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# THE ORIGIN OF MAN FROM A BRACHIATING ANTHROPOID STOCK

By Professor WILLIAM K. GREGORY
AMERICAN MUSEUM OF NATURAL HISTORY

## I. A COMPARISON OF THE LIMBS, HANDS AND FEET OF MAN, ANTHROPOID APES AND PRIMITIVE EOCENE MAMMALS[1]

Recent attacks on the "ape-man theory" by Professor Henry Fairfield Osborn have been misinterpreted by many newspaper writers and preachers to mean that what they choose to call the Darwinian hypothesis of man's origin has been demolished by America's foremost paleontologist, so that many now feel that man's anatomical bonds with the apes may safely be ignored or explained away. It is true that in stressing the wide psychical gulf between man and the apes Professor Osborn did not at first explicitly provide his "Pro-Dawn Man" with any assignable ancestors among the lower mammals. But those who prematurely welcomed Professor Osborn to the ranks of the anti-evolutionists seem to have overlooked several striking passages in his recent Des Moines address.[2] Here he definitely states that he is "not ignoring the overwhelming evidence of a remote community [of] origin between man and the anthropoid apes"; and that he is only "combating the special feature of the Lamarck-Darwin hypothesis that man once passed into highly specialized arboreal adaptations attained by the Miocene apes"; finally, he is "inclined to separate the human stock at a geologically earlier pre-Miocene period of anthropoid evolution." Moreover, Professor Osborn's diagram illustrating his "present theory of the ascent and phylogeny of man" agrees in general with my "family tree of man" (1921, 1924),

[1] Based on papers read before the Charlottesville, Virginia, meeting of the American Association of Anatomists and the American Association of Physical Anthropologists, April 18 and 19, 1930.

[2] Science, 71: 1–7, January 3, 1930.

the chief difference being that the point of initial differentiation of man and the anthropoid apes is placed one geologic epoch earlier in his diagram than in mine. Hence that which was often represented in the public press as a revolutionary overturning of the Darwinian hypothesis of man's origin differs only in details from that version of the Lamarck-Darwin theory which has been developed and expounded by Sir Arthur Keith since 1893, by Professor G. Elliot Smith for many years past and by the present speaker since 1916.

A careful study of Professor Osborn's recent papers shows that there are not less than fourteen points in which his theory is in entire accord with that which I am defending. These fourteen points will be discussed in the paper of which this is an abstract. On the whole they will probably arouse far less dissension in the world than did the fourteen points of Professor Osborn's former colleague at Princeton. Certainly they afford a basis for further progress toward agreement, especially since Professor Osborn concedes: (*a*) "the overwhelming evidence of a remote community [of] origin between man and the anthropoid apes"; (*b*) "the strong evidence for an Eocene arboreal stage in our ancestry," and (*c*) that "in the forest remain all the backward, conservative types, while on the plateaus and uplands are found the alert, progressive, forward-looking types." Thus we have made progress toward the conclusion that although man may have been a plateau-living biped for millions of years, his ancestry eventually merges with that of the conservative forest-living, originally arboreal anthropoids.

There are, however, ten remaining points in which Professor Osborn's theory diverges from mine, all of which are discussed in this paper as it will appear in the *American Journal of Physical Anthropology.* Of these, the most fundamental difference is that while admitting the existence of a common ancestral stock from which man and the anthropoid apes are both derived, Professor Osborn eliminates from the human line the "brachiating stage" through which the early anthropoid undoubtedly passed, while Keith, Gregory, Morton and others regard at least a moderate amount of brachiation as an indispensable prerequisite for the assumption of erect bipedal posture on the ground. Brachiation, as first used by Keith, means that method of progression in the trees in which the suspension grasp is employed by the arms, which are held above the head, while the backbone is in general vertical to the plane of progression. One need hardly say that the hind limbs of brachiators are of the grasping type. Other modes of progression are of course employed by the chimpanzee and gorilla when on the ground, and they do not invariably brachiate even when in the trees. Nevertheless they are evidently derived from partly brachiating ancestors, as shown by the construction of their skeletons.

In his Des Moines address referred to above, Professor Osborn did not discuss in detail the great mass of osteological and other anatomical evidence for the descent of man from early brachiating ancestors which has been set forth by Keith, Morton, Gregory, Schultz and others. He merely implied that resemblances of this kind might be due to the independent derivation of man and the anthropoid apes from Eocene mammals with divergent first digit. It is this last suggestion of Professor Osborn's that I desire to consider here.

At one time or another I have examined practically all the known types of hands and feet of Eocene insectivores, carnivores, protoungulates, artiodactyls, perissodactyls, rodents, edentates and primates. Many of these will shortly be described in Professor W. D. Matthew's memoir on the fossil mammals of the Lower Eocene. In all the more primitive representatives of the Eocene groups the hand is pentadactylate with a somewhat fan-shaped radiation of the metacarpals and digits. The thumb is well developed and divergent. The carpus is shallow, the bones in general being more or less widened, except the magnum or capitate, which in the front view is quite small. The centrale is distinct. The ungual phalanges are compressed and doubtless have sharp claws. This general type of hand was probably very near to the basic type for all the placental orders, but it has not taken even the initial steps toward the human type. None of the hands of non-primate mammals of Eocene age therefore offer any evidence in favor of Professor Osborn's suggestion that the human hand may be derived independently of the anthropoid ape type from some primitive Eocene mammal with a more or less divergent thumb.

The generalized primate type of hand was already in existence in Eocene times and had advanced far beyond the generalized placental type described above. In the Eocene lemuroid genus *Notharctus,* elsewhere described by me, the fingers are long and slender, the thumb relatively short but mobile, the capitate or magnum is extended vertically and the carpus decidedly narrow as compared with that of the ordinary Eocene mammal. This was the primary arboreal adaptation of the primate hand in Eocene times, and even in man the hand still abounds in unmistakable tokens of derivation from arboreal ancestors.

If we compare, for example, the skeleton of the hands of man, gorilla and chimpanzee, we shall see that while the hand of man is extremely different from that of the prototypal Eocene mammal, it is extraordinarily close to that of the gorilla in its fundamental features, differing chiefly in the length of the thumb and the shortness of the metacarpals.

Many deep-seated resemblances between man and the gorilla are to be seen in the carpal bones. In both forms the navicular (scaphoid) is placed vertically in a peculiar way so that the articular surface extends from the lunate down past the upper end of the capitate (magnum) to the lesser multangular (trapezoid). Almost every process on the carpal elements of gorilla is represented by a more or less reduced process in man. These processes are better seen in the so-called primitive races, such as Australians and Negroids, than in the more or less reduced, degenerate hands of pen-using white men.

Along with these resemblances between man and gorilla are numerous differences in the carpals of these two forms. Here belong especially the reduction of the pisiform in man, the enlargement of the lesser multangular in the rear view, the reduction of the great processes on the palmar side of the hamate, capitate (magnum), etc. These differences are doubtless associated partly with the fact that the gorilla still uses its hands in locomotion, while in man this function has normally long since been given up.

The persistence of so many and great resemblances notwithstanding the marked differences in locomotor habits between gorilla and man assuredly testify to the arboreal heritage of the human hand. Of all the anthropoids the nearest approach to man in the general construction of the bony hand is made by the gorilla. Now the gorilla, as may be testified from field experience, has not yet given up wholly the brachiating habits of his ancestors. Hence I infer that the strong resemblance in the hand skeleton of gorilla and man supports my contention made on other grounds that the skeleton of man retains many unmistakable souvenirs of a former brachiating stage.

If all these striking resemblances both in the skeleton and the general anatomy between the hand of man and that of the chimpanzee and gorilla are to be ascribed solely to parallelism, then what sort of morphological evidence would ever be accepted as evidence of genetic affinity?

If such degrees of resemblance between man and gorilla held only in the comparison of the hands alone, those who ascribe these resemblances to convergence or parallelism might have a stronger case, but the fact is that similar degrees of resemblance, associated also with differences, may be found in many other parts of the skeleton and soft anatomy.

Since space is lacking for the comparison of many parts of the skeleton of man with those of anthropoid apes and Eocene mammals, I shall deal here only with the humerus and the foot.

The facts show that the humerus of man is incomparably nearer to that of the brachiating chimpanzee than it is to the humeri of relatively primitive quadrupedal mammals of the Eocene. Comparative study shows that the humeri of the primitive Eocene mammals, which so far as known were all quadrupedal either on the ground or in the trees, have a relatively short stout shaft, the so-called supinator crest is large and prominent, there is a large entepicondylar foramen, the deltopectoral crest is flaring and ends above in a large greater tuberosity. In chimpanzee, gorilla and man, on the other hand, the shaft is long and narrow, the supinator crest is vertically elongate and narrow, the entepicondylar foramen is normally absent, the distal trochlea is separated from the capitellum by a prominent edge or ridge. Near the upper end the deltopectoral crest is low and vertically elongate, the bicipital groove is pronounced, the greater tuberosity is much reduced and tends to be paired with the lesser tuberosity, the head is globular and directed more upward and less backward than is the case in the humeri of Eocene quadrupedal mammals. Assuredly no unprejudiced authority, in the face of such cumulative evidence, could ascribe all these resemblances between the humerus of man and those of modern apes to pure parallelism, or still less to convergence. And it may be noted that by reason of his still essentially brachiating type of pectoral girdle, humerus, forearm and hand, man has not wholly lost the ability to brachiate effectively, at least in childhood or after practice and training.

As to the suggestion that the human foot might be derived from a generalized Eocene mammalian type with more or less divergent hallux, we may note that in these primitive Eocene mammalian feet the digits all diverge in a fan-like manner and there is as yet no suggestion of the progressive dichotomy or biramous condition which is so strongly impressed on the feet of all known primates, including those of Eocene times. This fundamentally biramous condition, which was characteristic of all the known families of Eocene primates, shows that even at this remote epoch the order of primates was thoroughly arboreal in habit. Even in man the biramous character of the foot is still so pronounced that it affords one of the clearest possible evidences that man shares with all other primates the primary arboreal heritage, while much the nearest to him in point of foot structure are the brachiating anthropoids.

In conclusion, it may be said again that the available evidence of comparative anatomy and paleontology appears to support the statement that in all the bones of his limbs, hands, feet, pectoral and pelvic girdles man is demonstrably nearer to the brachiating gorilla and the chimpanzee than to the primitive Eocene quadrupeds.

## II. THE IRREVERSIBILITY OF EVOLUTION AND THE ORIGIN OF THE HUMAN FOOT

In his recent papers on the origin of man Professor Osborn has cited Dollo's "law of the irreversibility of evolution" as debarring the whole anthropoid ape group from human ancestry on account of their loss of certain anatomical characters which have been retained by man. No doubt each modern anthropoid has many of these specializations, which should not be looked for in the ancestral common stock of both apes and man. But as to the particular characters which are to be classified under this heading there is considerable diversity of opinion. The object of the present paper is to examine several well-documented cases of the irreversibility of evolution in order to determine whether my previously published views as to the evolution of the human foot and the human dentition are in accord with this principle.

The skulls of titanotheres (extinct hoofed mammals that ranged from the lower Eocene through ascending geologic horizons to the summit of the Lower Oligocene of western North America and then became suddenly extinct) are fully figured in Professor Osborn's recently published monograph on the "Titanotheres." I had the pleasure of twenty years' close association with Professor Osborn in this work and made the measurements which are the basis of the following statements.

In the Lower Eocene the skull of the very primitive titanotheres then existent was elongate and the preorbital part of the face was about 47 per cent. of the basal length of the skull. In the final stage the preorbital length had shortened to 12 per cent. Here then is an example of differential or disharmonic evolution, one part shortening, while another lengthens. Such changes in proportion have been called by Professor Osborn *allometrons*.

During the same period a pair of bony protuberances, the so-called horns, grew out above the orbits, and finally they attained an elevation above the base of the nasal bone equal to 44 per cent. of the basal skull length. Here was an example of an excessive growth concentrated in certain definite spots. Such outgrowths have been called by Professor Osborn *rectigradations*.

In the top view of these same skulls equally interesting changes take place. The earliest skulls are relatively narrow both across the cheek arches and across the parietal region. Thus in the first stage the zygomatic breadth is but 50 per cent. of the basal skull length. In the succeeding stages the skull increases rapidly in absolute length but it also increases still more rapidly in width across the zygomata, so that in the latest stage the width may rise to 87 per cent. of the basal skull length.

Here then a period of rapid widening has supervened upon an earlier period in which the skull was relatively narrow. In one of Dollo's earliest papers on the irreversibility of evolution is figured the skeleton of the foot of an Australian marsupial *Trichosurus,* which may be taken to represent an ancestral stage, already highly adapted to limb-grasping habits, while compared with this is the foot of the gigantic ground-living form *Diprotodon,* the drawing reduced to approximately the same length. It will be seen that notwithstanding the enormous thickening and enlargement of the tarsals and fifth metatarsal in order to support the gigantic weight, the heritage of a former arboreal life is deeply impressed in the peculiar characters of this foot. One may notice, for instance, the divergent position of the great toe, the subequality of digits II and III and the greater length of digit IV as compared with digit III. Digit V, however, has received a great secondary increase in size.

Here then was a capital example of the fact that evolution is irrevocable, that later stages bear in themselves the more or less visible imprint of past adaptations to earlier methods of locomotion. This case likewise clearly instances the disharmonic or differential increase of one part as compared with its neighbor which occurs when an old method of locomotion (namely, tree-climbing) is abandoned and the habit of walking on the ground is assumed.

A fourth instance of the same principle is afforded by the known facts concerning the evolution of the feet of the titanotheres, as set forth in Professor Osborn's monograph. One of his figures[3] shows the forefeet of the earliest and later members of the group drawn to the same scale. It will be seen how massive and broad the gigantic later forms are in comparison with their diminutive narrow-footed ancestors. The upper figure on the same page shows the early, middle and late stages all reduced to the same absolute height. Now in the first stage, compared with other mammals, the foot is already remarkably high and compressed, but then a period of broadening supervenes. The carpal bones become broader and flatter, the metacarpals widen at different rates so that metacarpal IV becomes nearly as wide as metacarpal III, as in the hippopotamus. Meanwhile the phalanges or true digits have suffered a marked shortening, the ungual phalanges being relatively reduced.

Thus we see in these cases that, although evolution

[3] *Op cit.*, p. 801.

is irreversible, or rather irrevocable, the tendency toward length and narrowness, which is very obvious in the earlier forms, becomes masked by a tendency toward broadening, which involves radical alteration in the general pattern of the carpal and metacarpal elements.

During the same period of evolution of the titanotheres there were marked changes in the relative lengths of the various segments of the limbs. As the animals got heavier, they gradually gave up the light springing movements of their gracefully built ancestors and took on elephantine striding movements. This change in method of locomotion was accompanied by a marked alteration in the relative lengths of the different segments of the limbs. The femur became longer, the tibia shorter and the metatarsals much shorter. In brief, there was differential or disharmonic evolution of the relative lengths of the limb segments in adaptation to a new method of locomotion.

Still greater changes in the relative lengths of the various limb segments take place when an animal habituated to one medium begins to invade another. Take, for instance, the evolutionary history of the seals. They are of course an aquatic offshoot of the order Carnivora. Although we do not know, or have not yet recognized, their direct ancestors among the terrestrial mammals of the Eocene epoch, the construction of their brains, skull, dentition, soft anatomy and skeleton indicates that these terrestrial ancestors were placental carnivores with ordinary pentadactyl hands and feet. In the group of sea-lions (Otariidae) as well as in the true seals (Phocidae) the feet have undergone profound modifications which have enabled the animals to become highly efficient swimmers. The first digit of the hand of the sea-lion has become much enlarged; the hind foot has become fan-shaped with enlarged first and fifth digits. In the true seals the hind limbs are permanently extended backward and no longer capable of being drawn forward to support the body on land.

Here then is an example of the differential enlargement of certain digits and the rotation of the hind feet through an arc of 90°. Evolution is doubtless irrevocable, but when a race migrates into a new medium a real transformation of the limbs may ensue.

The ordinary pentadactylate feet of primitive Eocene terrestrial mammals had an evenly radiating or fan-like arrangement of the digits. But when the earliest ancestors of the primates took to the trees this even, fan-like symmetry of the digits of the hind foot was disturbed by the marked enlargement of the hallux and by its wide separation from the other digits. I have elsewhere reviewed the strong evidence tending to show that this biramous arrangement of the hind foot was a primary adaptation in the entire order and that even in man there are many indubitable traces of this condition. Traces of this biramous condition seem to be especially marked in the feet of Veddahs, figured by Paul and Fritz Sarasin.

In 1916 I summarized some of the changes which would be necessary in order to derive the human foot from a gorilloid type (using that term in a wide sense). Professor Schultz, after reviewing the embryological evidence, finds that many of these changes as inferred by me are actually passed through in the embryonic history of the human foot, in spite of the fact that in many other cases the embryonic history does not repeat the phylogenetic history.

The foregoing review of examples of fairly well-documented cases of evolution shows that the transformation of a gorilloid into a human type of foot would require no unusual or unprecedented changes either in degree or in kind.

In the first place, even in such a highly specialized foot as that of man, the old biramous heritage is inescapable, so that we must infer that the binding of the great toe to the others by means of the deep transverse metatarsal ligament is surely a neomorph. As it is evident how far nature can go in pushing a digit into a new position (as when the index finger in the Koala becomes aligned with the thumb), it was surely not difficult for nature to draw the outer toes and the inner toe together and to bring about the moderate twisting of the heads of all the metatarsals that was necessary for a firm stance on the ground. These changes were effected partly also by the differential growth of all the tarsal elements: the three cuneiforms and the cuboid becoming elongate proximo-distally, the talus being displaced on to the dorsum of the arch and the calcaneum assuming a much greater burden and becoming much widened transversely. The extreme reduction of the phalanges is so obvious from a morphological view-point as to require no special emphasis.

In this case the doctrine of the irrevocability of evolution is beautifully illustrated by the obviously gorilloid heritage underlying all these special adaptations to bipedal locomotion on the ground.

### III. Irreversibility and the Human Dentition

The human dentition also abounds in evidence both of the irreversibility of evolution and in traces of the derivation of man from a primitive brachiating ape ancestor of the "dryopithecoid" type. The recent intensive studies of Remane on the incisors, canines and premolars of man have left no reasonable doubt that the small canines of man have been derived by reduction from larger and more ape-like canines or that the simple-rooted lower premolars have been derived from more ape-like conditions. Similarly as to the molars, it has been shown by Gregory and Hellman that the molar patterns of primitive man abound in souvenirs of ape ancestry.

The "*Dryopithecus* pattern" of the lower molars of apes is characterized by the possession of three large cusps on the outer side of the molar, two on the inner side, and five principal grooves, a fovea anterior or precuspidal fossa and a fovea posterior or postcuspidal fossa of Hrdlička. In the molars of the oldest known fossil men this same arrangement of five primary cusps and five principal grooves and two foveæ is incontestably present. In many primitive human molars, however, a sixth cusp is often present. In general, human lower molars are relatively wide and short as compared with anthropoid molars, a period of widening having masked an earlier, more elongate form.

In modernized human molars the *Dryopithecus* pattern is almost completely transformed, chiefly by the reduction of cusp 5 and the loss of the fourth primary groove, so that a plus pattern appears, which at first sight has very little resemblance to the primitive *Dryopithecus* pattern. The plus pattern once acquired also masks the derivation from the *Dryopithecus* pattern. But Dr. Hellman and I have traced so many intermediate stages that the reality of this transformation can be doubted only by those to whom morphological evidence makes no appeal.

In the deciduous molars of man the *Dryopithecus* pattern is fully realized in the second but only very imperfectly foreshadowed in the first. The latter, however, in man is normally much more advanced toward the molar pattern than is the corresponding tooth of the modern anthropoid apes.

In conclusion, the question whether the law of the irreversibility of evolution forbids us to attempt to derive man from a brachiating anthropoid stock allied especially with the chimpanzee and the gorilla may be posed in another way, to wit: Is there, in fact, any known fossil form (other than *Pithecanthropus* and the extinct Hominidæ of Europe) which on the one hand is evidently related to the brachiating stock and on the other hand clearly foreshadows man in many weighty characters?

Photographs of the occlusal surface of the upper and lower deciduous teeth and first permanent molars of *Australopithecus* have been received through the kindness of Professor Raymond A. Dart. This interesting fossil anthropoid from Bechuanaland was described in 1925 by Professor Dart, who has recently succeeded in separating the lower from the upper teeth. It is by his express permission that I am enabled to discuss these photographs. The first permanent lower molar has the complete *Dryopithecus* pattern, together with the sixth cusp so often found in man. The tooth is relatively wider and more human than in any fossil or recent anthropoid known to me. The first deciduous premolar is submolariform as in man and not compressed and premolariform as in the chimpanzee and the gorilla.

The upper dental arch of the same form is even more suggestive of primitive human conditions. Space is not available here for a detailed discussion of this highly significant fossil, but it may be sufficient to state that, after a very careful comparative examination, Dr. Milo Hellman and I have compiled a table of resemblances and differences which may be summarized as follows:

DISTRIBUTION OF *Australopithecus* DENTAL CHARACTERS

| | |
|---|---|
| Nearer to chimpanzee | 0 |
| Nearer to gorilla | 2 |
| Nearer to chimpanzee and gorilla | 1 |
| Common to chimpanzee, gorilla, *Australopithecus* and primitive man | 3 |
| Transitional to, or nearer to primitive man | 20 |
| Total | 26 |

A few points of resemblance to the orang are associated with important differences, which indicate that, on the anthropoid side, *Australopithecus* is related to the African rather than the Asiatic genera.

Now in the light of all this additional evidence, if *Australopithecus* is not literally a missing link between an older dryopithecoid group and primitive man, what conceivable combination of ape and human characters would ever be admitted as such?

Evolution is truly irreversible, but its direction can and does change. The facts set forth in many papers seem to warrant the inference that in the remote predecessors of man nature for a long period seemed bent on breeding better and better brachiators. The orang and the gibbon are her most finished products in this direction. But before completing the experiment she segregated some of the more conservative brachiators, turned them out of their forest home and started their evolution in a new direction, that of upright walking on hard ground. *Australopithecus*, to judge from its skull and dental characters, was a pioneer in the new line, as held from the first by Dart.