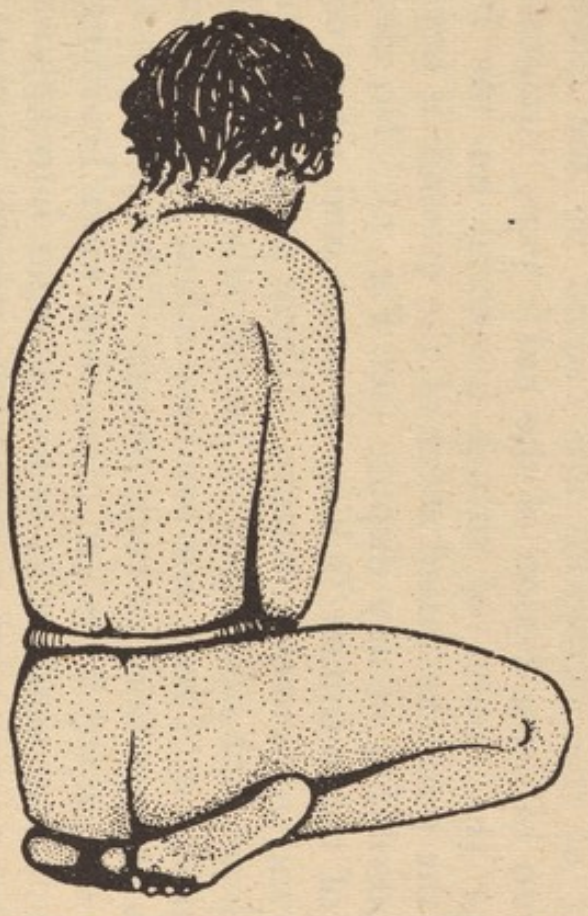

FIG. 2.—The posture of squatting adopted by the native of Australia.

and tailors—this must surely be classed as being a very bad case of ' ostrichizing ' evidence.

That the well-known squatting facets on the lower anterior border of the tibia and the upper anterior aspect of the astragalus are caused by the extreme position of dorsi-flexion of the ankle joint, maintained during the action of sitting hunkered on the heels with the buttocks raised sheer of the ground, is beyond the possibility of any dispute (see Fig. 1). No clearer case of the intimate linking of cause and effect could be found anywhere in nature. These peculiar articular facets are not developed in people who do not adopt this position of rest, nor are they found in the embryo, fœtus or new-born of such people. The facets in their fully developed form are more than mere bevellings of the adjacent surfaces of bones brought into apposition by the adoption of a very characteristic posture, for they are fully-formed joint surfaces, covered by articular cartilage and included within the capsule of the joint (see Fig. 3).

The squatting facets on tibia and astragalus are present in all Asiatic peoples who adopt the hunkered position of rest, but they are absent in all people who know the habitual use of chairs or of some other contrivance upon which to sit. Moreover, among those peoples who do not know the use of chairs there are various elected postures in squatting. It is well known that the Australian aborigine squats in his own peculiar, and for us very uncomfortable, position. He does not, as a habit, sit on his heels with his buttocks raised clear of the ground, like an Asiatic ; but he flexes his lower limbs completely, turns the soles of his feet inwards and backwards and rests his buttocks upon the lower part of his shanks and his inturned feet (see Fig. 2). In conformity with this peculiar posture, maintained for long intervals and adopted by all individuals, he has developed perfectly definite facets on the bones of his legs and these are obviously the outcome of his posture and are entirely different from

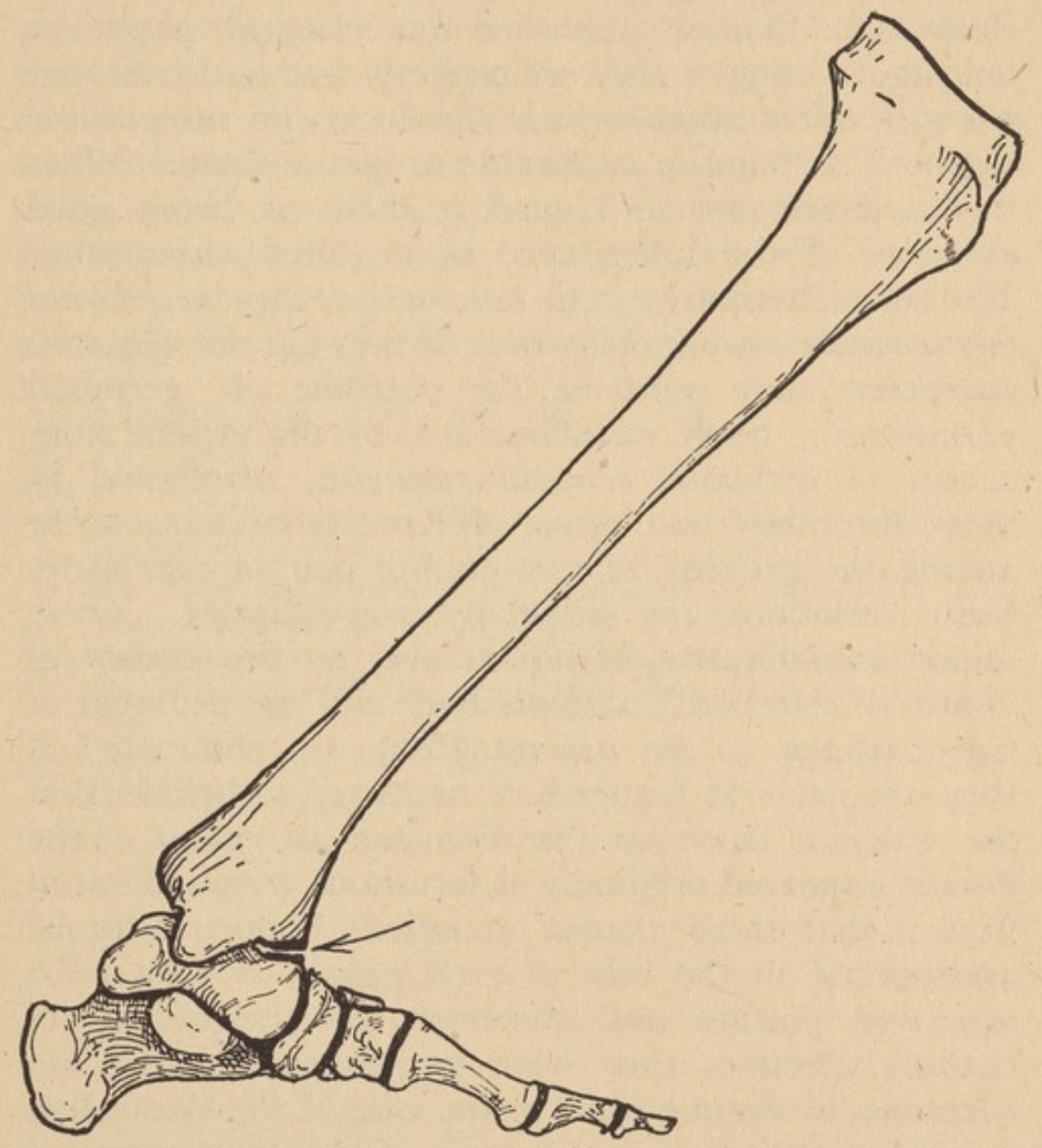

FIG. 3.—Bones of the left leg and foot to show the facets (indicated by the arrow) produced on tibia and astragalus by the Oriental posture of squatting.

those of the typical Asiatic squatter. (40) Moreover, these facets are present in children too young to have produced them by habit. They are definitely a part of the morphological heritage of the Australian aborigine.

Now these things have been known for many years (Havelock Charles published his classical paper as long ago as 1893) : they are perfectly well authenticated scientific facts about which there can be no possible dispute. It is quite impossible to ignore them. What is the alternative to regarding them as being good evidence of the inheritance of acquired characters? The only alternative is to say that, *as they are inherited they cannot be acquired characters.* If they are not acquired characters they must be the outcome of 'germinal variations'. Such variations are, by the general concensus of orthodox scientific opinion, manifested in those fortuitous and minor differences such as occur among the progeny of any mating pair of organisms. Such variations are essentially non-adaptive. These minor non-adaptive variations are, by the agency of 'natural selection', accentuated and perpetuated if they happen to be advantageous, or eliminated if they are not. It is therefore necessary to believe that the articular facets on the tibia and astragalus of the Asiatic appeared originally as fortuitous germinal variations : that these chance variations happened to be appropriate in the case of such people as adopted a squatting posture and therefore, by the agency of natural selection, they were perpetuated. It is also necessary to assume that, in the case of the Australian native, an entirely different series of fortuitous germinal variations produced an altogether different series of facets upon the bones and that these, happening to fit in with the habitual resting posture of the people, became perpetuated by selection and so became inherited. To demand belief in these things is to impose a burden on credulity at which even blind faith might be expected to baulk. Surely it is more

in accordance with the ordinary exercise of reason to accept these things as what they so clearly appear to be than to distort their apparently clear meaning in deference to the dictates of a teaching that there is no longer any reason to regard as being well established.

If we can agree to such a basis of understanding in this matter it may be worth while to examine one or two other examples of nature's experiments that appear to throw light upon the problem. In order to clear away some of the atmosphere of controversy that has settled about the subject, it will be well to take instances that have so far escaped from the verbal obscurity wrought by unprofitable controversy.

(35) THOMSON, J. A. 1908. op. cit. p. 180.
(36) —— loc. cit.
(37) —— op. cit. pp. 208–9.
(38) HAVELOCK CHARLES. 1893 and 1894. "Morphological peculiarities in the Punjabi and their bearing on the question of the transmission of acquired characters." Jour. Anat. and Phys. Vol. 28, pp. 1–19 and pp. 271–81.
(39) ARBUTHNOT LANE. 1888. "The anatomy and physiology of the Shoemaker." Jour. Anat. and Phys. Vol. 22, pp. 593–628.
(40) QUARRY WOOD, W. 1920. "The tibia of the Australian aborigine." Jour. Anat. Vol. 54, pp. 232–57.

VII

The *Pinnipedia* show a great resemblance to terrestrial carnivores in anatomical and ontogenetic characters. Owing to their adaptation to an aquatic habitat, they have acquired to a certain extent a fish-like form of body. . . . Fossil forms are rare, occurring first in the Miocene. Neither paleontology nor ontogeny furnishes satisfactory clues concerning their origin.

K. A. Von Zittel. *Text-book of Paleontology*, Vol. 3, "Mammalia," 1925, p. 78.

IN 1910 Professor Marett Tims wrote his report on the anatomy of the Weddel Seal embryos collected during the voyage of the *Discovery* to the Antarctic. One feature that particularly attracted his attention was the condition of the cervical region of these embryos.

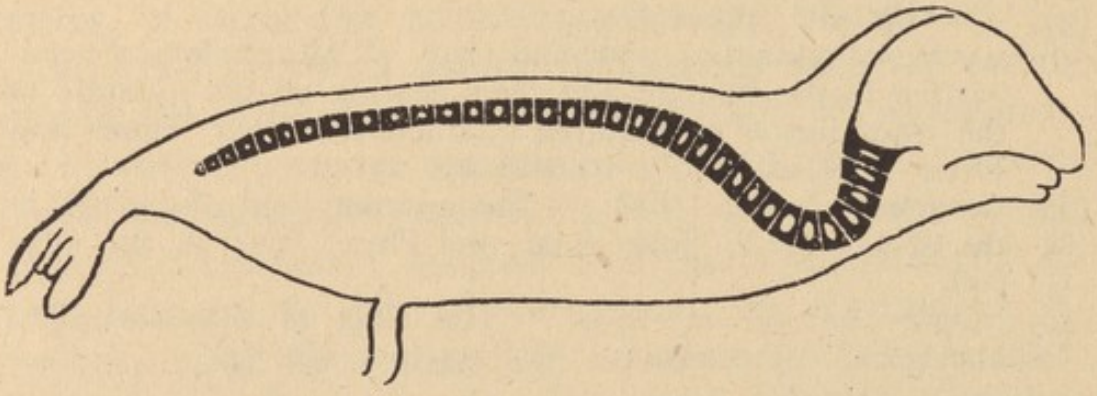

Fig. 4.—Mesial section of a seal embryo showing the abnormal curvature of the cervical portion of the vertebral column. (Modified from Marett Tims, 1910.)

He noticed that in all of them, no matter how young they were, the head was thrown backwards so that the neck was bent with its convexity forwards (see Fig. 4). Of this peculiarity he says: "The most interesting point which I have observed is the extraordinary downward curve in the cervical region of the vertebral column. The curvature involves the whole of the cervical and the anterior portion of the dorsal region. The bend is so considerable that the ventral surfaces of vertebræ are brought so close to the ventral body wall that the trachea and œsophagus are deflected to one side." For this peculiar condition Marett Tims could

offer no obvious explanation and he therefore submitted the facts to Hans Gadow. "Dr. Gadow made the suggestion to me that it might possibly be a sexual character present only in the males and caused by the habit of lifting the females when pairing. I therefore made median sections of both sexes and found that the curvature is a constant feature and further that it tends to become accentuated with the increasing age of the fœtus." (41)

The reason for describing this feature as the most interesting point that he had observed in the seal embryos was obviously that Marett Tims was surprised to find the cervical region of any mammalian embryo

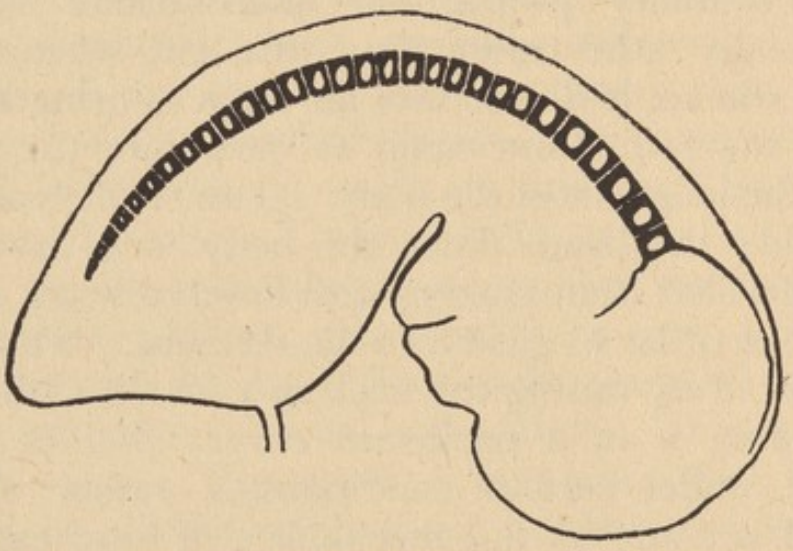

FIG. 5.—Mesial section of a human embryo showing the normal curvature of the cervical portion of the vertebral column. (Modified from Mall, 1906.)

bent into an "extraordinary downward curve", for it is typical of the embryo, when flexed in the uterine cavity, to have its neck bent in the opposite direction. The cervical region of the embryonic seal is convex downwards, the cervical region of the typical mammalian embryo is concave in the ventral direction (see Fig. 5). In order to accommodate itself in the space at its disposal the typical mammalian embryo is bent double, so that its chin may be said to rest on its chest. The primary curve of the vertebræ of the neck is the result of this general bending of the body.

But the primary curvature of the cervical region of

the vertebral column must be undone at some stage of development by the formation of a cervical curve in the opposite direction. In the case of the human infant there must come a time when the chin is raised and the direction of the face, from snout to ears, is brought to a line at right angles to the long axis of the body. This does not happen until the infant begins to hold its head up and this, as every mother knows, takes place when the baby is some three months old. This readjustment is produced by changing the primary curve of flexion of the neck into the secondary curve of extension. Once the secondary cervical curve has been established in the human infant it remains permanent.

The ordinary pronograde quadrupedal mammals need to do rather more than this, for, when looking straight ahead, it is necessary for them to bring the long axis of the face, from snout to ears, into the general line of the long axis of the body. This result is achieved by raising the head above the body axis, as when a horse, that has been grazing with lowered head, elevates its neck in order to gaze into the distance. This action is produced by raising the neck as a whole, rather than by bending it in a backward curve. But in certain animals, under certain conditions, a rather different demand is made on this mechanism of head extension. When a dog swims it is necessary that, not only shall the long axis of the face be extended in the same direction as the long axis of the body, but it must be extended so as to form a direct continuation of the line of the back. The head is not now elevated by raising the neck, but the neck is bent backwards so that snout and face and body are in one straight line. Anyone who has watched a dog swim must have noticed that it throws its head backwards so that the line of the nostrils, the eyes and the ears continues the line of the vertebral column. The nose is pointed straight forwards without the head being raised much above the level of the back. It is this action that produces a maximum of backward bending of the cervical portion of the vertebral column.

In doing this the dog is only producing, as an occasional posture, what thoroughly aquatic mammals have achieved as a permanent modification.

As to the phylogenetic origin of the seals, there are difficulties only when minor details are considered. It might be impossible on the available evidence to decide if the eared seals (*Otaridæ*) and the earless seals (*Phocidæ*) are derived from a common ancestor, or if the one group is more closely related to the bears while the other is more akin to the otters. That is a question of only minor importance, since everyone is agreed that all of them were derived, in the very distant past, from some carnivore that lived a normal mammalian terrestrial life. It seems very natural to suppose that, at the very outset of their departure from normal terrestrial life, the ancestors of the present seals produced this curious curvature of the cervical region only when actively engaged in swimming, as bears and dogs and other carnivores do today. It is equally natural to assume that, as the aquatic habit became more stereotyped in this particular phylum, this peculiar posture of the neck became more and more frequently adopted until, in the end, it became habitual in the adult. There remains the last stage. The cervical curvature has become habitual in all the adults over a very long series of generations. Has it ultimately become incorporated into the heritage of the animal, so that, in the end, its inception has been shifted back in ontogeny until it appears in the young animal before its mother has initiated it into its future aquatic life—for all baby seals (which are born on land) are introduced to their future environment by the solicitous care of their mothers. Has it even gone further and become developed during embryonic life as a part of the animal's normal hereditable characters? If we are agreed to discard all bias in favour of any theories, the common-sense answer would seem to be a decided affirmative.

Posture in squatting seems clearly to have produced skeletal peculiarities when it is habitual over long gener-

ations of human beings. These skeletal peculiarities are, in the end, developed in the embryo as a part of heritage and in advance of the actual exercise of the function. Posture in the carriage of the head and neck in the seals would seem to repeat the same story. When all is said and done the primitive terrestrial carnivora from which the seals probably arose flourished in the Eocene period and true seals, such as we know them today, were full-blown in the Miocene. There has been a vast span of time at nature's disposal in the ordering of these things compared with which the time involved in the production of the squatting facets would seem to be trivial and the time available to the individual human experimentor in the cutting off of rats' tails a mere impertinence.

Regarded in this way it would seem to be most in accordance with ascertained facts to look upon "the extraordinary downward curve in the cervical region of the vertebral column" of the embryonic seal as a feature, originally acquired in a long succession of its ancestors in the action of swimming, which has become incorporated into the common heritage of the race.

(41) MARETT TIMS, H. W. 1910. "National Antarctic Expedition." Nat. Hist. Vol. 5, "Mammalia," 1a. Seal Embryos. B.M. Publication. p. 10.

VIII

> Some will say that as Weismann's doctrine is contravened by the conclusions put forward, and as a large amount of evidence and current biological opinion is in favour of Weismann's views, any contrary facts, such as we have here, are probably due to other causes yet to be discovered. Such is Weismann's own attitude towards them. This may be magnificent, but it is not science.
>
> WALTER KIDD. *The Direction of Hair in Animals and Man*, London, 1903, p. 149.

THREE years before Walter Kidd wrote his criticisms of Weismann's attitude, he had read before the Anatomical Society of Great Britain and Ireland his paper on the ' Hair slope in Man '. In this paper he had boldly declared that in the case of the scalp hair : " It would seem that the action, through many generations, of methods of dressing hair afford the traction necessary to produce this peculiarity." (42)

To make such a statement more than forty years ago needed some courage, for at that time the doctrines of Weismann had not been subjected to any great amount of detailed criticism.

To make such a statement even now is to court disaster. In a recent notice of a very unadventurous publication on anatomy by the present writer, the reviewer has dealt as reviewers did with the works of Kidd, Samuel Butler and others many years ago. In the only journal devoted to the scientific study of Anatomy in Great Britain, the critic has pointed out to the student the snares involved in reading such a work, for he warns him against " being too easily persuaded by his (my) subtle and ingenious arguments ". He sums up the harmful influences that may be produced in the student's mind by saying : " Thus on more than one occasion he suggests that new structures are developed as the direct response to the demands of function, and he interprets the loss of structure as the direct result of their having become undesirable. The

reviewer believes that such teleological approach to the problems of evolution is sterile." (43) The word 'teleology' has been for so long a term employed to connote everything that is misguided, old-fashioned and stupid in the interpretation of nature's happenings, that by now, after near a century of this usage, it has somewhat lost its sting and it is almost refreshing to meet it again in 1942 employed as a stigma of the unpardonable sin.

It may be that some of the reviewer's criticisms were called forth by remarks that I had made on the general question of the direction of hair and that I have shared with Walter Kidd the obloquy of having adopted a sterile approach to the problems of evolution because both of us paid some attention to the subject of hair tracts. It may, therefore, be useful to state what is definitely known about these things, and in this statement we will not refrain from the inclusion of findings that may appear to be 'teleological' just because that very damning epithet may be casually applied to them.

It is a commonplace of everyday observation that hairs do not grow directly vertically from the surface of the skin, for they always issue with a definite slant and so tend to lie more or less flat against the surface of the body. In this way there is brought about a definite hair trend, which is best designated by the direction taken by the individual hairs from root to tip. If we use the terminology in vogue in describing textiles, we would say that the pile of the mammal's coat has a definite nap on it and that this nap has a definite direction to it, the direction being indicated by the axis from base to tip of the individual piles.

In the most primitive little mammals this hair trend presents a great uniformity and, regardless of zoological affinity, the hair pattern is the same in all primitive mammals. Roughly we may say that in the simplest disposition of the hair, a mammal may be stroked from head to tail without roughing up its coat. In more precise terminology the hair of the head and body is

directed from nose to tail (cranio-caudad), from back to belly (dorso-ventrad) and, on the limbs, from the front edge to the back (pre-axial to post-axial border) with a general tendency downwards. It has always seemed to people who have no claims to be scientific that the hair is arranged in this way because, since the animal habitually moves forwards, it is more appropriate that its hair trends should be directed backwards. Even people who *do* consider themselves scientific, and among them some of the most up-to-date of our present authorities, have, perhaps unwittingly, acquiesced in such a view. In an authoritative textbook published less than three years ago, the author says : " Primitively all the hairs of the body are directed cranio-caudally, a ' stream-line ' arrangement which is related to simple movements of the body in a forward direction, and this disposition of the hair is found in most small mammals of a generalized type." (44) So far, apparently, all men may go without incurring the charge of introducing the fallacy of teleological thinking.

The problem of the general direction of the mammalian hair trend would seem to be no more complex than that involved in the simple fact that the scales of fish, reptiles and scaly mammals and the feathers of birds are also directed backwards. This arrangement may be considered appropriate " as affording the least possible resistance to the passage of the animal through the air, water, burrows, brushwood, or any other heterogeneous environments which may be mentioned ". (45)

This primitive general hair trend is evidently " not lightly departed from by any individual animal in the course of its development ". Nevertheless it *is* departed from in many animals. The departures from basal simplicity may take the form of any degree of alteration of the primitive hair trend up to its complete reversal. Such alterations produce the familiar partings, whorls, convergences and reversals that are displayed in the hairy coats of most common domestic animals. Slight

deviations from the primitive pattern are at times correlated with body contour and proportions and, in each individual case, it is, as a rule, a simple matter to discern the correlation. Thus, as the general direction of the body hair is cranio-caudad and dorso-ventrad, the cranio-caudad direction tends to be more conspicuous in an animal with a very elongated body than in one with a short body. Some deviations from the primitive pattern would appear to be related to the relative conditions of movement and rest in adjacent areas of the surface of the body. Certain whorls and convergences appear to mark the site of parts which, once protruding from the surface, have disappeared, such as the horns in female Ungulates, the tail in man and, possibly, the umbilical cord in many animals. All such deviations may be classed together as changes brought about by morphological factors.

But it is at once apparent that there are a large number of alterations and complete reversals of hair trend that cannot possibly be explained by any appeal to morphological considerations. What other factor can be invoked to account for the presence of such alterations and reversals? It is here that, with Kidd, I see no alternative to the supposition that they have been caused by habit or use; and I would here call especial attention to those that appear to have arisen in response to the very definite and individually stereotyped methods employed by various mammals in performing the toilet of the coat. It is probably one of the most conspicuous shortcomings of the modern study of anatomy that so much exhaustive research is carried out on the detailed structure of dead and preserved animals in the absence of any attempt to correlate these findings with the life activities of the creatures concerned.

It is, nowadays, a fashionable plea that human anatomy must be taught as a study of the living as well as of the dead. This is a very well-justified plea and it is more the pity that so many of those who urge it most eloquently do not extend it so as to embrace the lower

mammals. It is very much to be doubted if long-continued and intimate observations on the toilet habits of lower animals have been the basis of most of the opinions expressed upon the subject of the causation of certain hair tracts. Had anatomists devoted their time and attention to these apparently trivial living activities, there would have been earlier and more general recognition of the innumerable beautifully adapted toilet implements with which so many mammals (among many other forms of life) have been endowed. Recent controversies concerning the lemur's dental hair-comb and the syndactylous toilet digits of some marsupials were occasioned solely by the neglect, by modern research workers, of that simplest form of research involved in watching living animals under, as nearly as possible, natural conditions. To the older anatomists, such as Cuvier and Owen, these things were well known. I have elsewhere called attention to other dental hair-combs, to other digital hair-combs and to the beautiful digital and other hair-brushes that exist in so many lower mammals. (46) Appreciation of these many and varied toilet implements, developed definitely and solely for the toilet of the hairy coat, is necessary before a realization of the importance of the business may be had by any anatomist. Having attained to an appreciation of the number and perfection of the specialized implements as anatomical structures, it is still necessary that the anatomist should spend much time in watching the animals performing the toilet of the coat. Only then will he realize that, though the business may appear to him as a very minor form of activity, it is one of the most constant of all activities. The very frequence of the repetition of the action more than makes up for its apparent triviality: for, as we have seen in other cases, it is the commonplace but frequent, rather than the dramatic but very occasional, activity that is important in these matters. I have some doubts if academic pronouncements, no matter with what profundity they may be made, are of any

very decisive value when made in the absence of some such apprenticeship in the anatomical study of the dead combined with ample observation of the living.

It is impossible to repeat here the descriptions of all the remarkable toilet implements with which various mammals are endowed. It is not necessary to define all the alterations and reversals of hair trend that seem so clearly to coincide with the direction in which the animal carries out the toilet of its hairy coat. Only two of the more striking hair reversals will be discussed and the discussion of these will be limited to their disposition in certain marsupials. The reason for this limitation of the scope of the inquiry is that I have had more abundant opportunities for prolonged and intimate observations on marsupials ; and that the multiplication of similar occurrences in other orders of mammals would be merely tedious repetition. Both the fields dealt with are those of digital scratching or combing and in relation to one field a specialized digital comb is involved.

It is a matter of common observation that, in different measure, in different animals, the toilet of the coat may be performed by the pes and by the manus. A dog scratches itself with its hind foot, a cat performs a certain part of its toilet with its fore paw. Many marsupials employ both manus and pes, and the office and the territory assigned to each is very rigidly defined. The marsupials considered here belong to the syndactylous diprotodont division of the Order. By this terminology it is meant that the animals have replaced the more primitive condition of having many small, pointed, front teeth by the specialization of fewer, larger and flatter incisors ; and that, on the pes, the second and third digits are dwarfed, conjoined and terminated by fine, sharp claws, placed side by side. It was well known to Richard Owen, over a century ago, that the marsupial syndactylous digits were highly specialized hair-combs developed " for the purpose of scratching the skin and dressing the

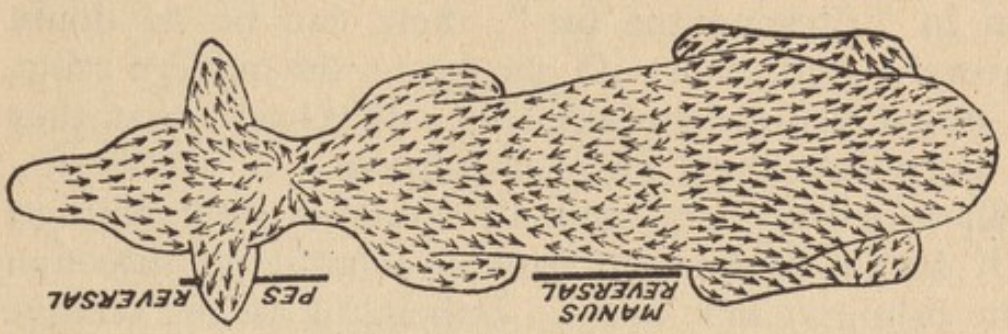

FIG. 7.—Hair tracts of *Wallabia greyi* (dorsal aspect).

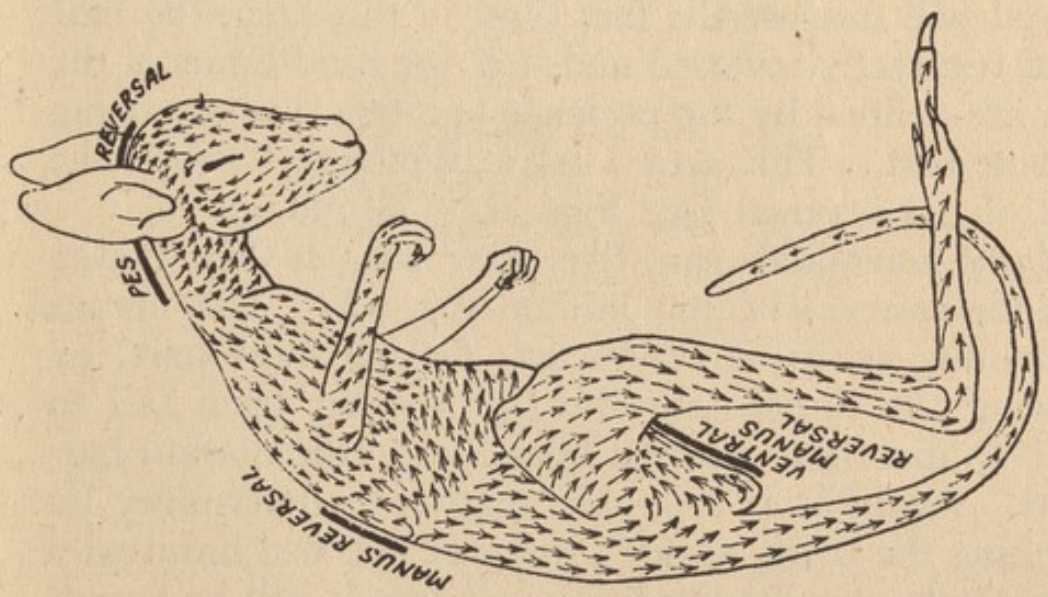

FIG. 6.—The hair tracts of a Kangaroo (*Wallabia greyi*) charted from a pouch-young.

fur, to which offices they are exclusively designed ". Owen's conclusions derived from careful observation of living animals has largely remained overlooked and it has recently tended to be obscured by the ridiculous claims of Pocock that in some forms they may assist in tree-climbing and in others in digging in the ground. Of the exclusive use of this strange anatomical specialization in " dressing the fur ", there can be no doubt whatever ; and, even with one eye on the modern critic, one might venture to suppose, with Owen, that they had been developed for that purpose.

When one of these animals scratches itself with its pes it does it by forward strokes—against the direction of the primitive hair trend. Depending on the relative length of the hind limb and the general build of the body, there will be a definite area of the head, and perhaps the anterior end of the trunk, that may be reached with the forward combing strokes of its hind foot and syndactylous toilet digits. By watching an animal at its oft-repeated toilet it is easy to determine the limits of this area habitually exposed to toilet operations conducted by the pes. Examination of the skin of the animal will disclose the fact that, in this area, the hair trend is directly reversed and that the hind limits of the area are defined by the presence of a whorl or a parting of some sort. This area I have, therefore, termed the area of pes reversal (see Figs. 6, 7, 8 and 9).

Many marsupials can, like man, scratch their bodies with their very delicately fashioned hands. This manus scratching, again, is conducted, for the most part, by drawing the finger-nails through the fur from tail to head—a direction reversed from that of the normal hair trend. Again it is a simple matter to determine, by watching the living animal, the area exposed habitually to this form of toilet operation. Again it will be found, on examination of the skin, that a definite hair reversal is present. This area I have, therefore, termed the area of manus reversal.

Probably the simplest presentation of the essential

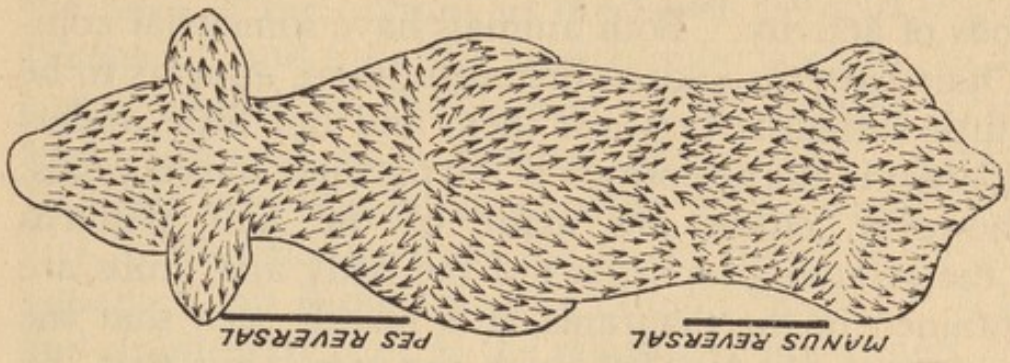

FIG. 9.—Hair traits of *Phascolarctus cinereus* (dorsal aspect).

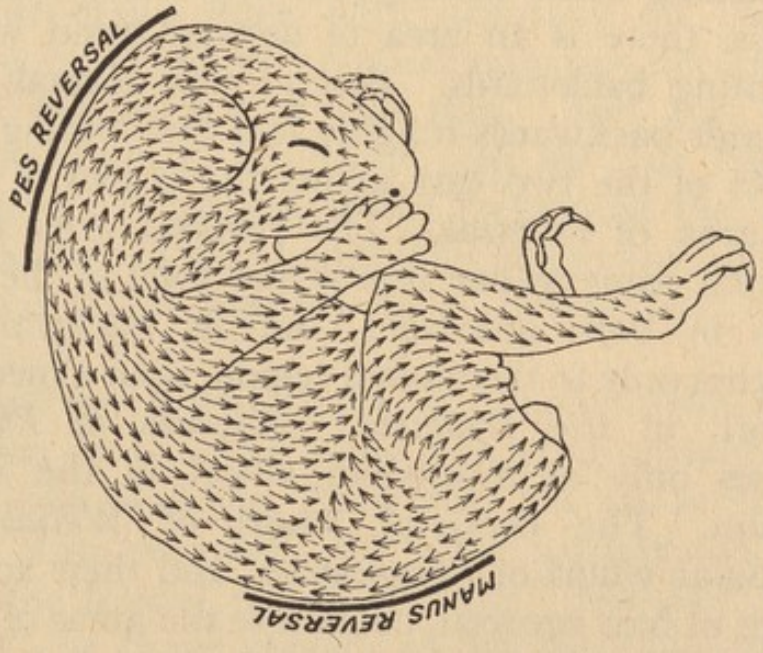

FIG. 8.—The hair tracts of a Koala (*Phascolarctus cinereus*) charted from a pouch-young.

facts concerning these two areas is by way of contrasting them in two animals of very different bodily proportions. For this purpose the short-armed, long-legged and long-bodied Kangaroo may be compared with the short-bodied and relatively long-armed Koala. Both animals are easily observed and the toilet operations of both are repeated with great frequency during the whole of their periods of activity. Both animals have somewhat complex hair patterns and, at first sight, there appears to be but little similarity between them and but little underlying order in the disposition of the partings and reversals. If, however, charts are made of the hair patterns and the relative proportions of the body and limbs are maintained in the diagrams, it is readily seen that the hair patterns are basally much the same, but that the whole design is shifted in the long axis of the body. Briefly, in the short-armed, long-legged Kangaroo (*Wallabia greyi*) (see Figs. 6 and 7) the whole hair pattern is shifted forwards (cephalad) when contrasted with that of the long-armed Koala (*Phascolarctus cinereus*) (see Figs. 8 and 9). Starting from the tip of the snout, and disregarding some minor, but extremely interesting hair fields, there is an area of normal trend with the hair pointing backwards. Behind this normal field, which extends backwards roughly to a line joining the anterior edges of the two ears across the crown of the head, is an area of reversal. The reversal area starts at the cranial convergence line at the level of the front of the ears in both animals; but its backward extension reaches only to the nuchal region, with a medial occipital whorl, in the *Wallabia*; whereas in *Phascolarctus* it ceases only at a median whorl in the interscapular region. The occipital whorl of *Wallabia* and the scapular whorl of *Phascolarctus*, and their accompanying fields of hair reversal, constitute the areas of pes reversal. It is over this area that the animal is accustomed to scratch its hair the wrong way with the syndactylous pedal toilet digits. This is in no way a speculative statement, for the functional rôle of the pes in toilet

operations in this area is constantly displayed whenever living animals are observed. The difference in extent and distribution of the areas appears to be obviously accounted for by the relative lengths of the body and the hind limbs in the two animals.

Behind the pes reversal area there is another normal tract, in which the hair is directed cranio-caudad from the back of the occiput to the lower cervical region in *Wallabia*; and from the interscapular area to the lower costal region in *Phascolarctus*. This normal tract is again followed by a reversal area, which extends in *Wallabia* from the lower scapular to the costal region; and in *Phascolarctus* from the lower costal to the sacral region. This is the area of manus reversal. It is large and situated far back in the relatively long-armed, short-bodied *Phascolarctus*. It is small and situated far forward in the relatively short-armed, long-bodied *Wallabia*. In both animals, the area of manus reversal terminates as a divergent parting line, behind which the hair trend again becomes normal. (For further details, see 47 and 48).

It should be noted that the actual charting of hair tracts is most easily done with accuracy on pouch embryos, so young that the hairs are only just becoming apparent on the surface of the skin. And this fact introduces the general statement that all hair tracts, however caused, are present in the embryo at the very earliest appearance of hair; and long before any actions of the animal could possibly have determined their development.

It is perhaps worth while going one stage further and thereby getting on to much more dangerous ground by noting that, like *Wallabia*, Man also has an occipital whorl and a scalp reversal. Of "The arrangement of the hair on the frontal region of Man" (see Fig. 10), Walter Kidd was brave enough to tell the Anatomical Society more than forty years ago: "The inference one would draw from these facts of hair direction is that probably most of them, certainly some, are produced

in the individual by inherited effects of dressing the hair in ancestors." (49) In the intervening forty years, although much adverse criticism has been brought to bear upon the conclusions arrived at by Kidd, no single fact controverting them has been forthcoming. (50) Indeed, it is difficult to see how any opposing facts can ever be brought forward.

Nevertheless, other explanations for these reversals have been suggested in the meanwhile. The latest and probably the most widely accepted and orthodox is that of Bolk. His conclusions are summed up as follows : " The only conclusion which could perhaps with some

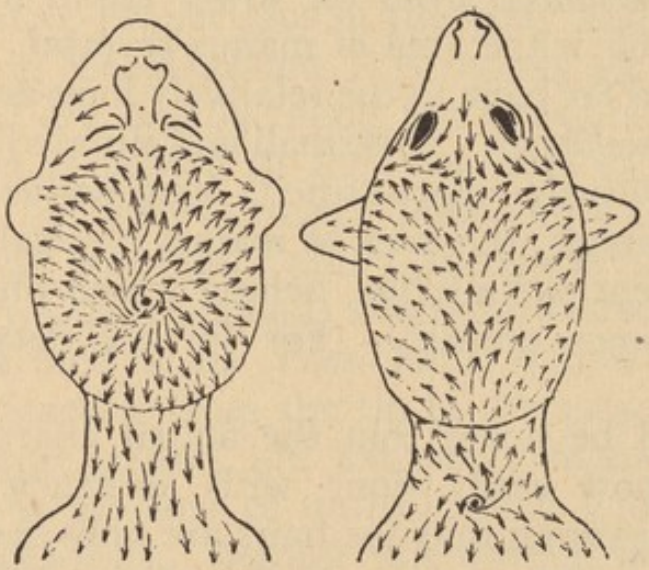

FIG. 10.—The head region of man and a Ring-tailed Opossum (*Pseudochirus occidentalis*) to show the occipital and nuchal whorls of hair.

justice be drawn from a comparison of the different conditions, is that the hair slope is not determined by external influences but that it is probably the expression of certain conditions of growth in the skin. We are still, however, entirely in the dark as to the actual connection between the process of skin-growth and the hair-slope." (51) This may not be a very satisfying explanation and at best it would seem to be a mere harking back to the older views of Voigt and of Schwalbe. We have already admitted that certain hair trends may possibly be determined by morphological factors, such as body proportions. etc. : but we can no longer pay,

even unwilling, homage to any theory that postulates that hair tracts bear any relation to mechanical tension of the skin. The tension lines of the human skin are well known and so are the human hair tracts, and it is most clearly apparent that they are unrelated to each other. (52)

I see no reason, therefore, to modify the opinion that I expressed in 1924: "Here we have a condition in which as soon as ever hair begins to appear upon the pouch young of a marsupial, and long before the little animal has any occasion to scratch itself, there is demonstrated the whole complexity of reversals, whorls and partings ingrained upon the coat by no more deep-seated, life-saving or useful process than the toilet methods adopted by its ancestors. If this is not, in the old, hackneyed, connotation of the term, a case of acquired characters being inherited, it is difficult to conceive what circumstances could afford a satisfactory demonstration of that phenomenon." (46)

It may appear presumptuous to repeat this claim in the face of certain experimental work which is held, by some, to have completely disproved the thesis. In 1931, Mildred Trotter and Helen L. Dawson conducted some experiments at Washington University, St. Louis, Missouri, and published their results in the 'Anatomical Record'. (53) They performed their operations on guinea-pigs. "In a series of twenty animals, during the period of one to three weeks after birth, an area of skin was rotated so that the positions of the cephalic and caudal poles were interchanged. Thus the direction of the hair on this area was reversed." So much for the technique of the experiment, which the authors claim caused the hair on the reversed areas to be "put in a position ideally adapted to test the hypothesis of Kidd and Wood Jones". "In all cases the hair maintained its original direction, responding in no way to the external, mechanical influences." The deduction is, therefore, that the hypothesis is proved to be incorrect!

There is surely no need to repeat what we have already said about the stupid business of cutting off rats' tails.

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IX

Of the Opossum from New Holland, John Hunter wrote :

> There is something in the mode of propagation in this animal that deviates from all others ; and although known in some degrees to be extraordinary, yet it has never been attempted, where opportunity afforded, to complete the investigation. I have often endeavoured to breed them in England : I have bought a great many and my friends have assisted me by bringing them or sending them alive, yet I never could get them to breed : and although I have a great many facts respecting them, yet I am not certain that I am possessed of sufficient information to complete our knowledge of the system of propagation in this class.
>
> JOHN HUNTER'S *Essays and Observations*. Edited by Richard Owen. 1861. Vol. II, p. 249, under heading : " Of the Animals of New Holland."

JOHN HUNTER knew well that there were some animals that, in the method of their reproduction, still hid their secrets from him. The common eel was a perpetual puzzle to him. " The natural history of the mode of propagation in the common eel has, I believe, never yet been described ; and this has probably in some degree arisen from the dissimilarity between their generative parts and those of fish in common, so as not to enable one to reason from analogy ; and, as the mode of propagation in animals can only be known when that operation is going on in them, and by following it through most of its stages, it has lain almost unintelligible in the eel from the difficulty of finding them in this state." (54) In order to find the eel " in this state " he " got eels every month in the year from the fishmonger with a view to catch them in the breeding season, as also of every size, but I never could distinguish any difference in these parts in any of the months ". More than a century had to pass before Schmidt discovered the marvellous fact that they only got into " this state " when in the depths of the Atlantic Ocean. As to the marsupials and the mysteries of their

reproduction, the business again had to wait for more than a hundred years after the death of Hunter : for it was the work of J. P. Hill on the Bandicoot, in 1899, that gave the first real hint of the correct solution. (55, 56, 57)

It was a curious turn of fate that prevented John Hunter from possessing "sufficient information" to carry knowledge of marsupial reproduction a stage further. "Sir E. Home, who published an account in 1785, (58) seems to have been the first to give a description of the female reproductive organs of the Kangaroo. This writer says that impregnated uteri had reached John Hunter before his death, but that from want of leisure the illustrious anatomist was prevented from giving them the attention they deserved." (59) Had Hunter examined the specimens, subsequently described by his son-in-law, it seems almost certain that his penetrating mind would have seized upon the clue that the material undoubtedly concealed. Most certainly his account would have prevented Owen (60) from rejecting the evidence provided by these specimens ; for Home's deductions were correct so far as they went, but Owen felt under no obligation to regard his statements as facts.

In order to follow the very remarkable happenings that are now known to take place in the process of reproduction among the marsupials, it is unfortunately necessary that some technical anatomical details must be appreciated.

It is beyond dispute that the most primitive mammalian type is preserved today in those egg-laying mammals known as the Monotremes. Although all the existing members of the Monotremes are very highly specialized in their own peculiar ways, it is obvious that they are highly specialized individual survivors of the most primitive mammalian phylum. This basal state of primitiveness is manifested in, among other things, their retention of the habit of laying eggs instead of producing living young, and in the arrange-

ment of the internal reproductive system of the females in conformity with this habit. It was this simplicity of the internal reproductive system of the females that prompted de Blainville, in 1816, to designate the Order as the *Ornithodelphia*. This satisfactory system of nomenclature will be adhered to here. Briefly, in the *Ornithodelphia* there are two ovaries and two oviducts. These oviducts remain separate in their whole length—they do not meet anywhere to form a single, median, uterus. The fact that the existing members of the *Ornithodelphia*

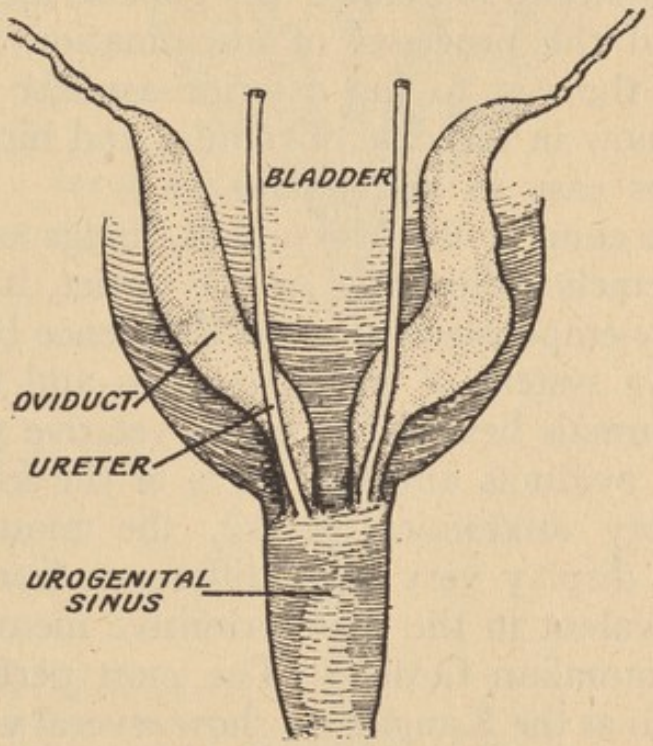

FIG. 11.—The internal reproductive system of a female monotreme (*Echidna*).

appear to show a preference for selecting the left oviduct as the main functional reproduction channel is merely of interest in connection with the accomplished dominance of the left oviduct in adult birds, for it does not controvert the statement that anatomically the two ovaries and oviducts are of equal and symmetrical development. These two oviducts open below into a chamber, which they share with the ducts of the kidneys, and this chamber is therefore termed the urogenital sinus. In all the existing members of the *Ornithodelphia* the ducts of the kidneys (ureters) open

into the urogenital sinus directly behind the separated openings of the two oviducts (see Fig. 11). In the process of reproduction, fertilization takes place by the route of the oviduct and the fertilized egg, or eggs, pass down the oviduct to the urogenital sinus and so to the cloaca and the exterior. In the case of the Platypus (*Ornithorhynchus*) the egg is brooded in a nest-chamber ; but, in some quite unexplained way, the egg of the Spiny Anteater (*Echidna*) finds its way into the mother's ventral pouch and is incubated there. These are only unsolved mysteries of detail : the general facts are clear enough and the processes of insemination and of the passage of the egg to the exterior are like enough to what we know in the case of reptiles and birds to make the business easy to understand.

When we come to the Marsupials, things are, in many ways, extremely different. At the outset, it cannot be too strongly emphasized that the difference between the reproductive system of the marsupials and that of the higher mammals lies mainly in the relative positions of the female oviducts and the ducts of the kidneys. In almost every anatomical detail, the most primitive marsupials display very little difference from the conditions prevalent in the most primitive members of the higher mammalian Orders. The most perfected marsupials, such as the Kangaroos, show several very striking divergences in their anatomical structure from those conditions prevalent in, say, rabbits or cats or any of the common, so-called, higher mammals. But it must be remembered that the most primitive marsupials are not pouched animals, for the marsupial pouch, or marsupium, is a specialization developed in perfection only in the most specialized members of the Order. It may then be asked, if the pouch and the other familiar features that are popularly accepted as the distinguishing features of the marsupial are not developed in all members of the Order, what is the hall-mark by which a marsupial animal may be recognized ? The answer is an apparently disappointing one, but it is one that

cannot be too strongly insisted upon: *A marsupial is a mammal whose kidney ducts lie mesial to its oviducts* (see Fig. 12). This appears to be a trivial distinction, but in fact all the peculiarities of marsupial reproduction are the outcomes of it.

We have seen that in the *Ornithodelphia* the ureters pass directly behind the oviducts. In the higher mam-

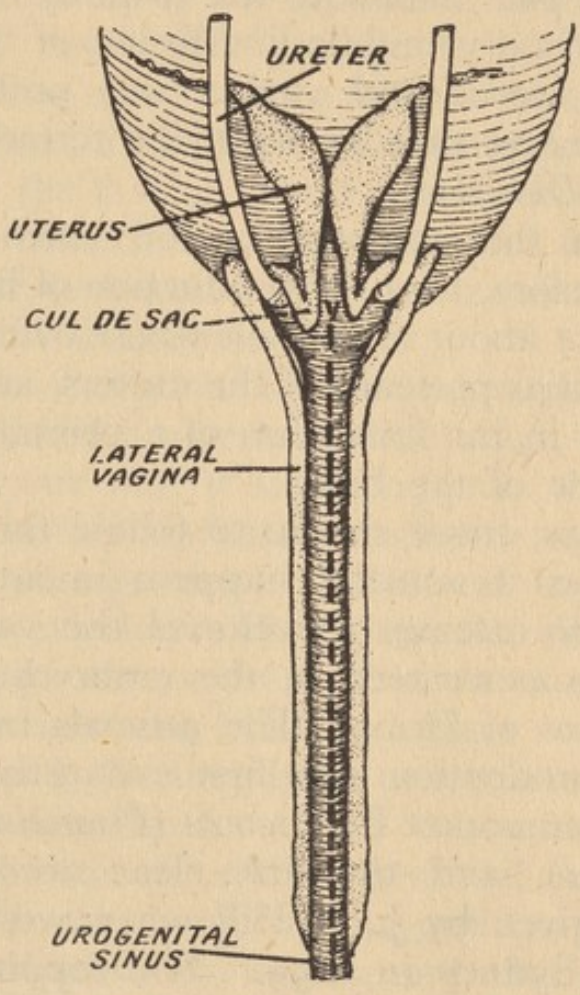

FIG. 12.—Internal reproductive system of a female pouch embryo of *Isoodon obesulus* (40 mm. head length), showing the great relative distance of the vaginal cul-de-sac from the urogenital sinus. The broken line marks the line of rupture to form the temporary median pseudo-vagina.

mals there is a stage in which it might be said that it is touch and go which side the ureters will pass the oviducts, and in the end they go to the lateral side of them. In the marsupials they pass to the medial side.

Now, in the higher mammals, as the ureters run lateral to the oviducts, they leave these two tubes as immediate middle-line structures. The two separate

oviducts are, therefore, free to fuse in the middle line. It is this fusion that caused de Blainville to give that best of all names to the higher mammals when he termed them the *Monodelphia*. In the *Monodelphia* the oviducts may meet and fuse between the ureters and in their fusion form a median uterus and vagina. By that curious twist of development that determined that the ureters should pass mesial to the oviducts in the marsupials, this primary middle-line fusion of the oviducts into a single uterus and vagina was prohibited. It was for this reason that de Blainville termed the marsupial Order *Didelphia*.

The problem that confronts us and which confronted nature is, therefore, how the production of living young is to be brought about in animals whose oviducts, separated by the initial presence of the ureters, are unable to meet and fuse in the formation of a primary uterus in the middle line of the body.

It is, perhaps, more simple to follow the process of reproduction as it actually happens in an individual animal, than to attempt to unravel the various anatomical arrangements seen in the embryos and adults of a wide series of forms. The animals in which the process of reproduction was first exhaustively studied are the two commonest Bandicoots (*Perameles nasuta* and *Isoodon obesulus*), and the first clear account of the business was given by J. P. Hill when working in the University of Sydney in 1899. The copulatory organ of the male is not unlike the forked tongue of a snake and insemination takes place by way of the two separate oviducts, which open into the urogenital sinus (see Fig. 12). Since these tubes have ceased to serve for the passage of eggs in the marsupials they are known, not as oviducts, but as the lateral vaginæ. The lateral vaginæ pass upwards upon either side of the urethra and, when they reach the base of the bladder, they are separated from each other by the whole interval that intervenes between the two ureters. Above the level of the opening of the ureters into the bladder there are

thickenings of the lateral vaginæ that may be termed the uterine sections of the tubes. Between the two uterine portions and the bars formed by the sling-like passage of the ureters to the bladder, the tubes tend to sag inwards towards the middle line as simple loops, known as the cul-de-sacs of the tubes (see Fig. 12). In the process of reproduction, the eggs, shed from the ovaries, are fertilized high up in the tubes and, as fertilized eggs, they begin to make their passage to the exterior. It is here that what almost seems to be a crisis in development takes place, for, instead of passing down the tube as eggs, after the fashion of the *Ornithodelphia*, the eggs hatch in the maternal passages and the living young make vascular connection with the maternal tissues in order to obtain nourishment.

This is the inception of the marsupial placenta. Having established a placental circulation, the embryos continue to grow and it would appear that it is the direct result of this intrauterine growth that prohibits their further passage down the lateral vaginal canals and so to the exterior. They pass, therefore, into the cul-de-sacs and so come to lie median to the openings of the ureters into the bladder. Here we might say they are trapped, for they have no obvious passage by which they can be born.

It is now that an astonishing series of events occurs. The two cul-de-sacs come into apposition in the mid-line: their adjacent walls fuse and ultimately break down, and their cavities become confluent as a single pregnancy chamber—a make-shift median uterus. But this median chamber still lacks an outlet. By some extraordinary means, a process, that appears to be in effect a simple rupture of tissues, takes place. This strange rupture takes place over the whole length of tissue that intervenes between the lower end of the fused cul-de-sacs and the upper part of the urogenital sinus. In *Isoodon* this distance is relatively a very considerable one, for the lateral vaginæ in this animal are of great length (see Fig. 12). Accompanying the forma-

tion of this rent in the maternal tissues, there is a considerable extravasation of blood ; and blood clot always marks the line of rupture along which the young animals subsequently pass. The young are, therefore, born through a long median passage, which is no more than a tear through all the maternal tissues that lie in the line of their passage. Immediately after the birth of the young there is therefore, in these animals, a make-shift median vagina in addition to a make-shift median uterine cavity. But the whole business is of only a very temporary nature, for the rent in the maternal tissues heals up as rapidly as any other accidental solution of continuity and, strangely enough, the umbilical cords of the embryos are incorporated in the scar tissue left by the healing. The placentæ are retained in the uterine cavity and are rapidly absorbed. So quickly is the whole process accomplished that, in one of the small carnivorous Native Cats (*Dasyurus viverrinus*), the whole of the rent in the maternal tissues is completely healed, and all the extravasated blood clot is absorbed, by the second day after parturition. The whole period of pregnancy in the lower marsupials is a very short one and, as a rule, it does not exceed some nine or ten days. The young are naturally born in a state of relative immaturity and, in those forms that possess pouches, they find their way immediately to the nipples situated within the pouch. In pouchless forms the young simply grasp the nipples, which are situated only a comparatively short distance in front of the cloacal orifice. The Bandicoot, like the other primitive marsupials, breeds at somewhat irregular intervals and has, as a rule, some four or five young at a birth. How often any individual animal breeds in its life-time is naturally unknown but, in captivity, they are long-lived and they breed at frequent intervals. It is, therefore, certain that the whole series of changes constitutes an oft-recurring phenomenon. Every time the female becomes pregnant, the young are delivered through a median rent in the maternal tissues. Every time this temporary

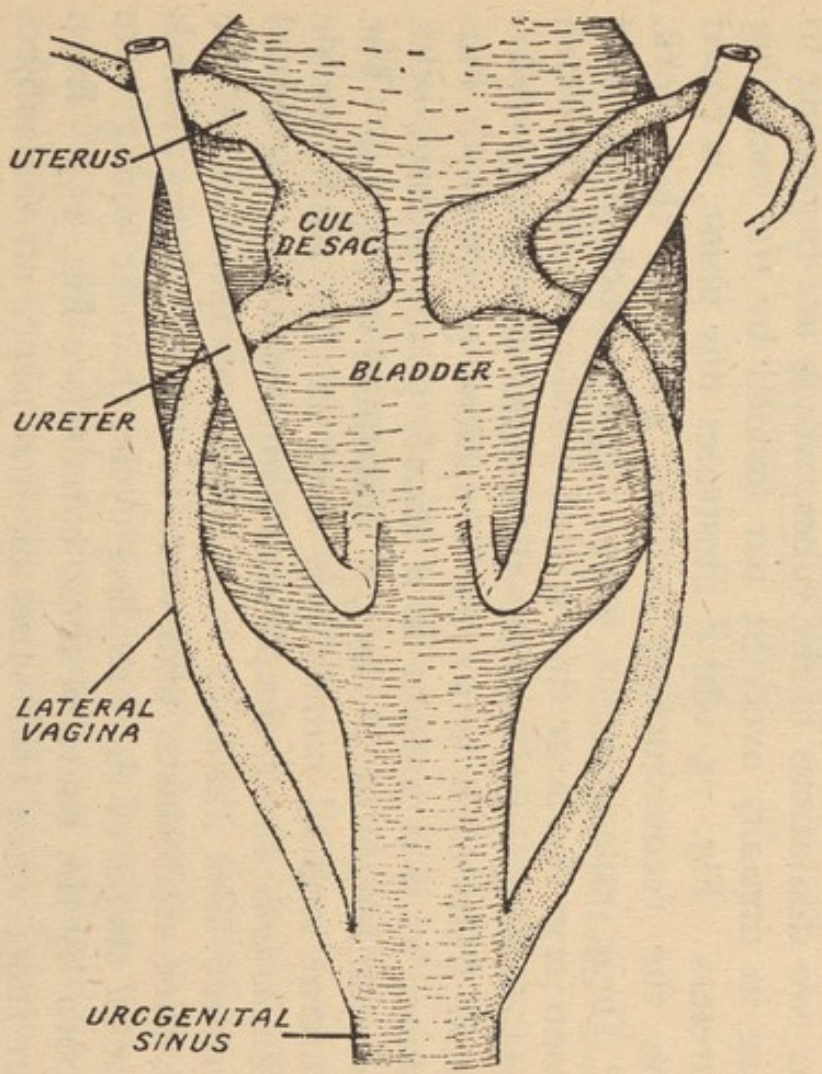

FIG. 13.—Internal reproductive system of a female embryo of *Trichosurus vulpecula* (22 mm. head length). (Based on the work of Buchanan and Fraser, 1918.)

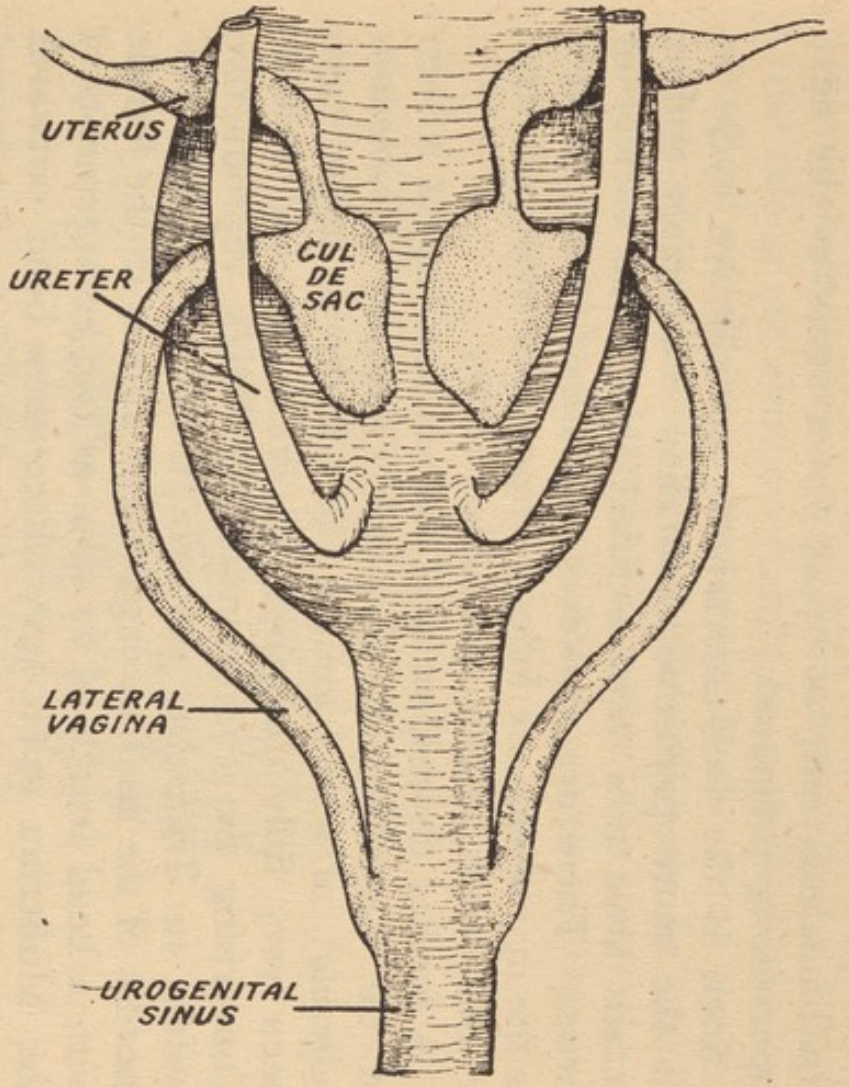

FIG. 14.—Internal reproductive system of a female embryo of *Trichosurus vulpecula* (38 mm. head length). (Based on the work of Buchanan and Fraser, 1918.)

and haphazard median passage is formed it undergoes rapid healing, only to break down again at the next supervening pregnancy.

Such is the well-ascertained reproductive cycle in all the more primitive Australian marsupials and its details have now been verified in a wide variety of forms. There are, however, variations in the process as the marsupials are followed from their most primitive to their most highly specialized forms.

A further development of the median vagina is seen in the Common Brush-tailed Opossum (*Trichosurus vulpecula*), of which animal the embryonic stages have been very fully described by Buchanan and Fraser. Concerning the condition of the female reproductive system in *Trichosurus* embryos they say: "The primordia of the median vaginæ first appear in the female with a head length of 22 mm. as two enlargements of the Mullerian ducts just where they bend outwards in the tissue of the genital cord to form the lateral vaginæ." (61) In this stage the cul-de-sacs are present as two dilatations of the tubes, which are beginning to sag in mesially over the bar formed by the incoming ureters. Fig. 13, which illustrates this phase, is based on the reconstruction outlines given in this work. "These enlargements grow rapidly backwards, and soon form two large thin-walled dorso-ventrally flattened cul-de-sacs, lying between the lateral vaginæ and separated from each other by a narrow partition." This stage, as it is present in a female pouch embryo with a head length of 38 mm., is illustrated in Fig. 14. The lateral vaginal canals are, even in the adult female *Trichosurus*, short, simple and comparatively wide-bored tubes; and naturally it was the assumption of all the earlier anatomists, who were unable to obtain animals at all stages of the breeding cycle, that the young were born by the route of these canals (see Fig. 15). Even in 1899, when Hill wrote his first paper on the subject of marsupial reproduction, he was still of this opinion. After describing the strange happenings in the repro-

duction of the Bandicoot he says : " As regards other forms there are some, e.g. *Trichosurus vulpecula*, in which the young are almost certainly born through the lateral vaginal canals, here comparatively short and simple in their course." During the following year he obtained material that enabled him to correct this statement and so to reconcile the contradictory statements made by

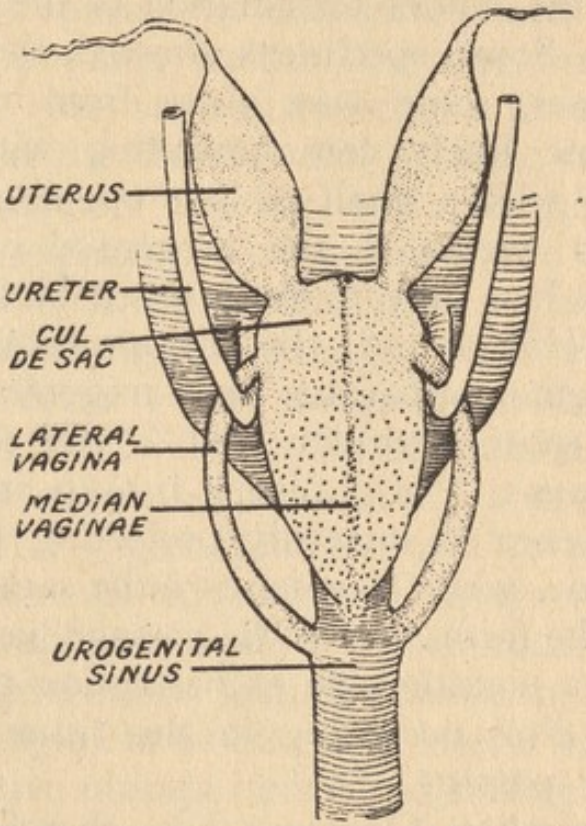

FIG. 15.—Internal reproductive system of an adult female *Trichosurus vulpecula*.

Brass and Forbes as to the normal condition of the parts in the adult female ; and settle, once and for all, the question of the route by which the young were born. Brass had described the median vaginal apparatus of the adult as consisting of the two fœtal cul-de-sacs approximated and enlarged, but still completely separated from each other by a median partition. (62) Forbes had described it as a single chamber, in which only slight traces of a former median partition were to be found. (63) Such a description was adhered to by Mackenzie, even in 1919, as being applicable to the normal adult condition, for he says : " The interior of the median vaginal canal is finely rugous, and on the

dorsal wall a faint streak scarcely deserving the name of elevation is seen, suggesting a division into two portions." (64) As a matter of fact, both descriptions are correct, but that of Brass applies to virgin females and that of Forbes and Mackenzie to those that have already borne young (see Fig. 15).

The same discrepancy in description had previously applied to the hinder termination of the cul-de-sacs in the adult. Some specimens showed them ending as blind recesses, some way away from the urogenital sinus; some freely communicating with the sinus; and some " with a small pinhole opening leading from the median vagina to the urogenital canal ". In a female that had very recently given birth to its single offspring, Hill found the communication between median vaginal apparatus and urogenital sinus to be " a large, quite irregular cleft ". Of this communication he says: " In outline it is quite irregular owing to the presence of inwardly projecting shreds of connective tissue, while fragments of the same occur in the lumen. The formation of the passage has been accompanied by a considerable extravasation of blood, large and small clots occurring in the tissue both in and around the passage." (56)

The Australian Opossum has, therefore, made an advance on the stage reached by the Bandicoot; for by means of these extraordinary, haphazard, proceedings it has at least gained a definitely new structure as a permanency. During pregnancy it converts the two cul-de-sacs into a median chamber and this median chamber, once made, would appear to persist in all individuals. During parturition it makes, by the simple process of rupture, a continuous median vagina communicating with the urogenital sinus. This rupture certainly heals completely in some animals, but it is possible that in some it may persist for a long while, or even permanently, as " a small pinhole opening ".

The most specialized of all the Australian marsupials —the Kangaroos and Wallabies—have even advanced

from the stage attained by the Opossums. In the pouch embryo of a Wallaby (*Thylogale eugenii*) with a head length of 34 mm. the median vagina already extends almost to the upper end of the urogenital sinus and constitutes the direct continuation of the two uteri. Each uterine neck, as it lies on the bar formed by the incoming ureter, is continued into a comparatively wide-bored tube, lined by epithelium and surrounded by a well-differentiated muscular wall. This tube, and its fellow of the opposite side, are embedded in a strand of tissue that lies behind the bladder and urethra, between the two incoming ureters (see Fig. 16). As the two tubes of the median vaginal apparatus are traced downwards they approach each other, finally joining to constitute a common median vaginal passage, which ends blindly in a mass of tissue which merges with the posterior wall of the urethra. This point of termination of the median vagina is situated immediately above the opening of the lateral vaginæ into the urethra to form the urogenital sinus. At this embryonic stage the opening of the lateral vaginæ is made by a common orifice, for the tubes of opposite sides join, just before their entrance, into a short, single chamber. The lateral vaginæ have shrunk to relative unimportance and, before they make their medial bend over the ureters, their lumen becomes reduced to an extremely small bore. All that remains to be completed after this embryonic stage is that the two median vaginæ fuse in the whole of their length up to the uterine necks. The process has started at their lower ends and the septum that separates them over the greater portion of their length consists of no more than the approximated epithelial linings of the two tubes. Higher up, where the uterine necks join them, the median tubes, though somewhat more widely separated, are still bound together in a common strand of tissue. At the lower end, where the two median tubes are united to form a single median vagina, the junction of the lumen of this cavity with the cavity of the urogenital sinus is interrupted only by the intervention of a small

mass of tissue, derived from the walls of the two chambers which are fused together over a short distance (see Fig. 16).

We have here, then, in the Wallaby embryo, a condition in which the whole median vaginal apparatus is fully developed as organized and epithelium-lined tubes. These tubes are already fused in part of their extent to form a common median vagina ; and this median vagina is only prevented from communicating with the

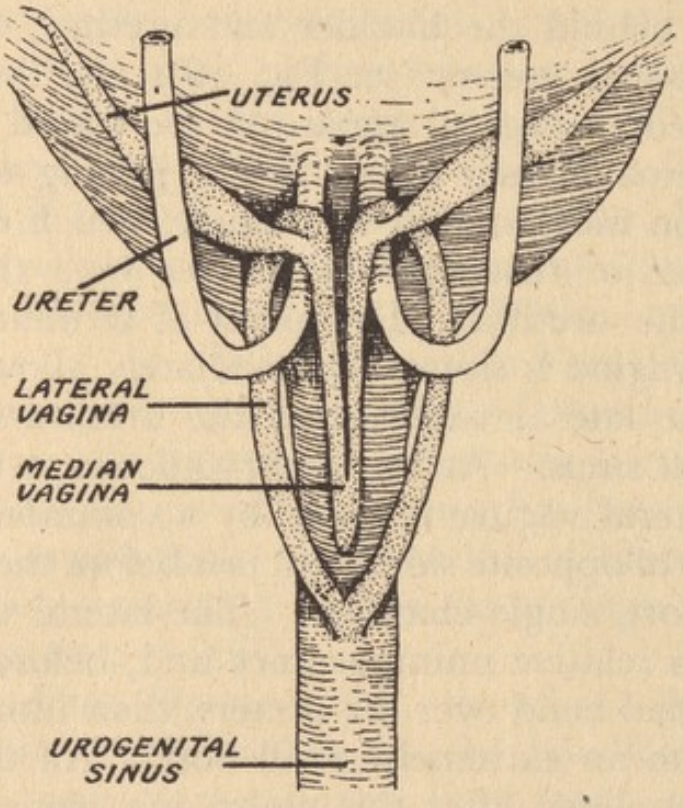

Fig. 16.—Internal reproductive system of a female pouch embryo of a Wallaby (*Thylogale eugenii*), 34 mm. head length.

urogenital sinus by the intervention of a small mass of tissue constituting a septum between them.

The condition typically present in adult virgin females of the *Macropodidæ* is well known, for large numbers of specimens of many species have now been examined. The ancient feud is settled and there is no longer need to quote Owen against Home, or Cuvier against Geoffroy St. Hilaire. (65, 66) There would appear to be a slight range of specific variation in minor details, but such variations do not in any way controvert any of the

general well-known conditions prevailing before impregnation and parturition. In all cases, the median cul-de-sacs have become converted into a true single median vagina, which is no mere tissue cleft, but a tube with properly organized muscular walls and with a

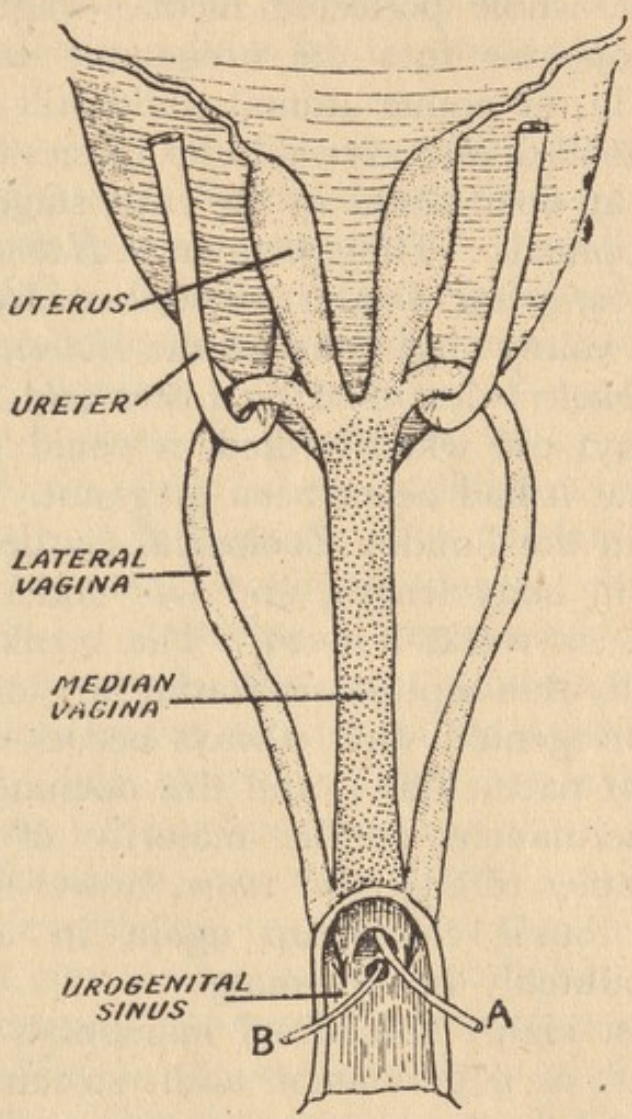

FIG. 17.—Internal reproductive system of an adult female Nail-tailed Wallaby (*Onychogalea unguifer*).

A. Probe passed into the opening of the median vagina.

B. Probe passed into the opening of the urethra. The arrows issue from the openings of the lateral vaginæ.

complete epithelial lining. In the Kangaroos this tube is some 7 cm. ($2\frac{3}{4}$ inches) in length, with a bore of slightly under half an inch (see Fig. 17). As a rule, this tube ends blindly by coming into apposition with the wall of the urogenital sinus at the level of the opening of the urethra into that chamber. The blind lower end

of the median vagina is separated from the cavity of the urogenital sinus by a septum, generally so thin as to be translucent : but, at times, even in young females that have undoubtedly never been pregnant, the two chambers are continuous.

That the whole perfected median vagina, with its definitive opening into the urogenital sinus, may be developed in the young animal whilst still in the virgin state is beyond doubt, even if in no species is it normally present as an open canal in the early stages of embryonic development. The specimen of *Halmaturus bennetti* (*Wallabia rufogrisea bennetti*) described by Brass was certainly a young virgin and, as the *Halmaturus ualabatus* (*Wallabia bicolor*) described by Lister and Fletcher was only 42 days old when it died, it could positively be asserted that it had never been pregnant. The animal was born in the London Zoological Gardens, was only 16 inches in body length, and was under observation during the six weeks it lived. The breaking down of the normally thin septum separating the median vagina from the urogenital sinus always occurs during pregnancy or at parturition ; and this opening once made remains permanent in the majority of species. In some examples of *Macropus major*, however, the orifice has been found closed up again in animals that have undoubtedly borne young.

The most highly specialized marsupials have, therefore, gained, as a permanent adult structure, an elongated and perfectly organized median vagina in which all trace of the septum that originally divided it into two lateral parts has disappeared. It has become lined with its own typical epithelium and bears no evidence whatever of its original make-shift origin. Moreover, in some virgin females it is already a direct channel of communication from the oviducts and uteri to the urogenital sinus, the cloaca and so to the outer world. Some species undoubtedly rehearse the ancient business of the breaking down and re-healing of the septum that normally separates the cavity of the median vagina

from that of the urogenital sinus: and this they do apparently at every successive pregnancy. But the most highly specialized members of the phylum, as a whole, have succeeded in obtaining, as part of their heritage, that median birth channel that is the birthright of the higher mammals whose ureters elected to pass lateral to the female ducts in the process of embryonic development.

What, then, would seem to be a just summary of the story of the phases of development of the female reproductive system in the marsupials? In all the great vertebrate phyla, with the sole exception of the Birds, some members have abandoned the ancestral method of reproduction, typified in the laying of eggs, and have adopted the business of producing living young. In the various phyla of the fishes, amphibians and reptiles, some adventurous individuals have become viviparous and, in every instance, profound adaptive changes have accompanied the alteration in reproductive economy. Among the mammals, the great adventure seems to have been taken by the ancestors of the present primitive Didelphians. The more primitive egg-laying Monodelphians have left few survivors and these, in all their adaptive refinements, are very highly specialized end products. Nevertheless, they show in their reproductive systems what may almost certainly be rightly considered as a comparatively unaltered perpetuation of the conditions prevailing in the ancestral form of all the existing mammals. This arrangement is of diagrammatic simplicity in that the two female passages or oviducts permit the passing of the fertilized eggs from the ovaries to the exterior. In these animals, the relation of the oviducts to the kidney ducts is a matter of no moment. But for some reason, for which at present there is no explanation, the kidney ducts, from occupying a neutral dorsal position in the *Ornithodelphia*, passed to opposite sides of the female genital ducts in the diverging phyla of the *Monodelphia* and the *Didelphia*. By passing to the medial sides of the female ducts in the *Didelphia*, the

kidney ducts prohibit that caudal meeting that produces the pregnancy chamber or chambers, with a median vaginal outlet, that typifies all members of the *Monodelphia*. A median birth channel is the natural outcome of the anatomical arrangement of the ducts of the kidneys and the female genital ducts in all the higher or Eutherian mammals. But, with the *Didelphia*, the primary formation of such a median passage for the birth of living young is prohibited.

From so much of the story as the surviving types can reveal to us, it would seem that, lacking this primary possibility of a median birth passage for living young, the primitive marsupials, like certain fishes, amphibians and reptiles, became viviparous. In this dilemma, the young, produced from the eggs hatched in the body of the female, became lodged in the female passages at the point where these run, as an inflexion, alongside the barrier caused by the kidney ducts passing from the dorsal body wall to the base of the bladder. At this point they developed the median cul-de-sacs of the female passages. The young embryos did what, under similar circumstances, the young of fishes, amphibians and reptiles had done before them : they established a vascular connection with the maternal tissues and so initiated one of the many types of placenta developed in the animal kingdom. The young, having thus organized a vascular supply, continued to grow ; the median partition, separating the two cul-de-sacs, broke down and a median pregnancy chamber was made on the emergency. This median pregnancy chamber demanded an outlet and, to meet the demand, the maternal tissues ruptured (over an area in the Bandicoots of nearly 2 inches) from the lower end of the pregnancy chamber to the urogenital sinus and cloaca and so to the outer world.

This birth passage, formed apparently in the first place as an emergency to meet an imperative need, is in the nature of a physiological wound and, as a wound, it undergoes rapid healing. After the healing of the

adventitious, traumatic, pseudovagina, the animal returns to its former condition, only to repeat the process at every subsequent pregnancy. Despite the countless millions of times the process has been repeated in the ancient, more primitive and unprogressive members of the marsupials, nothing has been gained as a permanency.

But in the marsupial phylum as a whole, the gain became, step by step, incorporated into the heritage of the animals. Once the median pregnancy chamber had been established at the first pregnancy in the *Phalangeridæ*, it became a permanency in the individual. The median outlet had, as a rule, to be remade each time the animal became pregnant: but something in adult anatomy, though not in embryological development, had been gained. Every parous female of *Trichosurus vulpecula* has a single median pregnancy chamber though it does not necessarily have a permanent median vagina. At this stage, the median pregnancy chamber becomes a permanent feature of the anatomy of the parous female and a very close approximation to this condition is seen in the adult virgin female, for the septum separating the two cul-de-sacs is merely membranous in its thickness. The condition that is only of very short duration in the parous female of the *Dasyuridæ* and *Peramelidæ* has, in the *Phalangeridæ* become permanent after the female has once been pregnant.

The highest specialization of the whole of the *Didelphian* phylum finds its expression in the peculiar development of the *Macropodidæ*—the Kangaroos and Wallabies. This specialized development took place only among the Australian radiation of the ancient Metatherian stock, for the American didelphians apparently never attained to this acme of marsupial development. In its most specialized members, the Australian radiation of the marsupials has achieved the triumph of attaining to the possession of a perfectly organized, epithelium-lined median vagina in all adult females. It would seem that the original emergency had been

taken advantage of in the most progressive members of the phylum and that, what started as a physiological wound, has become a perfectly organized anatomical structure.

It is of interest to quote the actual form of expression employed by Hill, when the whole curious story of reproduction in the Bandicoot first became clear to him. In his paper of 1899 he wrote : " Now the origin of this new and direct passage in the first instance presupposes, it seems to me, the existence of the median vaginal cul-de-sacs. These may have originally arisen as out-bulgings mechanically produced by the young to facilitate their passage from the contracted neck of the uterus into the lateral vaginal canal, here bent outwards and forwards in association with the medial position of the ureter. Whether or not this be the true explanation of the origin of the vaginal cul-de-sacs, if we grant their existence, then it seems probable that the median passage was discovered through what we can only describe as an accident, which, happening again and again, came eventually, owing to its value, to be adopted as a normal occurrence. In the lowly Perameles, the old, accidentally discovered passage has persisted, probably unmodified, in correlation with the retention by the genital organs as a whole of a persistently embryonic condition, while the specialized macropods have gone on to exhaust the possibilities implied in the possession of a median vaginal apparatus and have evolved a direct median passage, eventually epithelially-lined throughout its entire extent."

It might have been of the embryonic Bandicoot that William Browne wrote in 1613 :

> " Which, like the viper's young, that licke the earth,
> Eate out the breeder's wombe to get a birth." (67)

But it must be admitted that in doing it, they initiated a process which, if we are prohibited from believing that " features developed during the life of the individual in response to the action of use " may ultimately enter into heritage, is a happening very difficult to understand.

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X

> Is the 'nature'—the germinal constitution, to wit—all that passes from generation to generation, the capital sum without the results of individual usury; then we are freed, at least, from undue pessimism at the thought of the many harmful functions and environments that disfigure our civilization.
>
> J. Arthur Thomson, *Heredity*, 1908, p. 246.

We have considered only a few cases, out of a whole multitude that could be passed in review, in which there appears to have been a handing on in phylogeny of characters begot originally in response to habit, posture or even to accident. We have selected these instances solely because they have not previously been subjected to the distortions and evasions that have become traditional in the many discussions on this subject in the past. In some cases, such as that of the hair tracts, the operating cause would appear to be a very trivial, certainly not a life-saving one: and the same might be said of squatting. These instances do not represent the grand or dramatic in evolution. The actions of scratching the hair, or squatting on the ground, may not appeal to orthodox geneticists as being activities worthy of much attention; and yet it is their very triviality that makes them so important. Trivial though they may be, the structural changes that they effect would seem to have become a definite part of the heritage of the creatures concerned. Their very triviality is vastly outweighed by the constancy of their repetition. They give, I think, a very decided affirmative answer to the question we proposed at the outset of this inquiry: "May a feature, developed repeatedly during the successive lives of a long series of generations, be ultimately incorporated into the heritage of the species; so that in time, it will be developed in the offspring, not as a response to the action of use or environment, but as a permanent feature of the animal's

intrinsic characteristics?" To this question we have already seen that the work of the experimental embryologists has given us a theoretical sanction for an affirmative reply: the instances we have cited appear to give us very definite practical sanction for such an assurance.

But the real importance of this question lies not so much with the method by which the Bandicoot produces its young, or the way in which a Koala scratches itself: its gravest implications lie in its application to human social affairs. It is just here, where the matter touches humanity, that resistance to the belief in the inheritance of acquired characters has always been most determined.

That man differs from all other animals in that he has an external heritage as well as an internal inheritance is, of course, recognized by all. The external inheritance that man, alone among living things, enjoys is contained in the traditional lore and learning that is handed down in human societies, no matter what may be their stage of cultural evolution. With some societies it is merely a verbal heritage, with others a written or a printed one; and with all it is the most potent factor in shaping ideas, ideals and standards of conduct and ethics. There is no necessity to dwell, today, upon the paramount importance of man's external heritage, nor is there any need to call attention to the power for evil or for good of the inculcation, even during the lifetime of one generation, of a teaching that claims to be justified as being an essential part of the external heritage of any one section of mankind. The overwhelming importance of man's external heritage must be admitted by all.

But while making this admission we must not lose sight of the fact that man, in common with every other form of life, has his very real internal heritage.

One part of man's internal heritage, which he shares with every other living creature, is his own individual genetic or germinal constitution. In possessing this,

he naturally shows all those germinal variations that we are accustomed to meet with among all other forms of life. Man, considered as a zoological type, is, as we should expect in a mammal that may truly be termed a ' domesticated animal ', a highly variable form. It is strange that Thomson should have declared that " compared with most organisms, man is a slightly varying creature ". That statement he makes on more than one occasion in his work on Heredity and it is obvious that he attaches importance to it. But every human and comparative anatomist will be prepared to admit that the statement lacks any sort of validity. All the higher members of the Primates notoriously show a bewildering range of variation ; and it would be nearer to the truth to say that of all mammals man is the most variable, than to claim that he is " a slightly varying creature ". It is unnecessary to rehearse the enormous range that is covered by human variations that are well known to be true changes in germinal constitution. A vast amount of work has been done on the inheritance of these things and this work is permanent and remains, and must remain, beyond the possibility of any challenge as to its validity. Just as we must admit the importance of human external heritage, so must we admit the importance of the inheritance of an unusual number of internal germinal variations, in any sort of inquiry into the whole question of human inheritance.

But in addition to man's internal heritage of true germinal variations, the inheritance of which is admitted by all, he also exhibits, in a very high degree, the power of producing modifications as a consequence of use and of environment. Now this should be no surprise for us, since man is pre-eminently that form of life that has come to the occupation of almost every conceivable type of environment ; and that has become subjected to almost every possible sort of functional rôle as his life activity. Man may live at the poles or at the equator ; he may wield a sledge-hammer or a pen as a daily occupation ; he may spend half a lifetime sitting

at a desk or the same period in climbing mountain passes; he may be a pure carnivore or be a lifelong vegetarian.

"Use and environment" mean little in the life of a Koala, whose perpetual environment is a gum tree, and whose perpetual use is the climbing towards a new supply of gum leaves that constitute its sole diet. But in the case of man, "use and environment" are of infinite variety. It is not surprising, therefore, that man may be like to show an altogether exceptional range of variations in response to the demands of use or environment.

Is no whit of this ever passed on to succeeding generations? In Thomson's words, is the only thing passed on "the capital sum without the results of individual usury"?

We have seen that, in Nature, one of the factors that seemed to be of importance in the transmission of acquired characters was the repetitive nature of the stimulus derived from use or environment; and the other was the time factor; for repetition and long duration seemed far to outweigh the dramatic or the apparently important nature of the change in the perpetuation of modifications originally acquired during the lifetime of ancestors.

The human historic period is a short one: social usages have undergone changes, at longer or shorter intervals, throughout the whole of the historic period. Human environment and human occupations change as rapidly as do social systems. There is, therefore, no such long-continued and repetitive action of environment or use to be appealed to, in the short span of human history, as there is in the case of the paleontological record, or in the story of some of the use modifications that we have considered in lower mammals. And yet I think that the anatomist may claim that the development and inheritance of the squatting facets in man is a case that has met with no sort of explanation from the orthodox geneticist. In the absence of such

an explanation, it would appear to be justifiable to assert that we have here definite evidence of structural modifications, acquired during the human period, being transmitted by inheritance. It is, therefore, presumably not unreasonable to assume that, in regard to other characters, man is not exempt from the business ; that acquired modifications of many kinds may be handed on in him, just as certainly as they appear to be in other animals, provided the necessary conditions of time and repetition are fulfilled.

The fact that a man who, after the devotion of a life-time to the enterprise, had completely mastered the saxophone and yet, in his old age, begot a child with no musical appreciation whatever, would be regarded as negative evidence only by those who are prepared to be impressed by the evidence derived from the cutting off of the tails of white rats. And yet it is upon grounds but little better than this that the thesis of the non-inheritance of acquired characters in man has gained general acceptance in orthodox science.

It is easy to see what such a conclusion must inevitably lead to when theory is translated into actual social planning. If human germinal or genetic variations can alone be inherited, then it is obvious that only those individuals, elements, nations or races, deemed to have the best type of germinal constitution, should be encouraged or even permitted to reproduce their kind. Other individuals, elements, nations or races, deemed to be of inferior genetic constitution, should be prohibited from reproduction. Having accepted the thesis, only one difficulty remains and that is the attainment of universal agreement as to exactly what constitutes a really good germinal constitution, and just what stigmata denote a poor one. If we could come to agreement upon that point, then we might, possibly at the expense of some rather deeply-rooted social and ethical ideals, breed human beings as the pigeon fancier breeds pigeons. Having accomplished all this, we might be said to be

on the way to the inauguration of an era of the practice of human genetics. The dawn of such an era is apparently a consummation of the teachings of modern genetics that some people would consider desirable.

But there is a more immediate, and far more important, outcome of the comfortable doctrine that in man there is no possibility that acquired characters can be inherited. For if this doctrine is true, it follows quite definitely that no improvement of social conditions, no raising of the standard of living or of education can ever find its reward in the betterment of any human stock. And such a doctrine can be extended, as at present it is being extended, to warrant the teaching that no advancement in social organization and no amelioration of human conditions can ever hope to effect anything towards an ultimate improvement of humanity.

Unfortunately this doctrine may also be applied in such a way as to justify that cowardly acceptance of the avoidable evils of modern ' civilization ' that should at no time have received any support from science. The statement that : " then we are freed, at least, from undue pessimism at the thought of the many harmful functions and environments that disfigure our civilization ", seems to me to rank the teachings of modern genetics as among the least helpful of all the dicta of science. For a science which produces evidence that would give sanction for condoning the preventable degradation of human existence, imposed by certain of the conditions of modern civilization, can hardly be claimed as commendable, even were all its findings surely based on ascertained facts and unassailable premises. But when, as we have attempted to show, the premises upon which its claims are founded are by no means surely established, there can be little but condemnation for those who would venture to extend its teachings into the realm of human affairs.

That science should proclaim its theories with some assurance in scientific circles may be reckoned as a meritorious custom ; for the greater the assurance with which a thesis is urged, the more likely is it to be examined, criticized and, possibly, so far modified as to be virtually negatived. Even if, among scientific men in general, it gains an ultimate acceptance as a theory, it must be remembered that it remains no more than an accepted theory. It is a truism to say that even the most sublime theory may be slain by one little commonplace fact. Theories that remain alive merely because the facts that might slay them have not been forthcoming, or have not been properly presented, should be regarded, during a definite period of probation, with a certain amount of suspicion. This reserve should be maintained in the process of making them widely advertised among those incapable of judging their merits ; and this caution applies more especially in those cases in which the theories impinge in any way upon human ideals, human conduct or, especially, human cravings for ethical guidance. This reserve has not always been respected. In the question of the non-inheritance of acquired characters, and all its social implications, it has not even been attempted. A teaching, vulnerable in its foundations, culpable in its ' ostrichizing ' of unpalatable facts, has been broadcast regardless of its implications in the vastly important field of human sociology.

Every European who has watched a Chinese cashier manipulating his abacus must have felt admiration, both for the man, and for the instrument. The man must demand our respect because of the skill he displays in shifting the little balls, this way and that, along the rods upon which they are strung ; the instrument for its real simplicity, despite its apparent complexity, and for the ease with which it solves all the routine problems of the cashier's immediate preoccupation. The abacus is an instrument that is supremely competent to deal

with all the mathematical demands that are wont to be made of it. But I believe that all those, who are in the best position to make judgment in the matter, are agreed that the universal reliance that the Chinese place on the working of the abacus has somewhat hindered the development of a more widely-reaching system of higher mathematics among the members of that race.

I have, at times, been tempted to wonder if my unbounded admiration for the facility with which the modern geneticist solves his problems, by manipulating hypothetical little balls—called genes—along the bars of the chromosomes, may be in part due to my astonishment at his dexterity and to my mystification concerning the niceties of the working of his instrument. We have now a whole race of scientists trained in the refined use of the abacus of heredity. Their manipulation of the little balls of destiny has become an occupation demanding extraordinary skill and a deal of specialized knowledge and literature. Beyond any doubt they possess an instrument and a technique that enables them to keep tally of the petty cash transactions of heredity. It is doubtless a mere impertinence on the part of one who is not a professed, nor even an initiated, geneticist to wonder at times if the great reliance placed upon the workings of the abacus of heredity is not perhaps repressing the development of a possible higher mathematics of inheritance. For undoubtedly there is a higher sphere of inheritance and it must be sought, not through a microscope, not even by the most nicely adjusted experiments, carried on for a short time in the short life of one human being, but by a survey, incomplete though it must necessarily be, of what Nature, with time unlimited at its disposal, has effected among living things. We may be running the risk of becoming blind to the whole range of the possibilities of inheritance, if we concentrate too exclusively on the minutiæ of the means and modes by which, in certain cases, it appears to be effected.

The Chinese have their abacus. The Chinese also have a wealth of proverbs that conceal, or reveal, a vast store of wisdom. One of their proverbs tells us that it is useless to speak about the sea to a frog that lives at the bottom of a well.

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