

HOMOLOGIES OF THE MOLAR CUSPS IN PLACENTALS AND MARSUPIALS.

Article XIX.—STUDIES ON THE EVOLUTION OF THE PRIMATES.

BY WILLIAM K. GREGORY.

PART I. THE COPE-OSBORN "THEORY OF TRITUBERCULY" AND THE ANCESTRAL MOLAR PATTERNS OF THE PRIMATES.

(FIGS. 1-18 AND PLATE I.)

1. *Critique of the Cope-Osborn "Theory of Trituberculy."*

In 1895 Professor Osborn¹ applied to the cusps of the human molars the system of nomenclature which he had invented at an earlier period for the molar patterns of Eocene mammals, replacing such cumbrous terms as anterior palatal, anterior buccal, etc., with the simple and easily remembered terms protocone, paracone, metacone, hypocone, for the cusps of the upper molars, and protoconid, metaconid, hypoconid, entoconid and hypoconulid for those of the lower molars. "When we understand," he continued, "that all the teeth of all mammals have this key, this tritubercular key, we can unlock the comparisons through the series and point out the homologies," a statement which after certain reservations and restrictions have been made, is still, in the judgment of the writer, essentially true.

For some years past the "theory of trituberculy" upon which Osborn's nomenclature originally rested has fallen into disfavor. Unfortunately the original theory of trituberculy included four distinct propositions of very unequal value: the first proposition is that normal ungulates, carnivores and primates once passed through a stage in which the upper molars were tritubercular, or more properly trigonal, while the lower molars were tuberculosectorial, that is with a cutting trigonid and a crushing talonid. (Fig. 1, C, D).

This proposition rests upon the broadest basis of fact. During the past twenty odd years American Museum expeditions have collected many thousand specimens of fossil mammals, from a long and closely graded series of horizons in the Paleocene, Eocene and later formations of the West. These enormous collections, which are now being studied and described by Professor Osborn, Dr. Matthew, Mr. Granger, and the present writer, afford overwhelming proof of the statements made above, namely that trigonal

¹ The History of the Cusps of the Human Molar Teeth. International Dental Journal, July 1895. Reprinted in "Evolution of Mammalian Molar Teeth to and from the Triangular Type," 1907, p. 63.

upper molars and tuberculo-sectorial lower molars are truly ancestral in pattern and may be traced along divergent lines into the more complex molars of various groups of insectivores, carnivores, condylarths, perissodactyls, primates and other orders. On another occasion I hope to be able to supply visual evidence for these statements.

The second and later developed proposition of the "theory of trituberculy" was that triangular molars had been derived from the tricondont type with three cusps in fore-and-aft line, by the migration, or circumduction, of the two marginal cusps, outward in the upper jaw and inward in the lower jaw. A prodigious quantity of German and English text has been produced

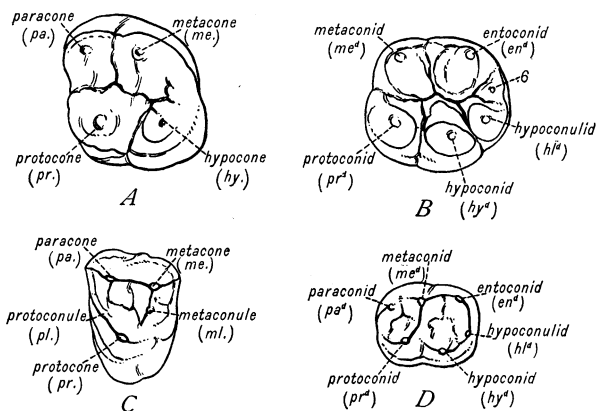


Fig. 1. The Osbornian nomenclature of the molar cusps.

- A. Second left upper molar of man (Kaffir).
- B. Second left lower molar of man (Australian black).
- C. Second left upper molar of *Pelycodus trigonodus*, a Lower Eocene lemuroid.
- D. Second left lower molar of the same.

C and D represent the primitive, tritubercular upper molar and tuberculo-sectorial lower molar.

in demolishing this frail hypothesis, often only for the purpose of setting up still frailer ones, such as the concrescence hypothesis which is supported even at the present day by Dr. Marett Tims (1914, p. 1) and Professor Bolk. But these authors have not realized that in disproving the cusp-circumduction hypothesis (if indeed they have disproved it) they have only rid the theory of trituberculy of a worse than useless encumbrance (Fig. 2). It is true that in the Order Triconodonta the genera *Menacodon* (Fig. 2D) and *Spalacotherium* (Fig. 2E) appear to supply evidence for the view that in their ancestors the para- and metaconids had been circumducted from an antero-posterior line, so as to make a triad of cusps, in the manner assumed in the Cope-Osborn hypothesis; but while, as I have elsewhere argued (1910, pp. 173-177), the assumed circumduction of cusps may very well have

occurred in the Metatherian order Triconodonta, there is little basis for assuming the same mode of origin for the quite differently appearing trigonids of the contemporary Trituberculata and later Placental Mammals.

A third correlated part of the original theory was that in ancestral stages the crowns of the upper and lower molars formed "reversed triangles," the lower triangle, or trigonid, with its apex external, the upper triangle, or trigon, with its apex internal. This proposition was not simply a generalization of observed facts; it involved also the inference that the inner cusps of the upper molars were in a sense homologous with the outer cusps of the lower molars and *vice versa*.

A fourth proposition of the original theory of trituberculy is that the

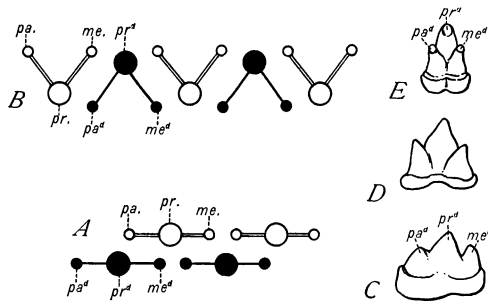


Fig. 2. The Cope-Osborn hypothesis of the circumduction of the para- and metacones.

- A. Triconodont stage with all three cusps in the same anteroposterior plane, as represented by *Amphilestes* (C).
- B. Tritubercular stage with the two minor cusps circumducted to the outer side in the upper teeth (white) and to the inner side in the lower (black).
- C. A lower molar of *Amphilestes*, Jurassic, England.
- D. A lower molar of *Menacodon*, Jura-Cretaceous, Wyoming. Inner side showing the paraconid and metaconid partly displaced to the inner side of the crown.
- E. A lower molar of *Spalacotherium*, Jurassic, England. Paraconid and metaconid completely displaced to the inner side of the crown.

This hypothesis is applicable, if at all, only to the origin of the molar patterns of the Triconodonta and not to other orders of mammals.

summit of the haplodont reptilian molar crown lies on the inner side of the upper, and on the outer side of the lower molars. This idea is closely connected with the proposition that in primitive types the upper and lower teeth form "reversed triangles." But while the latter is essentially true the former is open to considerable doubt, and has been especially attacked by those who uphold the "premolar analogy" theory. After many years of unbiased study of this problem I may briefly summarize my views on this highly debatable matter.¹

¹ See also the discussions of this subject by the present writer in "The Orders of Mammals" (1910, pp. 181-195) and, in collaboration with Professor Osborn, in the "Evolution of Mammalian Molar Teeth" (1907, pp. vi, 215-225).

First the "premolar analogy theory" assumes that the molars in pre-Tertiary times passed through precisely the same stages of progressive complication that are observed in the premolars of Tertiary phyla. This leaves entirely out of account the possibility that the final resemblances between premolars and molars may have resulted from the convergent evolution of non-homologous cusps. Nevertheless the resemblance between the fourth premolars and first molars, even in Paleocene times, was so pronounced, in so many families and orders, as to make it appear probable that in a general way the outer part of the fourth premolar is homologous with the outer part of the molars, and the inner part of the fourth premolar with the inner part of the molars. Hence I do not think there is sufficient evidence for the Scott-Osborn view that the main external cusp of p^4 is serially homologous with the main internal cusp of m^1 . On the contrary the fourth upper premolar appears to be truly more primitive in form than the first upper molar, especially in that its crown forms only a single pair, consisting of one external

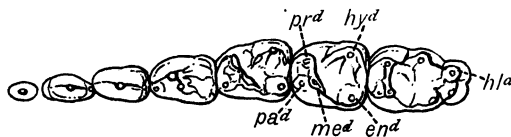


Fig. 3. Lower premolar and molar patterns of *Notharctus*, a Lower Eocene lemuroid. Crown view, twice the natural size.

Illustrates the complication of the molar pattern, through the great development of the talonid. The pattern of the fourth lower premolar is intermediate between that of the simple third premolar and that of the first molar. The wide basin of the talonid of the lower molars is correlated with the large size of the protocone of the upper molars, while the external position of the hypoconid implies the fact that in the upper molars the tips of the para- and metacones lie near the outer side of the crown.

and one internal cusp, while the first molar very often becomes divided into two moieties, the anterior moiety, consisting of the paracone and protocone and the posterior moiety consisting of derived cusps the metacone and hypocone, as more fully explained below (p. 253). Similarly the fourth lower premolar in all primitive Eutherian types appears to be more primitive in form than the first lower molar and it seems to show that the talonid has developed to fill up the interspace between the successive lower molars and to oppose the large internal cusp of the upper molars. As we follow the lower premolars forward we note that the talonid becomes shorter and narrower, until we reach the anterior premolars which have not yet acquired it. This sequence may be observed not only in many modern insectivores and lemuroids but also in many families of Eocene mammals.

The adaptive meaning of the simplification of the premolars as we pass forward is as follows: the anterior teeth are further away from the fulcrum,

which is the glenoid articulation, and further away from the insertion areas of the masseter, temporal and pterygoid muscles. Hence the anterior teeth sweep through a larger arc, that is, have greater velocity than do the molars, which are, on the other hand, in the best position for exerting slow vertical pressure. The premolars are thus intermediate in position and in function between the canines and the molars. But a greater velocity, associated with a smaller cross section and a sharper tip, imparts to the canines a relatively great piercing power. Consequently the anterior teeth retain the original haplodont crown, while in the cheek teeth this crown has become expanded and subdivided. These facts and considerations hold true not only in the mammals but also in *Cynognathus* and other extinct mammal-like reptiles.

In many Early Tertiary and primitive modern mammals as we pass backward from the simple conical first upper premolar through the progressively more complex p^2 , p^3 , and p^4 to the first molar we observe that the main high cusp of the premolars, which apparently represents the tip of the reptilian tooth, stands in anteroposterior line not with the protocone of the molars, but with the paracone and metacone (Plate I). As this is true not only in the examples cited by Dr. Wortman and others but in all primitive placental and marsupial mammals it constitutes the strongest point of the "premolar analogy theory" and tends to show that the paracone of the molars and not the protocone usually represents the tip of the original reptilian crown. If this is not the case we must suppose that the original summit of the upper molar crowns has been widely displaced inward, while the summit of the lower molar crowns has remained in the same anteroposterior line with that of the premolars (Fig. 3), an hypothesis which appears to be irreconcilable with the observed interlocking relations of the upper and lower cusps and depressions in any primitive mammal (Fig. 8).

That the outer side of the upper molar crowns is older than the inner side, namely that the region of the paracone and metacone is older than the region of the protocone, is clearly suggested also by the form of the deciduous molars (Fig. 4) and by the relations subsisting between the deciduous molars and the true molars in many families and orders of mammals. For several reasons the deciduous molars appear to belong to the same set with the permanent molars and to have been derived from the same strip of the dental lamina. The posterior deciduous molar and the first true molar are usually found in association and the posterior deciduous molar is practically always more molariform than the tooth which replaces it, which in primitive mammals is usually unlike the molars (Fig. 4). The premolars or replacing teeth, on the other hand, appear to belong to the same series

EXPLANATION OF PLATE I.

Homologies of the external, middle and internal rows of cusps in the premolar-molar series of primitive placentals and marsupials.

- A-D. *Zalambdodont* Insectivore series. Internal row (protocones) progressively reduced, middle row (para-, metacones) growing inward, as held by Mivart, M. A. Woodward, Gidley and Matthew. A after Matthew.
- E. *Dryolestes* (*Phascolestes*). Order Trituberculata (Pantotheria). Based on Osborn's figures. Interpretation of cusp rows doubtful.
- F-G. *Apternodus*, *Chrysochloris*. Order Insectivora, suborder Chrysochloroidea. Middle row growing inward, inner row reduced.
- H. *Didelphodus absarokæ*. Order Carnivora. Fam. Oxyclænidae (?) A primitive carnivore with all three rows well developed; the protocone row growing out, as usual, from the internal base of the crown.
- I. *Proscalops secundus*. Order Insectivora, suborder Soricoidae. A primitive talpid. After Matthew.
- J. *Tricentes*. Order Carnivora. Fam. Oxyclænidae. Outer row reduced in size. Inner cusps small in premolars, large in molars.
- K. *Peralestes*. A Mesozoic form of doubtful relationships. Interpretation of cusp rows doubtful. The inner row may represent the red series (paracones). Compare Marsupials. After Osborn.
- L. *Marmosa chapmani*. Order Marsupialia. Fam. Didelphiidae. The first molariform tooth is the deciduous molar. The enlarged metacones of the molars may represent the original tip of the crown (red series). Outer cusps greatly developed.
- M. *Didelphis*. Order Marsupialia. Fam. Didelphiidae.
- N. *Haplomylus*. Order Condylarthra. Fam. Hyopsodontidae. A tritubercular condylarth. Inner row enlarged, outer row small. After Matthew.
- O. *Omomys*. Order Primates. Fam. Tarsiidae. A tritubercular tarsiiform primate with enlarged protocones and reduced outer cusps. After Matthew.
- P. Q. R. Order Insectivora. Suborder Erinaceoidea. Fam. Leptictidae. Primitive relatives of the Erinaceidae. Inner row enlarged, outer row reduced.

Inspection of this series appears to support the following conclusion:

- (1) The three main rows of cusps (green, red, yellow) are respectively homogenous throughout the placental orders named.
- (2) The middle row (red) of the molar cusps are serially homologous with the single tips of the premolar crowns and are older than the inner row (yellow), or protocone series, which are ingrowths from the base of the crowns.
- (3) The outer row (green) are upgrowths of the external basal cingulum.
- (4) All three rows are well developed in primitive placentals, but frequently the outer row becomes reduced and the inner row becomes greatly enlarged.

as the vestigial "post-permanent" buds of the dental lamina. As we follow the deciduous molars forward there is a more or less gradual transition and simplification in form from m^1 through $dm^{\frac{3}{2}}$ and $dm^{\frac{2}{2}}$ to the more simple conical crown of $dm^{\frac{1}{2}}$. In every case observed the inner parts of the anterior upper deciduous molars, namely the region of the protocone, seem to represent an ingrowth from the outer portion of the crown, more or less similar to the internal extension of the crown in the upper premolars. The molariform character of the posterior deciduous molar, the more or less gradual transition in form from $dm^{\frac{3}{2}}$ to $dm^{\frac{1}{2}}$ and the shelf-like appearance of the inner

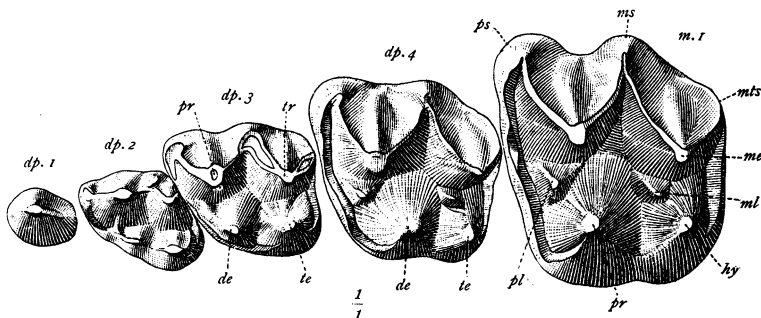


Fig. 4. Deciduous molars and first molar of *Palaeosyops leidy*, a Middle Eocene titanothere. After Osborn.

The first tooth of the series, wrongly marked dp^1 , is the first permanent premolar, p^1 , which, as in perhaps all other placental mammals, has no deciduous predecessor. The deciduous molars: dm^1 , dm^2 , dm^3 , (marked dp^2 , dp^3 , dp^4) show the shelf-like development of the internal cusps (corresponding to the proto- and hypocones of the true molars) and the progressive molarization of the deciduous series, the last being completely molariform. The first true molar is seen in association with the deciduous molars.

In this figure the cusps of the deciduous molars were originally named in accordance with the system devised by Professor Scott for the permanent premolars: the anteroexternal cusp being named "protocone" (pr), the anterointernal cusp "deuterocone," the posteroexternal "tritocone" and the posterointernal "tetartocone." In the present work the cusps of the deciduous molars are named in accordance with the system devised by Professor Osborn for the true molars.

cusps in the anterior premolars are all very widely distributed or even universal characters among mammals that possess a deciduous dentition. I base these statements upon a comparison of the deciduous and permanent dentitions in the following groups: Marsupialia Didelphyidae; Insectivora (various families as figured by Leche); Creodonta, Triisodontidae (*Pachyaena*¹), Mesonychidae (*Dissacus*¹), Hyænodontidae (*Hyænodon*, figured by Leche), Oxyænidæ (*Patriofelis*); Fissipedia: Cat, Dog, Badger, and Leche's excellent figures of the Viverridae, Mustelidae, Hyænidæ, Protelidae; Primates, Adapidae (figured by Stehlin), Cercopithecidae, Simiidae, Hominidae; Perissodactyla: Eocene and Oligocene Titanotheres, other Eocene Perissodactyls of several families, (figured by Stehlin); Artiodactyla: Eocene fami-

lies (figured by Stehlin), Tragulidæ, Suidæ; Tillodontia (*Esthonyx*¹); Tæniodonta, (*Onychodectes*¹).

The evidence obtainable from the deciduous dentition seems therefore to harmonize with the premolar analogy theory and to indicate that the "protocone" is a derived and not a primary cusp.

The view that one of the outer cusps (especially the paracone) and not the protocone represents the summit of the reptilian upper molar is fully in accord with the embryological facts² observed by Röse in the human teeth, by Taeker in the teeth of ungulates, by Leche in the teeth of marsupials and especially by M. F. Woodward in the teeth of various Insectivora. The latter author in discussing the conditions in the Insectivora, writes: "If the protocone represents the summit of the original protodont tooth of the ancestor of the Mammalia it must be the direct continuation of the primitive dentinal germ, and as such should be found to develop in a line with the axis of that structure. That this is not the case is well seen in Fig. 32, Pl. XXVI, [developing upper molar of *Talpa*] where the paracone is found



Fig. 5. Upper teeth of a small polyprotodont Marsupial (*Antechinomys laniger*). External view. $\times \frac{1}{2}$.

The canine, premolars and molars all have two large external roots, as in all primitive mammals.

to be identical with the primitive dentinal germ, and the protocone appears as a mere internal ledge growing out from the base of this structure, the

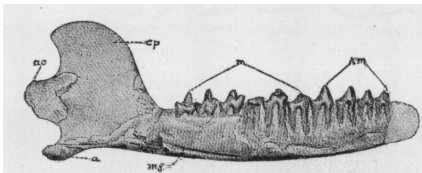


Fig. 6. Lower jaw of *Amphitherium preostii*, Jurassic, England. From Osborn, after Goodrich. \times circa $\frac{1}{2}$.

Showing the two roots of the premolars and molars, the conical compressed premolars and the very primitive tuberculosectorial molars.

metacone and subsequently the hypocone being similarly derived from a backward extension of the base of the primitive dentinal germ."

While this shelf-like development of the protocone might by itself fall under the suspicion of being cænogenetic, it perhaps gains in value when taken in connection with other evidence.

In both the upper and lower jaws the premolars and molars have two external roots (Figs. 5, 6). This is true not only in all the known Mesozoic

¹ By courtesy of Mr. Walter Granger.

² A summary of the embryological evidence is given in Osborn, 1907, pp. 208-215.

genera, belonging to several families of the Orders Triconodonta and Tribulculata, but also in all or most primitive mammals, both placentals and marsupials. The internal root, together with the protocone of the upper molars, is sometimes absent but the two external roots are always present in primitive mammals not only in the upper and lower premolars and molars but also in the deciduous molars.

In the lower deciduous molars (Fig. 7) the main *outer* cusp, or protoconid, appears to be the oldest part of the crown, while the inner cusps (paraconid,

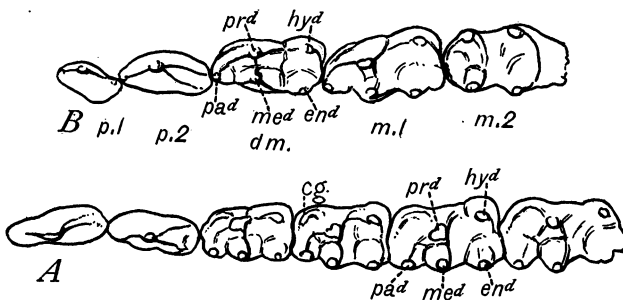


Fig. 7. A. Lower premolars and molars of *Didelphis* sp.

The protoconids of the lower molars appear to represent the tip of the premolars.

cg., anteroexternal cingulum, bordering a fossa for the tip of the enlarged metacone.

B. Deciduous molar and four permanent teeth of *Marmosa chapmani* Allen, a small Didelphid.

The deciduous molar (dm) is more molariform than the premolar which replaces it.

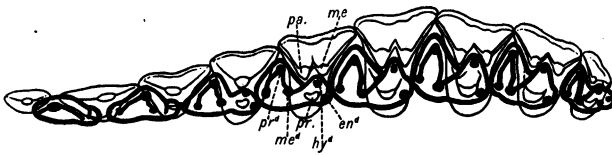


Fig. 8. Diagram illustrating progressive complication of the premolar-molar series and the interlocking relations of the upper and lower teeth in a generalized mammal.

The crown pattern of the lower teeth is shown in heavy black lines.

This diagram does not represent any particular genus, but is based upon the conditions observed in many early Tertiary mammals. With regard to the number of the teeth the diagram represents a hypothetical Mesozoic mammal with four premolars and five molars. The talonids of the lower molars are represented as being narrow, as they are in *Amphitherium* and other Mesozoic mammals. In most Tertiary mammals the talonids are wide.

metaconid, entoconid) appear to have arisen as upgrowths from the internal basal ledge.

When the upper and lower cheek teeth of any primitive mammal are carefully studied in articulation it is seen that the single conical cusp of the lower premolars and the protoconid of the lower true molars and deciduous molars correspond in function and topographic relations not with the "pro-

tocones" of the upper molars but with the main outer cusp or cusps of the upper premolars and molars, namely with the cusps which are supported by the two external roots.

I have long studied these interlocking relations of the upper and lower cheek teeth in many Tertiary and modern families, especially among the Marsupials, Insectivores, Carnivores, Primates, primitive Perissodactyls, Taligrada, Rodents etc. and I am confident that they lend strong support to the views long since expressed by Fleischmann, Schlosser and others to the effect that the mammalian jaws were originally anisognathus, (namely having the upper cheek teeth overhanging the lower cheek teeth), that the upper and lower cheek teeth originally alternated or interlocked and that the outer side of the upper molars is phylogenetically older than the inner side (Fig. 8).

But while I am thus obliged to reject the fourth proposition of the Cope-Osborn theory of trituberculy, to the effect that the protocones of the upper molars represent the original tip of the reptilian molar crown, yet the transverse widening of the crown or ingrowth of the protocone must have been effected at a relatively early epoch, since it is fully developed not only in the Paleocene and Eocene placental mammals but also in the Upper Cretaceous marsupials.

Whether the main internal cusp of the upper molars of the Jurassic genera *Peralestes* (Plate I, E, K), *Dryolestes*, *Kurtodon*, represent the protocones of later mammals or whether they are homologous with one of the main outer cusps (para-, metacone) is a difficult question. By analogy with the Paleocene zalambdodont genus *Palaeoryctes* and with later zalambdodonts they appear to represent the paracone series, while the internal cingulum indicated in Professor Osborn's figure of the upper molars of *Dryolestes* may represent the beginning of the protocone. The upper teeth of *Peralestes* suggest those of *Didelpys* and from a study of the interlocking relation of the upper and lower teeth in *Didelpys*, I infer that here the metacone represents the tip of the original two-rooted tooth (Plate I, Fig. M).

It may be objected that the trigonal and tuberculo-sectorial molar pattern may also have been attained in different ways among the Placental mammals, but to this I would reply that, notwithstanding contrary opinions, present evidence, in my judgment, points to the monophyletic origin of all the true Eutheria (namely the Carnivora, Ungulates, Primates, Insectivora), the ancestral stock probably having a dental formula, in the adult, of ^{3.1.4.3}_{3.1.4.3}, trigonal upper molars and tuberculosectorial lower molars. The molar and premolar patterns of all Eocene Carnivora, Ungulates and Primates show so many and detailed evidences of a fundamental unity of origin that I know no good evidence for the view that in the earliest representatives

of the different orders these patterns are merely homomorphic, or homoplastic, and not truly homologous. Later Eutherians sometimes exhibit convergent evolution between adjacent premolars or between premolars and molars, but this is far from disproving that all the primitive ancestral Eutheria of the Cretaceous had premolar and molar patterns which were severally homologous throughout the series.

Without going further into the controversy over the question of the origin of the tritubercular molar, which is still a very debatable matter, it may be noted here that the convenience and usefulness of the Osbornian nomenclature in expressing cusp homologies and homomorphisms in different families and orders of mammals has been recognized by the majority of palæontologists, especially in this country. But many zoölogists, anthropologists, anatomists and especially odontologists, are still without knowledge of the fact noted above that in the Paleocene and Eocene most of the known families of Eutherian mammals exhibit varieties of molar patterns which are very plainly and demonstrably modifications of the primitive tritubercular, or more properly trigonal, type. Nor do they realize, apparently, that the progressive changes in the premolars and molars of Creodonts, Condylarths, Primates, Insectivores, Perissodactyls, Artiodactyls and some other orders, in very many cases have long been quite well understood by American palæontologists.

I am aware that the primitive trigonal pattern is almost obliterated in not a few phyla, and that sometimes similar molar types are produced in different ways and involve partly non-homologous cusps, as where the postero-internal cusp of the upper molars is built up from the enlarged metaconule, as in many Artiodactyls, rather than from the basal cingulum, in the more typical manner. But in spite of such exceptions the Osbornian nomenclature of the molar cusps does in very truth provide the means of identifying homologous cusps in the diversely modified molars of Tertiary and modern mammals, as I will undertake to convince any fair-minded critic who will spend an hour with me in going over the Eocene mammals in the American Museum. Hence I object emphatically to the statements of Dr. Marett Tims in the last edition of *Tomes "Dental Anatomy"* (1914, p. 384) that although the Cope-Osborn system has "reduced to order" the nomenclature of the complex molar teeth of ungulates, yet "the reduction to order here referred to is unfortunately now again reduced to disorder. The terms Protocone, etc., may still be used to denote certain cusps, but certainly not with an assured implication of morphological significance, such as was intended when the terms were first adopted."

I deplore also the tendency of some writers to abandon the well established usage of the tritubercular nomenclature and to invent more or less

clumsy substitutes. What does it matter except to minds spoiled by a too literal use of words if the protocone was not the "apex of the original reptilian crown?" No matter how or when it arose, the protocone is the name for that cusp of the upper molars which in primitive mammals forms the main internal, or lingual, projection of the crown and which fits into the talonid of the lower molars (Fig. 9). The protoconid, on the other hand, originally wedges in between two upper molars (Fig. 8). Thus the protocone is as well defined a morphological concept as the sella turcica, or the entepicondylar foramen, and the same is equally true of all the other well recognized parts of the mammalian molars, as originally named by Osborn.

Hence it is not likely that American palæontologists will soon give up this convenient system for the at least equally cumbersome and hypothetical systems recently proposed by Bolk (1914) and extended by Schwalbe (1915).

Anthropologists and experimental zoölogists have diligently spread the thoroughly fallacious doctrine that morphology must be made an "exact" science and that results must be expressed in tables of indices and algebraic symbols. But, without disparaging the use of indices etc. as a method of describing facts, I often find it preferable to compare satisfyingly concrete and specific facts rather than abstract general symbols, and it seems far easier to call up a fairly distinct image of the second lower molar in *Pelycodus* than to remember that the cusp formula of this tooth according to Bolk is $\frac{Pa \ Pp \ 2}{3 \ D \ 4}$. This means in plain English only that all the cusps of the primitive tuberculo-sectorial lower molar are present, but gives no clue to the actual form of these cusps or to the precise appearance of the molar pattern, which are features of much practical importance.

But this is not to deny that Professor Bolk's system is easy to learn and that under certain circumstances it may be of real service. For example, the mere statement that the tuberculo-sectorial type of lower molar is the primitive pattern for Paleocene and Lower Eocene Eutherians may make but little impression upon opponents of the theory of trituberculy, but if I were to fill several quarto pages with the names of the Eocene genera and species (of many orders and families) in which the tuberculo-sectorial molar is present, and if I were to give the full Bolkian cusp formula for each molar, I dare say the resulting array of columns would be respectfully examined by anthropologists, statisticians and modern zoölogists.

In conclusion, I continue to endorse the Cope-Osborn theory, in so far as it derives all the more complex molar patterns of typical placental mammals respectively from the "tritubercular" and "tuberculo-sectorial" types of upper and lower molars. But I am forced to reject that theory both in its explanation of the origin of the tritubercular type and in its identification of the protocone as the summit of the haplodont reptilian molar. On the

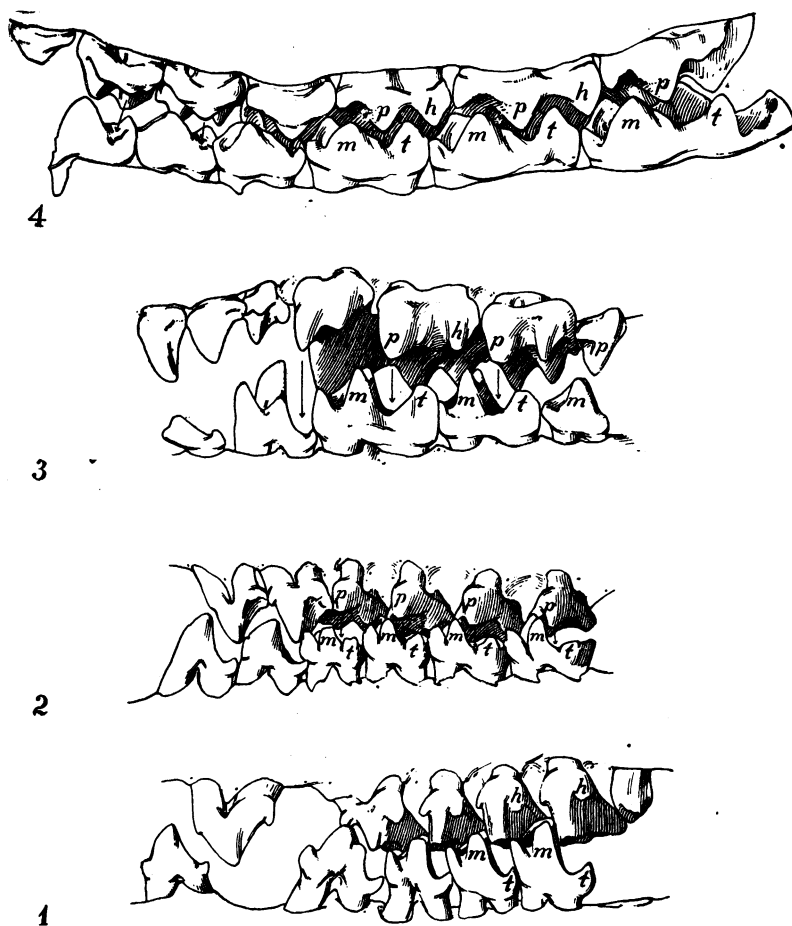


Fig. 9. Interlocking relations of the right upper and lower premolars and molars. Internal or lingual side view. (After W. K. Gregory in Osborn's "Evolution of the Mammalian Molar Teeth," 1907).

1. *Cenolestes* (Ord. Insectivora, subord. Zalambdodonta).
A specialized insectivorous-carnivorous type. This is not a primitive tritubercular type. The paracone (*p*) has grown inward and nearly usurps the position of the protocone.
2. *Didelphys* (Ord. Marsupialia, subord. Polyprotodontia).
Primitive insectivorous-omnivorous adaptations. A primitive marsupial with tritubercular upper molars and tuberculosectorial lower molars. The protocones (*p*) fit into the basin of the talonids (*t*). The trigonids fit between two adjacent upper teeth, *m*, metaconid.
3. *Erinaceus* (Ord. Insectivora, subord. Erinaceoidea).
Progressive insectivorous-omnivorous adaptations. The anteroposterior diameter of the molars has increased. The wide protocones fit into the broad talonid basins. The hypocones (*h*) jut inward into the basin of the trigonids of the lower molars.
4. *Telmatherium* (Ord. Perissodactyla, Fam. Brontotheriidae).
Herbivorous adaptations. Marked increase in anteroposterior diameters of the cheek teeth, the upper molars now including widely separated anterior and posterior moieties. Correlated expansion of the talonid basins. Premolars becoming submolariform.

other hand I now accept, in the main, the "Premolar-Analogy" Theory, as advocated especially by Wortman and by Gidley, which holds that the paracone of placental mammals usually represents the summit of the originally haplodont crown and that the protocone is an outgrowth from the inner base of the crown.

2. Application of the "Theory of Trituberculy" to the Molar Patterns of Primates.

In 1888 Professor E. D. Cope, in his article "On the Tritubercular Molar in Human Dentition,"¹ maintained that "first, the quadritubercular type of molar crown, illustrated by the first superior true molar of man, belongs to the primitive form from which all the crest-crowned (lophodont) molars of the hoofed placental mammals have been derived; and second, this quadritubercular type of molar has itself been derived from a still earlier, tritubercular crown, by the addition of a cusp at the posterior internal part of it.... In the inferior series," Cope continues, "I have shown that in known placental mammalia at least, the primitive molar crown is quinquetubercular, or tritubercular with a posterior heel."

In particular Cope held that the upper and lower molar patterns of man had been derived from the tritubercular, tuberculosectorial type exhibited in the Lower Eocene lemuroid *Anaptomorphus*. "This is the genus of Lemuroidea," he said, "which in its dental character most nearly approaches the anthropoid apes and man." Cope noted that the upper molars of man vary from the quadritubercular to the tritubercular condition, and he regarded the tritubercular form of human molars as a "reversion to the dentition of the Lemuridæ of the Eocene period of the family of Anaptomorphidæ." Cope's views will be discussed below. They are cited here in order to show that the Cope-Osborn theory of trituberculy was early applied to the elucidation of the morphology of the human molars.

In 1907 Professor H. F. Osborn² (pp. 157) said: "Cope's contention as to the tritubercular origin of the teeth of Primates rested upon the strongest possible proofs both from comparative zoology and from palæontology. The tritubercular pattern is still the prevailing one among the Lemuroidea, while the Anthropoidea radiate from trituberculy into quadrituberculy, and into crested forms. Osborn's recent revision³ of the American Eocene Primates proves that the molars exhibit a fundamentally triangular pattern

¹ Journal of Morphology, Vol. II, July 1888, pp. 7-23, pl. ii, iii.

² Evolution of Mammalian Molar Teeth to and from the Triangular Type. New York, 8vo, 1907.

³ Bull. Amer. Mus. Nat. Hist., Vol. XVI, 1902, pp. 169-214.

in every one of the twenty-two or more known species. The various types exhibit a familiar succession of stages from a more triangular condition with an extremely rudimentary hypocone to a quadrate, sextitubercular condition, stages which have already been treated in the evolution of the human molar teeth." (Fig. 10).

Professor Bolk, although attacking the theory of trituberculy at almost every point, has arranged a beautiful series of diagrams of the upper molar patterns in recent Primates, which series perfectly illustrates Professor Osborn's remark that "The tritubercular pattern is still the prevailing one among the Lemuroidea, while the Anthropoidea radiate from trituberculy into quadrituberculy, and into crested forms."

Professor Bolk's diagrams also illustrate a principle of dental mechanics which I described in 1910 (p. 188) and have since found to have a wide application: namely, that in the evolution of omnivorous, herbivorous and

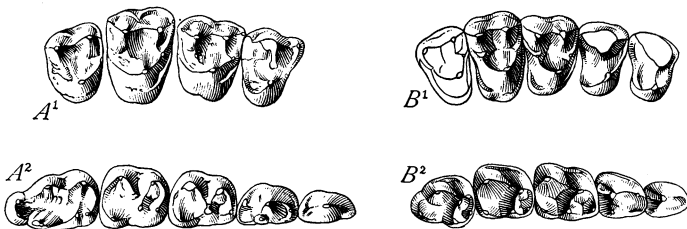


Fig. 10. Upper and lower premolars and molars of two primitive North American Eocene Primates representing the families Adapidæ (A¹, A²) and Tarsiidæ (B¹, B²), exhibiting the primitive tritubercular upper molars and tuberculosectorial lower molars.

A¹, A². *Pelycodus trigonodus*. Lower Eocene, Wyoming. After Matthew. $\times \frac{2}{1}$.

B¹, B². *Omomys* sp. Middle Eocene, Wyoming. After Matthew. $\times \frac{2}{1}$.

certain other types of molars the anteroposterior diameter of the whole crown steadily increases and all the main cusps widen anteroposteriorly, until an originally narrow trigonal upper molar of insectivorous type is transformed into an anteroposteriorly widened and more or less quadrate crown, with approximately similar anterior and posterior moieties (Fig. 9); meanwhile the lower molars enlarge the talonid and often lose the paraconid and the basin of the trigonid. Such a transformation may be followed in many families of Insectivores, Creodonts and Ungulates and is well illustrated in the comparison of the molar patterns of primitive Lower Eocene Primates with those of later Primates, as shown in the accompanying figures.

In all primitive mammals the trigonid of the lower molars wedges inside and between two adjacent upper molars (Fig. 11A) and the space between these molars is progressively obliterated by the widening of the inner side

of the crown. In such manner the primitive tuberculo-sectorial lower molar, which is provided with small cutting blades and sharp points for an insectivorous diet, is transformed into a bluntly cusped, crushing molar adapted for omnivorous or for herbivorous diet.

In the lower Primates the interlocking and alternating relations of the upper and lower molars constitutes a primitive condition seen in all primitive mammals and even plainly foreshadowed in *Bauria*, *Galesaurus*, *Sesamodon*, *Diademodon* and other Cynodont reptiles. In modern man, how-

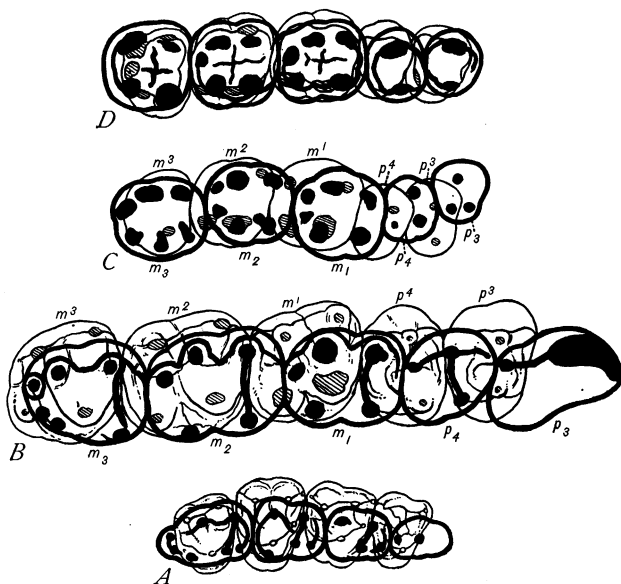


Fig. 11. Interlocking relations of the upper and lower cheek-teeth.

- A. *Pelycodus trigonodus*, a Lower Eocene lemuroid with primitive premolar and molar patterns.
- B. *Gorilla* sp.
- C. *Homo sapiens* (Australian black), with alternating or interlocking relations between the upper and lower molars.
- D. *Homo sapiens* (Negro), with end-to-end relations of upper and lower molars.

ever, the interlocking alternating arrangement is usually more or less replaced by a condition in which each lower molar articulates with only one upper molar (Fig. 11D). In some human skulls, however, the greatly reduced trigonid of the lower molars still retains a good contact with the posterior side of the upper molars, as observed by Topinard (1892) and others (Fig. 11C). Intermediate conditions are seen in the anthropoid apes (E).

Thus the molars of all Primates including man are believed to have

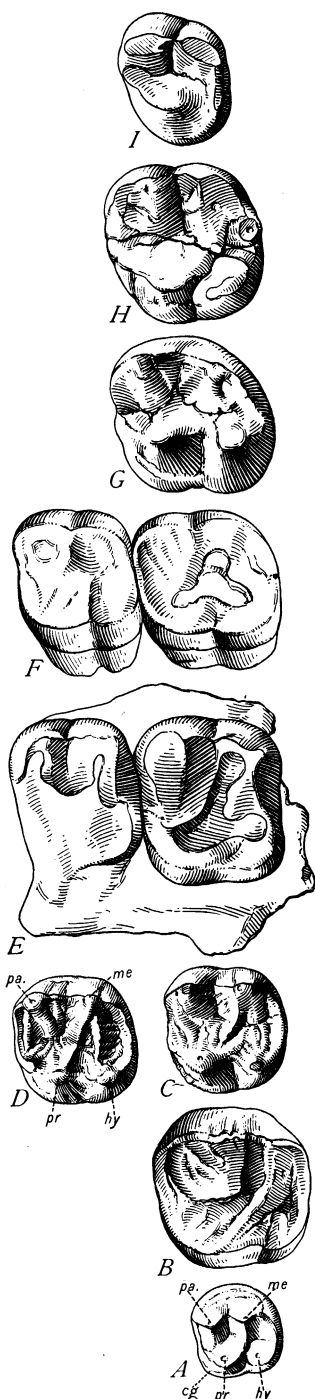


Fig. 12. Comparative series showing chiefly the second left upper molar in Hominidæ and Tertiary anthropoids. Three times natural size.

- A. *Pliopithecus antiquus* m². Upper (?) Miocene of Göriach, Austria. After Hoffman.
- B. *Dryopithecus punjabicus* m². Upper Miocene of Haritalyangar, India. After Pilgrim.
- C. *Pan* (*Anthropopithecus*) sp. Recent chimpanzee (m¹).
- D. *Dryopithecus rhenanus*. Lower Pliocene Bohnert of the Swabian Alps. From a cast. (m¹).
- E. *Sivapithecus indicus*. Referred m¹, m², much worn. From the Upper Miocene of Haritalyangar, India. After Pilgrim.
- F. *Palaopithecus sivalensis* m¹, m², much worn. From the Pliocene of Jobi, India. After Dubois.
- G. *Homo neanderthalensis* m². From the Pleistocene of Krapina. After Gorganovic Kramberger.
- H. *Homo sapiens* m². Kaffir from South Africa.
- I. *Homo sapiens* m². Brachycephalic Caucasian.

In the more primitive members of the series (A–D) the primitive trigon, consisting of the protocone, paracone and metacone, is reinforced by the large hypocone, which in *Homo neanderthalensis* becomes extremely prominent, the anteroposterior diameter of the crown having meanwhile increased. In the final stage (I), in correlation with the shortening of the whole tooth row and with the retrogressive character of the dentition, the hypocone disappears, and the small crown assumes a pseudo-tritubercular form.

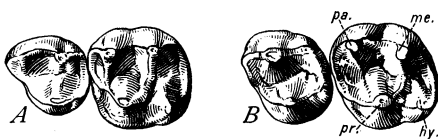


Fig. 13. Superior deciduous molars of a chimpanzee (A) and of *Homo sapiens* (B), showing agreement in fundamental pattern. The last deciduous molar as in all other mammals is molariform. $\times \frac{3}{2}$.

been derived ultimately from simple trigonal upper molars and tuberculo-sectorial lower molars (Fig. 10). The tritubercular upper molars of modern men are probably of retrogressive form (Fig. 12). The quadritubercular upper molars of lower and Pleistocene races clearly lead back through the quadritubercular molars of mid-Tertiary anthropoids to the trigonal, tri-

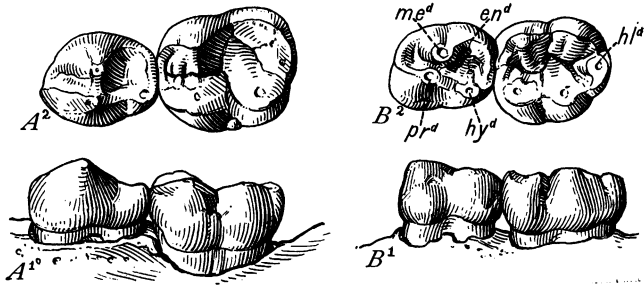


Fig. 14. Inferior deciduous molars of a chimpanzee (A^1 , A^2) and of *Homo sapiens* (B^1 , B^2) showing agreement in fundamental pattern.

As in the case of the upper deciduous molars, the anterior lower one in man is more molariform than in the chimpanzee, which thus retains a more primitive pattern in this tooth, as in others. $\times \frac{3}{2}$.

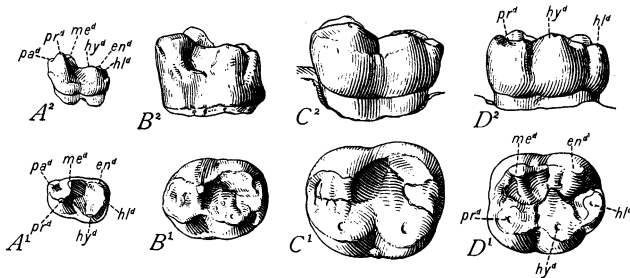


Fig. 15. Last lower deciduous molar of *Homo sapiens* (D), Chimpanzee (C), *Dryopithecus rhenanus* (B) (from a cast); compared with a permanent molar of an Eocene tarsiid (*Onomys*).

A^1 , $A^2 \times \frac{3}{2}$; remaining figures $\times \frac{3}{2}$.

In man (D) the tuberculo-sectorial pattern of the last lower deciduous molar is disguised, but in *Dryopithecus* it was largely retained.

tubercular molars of the earliest Eocene lemurs as will be shown more fully in Part II.

Comparison of the upper and lower molar patterns, both in the deciduous and permanent series, furnishes clear evidence that man is nearly allied to the Mid-Tertiary genera *Sivapithecus* and *Dryopithecus* and more remotely to the existing Chimpanzees and Gorillas (Figs. 11–15).

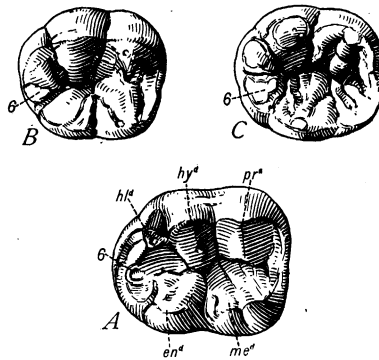


Fig. 16. Anthropoid heritage in the lower molar pattern of Man. All figures $\times \frac{3}{2}$.

- A. *Dryopithecus chinjiensis*. Upper Miocene, India. Left m_3 . After Pilgrim.
 B. *Homo sapiens*. Left m_1 , from the mandible of an Indian child.
 C. *Homo sapiens*. Left m_1 of an adult Australian black (♀).

In the primitive anthropoid (A) the molar crown is elongate, the posterior moiety is not wider than the anterior moiety and the entoconid is relatively small. In Man the opposite proportions are usually found. But the pattern of the crown in primitive human types is fundamentally the same as in *Dryopithecus* and *Sivapithecus*, consisting of five and sometimes six cusps arranged in the same manner. The main furrows also are arranged in much the same way, except that in Man, through the great enlargement of the entoconid the furrow that bounds the hypoconid internally is more or less excluded from contact with the base of the metaconid. In specialized human types the lower molars often lose the hypoconulid and also the sixth cusp (6); they become more or less rounded or subcircular in outline and the main furrows often tend to arrange themselves thus: + (Fig. 11, D).



Fig. 17. Anthropoid heritage in the lower molar pattern of Man (cont'd).

A primitive first lower molar of man (B), compared with that of two Miocene anthropoids, (A) *Sivapithecus indicus* Pilgrim (drawn from a cast of the type specimen) and (C) *Dryopithecus chinjiensis*, after Pilgrim.

All figures $\times \frac{3}{2}$ nat. size.

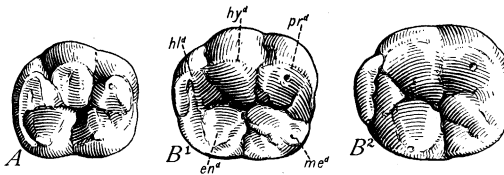


Fig. 18. B¹, B², two figures of the fossil human molar (left m_1) discovered by the Selenka expedition near Trinil, Java.

B¹ after Deek, B² after Walkhoff.

- A. *Dryopithecus chinjiensis*, after Pilgrim. Upper Miocene, India.

All figures $\times \frac{3}{2}$ nat. size.

The human molar seems to agree in general characters with the first lower molar of *Homo heidelbergensis* (Part II, fig. 27, E), but the variation in form among human molars is so great that perhaps no special significance should be attached to this fact.

PART II.—PHYLOGENY OF RECENT AND EXTINCT ANTHROPOIDS,
WITH SPECIAL REFERENCE TO THE ORIGIN OF MAN.

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I. INTRODUCTION.

The important collection of American Eocene Primates in this Museum has already been worked over, chiefly for the purpose of identifying the genera and species therein represented, by President Osborn (1902) and more recently by Doctor Matthew (1915). In 1912 these gentlemen generously entrusted to me the fuller study and description of this precious material, from the morphological and phylogenetic viewpoints, and they have also suggested that I should study the order of Primates as a whole, for the purpose of attaining some broad conception of the course of evolution and genetic relationships of its various branches. Accordingly, begin-

ning with the American Eocene family Notharctidæ I compared the skulls and postcranial skeletons of this group, which is well represented in our collections, with corresponding parts of the European Adapidæ and of various genera of recent lemuroids and other Primates. I then extend my studies to the remaining lemuroids, recent and extinct and finally to all the higher Primates. I had the privilege of examining the fossil lemuroid and other Primate material in the British Museum, and from the Museum of Comparative Zoölogy at Cambridge, Mass., I secured, through the kindness of Drs. Henshaw and Allen, the loan of a remarkably preserved specimen of the European Eocene lemuroid *Necrolemur*, which has been of the greatest service; while in this Museum I have at hand, in addition to the Eocene material already mentioned, a fairly representative collection of recent Primate skeletons, and casts of nearly all the important known extinct types of Asia, Africa, Europe and America. The photographs of recent Primate skulls, which had been made by my colleague Mr. A. E. Anderson for the late Dr. D. G. Elliot's great work on the Primates (1912) have also proved of signal value in my studies. About two hundred new illustrations of recent and fossil Primates have also been prepared for the present work with great skill, by Mr. Anderson and Mr. E. S. Christman.

Part I of the present series has dealt with the Cope-Osborn "theory of trituberculy" in its relation to the origin of the molar patterns of the Primates; Part II deals with the phylogeny of the great apes and man; Part III will treat of the catarrhine, or Old World Primates, and of the Platyrrhinæ, or monkeys of the New World; Part IV will discuss the phylogeny of the Lemuroidea and the possible relationships of the order as a whole with other mammalian stocks. Preliminary abstracts from the section on the Lemuroidea have already been published (1915).

A new synthetic study of the Primates seems timely because of the great additions that have been made during the last two decades to the material or objective side of our knowledge of the Primates. For during this period the Eocene lemuroids have been revised by Osborn (1902), Wortman (1903-1904), Stehlin (1912), and Matthew (1915), while new extinct lemurs of Madagascar have been described by Grandidier (1905), Standing (1908), and others. The fossil anthropoids of Europe (which are known chiefly from imperfect jaws and isolated teeth originally described by Gervais, Gaudry, Hoffman, Branco and others) have been restudied by Schlosser (1900, 1903), and Abel (1902), and the palæontological history of this group has been recently extended by the discoveries of Pilgrim (1915) in India and of Schlosser (1911) and Strömer in Egypt. Meanwhile great progress has been made in the knowledge of Pleistocene races of man, especially through the labors of Gorganović-Kramberger (1906), Schoetensack (1908), Boule (1912), Schwalbe (in numerous studies), Smith Woodward (1913),

Keith (1915) and others. I have naturally had recourse also to the well-known writings of Mivart, Forsyth Major, Dubois, Schlosser, Selenka and Winge and to the iconographic works of DeBlainville, Cuvier and Laurillard (*Planches de Myologie*, 1849) and especially the great monograph by A. Milne Edward and A. Grandidier (1875) on the anatomy of the Indrisinæ. This work is illustrated by 122 superbly executed plates, many of them in color, which set an almost unattainable standard for subsequent works of this character. In studying the morphology of the base of the cranium, including the architecture of the auditory region and the course of the internal carotid artery and its branches (regions and structures which afford pattern-complexes of high phylogenetic significance) I have thoroughly considered the important observations of Tandler (1899-1902), van Kampen (1905) and Zuckerkandl (1899).

But in spite of, or perhaps because of, all this wealth of material, there is still divergence of opinion regarding the classification of the major groups of the Primates and even more as to the origin and history of these groups.

In 1903 and 1904 Doctor J. L. Wortman, one of the pioneers of vertebrate palæontology in North America, whose withdrawal from palæontological work has been much regretted by his colleagues, made a notable and highly original attempt to work out the evolutionary relationships of the major groups and to reclassify the order on phyletic lines, as follows:

Order Primates

Primary Division Cheiromyoidea

Fam. Microsyopsidæ

“ Metacheiromyidæ

“ Cheiromyidæ

“ “ Lemuroidea

Fam. Lemuridæ

“ Indrisidæ

“ Nesopithecidæ

“ “ Anthropeoidea

Superfamily Arctopithecini

Fam. Hapalidæ

“ Paleopithecini

Fam. Anaptomorphidæ

“ Tarsiidæ

“ Neopithecini

Fam. Adapidæ

“ Cebidæ

“ Cercopithecidæ

“ Simiidæ

“ Hominidæ

In the present series of studies the writer will frequently return to this classification of Dr. Wortman's for detailed consideration and criticism. At present, however, it seems advisable to consider it in a broad and preliminary way, chiefly by merely stating the principal points in which it appears to the present writer to be objectionable or erroneous. In criticising Dr. Wortman's classification I shall almost necessarily put forward my own conclusions as to the interrelationships of the major groups of Primates, and thus the reader may be enabled to judge for himself, as these studies appear, how far my criticisms of Dr. Wortman's classification are justifiable and to what extent my conclusions seem to be legitimately drawn from the available evidence.

The first "primary division" Cheiromyoidea of Wortman appears to be an unnatural assemblage and not worthy of the high rank assigned to it. *Cheiromys* (*Daubentonina*) itself is surely a lemur of lemurs, an aberrant relative of the Indrisidæ, as I shall endeavor to show in detail in Part IV, and as most authorities have long held. Next the Metacheiromyidæ are not Primates at all, as shown by both Osborn and Matthew, but Edentates, related to the armadillos, the error having arisen through the malassociation of certain lemuroid remains with parts of a then unknown Edentate. Thirdly, the "Microsyopsidæ" in my judgment show no good evidence of relationship with the Cheiromyidæ. They are Eocene Primates (?) of very doubtful relationships and they resemble *Cheiromys* solely in the fact that they have a pair of enlarged lower front teeth of the gnawing type, a specialization acquired independently in many phyla of mammals and of little value as an indication of relationship.

Doctor Wortman did not, in my opinion, attain a clear conception of the interrelationships of the Lemuroidea, else he would not have omitted from this assemblage the Cheiromyidæ and Adapidæ and would not have failed to set apart the Lorises and Galagos in a family distinct from that of the lemurs of Madagascar, especially as he has given full family rank to the Indrisidæ and also to their near allies the Nesopithecidæ.

Even less fortunate it appears, is his treatment of the suborder Anthropoidea. For in assigning to this suborder the family Adapidæ and especially in placing the Adapidæ among the Neopithecini he has joined that which Nature has set far apart, while in removing widely the Hapalidæ from the Cebidæ he has separated two very closely allied descendants of a common ancestral stock. As to the Adapidæ, subsequent discovery may, conceivably, prove that the earliest members of the Notharctine or North American division of this family gave rise to the Platyrrhinæ, or monkeys of the New World. But between all known Adapidæ and all known Anthropoidea there is a wide structural hiatus: in the dentition, in the

whole architecture of the base of the skull, and to a less extent in the vertebral column and limbs. On the other hand all the Adapidæ both of America and of Europe are typically lemuriform in the architecture of the skull, save that they have not yet acquired certain minor specializations which have become characteristic of modern lemurs.¹ I conclude therefore that the Adapidæ should be assigned to the Suborder Lemuroidea and that the older North American representatives of the family are the most primitive known lemuroids.

As to the Hapalidæ, I can only state here that nearly all the characters

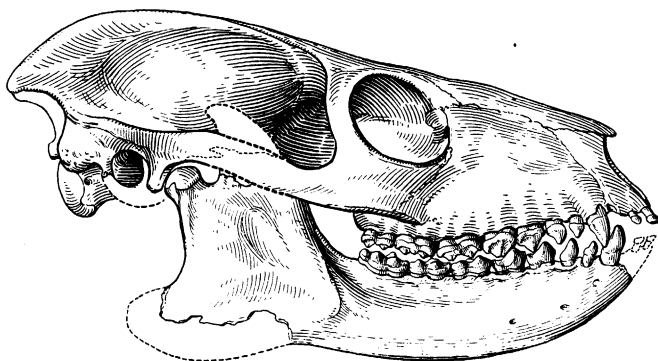


Fig. 1. Skull of an American Middle Eocene lemuroid *Notharctus formosus*, sp. nov.² Representing the American branch of the Adapidæ. $\times \frac{1}{4}$.

which, according to Dr. Wortman (1904, p. 220) indicate derivation from some early "Paleopithecine apes," are, in my judgment, either retrogressive or specialized characters which do not exclude the Hapalidæ from close alliance with the Cebidæ. Here belong the claw-like form of the nails,

¹ For a fuller discussion of this matter see the author's paper "On the Relationship of the Eocene Lemur *Notharctus* to the Adapidæ and to other Primates." Bull. Geol. Soc. America, Vol. 26, pp. 419-446, 1915.

² Type, Amer. Mus. No. 11466, a nearly complete skull and lower jaw from the Middle Bridger Beds, Grizzly Buttes, West; Bridger Basin, Wyoming.

Distinctive characters: Differs from *N. tyrannus*, *anceps* and *affinis* Marsh in the smaller and more slender lower molars, with narrower talonids; p_1 , p_2 spaced (diastemata closed in *tyrannus*, *anceps* and *affinis*); p_3 shorter than in *anceps*, with small talonid; p_4 with metaconid smaller than in *anceps*; m_3 has the two cusps of the entoconid region very small; paraconid small on m_1 , vestigial or wanting on m_2 , m_3 ; external cingula not extending on talonid. Lower canines small, with low crown (a female character?). Symphysis of mandible extends back to middle of p_4 . P^4 - m^3 with internal cingula weak (well defined in *anceps*). P^4 less progressive than in *affinis*.

Measurements of type.

p_1 - m_3 , 31.4	p^1 - m^3 , 27.3
m_1 - m_3 , 16.6	m^1 - m^3 , 13.7
$m_{3a.p.}$, 6.4	

The Bridger species of *Notharctus* have recently been studied by Mr. Walter Granger and the present writer and our revision of these forms will appear in Part IV of the present series of studies.

the feeble opposability of the hallux and pollex, the tritubercular form of the upper molars and the comparative slenderness of the lower jaw and the forward extension of the lacrymal. As will be argued more fully in Part III of these studies, the whole physiognomy and morphology of the Marmosets prove them to be specialized Platyrrhinæ, widely removed from the *Anaptomorphus-Tarsius* group.

In assigning the Eocene Anaptomorphidæ and the existing Tarsiidæ to the Anthropoidea under the "Superfamily Paleopithecini" Doctor Wortman took a bold course which may eventually be justified by further discovery and investigation. Indeed I shall offer some evidence for the conclusions, first, that *Necrolemur* of the Eocene of Europe, together with its ally *Microchærus*, form a family Microchæridæ, which should be referred to the Tar-

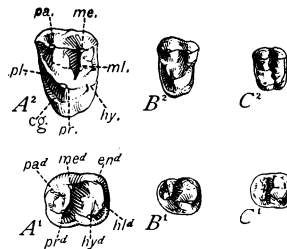


Fig. 2. Upper and lower molar patterns of primitive Eocene lemuroids.

- A. *Pelycodus ralstoni*. After Matthew.
- Fam. Adapidæ, subfam. Notharcinæ. Lower Eocene, Wyoming.
- B. *Omomy's* sp. After Matthew. Fam. Tarsiidæ. Middle Eocene, Wyoming.
- C. *Necrolemur antiquus*. From the specimen shown in Fig. 3 A.
- Upper Eocene, Europe.

All figures $\times \frac{2}{1}$.

In A and B the upper molars retain the primitive tritubercular pattern and the lower molars are tuberculosectorial. In C the pattern approaches that of the Catarrhinæ or Old World Primates, since the upper molars have four main cusps, while in the lower molars the paraconid has disappeared and the four main cusps are arranged in two transverse pairs. But these features may well have been independently acquired in the *Necrolemur* group and in the Catarrhinæ.

siiformes, and secondly that the known Microchæridæ exhibit certain important characters, not found elsewhere among the Lemuroidea, which may well be looked for in the immediate ancestors of the Anthropoidea, although the Microchæridæ themselves are plainly too specialized to lie in the direct line (*postea*, p. 264). But even if it should eventually be shown that some of the Tarsiiform series (Wortman's Paleopithecini) are allied to the remote ancestors of either the Platyrrhine or the Catarrhine division of the Anthropoidea, it would seem more judicious at present to let this division remain under the Lemuroidea, or even to give it coördinate rank with that group rather than to force it within the confines of the suborder Anthropoidea.

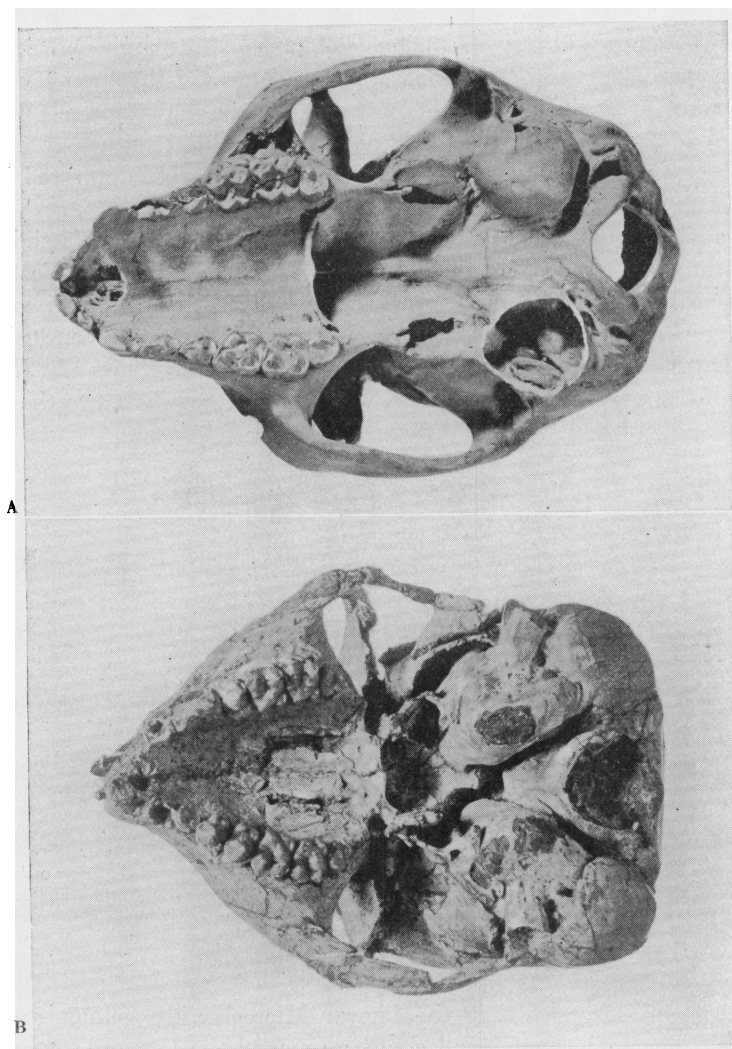


Fig. 3. Under side of the skull in two members of the suborder Lemuroidea, representing respectively the Lemuriformes (A) and the Tarsiiformes (B).

A. *Propithecus coquerelli*. Fam. Indridae. Recent, Madagascar. $\times \frac{1}{2}$.

B. *Necrolemur antiquus*. Fam. Microchœridae. Upper Eocene, France. $\times \frac{2}{3}$.

This specimen was loaned by the Museum of Comparative Zoölogy at Cambridge, Mass.

It has been freed from the matrix with great skill by Mr. A. E. Anderson.

In *Propithecus* the muzzle is wide, with enlarged canines, the palate is wide with parallel tooth rows. The zygomatic arches are stout; the wide posterior nares open behind m_2 ; the pterygoid alæ are elongate anteroposteriorly. The bullæ are of moderate size and completely enclose the small ring-like tympanic. The brain-case is of moderate width and the mastoid region not much swollen.

In *Necrolemur* the muzzle is narrow and pointed with small canines; the palate is narrow anteriorly with convergent tooth rows. The zygomatic arches are slender; the constricted posterior nares open far behind m_3 and the pterygoid alæ are much shortened. The bullæ are very large and expanded antero-internally and the large tympanic bone forms a tubular auditory meatus. The brain-case is very wide and the mastoid region much swollen.

Possibly the as yet undiscovered ancestral Catarrhinæ resembled *Necrolemur* in several of these characters, especially in the general appearance of the dentition, in the convergent tooth rows and in the swollen bullæ with tubular meatus.

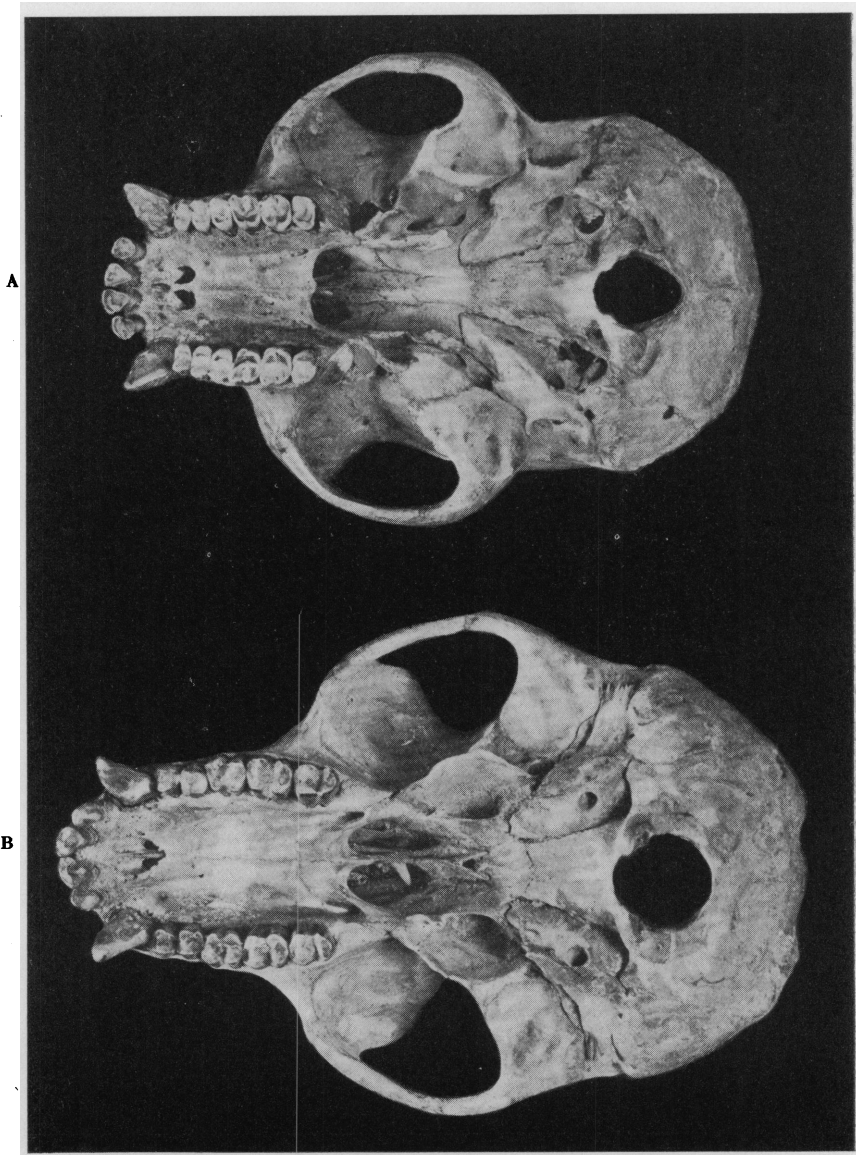


Fig. 4. Under side of the skull in two members of the suborder Anthropoidea, representing respectively the Platyrrhinæ (A) and the Catarrhinæ (B).

A. *Lagothrix lagotricha*. After Elliot.

B. *Nasalis larvatus*. After Elliot.

The Platyrrhinæ and the Catarrhinæ differ in so many important characters that they may have been derived from different families of Eocene lemuroids.

In the primitive Platyrrhinæ (A) the tooth rows and palate are relatively short, the three premolars are relatively large, the molars are small and rounded, retaining more or less of the tritubercular pattern. The posterior nares open near m^3 . The whole base of the cranium is elongate; the hamular fossæ for the internal pterygoid muscles are small. The auditory bullæ are elongate obliquely and the tympanic bones form widely open swollen zones adherent to the bullæ. The internal carotid canal is frequently located on the posterior side of the petiotic. The occiput is not very broad and is more or less rounded.

In the primitive Catarrhinæ (B) the tooth rows and palate are relatively long, the two premolars are small, the molars large and in the Cercopithecidae are divided into anterior and posterior moieties each bearing a transverse crest. The posterior nares open behind m^3 . The base of the cranium is short and wide; the hamular fossæ for the internal pterygoid muscles are large. The auditory bullæ are extended transversely and continuous with the elongate tubular tympanic. The internal carotid canal pierces the petiotic on its posteroventral surface. The occiput is broad and more or less flat.

In brief I conclude that on the whole Doctor Wortman's suggested rearrangement of the Primates constitutes a radical and unnecessary departure from long accepted standards. Indeed I much prefer the following elegantly simple grouping of "Les Quadrumanes Normaux" which was proposed by DeBlainville in 1816.¹

Singes du continent ancien

“ “ “ Les Singes [Catarrhinæ]

nouveau

Les Sapajoux [Platyrrhinæ]

Makis

Les Makis [Lemurs of Madagascar]

Les Loris [Lorises and Galagos]

L'Aye-Aye [Cheiromys]

In the present work, however, this grouping of DeBlainville's is hardly detailed enough for practical use and I therefore propose the following classification which I have gradually developed during the last few years:

Order Primates

Suborder Lemuroidea ²

Series Lemuriformes

Fam. Adapidae

Subfam. Nothartinae (*Pelycodus*, *Notharctus*, *Telmalestes*)

“ Adapinae (*Pronycticebus*, *Protoadapis*, *Leptadapis*, *Adapis*)

¹ Gregory, 1910. The Orders of Mammals, p. 77.

² The present classification of the Suborder Lemuroidea was first published, with definitions, in Nov. 1915. Bull. Geol. Soc. Amer., vol. 26, pp. 432-438.

- Fam. Lemuridæ
 - Subfam. Lemurinæ
 - " Chirogaleinæ
 - " Megaladapinæ
- Fam. Indrididæ
 - Subfam. Indrisinæ
 - " Archæolemurinæ (Nesopithecinae)
- Fam. Chiromyidæ (Daubentoniidæ)
- Series Lorisiformes
 - Fam. Lorisidæ
 - Subfam. Lorisinæ
 - " Galaginæ
- Series Tarsiiformes
 - Fam. Microchoeridæ [*Microchærus*, *Necrolemur*]
 - " Tarsiidæ [*Anaptomorphids* and *Tarsius*]
- Suborder Anthropoidea
 - Series Platyrrhinæ ("narines éloignées," DeBlainv. 1834)
 - Fam. Cebidæ
 - Subfam. Aotinæ (*Homunculus*, "*Nyctipithecus*," *Calli-
cebus*)
 - " Alouattinæ (Mycetinæ, *Alouatta*)
 - " Ateleinæ (*Lagothrix*, *Ateles*, *Brachyteles*)
 - " Pithecinæ (*Pithecia*, *Cacajao*)
 - " Cebinæ (*Cebus*, "*Chrysothrix*")
 - Fam. Hapalidæ
- Series Catarrhinæ ("narines rapprochées," DeBl.)
 - Fam. Parapithecidæ (Schlosser) (*Parapithecus*, *Mæripithecus*)
 - " Cercopithecidæ
 - Subfam. Oreopithecinae
 - " Cercopithecinae
 - " Semnopithecinae
 - Fam. Simiidæ
 - Subfam. Hylobatinæ (*Propliopithecus*, *Pliopithecus*, *Gri-
phopithecus*, *Hylobates*, *Symphalangus*)
 - " Simiinae (*Palæosimia*, *Simia*, *Sivapithecus*, *Dryo-
pithecus*, *Neopithecus*, "*Anthropopithe-
cus*" [*Pan*], *Gorilla*)

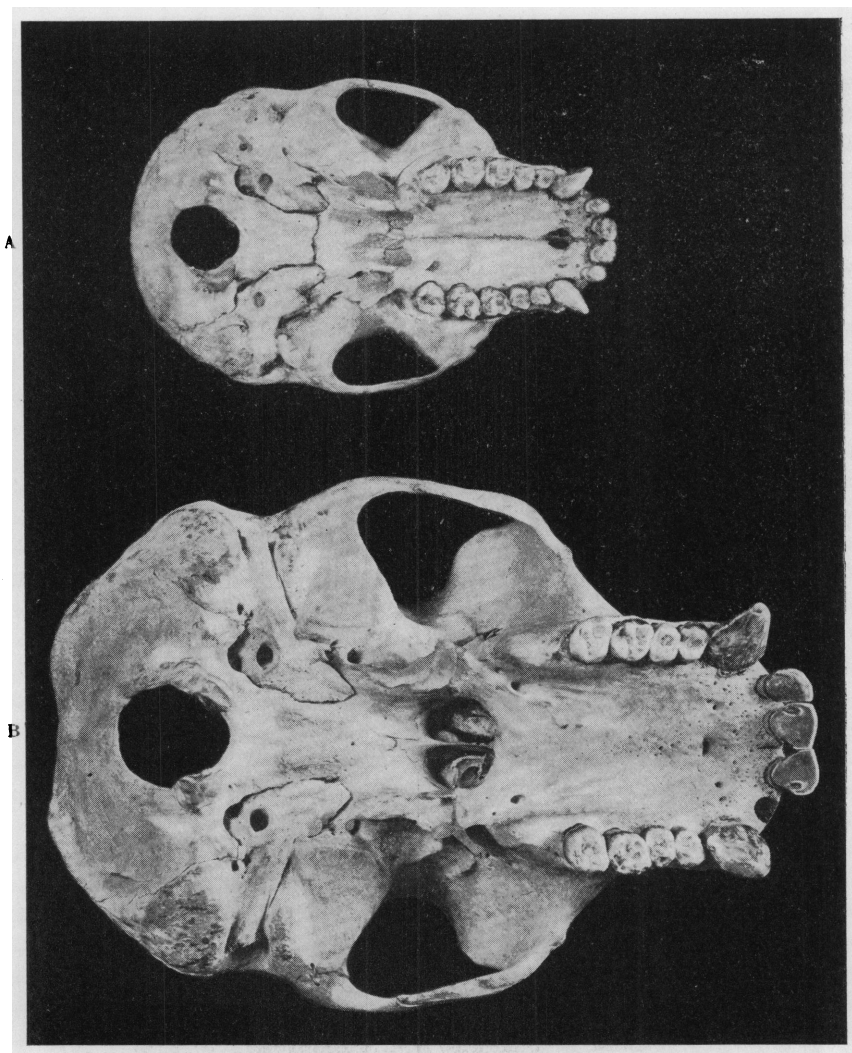


Fig. 5. Under side of the skull in (A) the gibbon (*Symphalangus syndactylus*) and (B) the chimpanzee (*Pan vellerosus*). After Elliot. (cf. Figs. 6-8).

Agreement in fundamental patterns is shown in the shape of the skull as a whole, in the number and form of the teeth (in this chimpanzee, however, the third upper molars have not erupted) and in the whole arrangement of the parts of the cranial base. The auditory region is identical in construction with that of the Cercopithecidae (Fig. 4B).

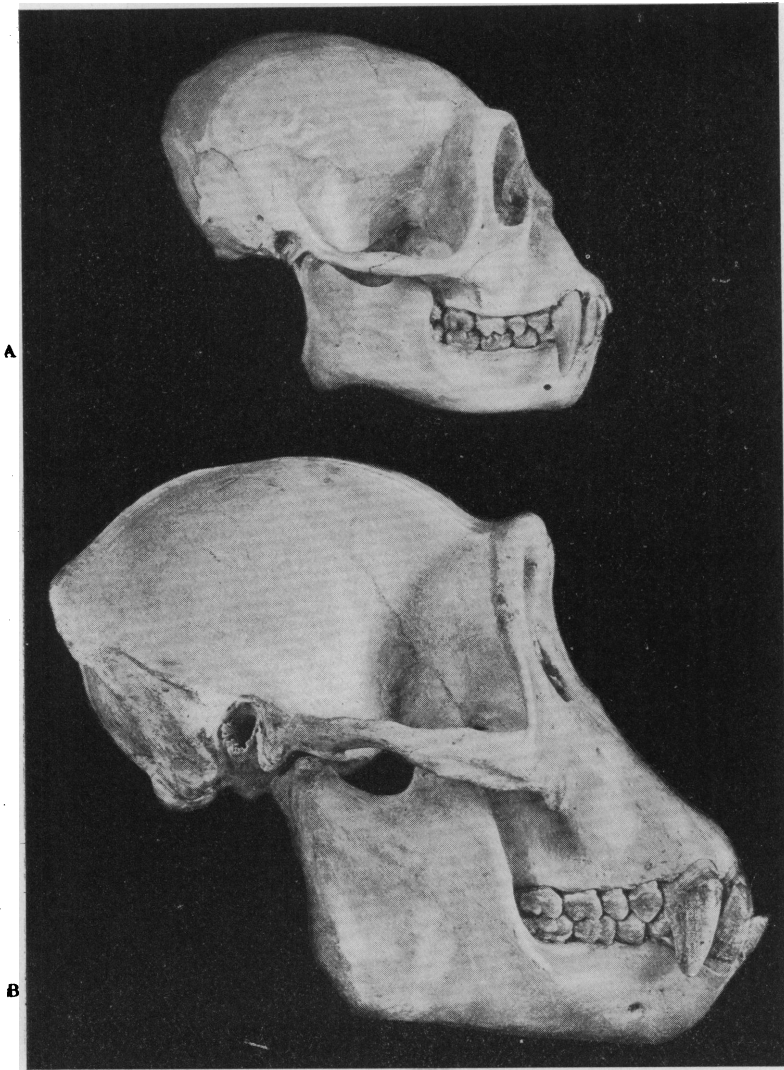


Fig. 6. Gibbon (A) and chimpanzee (B) skulls in side view (*cf.* Fig. 5). After Elliot.

Note the forward extension of the insertion areas of the temporal and masseter muscles. This gives to these muscles wide angles of insertion on the mandible with high crushing power for the molars and high piercing power for the erect pointed canines.

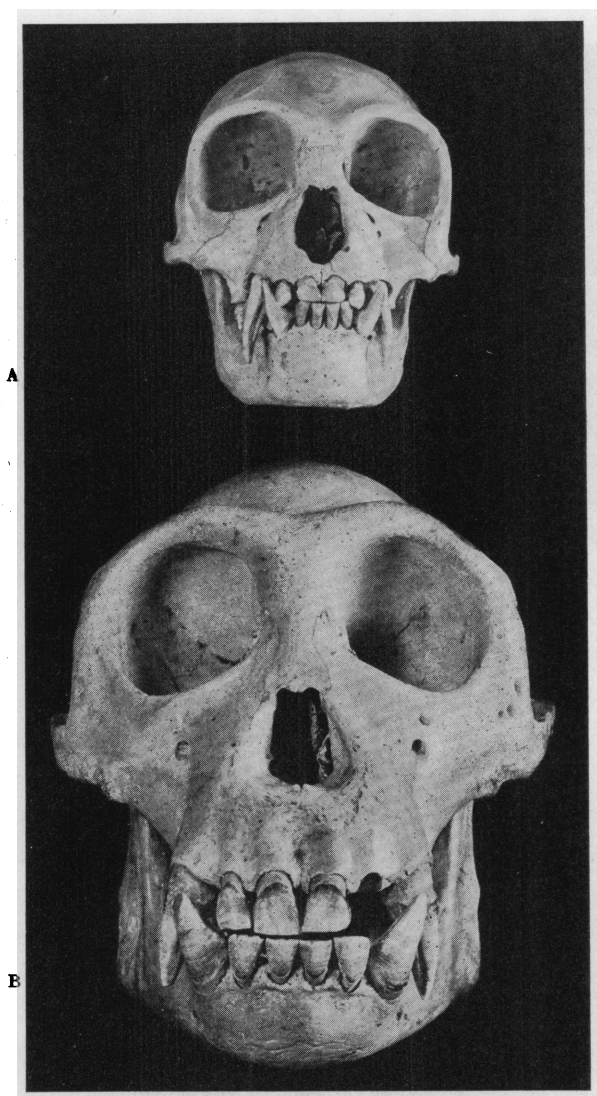


Fig. 7. Gibbon (A) and chimpanzee (B) skulls in front view.

A. *Symphalangus syndactylus*. After Elliot. $\times 1$.

B. *Pan vellerosus*. After Elliot. $\times 1$.

The opposite canines are widely separated, this bringing them near to the masseter muscles and increasing their piercing power. The axis of the lower canines is more or less parallel to the combined pull of the masseter and temporal muscles.



Fig. 8. Gibbon (A) and chimpanzee (B) skulls in top view (cf. Figs. 5, 6). After Elliot.

These top views illustrate the great width of the occiput and face in anthropoids, and the antero-posterior shortening of the whole skull.

The postorbital processes of the frontals and malars were originally developed in the lemuroid stage in connection with the forward extension of the temporal muscle, and served also as a brace for the base of the powerful masseter. In the higher anthropoids and early Hominidae the postorbital rims become everted and extend dorsally, forming the supraorbital tori. Similar ridges are also developed in certain baboons. They serve to protect the eyes and the frontal part of the brain, and through the action of the overlying facial muscles (frontalis, orbicularis and pyramidalis nasi) they intensify the expression of anger or excitement.

II. CHIEF ADAPTIVE CHARACTERS OF THE SKULL, DENTITION AND LIMBS OF THE ANTHROPOIDS AND MAN.

The Gibbons.

(Figs. 5A, 6A, 7A, 8A).

Of the existing anthropoids the gibbons are on the whole the most primitive in skull and dentition. On the other hand, as compared with primitive Eocene lemurs (*Notharctus*, etc.), they share with other anthropoids and Old World monkeys the following characters:

- the shortening of the face,
- the narrowing of the olfactory region,
- the forward growth of the orbits and frontals,
- the progressive separation of the orbital and temporal fossæ,
- the great widening of the brain-case,
- the backward growth of the occipital portion of the brain-case,
- the beginning of the downward deflection of the facial part of the skull.

In their incipient stages all these characters were doubtless characteristic of the ancestral catarrhine Primates as a whole and are to be regarded as primarily specializations for arboreal existence; they are correlated in part with a progressive enlargement of the cerebrum and a reduction of the olfactory portions of the brain. At the same time they foreshadow the end specializations of higher types.

The bony posterior walls of the orbit separate the eye and its muscles from the powerful temporal muscles, which are inserted on the posterior rim of the protruding orbits as well as on the sides of the brain-case. This voluminous anterior extension of the temporal insertion-area, together with the forward pushing of the brain-case, has no doubt conditioned in part the forward growth of the orbits, the shutting-off of the orbits from the temporal fossæ, and the retraction of the face. There is no sagittal crest, the opposite insertion-areas of the temporal muscles being widely separated by the flattened parietal vertex.

The jaws and dentition of the gibbons, as in all other anthropoids, are adapted chiefly for a frugivorous diet. The gibbons are more primitive than the other anthropoids in retaining the sub-tritubercular upper molars, in which the primitive trigonal pattern of the crown is only a little modified by the upgrowth of the postero-internal cusp, or hypocone, the inner side of the crown still being narrow and supported by an undivided root. All the molars lack the folds and wrinklins that are seen in the higher anthro-

poids. The lower molars have the four main cusps and the postero-median cusp, or hypoconulid, which are characteristic of the anthropoids and man. The middle part of the crown as in all Primates forms a broad basin for the reception of the main internal cusps (protocone) of the upper molars. The small premolars, or bicuspid, which, as in other catarrhines, are reduced to two above and below on each side, testify to the former loss of the two anterior premolars of the primitive placental dentition and to the marked shortening of the face in the remote ancestors of the gibbons. The very large saber-like canines may be either a defensive specialization or, more probably, a frugivorous one. The assumption of the tusk-like form has evidently conditioned the deepening of the anterior part of the lower jaw, the firm union of its opposite halves, and the rapid upward slope of its posterior border. The slenderness of the horizontal ramus is in all probability a retrogressive character: first, because in all other anthropoids the ramus is deep; secondly, because there is wide variation in this character in the genus *Siamanga* (see Bolk 1915); and thirdly, because an analogous reduction of the ramus is seen in the Cebidæ in several genera.

The incisors of the gibbons have remained rather primitive in form and consist of small procumbent chisel-like teeth, well adapted for holding and cutting fruits, the inner pair being only slightly enlarged and not excessively wide as in higher anthropoids.

Certain skull characters are undoubtedly connected with the upright pose of the gibbons, both in sitting and progressing, especially the downward facing of the foramen magnum, which brings the head at a sharp angle to the vertebral column.

The upright pose may have originated in connection with a change in the mode of locomotion. The primitive lemurs of the Eocene climbed, ran and jumped more upon the tops of the branches; the gibbons in progressing swing beneath the branches, the arms being held above the head. This acrobatic mode of locomotion, which has been appropriately called "brachiation" by Professor Keith, very probably took rise in the earliest anthropoids and has been carried to an extreme specialization in the excessively long armed gibbon.

Thus the habit of sitting upright, which first set free the hands for prehensile purposes and improved the power of supination, very probably preceded the habit of brachiation and the loss of the tail, as it has also in the genus *Indris* among the lemurs. The gibbons retain traces of the ischial callosities, which are fully developed in the lower Catarrhinæ but are lost in the higher anthropoids and man.

The Orang-utan.

The head of the orang-utan is distinguished by its marked shortness, roundness and great vertical diameter. The orbits are brought very close together, this reducing the entire nasal and orbital regions to an extreme narrowness. The orbits are very deep, the face is flat transversely and concave in the side view. The orbit is almost completely shut off from the true temporal fossæ. The brain-case is, so to speak, pushed forward over the face so that the basifacial axis is sharply inclined to the basicranial axis. Old males exhibit a sagittal crest, but possibly this is a secondary crest, produced by the upgrowth of the insertion-areas of the temple muscles, and it may not be homologous with the primitive sagittal crest seen in other orders of mammals.

As in all other anthropoids the massive teeth, jaws, and jaw-muscles are specialized for a frugivorous diet, the orang being able to tear open the tough rind of the fruit of the durian. The upper molar teeth are fully quadrangular with four-sided rather than triangular crowns. The surface of the crowns is low and flat with very numerous fine wrinklins on the enamel — an advanced specialization. The protocones or anterior internal cusps are only faintly connected with the external cusps, the para- and metacones. The premolars are relatively stouter than in the gibbon. The stout canines are highly effective in opening fruit and in fighting. The central upper incisors are very broad with flattened posterior faces. The long-crowned incisors and canines, as seen from below, form an evenly rounded or arched series.

The massive deep lower jaw has a wide distal end and a broad, high, ascending ramus; the condyle is raised above the level of the coronoid, in correlation with the forward displacement of the brain-case and the downward and backward displacement of the muzzle. The lower anterior premolar is stout and less elongate than in the gibbon, but more elongate than in the chimpanzee. Its oblique antero-external slope is worn, as in other anthropoids, by the postero-internal face of the upper canine. The posterior lower premolar is approaching the molar pattern, especially in its posterior moiety. The lower molars have five cusps as in other anthropoids, but the crowns are flatter and much wrinkled. The opposite premolar-molar series diverge slightly in front, in correlation with the widening of the muzzle and the wide separation of the opposite canines at this point.

The fore limbs of the orang are less extremely elongate than those of the gibbon, but are more elongate than those of the chimpanzee. This

excessive length of the arms and hands is not to be expected in the primitive anthropoid stock.

In keeping with its gigantic size the adult orang, although a master acrobat, is less agile than the gibbon and shows many structural adaptations that are connected with a massive thorax and abdomen.

The Chimpanzee.

(Figs. 5B, 6B, 7B, 8B).

The head of the chimpanzee is considerably longer than that of the orang; the most prominent feature in the top view is the extreme protuberance of the orbits and the outgrowth of bony ridges between, above and outside of the orbits. As in the gibbon all these outgrowths are connected with the forward extension and increase of the insertion-areas of the temporal and masseter muscles. The protrusion of the orbits and the development of orbital ridges may be regarded as part of the specialization for frugivorous diet, along with the deepening of the jaws. The sagittal crest of the males is apparently secondary.

The upper molars clearly retain the sharp V-like ridges of the primitive tritubercular pattern, but they add thereto a poorly developed posterior ridge running from the enlarged hypocone to the metacone. There is a decided tendency to divide the internal root into an anterior and posterior moiety, or rather, the formerly distinct roots may be in course of coalescing. The lower molars exhibit the four main cusps and the postero-median cusps which are characteristic of the great apes and man, and in the pattern of their crowns they distantly approach the human type although the antero-posterior diameter is still greater and the posterior moiety of the crowns not expanded. Traces of the primitive cross-ridges (protolophid, metalophid) are retained. The third upper and lower molars are somewhat reduced in size and degenerate in form. The rounded contour of the upper molars is correlated with the partly oblique, partly rotary excursion of the mandible. The molar crowns are coarsely wrinkled, the cusps being lower than in the gorilla. The upper premolars are comparatively small and are prominently bicuspid. The lower premolars are of normal anthropoid type, but are under the average size. The opposite premolar-molar rows are nearly parallel in the lower jaw but diverge in the upper jaw of old males. The canines form stout tusks. The anterior upper incisors are extremely wide with large wrinkled crowns. The muzzle as a whole is massive.

The Gorilla.

The gorilla carries to the logical extreme the frugivorous and fighting specializations which are foreshadowed in the chimpanzee. The head is lengthened by the forward growth of the muzzle and by the extreme backward growth of the skull-top. Thus the gorilla skull, to a certain extent, parallels that of the baboons. The supraorbital protrusion is now extreme. The secondary sagittal crest and widely flaring occipital crests attain an excessive development in old males, and are conditioned by the massive size of the muscles of the jaws and neck.

The canines form great tusks and hence the muzzle and lower jaw are very wide in front and the opposite premolar-molar series diverge anteriorly. The palate and basis cranii also reflect these swine-like adaptations. All these specializations are either absent or feebly developed in the females and young and may be looked upon as comparatively recent acquisitions which disguise the underlying similarity to the chimpanzee skull. The incisors are relatively narrow. The upper premolars are wide; the front lower premolar, in correlation with the tusk-like form of the upper canine, is shaped somewhat like that of a baboon, with a sloping well worn antero-external face. The molars all have conical cusps which are higher than in the other anthropoids and are less complicated by secondary folds and wrinkles. In correlation with the marked anteroposterior elongation of the head the upper molars are now divided into large anterior and smaller posterior moieties, but clear traces of the original trigonal pattern remain (Fig. 20B¹, B²). The lower molars (Fig. 27A) are also more elongate than those of the chimpanzee. The protoconid and metaconid are connected by a cross crest (protolophid) which fits between two adjacent upper molars (Part I, Fig. 11B). The fundamental pattern of all the premolars and molars are those seen in all anthropoids. The lower jaw is very massive with a long stout horizontal ramus and broad ascending ramus.

Thus the fundamental resemblances to the human skull are largely disguised in the male gorilla, which is distinguished by the great tusks and massive cheek teeth, the divergent tooth rows, the baboon-like muzzle and protruding orbits, in contrast with the opposite specializations in man. The young female gorilla on the other hand, except in the dentition, more distinctly approaches the human type than any other anthropoid, in all views of the skull (profile, front, top and back), in the interior and base of the brain-case and in the details of the tympano-petrosal region.

The limbs and body of the gorilla exhibit marked adaptations to its gigantic and clumsy stature. It has departed from the primitive slender-

limbed and arboreal type and exhibits a more or less transitional stage leading to bipedal ground-dwelling habits. As in the ground-sloths the long arms, stout, short legs and widely expanded pelvis are adapted for the support of the enormous thorax and abdomen.

The hands of the gorilla are more human than those of any other anthropoid, although the thumb is relatively smaller than in man and has not acquired the power of fully opposing itself to the other digits. So also the pes of the gorilla distinctly approaches the human type in the development of the heel, in the long metatarsals and short phalanges and in the diminution in volume of the digits from I to V. In the gorilla, however, the hallux is still of the old grasping type which is characteristic of all *Primates* except man (Fig. 31). Professor Keith has shown that this grasping type of pes assists the anthropoids in attaining a fully erect posture and balance while in the trees, but it is rather a hindrance to the upright position on the ground. (The structure of the gorilla foot is further discussed below, p. 330, 332.)

Man.

The anthropoids are chiefly frugivorous and typically arboreal; when upon the ground they run poorly and (except in the case of the gibbons) use the fore limbs in progressing. Thus they are confined to forested regions. Man, on the other hand, is omnivorous, entirely terrestrial, erect, bipedal and cursorial, an inhabitant primarily of open country. The anthropoids use their powerful canine tusks and more or less procumbent incisors for tearing open the tough rinds of large fruits and for fighting. Primitive man on the contrary uses his small canines and more erect incisors partly for tearing off the flesh of animals, which he has killed in the chase with weapons made and thrown or wielded by human hands. These implements and weapons also usually make it unnecessary for man to use his teeth in fighting and functionally they compensate for the reduced and more or less defective development of his dentition.

The comparative anatomical evidence alone is, I believe, sufficient to establish that in spite of these wide differences in habitus man is closely akin to the chimpanzee-gorilla group. All competent authorities will agree with MM. Boule and Anthony and Professor Keith that man bears an indelible stamp of remote arboreal ancestry, that upright or semi-upright progression in the trees was a prelude to the profound changes initiated by the assumption of bipedal progression upon the ground. The change from arboreal to terrestrial life must have been correlated with a great change in food habits from a chiefly frugivorous to an omnivorous diet.

In all known anthropoids, both recent and extinct, the powerful jaws and teeth seem to be adapted for tearing open the tough rinds of larger fruits, while early man, on the other hand, was a great hunter and flesh eater, like most primitive tribes of the present day. And every observer knows what efficient structures the incisors and canines of savages are in tearing off pieces of flesh.

Hence all the non-anthropoid and distinctively human features in the dentition of man seem to be relatively late specializations, which constitute a functionally correlated series. This complexly interrelated series of more or less simultaneous changes included the following elements (Fig. 9A):

- (1) Shortening of the muzzle and symphysis.
- (2) Retraction of all the anterior teeth, the incisors becoming more erect, the canines decreasing in size and the "edge-to-edge bite" becoming further emphasized.
- (3) Reduction in size of the front lower premolar and the completion of its bicusped character (Fig. 27E, F, G).
- (4) Development of a chin (a late feature).

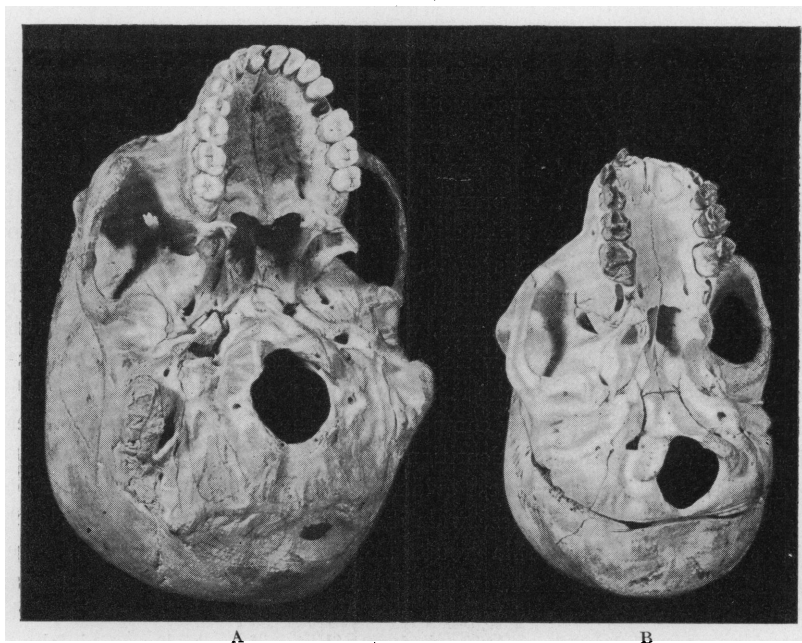


Fig. 9. Under side of the skull in a female Australian black (A) and in a young gorilla (B). The agreement in the underlying structure of the brain-case is masked by the wide differences in the dentition and in the upper jaw and its related parts.

The structure of the auditory region is fundamentally the same, but in man the carotid canal is larger and the tympanic spout develops an inferior crest.

(5) Increasing convergence of the opposite tooth rows and widening of the intercondylar diameter of the mandible.

(6) Rounding of the molar crowns, progressive obliteration of the anthro-poid, or *Dryopithecus*, pattern (*postea*, p. 293) of the molars and in some cases progressive loss of the hypoconulid on the second and third lower molars. Progressive reduction of the third upper molar from a more quadrilateral to a more tritubercular pattern.

(7) A change in the predominant movement of the mandible from a more ruminant-like, obliquely transverse movement, to movements in all directions and of a partly rotary character. (Especially correlated with the reduction of the canines.)

(8) A long and complexly interrelated series of changes connected with the assumption of the upright posture, the enormous increase in the brain-case and the consequent balancing of the head upon the neck. This influenced the dentition, especially by changing the insertion areas of the jaw muscles (*cf.* Miller, 1915) and perhaps permitted retrogressive changes, due to the diminished functional importance of teeth as compared with brains.

(9) A final shifting and readjustment of the whole lower dental arch in such a manner that the upper incisors finally overhung the lower incisors, and that each lower molar, which formerly articulated with two upper molars, came to articulate chiefly with only one upper molar (Part I, Fig. 11).

In brief, the skull and dentition of man in comparison with those of all anthropoids exhibit the following adaptive characters:

- enormous expansion and deepening of the brain-case;
- extreme shortening of the face;
- retraction of the front part of the lower dental arch;
- reduction in size of the dentition;
- tooth row forming a more or less rounded arch;
- canines not protruding much above the level of the other teeth;
- anterior premolars transversely widened and fully bicuspid rather than compressed in form;
- fusion of the premaxillaries with the maxillaries;
- lower jaw with progressively protruding chin, early losing the inferior symphyseal ledge;
- reduction of the supraorbital crest;
- extreme retraction of jaws beneath brain-case;
- articular eminence for the lower jaw small and strongly convex, permitting motion in all directions;
- glenoid fossa very deep;
- zygomatic arch feeble;

mastoid processes large and prominent;
tympanic plate (which is elongate and spout-like in the lower anthropoids) abbreviated;
carotid canal (which pierces the petrosal) much enlarged.
The limbs and backbone abound in well-known adaptations to erect bipedal terrestrial locomotion, some of which are discussed below (p. 327-336).

III. THE FAYÛM OLIGOCENE ANTHROPOIDS.

***Parapithecus* Schlosser.**

(Figs. 10A, 11A, 17A).

The anthropoids of the Lower Oligocene of Egypt, which have been carefully figured and described by Schlosser (1911), are of capital importance in the history of the higher Primates. Of these the genus *Parapithecus*, known from a well preserved lower jaw with complete dentition, is, as noted by Schlosser, by far the most primitive of all known Old World monkeys and apes. The animal was of very small size, not bigger than a squirrel monkey. Its dentition and jaw appear to be adapted not for eating large fruits with heavy rind as in the typical anthropoids but small fruits and perhaps insects.

The opposite rami of the lower jaw converged rapidly toward the narrow chin, which sloped sharply backward. The two incisors (on each side) were narrow and gently procumbent. The canine was small and not tusk-like, its tip no higher than that of the incisors and premolars, its crown low, conic with an incipient posterior basal cusp and a well marked internal cingulum. The two premolars were incipiently bicuspid, each with a large external cusp, a low postero-internal cusp and a low posterior cingulum. The first two molars have low crowns with the five cusps normal in the anthropoid-man series (protoconid, metaconid, hypoconid, entoconid, hypoconulid, or mesoconid), the paraconid being absent; the trigonid basin small, the talonid, or posterior moiety of the crown, large. The four principal cusps are arranged in transverse pairs the metaconid internal and slightly posterior to the protoconid, and connected with it by a low ridge, the protolophid; the entoconid slightly posterior to the hypoconid, the latter enlarged; all cusps very low, rounded, not wrinkled; an external cingulum; hypoconulid median; molars narrow; third molar with narrow posterior moiety. Mandibular ramus fairly stout but not deep, coronoid process high, recumbent, extending much above condyle, the latter widened transversely. These characters imply that the skull was of much lower grade than that of the typical anthropoids.

The dental formula as provisionally given by Schlosser namely I_1 , C_2 , P_3 , M_3 , should, perhaps, be changed to I_2 , C_1 , P_2 , M_3 , for the following reasons:

(1) the second tooth of the series looks to me more like I_2 of *Pliopithecus*; its crown is likewise separated by a small cleft from the tooth which I identify as the lower canine;

(2) a comparison of the premolars of *Parapithecus* with those of *Propliopithecus* and *Pliopithecus* indicates that we have here *two* premolars not *three* as suggested by Schlosser; these premolars are more primitive or less bicuspid than in later types;

(3) the tooth which I call the canine and which Schlosser calls the first premolar is more caniniform than the anterior premolars and is comparable with the canine of *Propliopithecus*;

(4) This interpretation brings *Parapithecus* into harmony with its nearest allies and with all other catarrhines, with which it agrees also in the fundamental pattern of the premolars and molars.

The reduction of the dental formula in *Parapithecus* and all other Old World Primates from the primitive Eutherian formula of 3. 1. 4. 3 to I_2^2 , C_1^1 , P_2^2 , M_3^3 , offers good evidence that at a very early period the muzzle and jaws in the Old World Primates were shortened to such a degree that one incisor, and two anterior premolars, on each side, above and below, had been crowded out, as in the Eocene *Anaptomorphus æmulus*. Such crowding and elimination may still be traced in the Lemuroidea, since the oldest family, the Adapidae, retain the formula I_2^2 , C_1^1 , P_4^4 , M_3^3 , while the most specialized genera of the Indrisinae reduce the formula to I_1^1 , C_1^1 , P_2^2 , M_3^3 .

Accordingly *Parapithecus* appears to stand as structurally ancestral to the whole anthropoid-man series, and as derived in turn from Eocene, insectivorous lemuroids. Dr. Schlosser has suggested that *Parapithecus* is related to the Eocene Anaptomorphidae and such relationship may eventually be demonstrated. The molars and premolars do indeed suggest derivation from a far more primitive insectivorous type, represented in *Omomys* sp. as figured by Matthew (1915, p. 449), but in this otherwise very primitive member of the Anaptomorphidae the incisors are apparently not fitted to give rise to those of *Parapithecus*. *Anaptomorphus æmulus*, as above noted, has the right dental formula, $\frac{2.1.2}{2.1.2}3$ (Matthew, 1915, p. 457), but in the absence of intermediate types it would be rash to regard it as ancestral to *Parapithecus*. *Tetonius* ("*Anaptomorphus*") *homunculus* is aberrantly specialized in many characters and the same is true of all other known genera of the Anaptomorphidae, which as a family appear to be allied with *Tarsius* rather than with the catarrhine series.

The lower jaw and teeth of one of the South American monkeys (*Chryso-*

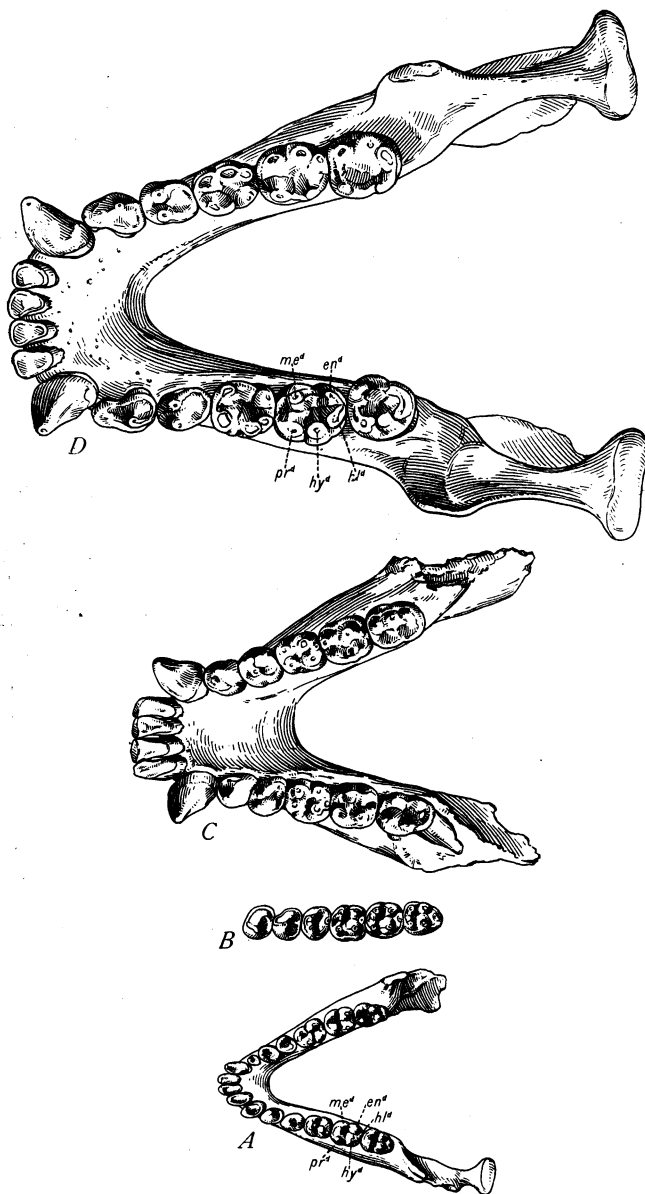


Fig. 10. Lower jaws and teeth of Parapithecidae and Hylobatinae. Dorsal view. Natural size.
 A. *Parapithecus fraasi*. Lower Oligocene, Fayûm, Egypt. After Schlosser.
 B. *Propithecus haeckeli*. Lower Oligocene, Fayûm, Egypt. After Schlosser.
 C. *Pliopithecus antiquus*. Lower Pliocene, Germany. After DeBlainville, modified from a cast of the same specimen.
 D. *Hylobates* (*Symphalangus*) *syndactylus*. Recent, Asia. After DeBlainville, modified from specimens.

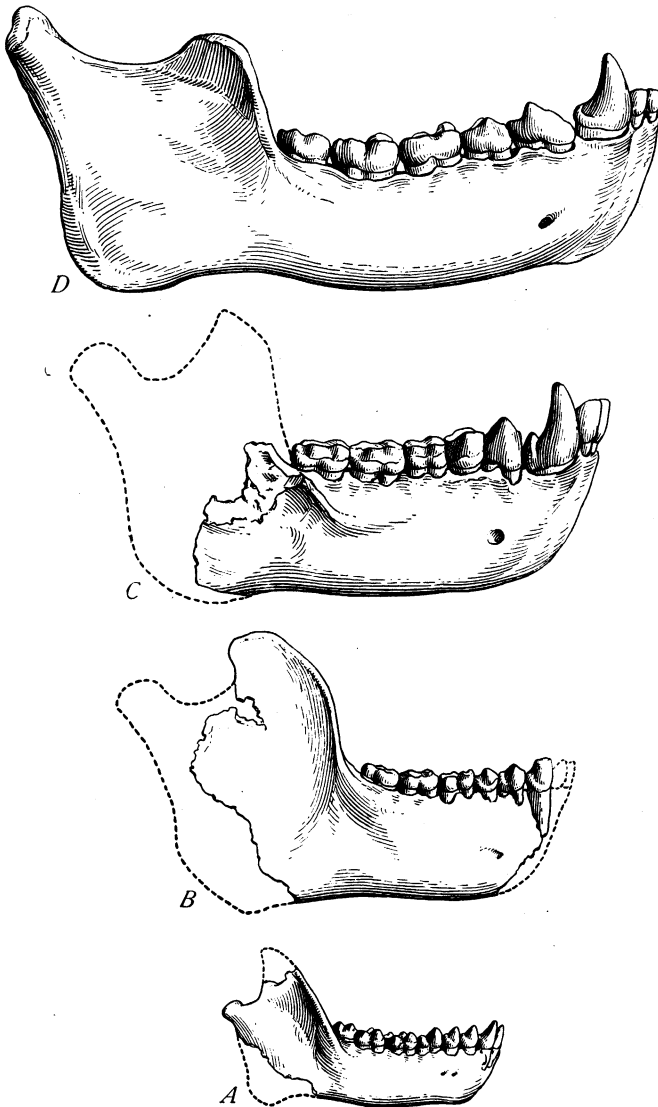


Fig. 11. Lower jaws of *Parapithecidae* and *Hylobatinae*. Side views. Natural size. For explanations see fig. 10. In Figs. A, B, C, the missing parts are restored hypothetically by the author.

thrix) as noted by Schlosser resemble those of *Parapithecus* in several characters. But all the Platyrrhinæ retain three lower premolars, and may rather represent a parallel series also derived from Eocene Lemuroids.

In conclusion, unquestionably the jaw of *Parapithecus* is structurally intermediate between a lower insectivorous anaptomorphoid stage and a higher anthropoid stage.

***Propliopithecus* Schlosser.**

(Figs, 10B, 11B, 17B).

This genus, so far as known from the lower jaw, is justly regarded by Schlosser as structurally ancestral to *Pliopithecus* and the higher anthropoids, and the characters about to be mentioned appear to be primitive for the man-anthropoid series. Although larger than *Parapithecus* the genus under consideration was much smaller even than a modern gibbon.

The jaw and dentition appear to be adapted for eating fruits with fairly heavy rinds. Unfortunately the incisors are not preserved but may well have approached those of *Pliopithecus*. The canine in side view has a low crown, rounded at the tip and sub-premolariform. In section it is roundly oval. It has a strong internal basal cingulum and a low internal basal cusp. Its fang is very stout and vertical. The anterior lower premolar (p_3) has a large single external cusp, a low internal cingulum and a very small postero-medial cusp. The posterior premolar (p_4) has a truly bicuspid anterior moiety with a small trigonid basin, or anterior valley, and a very low talonid basin with a postero-medial cusp. The first molar consists of four main cusps arranged in pairs and of a single postero-medial cusp, or hypoconulid. The paraconid is wanting and the metaconid is connected by a faint transverse crest with the base of the protocone. The hypoconid is the largest cusp, with a large antero-internal slope. It is connected by a very faint crest with the protoconid, this crest apparently foreshadowing the "crista obliqua" of later types. As in all anthropoids the depressed middle of the crown forms a basin for the reception of the massive protocone of the superior molar. The furrows formed by the intersection of the bases of the cusps make a pattern that foreshadows the "*Dryopithecus* pattern" described below. The large hypoconulid, or postero-medial cusp on m^1 lies nearer to the entoconid than to the hypoconid. There is a well marked external cingulum. The posterior moiety of the third lower molar is narrow. The horizontal ramus, or body, of the mandible is deep and the ascending ramus very broad, the coronoid process high and wide. The chin may well have been fuller (less sloping) than in *Parapithecus*.

From these characters we may infer with confidence that the upper dentition and skull had the following characters: (1) upper canine not greatly enlarged. (If it had been the anterior lower premolar would have been enlarged and compressed and the lower canine would have been tusk-like.) (2) Upper premolars more or less bicuspid. (3) Upper molars quadritubercular, with wide protocone and low hypocone, but retaining clear traces of an earlier trigonal pattern. (4) Skull more or less like that of a small gibbon but with much shorter, more massive jaw, and presumably stouter malars. As to the affinities of *Propiopithecus* with the later types Dr. Schlosser held that it was not only directly ancestral to the *Pliopithecus*-Gibbon line but also to all the higher anthropoids and man — a view which appears to the present writer to be in accord with present evidence (*postea*, pp. 294, 303, 304).

It may be objected that *Propiopithecus* should be regarded rather as a collateral ancestor of these later types than as a direct ancestor, and it may be argued that there may have been other genera of anthropoids living at that time in Egypt or elsewhere, which were the true and direct ancestors of the later types. But before postulating the existence of such genera a critic may well be required to show what characters of the already known genus definitely exclude it from such ancestry. In the reviewer's judgment the characters cited by Dr. Pilgrim (1915) for this purpose are wholly insufficient and are indeed primitive anthropoid characters.

IV. THE SIWALIK UPPER MIOCENE AND LOWER PLIOCENE ANTHROPOIDS.

As described by Lydekker ¹ in 1886, the fossil Primates of India included extinct species of macaques, baboons and semnopithecques, and two anthropoid apes apparently related respectively to the orang and the chimpanzee. This composite assemblage of genera now widely separated in Africa and Asia tended to confirm the faunal kinship of these continents with each other and with Europe during the later Tertiary and inspired the hope that eventually the Siwaliks series would yield important evidence on the origin and interrelationships of the great apes and man.

In recent years the Geological Survey of India has secured more of these fragmentary but very important fossils, which have lately been accurately described and figured by Dr. Guy E. Pilgrim in a memoir entitled "New Siwaliks Primates and their bearing on the question of the Evolution of Man and the Anthropoidea." ²

¹ Indian Tertiary and Post-Tertiary Vertebrata. Siwalik Mammalia Supplement I. Mem. Geol. Surv. Ind., Ser. X, Vol. IV, Part I.

² Records of the Geological Survey of India, Vol. 45, Pt. 1, Febr. 1915.

According to Pilgrim the Primates of India appear first in the Chinji zone (Lower Siwaliks) which is regarded as of Lower Sarmatian (Upper Miocene) age; they extend through the Nagri and Dhok Pathan zones (Middle Siwaliks) of Pontian or Lower Pliocene age, and culminate in the upper zones of the Upper Siwaliks, of Upper Pliocene age (Fig. 37).

All belong exclusively to the Catarrhine or Old World division of the suborder Anthropoidea. More in detail the Lower Siwalik series (Chinji zone, Upper Miocene) includes: (a) two species of *Dryopithecus*, a primitive genus of the great apes, hitherto known only in the Upper Miocene and Lower Pliocene of Europe; (b) *Palæosimia*, a supposed ancestor of the orang, and (c) *Sivapithecus*, a genus regarded by Pilgrim as related to the ancestors of the Hominidæ.

The Lower Middle Siwalik series (Nagri zone, ?Upper Miocene) includes a gigantic species of *Dryopithecus* (*D. giganteus*). The Upper Middle Siwalik series (Dhok Pathan zone, Lower Pliocene) includes *Palæopithecus*, an anthropoid which was regarded by Lydekker as closely related to the gorilla and chimpanzee.

The Upper Siwaliks (Upper Pliocene) include an orang and several species of macaques, baboons and semnopithecues.

Through the kindness of Dr. Pilgrim the American Museum of Natural History has secured casts of the principal types of Siwalik anthropoids and these, together with the extremely accurate figures given in Dr. Pilgrim's memoir, have enabled the reviewer to make careful comparisons with other recent and fossil anthropoids.

***Palæosimia rugosidens* Pilgrim.**

(Fig. 12A).

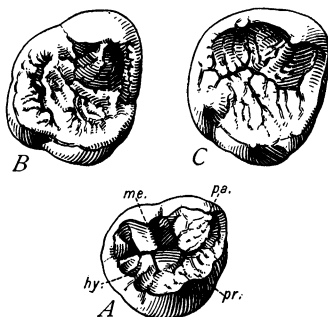


Fig. 12. Comparison of the third right upper molar of *Palæosimia rugosidens* Pilgrim with those of two modern Orang-utans. $\times \frac{3}{2}$.

- A. *Palæosimia rugosidens*. Lower Siwaliks (Upper Miocene), India. After Pilgrim.
- B. *Simia satyrus*. After Selenka.
- C. *Simia satyrus*. After Selenka.

This anthropoid is represented only by the third upper molar of the right side (pl. 2, fig. 9). As observed by Pilgrim this tooth distinctly foreshadows that of the orang, in its general pattern and in the characters of the enamel folds and wrinkles, the differences all being obviously primitive characters. This specimen comes from a low horizon (Chinji zone) and its characters suggest that the orang line had even at that time become rather widely separated from the forerunners of the chimpanzee and gorilla. Accordingly, Dr. Pilgrim considers *Palæosimia* "as branching off from the *Dryopithecus* line previous to the chimpanzee and gorilla and passing through a marginal hypothetical species of *Dryopithecus*" (p. 67).

***Sivapithecus indicus* Pilgrim.**

Figs. 13A, 14A, 15A, 16A.

This highly important genus and species were originally established on a third right lower molar (Pilgrim 1915, pl. 1, fig. 7) from the Chinji zone of the Lower Siwaliks, but the author employs as a neotype or topotype (wrongly called "type") a specimen from the same locality and level consisting of a right mandibular ramus (pl. 1, fig. 7), containing in excellent preservation the second and first molars, the posterior premolar and portions of the roots or alveoli of the anterior premolar and canine. A supplementary series from a later horizon (the Nagri horizon of the Middle Siwaliks is referred by the author to the same species and consists of: (a) a fragment of the mandibular symphysis (pl. 2, figs. 1, 1a-d) containing the left canine and parts of the roots and alveoli of the incisors and front premolar; (b) a front lower premolar (pl. 1, figs. 9, 9a, 9b); a lower molar (not figured). An upper canine from the Lower Siwaliks of Chinji (pl. 2, figs. 3, 3a-d) is provisionally referred to the same genus, while a fragment of the right maxilla (pl. 2, fig. 2) containing the much worn first and second upper molars are doubtfully referred to this genus.

After an exceedingly detailed study of these precious fragments Dr. Pilgrim has attempted a preliminary and partly hypothetical restoration of the mandible of *Sivapithecus* in left side view and as seen from above. The reviewer has given prolonged consideration to this restoration, first with reference to the propriety of associating the scattered fragments in a single generic concept and secondly with reference to the placing and orientation of the various parts. While the generic association of the fragments seems probable the reviewer has been led to a different conception of the jaw as a whole.

This anthropoid shows a rounding and broadening of the molar crowns.

which in these particulars foreshadow the human type, although the first and second molars are more primitive and less widened than in man. The molar crowns present a widened modification of the "*Dryopithecus* pattern," described below, a pattern which is further obscured in man; the posterior

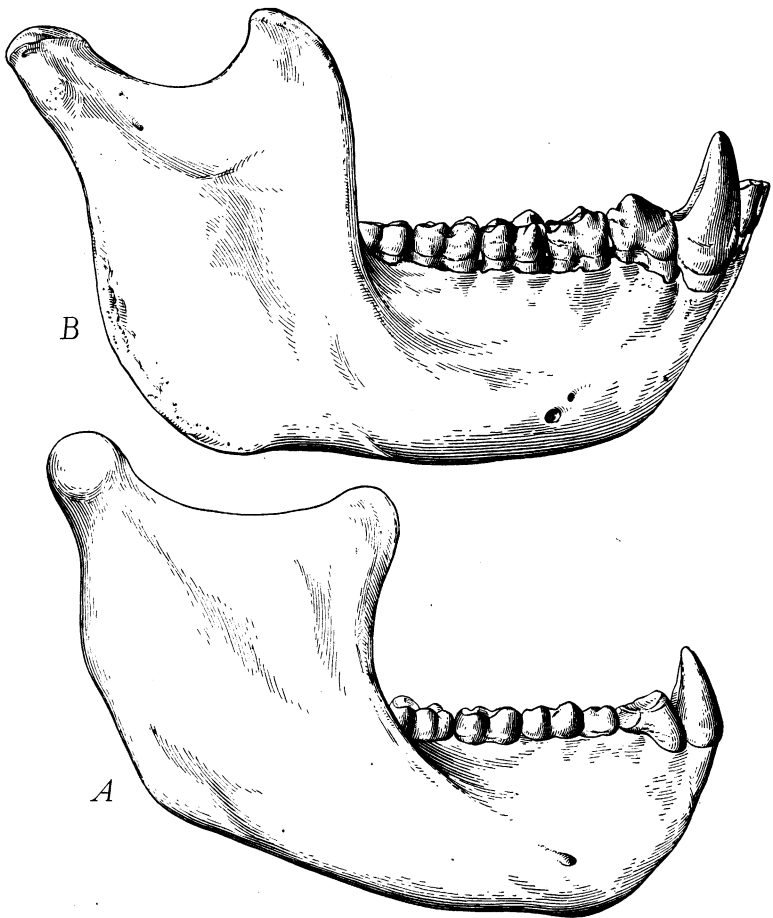


Fig. 13. Comparison of *Sivapithecus* and *Simia*. Side view of lower jaw. Both figures $\times \frac{2}{3}$.
A. *Sivapithecus indicus*. Partly hypothetical and provisional restoration by Pilgrim.
B. *Simia satyrus*. Male specimen.

premolar is bicuspid, and foreshadows the human type. Although the lower border of the mandible is not preserved, enough remains to show that the mandible was deep and massive, as it was in all early anthropoids and men. The ascending ramus was undoubtedly wide, as indicated by the forward

extension of its lower outer ridge and by the massive character of the mandible.

One of the most noteworthy human characteristics of *Sivapithecus* is the remarkable agreement in the breadth indices of all the lower cheek teeth as given by Dr. Pilgrim as follows:

	<i>Sivapithecus</i>	Man
m ₃	93.7	91.6
m ₂	94.6	94.4
m ₁	92.1	92.
pm ₄	116.5	112.7
pm ₃	110.1	111.6

The premolars also approach the human type in fundamental pattern.

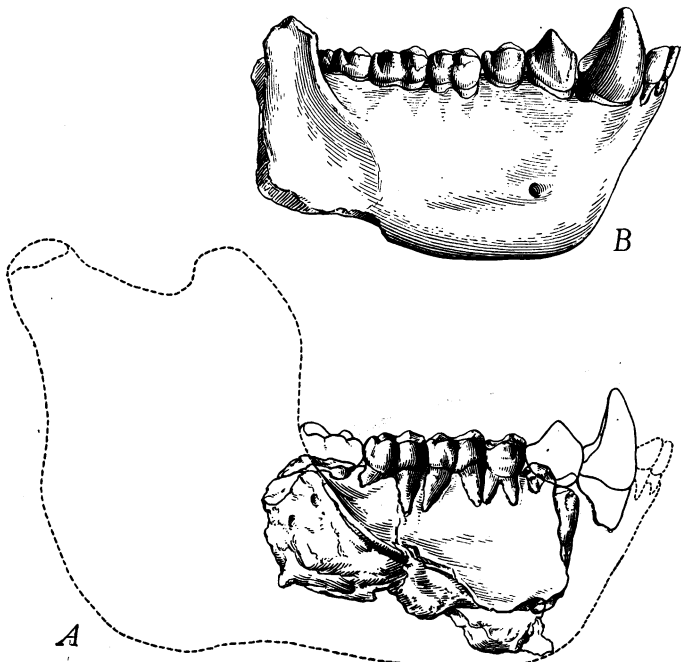


Fig. 14. Comparison of *Sivapithecus* and *Dryopithecus*. Side views of lower jaw. Both figures $\times \frac{2}{3}$.

A. *Sivapithecus indicus*. New restoration based on casts of the original specimens. Side view (Compare fig. 13A).

The fully shaded part represents the topotype or principal specimen. The third molar (outline) is the type. The canine and anterior premolar are referred specimens belonging to other individuals. The anterior premolar may be somewhat too large. The dotted parts are hypothetical.

B. *Dryopithecus fontani*. From Branco, after Gaudry.

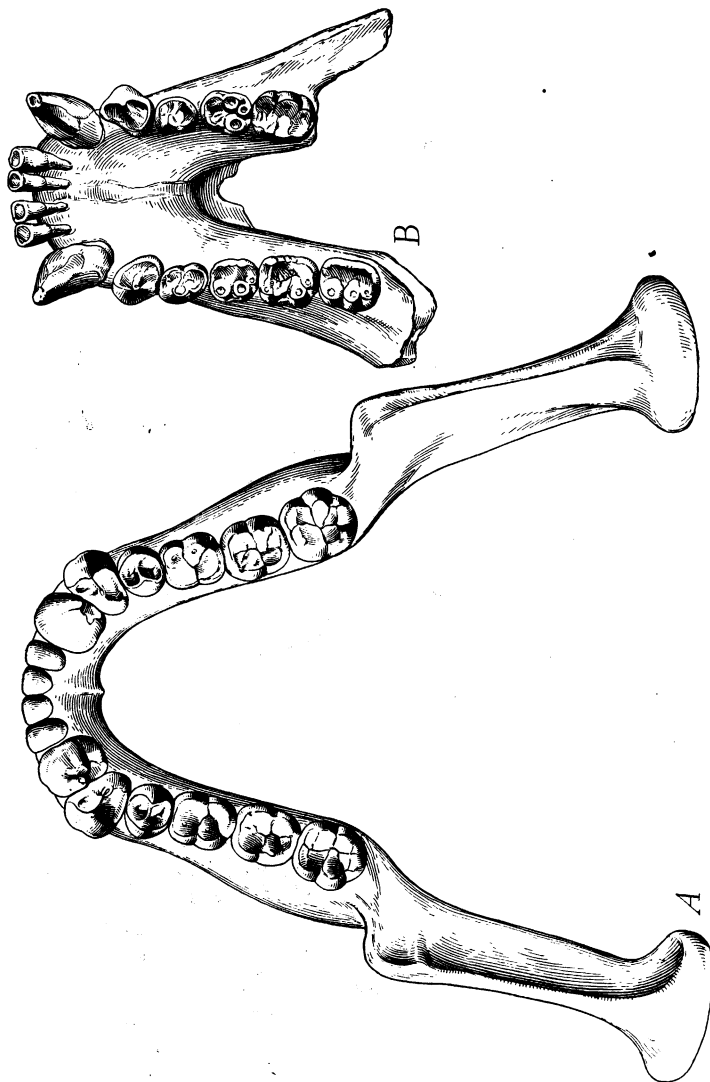


Fig. 15. Comparison of *Sivapithecus* and *Dryopithecus*. Lower jaws, top view. $\times \frac{2}{3}$.

A. *Sivapithecus indicus*. Provisional and partly hypothetical restoration by Pilgrim.

The subhuman character of the *Sivapithecus* jaw and dentition, as thus represented, is criticised adversely in the text.

B. *Dryopithecus fontani*. Upper Miocene, Europe. After Branco.

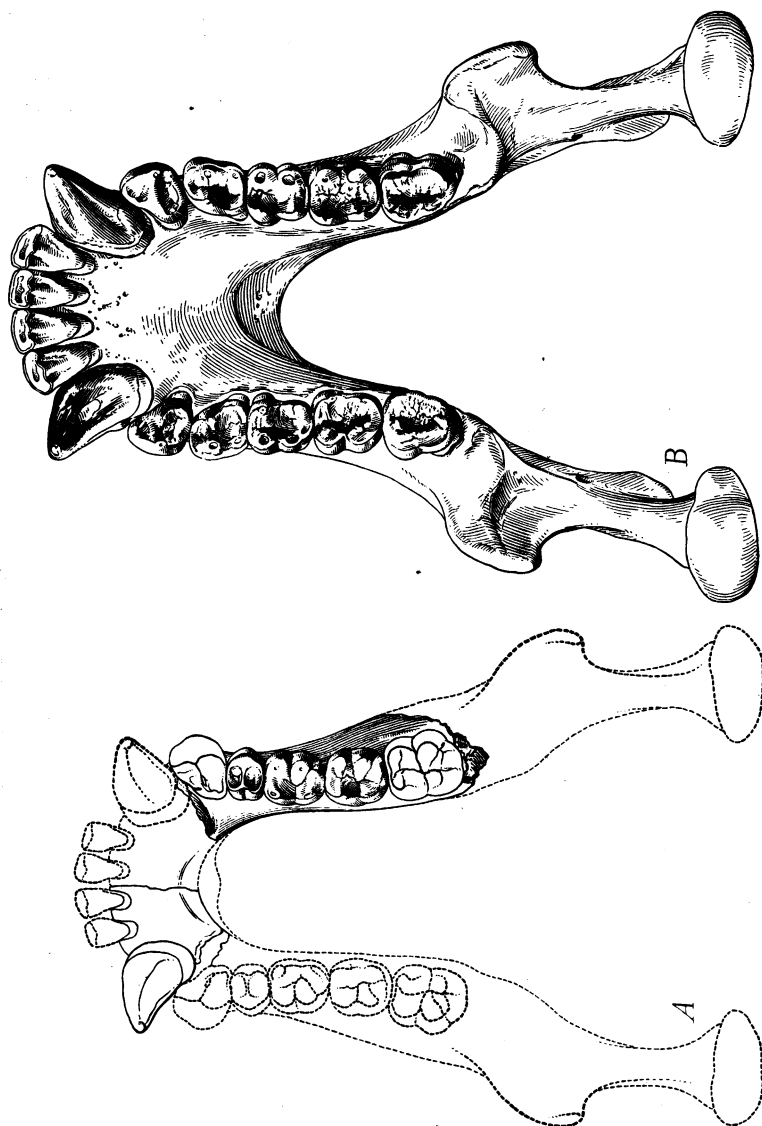


Fig. 16. Comparison of *Sivapithecus* and Orang. Lower jaws, top view. $\times \frac{2}{3}$.

A. *Sivapithecus indicus*. New restoration. Compare with Fig. 15A, B. Conventions as in Fig. 14A. The anterior premolar is probably too large.

According to the author's view *Sivapithecus* is nearly allied to *Dryopithecus*.

B. Male Orang jaw.

In Dr. Pilgrim's provisional restoration the symphysis is very short; the canines are set more internally to the front premolars, as in man, instead of fully in front of them, as in typical anthropoids, and the opposite halves of the mandible are made more divergent than in anthropoids.

Among my reasons for doubting the accuracy of Dr. Pilgrim's restoration are the following:

First, that, so far as it is preserved, the jaw fragment and all the cheek teeth are unquestionably closer in structure to *Dryopithecus* and even to the orang than they are to *Homo*. The same is true of the referred canines.

Secondly, when the three molars and posterior bicuspid are placed parallel to those of an orang the premolar and canine alveoli also agree in general position and the canine is not much if any more internal to the anterior premolar than it is in some orangs.

Thirdly, the presence of a heavy ape-like canine and anterior premolar seems quite inconsistent with the extremely shortened symphysis assigned to *Sivapithecus* in Dr. Pilgrim's provisional restoration.

Fourthly, I think that Dr. Pilgrim's figures of the symphysial fragment (pl. 2, figs. 1-1a) are not *true* side, top, front and inside views but all oblique views, which foreshorten the apparent length of the symphysis and cause the canine to appear too far internal to the front premolar.

Fifthly, the teeth and the front part of the jaw are very different in details from those of *Homo heidelbergensis*, *H. neanderthalensis* (Krapina jaws) or any other known human types.

In brief I would be inclined to restore the *Sivapithecus* jaw more after the pattern of a female orang than after that of early races of man. Conceivably *Sivapithecus* might be related to *Palæosimia* which is known only from a third upper molar. This is a well rounded tooth, as is also the third lower molar of *Sivapithecus*, but is distinguished by the wrinkling of the enamel.

By far the most unhuman features of the *Sivapithecus* jaw are the ape-like canine and front premolar. Those investigators who do not accept as a fact the frequent reversal of evolutionary tendencies, who expect very remote ancestors to foreshadow all the characters of their specialized descendants, and who, not finding such ancestors, make every group indefinitely polyphyletic and push all phyletic lines backward as nearly parallel lines meeting only at excessively remote periods, will undoubtedly see in the ape-like canines and front premolars of *Sivapithecus* an almost insuperable objection to close kinship with man. They will regard this genus as merely an extremely brachycephalic offshoot of the *Propliopithecus*-*Dryopithecus* group with no special affinity to the Hominidæ. At the other extreme Pilgrim would remove it very far from all the Simiidæ and place it in or

near the ancestral line of the Hominidæ, finding the common stem of Simiidæ and Hominidæ only in a remote and unknown Eocene common stock.

The presence of ape-like canines and front lower premolars does not in itself necessarily exclude *Sivapithecus* from kinship with man, but rather, as Dr. Pilgrim thinks, it may well be a character which should perhaps be expected in a mid-Tertiary human precursor. However, even if it should be thoroughly established that *Sivapithecus* is directly ancestral to the Hominidæ, this would not, in the reviewer's opinion, warrant its removal from the Simiidæ to the Hominidæ, unless it could be shown that in the totality of its skeletal characters the genus was more manlike than ape-like.

***Dryopithecus* Lartet.**

(Figs. 14B, 15B, 17D, 18-21 24B, 25B, C).

The genus *Dryopithecus* was formerly known only in the Upper Miocene and Pliocene of Europe. Several lower jaws with teeth have been described by Lartet, Gaudry, Branco, Harlé, A. S. Woodward. Isolated lower molars have been described by Branco, Abel, Schlosser and others. A couple of upper molars have been figured by Branco. The Indian material referred to this genus by Pilgrim is of similar fragmentary character, but is of great importance not only in further emphasizing the faunal affinities of the Siwalik series with the Upper Tertiary of Europe, but also in its bearing on the phylogeny of the anthropoids.

The pattern of the lower molars of *Dryopithecus* may be broadly described as follows: There are five main cusps, three of which (protoconid, hypoconid, mesoconid) are on the external side of the crown and two (metaconid, entoconid) on the internal side. The metaconid, which is the highest cusp, is directly internal to the protoconid; the hypoconid is opposite the valley between the metaconid and the entoconid; the mesoconid (or hypoconulid) is on or near the postero-median border of the tooth, behind the hypoconid and entoconid. The external basal cingulum is more or less reduced but sometimes persists opposite the posterior part of the protoconid. In front of the protoconid and metaconid is a remnant of an earlier trigonid basin in the form of a transverse valley; into this depression fitted the hypocone of an upper molar. At the back of the tooth there is a very thick cingulum which sometimes is confluent with the mesoconid. The surface of the lower molar crown is likewise characterized by the arrangement of certain furrows; the hypoconid is limited anteriorly and posteriorly by two deep transverse furrows which converge into a prominent inverted V(Δ), the narrow end of which is at the centre of the crown. From the narrow end and

sides of this truncated V other furrows radiate as follows: (a) an anterior central furrow between the protoconid and metaconid, (b) a posterior central furrow between the mesoconid and entoconid and (c) one or two internal furrows between the metaconid and entoconid.

This general pattern is not only characteristic of all species of *Dryopithecus* both European and Indian, but also of the new genus *Sivapithecus* which Pilgrim regards as ancestral to *Homo sapiens*. The *Dryopithecus* lower molar without doubt also reveals the fundamental ancestral pattern

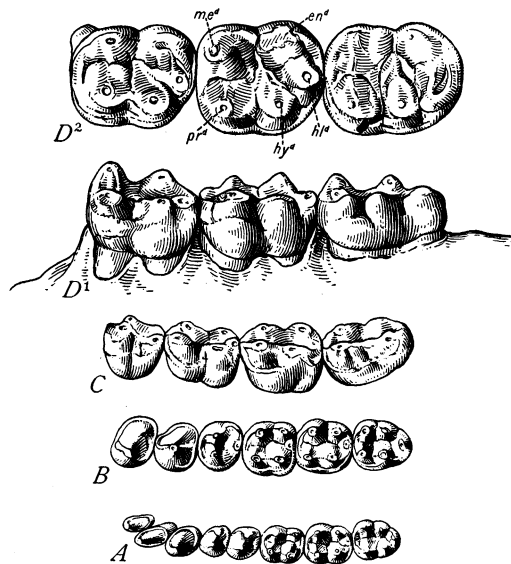


Fig. 17. Comparison of lower teeth of *Parapithecus*, *Propithecus*, *Pliopithecus*, *Dryopithecus*.
× $\frac{3}{2}$.

- A. *Parapithecus Fraasi*. Lower Oligocene, Fayûm, Egypt. After Schlosser.
- B. *Propithecus Haeckeli*. Lower Oligocene, Fayûm, Egypt. After Schlosser.
- C. *Pliopithecus antiquus*. Lower Pliocene, Europe. Oblique view. After Abel.
- D¹, D². *Dryopithecus fontani*. Upper Miocene, Spain. After Smith Woodward. D¹ outer side, D² crown view.

in the Orang, Gorilla, Chimpanzee and even Man, but it is more or less masked in each of these genera by secondary modifications. Judging from many analogies in other mammalian groups the *Dryopithecus*-pattern was ultimately derived, I believe, from the very primitive pattern exhibited in the genus *Parapithecus* Schlosser from the Lower Oligocene of Egypt; which is also structurally ancestral to the *Propithecus*-Gibbon series.

Although this conception of the morphology and relationships of the *Dryopithecus* molar is based upon the specimens figured by Gaudry,

Schlosser, Abel, Branco, Harlé, Pilgrim and others, none of these authors should be considered as responsible for the present interpretation and formulation of the facts.

Difficulty has been caused by the shifting relations of the hypoconulid ("mesoconid") to the mid-line in *Dryopithecus* and other Primates. Branco, Schlosser, Abel and Pilgrim seem to have assumed that the primitive position of the hypoconulid is on the outer side of the crown in line with the protoconid and hypoconid and they speak frequently of an "inward displacement of the mesoconid." But a central position of this cusp is the primitive condition in many mammalian groups. It is seen in the Lower Eocene Anaptomorphidæ, it persists in the oldest known anthropoids *Propliopithecus* and *Parapithecus* from the Lower Oligocene of Egypt and continues into the *Pliopithecus*-gibbon line. Its position is variable in *Dryopithecus*, where it is occasionally more or less displaced toward the outer side as it is more or less in the Orang, Chimpanzee, Gorilla and *Eoanthropus*. In all genera it is more central in the conservative first lower molar than in the more progressive second and third. It strikes behind the inner part of the metacone and externally to the hypocone of the upper molars. In the milk teeth it is often more or less central in position. In *Sivapithecus* it is intermediate in position, somewhat further inward than in Abel's "Second Type" of *Dryopithecus fontani*. In man it is usually more median in position, especially in m_1 , but is occasionally somewhat displaced to the outer side. The median position of the hypoconulid in man may be either a primitive or a secondary character. The frequent disappearance of the hypoconulid on the second and third molar in man is correlated with the rounding of the whole molar crown and with the rotary action of the lower jaw.

***Dryopithecus chinjiensis* Pilgrim.**

(Figs. 18A and Part I, Fig. 18A).

The type consists of an isolated third lower molar (op. cit., pl. 2, figs. 6, 7) from the Chinji horizon of the Lower Siwaliks. The author assigns this tooth to the genus *Dryopithecus* with some doubt; but that is evidently only because nowadays "genera" are about equivalent to the old-fashioned "good species." The author's excellent figure of the type clearly reveals the generic pattern as described above and the differences between this tooth and those referred to *D. fontani* of Europe are no greater than the differences between the latter and the type of *D. darwini*. The author suggests (p. 66) that *D. chinjiensis*" . . . might indeed even be the direct

ancestor of the Gorilla," and a careful comparison of the figures of the first and third lower molars (the only ones known) reveals striking fundamental

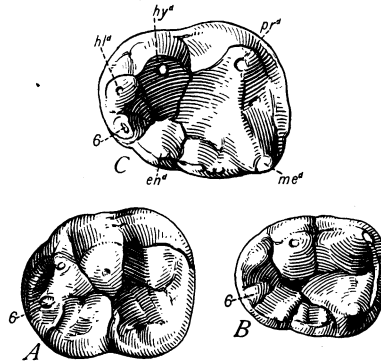


Fig. 18. Comparison of the third left lower molar of *Dryopithecus chinjiensis* (A), *D. punjabicus* (B) and *Gorilla* sp. (C). $\times \frac{3}{2}$.
A and B after Pilgrim.

resemblances to the corresponding teeth of the Gorilla, the differences being all apparently primitive characters.

Dryopithecus punjabicus Pilgrim.

(Figs. 18B, 19B, 20A, 25B, 34A.)

The specimens referred to this species are believed to have come from the summit of the Chinji zone (Lower Siwaliks) and from the lower part of the Nagri zone (Middle Siwaliks). The type consists of parts of the mandible containing the third right lower molar and the second left lower

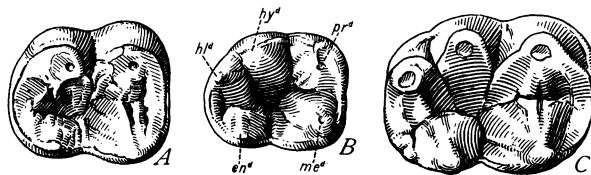


Fig. 19. Comparison of the second left lower molar of *Dryopithecus punjabicus* (B), Orang (A) and *Gorilla* (C). $\times \frac{3}{2}$. B after Pilgrim.

molar. The third lower molar shows all the generic characters above noted; its specific characters need not be considered here, except to note that it is elongate tapering posteriorly, with low cusps, and with the internal margin

broken up into numerous small cusps by sharp transverse furrows. It is more primitive than the third lower molar of the Chimpanzee and it also suggests the contour of the third lower molar of the Gorilla. The second lower molar is elongate, narrow posteriorly and has an accessory cusp behind the metaconid. (Apparent vestiges of this cusp appear in certain chimpanzees).

The author refers to this species a specimen from the Nagri horizon of

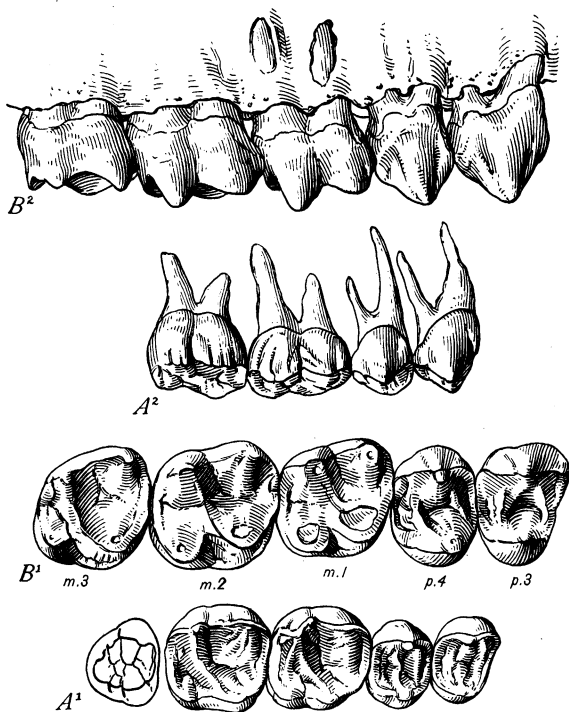


Fig. 20. Comparison of upper cheek teeth of *Dryopithecus punjabicus* (A¹, A²) and Gorilla (B¹, B²).
× $\frac{1}{4}$.

A¹, A² after Pilgrim.

the Simla Hills, which is highly important, since it is a maxilla containing both premolars and the first and second molars in excellent preservation (pl. 3, figs. 1, 2). The author observes that in comparison with the upper molars of the European species of *Dryopithecus* (as figured by Branco and by Schlosser) the Indian specimens agree so closely, apart from minute differences, as to make it fairly certain that they belong to the same genus. The author refers it to *D. punjabicus* on account of the "remarkable analogy in

structure and ornamentation of these molars and those of the Chinji mandible" (type), special points of resemblance being the serration of the outer edge of the tooth, the lowness of the cusps and the complex character of the enamel folding. To the reviewer these upper teeth, as well as the isolated ones figured in Pl. 2, figs. 4, 5, bear also a highly significant resemblance to those of both the Gorilla and the Chimpanzee, not only in the general plan of each premolar and molar but also in a great many details.

***Dryopithecus giganteus* Pilgrim.**

(Fig. 21 B.)

This species comes from a higher horizon, very near the boundary between the Lower and Middle Siwaliks, and is referred to the Nagri horizon of the Middle Siwaliks. The type and only known specimen is a third right lower molar, which is not only much larger than that of any other species of the genus but is much larger than that of the Chimpanzee, in

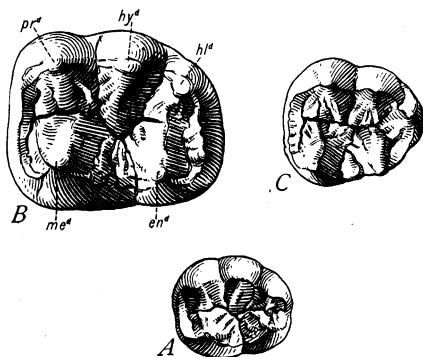


Fig. 21. Comparison of third right lower molar of *Dryopithecus rhenanus* (A), *D. giganteus* (B) and Chimpanzee (C). $\times \frac{3}{2}$.

A from a cast of a specimen figured by Branco.

B from a cast of the type.

which this tooth is more or less retrogressive. To the reviewer this tooth is curiously suggestive of the corresponding tooth in certain chimpanzees, especially in the general pattern, course of all furrows, character and position of the wrinkles, the most important difference being the greater size and the fact that in the modern genus the posterior part of the tooth is usually narrower. *D. giganteus* therefore appears to be rather closely allied to the ancestors of the Chimpanzee. The wide range in size in the species of *Dryopithecus* is noteworthy.

***Palæopithecus sivalensis* Lydekker.**

(Fig. 22 B, C.)

The type consists of a palate containing the teeth of one side except the incisors. The horizon is the Dhok Pathan zone or Upper Middle Siwaliks, regarded as of Pontian or Lower Pliocene age. Lydekker referred this specimen to a new genus *Palæopithecus* in 1879, but later (1886, p. 3)

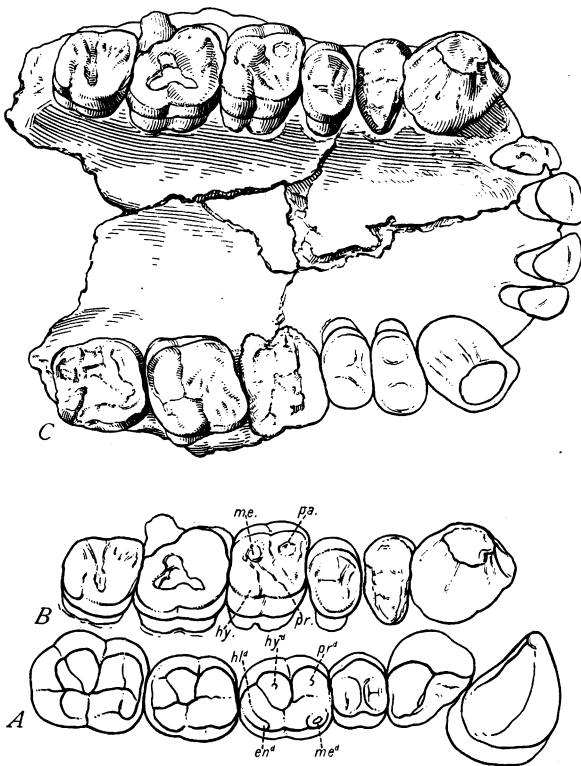


Fig. 22. Upper teeth and palate of *Palæopithecus sivalensis* (C). After Dubois. $\times \frac{1}{4}$.

Upper teeth of *Palæopithecus* (B) compared with lower teeth of *Sivapithecus* (A).

The canine, anterior premolar and third molar of *Sivapithecus* belong to different individuals.

The relations between the lower teeth of *Sivapithecus* and the upper teeth of *Palæopithecus* seem hardly close enough to be indicative of generic affinity.

came to the conclusion that it was "an ape generally distinct from both *Gorilla* and *Simia*, but so close to *Troglodytes* [the Chimpanzee] as to leave little doubt as to its identity — an identity rendered the more probable by the occurrence of *Cynocephalus* in the same region. In those respects

in which the Siwalik *Troglodytes* differs from the existing African species it shows in a still more marked degree the approach to the human type of dentition presented by the latter, and serves, in a small degree, to bind still closer the connection between the *Simiidae* and the *Hominidae*. In the inclination of the two series of cheek-teeth and the relative lateral position of the premolars to the true molars the genus *Hylobates* makes an approach to the human type which is wanting in all the larger existing *Simiidae*, and it is very noteworthy to find a similar relation obtaining in the Siwalik *Troglodytes*, accompanied by a more human-like structure of the upper premolars."

Dubois (1897) dissented from Lydekker's conclusions, gave a corrected figure of the type and concluded that one should rather assign to *Palæopithecus* a position in the family *Simiidae* lower than that of any of the four living genera (p. 90); also (p. 96) that the Indian *Palæopithecus* may have been a later member of an older group of anthropoids that included the European Miocene genera *Pliopithecus* and *Dryopithecus*.

Dr. Pilgrim (1915) gives an extended analysis of the known characters of *Palæopithecus*, in which he lists eleven characters in which the type differs from the chimpanzee, seven in which it differs from man, three which distinguish it from *Dryopithecus* and so forth. To the reviewer many of the characters which distinguish *Palæopithecus* from both the chimpanzee and the gorilla appear to be simply primitive characters, which may either prove to be characteristic of the Upper Siwalik ancestors of these apes, or may at that time have been retained by *Palæopithecus* as a conservative genus. The narrow palate, relatively small incisors and slightly convergent tooth rows are, for excellent reasons, to be ascribed to the ancestral anthropoids, since the opposite characters are characteristic specializations of all the larger existing *Simiidae*. In the existing chimpanzee, which is strongly brachycephalic, the upper cheek teeth are evidently beginning to suffer retrogressive changes such as have been carried to far greater lengths in brachycephalic races of man. Thus, the molars are assuming a rounded or subcircular contour, while the number of internal roots in the molars and of external roots in the premolars is apparently in process of reduction, by coalescence, from two to one. Hence in *Palæopithecus*, a more primitive anthropoid, it is not surprising to find more distinctly quadrilateral molars, with two distinct internal roots, and wider premolars with two distinct external roots.

Several of the characters in which *Palæopithecus* differs from the chimpanzee bring it closer to the gorilla: here belong the stouter canines, the somewhat higher cusps of the molars, the more quadrilateral molars, the greater width of the anterior premolars. To the reviewer it seems closer

to the gorilla notwithstanding the laborious arguments of Dubois and Pilgrim.

The dentition as a whole is also similar to that of *Dryopithecus punjabicus*, from which *Palæopithecus* may well be descended.

Pilgrim notes that it resembles *Pliopithecus* especially in the width and shortness of the premolars and first molar, the narrow palate and straight tooth row, the small incisors and general characters of the molars, so that as already said Pilgrim and Dubois regard it as a relative of *Pliopithecus*, from which according to Pilgrim it is distinguished by its greater size (the tooth row being nearly as long as in a chimpanzee), wrinkling in the enamel and reduction of the internal cingulum. The reviewer, on the other hand, regards the points of resemblance to *Pliopithecus* as all primitive characters.

Palæopithecus also resembles the Lower Siwalik genus *Sivapithecus* Pilgrim (to be noted below), in the general appearance of the molars, with relative width of the molars and anterior premolars, in the height of the cusps and in the amount and character of the wrinkling of the enamel. Lydekker indeed suggested that the jaw of *Sivapithecus* should be referred to *Palæopithecus*, a suggestion that has not yet been definitely disproved, since Dr. Pilgrim's principal objection to it is the assumed wide difference in the front part of the lower jaw in *Palæopithecus* and *Sivapithecus*; but this difference does not exist, if the reviewer's restoration of *Sivapithecus* is more correct than that of Dr. Pilgrim.

In brief I think that Dubois and Pilgrim have largely misinterpreted the relationships of *Palæopithecus* and that it is quite close to the ancestor of the Gorilla, from which it differs only in primitive characters.

V. THE EXTINCT ANTHROPOIDS AND MEN OF EUROPE; ALSO PITHECANTHROPUS.

***Pliopithecus antiquus* Gervais.**

(Figs. 10C, 11C, 23A).

This Upper Miocene and Lower Pliocene genus has been regarded by nearly all authors except Dubois (1897) and Pilgrim (1915) as an ancestral Gibbon, Hoffman (1893) after a very careful investigation even placing it in the genus *Hylobates*. Its resemblances to the Gibbons are indeed so numerous and so fundamental that I do not doubt that it is at least nearly related to that group and in most if not all characters structurally ancestral. Dr. Pilgrim (1915) on the contrary thinks it is excluded from the direct ancestry of the Gibbons by at least the following characters: "1) The greater proportionate breadth of the teeth in the front of the jaw in *Pliopithecus*,

particularly marked in the case of pm_3 , but noticeable in all the premolars, upper as well as lower, and in the first molar above and below.

2) The much longer symphysis in *Pliopithecus*.

3) The greater divergence of the mandibular rami."

But, to deal with these in reverse order, why is the greater divergence of the mandibular rami regarded as a specialization in *Pliopithecus*, and why are the more parallel rami of the Gibbons regarded as more primitive? From the reduction of the dental formula and crowding out of one pair of incisors and the two anterior pairs of premolars in all Old World Anthropeidea, and from the evidence that all this series eventually ran back into small insectivorous-frugivorous, short-faced lemuroids analogous to *Necrolemur* and the Anaptomorphidæ it seems quite probable that in the remote ancestors of the series the front of the jaw was quite narrow, with small semi-procumbent canines and incisors, the mandibular rami divergent rather than parallel. Such a jaw, as shown above, is already known in the Lower Oligocene *Parapithecus*. On the other hand the parallel rami, wide muzzles and chins of the Gorilla, Chimpanzee and Orang are obviously correlated with the widened incisors and tusk-like canines. The Gibbon, too, has acquired almost sabre-like, wide-spread, although slender, upper canines, and somewhat wider incisors; in connection with these features its jaw has widened distally and its mandibular rami have become parallel rather than convergent. To the same sabre-like form of the canines as a primary adaptation may reasonably be credited the elongate compressed form of the front lower premolar, as

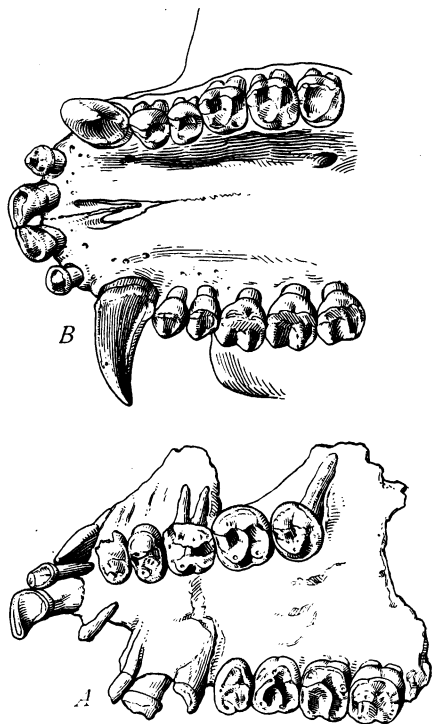


Fig. 23. Upper teeth and palate of (A) *Pliopithecus antiquus* (after Hoffmann) and (B) *Hylobates lar*. Both figures $\times \frac{1}{2}$.

This figure well illustrates the relatively close structural and genetic relationships of these genera. The modern genus has become specialized in the widening of the median incisors, in the laniary form of the canines, in the anteroposterior elongation of the premolars and in the reduction of the cingulum of the molars.

well as the oblique downward prolongation of the front portion of its crown, features developed in far greater degree in the baboons, where their association with the tusk-like form of the upper canine is very obvious. *Pliopithecus* on the other hand in the divergent rami, in the smaller canines and in the wider premolars has retained the characters seen in greater emphasis in the far older Oligocene genus *Parapithecus*.

The greater width of the upper premolars in *Pliopithecus*, as compared with the Gibbons, means only that in the Gibbons the relative antero-posterior diameter of these teeth has increased, perhaps in correlation with a slight lengthening of the premolar region in the lower jaw, and the same is true of the greater relative width of the first upper and lower molars. As noted above in many mammals there is often a tendency for molars to transform from a relatively wide and triangular crown to an anteroposteriorly elongated quadrangular crown. This tendency has affected the Gibbon far less than the Gorilla, but the Gibbon has not escaped it entirely as the foregoing comparison with *Pliopithecus* indicates. The greater breadth of the lower premolars in *Parapithecus* and *Propliopithecus* by no means excludes them from the ancestry of the Gibbons. In the remote forerunners of the whole anthropoid series there was as above noted a marked fore-and-aft crowding of the front of the jaw, a process seen also in the Anaptomorphidæ, where it also results in a relative widening of the premolars.

As for the much longer symphysis in *Pliopithecus*, that is associated perhaps with the far heavier mandibular rami, very wide ascending ramus and heavy jaw muscles. Such a type of jaw is clearly foreshadowed in *Propliopithecus* and is carried to an extreme in the male Orang. While there is a truly amazing variation in the form of the jaw in the Siamang, as shown by Bolk (1915), the very slender jawed types with a weak symphysis have a degenerate look, which as in the case of certain Cebidæ and Lemuridæ is, I believe, a late acquisition.

Among the characters which in Dr. Pilgrim's view tend to exclude *Propliopithecus* and *Pliopithecus* from the ancestry of the Gibbons is "the fact that m_3 is shorter than m_2 ." "There can, however, be no doubt," continues Pilgrim (p. 63), "that the latter character is typical of an advanced stage of evolution." But in the far older Anaptomorphidæ of the Lower and Middle Eocene m_3 is usually a *smaller* tooth than m_2 and is sometimes even shorter. The further fact that it is shorter than m_2 in both the known Oligocene genera, *Propliopithecus* and *Parapithecus*, suggests that this is a primitive character rather than that these genera should be excluded from the ancestry of *Propliopithecus* and the Gibbons.

"The question of the canines in this branch merits consideration," says our author (*loc. cit.*). "Are the small canines in *Propliopithecus* an instance

of precocious reduction, similar to what has occurred at an extremely recent period in the case of the *Hominidæ*, or were the canines of the Anthropoidea primitively small? The answer to this can only be hazarded as a guess." But to the present writer the evidence on this matter seems fairly decisive. The canines are quite small in most of the Lower Eocene Anaptomorphidæ and in the oldest known Anthropoid, *Parapithecus*. In *Propliopithecus*, *Pliopithecus* and *Dryopithecus* the progressive enlargement of the canines can be traced to its extreme development, in the modern giant apes. Dr. Schlosser's view is that in the Primates generally the canine may have originated as a front premolar which gradually became caniniform, and that the original lower canine came to function as an incisor. This hypothesis, although favored by Dr. Pilgrim (p. 64), is, in my judgment, totally erroneous and based upon a false analogy supplied by the Lemuridæ. For the lower canine of all anthropoids and in the Adapidæ and Cebidæ fits in front of the first maxillary tooth, which is surely an upper canine. Hence the lower canine of anthropoids is homologous with the lower canine of lemuroids.

In conclusion it may be remarked that the present writer during the past fifteen years has had perhaps unusual opportunities for studying the evolution of the teeth in many phyla of mammals. From this experience has grown the impression that mere quantitative differences in degree, or proportion, should not, in themselves and without further evidence, be deemed sufficient to exclude an earlier form from the ancestral line of a later form. In many cases I believe there are marked changes and even reversals in the trend of evolution as we follow the lines onward — of which many fairly well tested instances might be cited.

Such a reversal of trend may well be illustrated in the history of the dentition in the line leading to the Gibbons. At a very remote period, perhaps in the Lower Eocene, there was probably a marked anteroposterior crowding of the front part of the lower jaw, with a consequent elimination of one incisor and two premolars on each side, and a widening of the lower premolars, this stage being represented by *Parapithecus* and *Propliopithecus*. Subsequently there was a secondary increase of length in the front part of the rami, associated with an increase in anteroposterior diameter and a decrease in width in the lower premolars, a rapid enlargement of the canines, a widening of the distal end of the jaw and a parallel realignment of the lower tooth rows.

In brief it appears to the present writer that the genera *Parapithecus*, *Propliopithecus*, *Pliopithecus* and *Hylobates* (in the broad sense) offer a fairly good series characterized by the following changes: (a) increasing verticality of the incisors, (b) sabre-like elongation of the upper canines, (c)

shortening and widening of the symphysis, (d) anteroposterior lengthening of the premolars, (e) weakening of the body of the mandible, (f) rounding of the molar crowns and of all the molar cusps.

***Dryopithecus darwini* Abel.**

(Fig. 24B.)

This species, from the Upper Miocene of the Vienna Basin, is known only from the type, a third left lower molar.

From the writings and illustrations of Professor Abel (1902, p. 34) and Dr. Pilgrim (1915, pp. 15, 70) we learn that the third lower molar of this species has the following characters: both in length (13.5) and breadth (11.8) it exceeds the other European species of the genus and also *D. punjabicus*, but is considerably smaller than *D. chinjiensis* and much smaller than *D. giganteus* (length 19.1, breadth 15.3). Its breadth-index exceeds that of allied species and equals that of the Orang. The crown is low and the anterior moiety is much wider than the posterior one. The protoconid is very large and the hypoconid narrow. There is a massive external cingulum which is arranged almost precisely as in *Pliopithecus antiquus*. The enamel folds and wrinkles are more numerous and stronger than in the other European species and the deep furrows that form the characteristic *Dryopithecus* pattern fork at the ends. The inner side of the crown bears an accessory transverse furrow, as in *D. punjabicus*, *D. rhenanus* and *Homo*. The hypoconulid ("mesoconid") is placed further in toward the centre of the crown than in *D. fontani*.

D. darwini is undoubtedly widely different from Abel's 2nd type of *D. fontani*, in which m_3 is elongate, with a weak cingulum and externally placed hypoconulid; but it approaches Abel's "1. Type" of *D. fontani* which is a wider tooth, with inwardly placed hypoconulid.

From *D. rhenanus* the species under consideration is distinguished by its greater breadth, more wrinkled crown, more central hypoconulid. From two of the Indian species, *D. giganteus* and *D. chinjiensis*, it is readily dis-

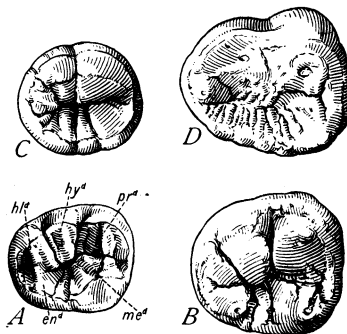


Fig. 24. Comparison of the third left lower molar of (A) *Dryopithecus rhenanus*, (B) *D. darwini*, (C) Strandlooper Bushman, (D) Orang. All $\times \frac{3}{2}$.

A and B from photographs by Abel.

Note the secondary furrows between the metaconid and the entoconid.

tinguished, but it is less distinct from *D. punjabicus*, to which it may be allied. The strong basal cingulum, as noted by Abel, seems to be a primitive character derived from *Pliopithecus*-like ancestors.

Professor Abel also notes that this tooth in its whole appearance and size, and in the arrangement and abundant branching of the furrows, approaches the men of Krapina; it differs, however, in the narrowness of the posterior moiety of the crown — a primitive character.

***Dryopithecus fontani* Lartet.**

(Fig. 14B, 15B, 17D¹, D².)

This species is known chiefly from several lower jaws which have been figured by Lartet, Gaudry, Harlé, Smith Woodward and others. Abel (1902, p. 33) has distinguished two types of this Upper Miocene ape of France and Spain. In the first type the molars are a little wider than long, the hypoconulid is more central and posterior in position. In the second type the molars are considerably longer than broad and the hypoconulid is more external in position, almost as much as the hypoconid and protoconid. Both types have a weak basal cingulum on the front and outer sides.

The third lower molar is a little smaller than in *D. punjabicus* which, according to Pilgrim (1915, pp. 14, 15), is distinguished further by minor details such as the absence of fine wrinkles and the absence of a serrated margin on the metaconid and entoconid. From *D. chinjiensis* and *D. giganteus* the species under consideration is distinguished by its smaller size. The lower cheek teeth of *D. fontani* are of primitive anthropoid type of relatively very small size, with few wrinkles, with considerable remnants of the external cingulum and a relatively short first molar.

The jaw of *D. fontani* is of great interest on account of its relatively primitive character. The massive horizontal ramus is shorter than that of the Gorilla, which is secondarily elongated. The region of the swollen symphysis is of generalized anthropoid type, as shown in Dr. Smith Woodward's comparative cross sections (1914, p. 317). *D. fontani* is, in one sense, a collateral ancestor of the Gorilla, but perhaps not the direct ancestor, which may well be *D. chinjiensis* of India. In most characters it is intermediate between the far older *Propliopithecus* of the Fayûm and the modern Gorilla.

The varied relative lengths of the third lower molar in the anthropoids and man have led Dr. Pilgrim to exclude forms with a short m_3 from ancestral relations with those with a long m_3 . The third lower molar in *Proplio-*

pithecus is relatively and absolutely short. According to Pilgrim (1915, p. 72) the ratio of length of m_3 to that of m_2 in this genus is only 96.4 as compared with 110.1 in *Pliopithecus* in which the third molar is relatively very long. In the Gibbons m_3 is extremely short (80–88); in *Dryopithecus fontani* it is relatively much longer than is *Propliopithecus*, but only slightly longer than in the Gorilla (101.2) and considerably longer than in the Chimpanzee.

Perhaps the majority of palæontologists of the present time, who believe in orthogenesis, the irreversibility of evolution and the polyphyletic origin of families, will assume that a short molar must keep on getting shorter, that it can never get longer and then again grow relatively shorter and therefore that *Propliopithecus* with its extremely short third molar and *Dryopithecus* with its long m_3 are alike excluded from the ancestry of the Gorilla, in which there is a slight retrogression in length of m_3 . After many years reflection and constant study of the evolution of the vertebrates however, I conclude that "orthogenesis" should mean solely that structures and races evolve in a certain direction, or toward a certain goal, only until the direction of evolution shifts toward some other goal. I believe that the "irreversibility of evolution" means only that past changes irreversibly limit and condition future possibilities, and that, as a matter of experience, if an organ is once lost the same (homogenous) organ can never be regained, although nature is fertile in substituting imitations. But this does not mean, in my judgment, that if one tooth is smaller than its fellows it will in all cases continue to grow smaller. Frequently this is the case, but sometimes a relatively small member of a series will enjoy a secondary increase in size, or a relatively narrow structure will widen. Finally I believe that "the polyphyletic origin of families" is to some extent a contradiction in terms; for if the families are of widely diverse or convergent origin then they are not natural. On the contrary natural families perhaps usually arise from a single genus or from closely allied genera.

Hence I know no proved general principles which forbid us to believe that the last lower molar of anthropoids has always been rather variable in relative size; that it was at first small, but became larger and lengthened in *Pliopithecus* and *Dryopithecus*, becoming a little shorter in the Gorilla, much shorter in the Chimpanzee and excessively short in the Gibbon.

In the last named genus the sabre-like enlargement of the canines has thrown more work upon the masseter muscles and upon the malar bone and less upon the temporals. This may be associated with the retrogressive character of m_3 . In the Gorilla, on the contrary, although the masseters are large the temporals are of enormous size and hence the third lower molar is also large. In the Chimpanzee the temporals are relatively smaller

than in the Gorilla and so also is the third molar. In Man the temporals are relatively small but the whole tooth now is so short that the large masseters still exert a strong and less oblique pressure upon the third molars which are consequently still of a fair size, although the first molars, which are in the position of greatest vertical pressure, have now become dominant.

From these and similar considerations I should expect that in *Propliopithecus*, from the small size of m_3 , the temporals would be relatively small, while from the vertical position of the canine and massive horizontal ramus the masseters ought to be powerful. In *Dryopithecus fontani* the temporal muscles would be only less developed than those of the Gorilla, while the massive symphysis and deep horizontal ramus indicate that the masseters also were powerful.

In conclusion I am unable to accept Dr. Pilgrim's view (*op. cit.*, pl. 4) that the Gorilla and Chimpanzee have been derived from none of the six known Indian and European species of *Dryopithecus* but trace their origin on separate parallel lines to an unknown proto-anthropoid stock that lived somewhere far back in the Lower Miocene. Such a view may possibly prove to be true; but before assuming it, what characters definitely exclude *D. chinjiensis*, *D. punjabicus* and *D. fontani* from at least very close kinship with the true ancestors of both the Gorilla and the Chimpanzee? While differences between the Miocene and modern genera are striking, my difficulty in fact is to find provedly aberrant characters which will definitely and positively exclude these forms from such ancestry. According to Dr. Pilgrim the cleft between Gorilla and Chimpanzee is so great that the latter is very widely removed from the known species of *Dryopithecus* in the Upper Miocene in India. But to me after comparing repeatedly the Indian types with the Gorilla and Chimpanzee the evidences at least of close kinship are of the most convincing character. According to this view the European *D. fontani* may even be directly intermediate between the Asiatic types on the one hand and the modern African Gorilla on the other; while the allied *D. rhenanus* may stand nearer to the direct ancestors of the Chimpanzee.

***Dryopithecus rhenanus* (Pohlig).**

(Part I, Figs. 12D, 15B; Part II, Figs. 21A, 24A, 25C, 26B).

While *D. fontani* is of Upper Miocene age *D. rhenanus* comes from the Lower Pliocene (Swabian Böhnerz). It is represented chiefly by two upper molars and a number of lower molars, from the Swabian Alps, which have been very carefully figured by Branco (1898, Taf. I, II). According to Abel (1902, p. 2) the real type of the species is a femur from the sands of

Eppelsheim, described by Pohlig (1895) as *Paidopithecus rhenanus* and by Dubois (1897) as *Pliohylobates eppelsheimensis*. These were later referred by Schlosser (1902), along with the upper and lower molars, to the genus *Dryopithecus*. Abel defines the species as follows: Molars longer than broad (except the lower m_1), the hypoconulid placed well in toward the centre. Basal cingulum as a rule not present, except on the last lower deciduous molar.

The trigonid basin is represented by a transversely oval pit at the front end of the crown, while a similar pit at the hinder end lies between the remnant of the posterior cingulum and the ridge connecting the entoconid and the hypoconulid. This ridge is quite prominent in this species and in *D. giganteus* but not in other species.

The upper molars are quadritubercular with strong folds and wrinkles.



Fig. 25. Comparison of left upper molars.

- A. *Grhipopithecus suessi*, m^3 . After Abel.
- B. *Dryopithecus punjabicus*, m^1 . After Pilgrim.
- C. *Dryopithecus rhenanus*, m^1 . From a cast of a specimen figured by Branco.
- D. Chimpanzee, m^1 . A. M. N. H. No. 35550.
- E. Orang, m^1 . A. M. N. H. No. 35549.

They are distinguished from the upper molars referred to *Dryopithecus punjabicus* by the following characters observed by Pilgrim (1915, p. 20). In the Indian species, "the breadth index of the molars is greater. The cusps are probably lower. The outer cingulum is less clear. . . . The furrows on the outer cusps cross the edge of the tooth, and so produce in side view a serrated appearance, which appears to be absent from *Dryopithecus rhenanus*." The patterns of both the upper and the lower molars of *Dryopithecus rhenanus* approach those of the Chimpanzee in many characters, except that in the latter the molar crowns are more rounded, less quad-rangular and the third molars are often rounded and more degenerate in form. *D. rhenanus* may therefore represent a closely related if not directly ancestral phylum leading to the Pleistocene and Recent Chimpanzees.

Neopithecus.*Neopithecus brancoi* (Schlosser), Abel.*Anthropodus brancoi* Schlosser.

(Fig. 26A.)

Dr. Schlosser (1902, p. 266) suggests that the age of this specimen may possibly be Upper Pliocene. This genus and species is represented by a third lower molar from the Swabian Bohnerz. It is smaller than any species of *Dryopithecus* and is distinguished from all other anthropoids by its narrowness, the breadth index being only 75.7, while in *Dryopithecus* the index ranges from 80.1 to 87.4 (Pilgrim). Gaudry suggested that it was a last

lower milk molar but this view was vigorously combatted by Schlosser (1901, p. 262), who states that a milk molar may always be recognized by its strongly divergent roots which afford space for the replacing tooth beneath it, and by its thin enamel, the opposite characters being shown in the molar under consideration. Schlosser notes that this tooth has the characters of a permanent m_3 , that the posterior root is compressed and prolonged backward, while the median posterior cusp (hypoconulid) is unusually large and forms a third lobe. In

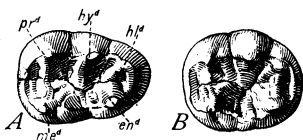


Fig. 26. A. Third lower molar of *Neopithecus* (*Anthropodus*) *brancoi* Schlosser. $\times \frac{3}{2}$. Drawn from a reversed image of a cast of the type, which is a third left lower molar.

B. Third right lower molar of *Dryopithecus rhenanus*. $\times \frac{3}{2}$. From a cast of a specimen figured by Branco.

the living anthropoids and in man this strong development of the posterior cusp of m_3 is no longer evident, but as it is found in almost all of the more ancient mammals and is present in *Pliopithecus*, the ancestor of the Gibbon, its presence in a fossil anthropoid, says Schlosser, is not surprising.

Under the name *Anthropodus* (which, as noted by Abel, was preoccupied by *Anthropodus* De Lapouge) Dr. Schlosser gave the following generic definition:

Anthropodus n. g. Only lower m_3 known, much longer than broad, without basal cingulum, consisting of five principal cusps, whereof the first inner cusp (metaconid) is higher and larger than the remaining second inner cusp (entoconid). Second outer cusp (hypoconid) and posterior cusp ("mesoconid") alternating; first outer cusp (protoconid) standing only a little further back than the first inner cusp (metaconid). Secondary intermediate cusps present behind metaconid and between entoconid and

mesoconid. Cusps provided with enamel grooves running toward the midline — one for each cusp except the metaconid which has three grooves. Peculiar topography (Sonstiges Relief): furrows and grooves weakly developed. Posterior root of m_3 , as a result of the talonid-like extension of m_3 , strongly extended posteriorly.

As specific characters Dr. Schlosser gives the dimensions of m_3 (length 10.3, greatest breadth 7.8, height of the metaconid 5.3) and the estimated measurement of the three lower molars (35 mm.) and of the premolars and molars (46.-48. mm.).

From the corresponding molars of *Dryopithecus* that of the present genus, continues Dr. Schlosser, is distinguished by its relatively slight breadth, by the relative lowness of the several cusps, by the strong development of the mesoconid, by the weakness of the enamel wrinkles and above all by the weak relief of its grinding surface; although the course of the principal enamel furrows is essentially the same in the two genera. At first sight it is much like a human tooth, but the latter is very much shorter and wider, with more massive higher cusps, and consequently deeper in-sinking of the middle of the crown; finally the enamel furrows and grooves in man are decidedly coarser and the whole relief of the crown somewhat more complicated and irregular. In all these details, except the less strongly developed cusps, *Anthropodus* is more primitive than either *Dryopithecus* or *Homo*. The origin of *Anthropodus* continues Schlosser (p. 267) is still obscure; the only certainty is that it is nearly related to *Dryopithecus*. It differs from *Pliopithecus* in the more complicated pattern of the crown through the appearance of enamel foldings and also in the disappearance of the basal cingulum; it is, however, more primitive than *Pliopithecus* in the posterior elongation of m_3 .

To the writer the type m_3 of the species under consideration presents an underlying resemblance to a certain m_3 of *Dryopithecus rhenanus* of which a photograph is given by Abel (1902, Pl., fig. 4), except that in *Neopithecus* the enamel is covered with coarse grooves, the tooth as a whole is elongate, narrow and the posterior pit is filled up. But, in spite of all efforts, the more precise relationship of *Neopithecus* remains obscure. It may well be a late descendant of some primitive species of *Dryopithecus* that still retained an elongate narrow m_3 . The enamel folds and wrinkles seem to have been acquired independently in all phyla of the man-anthropoid series.

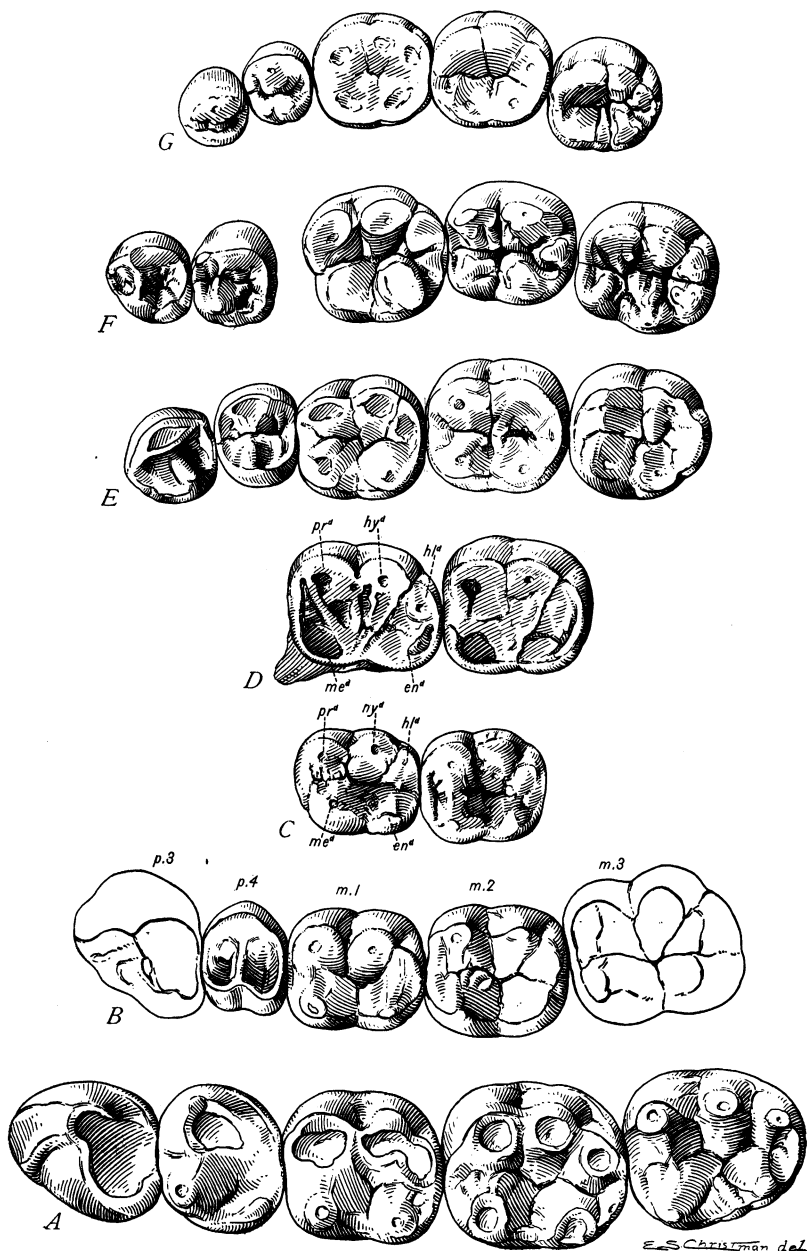


Fig. 27. Right lower premolar-molar series of primitive men and of anthropoids. Crown views. \times circa $\frac{3}{2}$.

- A. *Gorilla* sp.
- B. *Sivapithecus indicus*. After Pilgrim.
- C. *Pan* sp. Much worn molars of an old chimpanzee. After Miller.
- D. *Pan vetus*. Much worn molars of the Piltdown mandible; from a photograph published by Smith Woodward ($\times \frac{3}{2} +$).
- E. *Homo heidelbergensis*. From a photograph published by Schoetensack.
- F. *Homo sapiens*. Molars of an old female Australian black. Premolars of a male negro.
- G. *Homo sapiens*. Lower premolar-molar series of a Strandlooper Bushman (Gift of Dr. R. Broom).

From this series it appears that Mr. Miller is well warranted in stating that the Piltdown molars are generically referable to *Pan* rather than to *Homo*.

Anthropopithecus (Pan).**Pan vetus** *Miller.*

(Figs. 27D, 28, 29B, 30B, 31B, 32A, 33A).

In an earlier paper (1914) I have reviewed the controversy over the Piltdown remains (*Eoanthropus dawsoni*), emphasizing the entirely human character of the brain-case, the essentially ape-like character of the lower jaw and teeth and the doubts as to their association already expressed by several authors. With some doubts, which were even more strongly felt

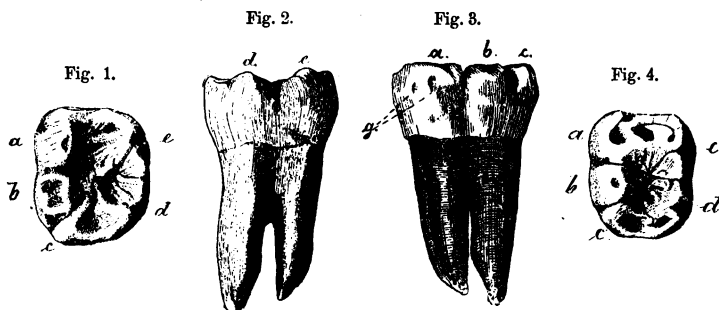


Fig. 28. Three views of first left lower molar figured by Nehring in 1895 as a human tooth, from the diluvium at Taubach near Weimar, together with a crown view (Fig. 4) of the corresponding tooth of a chimpanzee. All after Nehring. About $\frac{3}{2}$ nat. size. Fig. 1 crown view, Fig. 2 lingual side, Fig. 3 labial side.

Mr. Miller remarks that this tooth resembles the first lower molar of the Piltdown mandible and likewise represents a Pleistocene species of chimpanzee. Nehring himself noted its strong resemblance to a chimpanzee molar, but in spite of that referred it to *Homo*.

by my colleague Dr. Matthew, I was led to accept provisionally the association of the jaw with the skull, chiefly because the jaw is stated to have been found within a yard of the point where a piece of the occiput was discovered, and at precisely the same level. In this connection I said (op. cit., p. 194) that: "Fossil remains of anthropoids of any age have hitherto been exceedingly rare, and the chances that a jaw of a hitherto unknown type of ape should be washed into the same gravel bed with a human skull of conformable size, and that both should become mineralized in the same manner and degree, may be regarded as extremely small." The chances of such a coincidence occurring were, no doubt, extremely small, but nevertheless the event must have happened, for I consider that Mr. Gerrit S. Miller (1915) has practically demonstrated that the Piltdown lower jaw

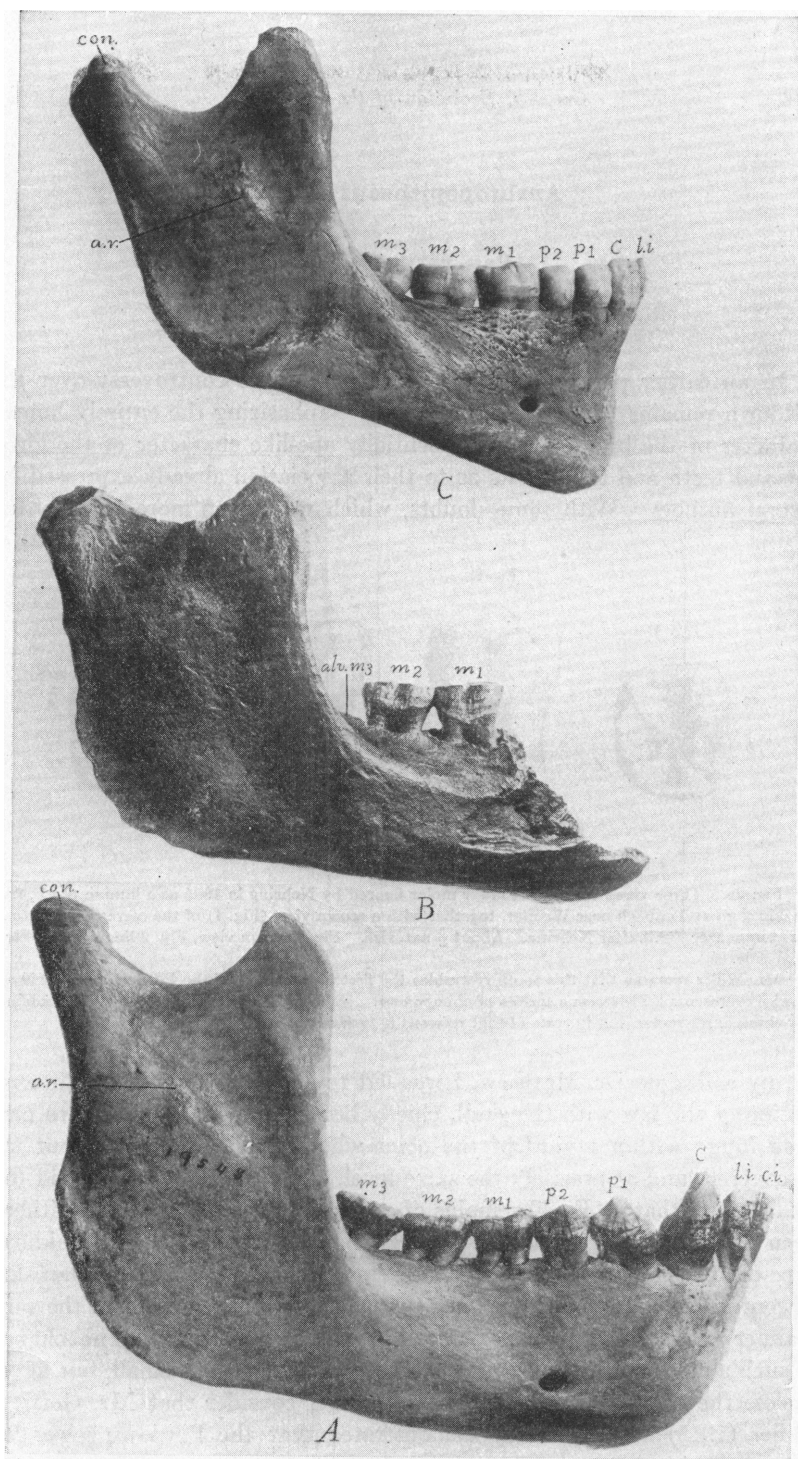


Fig. 29. The Piltdown lower jaw (B) from a cast in the Williams Collection, compared with a female orang (A) and a modern man (negro) (C). External views. $\times \frac{1}{4}$. *alb. m3*, socket for third lower molar; *a.r.*, ascending ramus; *c*, canine; *c. i.*, central incisor; *con.*, condyle; *l. i.*, lateral incisor; *m1*, *m2*, *m3*, molars; *p1*, *p2*, first and second premolars (equivalent to *p3* and *p4* of lower mammals). After W. K. Gregory (1914).

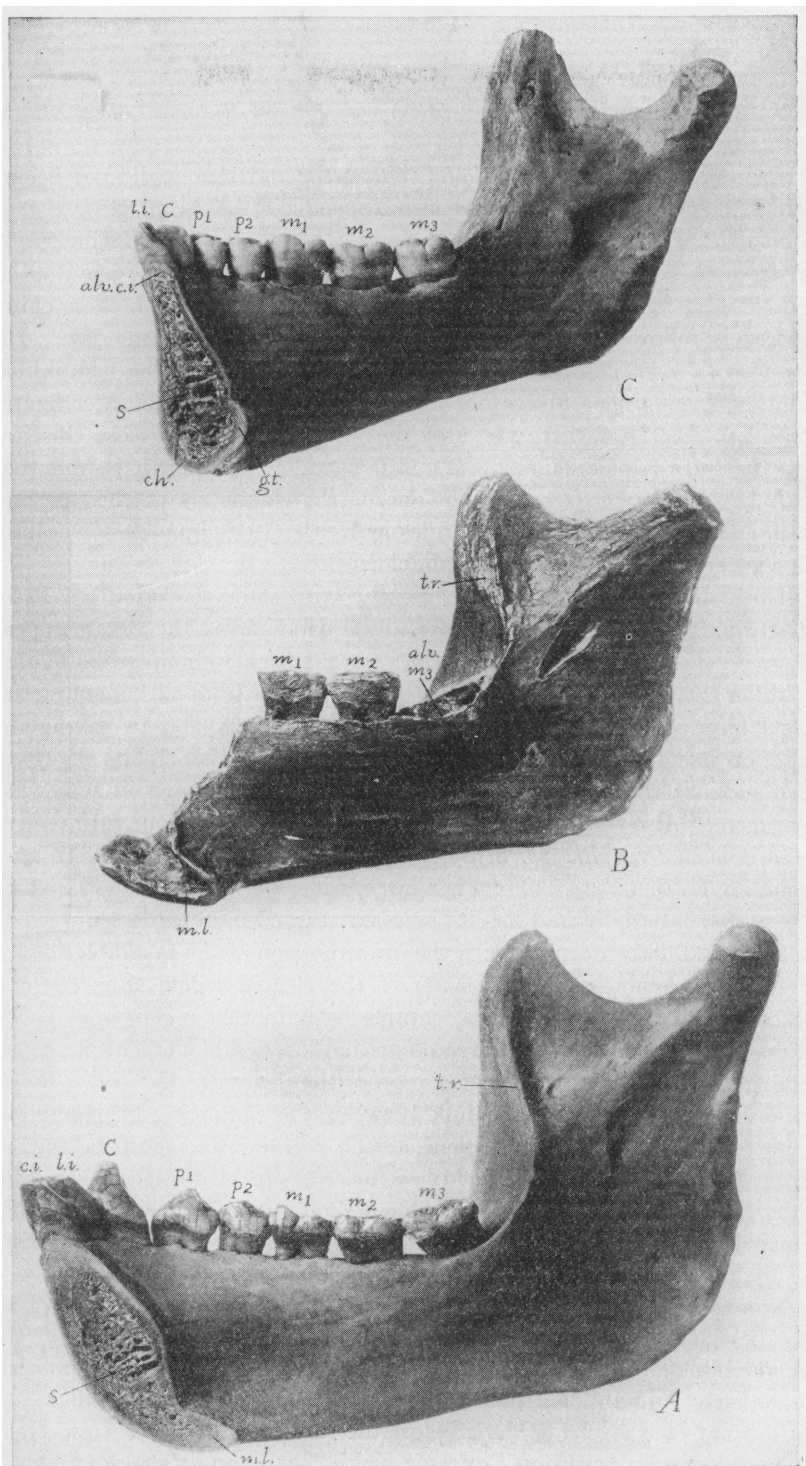


Fig. 30. Lower jaw of the Piltdown man (B), of a female orang (C) and of a modern negro (A). Inner side. $\times \frac{3}{4}$. *alv. c. i.*, alveolus for central incisor; *ch.*, bony chin; *g. t.*, genial tubercle; *m. l.*, mental ledge; *t. r.*, ridge in area of temporal muscle; *s*, section through symphysis. (*op. cit.*, 1914.)

represents a Pleistocene species of Chimpanzee and that it did not belong with the associated brain-case (see also Appendix B, below, p. 348).

In all views of the jaw — from beneath, from above, from the inner side and from the outer side — it is generically identical with the aged specimens of *Pan* figured by Miller. Every curve and contour in these chimpanzees is followed with minor variations in the Pleistocene jaw. Dr. Woodward's own comparative figures (1914, p. 317) of the symphyseal region of *Eoanthropus* and other anthropoids, as well as his later figures (1915, pp. 16–21) of three views of the jaw, all show how close this jaw is to that of a female chimpanzee and how widely different it is from that of *Homo heidelbergensis*. And not one of the characters of the jaw and teeth, as most ably analysed by Professor Keith (1915, pp. 430–478) establish a generic difference from the chimpanzee.

The two molar teeth although greatly worn show the primitive *Dryopithecus* pattern, which is disguised in all the Hominidæ; the molars appear to agree generically with those of the very old female chimpanzees figured by Miller (*op. cit.*, pl. 2, figs. 2'', 1'', 4). They differ from all human molars that I have seen in being relatively long and narrow and in having the posterior moiety less widened transversely. From the molars of *Homo heidelbergensis* they differ in the same characters, although in somewhat less degree. Also the long axis of m_1 in *Pan vetus* is continuous with that of m_2 as it is in *Dryopithecus*, *Sivapithecus* and all other apes, while in man (including *H. heidelbergensis*) m_1 is a large, wide, well-rounded tooth, which is displaced internally and has its long axis turned more or less inward at the front end, in conformity with the inward sweep of the mandible.

The completely human character of the glenoid region (Fig. 33) and the complete absence of simian features both in this region and in the region of the temporal muscle area offered an insuperable difficulty, as long as one accepted the supposed association of the jaw with the skull. By all well-founded analogies a true link between the Simiidæ and Hominidæ should have more intermediate characters in both jaw and temporal region; but, as fully expounded by Mr. Miller (*op. cit.*, pp. 14–18), the whole conformation of this region in the Piltdown skull demands a human or sub-human lower jaw, while the anthropoid jaw demands anthropoid glenoid and temporal regions.

Now that this anomalous composite called *Eoanthropus* has been resolved into its diverse elements we realize again that the transformation of the Simiidæ into the Hominidæ took place at a much earlier period; and that the entirely human dentition of *Homo heidelbergensis* shows that this transformation was effected long before the Mid-Pleistocene; a view which has been strongly urged by Professor Keith, but upon other grounds.

If the Piltdown skull, which is entirely human, bore a human jaw, as now seems likely, then there is no necessity for pushing the point of divergence of *Eoanthropus* and *Homo* far back into the Lower Pliocene, as in Professor Keith's diagram (1915, p. 509).

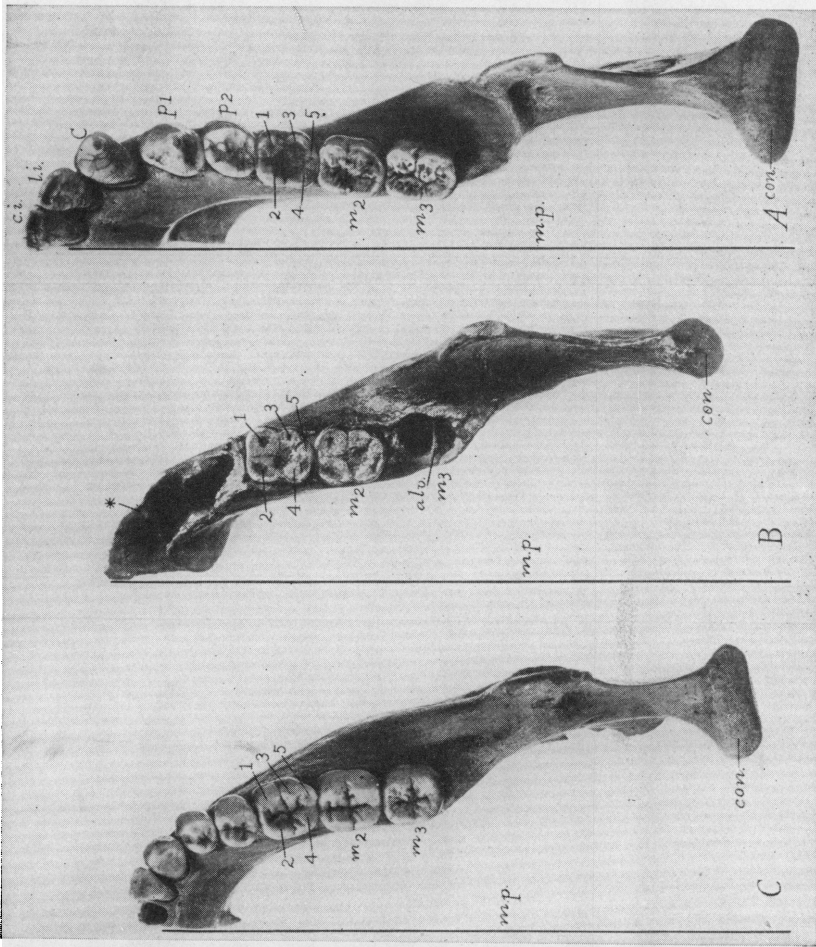


Fig. 31. The same three specimens of Figs. 29 and 30, viewed from above. (*op. cit.*, 1914.) 1, 2, 3, 4, 5, cusps of the lower molars; *m. p.*, median plane; *, broken edge.

In A and B the median plane (*mp.*) is incorrectly placed. It should be further away from the condyle in A and somewhat nearer to the condyle in B.

The persistence of one of the great apes in the Pleistocene of Europe, as a survivor of the *Dryopithecus* group of the Upper Miocene and Pliocene, is analogous with the persistence in the same region of hippopotamus and

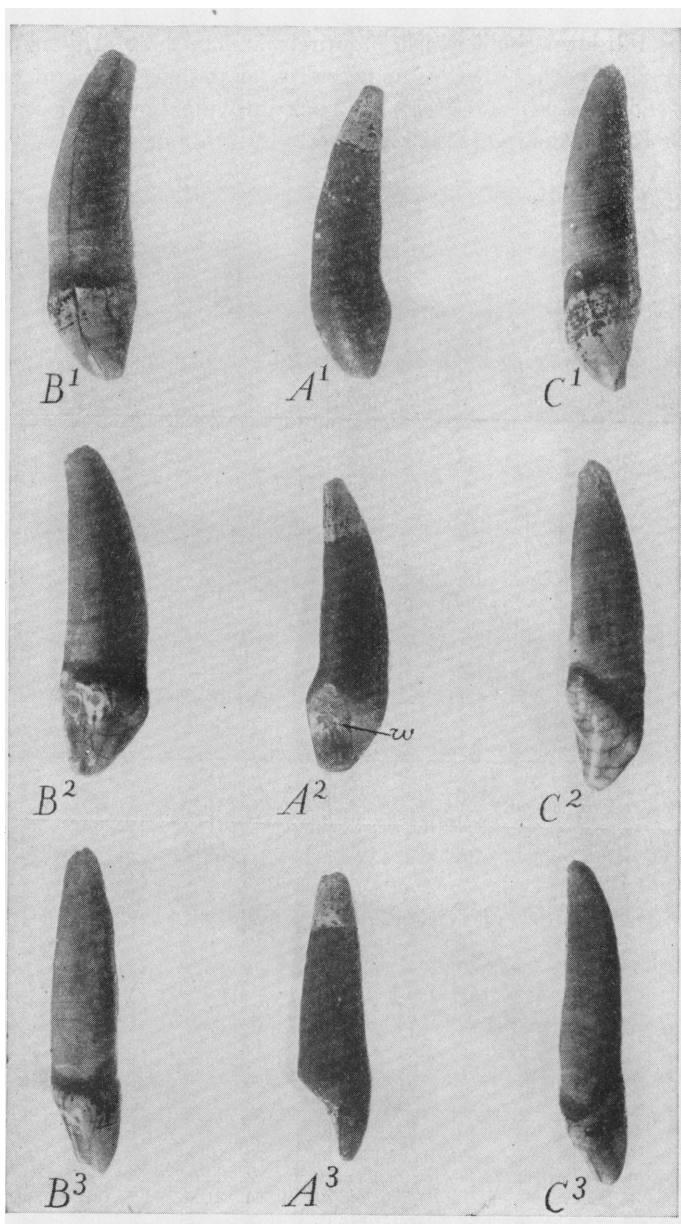


Fig. 32. Canine tooth (cast) of the Piltdown man (A) in comparison with the left upper (B) and right lower (C) canines of a female orang. $\times \frac{1}{2}$. The lower canine is turned upside down to facilitate comparison with the others. In A the tip of the root is restored. (op. cit., 1914.)

A¹, B¹, C¹. Seen from the outer or labial side.

A², B², C². Seen from the inner or lingual side. *w*, worn surface.

A³, B³, C³. Seen from the front; or antero-internally.

other forms at present confined to the tropics. The fact that the Pleistocene species is distinguished from the modern type by a somewhat more robust mandible and larger molar teeth also finds precedents among other mammalian phyla.

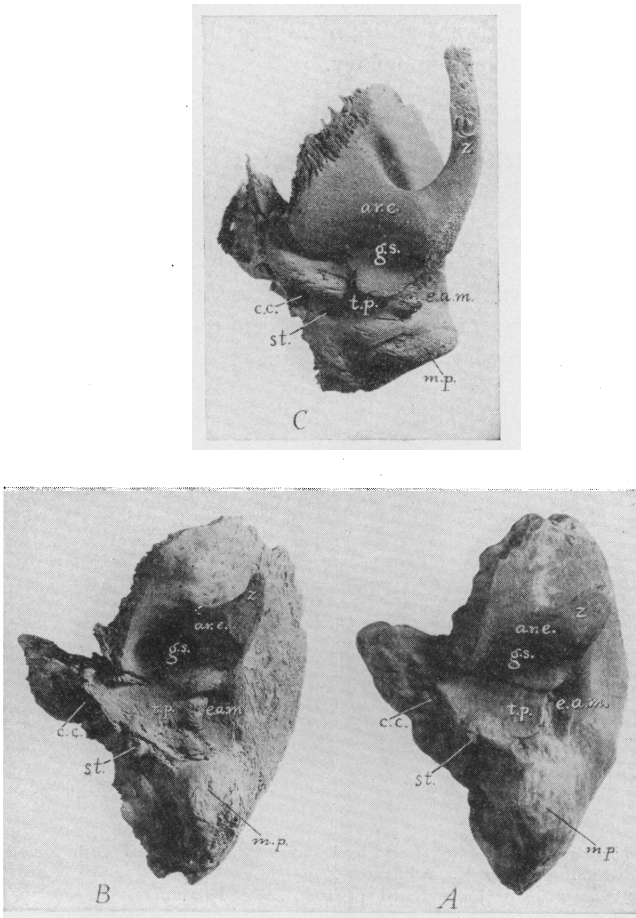


Fig. 33. Temporal bones of the Piltown man (A), of a negro (B) and of a female orang-utan (C) Two-thirds natural size. (*op. cit.*, 1914.)

ar. e., articular eminence (for lower jaw); c. c., carotid canal; e. a. m., opening leading to middle ear; g. s., glenoid socket (for lower jaw); pet., bone surrounding internal ear; st., pit for styloid process; t. p., tympanic plate; z, root of zygomatic arch.

As to the canine tooth, in my earlier paper I recorded the observation of Mr. A. E. Anderson, that this tooth agreed better with the left upper canine of apes than with the right lower one, as originally identified by Dr.

Smith Woodward. I was at that time not entirely convinced of this identification, but its correctness seems to have been confirmed by Mr. Miller (p. 12) who finds left upper canines of aged female chimpanzees which closely approximate the Piltdown canine both in form and in the manner of wearing down. I also consider the resemblances to the right lower milk-canine of man, noted by Dr. Woodward (1915, p. 22, Fig. 9), as not being sufficiently close to be demonstrative of homology.

***Pithecanthropus erectus* Dubois.**

(Fig. 34 C¹, C².)

The molars referred by Dubois to *Pithecanthropus* are remarkable for their extraordinary size, for the widely divergent roots, and for the similarity of the contour of the crown to that of an Orang (B). The contour is certainly

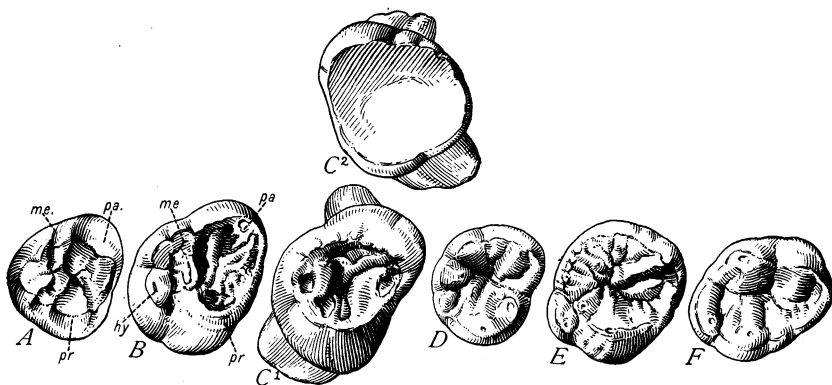


Fig. 34. Third right upper molar referred by Dubois to *Pithecanthropus* (C) in comparison with various human and anthropoid types. All figures $\times \frac{3}{2}$.

- A. *Dryopithecus punjabicus*, referred specimen. After Pilgrim.
- B. Modern Orang.
- C¹. *Pithecanthropus erectus*. Cast of referred specimen (m^s right).
- C². *Pithecanthropus erectus*. Cast of a second referred specimen (m^s left).
- D. *Homo sapiens*. Australian black (♀).
- E. *Homo sapiens*. Kaffir.
- F. *Homo sapiens*. Brachycephalic Caucasian.

nearer to that of the Orang and *Dryopithecus* than to the human types. The possibility is that *Pithecanthropus* may be related both to *Homo* and to *Sivapithecus*.

Homo.***Homo heidelbergensis* Schoetensack.**

(Fig. 27E.)

The jaws and dentitions of all known anthropoids appear to be adapted for a chiefly frugivorous diet; and they have protruding canines, gently procumbent incisors, and more or less parallel tooth rows. On the other hand the jaw and dentition of *Homo heidelbergensis* appear to be adapted for an omnivorous diet; its canines are small and do not protrude above the level of the adjoining teeth and its opposite tooth rows form an arch in the human fashion. Moreover the form and crown pattern of every tooth is distinctly human, and it is chiefly the lack of a chin, the restricted space for the tongue, the great depth of the horizontal ramus and the great width of the ascending ramus that recall the ancestral anthropoid characters. From the typically human character of the dentition of *Homo heidelbergensis* and from its relatively great antiquity as compared with other human remains we learn that the transition from anthropoid to human characters in the dentition took place at an epoch far anterior to the Mid-Pleistocene.

The sharply worn tips of the vertically placed incisors indicate an "edge-to-edge bite" of the upper and lower incisors which would be well fitted for pulling and tearing meat from bones. The stout premolars and molars and enormous jaws would be well able to chew the meat and crack the bones. If it be objected that a carnivorous animal should have large canines it may be replied that the human manner of killing the food and of eating it is wholly different from that of quadrupedal carnivores. The canines of the anthropoids were, I believe, evolved for a frugivorous diet and secondarily may be of some value as fighting weapons; but when the ancestors of man came down from the trees and took up a cursorial and predatory life, using weapons instead of teeth in fighting, the canines were shortened as the face and dental arch were retracted, and the short vertical canines and stout bicuspid proved just as effective in piercing bones as the large canines and premolars had been in piercing the tough rinds of fruits. The work of the canines and incisors may also have been made easier by the use of flints for cutting the food (see below p. 325).

While the dentition of *H. heidelbergensis* is distinctly human, the photographs published by Dr. Schoetensack and the casts of the type reveal certain slightly primitive characters. In the first place the dental arch is not so convex and the divergence of the opposite rami is not so great as it is in brachycephalic human skulls, although greater than in many dolicho-

cephalic skulls. Consequently the premolars are not so much crowded inward, with reference to the first molar. Secondly, the patterns of the premolar crown retain clearer traces of derivation from a *Sivapithecus*-like type (Fig. 1), and the premolars are relatively larger in size than in most modern jaws. Thirdly, although the molars show the well rounded wide human character, with large hypo- and entoconids and the human modification of the "*Dryopithecus*" pattern of the furrows which make a + in the middle of the crowns, they are all less widened than in many modern skulls; m_1 is not larger than m_2 , m_1 retains more of the "*Dryopithecus*" pattern, all the molars retain the hypoconulid and m_3 has the hypoconulid projecting backward. Finally, while the jaw itself is of gigantic size the teeth are actually smaller than in certain Australian and Kaffir jaws. In other words the dentition of *Homo heidelbergensis* differs from that of *H. sapiens* only in retaining certain primitive characters which are frequently lost in the higher types. The mandible itself also differs from the higher type solely in its greater size and numerous more primitive characters.

Hence I recognize no character in this species which would definitely exclude it from ancestry to *H. sapiens* and as it differs from the later type and also from *H. neanderthalensis* only in its more primitive characters and far greater geological age I see no reason for regarding it as an aberrant side line.¹

The gigantic size of *H. heidelbergensis* might be cited as a specialization that would exclude this species from the direct line leading to *H. sapiens*, on the ground that in many other phyla of mammals the gigantic members are supposed not to be ancestral to the smaller existing races. But, however, it may have been in other phyla, a large stature, or more precisely a massive head and thorax, may well be expected in the ancestral Hominidæ. When the ape-men definitely abandoned the forests and intruded themselves into the gigantic and well-armed fauna of the plains we may be sure there was no place for undersized gibbon-like beings of pacific habits, but all the conditions at first favored the evolution of powerful and aggressive hunters and fighters, killing with the crudest weapons and tearing off the raw meat with their powerful jaws. As the jaw of the Heidelberg Man is lower in type than that of the Neanderthals it seems likely that his intelligence was also of a lower order, the face extremely heavy, and the forehead retreating, a conception well worked out in Professor Rutot's restoration. The total absence of palæoliths or other artifacts (aside from the highly questionable "eoliths") until the Pre-Chellean epoch also suggests that the earlier races were much

¹ The significance of the "taurodont" character of the roots of the molar teeth is discussed below (p. 325).

less intelligent than the Neanderthals, who knew how to make a number of kinds of stone implements. Finally, as the teeth are at least generically identical with those of *H. sapiens*, I see no good evidence either for regarding the Heidelberg race as a distinct genus or for pushing far back into the Lower Pliocene the supposed point of divergence between the lines leading to *H. heidelbergensis* and *H. sapiens*, as in Professor Keith's diagram (1915, p. 501).

***Homo dawsoni* (Smith Woodward).**

Eoanthropus dawsoni Smith Woodward.

Mr. Miller ((1915), p. 4) suggests that "A mandible as heavy as that of the Pleistocene *Homo heidelbergensis* would probably be in due proportion" with the massive brain-case of the Piltdown race. Since Mr. Miller has also adduced strong reasons for believing that the Piltdown skull bore a human jaw and not a chimpanzee jaw, the possibility of referring the human Piltdown remains to *H. heidelbergensis* must be considered, especially as the precise age of the Piltdown remains has never been positively settled.

In 1914, when studying the fragments of the Piltdown brain-case I was impressed by the fact that they offered no salient distinctions from *H. sapiens*, the most remarkable feature being their great thickness. Even the pattern of the meningeal vessels impressed upon the cerebral surface of the parietal is similar to that of some human skulls. Similarly, in the lower teeth of *H. heidelbergensis*, the only differences from *H. sapiens* appear to be primitive characters.

The affinity of the Piltdown skull with the Heidelberg jaw, if it ever be established, will go far toward clearing up the origin of *H. sapiens*, a species which is now left without known ancestors in the most recent phylogenies (cf. Keith, 1915, p. 501; Osborn, 1915, p. 491). But as such affinity is so far only suspected, and as the evidence for referring the Piltdown skull to *H. sapiens* is also incomplete, it may be left provisionally in a third species *Homo dawsoni* (Smith Woodward).

***Homo neanderthalensis*.**

(Fig. 35B).

Professor Adolff (1907) has pointed out that the Neanderthal molars differ widely from those of *H. sapiens*. The pulp cavity is very large and extends far down the interior of the tooth, limiting the fangs proper to the lower end of the tooth. The roots are not sharply constricted from the

crowns but form with the crowns a stout column, tapering gently toward the bottom and extending deeply into the jaw and adapted to a sweeping motion of the jaw. To designate this somewhat ox-like character of the

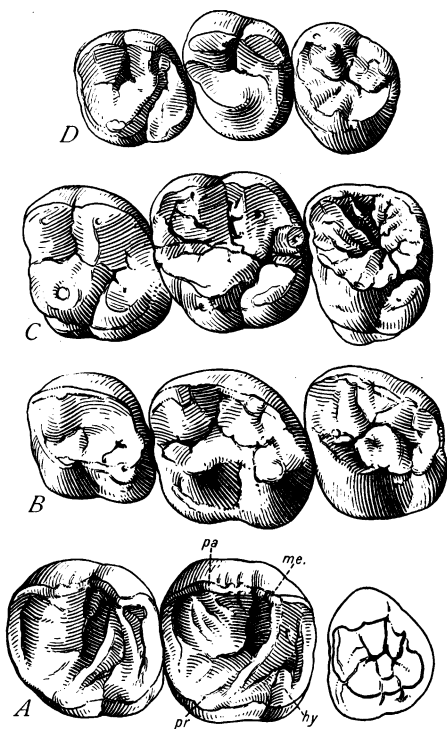


Fig. 35. Comparison of upper molars of men and anthropoids. $\times \frac{3}{2}$.

- A. *Dryopithecus punjabicus*. After Pilgrim.
- B. *Homo neanderthalensis* (Krapina). After Gorganovic-Kramberger.
- C. *Homo sapiens*. Kaffir.
- D. *Homo sapiens*. Brachycephalic Caucasian.

This shows the wide variation in form of the upper molars of *Homo sapiens*, some specimens approaching *H. neanderthalensis*, with very large quadritubercular crowns, others of retrogressive type, with small tritubercular crowns. The first molar, as usual in anthropoids, is more conservative in pattern, the third molar more irregular and retrogressive.

Neanderthal molars Professor Keith (1913) invented the term "taurodont" in contradistinction to the "cynodont" molars of *H. sapiens* which have a small pulp cavity and long separate fangs. This peculiar adaptation, which is seen in an incipient stage in *H. heidelbergensis*, is unlike anything known in the anthropoids and supports the suggestion (p. 277 above) that there was a very early and marked change in diet in the forerunners of man. Professor Keith (1915, p. 151) interprets the adaptive significance of this taurodont character of the Neanderthal molars as follows:

"The wide palate [known from the Gibraltar skull], the wide dental crowns and big bodies of the teeth seem to indicate powerful side-to-side grinding movements of the mandible during mastication. On the evidence of the teeth and palate one is inclined to regard Neanderthal man as specially adapted to live on a rough vegetable diet." But, in speaking of the Krapina remains, Professor Keith says

(op. cit., p. 133): "The superimposed strata [of the cave in which the Krapina Neanderthaloids were found] showing nine different horizons marked by human occupation — hearths, tools, and debris of meals — proved to be the richest treasury of the Neanderthal race ever opened by

the explorer's spade. Over two hundred fragments of human skeletons were found, representing at least ten individuals of all ages and both sexes. One hundred upper and one hundred and twenty lower human teeth were collected, all of them showing, in a varying degree, the characteristic form we now associate with the Neanderthal race. Over two thousand fragments of bones of the animals of the period were found, including those of the same ancient form of rhinoceros as occurred at Taubach (*R. Mercki*). The cave-bear occurred abundantly; it was evidently a favorite article of diet. The rhinoceros bones had been broken open to extract the marrow. The mammoth and many other ancient and modern animals were also represented. Some of the human bones were charred, and some had been apparently split open: on that slender basis the Krapina men have been suspected of cannibalism. The implements, like those at Taubach, are not of the typical Mousterian forms, but experts ascribe them to the culture of that period. Some evidence, as at La Quina, was noted of bone having been shaped for use as a tool; perhaps wood was also worked."

Hence in view of this archæological evidence I think it is more than doubtful whether Neanderthal man was "specially adapted to live on a rough vegetable diet." Possibly he was at times a vegetarian by necessity, but in the face of this evidence of his prowess as a hunter one can hardly deny that animal food formed a large part of his diet. Many or perhaps all the early Palæolithic implements with sharp points or with serrate edges would be adapted for piercing the bones, for cutting the tendons, and for stripping off the hide. These implements would materially assist the teeth in the work of getting the food into the mouth; but the very stout deeply implanted molars, with their rough surfaces, would be well adapted for chewing the meat and crushing small bones.

Professors Adloff and Keith both think that the taurodont character of the molars is sufficient to exclude the Neanderthal race from ancestry to *H. sapiens* and hence with other authorities they regard the Neanderthal race as wholly extinct. Now, there are, indeed, many cases in which known Pleistocene genera have some specialized character that appears to exclude them from direct ancestry to the existing types, and it may well be that the same is true in this instance. But it should by no means be regarded as an established fact. Among the Neanderthals themselves there is considerable variation in the degree of "taurodontism" and the same is true of *Homo sapiens*. As regards the form of the upper molars it seems likely that the tritubercular pattern of the second and third upper molars in many skulls of *H. sapiens* is a retrogressive pattern, derived by degeneration from the more vigorously developed, more quadritubercular molars of lower races. At any rate there is a very wide range of form in the molar patterns

of *H. sapiens*, so that the Kaffir molars shown in Fig. 35C are actually more like those of the Krapina men than they are like those of typical white men. Hence it seems possible that there may also have been a loss of "taurodontism" in *H. sapiens* correlated with the reduction in size of the jaws and with the use of cooked food.

Consequently I incline to Professor Keith's earlier view (1911, p. 87) which he expressed as follows: "So peculiar are the roots, [of the Neanderthal and in less degree of the Heidelberg molars] so unlike the same structures in the modern type of man and in anthropoids, that Dr. Adloff thinks the Heidelberg man, and the Neanderthal type to which he belongs, cannot be regarded as a stage in the evolution of modern man. In the writer's opinion the form of root just described is a specialization which appeared and subsequently disappeared when the special adaptation was no longer required. The case is similar to the biceps of the blacksmith; the hypertrophy disappears when vigorous demands cease to be made on it. When knowledge ameliorated the quality of the human diet, the overgrown condition in the roots of the teeth disappeared."

There is a tendency among both anthropologists and palæontologists to assume that a marked difference in a given adaptive character between an earlier and a later type excludes the former from ancestry to the latter; because, it seems to be further assumed, evolution is orthogenetic and does not reverse itself! The Neanderthals, say Professors Adloff and Keith in effect, have more specialized molars than modern races have, therefore they cannot be ancestral to them. But what disproves the opposing view that in these characters, modern races (including even the Crô-Magnons) are retrogressive?

M. Boule's extremely careful studies of the postcranial skeleton of the Chapelle-aux-Saints man led him (1912) to the following views: (a) that many of the resemblances between the Hominidæ and the anthropoids are largely homoplastic, or convergent, (b) that the limb structure of man shows in certain features more fundamental resemblances with that of the cynomorph monkeys than with that of the anthropoids, (c) that the Hominidæ have been derived neither from the anthropoid stem nor from any other known group but from a very ancient primate stock that separated from the main line even before the giving off of the lemuroids. Other anthropologists also emphasize the wide genetic separation of the Hominidæ from the anthropoids. "We must vigorously oppose the view often met with in lay circles," says Dr. Bruno Oettking (1915), "that man developed directly from the anthropoids. . . . Granting variability, we must assume that from a highly developed vertebrate — a hypothetical paleoprimates — there developed both the anthropoid apes and a being representing man's ancestor."

Now it is of course not the intention of the present writer to urge that the Hominidæ were derived from any still existing genus of anthropoids. But I believe that a concrete and approximately accurate notion of the facts would be given if one were to affirm that the Upper Miocene ancestors of the Hominidæ were at least very closely akin to the Upper Miocene common ancestors of the chimpanzee and gorilla, that they were in fact heavy-jawed, stout limbed, tailless and semi-erect anthropoid Catarrhinæ, with quadritubercular second and third upper molars and *Sivapithecus*-like lower molars.

It was suggested above (p. 321) that the entirely human character of the dentition in the Mid-Pleistocene *Homo heidelbergensis* indicates that the real transitional stages between the anthropoids and the Hominidæ are to be sought in a far earlier epoch, perhaps the Upper Miocene. Hence it is not surprising to find that the Upper Pleistocene *Homo neanderthalensis* differs in many important characters from the recent anthropoids, although retaining quite a few other important anthropoid characters that have been lost in later Hominidæ.

All M. Boule's elaborate discussion of limb ratios and of indices rests upon a comparison of *recent* anthropoids with recent and Pleistocene Hominidæ. But until it is possible to compare the skeletons of Upper Miocene anthropoids with those of their diversified descendants M. Boule's ratios and indices merely record the facts of present divergence and are of ambiguous phyletic significance. We do not know precisely how far the chimpanzee and gorilla have diverged in the characters of the limbs from each other and from the common man-anthropoid stock of the Upper Miocene. But, from the anatomy of the brain, genito-urinary organs and countless other structural and physiological resemblances, we infer with practical certainty that the Hominidæ and the existing anthropoids are the divergent derivatives of a common ancestral stock. And nearly all authorities have recognized that even the existing anthropoids, especially the gorilla and chimpanzee, have on the whole retained the ancestral habitus, with minor changes, while the Hominidæ represent an aberrant terrestrial, bipedal offshoot, primarily of predatory and omnivorous habits.

The whole skeleton of *Homo neanderthalensis* abounds in low characters not found in such an assemblage in any existing specimens of man. But in spite of the opinion of very eminent authorities, no one and no group of these characters, appear to the present writer to exclude this species either from derivation from Upper Miocene anthropoids or from ancestry to *H. sapiens*.

The huge size and strength of the skull, jaws, and dentition are in harmony with the view that the ancestral Hominidæ were ferocious and preda-

tory terrestrial anthropoids. In the great size and depth of the face *H. neanderthalensis* surpasses any recent Hominidæ, which are all more or less retrogressive in the face, dentition and jaws and highly progressive in the brain-case. Consequently all the wide differences in cranial indices ("Kalottenhöhe" etc.) between the Neanderthals and *H. sapiens* do not in themselves exclude the older species from ancestry to the later. Of course the Crô-Magnons and other high types may very well have come into Europe from Asia and the European Neanderthals may simply have crossed with the invading race; but the ancestors of the Crô-Magnons in Asia must have at some earlier time have passed through a Neanderthaloid stage of evolution and perhaps it was some of the older strains of these Pro-Neanderthaloids and not the Mousterian population, which may have given rise at different times and in widely separated regions to the composite group called *H. sapiens*.

It is hardly necessary to believe with Dr. Smith Woodward (1915) that the projecting brow-ridges of male Neanderthals, chimpanzees, and gorillas are quite independently derived characters and that the smooth round brain-case of the young chimpanzee gives the type immediately ancestral both to apes and man. Young mammals usually have relatively larger and more swollen heads than their parents and the heavy crests are not completed until the jaw muscles attain their full size. Through neglect of the phenomenon of cænogenesis certain authors have been led to the absurd conclusion that the swollen brain-case of man and of the smaller Cebidæ is more primitive in form than that of other mammals, a conclusion implying a complete inversion of the palæontological and neontological record. Such a conclusion must have rested upon a complete ignorance of the small brain-case of Eocene mammals of many families and orders. Very likely all the known Miocene genera of anthropoids had brow-ridges, at least in the males, as may be inferred from the massive character of their lower jaws, and the same was probably true of *H. heidelbergensis*, as it was also of *Pithecanthropus* and is of many low specimens of existing Hominidæ. The projecting brow-ridges are associated with stout temporal and masseter muscles and large canines and if the Hominidæ are derived from Upper Miocene anthroids they probably had brow-ridges.

The backbone of the Chapelle-aux-Saints man, as admirably described by Boule, resembled that of a chimpanzee and differed from that of recent Hominidæ especially in the form of the cervical vertebræ and in the forward curvature of the neck, characters associated with many ape-like peculiarities of the skull. The forward curve of the lumbar region was also less pronounced than in existing Hominidæ and the whole conformation of the skull and backbone shows that the upright posture and the balancing of the

skull upon the column were very imperfectly developed in this upper Pleistocene species. The extremely robust ribs, which in volume greatly surpass that of any modern races, testify to the massive musculature of the thorax, which is in harmony with the gigantic and very powerful head and neck.

The pelvis is prevailingly human in character, having the widely expanded ilia of man rather than the long narrow ilia of the chimpanzee. This human character of the pelvis suggests an equally human development of the enclosed viscera. It also implies essentially human conformation of the glutæi, psoas, iliacus and many other locomotive muscles. Although the difference between the human pelvis and the anthropoid types of pelvis is very marked the former is clearly a structural derivative of the latter. A spreading, basin-like ilium has in other phyla of mammals very frequently been evolved out of a narrow blade-like ilium, as in many groups of ungulates. Moreover there is a steady rise in the pelvic index, *i. e.*, in the breadth of the ilium, as we pass from the Eocene lemuroids, through the South American and cynomorph monkeys to the gibbon, orang, chimpanzee, gorilla, and man.

The legs of the Neanderthal race were of human type, distinguished by the relatively short tibia, the partial retroversion of the head of the tibia, showing that the knee was slightly bent even in the erect pose, and the presence of accessory facets for the tibia on the astragalus, similar to those observed in cynomorph monkeys and in modern human races that squat instead of sitting. "There are other features," observes Professor Osborn (1915, p. 238), "which would tend to show that the ancestors of the Neanderthaloids had been ground dwellers rather than tree dwellers back into a very remote period of geologic time; the arms are much shorter than the legs, whereas in tree dwellers they are much longer. . . . Thus, to sum up the bodily proportions of the Neanderthals:

Arm short in proportion to leg, average index 68 percent.

Forearm short in proportion to upper arm, average index 73.8 per cent.

Shin bone short in proportion to thigh bone, average index 76.6 per cent.

Stature extremely short in proportion to size of head."

The foot of the Neanderthals is essentially human with a few primitive features of the astragalus. The lack of truly intermediate stages between the human and the anthropoid types of foot may well be cited by those who regard the Hominidæ as a family of mysterious, unknown affinities which branched off in the Eocene or even earlier. The human foot is so completely adapted for erect bipedal progression on the ground and it is so markedly different from the anthropoid foot, which is adapted for grasping the limbs of trees, that the opinion has been expressed that the human foot has not

been derived at all from the anthropoid type. Briefly the contrast between these two types of foot is as follows:

(1) The hallux in the anthropoids is highly opposable. It is sharply divergent and articulates by a saddle-shaped facet on the obliquely placed entocuneiform and is operated by very powerful flexor and adductor muscles. Its plantar surface faces the other digits and its dorsum is turned sideways. The cleft between the hallux and the other digits extends far toward the proximal end of the foot, and the tip of the hallux does not extend to the end of the other digits. The foot as a whole is broad, spreading and flat

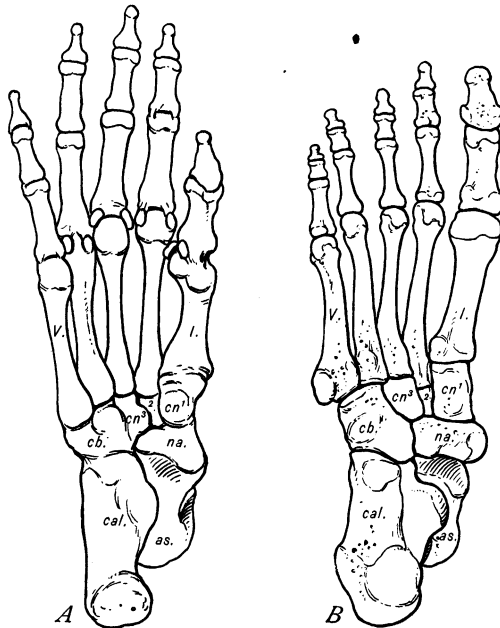


Fig. 36. Plantar aspect of the foot in (A) an infant gorilla and in (B) man (Australian black, ♀), contrasting the semi-arboreal and the cursorial terrestrial types.

In order to show the comparative lengths of the phalanges the distances from the tip of the second metatarsal to the back of the tuber calcis are reduced in both figures to the same absolute length.

and the sole faces inward. The digits are curved inward and, in proportion to digit I, digits II, III, IV are all larger than in man. The phalanges are relatively long and are much flexed. The trochlea of the astragalus is tilted outward, in accordance with the marked supination of the foot. Such a foot is adapted for grasping the branches and practically serves also to some extent as a hand. By means of its strong grasping power of the pes the animal can stand completely erect when in the trees (Keith, 1911), but the anthropoid pes is very ill adapted for walking on smooth ground,

where there is nothing to grasp, and causes the animal to be very unsteady and clumsy when it attempts to walk fully upright on the ground.

(2) In the pes of man on the other hand the hallux is not at all opposable. It is not divergent but nearly parallel to the other digits. Its planar surface faces downward. It articulates by a concave or flattened facet with the more rectangular entocuneiform. The great flexors and adductors of the hallux coöperate with other muscles in giving a powerful thrust upon the ground. The cleft between the hallux does not extend much beyond the phalanges, so that the hallux and other digits are encased in a common integument extending to the end of the metatarsals. The tip of the hallux often extends beyond the other digits. The foot as a whole is narrow, compressed, and arched, and the sole faces entirely downward. The digits are straight; digit I is much the largest and longest while the other digits are all weak. The phalanges are short and not flexed. The trochlea of the astragalus faces superiorly instead of obliquely, in accordance with the fully pronate position of the foot. Such a foot is adapted solely for erect, bipedal locomotion in walking, running, and jumping. There are of course other differences between the human and anthropoid types of pes but the above mentioned ones are sufficiently distinctive.

Now it is an incontestable fact that a steady general progression toward the human type of foot may be observed if one will arrange a series in the following order: (1) Eocene lemuroid *Notharctus*, (2) Old World monkey, (3) young gorilla, (4) *Homo*. This may not be a true genetic series, but I believe that it reveals the general course of evolution as follows:

The oldest known type of Primate foot, that of the Middle Eocene *Notharctus*,¹ was fully adapted for very firmly grasping the branches and proves that this primary adaptation of the Primate foot was acquired at a very early date, perhaps in the Paleocene. The metatarsals are very short. The hallux is even larger than it is in *Lemur*. It has a large broad process at its proximal end for the attachment of the peroneus longus muscle and this process interlocks with the surrounding elements in such a way that it narrowly limits the opposability of the hallux, which is always sharply divergent from the other digits. The phalanges of the hallux are of large size and the distal phalanx is widely flattened and affords a firm attachment for the powerful flexors. The phalanges of the other digits are long, but much less so than in modern lemurs. The fourth digit was probably the longest. The astragalus of this type has a narrow, asymmetrical flat trochlea without marginal keels, a relatively long oblique deck and a narrow slender head. This type of foot is carried to its extreme development in the modern

¹ This will be fully described in Part IV of the present series of studies.

Indrisine lemurs. It is primarily adapted for a very firm grasp of the branches and secondarily for leaping. In walking on the ground the hallux serves as a wide strut, that projects inward, as may be observed in modern lemurs.

(2) The foot of an Old World monkey differs from the primitive type chiefly in (a) the reduction of the peroneal process of the hallux, which has therefore more flexibility, more opposability, (b) the lengthening of the metatarsals and (c) the readjustment of the lengths of the digits so that digit IV is slightly shorter than digit III. (d) The astragalus has a wide trochlea with marginal keels. (e) In walking the hallux is not turned inward quite as sharply as it is in the lemurs. Such a type of foot is somewhat better adapted for free and active quadrupedal running along the tops of the branches as well as on the ground; and it also serves for grasping.

(3) The foot of the gorilla shows some approach toward the human type, especially in the following characters: (a) in adaptation to the gigantic size and weight of the animal, the phalanges are notably shorter than in preceding types and the metatarsals are stouter; (b) the digits decrease in massiveness from I to V; (c) the astragalus has lost the trochlear keels and is widened, so that in general form it distinctly approaches the human type; (d) the tuber calcis is expanded and forms a true heel; (e) the foot as a whole shows the beginning of an arch; (f) in walking on the smooth ground the phalanges, being shorter, are not flexed so much as they are in lower Primates, and the sole of the foot is planted more directly upon the ground.

(4) It may well be that the gorilla, as the result of its giantism and of its partial assumption of terrestrial habits, is acquiring at a late date characters which the Hominidæ acquired more perfectly at a far earlier period, perhaps in the Upper Miocene. But in order to transform a gorilla-like foot into a human foot it is chiefly necessary: (a) to increase the length of the hallux, (b) to adduct it, and rotate it on its own axis so that its plantar surface shall be applied to the ground instead of facing toward the other digits. (c) Next it would be necessary to shorten still further the phalanges and (d) to narrow the whole foot, that is to make all the digits parallel instead of divergent. (e) The tuber calcis and cuboid must be enlarged and (f) the whole foot must be "pronated" or made to face downward rather than inward. As a result (g), the trochlea of the astragalus is made more symmetrical, deeper on the tibial malleolar facet, (h) the head of the astragalus is widened.

Those who lose sight of the fundamental principle of the change of function and who expect remote ancestral stages to foreshadow *all* the features of the final stage will hardly realize that by the foregoing relatively slight morphological changes a gorilloid type of foot could be easily made over for service on the ground. And if man has descended from any primi-

tive Primate, whether lemuroid, cynomorph or anthropoid, such are the changes which undoubtedly must have occurred.

But, it may be objected, this is not what actually did happen in other and better established instances, as when the arboreal marsupial foot was made over into the various ground-living types, or when the arboreal primitive placentals were transformed into the swift running carnivores and ungulates of the Eocene. To such an objection I would reply that in these other instances we have to do solely with the transformation of arboreal plantigrade quadrupeds into terrestrial digitigrade quadrupeds. In such cases the hallux, upon the adoption of terrestrial quadrupedal progression, is very often lifted clear of the ground and rapidly dwindles away, as in the *Dasyuridæ*. And in such cases the hallux in the primitive arboreal forms is by no means as large and powerful as it is in the primitive lemuroids and anthropoids. But in the transformation of a gorilloid form of foot into the human type we have to do with widely different conditions, namely the transformation of erectly sitting, brachiating quadrupeds into erectly walking, plantigrade bipeds. When the Miocene ancestors of the *Hominidæ* began to spend more time on the ground and less time in the trees it was perfectly natural that their powerful hallux should have been utilized as the main axis of the foot, instead of the weaker digits II, III, IV; because on rough forest ground the strongly grasping hallux with its powerful flexors and adductors would be almost as useful in maintaining the balance in the upright pose as it would in the trees.

The assumption of the erect attitude in the *Hominidæ* has involved many other readjustments and reversals in the proportional lengths of the limb segments — readjustments, of which the true significance has been largely missed by those who put their trust in ratios and indices. It is often held that the relatively long arms and short legs of the chimpanzee and gorilla as compared with those of man are aberrant specializations which remove these apes from the direct ancestry to man. But long arms and short legs are used in brachiating, and short legs are especially advantageous in squatting, the favorite posture of the gorilla. Now both brachiating and squatting form I believe a necessary introduction to the upright posture of man. The habit of brachiating, or swinging from branch to branch with the arms, trained the arms in the all important power of supination and improved the brain, eyes and all the balancing mechanism. The habit of sitting upright conditioned the loss of the tail and the further development of all those characters of the backbone, thorax and pelvis which give to the anthropoid skeleton a distinctly subhuman look. Moreover the habit of sitting upright tended greatly to encourage the use of the hands.

But long arms and short legs are also very useful in progression upon the

ground and especially in the forest, as one can readily see from Mr. Raymond L. Ditmar's excellent motion pictures made in the New York Zoölogical Park. This peculiar method of taking great strides with the forearms, in a semi-erect posture, again forms a necessary prelude to fully erect bipedal progression. It must have been abandoned only when the primitive apemen took to carrying weapons or food in their hands, and when through the use of jagged flints the arms became terrible fighting weapons.

With all respect to the contrary views of very eminent authorities, such as M. Boule and Professor Klaatsch it seems perfectly evident that the long legs and short arms of man form a secondary specialization for erect bipedal progression upon the ground and that all resemblances in the proportions of the fore and hind limb between man, the cynomorphous monkeys and certain lemuroids are entirely secondary. Both the long femur and the long tibia of man greatly lengthen the stride and increase the speed, factors of vital importance in a hunting and fighting animal, but of less importance to the clumsy frugivorous anthropoids. The short arms in man are also more powerful and of greater advantage in fighting with weapons. On the other hand the opposite proportions, namely long legs and short arms, in the tree living anthropoids would be inconsistent with the fully upright posture in sitting and with the habit of brachiation, and such arboreal animals as happen to have long legs and shorter arms, as in the *Galago*, although accidentally approaching man in this respect, have these proportions because they are specialized for leaping, in a manner utterly different from the erect bipedal progression of man. Moreover long hind limbs, while permissible in a small arboreal animal like the gibbon, would be quite inconsistent with the upright pose, in the trees, of a heavy animal like a full grown chimpanzee or gorilla, since they would make it more difficult to maintain the balance.

M. Boule is impressed by the fact that in some of the cynomorph monkeys the disproportion in length between arms and legs is less than it is in the anthropoids and he therefore seems to favor the view that man may have been derived from some arboreal form more or less resembling the cynomorphs in the humero-femoral ratio. But the cynomorphs have relatively short arms and long legs precisely because they are quadrupeds, and they walk upright only with the greatest difficulty. It is true that they can sit partly upright, but in the whole skull, backbone, and pelvis they are far less man-like than the anthropoids.

In brief I can discover no valid objection to the view that the Upper Miocene forerunners of the Hominidæ had short stout femora and long arms much like those of baby gorillas. As terrestrial bipedal progression was adopted the femora and tibiæ lengthened out while the forearm was reduced in length but gained in thickness.

Those who admit that the trend of evolution sometimes changes, following a change of habits, can find plenty of precedence for the reduction in size of one part and the increase of another: the reduction of the face and jaws and the great increase in the brain-case in man being a case in point. Among the Lemuroidea many analogous cases of reversal in evolutionary trend occur. *Megaladapis* is undoubtedly an aberrant derivative of some normal primitive lemur like *Lepilemur*, but *Megaladapis* has the hind limb bones secondarily shortened and widened, while all the primitive lemurs have them long and slender.

An admirable example of a profound readjustment of proportions, following upon a change in habits, is furnished by the limbs of Pinnipedia, of all families. The pinniped foot resembles broadly a much enlarged human foot which has been flattened out and spread apart. The hallux is much enlarged and exceeds the other digits in size and length. Now although the direct ancestors of the Pinnipedia are not known it is practically certain that they have been derived from primitive terrestrial carnivores of some sort, as shown especially by the morphology of the skull. But no primitive terrestrial carnivore or even terrestrial Eutherians of any known family had hands and feet like those of pinnipeds. Primitive carnivores and primitive placentals were on the contrary digitigrade animals with short metapodials and a normal hallux, which is never as large as it is in the pinnipeds. The change of habits from terrestrial to aquatic life has conditioned a profound readjustment in the proportions of all parts of the limbs: not only has the hallux become very large and long and the other digits variously readjusted in length and proportions, but the femur has become extremely short and broad and the whole pelvis has been remodeled on lines quite foreign to the pelvis of terrestrial mammals.

A change from normal terrestrial to fossorial habits has in the Talpidæ produced a profound readjustment of limb proportions. The primitive terrestrial type is still extant in the Thibetan *Uropsilus soricipes*, which is a true talpid in skull and dentition but retains very primitive shrew-like limbs. At the other extreme the specialized fossorial habits of *Talpa* have conditioned an excessive widening of the hands and shortening of the metatarsals, an excessive widening and shortening of the clavicle which has lost all resemblance to a normal clavicle, a great widening and remodeling of the humerus, and a great lengthening and narrowing of the scapula. But if one were to compile an imposing series of comparative limb ratios and indices of *Talpa* and *Uropsilus* the contrasts would be so enormous that no conservative statistician would dare to suggest that there is a close relationship between these two genera.

A constant and long continued study of the evolution of very many orders and families of fishes, amphibians, reptiles and mammals has brought

to my notice so many striking examples of profound readjustments in proportions and indices following upon marked changes in function that it seems amazing to me that the relatively small morphological differences between the limbs of *Gorilla* and those of *Homo* should frighten some authors into constructing purely hypothetical phylogenies in which these two related genera are placed far apart.

In short I hold that as the ancestral Hominidæ gave up arboreal frugivorous and semiquadrupedal habits and assumed the life of hunters upon the ground, the hind limb, especially the femur became longer, the hallux was lengthened, rotated about its own axis and brought into alignment with the other digits, the forearm shortened and the pollex became larger.

VI. PHYLOGENETIC SUMMARY AND CONCLUSIONS.

1. *Phyletic Relations of the Tertiary and Quaternary Anthropoids.*¹

(Fig. 37.)

Parapithecus and *Propliopithecus*.—The earliest known member of the anthropoid series, the genus *Parapithecus* of the Lower Oligocene of Europe, foreshadows the true anthropoids in the fundamental pattern of its premolars and molars and appears to be structurally intermediate between an Eocene partly insectivorous anaptomorphoid stage with pointed jaws and small canines and a true anthropoid stage.

Parapithecus must be regarded as a persistent primitive type, for its contemporary *Propliopithecus* is already a true and very primitive anthropoid ape, with a deep jaw and with the highly characteristic dentition, although much smaller and more primitive even than the modern gibbon, as rightly maintained by Dr. Schlosser.

Pliopithecus.—This genus of the Upper Miocene and Lower Pliocene of Europe appears to be intermediate between *Propliopithecus* and the modern gibbon. Its jaw is more primitive than that of the latter in its divergent rami, smaller canines, wider premolars and un-reduced third lower molar.

Palæosimia.—This genus, from the Upper Miocene of India, so far as known, appears to be ancestral to the orang-utan.

Sivapithecus.—This Upper Miocene Indian genus appears to the present writer to be closely related to *Dryopithecus*, as a descendant of a common stem resembling *Propliopithecus*. In another direction it appears to be related to *Palæosimia* and the orang. It approaches man not only in the greater breadth index of the premolars and molars, but also in their

¹ Until all or nearly all these genera and species are known from both the upper and the lower molars the exact relationships and status of some of them must remain indefinite.

fundamental pattern. It retains the high conic canines, which were probably reduced in the Hominidæ. According to the writer's interpretation *Sivapithecus* also exhibited an ape-like arrangement of the cheek teeth, in parallel rather than convergent rows. It should therefore be referred, by definition, to the Simiidæ rather than to the Hominidæ.

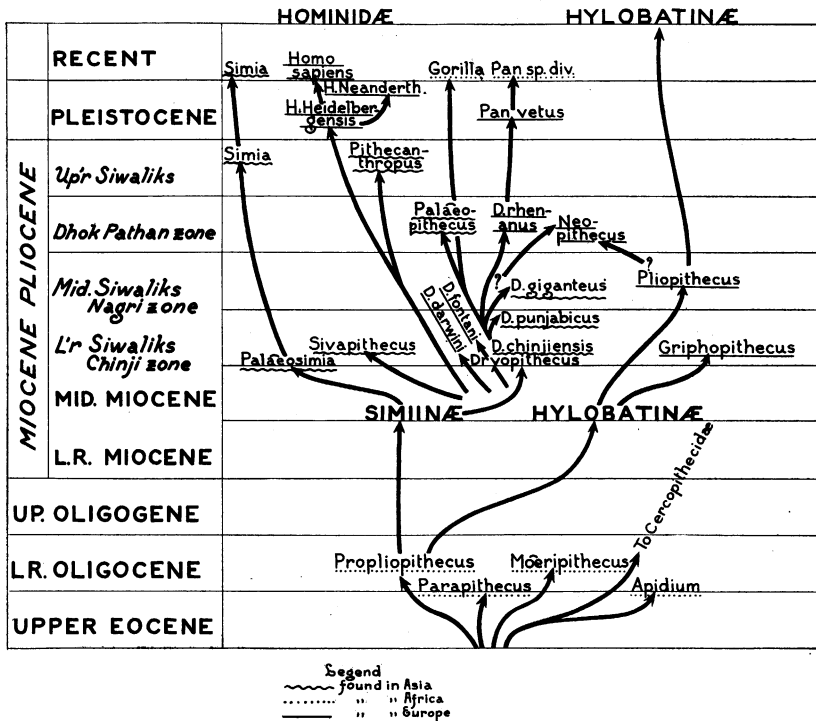


Fig. 37. Geological succession and provisional phylogeny of the Hominidæ and Simiidæ, as interpreted from available evidence by the author.

Dryopithecus.— This Upper Miocene and Lower Pliocene genus, which is known from three species in India and three in Europe, retains strong evidence of derivation from a form like *Propithecus*, but is much larger and more progressive. Its molars and premolars are ancestral in pattern not only to those of the chimpanzee and gorilla, but also to those of man.

Dryopithecus chinjiensis (of India) may be the remote ancestor of the gorilla line.

Dryopithecus punjabicus (of India) seems to be closely allied or ancestral both to the gorilla and the chimpanzee.

Dryopithecus giganteus (of India) is very much larger than the other species and appears to be closely related to the chimpanzee.

Dryopithecus darwini (of Europe) is known from a third lower molar, which is unusually short and wide and has deep furrows and wrinkles. Its exact relationships are uncertain; perhaps it is related to *Pithecanthropus*.

Dryopithecus fontani (of Europe) is known from lower jaws and teeth, which appear to be allied in many characters to *D. chinjiensis* and to the modern gorilla.

Dryopithecus rhenanus (of Europe) is in some ways more specialized than *D. fontani* and may be intermediate between *D. punjabicus* and the chimpanzee.

Palæopithecus.—This genus is known from a palate and upper teeth from the Lower Pliocene of India. It appears to the present writer to be related to the gorilla.

Neopithecus (“*Anthropodus*”).—A third lower molar of doubtful relationships, perhaps related to *Dryopithecus rhenanus*, but with a narrow m_3 .

Anthropopithecus (*Pan*) *vetus*.—An extinct Pleistocene species represented by a lower jaw found near the Piltdown skull. The last survivor of the *Dryopithecus* group in Europe. Teeth and jaw differ greatly from those of the oldest known man, *H. heidelbergensis*, and are not generically separable from the modern *Anthropopithecus* (*Pan*), as held by Miller.

Pithecanthropus.—The two upper molars referred to this genus are of very large size; in pattern and contour they suggest relationships with the *Dryopithecus*-group as well as with *Sivapithecus* and *Homo*.

2. Origin of the Recent Anthropoids.

The Gibbons.—In a recent phylogenetic diagram Dr. Pilgrim (1915) unites the gibbon stem with the human stem in the Upper Oligocene and places a very deep cleft between this gibbon-man trunk and the *Pliopithecus-Dryopithecus* group and its derivatives the modern great apes. This view of the nearer relationship of man to the gibbons rather than to the “giant apes” may be said to be flatly opposed by the anatomical results of many investigators. “The brain of the gibbon,” says Keith (1896) p. 372, “is comparatively small and simple, resembling in its form and topography much more the brains of cynomorphous monkeys than those of the three great anthropoids.” The brain of the Giant Apes on the other hand in the words of M. Weber (1904, p. 809) . . . “ist ein vereinfachtes Menschengehirn, dem aber nichts Wesentliches fehlt.”

Again, in summarizing the results of his complete dissection of eighty specimens of the higher Primates, Professor Keith gives a tabular analysis (1911, p. 509) of over a thousand characters observed in the gibbon, from which the following comparison is taken:

Total number of characters examined over 1000	Common to gibbon and cynomorphs 323	Common to gibbon and to all other anthropoids and man 133	Common to gibbon and man alone 84
	Common to chimpanzee and cynomorphs 980	Common to chimpanzee and to all other anthropoids and man 133	Common to chimpanzee and man alone 98

But these figures hardly convey a correct impression of the relative degrees of affinity of the gibbon to man and to the great apes, since the characters are recorded numerically and are not evaluated according to their phylogenetic importance.

"As to the position of the gibbons in the series of primates," remarks Keith (1896, p. 376), "there is a tendency at present, with which the writer is in sympathy, to remove the gibbons altogether from the company of the anthropoids and place them in a position intermediate between the great apes and the cynomorphous monkeys. . . . They are really cynomorphous monkeys adapted to locomotion in an upright posture" (1896, p. 376). The present writer, however, regards the Hylobatidæ rather as aberrant Simiïdæ, widely removed from the Cercopithecidæ.

In short the dental, osteological and anatomical characters of the gibbons appear to indicate that these apes represent an earlier offshoot of the anthropoid stem, as held by most authorities, and that the giant apes and man represent a later radiation. Comparative anatomical evidence sufficiently establishes the fact that the gibbons have been derived from the same brachiating and frugivorous catarrhine apes that gave rise to the whole man-anthropoid series. The derivation of the Gibbons from *Pliopithecus* of the Upper Tertiary of Europe is defended above (p. 301).

Apart from their primitive anthropoid characters the gibbons resemble man chiefly in the features wherein they have avoided the specializations of the giant apes. The rounding and reduction of the third lower molars are probably secondary characters analogous with similar retrogressive characters in the orang, chimpanzee and man.

The Orang-utan.—Professor Keith's vast labors on the anatomy of the anthropoids show: first that from the viewpoint of comparative anatomy the orang stands on a much higher plane than the gibbon, that is it has advanced further on the road toward extreme arboreal, frugivorous adaptation, toward a higher brain and mentality and toward gigantic size; secondly, that it stands well apart from the chimpanzee-gorilla group; and thirdly, that in the majority of its characters the orang is less man-like than the gorilla and chimpanzee.

The possible derivation of the Orang from the Miocene Asiatic genus *Palæosimia* is discussed above (p. 286).

The Chimpanzee.—Many features of the skull and skeleton of the chimpanzee are prophetic of the more specialized conditions in the gorilla. These two apes are indeed so closely allied that until recently both were referred to a single genus *Anthropopithecus*. Certain chimpanzees have exhibited strong resemblances to the gorilla, so that their status as chimpanzees was only determined by careful investigation (Keith, 1899), while on the other hand immature and female gorilla skulls to some extent suggest those of the chimpanzee.

The anatomist Tyson in 1699 published an excellent account of the anatomy of the chimpanzee, which he regarded as a distinct type of man (*Homo sylvestris*), and since then all observers have noted the close relationships of this ape to man in its anatomy, physiology and mental activities.

The derivation of the chimpanzee-gorilla group from one of the Miocene species of *Dryopithecus* is discussed above (p. 296–298, 337).

The Gorilla.—Morphologists who have had the opportunity of studying the young female gorilla, as well as the gibbons and other anthropoids now or lately living in the New York Zoölogical Park, can hardly fail to be impressed with the superiority of the gorilla's claim to human kinship as compared with that of the other anthropoids, especially the gibbon. This is shown not only in the face, hands and feet and other parts of the body, but in the deep-seated functions of the digestive and reproductive systems. The gorilla, is in fact extremely manlike in many organs of high morphological significance, such as the brain, the sternum, the region of the auditory bulla, the external ear, the genital organs, the mammæ, the heart, and the eye. The musculature of the gorilla also presents many human characteristics. (*Cf.* Duckworth, 1915.)

In adopting a partly terrestrial habit the gorilla has entered upon a line of adaptation which in the forerunners of man resulted in a fully bipedal, cursorial type, capable of invading the plains. But as the gorilla is largely frugivorous and limited to the forests and their neighborhood the only course left for it (apart from its inevitable extinction by man) would have been to go on increasing still further in size until it might have surpassed even the Kadiak bear in bulk. Such a beast might have ambled along on all fours, partly supporting itself upon its knuckles as the gorilla now does.

The probable derivation of the gorilla from one of the Miocene Asiatic species of *Dryopithecus* is discussed on pages 297, 337.

3. *The Origin of Man.*

Most anthropologists have specialized almost exclusively in their own field and have not acquired a practical knowledge of the evolution of the mammals, so far as it is known in many orders and families of mammals throughout the Tertiary and Quaternary Periods. Such specialists are impressed by the great and obvious differences between mankind and the existing anthropoids. They often magnify the phylogenetic importance of these differences, sometimes to the extent of supposing that the derivation of man is still veiled in complete mystery, or that the separation of the Hominidæ from the ancestral primate stock took place even before the differentiation of the Lemuroidea and Anthropeidea.

Many palæontologists, impressed with the vast antiquity of *Homo sapiens* as estimated in years, and with the fact that even the older Pleistocene species of Hominidæ were already widely separated from the anthropoids in tooth and limb structure, are inclined to push back the point of separation of the Hominidæ and the anthropoids into the early Tertiary.

In the present work the chief conclusions, which appear to be of a conservative character, are as follows:

1) Comparative anatomical (including embryological) evidence alone has shown that man and the anthropoids have been derived from a primitive anthropoid stock and that man's nearest existing relatives are the chimpanzee and gorilla.

2) The chimpanzee and gorilla have retained, with only minor changes, the ancestral habits and habitus in brain, dentition, skull and limbs, while the forerunners of the Hominidæ, through a profound change in function, lost the primitive anthropoid habitus, gave up arboreal frugivorous adaptations and early became terrestrial, bipedal and predatory, using crude flints to cut up and smash the varied food.

3) The ancestral chimpanzee-gorilla-man stock appears to be represented by the Upper Miocene genera *Sivapithecus* and *Dryopithecus* the former more closely allied to, or directly ancestral to, the Hominidæ, the latter to the chimpanzee and gorilla.

4) Many of the differences that separate man from anthropoids of the *Sivapithecus* type are retrogressive changes, following the profound change in food habits above noted. Here belong the retraction of the face and dental arch, the reduction in size of the canines, the reduction of the jaw muscles, the loss of the prehensile character of the hallux. Many other differences are secondary adjustments in relative proportions, connected with the change from semi-arboreal semi-erect and semi-quadrupedal pro-

gression to fully terrestrial bipedal progression. The earliest anthropoids being of small size doubtless had slender limbs; later semi-terrestrial semi-erect forms were probably not unlike a very young gorilla, with fairly short legs and not excessively elongate arms. The long legs and short arms of man are due, I believe, to a secondary readjustment of proportions. The very short legs and very long arms of old male gorillas may well be a specialization.

5) At present I know no good evidence for believing that the separation of the Hominidæ from the Simiidæ took place any earlier than the Miocene, and probably the Upper Miocene. The change in structure during this vast interval (two or more million years) is much greater in the Hominidæ than in the conservative anthropoids, but it is not unlikely that during a profound change of life habits evolution sometimes proceeds more rapidly than in the more familiar cases where uninterrupted progressive adaptations proceed in a single direction.

6) *Homo heidelbergensis* appears to be directly ancestral to all the later Hominidæ.

4. On the evolution of human food habits.

While all the great apes are prevailing frugivorous, and even their forerunners in the Lower Oligocene have the teeth well adapted for piercing the tough rinds of fruits and for chewing vegetable food, yet they also appear to have at least a latent capacity for a mixed diet. The digestive tract, especially of the chimpanzee and gorilla, is essentially similar to that of man and at least some captive chimpanzees thrive upon a mixed diet including large quantities of fruits, vegetables and bread and small quantities of meat (Keith 1899). Mr. R. L. Garner who has spent many years in studying the African anthropoids in their wild state, states¹ that "their foods are mainly vegetable, but that flesh is an essential part of their diet." Other observers state² that the gorilla and chimpanzee greedily devour young birds, as well as eggs, vermin and small rodents.

Even the existing anthropoids, although highly conservative both in brain development and general habits, show the beginning of the use of the hands, and trained anthropoids can perform quite elaborate acts. At a time when tough-rinded tubers and fruits were still the main element of the diet the nascent Hominidæ may have sought out the lairs and nesting places of many animals for the purpose of stealing the young and thus they may have learned to fight with and kill the enraged parents. They had also

¹ Science, vol. XLII, Dec. 10, 1915, p. 843.

² Keane, Ethnology, Cambridge 1901, p. 111.

learned to fight in protecting their own nesting places and young. And possibly they killed both by biting, as in carnivores, and by strangling, or, in the case of a small animal, by dashing it violently down.

We may conceive that the Upper Tertiary ape-men in the course of their dispersal from a south central Asiatic centre (Matthew, 1915, pp. 210, 214) entered regions where flint-bearing formations were abundant. In some way they learned perhaps that these "Eolith" flints could be used to smash open the head of a small strangled animal, to crack open tough vegetables, or to mash substances into an edible condition. Much later, after the mental association of hand and flint had been well established, they may have struck at intruders with the flints with which they were preparing their food and in this way they may have learned to use the heavier flints as hand axes and daggers. At a very early date they learned to throw down heavy stones upon an object to smash it, and this led finally to the hurling of flints at men and small game. Very early also they had learned to swing a heavy piece of wood or a heavy bone as a weapon. For all such purposes shorter and stockier arms are more advantageous than the long and slender arms of a semi-quadrapedal ancestral stage and I have argued above (p. 333) that a secondary shortening and thickening of the arms ensued.

One of the first medium-sized animals that the nascent Hominidæ would be successful in killing was the wild boar, which in the Pleistocene had a wide Palæarctic distribution.

From the very first the ape-men were more or less social in habits and learned to hunt in packs. Whether the art of hunting began in south central Asia or in Europe, perhaps one of the first large animals that men learned to kill after they invaded the open country was the horse, because, when a pack of men had surrounded a horse, a single good stroke with a coup-de-poing upon the brain-case might be sufficient to kill it.

I have argued above (p. 321) that the retraction of the dental arch and the reduction of the canines is not inconsistent with the use of meat as food, because men learned to use rough flints, in place of their teeth, to tear the flesh and to puncture the bones, and because the erect incisors, short canines and bicuspid were highly effective in securing a powerful hold upon the tough hide and connective tissue. It must be remembered that with a given muscular power small teeth are more easily forced into meat than large teeth.

After every feast there would be a residuum of hide and bones which would gradually assume economic value. The hides of animals were at first rudely stripped off simply to get at the meat. Small sharp-edged natural flints could be used for this purpose as well as to cut the sinews and flesh. After a time it was found that the furry sides of these hides were

useful to cover the body at night or during a storm. Thus the initial stage in the making of clothes may have been a biproduct of the hunting habit.

Dr. Matthew (1915, pp. 211, 212) has well suggested that men may have learned to cover the body with the skins of animals in a cool temperate climate (such as that on the northern slopes of the Himalayas) and that afterward they were able to invade colder regions. The use of rough skins to cover the body must have caused exposure to new sources of annoyance and infection, but we cannot affirm that natural selection was the cause of the reduction of hair on the body and of the many correlated modifications of glandular activity. We can only affirm that a naked race of mammals must surely have had hairy ancestors and that the loss of hair on the body was probably subsequent to the adoption of predatory habits.

The food habits of the early Hominidæ, and thus indirectly the jaws and teeth, were later modified through the use of fire for softening the food. Men had early learned to huddle around the dying embers of forest fires that had been started by lightning, to feed the fire-monster with branches, and to carry about firebrands. They learned eventually that frozen meat could be softened by exposing it to the fire. Thus the broiling and roasting of meat and vegetables might be learned even before the ways of kindling fire through percussion and friction had been discovered. But the full art of cooking and the subsequent stages in the reduction of the jaws and teeth in the higher races probably had to await the development of vessels for holding hot water, perhaps in Neolithic times.

This account of the evolution of the food habits of the Hominidæ will probably be condemned by experimentalists, who have adduced strong evidence for the doctrine that "acquired characters" cannot be inherited. But, whatever the explanation may be, it is a fact that progressive changes in food-habits and correlated changes in structure have occurred in thousands of phyla, the history of which is more or less fully known. Nobody with a practical knowledge of the mechanical interactions of the upper and lower teeth of mammals, or of the progressive changes in the evolution of shearing and grinding teeth, can doubt that the dentition has evolved *pari passu* with changes in food habits. Whether, as commonly supposed, the food habits changed before the dentition, or *vice versa*, the evidence appears to show that the Hominidæ passed through the following stages of evolution:

- 1) A chiefly frugivorous stage, with large canines and parallel rows of cheek teeth (*cf. Sivapithecus*).
- 2) A predatory, omnivorous stage, with reduced canines and convergent tooth rows (*cf. Homo heidelbergensis*).
- 3) A stage in which the food is softened by cooking and the dentition is more or less reduced in size and retrograde in character, as in modernized types of *H. sapiens*.

5. APPENDIX A. M. BOULE'S CONCEPTION OF *Eoanthropus* AND OF THE ANCESTRAL HOMINIDÆ.

In the course of a critical discussion of recent archæological and palæontological work in England M. Boule (1915, pp. 60, 62) says of the Piltdown mandible that it completely resembles the mandible of a chimpanzee; that notwithstanding what had been said of it, its molars are more simian than human in type, so that if it had been found alone in the gravel beds of Piltdown, along with the remains of Pliocene mammals, one would not have failed to call it *Troglodytes Dawsoni* and to declare that it gave evidence of the existence in England, during the Pliocene, of an anthropoid ape. But after noting the anatomical difficulties in the way of conceiving this simian jaw as having articulated with a fully human brain-case M. Boule goes on to say that although this purely anatomical argument is not without value, yet it relies too much upon the old Cuvierian doctrine of correlation (*il a le tort d'être imprégné d'un vieux parfum cuviérin*) and it is based too exclusively upon morphological data drawn from existing human conditions. But, continues M. Boule, palæontologists know how fertile nature is in making unforeseen combinations and she could easily enough associate a human condyle and glenoid fossa with a simian jaw in such a way that the association would not appear absurd either mechanically or physiologically. [To the present writer this argument seems to be almost a *petitio principii*.] It seems that in the evolution of a bony head, when the face diminishes the mandible diminishes more slowly, lagging some distance behind, so to speak, in the retreating movement. This phenomenon appeared very clearly to him, says M. Boule, in both the Chapelle-aux-Saints and the La Terrassie skulls of *Homo Neanderthalensis*.

Passing to the circumstances and conditions of deposition of the Piltdown remains M. Boule (p. 62) notes that it is difficult to imagine the presence, at the same point in the depths of an ancient alluvial formation, of remains belonging to two species of large Primates, and to explain, as a mere chance, the fact that these remains should have the same physical characters, should belong to beings of the same form and should pertain to complementary parts of the skeleton. [This point is critically considered in Dr. Matthew's "Note on the Association of the Piltdown Skull and Jaw" (*postea*, p. 348).

However the chimpanzee jaw may have happened to become associated with the human remains, the fact that it is a chimpanzee jaw is demonstrated, the reviewer believes, by a comparison of the Piltdown mandible with the specimens figured by Miller (See also p. 312 above.).]

On the other hand, continues M. Boule, the presence of an anthropoid in western Europe in the Pliocene epoch would be nothing extraordinary. [In addition to the chimpanzee molar from the Pleistocene of Taubach near Weimar, originally described by Nehring (1895) as a human tooth and identified by Miller as belonging to a chimpanzee, there were chimpanzees in the Pliocene and Upper Miocene of Europe, because a comparison of the molars of *Dryopithecus rhenanus* with those of existing chimpanzees has convinced the reviewer that the former was very closely allied, or even directly ancestral, to the Pleistocene and Recent chimpanzees (*supra*, p. 309).]

So that without rejecting M. Smith Woodward's interpretation, which, says M. Boule, "I believe to be perfectly possible, even probable, it would seem to me prudent for the present to hold the question open and to leave the point of the association of mandible and skull in doubt."

The Piltdown documents, continues our author, are unfortunately incomplete. The interpretation of them is still doubtful on essential points. But for all that they constitute one of the most important and instructive of discoveries. Even supposing that the skull and the mandible be entirely independent yet the fragments of the cranium apprise us of the existence, at a very remote geological epoch, of a hominid with a brain-case essentially human; they show further that this man is connected more distinctly with the line of ascent of *Homo sapiens*, than with that leading to *Homo Neanderthalensis*. The latter would represent, therefore (says M. Boule), as I have long maintained, a very different branch from that of *Homo sapiens*, and hence the point of origin of our direct ancestor should be pushed back very far into the past. Up to the present time one could only cite in support of this fact a small number of discoveries, which were without geological guarantees, without satisfactory legal status, and consequently without any demonstrative value. But here we are in the presence of a fact that is new, thoroughly observed and of clear and precise significance.

The author, after gladly acknowledging the merits of Mr. Smith Woodward's researches, begs his pardon for this final criticism: Why make a new genus for the Piltdown fossil, since according to Mr. Smith Woodward himself, its characters are essentially human, and since he now attributes to it a cerebral capacity as large as that of many existing types? And, especially, why choose the name *Eoanthropus*? Does Mr. Smith Woodward really believe that he has discovered the auroral form of humanity? If, from a palæontological viewpoint, says M. Boule, we compare the evolution of the Hominidæ with that of the Equidæ, we see that the name *Eohippus*, invented by Marsh, corresponds truly to a very ancient Perissodactyl, in which we begin to perceive the tendencies toward the soliped type. Then come other forms: *Meshippus*, *Protohippus*, *Pliohippus* etc., connecting

this *Eohippus* with the true *Equus*. Now it is quite certain that *Eoanthropus* does not bear the same relation to *Homo* as *Eohippus* does to *Equus*. It rather represents, for the Hominidæ, about what the *Protohippus* stage does for the Equidæ. And Mr. Smith Woodward, who still retains for the Neanderthal man the name *Homo primigenius*, the incorrectness of which, says M. Boule, I have elsewhere shown, was no better inspired when he devised his *Eoanthropus* for a *Homo*.

Then follows, as a climax and abrupt ending, the conclusion to which all M. Boule's own researches in palæanthropology and palæontology have evidently led him:

Some day, he says, one will discover a hominid of small stature, and almost erect posture, with a brain-case very voluminous in relation to the total volume of the body, but very inferior in absolute value to that of all the Hominidæ now known. And that will be the veritable *Eoanthropus*.

To the reviewer it seems that this striking conclusion, backed as it is by M. Boule's eminent position, and by the high importance of his various memoirs, will be likely to receive a degree of acceptance far greater than that which it truly merits. Unfortunately M. Boule does not enlighten the reader as to his reasons for deriving the Hominidæ from dwarfish beings with swollen heads; but we know that in his memoir on the Chapelle-aux-Saints man he was much impressed by the (to him) profound differences in the structure of the limbs between this ancient Hominid and all known Anthropoids, so that he finally ascribed many of the resemblances between the two groups to a far-reaching parallelism, extending even to blood reactions, brain structures and characteristics ordinarily regarded as indicative of a common origin. We know too that in that memoir he finally suggested that the point of divergence between the Hominidæ and other Primates might prudently be regarded as occurring very far down upon the Primate stem, perhaps even before the divergence of the lemurs from the remaining Primates and he insisted that the poverty of the palæontological record must render nugatory any attempt to work out the phylogeny of the Hominidæ from existing data.

The reviewer on the contrary has maintained (*vide supra*) that even if we had no direct palæontological evidence, the data of comparative anatomy are sufficient to demonstrate that the anthropoid apes are the nearest existing relatives of mankind; that the divergence of the Hominid branch occurred not in a pre-lemuroid or even pre-catarrhine stage, but from the anthropoid stem after the separation of the gibbons; further, that from the palæontological side the fundamental unity in premolar and molar patterns between Tertiary anthropoids and Quaternary Hominidæ reinforces the anatomical evidences for unity of origin of these groups. The reviewer is

also of the opinion that the enlarged braincases of certain small-bodied lemuroids and platyrrhines and of human foetuses offer no real evidence that the ancestral hominid had a swollen braincase. As for the swollen head of the human foetus that is evidently a cænogenetic character, as it is in many other mammals. The reviewer also holds that the anatomical and palæontological data give evidence of a profound change of function and structure in the human dentition, a change from a pre-human frugivorous stage to a sub-human omnivorous-carnivorous stage; that the immediate ancestors of the Hominidæ, after the loss of the chief anthropoid characters were of large size, powerful build and predatory habits and that the bipedal adaptations were assumed at a relatively late geological epoch (Middle Tertiary).

6. APPENDIX B. NOTE ON THE ASSOCIATION OF THE PILTDOWN SKULL AND JAW.

By W. D. MATTHEW.

The finding of the cranial fragments and lower jaw associated in the same stratum and locality, and in similar state of preservation, has been presented as an argument for their pertaining to the same individual. Curiously enough this evidence has been discussed and weighed with purely theoretical and *à priori* reasons, as though it were a unique case in palæontologic discovery. But it is a very common occurrence among fossil mammals. Every collector, every cataloguer of such collections must have had again and again to decide whether a "lot" of fragments found together represented one individual or more than one, and what parts should be assigned to each if two or more animals were present. In the experience of the American Museum collecting there have been thousands of such cases to decide, and the probabilities and methods of determining them are well known and have been thoroughly tested. The conditions of discovery vary between extremes in which all the remains belong certainly to a single individual, and the so-called "general quarries" and miscellaneous pots in which remains of many individuals are commingled, often with no probable association of parts. For the most part the extent to which the animals represented can be sorted out, and the degree of probability that attaches to the association of different parts as of the same individual, must be decided by the particular circumstances in each case. Few general rules can be laid down. Duplication of parts affords of course conclusive proof of the presence of more than one individual. The presence of parts recognized as belonging to different kinds, ages or sizes of animals, proving that

more than one individual is represented casts doubt upon the pertinence to a single individual of bones which would otherwise be associated with reasonable probability. Such associations must be scrutinized with care. The mere fact that they are found together, and are anatomically proven to belong to the same order or even genus, has but little weight as evidence for pertinence to one individual. Yet if numerous fragments of different parts which might be tentatively assigned to a single animal are found to fit together in part, there will be good reason to conclude that the lot of fragments is mainly of one individual and only a few odd bones of others have become intermingled. If, on the other hand, a lot of fragments are found together which may reasonably belong to a single individual, and there is no evidence at all of any intermixture, the lot being found well separated from any other fossil remains, there is a high degree of probability that they do all belong together; and this probability is higher in proportion to the number of bones or fragments present.

If the Piltdown remains were subjected to the ordinary practical criticism with regard to their association that would be accorded to any lot of fossil mammals for cataloguing and record at the American Museum, or any similar institution, the question of association would turn largely upon the foregoing considerations.

It would be clear in the first place that there is unquestionable evidence of admixture of animals belonging to different groups. The teeth or fragments of *Stegodon*, *Mastodon*, *Hippopotamus* etc. are stated to be found in the same deposit; it is a gravel deposit, and this is well known to add greatly to suspicion of intermixture. Some of the remains are stated to be in a rolled and water-worn condition presumably derived from an older deposit, others including the primate remains, *Hippopotamus*, *Castor* and *Cervus* are considered to be of the same age as the gravel. The latter are then unquestionably a mixed lot, and the mere association has little weight as evidence that all the primate remains belong to one individual. So far as the cranial fragments are concerned, some of them are found to fit together; this is strong positive evidence that all the cranial fragments belong to one individual, and as all are characteristically identical with the genus *Homo*, it may be accepted as a practical certainty that they do belong together. The fragments of nasal bones may, but with somewhat less certainty, be assigned to the same individual. If various parts or fragments of the skeleton were present, I should regard it as strong presumptive evidence for associating the lower jaw with the skull. In the absence of any skeleton fragments no such presumption exists. There is not much more probability that the lower jaw would remain in association with the skull than that any of the other bones of the skeleton would so remain. Theoretically there

should not be any more, but in practice one finds the skull more often associated with the lower jaw than with any particular skeleton bone. There is therefore more probability that a primate skull and jaw found associated would pertain to the same individual than that a primate skull and ulna found together would be from the one animal. But in neither case is the probability of very high degree, unless there is an entire absence of admixture of remains of any other animals, which in this instance is not the case.

The canine tooth if it belongs to the upper jaw does considerably add to the probability of the association with the skull, provided it were evident from the freshness of the root surfaces that it had been buried in the alveolus up to the time that the cranium was broken in fragments. Otherwise it has little weight. If it were, as Doctor Smith Woodward considers it to be, a lower canine, it would not afford any confirmatory evidence for association of skull and jaw.

In brief, a critical consideration of the available evidence for association of the primate remains from Piltdown, on the same lines that have been used in associating the thousands of more or less similar Tertiary mammal specimens that I have had occasion to examine for cataloguing purposes, would lead to the conclusion that they may probably represent either one or three individuals, but that they might be tentatively associated as of one individual provided they belonged to a single known type or that no anatomical discrepancies or improbabilities were involved. But the argument from association is quite too slight to outweigh any such contrary evidence, and certainly not adequate to base upon it the erection of a new type of primate combining characters hitherto found dissociated in distinct generic types.

This opinion is based solely upon examination of the casts and of the published evidence. I do not question that much additional evidence would appear upon a critical examination of the original specimens, and it is stated with due deference to the judgment of those who have had that privilege. I think proper to express it only because I have had somewhat exceptional opportunities of examination and judgment upon a great number of cases which I deem to be more or less similar.

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