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THE TREND OF HUMAN EVOLUTION

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ACCELERATION AND DECELERATION IN THE RATES OF EVOLUTION

In his book, "Tempo and Mode of Evolution," G. G. Simpson states (p. 125) that while most phyletic lines evolve regularly at rates more or less comparable to those of their allies, some lines seem to evolve with exceptional rapidity while others change so slowly that they hardly seem to be evolving at all. The simultaneous occurrence in the recent fauna of generalized lemuroids, specialized and aberrant lemuroids, and many monkeys, few apes, and the unique species of man can be explained, according to the author, only by the postulate that the more primitive lemurs evolved more slowly, and apes and man more rapidly, than the average rate for primates.

There are very good examples for such differences in the rates of development of monkeys, apes and man despite the scarce fossil material available in the higher primate groups. In Locality I of Choukoutien, for example, several skulls of macaques have been recovered which differ only in size and robustness from macaques living today in North and West China (*Pithecus tibetanus* and *Pithecus lasiotis*). This fossil macaque, described by C. C. Young as *Macacus robustus,* because robustness is its only characteristic feature, was contemporaneous with *Sinanthropus pekinensis* and shared its habitat with him. Nevertheless, except for a relatively slight reduction in size and robustness, the macaque does not present any change in the basic character of its essential features over a period of about 500,000 years, while Sinanthropus, as an early hominid type, underwent great changes during the same period. So we have an almost complete standstill in one case and rapid development in the other. It seems very likely that orangutan and Pithecanthropus contrast in the same way. Except for the size of the teeth, the fossil orangutan from South China and Java scarcely differs from the living orangutan while Pithecanthropus changed in almost every detail during the same period, retaining only his general human character.

Another example which could be interpreted as a standstill in evolution is the case of *Paidopithex rhenanus. Paidopithex rhenanus,* represented by a well preserved femur, is a fossil primate from the Lower Pliocene of the valley of the Rhine. Its general form, proportions, and every detail are identical with those of the femur of recent *Hylobates* (gibbons) of South Asia and Indonesia, the only differences being the size of the *Paidopithex* femur which is much larger

than that of any living *Hylobates*. This fact proves that a typical gibbon, already specialized, had evolved in the Tertiary without, in the meantime, changing its essential morphological character.

Even modern man himself would seem to have stopped his evolution at the beginning of the Pleistocene if the fragmentary braincases of Piltdown (England) and Kanam (East Africa), which show all the morphological characteristics of modern human skulls, really belong to the geological horizons from which they have been taken. This would mean that the modern type of man discontinued evolution for a period of at least five hundred thousand or even a million years. If a change of environment could be responsible for discontinuation or reassumption of evolutionary courses, as many people claim, then it must be presumed that the environmental conditions in England and East Africa, so far as man is concerned, were the same during the whole Pleistocene period, which is certainly not true. In addition, such a spatially limited standstill in human evolution is even less probable since incontestable facts prove that human evolution did proceed relatively rapidly at the same time in other regions (China and Java) although the environments cannot have differed essentially from those in East Africa.

People who believe in such an early appearance of the modern type of man always use the same means to invalidate facts contrary to their theory. Since the first human fossil came to light there have been claims that forms which were more primitive but geologically more recent than more advanced forms living earlier, have stopped evolution forever. For this reason they have to be assigned to another human "species" or "genus" than the unknown one which led to modern man. Such fossils are interpreted as remainders of long extinguished forms, natural experiments that failed.

If this were true, no essay on the trend of human evolution could be written. However, as more fossil material comes to light it becomes more and more evident that each morphological feature characteristic of modern man can be traced back to fossil forms to which recognition as human ancestors had been denied by somebody. This tracing leads to earlier stages whose specificities get more and more lost by merging into a "generalized" simian pattern. In addition, none of these features is independent. All are closely correlated, irrespective of the evolutionary stage in which they are observed. The maintenance of their correlation proves that any change of any individual feature must depend on changes in other features. It is just this persistence that makes the tracing possible. Were specific features nothing but accumulations of structural peculiarities varying at random in each stage without keeping to their original correlations, no evolutionary trend would be recognizable.

Specialization and Correlation

Human evolution is specialization. If modes of evolution exist in which no specialization takes place, man does not belong to such a category. Therefore the trend of man's evolution is determinable if the type of his specialization is known and can be traced back to its first manifestation. The organization of the human body, and the static and dynamic conditions to which the whole body and its individual parts are subjected, are better known than those of any other creature. This knowledge permits recognition of the function of every structure and the effect that eventual changes in one structure may have on all the others to which this structure is correlated. Any organization whatsoever can work only if all parts of which it is composed are adapted to each other and cooperate harmoniously.

The fundamental specialization by which man differs from any other mammal, and particularly from those which come closest to his own organization, is the perfectly erect position and the complete release of the forelimbs from use

in the locomotion of the body. "Bipeds" occur in fossil and living reptiles, birds and mammals. In the first two classes, however, upright posture is confined to the prepelvian part of the skeleton, while in all cases the pelvis itself and the hind limbs retain their original quadruped orientation and corresponding structural peculiarities. In some primates, upright stance and gait, with or without auxiliary support of the forelimbs, have been achieved. But in man alone the heels rest on the ground; the legs are stretched in hip and knee joints to the maximum extent; the pelvis is tilted forward; the vertebral column is curved alternately forward and backward; and finally the skull rests with the center of the base on top of the spine (figure 1c).

A perpendicular dropped from the vertex of the head when the body is in a relaxed posture runs through approximately the atlanto-occipital joint, passes tangentially the cervical and lumbar convexities of the spine and goes nearly through the hip joints and the knee and ankle joints. In a forced extension of the whole body it runs through the spine and all the joints mentioned. In addition, the legs are adduced to the midline so that knees and ankles touch each other. In such a posture the center of gravity is placed within the perpendicular near the promontory of the pelvis, and the weight of the body is carried in equilibrium by the pelvis and the legs. By this arrangement the least possible muscular energy is required to keep the body in balance, and the tension of fasciae and ligaments is used to substitute for muscle action. In the semi-erect position of dinosaurs, birds and kangaroos a similar principle has been applied by ossification of the tendons of the dorsal muscles of the trunk and of the leg. None of the anthropoids, apes or monkeys is capable of

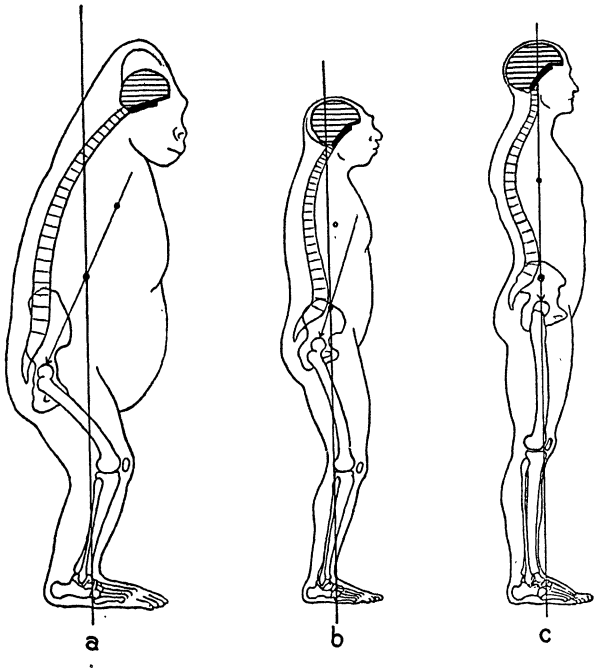

FIG. 1. Gorilla (a), Neanderthal Man—La Chapelle-aux-Saints (b), modern man (c) in erect position. After J. Dudley Morton (the human foot, 1935).

The axes and the location of the center of gravity are indicated. Situation of cranial cavity and base of braincase roughly indicated after F. Weidenreich.

taking the same posture as man. The construction of the individual bones of their skeletons, their proportions and their arrangement, have not entirely lost the original quadrupedal character (fig. 1a).

Practically all individual bones of the human skeleton give evidence of their adaptation to the special statics and dynamics of upright posture. Even minute details may owe their shaping to these factors. Foot bones as well as cranial bones are built in accordance with the particular requirements of their location and function. In the vertebral column, not only the form of the body of the vertebrae but also the direction of their articular facets and that of their neural spines, depend entirely on the place the respective vertebrae occupy in the carrying system of the trunk. For thirty-five years I have studied the human skeleton in order to find out how far form and features of the individual bones answer to the special requirements of the erect position. I studied the pelvis (1913), the foot and the lower extremities (1921/1922), hand and foot (1931), the spine and the skull (1924), and the general effect of muscular action on the skeleton (1922). The result of these studies is the conclusion that the shaping of each of even the simplest units of the human skeleton depends upon that of other units, that is to say, that all are strictly correlated and fit perfectly with the special organization of the body.

Most of my contributions to the problem of correlation and adaptation have been ignored, even by authors dealing with the same question, perhaps because they were written in German, but certainly also because the time had not yet come for an approach to the problem of evolution from the functional side. Considerations that were suspected as "Lamarckian" were banned. Nevertheless, only the functional approach to morphological problems will lead to the understanding of specific forms such as those of man, and their changes in the course of evolution. All those interested in studies of this kind are referred to a paper recently published by the Dutch author, E. J. Slijper. In this investigation, the author deals with the vertebral column and the spinal musculature of mammals, and shows conclusively that their specific form depends entirely on the special static and dynamic requirements of locomotion.

Since completely erect posture represents the specialization typical of modern man, and all skeletal bones are correlated and adapted to that position, any basic deviation from the stance and gait of the type must become manifest by differences in the construction and form of the individual bones. In other words, if man has derived from a primate whose physical organization was genuinely that of a quadruped, man's forerunners, wherever and whenever they may have lived, must display quadrupedal characteristics of the skeleton. The more remote they are from the most recent—most adapted—form, the more they will show them, or the other way round: the quadrupedal characteristics must be more obscure and the bipedal ones more obvious the closer the forerunners come to the modern human type. If the gradual changes of these characters can be determined, one way or the other, the trend of phylogenetic evolution of man will be evident by mere comparison. Nothing is known so far about those earliest phases in which features, recognizable without any doubt as "human" in character, are dawning. All that has been written about, and all the names given those hypothetical archetypes, are nothing but phantoms construed from deductions from the anatomy of present man and his immediate predecessors. Living and fossil human forms must have retained some structures of the most "primitive" primates, but the correct phylogenetic interpretation of these traces depends on the recognition of the character of their functional changes.

1. *Extremities and trunk*

The foot is that part of the human skeleton whose structural details should give the most reliable information of its original appearance before it was adapted to an erect position. The arrangement of the tarsal and metatarsal bones and their forms are still those of a five pronged instrument constructed for grasping and keeping objects in its grip, like a hand. This is the functional meaning of the longitudinal and transversal arches of the foot and the decrease in length of the metatarsal and phalangeal rays. The human foot still possesses all the muscles necessary to spread and flex the toes and abduct or adduct the hallux despite the loss of their ability to act in this way. In addition, although all the original foot joints are still functioning, their mobility has been greatly restricted or arrested. At the same time, the muscles have been replaced in part by ligaments and fasciae wherever the static and dynamic conditions allow for such a substitution. In this way, a restricted mobility but a greater stability, and, above all, elasticity, have been achieved. These are exactly the prerequisites for securing the support of the body on such a small base as the human foot offers in bipedal stance and gait.

As the center of gravity shifts backward (cf. fig. 1a and c), a result of the adoption of the erect posture, the heel bone is pressed down to the ground and strengthened in its new task by a substantial increase in height and a broadening of its base, the *tuber calcanei,* to enable it to carry the body weight. Thus the tuber, and only the human tuber, has developed an accessory process on its lateral side—*processus lateralis tuberis calcanei.* In none of the anthropoids, not even in the mighty gorilla, does such a process exist, the tuber being represented here only by a medial process (Weidenreich, 1921/22, 1940). The relatively late acquisition of the lateral process follows from the fact that not even in living man are the two structures merged into one but may remain more or less separated. Unfortunately, the position of the lateral process and its relation to the medial one cannot be checked in fossil man. Only two or three heel bones have been recovered with the region in question preserved. They belong, however, to late Neanderthal phases or to fossil neoanthropic man,[1] and for this reason do not differ essentially from those of modern Australians in which the lateral process is occasionally completely isolated.

The precise evolutionary phase in which man lost the grasping (climbing) character of his foot is a matter of speculation. Probably it happened at a very early period. Such an early dating can also be inferred from the state of other bones of the lower extremities. Although the material on hand is very scanty, and foot and hip bones are missing in all Archanthropines,[1] the character of the two tibiae of *Homo soloensis* and of several fragmentary femora of Sinanthropus prove that these types had passed the climbing and quadrupedal stage of locomotion long ago. They all exhibit structures characteristic of a creature walking erect. Neither in their proportions nor in any other peculiarity of their extremities have they retained any clear simian feature. It is true the limb bones differ from the standard type of modern man in some minor details, but the deviations are not of a kind to exclude erect position. Therefore, Eugène Dubois, who gave Pithecanthropus the surname *"erectus,"* may have been right although it still remains doubtful whether the Trinil femur is typical of Pithecanthropus and may not be the femur of a more advanced human form which was accidentally de-

[1] The term "neoanthropic" man is used for the modern human form. "Paleoanthropic" man means the immediately preceding group of fossil man, the Neanderthalians and corresponding groups. The term "archanthropic" man comprehends all the forms of early hominids who precede the Paleoanthropines (cf. Weidenreich, 1946).

posited at the same site as the skull fragment.

The only hip bones and vertebrae known are those of Paleoanthropines.[2] The former show the usual neoanthropic pattern indicating that the pelvis must have been subjected to the static and dynamic conditions of erect position for a long period of time. Regarding the vertebral column, the best known is that of the man of La Chapelle-aux-Saints, described and reconstructed by M. Boule. As the special features of the individual vertebrae which indicate the degree of the cervical and lumbar curvatures of the column (see above) show no essential deviations, Boule modeled the column after the general modern pattern. But, since he found some of these features of the individual vertebrae less pronounced than they are in the majority of human individuals of today, he bent the model column slightly forward (fig. 1b). I do not believe that Boule's reconstruction is representative of all Neanderthalians. Indeed, McCown and Keith state with regard to the lumbar curvature of the Mount Carmel population: "Our evidence points to this curvature being developed at least to the extent found in modern native races." Boule, however, may be right so far as the posture of the skull is concerned. Size, length and direction of the neural spines of the cervical vertebrae suggest that the muscles attached to them may have been considerably stronger than those of neoanthropic man. The formation of the nuchal region of the archanthropine skull lends strong support to such a suggestion. Early man was certainly bull-necked.

The character of the bones of the upper extremity of Archanthropines and Paleoanthropines fits in well with that of the lower extremity. Humerus, clavicle and one wrist bone of Sinanthropus, the only upper extremity bones of Archanthropines preserved, completely conform to those of neoanthropic man in form and proportions, and the same is true of the upper extremity bones of the Neanderthalians. It may be that these bones are a little longer in proportion to the leg bones but they certainly do not fall outside of the limits of normal variation found in modern man.

To summarize what we know of the skeleton of trunk and extremities of fossil man, all specimens display a neoanthropic pattern; therefore it can be taken for granted that man achieved upright position as soon as he became morphologically discernible as man. The long bones of the lower extremity are much more robust in the earlier stages than in any of the neoanthropic forms. The femur of Sinanthropus, although not exceeding that of the neoanthropic type in circumference, excels in the thickness of its compacta and a corresponding narrowness of the medullary canal. These properties are indications of a greater massiveness of the skeleton of early man. We will return to this question later.

2. *The skull*

The only skeletal part of early man that does not show the same degree of adapta-

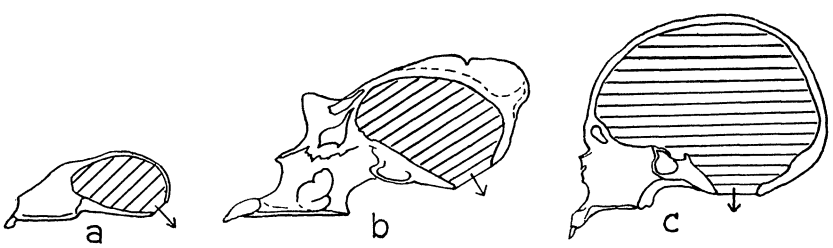

FIG. 2. Mid-sagittal sections through the skulls of lemur (a), gorilla (b), and modern man (c), showing the differences in the topographical orientation of braincase and face. In part after W. L. H. Duckworth.

tion to upright position as do trunk and extremity bones is the skull. Among the primates the skull of the lemurs comes closest to the original quadrupedal mammalian type (figs. 2 and 3a). The two main constituents of the skull, the braincase and the face, are arranged in a straight horizontal line so that the snout (upper and lower jaws) is in front and the braincase continues into the spine in the rear. The change in the manner of locomotion and the adaptation of the skull to the erect position require a fundamental alteration in the primary topographical arrangement of the two constituents of the skull. If the spine passes from a horizontal orientation to a vertical one, and the skull joins in this movement without abandoning its original connection with the spine, the face would be placed on top of the skull and the eyes would look upward. Of course such a twisted posture could be corrected by bowing the head to such an extent that the longitudinal axis of the skull would form a right angle with the longitudinal axis of the spine. Such a position, however, would consume the total range of mobility of the atlanto-occipital joint. Nature used another way of adaptation. The base of the skull itself has been deflected to maintain the connection between the occipital part of the braincase and the spine. The rest has been brought into a horizontal line and the face reduced in size and length to such an extent that it could be lodged almost entirely beneath the deflected front part of the braincase (figs. 2 and 3c; 5).

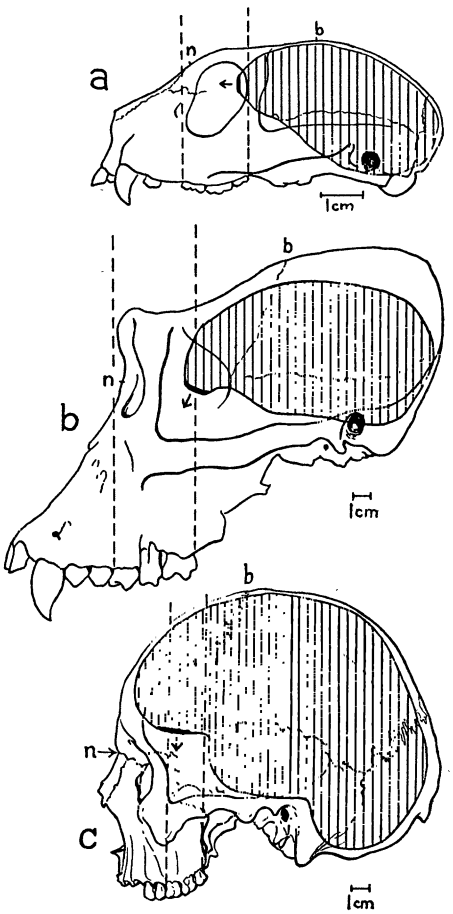

FIG. 3. Skull of lemur (a), gorilla (b), and modern man (c), in lateral view, showing the differences in the topographical orientation of braincase and face and in the orientation, size and form of the brain (cranial cavity shaded). The different directions of the olfactory nerves (lamina cribrosa) are indicated by arrows. b—bregma, n—nasion.

The original quadrupedal character of the skull must have been lost long before the human stage was reached. In monkeys and apes the frontal pole of the braincase has already been raised and overlaps the rear parts of the facial skeleton (figs. 2 and 3b). This slanted position of the braincase corresponds to the semi-erect posture of the trunk. All the known skulls of the Archanthropines have already passed this simian stage. Only the foremost parts of the eyesockets are still thrust beyond the frontal pole of the braincase. The vigorously strengthened upper margins of the "exposed" eye sockets—*tori supraorbitales*—one of the most conspicuous features of this phylogenetic stage of human evolution (fig. 4b), and a slight "facial prognathism," are all that has been left from the protruding snout of the simian stage.

The base has not reached its maximum deflection in either the Archanthropines nor in the classic Neanderthalians. The deflection is only completed in neoan-

thropic man. The form of the original human braincase, such as is typical of the Archanthropines, is comparable to a flat, oblong, loaf-like body. Its neoanthropic form is more globular. The transformation looks like a "rolling-up," that is to say, the flat, loaf-like braincase bends around a transverse axis which runs approximately through the mandibular joints of both sides. In this way the frontal and occipital poles move closer together, resulting in the reduction of the length of the base and the lifting high up of the apex of the curvature (fig. 5). All individual cranial bones undergo corresponding changes in their proportions, forms and topographical relations. The base of the temporal bone, situated in the center of this "movement," is the most affected in all its details. As long as the braincase is stretched and flat, the temporal base occupies a greater area between the sphenoid and occipital bones. When the skull is rolled up, the whole basilar part of the temporal bone is jammed between the adjoining bones and at the same time is pushed up into the cranial cavity. The characteristic changes which the individual portions of the temporal bones undergo as a result of this process have been described in an earlier paper (1943). Their state can serve as a standard for the degree of transformation at-

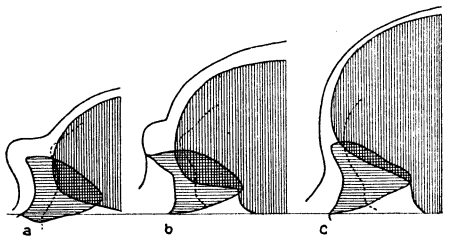

FIG. 4. The topographical relation between orbit and cranial cavity in chimpanzee (a), Sinanthropus (b), and modern man (c). The brain (vertically lines) expands forward and overlaps the orbit (horizontal lines). The supraorbitals disappear correspondingly.

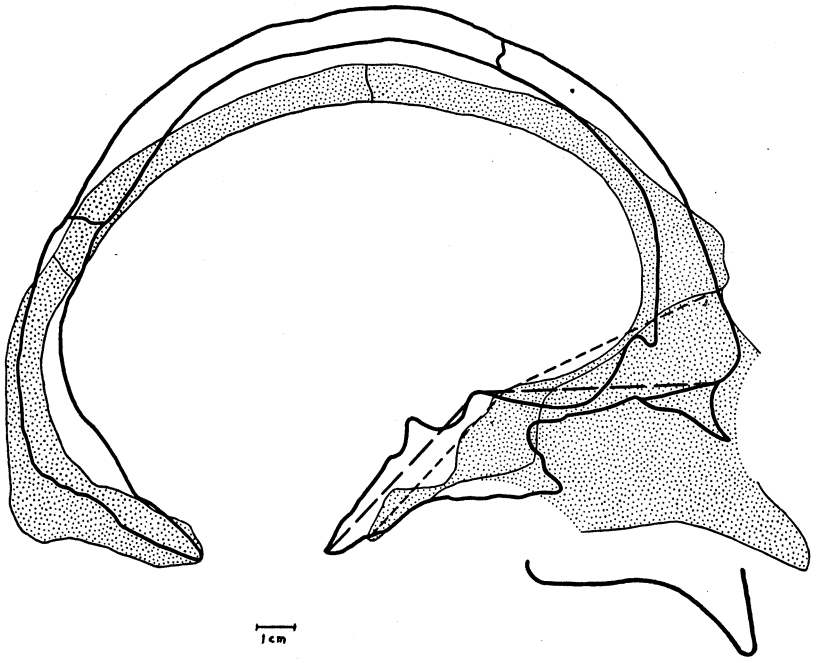

FIG. 5. Mid-sagittal diagrams of the skulls of *Homo soloensis* Skull XI (stippled) and modern man—Tasmanian (heavy lines), showing the differences in the deflection of the base (indicated by interrupted lines), the shortening of the base and the vertex elevation of modern man. The face of Sinanthropus has been substituted for the missing face of *Homo soloensis*.

tained by the skull and, consequently, as a clue for the classification of the type.

Concomitant with the transformation of the braincase, the face recedes beneath it (figs. 2, 3c and 5). The mighty supraorbitals disintegrate correspondingly (fig. 4c) until nothing is left but a faint swelling at the medial part of the eyebrow region—the superciliary ridge. The facial "prognathism" becomes further reduced to "orthognathism" and "hyperorthognathism," and the cheeks appear correspondingly more "sunken." The nasal bridge, the anterior nasal spine, and the chin, jut out from the profile as the remaining foremost landmarks of the otherwise shrunken face.

3. *Dentition*

Almost all the alterations of the dentition in the course of the phylogenetic evolution of man can be regarded as a consequence of the reduction of the face and of its adaptation to the upright position. The dentition of the earliest hominids differs from that of the anthropoids, living or fossil—with the exception of the Australopithecinae—by having no tusk-like canines and no sectorial-typed first lower premolars. But they agree with them in the general pattern of the lower molars. They agree, furthermore, with the gorilla, but not with the orangutan and chimpanzee, in having small incisors but large molars. Crown and roots of the Archanthropine teeth, especially those of the giant forms, far exceed in size those of neoanthropic man. Reduction is already apparent in the Paleoanthropines. The shortening of the jaws necessitates a shortening of the entire row of molars and a shortening of individual teeth; the last of the row, the third molar, being particularly affected, becoming smaller in all dimensions. In the paleoanthropine Heidelberg jaw this molar is already reduced to an extent characteristic of modern man. In the other teeth the shortening of the length results in a relative increase in height. The reduction of the crown pattern appears as a progressive simplification with the number of the molar cusps decreasing and the originally complicated wrinkle system becoming ironed out. In modern man the third molar tends to disappear entirely. In many cases its eruption is delayed or never occurs, or the tooth does not develop at all. Exactly the same process takes place in the dog. Dwarf dogs, compared with large dogs, have undergone a remarkable reduction of the molars in number, size and details of their pattern (simplification); the reduction of the teeth here goes hand in hand with the reduction of the jaw and the transformation of the braincase in the wake of the relative enlargement of the brain (Weidenreich, 1941).

4. *Robustness of the bones*

Two of the most typical features of the cranial bones of early man is their thickness and massiveness (Weidenreich, 1942, 1947). These qualities are not confined to the bones which build the walls of the cranial cavity but include the whole facial skeleton. The thickness and massiveness is chiefly due to the thickening of the outer and inner tables of the cranial bones, while the mass of spongy substance between (diploë) is small in comparison with the condition in modern man. In the lower jaw of Meganthropus the density of the enormously thickened compacta layers looks almost like an eburnation. The mass of the supraorbitals, however, consists mainly of dense spongious substance. The cranial bones of the Archanthropines exceed by far those of all known Paleoanthropines in thickness and massiveness. Meganthropus, *Pithecanthropus robustus* and *Homo soloensis* top the list for robustness, *Pithecanthropus erectus* and Sinanthropus follow. The extraordinary robustness of all these different early types—evidently still surpassed by the cranial bones of Gigantopithecus of which only some of the teeth are known—suggests that this robustness is not an accidental variation but represents a general character of earliest homi-

nids. The shafts of the femur of Sinanthropus and the tibia of *Homo soloensis* indicate that it was not confined to the bones of the skull but may also have affected the extremities. This type of robustness does not show in living anthropoids nor in any other living primate but there is some indication that it may have occurred in certain fossil primate forms (Australopithecinae, Dryopithecus). Although it is not yet possible to tell from whom the hominids inherited this special feature, what happened to it in the course of subsequent phylogenetic evolution can be described. A tendency toward reduction has already set in within the Archanthropine group itself, as *Pithecanthropus erectus* and Sinanthropus reveal. The clumsiness of the Rhodesian skull, the Heidelberg jaw, the general thickness of the Neanderthalian skulls and the robustness of their femora demonstrate that the old Archanthropine feature in question is still recognizable although it has lost much of its original character. The reduction continues even in neoanthropic man: it is less in upper Paleolithic man than in recent man, less in "primitive" races than in more "advanced" ones of present mankind. In the temporal bone the reduction generally reaches a high degree: the apex region of the pyramid appears eroded and a wide *"foramen lacerum"* takes its place; the tympanic bone, which is a thick plate in Archanthropines, is almost paper thin and not infrequently even perforated (Huschke's foramen). But the original thickness of the bone seems to be preserved in some special places. I interpret the so-called ear exostoses at the entrance of the *meatus acusticus externus* as such relics. The *tori mandibularis* and *palatinus* may be interpreted in the same way.

Another phenomenon, very characteristic of the Archanthropines, which may have some connection with the robustness of the cranial bones, is the early closure of the sutures. In all the Archanthropines the main sutures are ossified and in most specimens fused to such an extent that they are scarcely recognizable from either inside or outside. Under similar conditions in modern man, the cranial sutures are either open or just at the beginning of fusion. Complete ossification of the cranial sutures, even their entire disappearance at an early stage, is typical of anthropoids.

5. *The brain*

It follows from all the recorded facts that the adoption of upright position and the correlated adaptation of all skeletal parts is the fundamental specialization of man. There is, however, a second one seemingly partially correlated to the first but surpassing it in significance. This is the enlargement and differentiation of the brain. However, the trend toward the expansion of the brain, particularly the pallium, in the course of evolution is not a privilege of man or the primates. It is a characteristic feature of many mammals and also apparent in reptiles and birds. As early as 1876, O. C. Marsh made the following statements: (1) All mammals at the beginning of the Tertiary had small brains; (2) the size of the brain gradually increased during the Tertiary period; (3) this increase was confined mainly to the cerebral hemispheres . . . ; (4) in some groups the convolutions of the brain have gradually become more complex; (5) there is some evidence that the same general law of brain growth holds good for birds and reptiles from the Cretaceous to the present time. The paleontological facts which have come to light in the meantime have largely corroborated the truth of Marsh's theses. However, the mere increase in size is not that specialization of the human brain upon which all physical development and achievement depend. All attempts to read the degree of mental efficiency from morphologically recognizable features such as size or form of the brain or of its lobes or of the convolutions, have failed. It can only be said that a certain amount of brain substance is necessary for normal psychical functioning.

Anthropoids with a maximum cranium capacity of 650 cc. behave like apes and a living adult human being with no more brain may operate its vegetative system but is an idiot. Pithecanthropus, the most primitive human form whose brain size can be calculated, has a cranial capacity of 775 cc. (Skull II). Provided that mental faculties are only a matter of the amount of brain mass, the doorstep to humanity would be passed if the cranial capacity lies between 650 cc. and 750 cc. On the other hand, the maximum brain size attained by a fossil non-neoanthropic hominid is 1620 cc. (Man of La Chapelle-aux-Saints). However, this increase of about 900 cc., tantamount to the size of the Pithecanthropus brain, cannot be taken as a measure of man's cerebral specialization or progress in phylogenetic development. For among adult neoanthropic men with normally functioning brains, the cranial capacity ranges from about 900 cc. to 2000 cc. Nobody has ever been able to tell which internal structures of the brain allow a margin of half of the possible total amount for normal or even supernormal functions. The list of "elite" brains includes famous personalities whose brain mass or cranial capacity ranges from 1100 cc. to over 2000 cc. There is a certain relation between brain size and body size; tall individuals may have larger brains than small individuals, yet small individuals may also have relatively large brains. However, these differences are minimal when compared with the normal fluctuations of brain size and can, therefore, be disregarded. In addition to all this, there are no data which prove incontestably that the human brain gained in average size between the paleoanthropic and neoanthropic phases. The most reliable figures available indicate instead a slight decrease.

All these discrepancies are easier to understand if it is realized that operation and regulation of the vegetative system of the human body require a very small amount of brain substance, as the brains of idiots indicate. Adult idiots may do it with not more than 350 cc. The brain substance exceeding this amount seems, therefore, available for psychical functions. These functions have their main seat in the cells of the cerebral cortex and in the fiber systems. To my knowledge, however, no investigation has ever been made to find out whether there is a constant relation between the total size of the brain or that of the pallium, and the efficiency of the cortex and fiber systems, and if not, how the brain can fulfill all its mental potentialities whether it weighs 1100 gr. or 2000 gr.

In any case, the latest phase of specialization of the human brain must take place in the cortex and be independent of the actual size of the brain and, consequently, also of that of the braincase. The main morphologically recognizable difference between the brain of Archanthropines and the brain of Paleoanthropines is the greater fullness of the latter (Weidenreich, 1947). All parts of the pallium have a share in the enlargement, the four lobes in almost equal proportions. But there is no change in the general form. All the brains of the evolutionary stages preceding the stage of modern man are flat and show no vertex elevation irrespective of their absolute length or their vertical diameter, the latter rising from 95 mm. in Pithecanthropus II to 116 mm. in La Chapelle-aux-Saints.

A characteristic change of the brain occurs, however, before the definite stage of neoanthropic man has been reached. Its vertex rises to a hump-like elevation while its total length shortens. This is the result of the "rolling up" of the braincase, the deflection of the base, and the final adaptation to upright position as has been described above (cf. fig. 5). But there seems to be no direct correlation between the increase of the cortex differentiations and the special shaping of the brain. Neither is the growing fissuration of the pallium correlated to it. This phenomenon is a part of the general expansion of the brain in the course of evolution and accordingly takes place in most mam-

malian orders. The folding process of the cerebral surface first produces the main divisions, the lobes, and then the subdivisions, the convolutions. In primates the increase of the fissuration keeps pace with the advancing general organization of the subgroups and so complements the expansion of the pallium in cases in which the space for the expansion of the braincase itself is limited. Among the primates, man has the most expanded brain, the most developed and complicated fissuration and, in accordance therewith, the most highly differentiated cortex structures.

But man exceeds all vertebrates including the primates in another feature which so far has escaped attention. Man has the smallest spinal cord in proportion to the size of the brain. In the course of evolution the human brain has "swallowed" the spinal cord, that is, it took over the functions of the latter more and more, bringing the reflex actions under the control of consciousness and will. Unfortunately, the gradual diminution of the cord cannot be tested in fossil man for the vertebral column is missing or does not permit calculations of the volume of the vertebral canal. But in living anthropoids the cord is clearly greater in proportion to the size of the brain than in man.

The transformation of the skull

The transformation of the human skull in the course of evolution follows a very definite line to which all essential structures hold, even in minute details. Not a single fossil human type has come to light which shows any indication of deviation from this line. Irrespective of the site from which the specimens were recovered or to what geological period they may be attributed, all exhibit the characteristics of the respective features either of the earliest stages or those of later or latest ones, the latter with the typical signs of disintegration of the original pattern. Dozens of examples can be given, but for want of space only one of the most conspicuous features, the *supraorbital tori* have been selected. As I have shown earlier (1939, 1943) these structures are the front part of a reinforcement system which originally runs around the braincase at its greatest circumference, the *occipital torus* representing its rear portion. In modern man the *supraorbital tori* have almost entirely disintegrated, a small swelling at the medial ends of the eyebrows is all that is left. What the tori looked like at the very dawn of mankind is unknown, but we may not be too far afield in suggesting that their formation was similar to those of the living gorilla (fig. 6a): a strong, exceedingly protruding and continuous bar crossing the forehead at its base along the margins of the orbits. Their lateral ends jut far out while behind them the braincase shows the characteristic postorbital constriction. Viewed from above, the bar exhibits a distinct forward directed convexity. In the Archanthropines (figs. 6b, c, d) the front contour differs from that of the gorilla (a) by forming an almost straight line and having the lateral ends considerably thickened. But *Homo soloensis* (d) already indicates the beginning of the disintegration of the torus by breaking its continuity into two separate portions, a process which is in full swing in the Paleoanthropines (e, f). At the same time, the tori shrink and their ends bend backward to conform more and more to the rounded front contours of the braincase proper (see also fig. 4c). The postorbital constriction disappears to the same degree. The disintegration is completed in the final stage of neoanthropic man.

Nothing can better prove the unity of the hominid type than the study of gradual changes of features such as this one. People who deny the unity and imagine that *Homo sapiens* did not derive from a Neanderthalian or Sinanthropus type and that, therefore, features like his superciliary ridge are not necessarily relics of the supraorbital tori of earlier hominids but may be a newly developed ornament, are not sufficiently acquainted with comparative anatomy. Figure 6 also gives two ex-

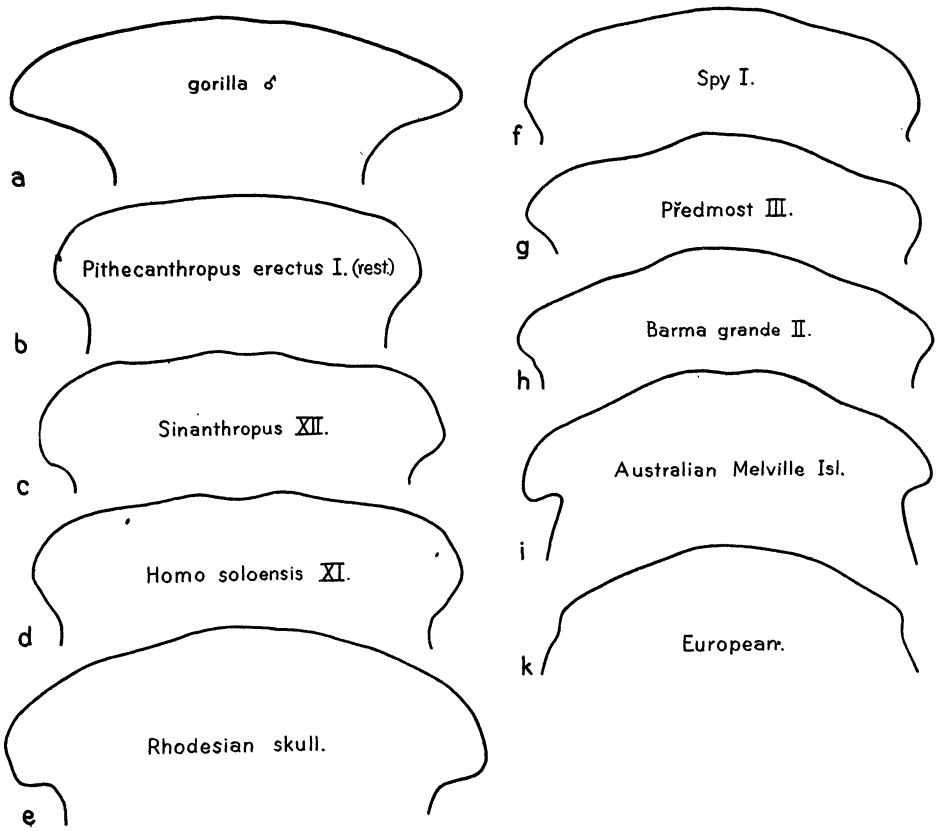

FIG. 6. The gradual disintegration and disappearance of the supraorbital tori in the course of human evolution. The tori viewed from above.

amples of Upper Paleolithic *Homo sapiens,* the Předmost Skull II (g) and the Barma grande Skull II (h). As all the features of these forms show, they are morphologically intermediate between the Paleoanthropines and living man. Despite all protests, negations or incredulity, none of the sceptics has been able to produce conclusive anatomical or biological evidence of specialization in any fossil hominid which would not fit the scheme of human specialization described and would lead definitely away from the established line of human evolution.

Figure 6 illustrates, in addition, another phenomenon characteristic of human evolution. The skulls depicted, Rhodesian (e) and Australian aborigine of today (i), show an extraordinary development of the supraorbital tori in the first case, and its equivalent, the superciliary ridges, in the second case. They contrast strikingly with other representatives of the phylogenetic groups to which they must be attributed on account of the character of other features they exhibit. The supraorbitals of the Rhodesian surpass in heaviness even those of some of the Archanthropines, nevertheless the curvature of the front contour conforms to that of the Paleoanthropines to which the skull belongs morphologically. In the Australian skull, the "superciliary" ridges are even more pronounced than in neoanthropic Upper Paleolithic man (cf. i with g and h), not to speak of modern Europeans (k). Reversions like these are common and well known occurrences. If they oc-

cur in neoanthropic man they are called "atavisms." Such "atavisms" are not confined to neoanthropic man but may be found in each phase of human evolution. When they are found in Archanthropines they point to still unknown earlier forms. Their mere existence proves that seemingly new features are not necessarily new creations but may have their roots in the past. It seems to me that not all students of human evolution are fully aware of this truth.

In addition to these reversions there is another phenomenon in human evolution which has not attracted the attention it deserves, particularly when the factors and mechanisms of the transmission of specific characters to descendants are discussed and interpreted. It has been shown that there is a strict correlation between almost all those features. It is superfluous to emphasize that such a correlation must exist in every evolutionary stage to guarantee the workability of the organism regardless whether it is already fully adapted to new conditions or still on its way. Considered from this point of view, it seems difficult to understand that some features which are typical of later stages of evolution can make their appearance in earlier stages although other features which are parts of the same correlated system still maintain their original character.

In the lower jaw of Sinanthropus the mental spine, a typical structure of modern man, is almost perfectly developed, although the chin, which is combined with the spine in modern man, is still missing. The strong *occipital torus,* one of the most characteristic features of the Archanthropines and an essential piece of the reinforcement system of the braincase, may already be disintegrated in Paleoanthropines to a degree found in modern man, although the front piece of the same system (the *supraorbital tori*) remains intact. The reverse condition, the disappearance of the supraorbitals but the maintenance of the *occipital torus* can happen too, but this condition has so far been observed only in neoanthropic man.

Orthogenetic Evolution

All the facts presented prove that the specialization of man in the course of his phylogenetic evolution is twofold. There is first the general "bipedal specialization" consisting of the adoption of the erect posture and the adaptation of the whole skeleton and body to it, and second, a particular brain specialization consisting of an enlargement of the brain as a whole, in addition to an expansion of the cerebral surface—increase of its fissuration—combined with a high degree of cortex differentiation. So far as the brain is involved, the bipedal specialization causes an adaptation of the form of the brain to the basilar deflection of the braincase. Although the two specializations are morphologically distinguishable, it is impossible to say which one set in first. Apparently they proceeded hand in hand, both reaching their climax in the modern human type. Yet, as indicated above, the brain specialization is a more general biological character, not necessarily confined to man, while the bipedal specialization is typical only of man.

Considered as a whole, human evolution has taken an orthogenetic course; it tends to proceed in one direction without any indication of deviation. Should there be an aversion to the term orthogenesis because it may imply predestination, I have no objection to calling it "rectolinear evolution." The mystery behind it remains the same for there is so far no indication that the recognizable stages of transformation which succeeded each other, or the individual features which characterize each of the stages, take their origin from "chance variations." The strict correlation which is evident even in the smallest morphological details renders, in my opinion, that interpretation unlikely. Although the most primitive hominid forms known so far come close to the stage in which they become scarcely

distinguishable from "apes," they are already specialized as hominids.

Environmental Influence

This raises the question of whether, and how far, environmental conditions can be made responsible for the course taken by human evolution. All the facts produced by human paleoanthropology are certainly incompatible with many earlier statements concerning the effects of environment, especially so far as they refer to climate. For example, the apelike forerunners of man living an arboreal life in tropical forests are said to have given up this habit when high mountains (the Himalayan range) rose and changed the climate to the effect that the forests on the arid slopes disappeared. The apes on the dry mountain side were forced to descend to the ground, walked around here and became hominids while those living on the slopes with high precipitation continued their arboreal life and remained, therefore, apes until today. If this were true, the remains of early man should be found in the arid regions north of the Himalayan range and the apes south of it. In reality, the most primitive types of man have been recovered from regions which never changed their tropical or subtropical conditions (South China and Java), while the orangutan remained their companion all the time.

Furthermore, it has been claimed that the Last Glacial Period which came over Europe forced the Neanderthal man, living there in the mild Interglacial, to use all his wits to escape the inclemencies of the new climate, and this exceptional strain of his mind made his brain grow so that man became *"Homo sapiens."* This sounds like a joke but this kind of reasoning was very common for a long time. In reality, the only direct morphological evidence of transitional forms between Neanderthal man and *"Homo sapiens"* came from Palestine (Mt. Carmel population), but these intermediate types lived there long before the Last Glacial and may never have passed through a real Ice Age.

Beside climate, diet above all things has been used to account for producing morphological transformations on a great scale. Yet what human evolution reveals does not lend support to this theory. All the Archanthropines were probably omnivorous. Sinanthropus, at least, was a hunter, living on meat and fruits (hackberries) and using fire. His eating habits cannot have differed greatly from those of primitive tribes of our day. Nevertheless man's dentition has changed considerably since (see above). Besides, it is difficult to comprehend how the patterns of the molars of apes and man could have been affected by a special kind or change of food. Almost all apes, and certainly all anthropoids, are frugivorous and take practically the same kind of food. Nevertheless, the pattern of their teeth is so specific that it can be used to identify each type. In addition, this pattern remains intact only for a very short fraction of the life span; it is usually worn away soon after the eruption of the tooth. Moreover, it has never been made clear how food can alter the entire chewing system (jaw bones, muscles, teeth, etc.) which represents an integral part of the skull and, as such, is demonstrably dependent on the special formation of the skull (see above).

The search of morphologists for environmental factors directing evolution lost much ground when the geneticists claimed that experiments on living organisms proved incontestably that acquired characters are not inheritable. The transmission of new characters would only be possible if these characters were the effect of changes of the genes. However, the essential question, which factors start the "mutations," remained unanswered as before. In any case it is hard to understand how "chance" mutations, meaning purely "accidental" hereditary changes, can work in such an elaborate correlative system as the human organization. They could do it only if the muta-

tions fitted in with this system but not many "chances" would be left in such a case. The usual argument that time allows for any chance mutation and its eventual establishment, is scarcely applicable to the rapidly proceeding final stages of human evolution. For the period of time in which the hominids passed from the early Archantropine stage to that of neoanthropic man did not last "millions of years" but not more than about 500,000 years (about 15,000 generations) as estimated from reliable geological data.

Summary

The trend of human evolution is toward specialization. This specialization is twofold. It consists: (1) in the adoption of erect posture and a strictly correlated adaptation of the entire human organization to this position; and (2) in the expansion of the brain, especially of the surface of the pallium, and in an intensive differentiation of the internal cortex structures. Human evolution took an orthogenetic course. The facts available do not indicate that environmental conditions played a decisive role in this development.

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