

no offspring its acquired characters cannot be inherited. The evolution of the worker must be explained as the result of natural selection, preserving those queens that produced the workers best adapted to the needs of the species.

If such complex adaptations as the mechanism for cross fertilization in orchids, and modifications observed in the worker of the honey-bee have arisen through the action of natural selection without the aid of the inheritance of modifications, a strong presumption is raised in favor of the view that natural selection and not inheritance of acquired characters, has been the prime factor in evolution generally. This being granted, should we not return to the position taken by Darwin, that while natural selection is by far the most important factor in evolution, it has been aided by the favorable variations resulting from the inheritance of acquired adaptive modifications?

The amount and kind of evidence that is required to prove any generalization depend upon its theoretical probability. Now if we accept Darwin's view as to the inheritance of acquired characters, we must also accept his theory of heredity or some theory closely allied to it. The study of heredity, however, makes it clear that the only theory that corresponds with what is known of the origin of the germ cells and the subsequent development of the embryo utterly fails to explain the inheritance of acquired characters. If acquired characters are ever inherited, our theory of heredity must include some form of pangenesis and of preformation. But the only theory that agrees with the facts of development must include the contrary principles of continuity of the germ plasm and epigenesis. This makes the inheritance of acquired characters seem theoretically improbable, and necessitates a critical examination of the testimony in its favor. This evidence may be classified as follows:

1. Indirect evidence.

(a) Analogy between congenital and acquired characters.

(b) Apparent uselessness of nascent structures observed in fossils.

(c) Reflex actions.

(d) Instinct.

2. Direct evidence.

Reported cases of inherited effects of (a) use or disuse, of (b) climate, and of (c) food.

3. Experimental evidence.

(a) Brown-Séguard's experiments on guinea-pigs.

(b) Experiments of Hoffman, Carrière, and Buckman on plants.

It will be most convenient to take up this evidence in the reverse order. Beginning with the experimental evidence, Brown-Séguard's experiments were supposed to show that epilepsy induced in guinea-pigs by operation is inherited by their offspring. But Romanes repeated these experiments as carefully as possible, and his results were inconclusive.

Carrière and Buckman were able to produce change in plants increasing in successive generations, by growing them on different soils. But here the principle of selection was employed, and it is impossible to say how far the result is due to selection and how far to the inheritance of acquired characters. It is also to be remembered that food is one of the factors in the environment that may affect the germ plasm directly. It is possible, therefore, that the changes observed in the succeeding generations of plants may be due to the new constituents of the sap affecting the germ plasm directly. The new characters would not then be acquired characters in the technical sense, but true congenital variations. Moreover, these experiments are offset by a number of experiments made by careful observers especially to test the question of inheritance of acquired characters, which have given purely negative results. Fay found that when both parents are congenitally deaf, twenty-six per cent. of the children are deaf. When one parent is congenitally deaf and one has acquired deafness, the percentage of deaf children is 6.5 per cent., while where both

parents have acquired deafness it is only 2.3 per cent., and this last percentage may be due to an error in determining whether the deafness is congenital or acquired.

So the experimental evidence, which should be expected to give the most conclusive answer, is after all unsatisfactory.

The direct evidence as a whole is worthless. Most of the cases have been reported by unscientific persons unskilled in exact observation. The cases in which there have been competent observers can be explained as well either as the result of selection of congenital variations or as the result of the direct effect of environment upon the germ plasm.

It is the indirect evidence that offers by far the best cases in favor of the inheritance of acquired characters. In the first place, that the effects of use and disuse of parts and the effects of external conditions, climate, food, etc., are inherited, is a matter of common belief. We know the effects of these causes upon the individual, and we know that very minute individual peculiarities frequently are inherited. It is reasonable to suppose then that peculiarities caused by external conditions are inherited with the rest. No one can claim, however, that this line of evidence offers more than a presumption in favor of the inheritance of acquired characters. A better line of indirect evidence is furnished by those adaptations which apparently could not have been of use in the early stages of their evolution, and many palaeontologists believe that they find in extinct species such nascent structures and that these prove the inheritance of acquired characters to be the prime factor in evolution. This is regarded as especially true of those cases in which a high degree of co-adaptation is required. Spencer, for example, presents the case of the giraffe as a form undoubtedly due to the inherited effects of functional activity. For as he rightly says, in order that the giraffe may carry his long neck, the forelegs must be lengthened, and the hind legs shortened. In fact, the whole shape of the body has to be altered, involving changes in a great many tissues and organs. If a breeder is trying to produce a variety having a new combination of characters, he selects individuals, some having one character, some another, and still others a third, and so on; and by causing these to breed together finally obtains individuals in which these characters are all combined. The Boston terrier and the Plymouth Rock fowl are excellent examples of such a blending of characters by artificial selection.

Now Spencer argues that it is impossible for co-adaptation to be produced by an analogous process in nature, for it is inconceivable in the case of the giraffe, for example, that any one of its peculiarities occurring alone in an individual could be of sufficient value to lead to the preservation of the animal by natural selection. In fact, some peculiarities without the others, for instance, the long heavy neck without unusually strong shoulders to support it, might be so great a disadvantage as to lead to speedy elimination. In order that the giraffe should be produced by natural selection, according to Spencer, it would be necessary for all of the co-ordinated adaptations to appear at the same time and in a large number of individuals. For, in the first place, these variations could be of no value unless all were present and co-ordinated; and in the second place, unless they occurred at the same time in a large number of individuals, they would be lost by the swamping effect of intercrossing. Moreover, they must continue to vary in the right direction in a large number of individuals. All of this Spencer holds to be impossible without the aid of the inheritance of acquired characters.

A new variety may be supposed to arise in one of two ways, either (1) from the blending of a series of adaptations each in itself of selective value, or (2) by the co-adaptation of a number of variations each so slight as not alone to have selective value, but when combined with the others producing a form sufficiently superior to its fellows to be preserved in the struggle for existence. Even Spencer would admit that the first method is easily ex-

plained by natural selection, if the swamping effect of intercrossing can be eliminated by some mode of isolation. But, if new forms are produced in the other way, by co-adaptation of variations in themselves not of selective value, as Spencer supposes in the case of the giraffe, natural selection is not so easy an answer.

These phenomena of co-adaptation present one of the best lines of evidence that has ever been brought forward in support of the theory of the inheritance of the effects of use, and yet it does not seem to be at all conclusive. To begin with the case of the giraffe, it would seem that the development of this species from an antelope-like ancestral form may be explained by the mingling of adaptations as well as by the sudden appearance of true co-adaptations. Those who take the opposite view, while insisting upon the adaptive value of functional modifications, that is, characters acquired as the result of the use of parts, seem to forget, as has been pointed out by C. L. Morgan and others, that purely fortuitous, or accidental, congenital variations in the same direction may occur at the same time. The element of environment that has led to the evolution of the giraffe was evidently the need of reaching high foliage. Now in order that the animal shall reach this foliage the head must be raised high from the ground, and this may be accomplished by lengthening the neck or by lengthening the fore-limbs, or by lengthening both at the same time. At the beginning, therefore, of giraffe evolution, those animals which varied toward greater length of neck and those which varied toward greater length of fore-limb or greater height of shoulder would have an equal chance of surviving in the struggle for existence, provided the muscles necessary for carrying this increased weight were equally capable of being strengthened by exercise. These individuals would breed freely together, and finally offspring would be produced having both neck and fore-limbs longer than in the ancestral form. Again, the effects of exercise would compensate for the increased weight, and, again, the individuals best developed would survive. Now we know practically that every part must have varied on both sides of the average character of the race. A large number of individuals inheriting the above characters must have presented congenital variations of the co-operating parts of the body of the same character as those modifications produced in the others by functional activity. Such congenital characters might occur separated, some in one individual, some in another; but wherever they occur the animal will have a distinct advantage, for so much will be, so to speak, ready-made, and just so much less to be developed by exercise. You can make an athlete of a man with a congenitally strong back and weak legs more quickly than you can make one of a man whose back and legs are both congenitally weak. In time, by careful training, the two men might become equally strong, but in natural selection time counts. The sooner an animal can hold its own with its fellows, the better its chance for surviving to produce offspring.

It seems to us then, that if we remember that fortuitous, congenital variations and modifications due to functional activity may be of the same character and may occur side by side, there is no longer any difficulty in the theory that even so complicated a co-adaptation as is presented by the giraffe may arise by blending of minor congenital adaptations and therefore may be explained by natural selection. Moreover, it is to be borne in mind that it is a fallacy to speak of any one character as being selected. It is not a single character that is even preserved by natural selection, but it is the individual as a whole that is selected. While a favorable character may not of itself be of selective value, it may be perpetuated because it occurs combined with other favorable characters either congenital or acquired, all so blended as to give their possessor superior advantages. Individually acquired modifications may, therefore, become important factors in evolution, not because they are inherited, but because by their acquirement the individual is able to supplement the deficiencies in its congenital characters. And when thus supplemented by individually acquired adaptive

modifications, the inheritable congenital characters may be preserved by natural selection and continued from generation to generation, until by the operation of fortuitous variation and natural selection the acquired modifications are replaced by congenital characters of the same kind. So we may have two forms of co-adaptation: first, co-adaptation of mingled congenital and acquired characters, which precedes and prepares the way for the second, co-adaptation of purely congenital characters.

The question whether co-adaptation by the blending of favorable congenital variations really occurs in nature is answered best, according to Romanes, by a study of reflex actions and of instincts. Turning now to the evidence from reflex actions, it seems to us that Romanes has been unfortunate in selecting this line of evidence upon which to pin his faith in the occasional inheritance of acquired characters. He asks what use an animal can have for lower reflex centres when the higher brain centres are capable of originating the same nervous impulses. Now no one who has ever learned to dance, to swim, or to ride a bicycle will fail to appreciate the superiority of reflex over conscious action. No one can become an expert swimmer or rider until the movement is of the nature of a reflex, although the higher centres, the rational processes, may still be indispensable in case of accident. Romanes argues at length in regard to the apparent uselessness of many reflexes, together with the completeness of the mechanism required, and the consequent difficulty of explaining them by natural selection, and then proceeds to show that "if function produces structure in the race as it does in the individual," all is easily explained.

Now, in the first place, does function produce structure in the individual? Function may be said to produce size, strength, hardness, flexibility, and the like, but no case is on record where new muscles, new nerves, or any other new structure has been produced by any amount of functioning. Moreover, how can a structure be the result of a function when the function arises from the activities of the structure in question? A given intelligent act cannot take place until the whole neuro-muscular mechanism concerned in that act is complete, any more than if it were a reflex; and it is not evident how one can be explained by gradual development any better than the other. (It is like saying that a man can make a bicycle by riding it.) But even if we allow that a reflex mechanism may be the inherited result of intelligent action, this action must have been of a great deal of use to have been repeated often enough to make so great an impression on the organism. And if it has been of so great use it may well have had a selective value, and its development may then be explained by variation and natural selection.

It would seem, therefore, that reflex mechanisms and actions may be explained best by the principles of change of function and natural selection. When you learn to ride a bicycle, or better, when you learn to swim, you develop a new set of reflexes, but no new sense organs, nerves, or muscles, only the old ones in new combinations. Now the study of the morphology of the nervous system in any great group of the animal kingdom shows that a change of function in different parts of the nervous system is just what has taken place as we go higher in the scale of organization; and it is easy to see how any variation toward more intimate union of parts habitually used together would be preserved by natural selection until their interaction would be so easy as to become reflex.

Turning to instinct—if we regard it as "hereditary habit," that is, if we suppose it to contain an element of transmitted experience, all is easily explained. The simple instincts are easily explained by natural selection, "but in all cases where instincts become complex and refined, we seem almost compelled," according to Romanes, "to accept Darwin's view that their origin is to be sought in consciously intelligent adjustments on the part of ancestors." He cites the case of a species of wasp of the genus *Sphex*, which paralyzes caterpillars by stinging

them in each of the nine minute nerve centres before depositing them in the cells for the larva to feed upon. He regards it as impossible that such an instinct could have arisen by natural selection unaided by originally intelligent action. In regard to this it may be said that, if the complicated maternal instinct of the *Sphex* wasp is an "inherited habit," its ancestors must not only have possessed great industry, but also a very remarkable knowledge of anatomy. Moreover, it has been shown very recently (1898) by Mr. and Mrs. Peckam ("Instincts and Habits of the Solitary Wasps") that the instinct of *Sphex* is not so exact as was formerly supposed. Not only is there a great deal of individual variation in the instinct of this species, but there is a gradation from this through other genera to those having much simpler instincts. They have shown that instinct may be acted upon by natural selection, just as may any other function or structure.

In conclusion it may be said, therefore, that in the writer's opinion, while acquired characters are of great importance to the individual, and their periodic recurrence in successive generations may be necessary in the formation of co-adaptations as an aid to natural selection, the inheritance of acquired characters is not only not the prime factor in evolution, but that it is not a factor in any degree.

Differential fertility appears to be an important factor, being, according to the circumstances, either an aid or a hindrance to evolution; preferential mating is the best explanation of the origin of certain secondary sexual characters; and some form of isolation must be present, or else divergent evolution is impossible, and without isolation it would be impossible to explain the differentiation of species by characters of less than selective value; but the chief cause of organic evolution is natural selection, or the survival of the fittest in the struggle for existence.

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EVOLUTION OF MAN.—The science of anthropology has advanced with surprising rapidity since the discovery of the two principles, evolution and psychic unity, the latter contributing evidence in support of the theory of evolution similar to that furnished by the homologies of biology. From each of the recognized divisions of anthropology evidence has been accumulated to establish the unity of the human species and to warrant the assumption that it has developed from the original mammal through the lemuroid and anthropoid stages. A few zoologists would derive man directly from the lemurs, but while it is recognized that man has many characters in common with the half-apes and even with lower forms, anthropologists are unanimous in deriving him from a generalized anthropoid precursor. The phylogeny of the mammalian group is given in the preceding article upon *Evolution*, so that we may devote our attention here to the problems involved in the determination of man's immediate ancestry. We shall seek such evidence as

may be found within the human group, neglecting argument by analogy, which can never be wholly convincing.

I. SOMATOLOGY.—The modern science of physical anthropology interprets the data supplied by embryology, ethnic and comparative anatomy, and statistical anthropometry by the aid of the theory of evolution which alone renders them comprehensible.

1. *Embryology.*—In addition to the indications of relationship to lower animal forms there are many marks of phylogenetic proximity to the anthropoids in the human foetus. By the dictum of "the first biogenetic law" we interpret the greater resemblance of the young of anthropoids and man to mean that both sprang from a common ancestral type. Not to deal too exclusively with general statements let us review a few of the more salient facts.

The lanugo of the foetus recalls the hairiness of primitive man and his immediate ancestor, a condition seen even now in an occasional unfortunate adult. The free projecting tail of the embryo certainly pertains to an earlier form than the anthropoid but not necessarily earlier than the lower primates. Again it is to be noted that this character sometimes persists in human beings until maturity, either with or without free vertebrae. Until the very end of the nineteenth century rumors of the discovery of tribes of tailed men were circulated from time to time. It has been suggested that such fables may have arisen from the practice of wearing a sort of caudal appendage, as among the Sioux Indians and the Nagas of Manipur. The theory of an ontogenetic shifting of the pelvic girdle is generally accepted, reducing the number of presacral vertebrae from the number existing in most of the anthropoid families and from the ancestral condition. The presence of cervical and lumbar ribs in the embryo recalls the type prevailing among the anthropoids where the orang alone has as few as twelve pairs. The shape of the entire thorax in the embryo is of the primary type seen in the lower apes. One of the most noticeable simian characters to be seen in the embryo is the proportionately long fore-arm which in the embryo of two and a half months equals 88.88 per cent. of the length of the humerus as compared to 72 to 73 per cent. in the adult European, 78 or 79 in the adult negro, and 90 to 94 in the chimpanzee. The os centrale of the human embryo is found in but one group of anthropoids among adults, though it occurs in most monkeys. The short lower limbs of the foetus suggest the adult anthropoid condition. The fibular malleolus, much less important than the tibial in apes, is less developed in the foetus and among Australians and other low races. The opposable condition of the great toe in foetal, and even infantile life is an often cited example of the retention of an ape-like character.

Among the muscles we may refer to the condition of the pyramidalis which in the child resembles that of the apes and lower mammals; also to the *interossei pedis* muscles which in the human embryo are distributed as in some of the lower apes and in lesser degree the chimpanzee and orang. The vermiform appendix is proportionately larger in the foetus.

In the brain, the most distinctively human of all the organs of the body, the ontogenetic changes in the character of the surface and the disposition of the vesicles repeat phylogenetic development in a marked degree. Resemblance between the young of the two groups is nowhere more striking than in this organ. Hints of the anthropoid condition are not numerous in the sense organs of the embryo, but in the external ear such conditions are fairly prominent; the tip shifts downward and not until the eighth month does the human ear fold begin to roll inward. The palatal ridges of the embryo (six or seven) suggest the anthropoid condition, though they are rather more numerous in the apes. The milk teeth of man and anthropoids are closely similar and the dental formulae are identical in the two groups.

These are a few of the more important characters that point to an anthropoid ancestry. They are but a fraction of the number of characters that occur in the human em-

bryo which are indicative of lower stages of development, but taken altogether they lend strong support to the evolutionary hypothesis.

2. *Ethnic and Comparative Anatomy.*—Together with physiology and anthropometry it comprises the greater part of the science of somatology as now taught in our universities, and the evidence of the relationship of man to the anthropoids is rapidly accumulating, both from the work done in our laboratories and from that accomplished among what we are pleased to term the lower races, though it must be understood that in many respects these races as well as some of the lower animals exhibit characters of decided superiority. We may summarize the facts as follows: Man resembles the anthropoids more closely than do the latter the American monkeys. In other words, the gap between the human and the nearest non-human group is far less striking than that between many mammalian groups. Among skeletal characters we find that the spinous processes of the cervical vertebrae are simple and undivided among low races. The clavicle and the scapula are proportionately longer and hence more simian in the negro than in the Caucasian. The arm of the negro exhibits two opposing characters: it is higher in its shorter humerus and lower in the longer radius than the white; the proportion of the radius is more exaggerated in the Veddahs of Ceylon. With a slightly shorter femur and a tibia of equal length the negro possesses lower limbs of a more simian type than the white. In the torsion of the humerus the black races stand midway between the anthropoids (130°) and Europeans (164°). The condition known as perforate humerus or the occurrence of the supratrochlear foramen, which is most frequent in Veddahs and Bushmen, is common in the gorilla and the orang. Among non-European races it is not the blacks alone that retain the ape-like prehensile foot beyond the period of infancy; many Eastern peoples possess this character, notably the Japanese. However, it is a pincer foot, not a hand foot.

The skull continues to be the most significant portion of the skeleton for classificatory purposes notwithstanding some contradictions presented by single characters. The projecting brows of the gorilla are seen in certain prehistoric crania to be described later and in the Melanesians as well as in rare instances among Caucasians. Many human groups possess the flat nose of the anthropoids. The fusion of the nasal bones that is normal in apes occurs more frequently in lower races than in higher. Australians, Hawaiians, and others have no sharp line of demarcation between the nasal opening and the maxilla beneath it. The temporal crest assumes a simian appearance among the Oceanic blacks. The meeting of the temporal with the frontal in the form known as pterion in K is most frequent in the Veddahs, Australians, and negroes; in anthropoids it is seen in the gorilla. Considerable variation in the foramina of the skull occur: the parietal are more frequently wanting in the higher races, the middle lacerated is larger in Europeans than in lower races and is wanting in anthropoids. The palatine suture of certain low races by its curved and irregular course resembles that of the apes. The form of the palate among low races often resembles the U-shaped alveolar arch of the anthropoids and occurs occasionally among Caucasians as an individual variation. The teeth of the Australians increase in size backward as in the apes. The New Caledonians not rarely develop a third pre-molar, the normal condition in New World monkeys. The shortened inferior maxillary of the European is causing a reduction in the number of teeth so that the upper outer incisors are sometimes wanting and the wisdom teeth as well. This change is also taking place among Amerinds. We have observed cases of suppressed third molars among the Esquimaux and all stages between rudimentary third molars and those larger than the first and second molars among other Amerinds. The hyoid of negroes resembles that of apes more closely than does that of Caucasians. The prognathism of the ape is conspicuous in the extinct Kalangs of Java, the Akkas and other Africans.

The only well-marked gap existing between the crania of man and anthropoids is in capacity. The highest recorded capacity for the latter is about 590 c.c. while the lowest for the former is that of a normal Veddah skull of 950 c.c. While the methods of determining cranial capacity are unsatisfactory, and the results of different observers are scarcely comparable one with another, yet approximately correct averages have been recorded for most human groups which show that the lowest capacity exists among the dwarf races of Africa, the Veddahs of Ceylon and their neighbors, the Andamanese. The question of capacity is the most interesting one concerning fossil human crania.

3. *Variation.*—Notwithstanding the potent influence of mixture of races, the constant mingling of blood owing to conquest, slavery, or friendly alliance, all tending toward uniformity of type, the human body is in the highest degree variable. The tendency toward uniformity has produced a well-defined species with varietal differences within the group; but each organ of the body and the proportions of the whole vary to such a degree that the examination of a large series of anthropometric data cannot but cause the investigator to marvel at the continuance of the human type. We now know that the black, white, yellow, and red varieties of the race perfectly intergrade; hence we need not expect by such comparisons as have been made in the preceding paragraphs to discover differences in the various human groups that shall equal those existing between this species and the anthropoids belonging to four separate families.

Even in the size of brain case, the range of normal variation in man is from 900 to 1,800 c.c. while the range from microcephalic idiots to pathologic megalcephalic skulls is from 350 to 3,500 c.c. The range of variations in cranial capacity in a small series of 42 Auvergnat skulls was 676 c.c. The range from the earliest times to the present is inconsiderable and inconclusive. The proportions of the brain case are fairly constant within the tribe but not in the larger divisions of the species: we have long-and-round-headed Caucasians, Mongolians, negroes, and Amerinds, with all possible intermediate forms. In the torsion of the humerus, often cited as a good zoological character separating man from the other animals, the variation is from 164° in Europeans to 134° in Australians, the minimum being at least seven degrees below the average for the gorilla, less than the gap separating the lowest anthropoid from the lower apes and monkeys which, in their turn, are lower than the marsupials and others. Independently of the normal variation in the length of the humerus, the difference between the right and left sides sometimes amounts to 2 cm. The other long bones exhibit a corresponding variability; indeed, the tibia has been termed the most variable long bone in the limbs of man. The thickness of its shaft varies from forty to one hundred per cent. of the antero-posterior diameter and the outline varies from almost a circle through oval, triangular, and quadrangular forms. Physiological causes are supposed to bring about the platycnemid or flattened condition and the retroversion of the head as well as various degrees of curvature of the shaft. Examples of similar variations might be multiplied indefinitely from an examination of other parts of the skeleton and of the other tissues, particularly the muscles, where variation becomes excessive, and we yet continue in our laboratories to record cases of "new muscles."

II. ETHNOLOGY.—The study of the culture of living races furnishes little evidence in favor of our thesis; although it is true that in the Amerindian division the Fuegians, the Seri of the Gulf of California, and perhaps the Botocudo stand out little above the apes. Subsisting mainly upon raw food and manufacturing implements and weapons of the simplest sort they are not industrially much superior to the anthropoid that has learned to preserve the conveniently shaped stone for breaking coconut shells. Among the blacks, the Andamanese, the Veddahs, some Australians,