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# THE
# ORIGIN AND EVOLUTION
# OF THE
# HUMAN DENTITION

WILLIAM K. GREGORY

# THE ORIGIN AND EVOLUTION
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# HUMAN DENTITION

BY

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BALTIMORE
WILLIAMS & WILKINS COMPANY
1922

PUBLISHED FOR THE
JOURNAL OF DENTAL RESEARCH, INC.
NEW YORK

COMPOSED AND PRINTED AT THE
WAVERLY PRESS
BY THE WILLIAMS & WILKINS COMPANY
BALTIMORE, MD., U. S. A.

*DEDICATED*

*To Henry Fairfield Osborn, LL.D., Hon. D.Sc., etc.*
*Author of "Evolution of Mammalian*
*Molar Teeth to and from the*
*Triangular Type."*

# PREFACE

Parts I to V of this book were published in five successive numbers of the JOURNAL OF DENTAL RESEARCH, Vols. II and III, beginning in March, 1920. The purpose of the book is to give a brief and concise review of the origin and evolution of the human dentition from the palæontological viewpoint; but how far brevity and conciseness have been achieved, in the midst of so many debated subjects requiring detailed discussions, must be left to the reader's verdict.

The facts and interpretations of facts here set forth are such as have presented themselves during the course of the author's palæontological studies at Columbia University and at the American Museum of Natural History, where since 1900 the author has had the inestimable privilege of close association with Professor Henry Fairfield Osborn.

As fully set forth in Professor Osborn's work on the Evolution of Mammalian Molar Teeth (1907), we owe to the late Professor E. D. Cope of Philadelphia the discovery (1883) that the "tritubercular type was ancestral to many if not all the higher types of molar teeth." "This," writes Professor Osborn, "is one of the most important generalizations ever made in mammalian comparative anatomy." He further says that in his opinion "the evidence in favor of it is so overwhelming that primitive trituberculy is no longer an hypothesis or a theory but an established fact." Similarly Doctor J. L. Wortman, author of a standard work on the Comparative Anatomy of the Teeth of the Vertebrata (1886), and the discoverer and describer of many important types of Eocene mammals, writes thus of Cope's theory of Trituberculy (1921, p. 187):[1]

> "The broad generalization sought to be established by this theory is one of the most important and far reaching deductions within the whole range of mammalian morphology, and is a performance in every way worthy of

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[1] See the bibliography for complete versions of this and similarly abbreviated references.

the great master mind that conceived it. It is one of the many enduring monuments that will stand to the credit of this greatest of all American morphologists as long as the science is cultivated.

"It is to be observed that Cope's theory of Trituberculy, as the name implies, sought only to reduce the highly developed and complex molar patterns to the basis of the simple three-cusped stage, and his researches and discoveries were largely to this end. These studies were mostly made upon the Amblypoda, Phenacodonts, Ungulates, Primates, Carnivores and related groups, and it is largely upon the molar evolution of these orders that the generalization rests. In this, Cope's researches have been epoch-making and it was almost wholly through these efforts that the evolution of the complex and complicated molar patterns of these forms was first completely understood. In the further development and elaboration of this subject, the researches of Cope have been powerfully supplemented by the work of Scott and Osborn, especially the latter, who has contributed greatly to our knowledge along these lines."

These statements by Professor Osborn and Doctor Wortman in support of Cope's generalization rest upon the broadest basis of fact. Since 1891 expeditions from the American Museum of Natural History 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 still being described in American Museum publications, afford cumulative evidence (which only those who know the material at first hand can fully appreciate) for Cope's and Osborn's conclusion that trigonal 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 carnivores, condylarths, perissodactyls, primates and other orders. Nor should we forget the reënforcement of this conclusion afforded by the great collections of European fossil mammals, as described during recent years by Depéret, Schlosser, Stehlin and many other palæontologists.

In 1895 Professor Osborn 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 of protocone, paracone, metacone, hypocone, for the cusps of the upper molars,[2] and protoconid, metaconid, hypoconid, entoconid and hypoconulid for those of the lower molars.[3] "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.

Unfortunately the numerous and fundamental contributions of Professors Cope and Osborn to the subject of the evolution of mammalian molar teeth from the tritubercular type onward, are too often lost sight of as a result of the altogether disproportionate attention that has been devoted to the "Cope-Osborn hypothesis" of the origin of the tritubercular molar from the triconodont molar.[4] This "frail hypothesis," as the writer has called it (1916, p. 240) was that triangular molars had been derived from the triconodont type with three cusps in fore-and-aft line, by the migration, rotation, or circumduction, of the two marginal cusps, outward in the upper and inward in the lower jaw.

The Cope-Osborn hypothesis has been rejected, as insufficient or in conflict with other evidence, by several authors, including Dr. J. L. Wortman (1903–'04). Professor Osborn in 1907 (p. 8) restated the evidence in its favor and concluded, "there is thus evidence for cusp rotation, but it is not an essential part of the tritubercular theory, because, as above stated, the denticles (para- and metacones) may have arisen on the inner and outer sides of the crown from the outset."

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[2] protocone = mesiolingual
paracone = mesiobuccal
metacone = distobuccal
hypocone = distolingual

[3] protoconid = mesiobuccal
paraconid (absent in man)
metaconid = mesiolingual
hypoconid = distobuccal
entoconid = distolingual
hypoconulid = distal

[4] Wortman (1921, p. 187) attributes to Osborn the authorship of this hypothesis; but Cope (in his Origin of the Fittest, p. 347) refers to it as his own, and Osborn has always (1888, p. 243; 1907, p. 4) given Cope the credit for it. It is clearly set forth in Cope's article on the Creodonta in the *American Naturalist*, 1884, p. 259.

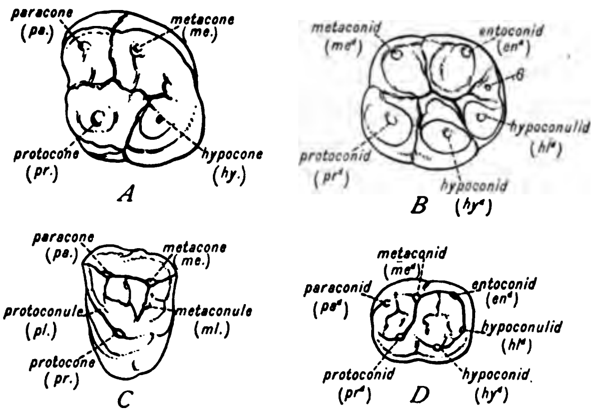

FIG. A. THE OSBORNIAN NOMENCLATURE OF THE MOLAR CUSPS

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 species.

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

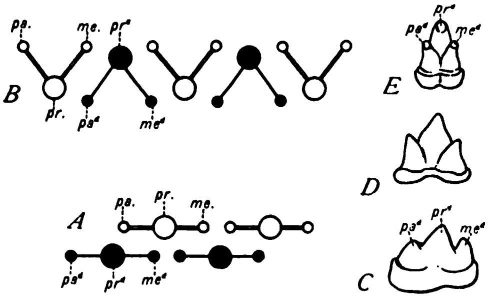

FIG. B. THE COPE-OSBORN HYPOTHESIS OF THE CIRCUMDUCTION OF THE PARA- AND METACONES

A.—Triconodont stage with all three cusps in the same antero-posterior 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.

In the present work (Part I) as well as in previous ones (1910, p. 193; 1916, p. 242–3), the author supports the view that in the remote ancestors of typical mammals the para- and metaconids of the lower molars probably arose, in situ, as up-growths from the cingulum, but that in *Spalacotherium*, *Menacodon* and their allies there may have been a migration or shifting of the para- and metaconids. The view of Cope and Osborn that the so-called protocone (mesio-lingual cusp) of typical upper molars represents the original apex of the crown, has been attacked by many authors, as set forth by Osborn (1907) and the present writer (1916).

Recognizing the cumulative weight of the evidence that in the upper molars of early Tertiary mammals the so-called protocone is not the oldest, or first cusp, but represents an upgrowth from the basal tubercle or cingulum [as maintained especially by Wortman (1903–'04), Gidley (1906), Matthew (1910), Gregory (1916)], and that the primitive tip of the reptilian crown lies in the paracone (or para + metacone), the author has formulated in the present work (Parts I, II, fig. 44) the following principles:

(1) That in the triangular upper molars of early Tertiary mammals there are two principal "trigons," (a) the *primary trigon*, consisting of the divided "original tip" (para + metacone) and the external cingulum, and (b) the *secondary trigon*, comprising the inwardly grown "protocone" and the divided original tip.

(2) That the homologue of the trigonid of the lower molars is not the *secondary* but the *primary* trigon.

It follows from these principles, and from studies of the occlusal relations of the upper and lower teeth, that Cope's conception of the origin of the tritubercular molar and, consequently, the whole nomenclature of the mammalian molars proposed by Professor Osborn, probably rest upon a misconception, by which the *secondary* trigon of the upper molar was viewed as corresponding with the *primary* trigonid of the lower molar.

But are we therefore to agree with Dr. Wortman (1903, 1921) and abandon the use of the Osbornian nomenclature? Gidley (1906), Matthew (1910) and the writer (1916) hold that as these names are far more widely used by palæontologists than any others, it is not likely that they will readily give up such a convenient system for any of the cumbersome substitutes that have been proposed. Even although the "protocone" of the upper molars is probably not the oldest cusp of the mammalian molar crown, its name need not carry the implication of oldest, if used as a conventional name for that cusp. And even although the protocone of the upper molar has probably arisen with and is functionally analogous with the talonid, or posterior part of the lower molars (see Parts I, II), it would be in the highest degree confusing either to abandon the Osbornian nomenclature at this late date or to try to rectify it in accordance with the newer ideas. Such a compromise will no doubt be unacceptable to rigorous idealists who do not recognize that the terminology in question consists of more or less arbitrarily chosen symbols, which, although not always appropriate, have the merit of being well defined, practicable and in wide use.

For readers who desire to gain a preliminary idea of the contents of this work is suggested, first, an inspection of *figs. 346–353* inclusive, illustrating the stages in the evolution of the human skull and dentition from fish to man, and secondly, a cursory review of the summaries and conclusions at the end of each part.

In spite of the efforts of the author and of the editor to make this work accurate and reliable in all details, many minor errors and some more important ones, in the original publication of the parts in the JOURNAL OF DENTAL RESEARCH, have already been detected.[5] These corrections and changes have been made in the text or are noted on pages following this preface. The author is under especial obligation to Dr. Milo Hellman for critical reading and notes on Parts I–V, and to Dr. W. D. Matthew for critical notes on the section dealing with the Mesozoic mammals.

It will be observed that the author contributes nothing new to the Piltdown problem, but leaves it *in statu quo*. While Part V was in press, and since that time, Professor Osborn, Dr. Matthew and Professor J. H. McGregor have each examined the original Piltdown remains, and the later ones described (1917) by Smith Woodward. They have all come to the conclusion that the more recently discovered lower molar tooth is much like the original type, and that it

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[5] See the *Journal of Dental Research*, 1920, ii; under "errors and changes," p. 41 (general matter for vol. II, December issue).

lends strong evidence in favor of Smith Woodward's conclusion that the ape-like lower jaw belongs with the man-like skull. Professor Osborn also indorses Woodward's conclusion that the ape-like canine is a lower and not an upper one, and the same view is held by Dr. Milo Hellman, whose intimate knowledge of the occlusal surfaces of teeth lends weight to his opinion.

In conclusion the author's deep appreciation and thanks are due to the executive officer of the board of editors of the JOURNAL OF DENTAL RESEARCH, Professor William J. Gies, for his unwearied patience and splendid support at every stage of the work. To Professor Osborn, Director Lucas, and Dr. Matthew, of the American Museum of Natural History, the author owes the privilege of reproducing many illustrations belonging to the Museum, including plates from D. G. Elliot's memoir on the Primates, and most of the American fossil mammals figured in this work. During the past twenty years Dr. Matthew has constantly placed at the disposal of the writer his wide and intimate knowledge of the dentition of the fossil mammals of America, and we have had many stimulating discussions bearing upon the facts and theories of dental evolution. The courtesy of others who loaned illustrations is acknowledged in the legends of the figures.

WILLIAM K. GREGORY.

*American Museum of Natural History*
*New York City, December, 1921*

# ERRORS AND CHANGES

Page 39; sixth line from the bottom: "known from a fragment of a lower jaw." *Note.*—Dr. W. D. Matthew, who has recently examined this fragment in the British Museum, has kindly given the author the following note: "This is a fragment of an *upper* jaw. It shows under binocular microscope three complete teeth, which agree fairly well with the posterior molars of *Tritylodon*, and the roots or alveoli of three others in advance of them. It differs from *Tritylodon* in size, in the sharp incurvation of the maxilla a little above the teeth, and the more anterior position of the zygoma, if the above identification be correct, but may be provisionally referred to the same family."

Page 45; line 2: *Family* **Spalacotheriidæ**. *Note.*—After examining the specimens in the British Museum, Dr. W. D. Matthew has written as follows to the author: "It appears to me more probable that *Spalacotherium* is related to the Trituberculata in spite of the difference in the angle. The teeth are quite close to *Stylodon* and its allies, and of a type that appears to me fundamentally distinct from *Triconodon* and equally distinct from *Phascolotherium*."

Page 49; *fig. 26:* lower jaws of *Amblotherium*. *Note.*—Dr. W. D. Matthew notes that the jaws and teeth of *Amblotherium soricinum* are much like those of *Stylodon*, and that in the jaw of *A. mustelula* the teeth are poorly exposed and very much worn.

Page 51; *fig. 28:* lower jaws of *Stylodon*. *Note.*—Dr. W. D. Matthew, who has recently examined these specimens, has written to the author as follows: "These are imperfectly exposed. The tooth has in fact a trigonid with high protoconid, smaller but well developed inner cusps and a small-cusped talonid. They are Amphitheriidæ, differing from *Amphitherium* in the higher trigonid and smaller heel."

Page 57; *fig. 33:* upper and lower molars of *Peralestes*. *Note.*—After examining the maxilla of *Peralestes longirostris*, Dr. W. D. Matthew notes: "The differences from the *Kurtodon* type are chiefly due to the presentation of the views. They are essentially the same, differing only in the presence of a distinct intermediate cusp on the postero-internal crest. This I take to be the upper dentition of *Spalacotherium*."

Dr. Matthew's *provisional* conclusions are: (1) that "*Spalacotherium*," the lower teeth, and "*Peralestes*," the upper teeth, belong together; (2) that both are allied with *Kurtodon;* (3) that both the stylodonts and spalacotheres are closely related to or derived from the older genus *Amphitherium*, but more specialized in the reduction of the talonid in the lower teeth; (4) that it is probable that *Spalacotherium* and the other Trituberculata are fundamentally distinct from *Triconodon* and equally distinct from *Phascolotherium;* (5) that the main tips of the upper molar crowns of *Stylodon* and of *Peralestes* are serially homologous with the main tips of their premolars, and that they represent the para + metacones of Tertiary mammals; (6) that the Trituberculata of the Mesozoic are paralleling the zalambdodonts of the Tertiary in the evolution of their molar teeth, and that (7) they therefore throw no new light on the ultimate origin of the tritubercular molar.

None of these conclusions is in conflict with the interpretation of the origin and evolution of the molar teeth adopted in the present work. Dr. Matthew feels reasonably certain that the main tips of the upper molars in *Kurtodon* and *Dryolestes* are serially homologous with those of the premolars, as set forth in Parts I and II of this book.

Page 117. Dr. W. D. Matthew notes that the premolar of *Mixodectes* sp. (*fig. 50*) is probably wrongly associated with the other teeth.

Page 425. Dr. Milo Hellman notes, in comment on section "(9)": The last part of the sentence referring to molar occlusion is true only of the third molars. In the first and second molars the disto-lingual slopes of the disto-buccal cusps of the upper molars come into occlusal relation with the mesio-buccal slopes of the mesio-buccal cusps of the lower molars distal to them. It would therefore appear that the molar occlusion in man has not entirely lost its primitive character even on the buccal side. In instances where this occlusal relationship is disturbed, it should more properly be considered either as an individual variation or as an anomalous manifestation. (Disto-buccal cusp = metacone. Mesio-buccal cusp of lower molars = protoconid.)

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# PART I

## Stages of Ascent from the Silurian Fishes to the Mammals of the Age of Reptiles

# I. EARLY STAGES OF VERTEBRATE EVOLUTION, SEEN IN THE FISHES OF THE PALEOZOIC ERA

The later chapters in the evolution of the human dentition can only be understood in the light of the whole story, so it is advisable to begin at the beginning, or as near to the beginning as the palæontological record extends.

## THE OSTRACODERMS OF THE UPPER SILURIAN AND DEVONIAN

The problem of the origin of the vertebrates we must necessarily ignore, because the innumerable answers to it cannot be tested by an appeal to the palæontological record. We can, however, begin at a very early stage, represented by the ostracoderms of Silurian and Devonian times, which are on the whole the most primitive of all known chordates. It is true that the modern *Amphioxus* and the cyclostomes have acquired a world-wide reputation as primitive chordates but, in the absence of palæontological evidence, their real status is still unsettled; and, in their present conditions, they teem with specializations which conceal their primitive characters. The Paleozoic ostracoderms, on the other hand, afford definite information of a pregnathostome stage of evolution which is lower and, as a whole, older, than any other group of vertebrates. Although much excellent material is preserved in the museums of the world, none of these lowly fish-like chordates shows the least evidence of having attained "gill-arch jaws" of the normal vertebrate type. Some of them had a capacious mouth and, in the latest and more specialized ones (*Bothriolepis*, *Pterichthys*), the ossified dermal plates around the slit-like mouth acquired jagged edges and may have functioned in the prehension of food; but no known ostracoderm had either teeth or calcified oral and branchial arches. For the most part they probably fed on small organisms found in the mud on the bottom of the streams in which they lived. Possibly they may have extracted the nutriment from the mud by ciliary tracts, as in *Amphioxus* and the larval lamprey. One of them (*Birkenia*) was shaped somewhat like *Amphioxus* and could perhaps dart about freely in the water, but most of them were depressed in form and probably lived on the bottom. None of them had attained the swift-swimming, predatory form, armed with strong teeth, which, there is much evidence to indicate, was the starting-point for the development of vertebrates higher in the scale.

## THE DEVONIAN SHARKS

The numerous group of sharks, dating back to the Upper Silurian but well known only in the Devonian and later periods, are with good reason regarded as primitive in their class characters, since they all have the primitive vertebrate ground-plan of the endoskeleton. While most of the known ostracoderms had over-emphasized the exoskeleton, the elasmobranchs very early built up an endoskeleton by precipitating calcium salts in the connective tissues and septa, which form a nucleus or core of the endoskeleton. They were active, predatory, fishes and developed further than did the ostracoderms the method of moving by rhythmic contraction of the muscle segments, or myomeres, arranged on either side of the mid-line. The development of the endoskeleton stiffened the median axis against the thrust of the myomeres and made possible the assumption of aggressive habits.

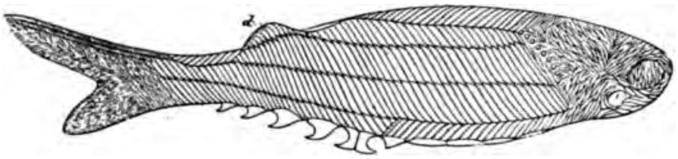

FIG. 1. *Birkenia elegans*, A PRIMITIVE FISH FROM THE UPPER SILURIAN OF SCOTLAND

Illustrating a stage of evolution before the formation of teeth and jaws. Natural size. After Traquair.

In the earliest known sharks the mouth is supported by cartilaginous jaws of the "gill-arch" type. Even modern sharks retain much evidence tending to show that the cartilage jaws are serially homologous with the gill arches, and that the primitive jaw muscles for squeezing the upper and lower halves of the oral arch together are serially homologous with the constrictor muscles of the gill arches.

It is well known to all students of odontology that, in typical sharks, the skin all over the body is covered with shagreen denticles, and that the primitive dental lamina of sharks is merely a rolled-up fold of skin bearing the dermal denticles, and carried around onto the inner side of the mouth. The whole surface of the throat is also covered with this denticle-bearing skin, and it is for this reason that in later groups of fishes we often find teeth on the pharyngeal parts of the gill arches.

In this primitive vertebrate stage the primary or cartilage jaws articulate posteriorly with the sides of the primitive cartilaginous brain case and are also supported by the second, or hyoid, arch. The endocranium itself is a complex of the connective tissue surrounding the capsules of the sense organs and the anterior end of the notochord. The denticulate skin covering the whole body represents the dermal skull, the bony sheaths of the jaws, and the scaly areas on the body of the higher fishes.

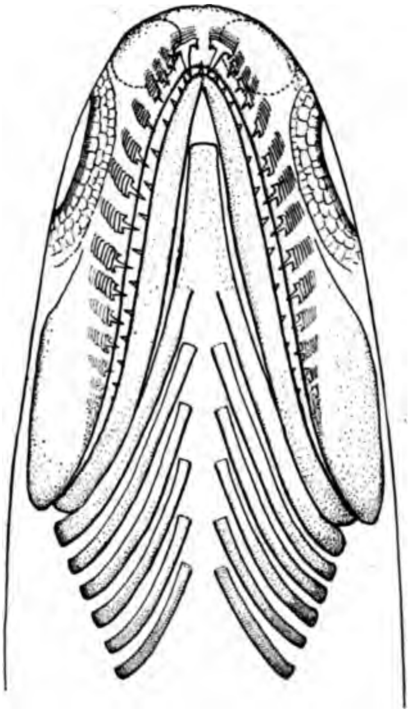

FIG. 2. UNDER-SIDE OF THE HEAD OF *Cladoselache fyleri*, A PRIMITIVE SHARK FROM THE UPPER DEVONIAN OF OHIO

Showing the primary jaws, homologous with the branchial arches, and bearing teeth on the skin inside the mouth. The eyes are surrounded by rows of sclerotic plates, which are homologous with the teeth and with the shagreen denticles of the skin. After Dean.

It is only in respect to the ground-plan, or class characters, that sharks are primitive, because most of the known sharks even in the Devonian are already diversely specialized in the dentition. The primitive shagreen denticles often fused into great dental plates of diverse form, as in many of the rays, adapted for crushing shellfish. The sharks remained primitive, however, in that they never developed sockets for the teeth in the upper and lower jaws.

## THE DEVONIAN GANOIDS AND LUNG-FISHES

The undiscovered links between the ostracoderms and sharks, and between the predecessors of the sharks and the oldest ganoid fishes, may some day be found in the Upper Silurian. At least in the Lower Devonian the primitive ganoid fishes were already established. These exhibit a distinctly higher stage in the evolution of the vertebrates than did the sharks. The teeth are now sharply differentiated from the rest of the exoskeleton and are often set in distinct sockets or grooves in the derm bones of the jaws; the head skeleton is complex, consisting, first, of an outer mask of derm bones, the histological elements of which are identical with those of the scales, and second, of the inner or endocranium, homologous with the cartilage skull of the shark, but now invaded by bony tissue. So, too, the primary or cartilaginous lower jaw (Meckel's cartilage) has been sheathed in a thick coating of dermal bones, and similar derm bones cover the roof of the mouth and the lips, giving rise to external or secondary jaws (premaxilæ, maxillæ), to the vomer and parasphenoid, and to the dentigerous tracts which partly cover the primary upper jaw or ossified pterygoquadrate cartilage.

These earliest ganoids, using the term in its wide sense in allusion to their shiny ganoid scales, include three very distinct groups. The first, or actinopterygian series, of which the fullest palæontological record is known, leads up through long successive ages to the highly specialized modern teleosts, including by far the greatest number of existing fishes. In these the locomotor apparatus attains its highest perfection for progression through the water. The tail passes from the heterocercal, or shark-like, type, to the homocercal, or "fish-tail," type. The primitive scales covering the fin-webs become fused in rows and give rise to the bony dermal rays, which support both the median and paired fins, and form one of the dominant features in the economy of these fishes. The jaws become diversely specialized away from the primitive predatory type, in adaptation to nibbling, grinding, sucking, etc. Very often pharyngeal teeth on the gill arches become of great functional importance.

In wide contrast to the actinopterygian series is the dipnoan group which failed to become progressively specialized except along certain degenerate, eel-like lines. Their modern representatives are equipped with a well-developed lung in addition to their gills, which serves them especially when the pools in which they live either dry up or become deficient in oxygen. The Devonian dipnoans already bore the main characteristics of the group, and very probably likewise were provided with lungs. Although paralleling the amphibians in

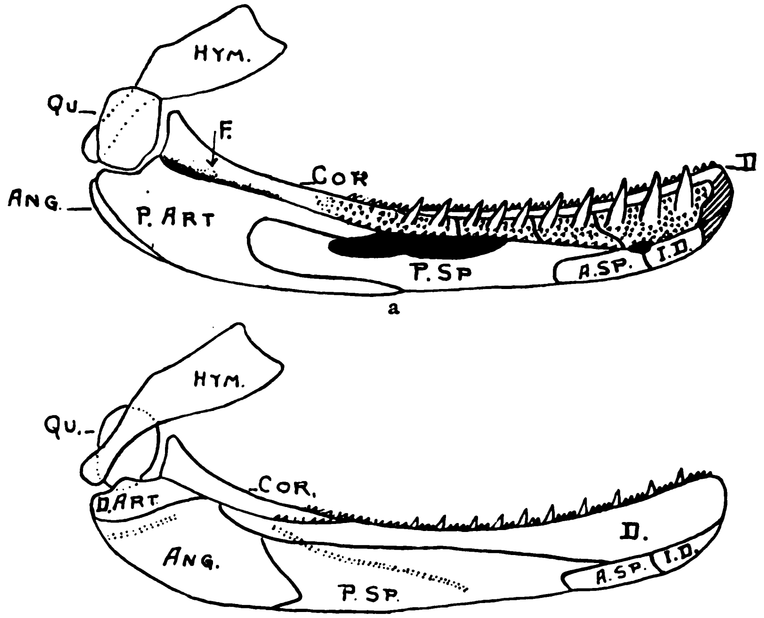

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FIG. 3. LOWER JAW OF *Eusthenopteron foordi*, A CROSSOPTERYGIAN GANOID FROM THE UPPER DEVONIAN OF SCAUMENAC BAY, QUEBEC

The primary lower jaw (Meckel's cartilage) is completely covered with derm bones, which are severally homologous with those of the earliest tetrapods. The teeth are of the labyrinthodont type and are limited to the dentary and the coronoid series. After Bryant. Upper figure (a), inner side; lower figure (b), outer side. *F*, mandibular fossa (for the insertion of the jaw muscles); *D*, dentary; *Cor*, coronoid series.

many respects, they are definitely removed from the ancestral line of the Tetrapoda, or four-footed vertebrates, through the early aberrant specialization of the dentition. This consists chiefly of clusters or aggregations of dental tubercles arranged in two fan-like series on

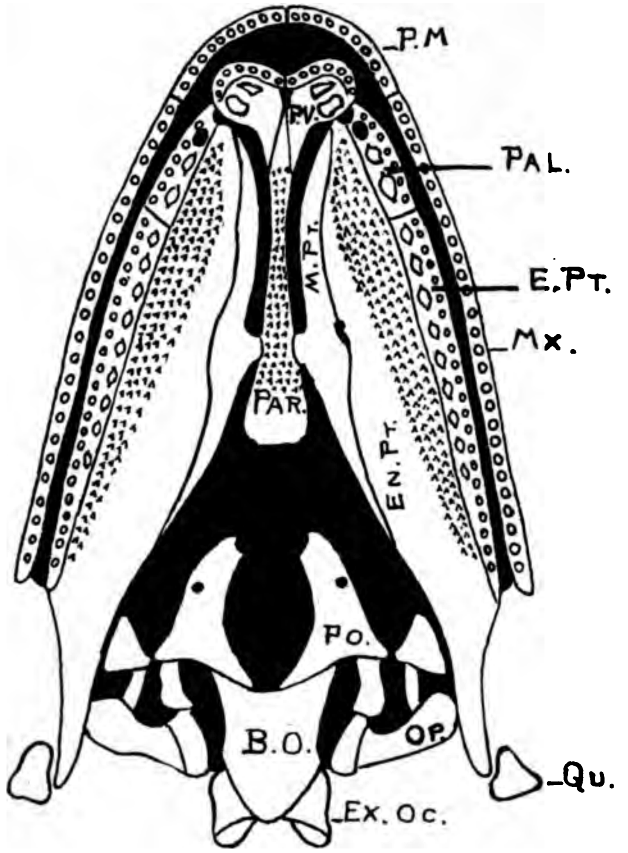

FIG. 4. PALATAL ASPECT OF THE SKULL OF *Eusthenopteron foordi* (CF. *fig. 3*)

Showing the dentigerous tracts, located as follows: (1) on the marginal or secondary jaws, including the premaxillæ and maxillæ; (2) on the primary upper jaws, or palatopterygoids; and (3) on the derm bones beneath the anterior part of the primary brain case, namely, the vomers (prevomers) and parasphenoid. After Bryant.

the roof the mouth, opposing a similar series on the inner side of the lower jaw. Histologically, these tubercles are homologous in construction with the teeth and scales of the primitive crossopterygians described below. The apparatus as a whole is primitively adapted for crushing and in modern forms for cutting, but in this group the earliest representatives are less carnivorous in construction than are their modern derivatives. The dermal cranium and the endocranium, as well as the mandibles, are profoundly modified to provide a firm base for these crushing plates.

The dipnoans, as well as certain types of sharks and rays, afford well proved examples of the development of the complex dental apparatus through the concrescence of small tubercles but, as they are definitely out of the line of ancestry of the tetrapods, it would be futile to cite them as evidence for the theory of origin of complex mammalian molar teeth through concrescence of separate teeth.

The second group of ganoids includes the crossopterygians, or lobe-finned series. These parallel the actinopterygians in the development of dermal fin rays, but never progress so far in building up an efficient homocercal tail. They differ widely from the first series in the strucure of the paired fins, which had a more or less elongate fleshy axis in addition to the fringing dermal rays. All the available evidence points to the members of this series (*Osteolepis*, *Megalichthys*, *Eusthenopteron*, etc.) as standing relatively near to the ancestors of the Tetrapoda, or four-footed vertebrates, but here again the connecting links are lacking from the fragmentary geological record.

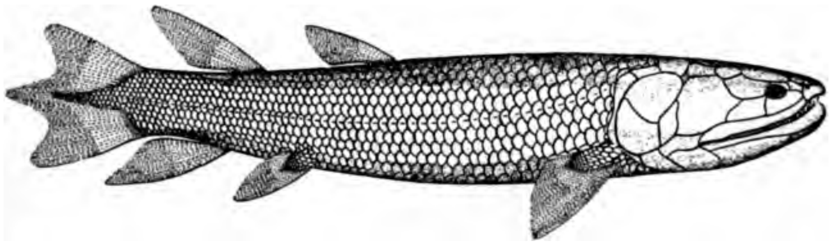

FIG. 5. RESTORATION OF *Eusthenopteron foordi*, A CROSSOPTERYGIAN GANOID FROM THE UPPER DEVONIAN OF SCAUMENAC BAY, QUEBEC

Illustrating the general type of fish from which the land-living vertebrates probably arose. After Bryant.

The group is represented, at the present day, by two more or less degenerate survivors, *Polypterus* and *Calamoichthys* of Africa. In these fishes the "air-bladder" retains traces of the vascular condition which is better developed in the living dipnoans and surviving primitive actinopterygians (*Amia*, *Lepidosteus*); that is to say, the "air-bladder" in all the more primitive ganoids probably already functioned to oxygenate the blood and to supplement the function of the gills, because the living dipnoans and some of the living ganoids are, in fact, able to breathe atmospheric air.

## II. THE EMERGENCE OF FOUR-FOOTED, AIR-BREATHING VERTEBRATES (PRIMITIVE STEGOCEPHS) IN THE UPPER DEVONIAN AND LOWER CARBONIFEROUS AGES

Perhaps as far back as the middle Devonian some of the crossopterygians became adapted to a periodic drying up of the streams and were able to live by means of their lungs, as are the modern lungfishes. In some of them the stout pectoral and pelvic paddles began to be used in crawling, and this was doubtless the initial step in the origin of the paired limbs of land-living vertebrates. Anatomical evidence is very decisive that the pectoral and pelvic limbs of four-footed vertebrates are truly homologous with the pectoral and pelvic paddles of fishes. Some who delight in turning the geological record upside down have argued that fishes have been derived from tetrapods, but this has found scant favor among the majority of anatomists and palæontologists, and recent investigations have practically established at least the common origin of the crossopterygians with the tetrapods.

As a whole the geological and comparative anatomical records show that the great advances have been made through revolutionary changes in the general trend of development, as when the birds arose from the reptiles. The primitive crossopterygians gave rise to the earliest tetrapods (which are first known from footprints in the Upper Devonian of Pennsylvania) through a profound revolution, in which the locomotor apparatus, evolved in earlier stages for progression through the water, had to be largely remodeled for progression on land. The dermal rays of the fins and the hitherto important caudal fin were sacrificed, while the pectoral and pelvic paddles were bent around so as to make a knee-joint and an elbow-joint, and to bring the sides of the paddles in contact with the ground. The five-toed hands and feet of the most primitive amphibians probably grew out from the fleshy stumps of the paired paddles.

The earliest tetrapods still went through an aquatic stage of development with more or less functional gills which are retained in many existing Amphibia; but the loss of the gills in the adult conditioned a

FIG. 6. PALATAL ASPECT OF THE SKULL OF *Eryops megacephalus*, A STEGOCEPHALIAN FROM THE PERMIAN OF TEXAS

The labyrinthodont teeth are, for the most part, indicated by their broken stumps or sockets. They are located chiefly on the marginal bones of the upper jaw, with a few larger teeth on the prevomers, palatines, and ectopterygoids. Amer. Mus. Nat. Hist., no. 4,190.

marked change in the region of the bony gill-covering, or opercular bones. Hence, in the earliest tetrapods, the true or dermal skull has lost the opercular bones and stops at the posterior end of the primary upper jaw and of the bones that cover it, including the squamosal.

While these profound changes were going on in the elements of the skull, the dentition changed surprisingly little, because the earliest reptiles and amphibians of the Coal Measures and succeeding ages still retained the labyrinthodont teeth which are so characteristic of their crossopterygian predecessors. The elaborate infolding of the bases of these teeth apparently served to strengthen their connection with the tough bony skin, as may be seen in the modern garpike. These labyrinthodont teeth are distributed along the margins of the mouth in the premaxilla, maxilla and dentary, and also in some cases in clusters of small tubercles, or in a few large teeth, on the roof of the mouth and on the inner side of the lower jaw. The histological composition of these teeth was homologous with that of the scales. and of the skull plates, of the more primitive crossopterygians.

Thus, the primitive amphibians and reptiles, no less than their crossopterygian ancestors, were predatory animals with strong jaws and sharp, more or less laniary, teeth. This predatory type gives rise to a wide adaptive deployment into variously specialized dental types fitted respectively for crushing shelled invertebrates, for an herbivorous diet, for fish catching, etc.

## III. THE STEM REPTILES (COTYLOSAURIA) AND THE MAMMAL-LIKE REPTILES (THERAPSIDA) OF THE LATE PALEOZOIC AND EARLY MESOZOIC ERAS

It used to be thought that even the oldest reptiles were extremely different from the contemporary amphibians but, as a result of the intensive investigations of recent years, one "diagnostic" class character after another has given way, and more and more characters in common have been shown to connect the primitive reptilian order Cotylosauria with the amphibian order Temnospondyli. From certain more primitive stegocephs of the Coal Measures (e.g., *Loxomma*, *Pteroplax*) to the stem reptiles of the same period was but a short step, involving chiefly the suppression of the "tadpole" stage of development.

In the Permo-Carboniferous beds of Texas is found a group of reptiles, the Cotylosauria, which, in its ordinal characters, is structurally ancestral to all the higher vertebrates. In these animals the temporal region of the skull is still covered by the dermal skull roof, the inner surface of which covered and perhaps gave attachment to the primitive temporal muscle mass. Most of the known members of this group were for the most part already specialized for feeding on invertebrates but, by analogy with many other cases, it can be predicted that the stem forms were more or less carnivorous.

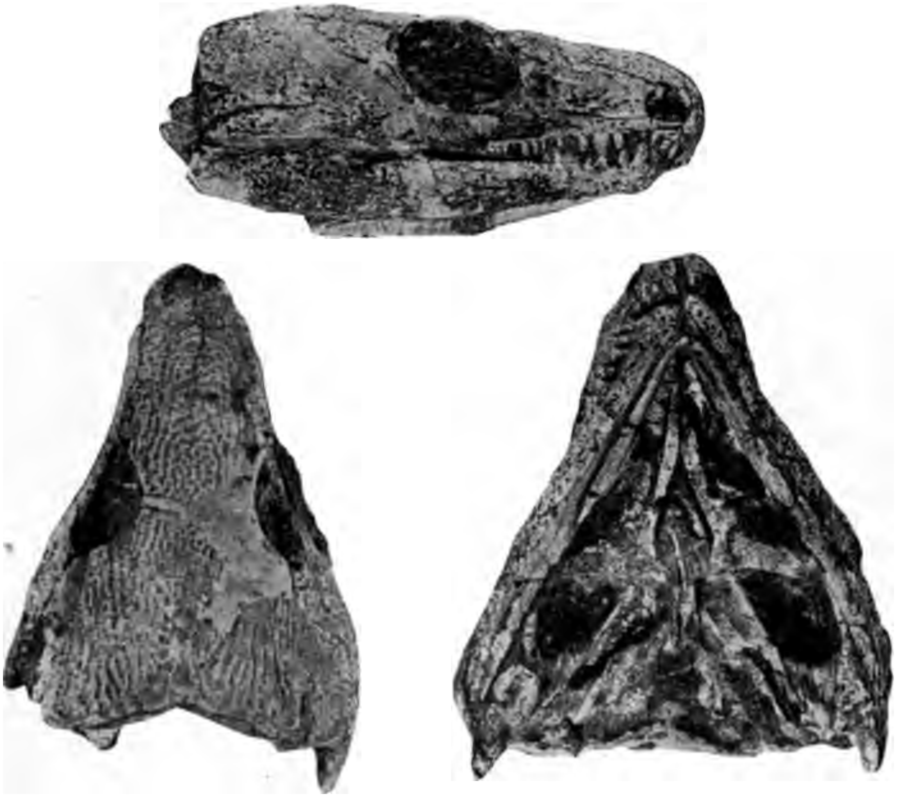

Fig. 7. Skull of *Captorhinus angusticeps*, a Small Cotylosaurian Reptile from the Permian of Texas

Showing the unfenestrated roof of the temporal region, the simple teeth, and the effective bracing of the jaws on the palatal side of the skull. Amer. Mus. Nat. Hist., no. 4,334.

Carnivorous or predatory habits are likewise characteristic of the pelycosaurs, a contemporaneous group which, in the construction of their temporal region, exhibit a stage following the cotylosaurs. The primitive dermal roof is now perforated on each side and the resultant opening is surrounded by the postorbital, jugal, and squamosal, bones, and is homologous with the "lateral temporal fenestra" of the existing *Sphenodon*. The teeth, being confined mostly to the margins of the jaws, were embedded in distinct sockets and have lost most of their labyrinthine structure. In some cases there are clusters of crushing teeth on the roof of the mouth.

FIG. 8. SKULL OF *Dimetrodon incisivus*, A LARGE PELYCOSAURIAN REPTILE FROM THE PERMIAN OF TEXAS

Showing especially the carnivorous dentition, the deep compressed skull, the single temporal fenestra, and the mammal-like zygomatic arch, composed chiefly of processes from the jugal and squamosal bones. Amer. Mus. Nat. Hist., no. 4,636.

From some primitive member of the pelycosaur series it is believed the mammal-like reptiles (Therapsida, "Theromorpha" in part) arose. Numerous and diverse representatives of this order occur in the Permian of South Africa and Russia, and in the Triassic of South Africa. There is a single temporal opening on each side, homologous with the lateral temporal fenestra of the pelycosaurs, bounded below by the stout zygomatic arch, which is composed of the jugal, postorbital, and squamosal. The more primitive types are carnivorous, with laniary teeth embedded in sockets on the margins of the jaws. Aberrant side lines acquired specialized dentitions, some (anomodonts) losing the teeth entirely, which are functionally replaced by a horny beak. Others, the dinocephalians (plate 1) develop very strong piercing teeth around the front part of the jaws, but have dwindling lateral teeth. Dental clusters on the roof of the mouth are usually small or absent entirely.

Notwithstanding the diverse specializations which exclude many of the Therapsida from the line of mammalian ancestry, the group as a whole shows a strong tendency to assume mammalian characteristics,

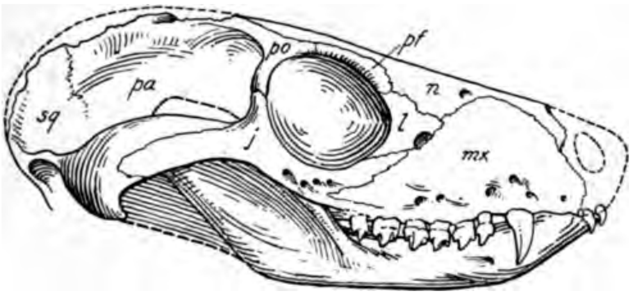

FIG. 9. SKULL OF *Ictidopsis elegans*, A SMALL MAMMAL-LIKE REPTILE FROM THE UPPER TRIASSIC OF SOUTH AFRICA

Showing the sub-mammalian characters of the whole skull and dentition. ×3/2. Amer. Mus. Nat. Hist., no. 5,630.

and some of them come almost to the dividing line between reptiles and mammals. First and most important, they were much more active than their cold-blooded reptilian ancestors. Many of them were able to raise the body well off the ground in running, and, in the higher therapsids, the limbs and girdles steadily approach the lower mammalian type. As shown by endocranial casts, the olfactory parts of the brain were submammalian in type and the respiratory system, as indicated especially by the development of a submammalian palate, was also highly progressive. In the almost mammal-like cynodonts there was a sharp regional differentiation of the backbone and ribs into cervical, dorsal, and lumbar, regions, so that it seems quite possible that these animals had the beginning of a mammalian diaphragm.

In the lower members of this series (Gorgonopsia, Therocephalia) the construction both of the upper and lower jaws is of primitive reptilian type but, in the later or Triassic Therapsida (Cynodontia), there is a progressive approach to the mammalian construction both of the dentition and of the jaws. According to Broom (1913), the teeth are now limited to two sets; the molar teeth having no successors and the antemolar teeth being preceded by a deciduous series. Cross sections of the skull of *Sesamodon browni* (Amer. Mus. No. 5,517), made by Dr. Broom and now in the writer's care, show, that in the molar region, at least in the adult, there was but a single set, without successors. The skull and lower jaw of *Diademodon platyrhinus* (Amer. Mus. No. 5,518), described by Broom, is also in the writer's care, and fully validates Broom's statements that the tips of replacing teeth may be seen in the empty alveoli of the upper and lower canines, and of the third lower (deciduous) premolar; also, that there are no replacing teeth beneath the molars; and that, in the imperfect upper jaw, there is "clear evidence of one replacing tooth—the third left incisor." In the type of *Lycognathus ferox* Broom (Amer. Mus. No. 5,538), a section across the skull and lower jaw through the posterior premolar region shows that, in this old animal, there were no teeth beneath the functional set; in other words, the single replacement had taken place. "We may thus safely conclude," writes Dr. Broom

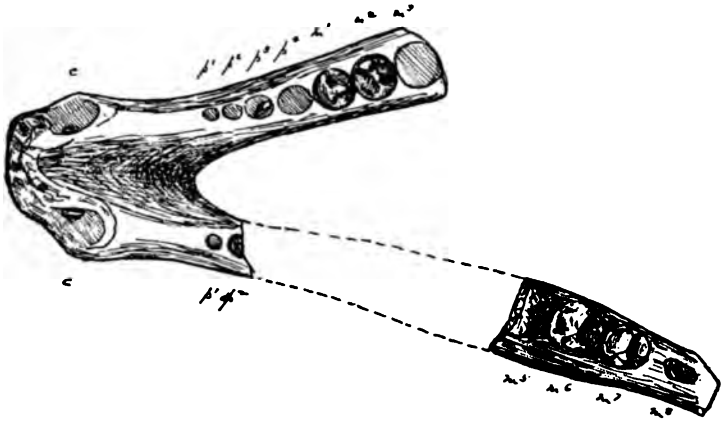

FIG. 10. LOWER JAW OF *Diademodon platyrhinus*, A MAMMAL-LIKE REPTILE FROM THE UPPER TRIASSIC OF SOUTH AFRICA

Showing successional canines and premolar. x 5/4. After Broom

(1913, p. 467), "that as the Cynodont approaches full maturity the incisors, canines and premolars are replaced as in mammals, and as no completely adult specimen has ever shown any trace of a later succession we may conclude as probable that there is only a single succession." At the lower end of the therapsid series in the order or suborder Dinocephalia, the type specimens of *Taurops macrodon* Broom (Amer. Mus. No. 5,610), and of *Moscognathus whaitsi* (Amer. Mus. No. 5,602), afford a positive demonstration of the following facts: (1) there were two and only two sets of teeth; (2) the three incisors, the canines, and seven or eight of the postcanine teeth, were deciduous and replaced by a second or permanent set; (3) the teeth were arranged in two rows, an outer or deciduous series (exostichos) and an inner or replacing set (endostichos); (4) there is no evidence of replacement of the true molars; (5) the succession of the teeth was vertical, not intercalating (Plate 1). The bearing of these facts is discussed below.

The dentition of cynodonts is differentiated into incisors, canines, premolars and molars, which in certain respects strongly suggest the more primitive mammalian types. Moreover, in this group there is a considerable adaptive radiation in the dentition, paralleling that of the mammals. Beginning with the simple recurved teeth of the gorgonopsians and therocephalians, we have, on the one hand, the compressed, sectorial, teeth of *Cynosuchus*, *Ictidopsis*, *Cynognathus*, *Lycognathus*, *Pachygeneleus*, etc., in which the molars have postero-lateral cusps suggesting those of the triconodonts among mammals; on the other hand, we have *Diademodon* and its allies, in which the upper molar teeth are wide ovals bearing several cusps, which may be homologous with the cusps of the primitive mammalian molar crown. Watson, indeed, has demonstrated (1913) several structural stages in the evolution of this transversely widened crown of the upper molars of *Diademodon*, indicating its derivation from the compressed sectorial type through the progressive development of a lingual shelf, after the fashion seen in the earlier stages in the evolution of mammalian premolars (*fig.* 11).

The skull of Cynodonts as a whole is of protomammalian type and the zygomatic arch is especially mammalian, but differs in the retention of the primitive postorbital bone, which is lost in the mammals.

In the lower jaw the dentary finally becomes the predominant element, while the several bones behind the dentary, which are of large size in all typical reptiles, are progressively reduced. The dentary now has a wide ascending ramus of submammalian type, but it has not yet acquired a condyle for the reason that it was still entirely embedded in the temporal muscle and had not yet gained the secondary contact with the squamosal,[1] which gave rise to the mammalian joint between the skull and the lower jaw (cf. Gaupp, 1913).

There is evidence tending to show that the reduced angular of the cynodont jaw was already in contact with the tympanic membrane

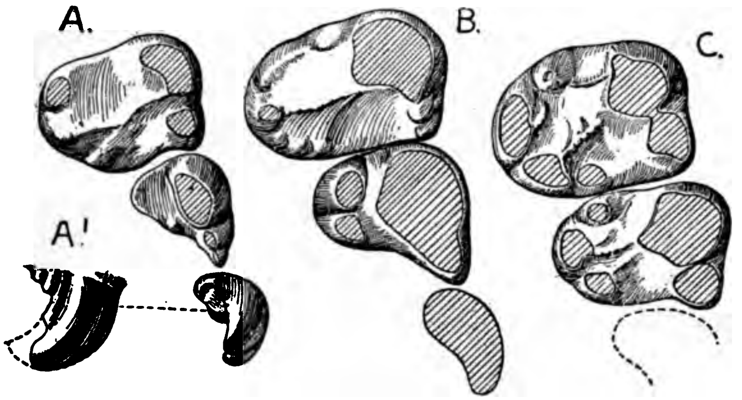

FIG. 11. THE LAST THREE MOLARS OF *Diademodon*. × 3. AFTER WATSON

**Showing the apparent mode of formation of the lingual part of the crown through the ingrowth of the basal cingulum.**

*A, A', Diademodon browni; B, D, entomophonus; C, D, mastacus*

(Palmer, Watson), foreshadowing the transformation of these finally minute jaw elements (quadrate, articular, angular) into the accessory auditory ossicles of the mammals. So, too, in the upper jaw the quadrate bone, which in primitive reptiles is very large, is here reduced to relatively small proportions.

Much work has been done in recent years to support Reichert's theory that the incus and malleus of the mammalian middle ear represent respectively the greatly diminished quadrate and articular elements of reptiles. As I first showed in 1910, and as recognized by Gaupp, Watson and Broom, these extinct mammal-like reptiles of

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[1] Except *Gomphognathus*. Petronievics: *Proceedings of the Zoological Society* (London), 1919.

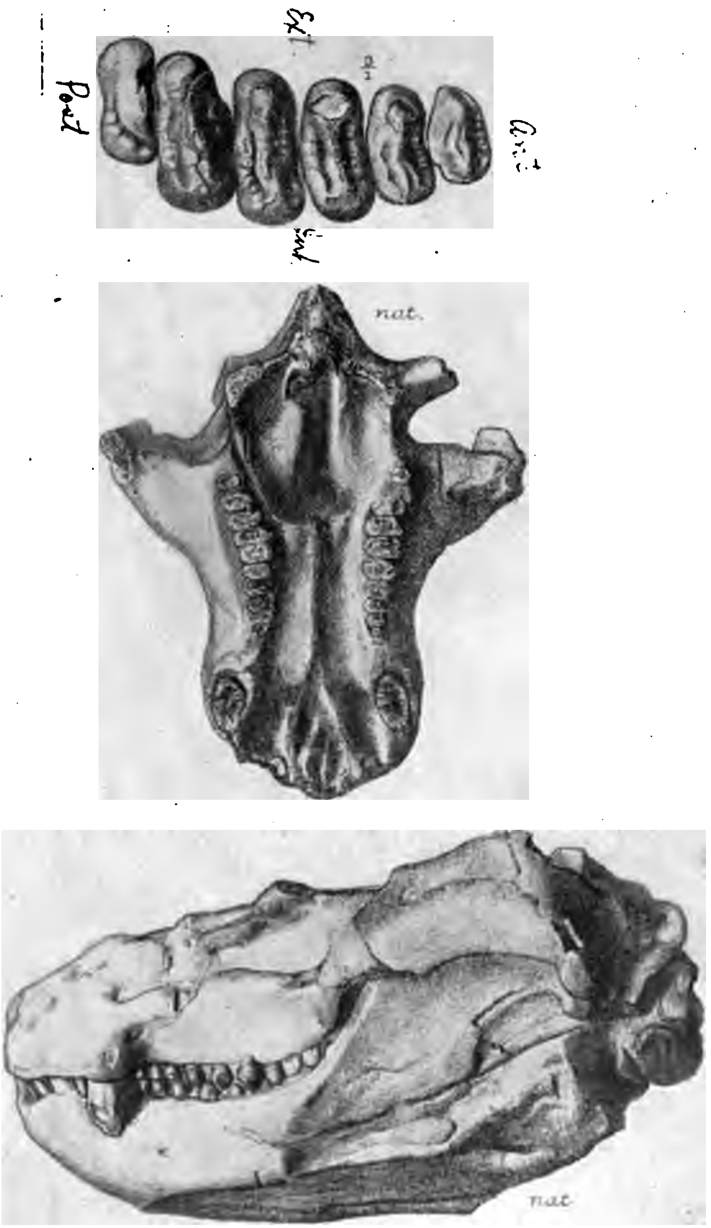

FIG. 12. SKULL AND RIGHT UPPER CHEEK TEETH OF *Trirachodon*, A MAMMAL-LIKE REPTILE FROM THE UPPER TRIASSIC OF SOUTH AFRICA. AFTER SEELEY

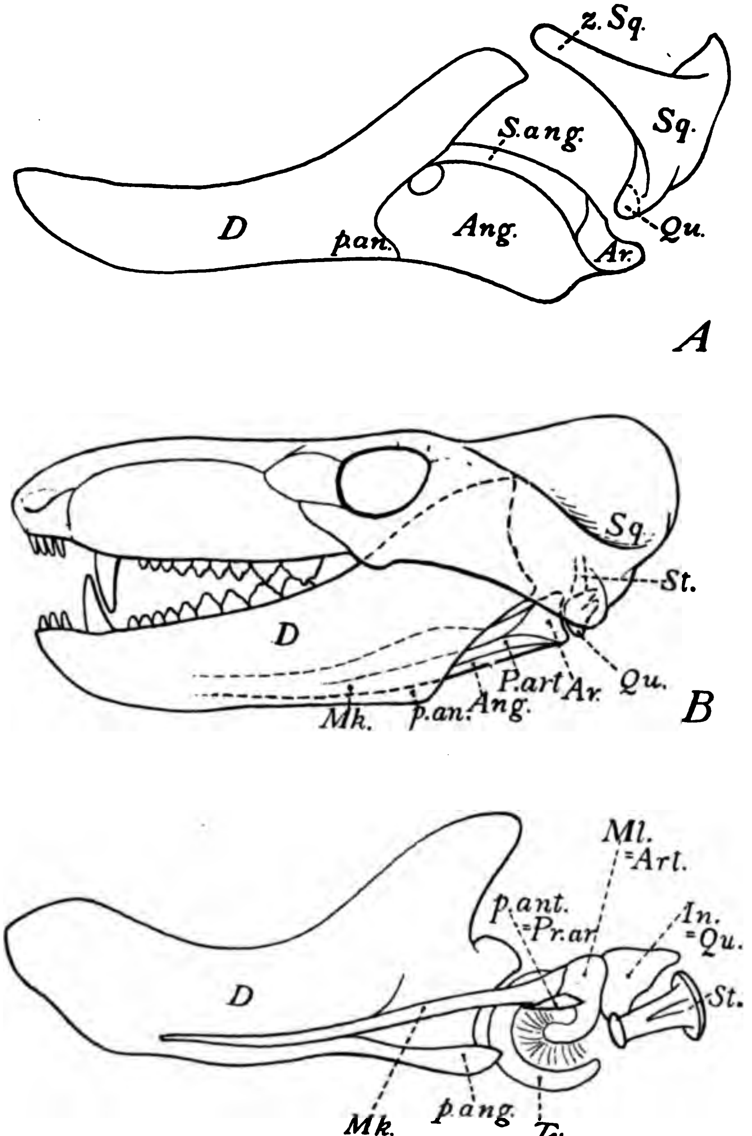

Fig. 13. Diagram Illustrating the Morphology of the Lower Jaw and of the Auditory Ossicles in Mammal-Like Reptiles and Mammals

(See legends on page 21)

South Africa afford an almost ideal transitional stage between the primitive reptilian condition, in which the posterior elements functioned chiefly as jaw bones, and the mammalian condition in which they have been entirely surrendered to the middle ear, the jaw functions being restricted to the dentary and the squamosal.

Doubtless objections to this theory will continue to be made by those who are either not familiar at first hand with the anatomy of the therapsid reptiles, or rely on illusory evidence and fortuitous resemblances, such as that furnished by the development of the middle ear in frogs and other groups that are widely removed from the ancestry of the mammals.

The cynodonts thus foreshadow mammalian conditions in the jaws and dentition in the following characters:

(1) The dentition is differentiated into incisors, canines, premolars and molars.

(2) The upper teeth overhang, or bite outside of the lower teeth.

(3) In occlusion the upper and lower teeth alternate, each lower lying between two uppers.

(4) The cynodonts, although closely related in skull structure, in-

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A.—Primitive therapsid condition: a jaw of reptilian type, in which the elements behind the dentary are not reduced.

*D*, dentary; *p. an*, angular process of dentary, embracing the angular (*Ang*); *S. ang*, surangular; *Ar*, articular; *Qu*, quadrate, largely covered by *Sq*, squamosal; *z. Sq*, zygomatic process of squamosal.

B.—Cynodont condition: jaw of sub-mammalian type; the dentary the predominant element, with a very wide ascending ramus; post-dentary elements reduced, the primary jaw (articular, Meckel's cartilage) and attached derm bones passing downward and forward, and being received in the fossa on the inner side of the dentary; stapes in contact with quadrate; the latter small and largely covered by the squamosal.

*D*, dentary; *Mk*, Meckel's cartilage; *p. an*, angular process of dentary; *Ang*, angular; *P. art*, prearticular; *Ar*, articular; *Qu*, quadrate; *St*, stapes; *Sq*, squamosal.

C.—Condition in mammalian embryo (*Macropus*, after Bensley), seen from the inner side: the dentary the sole functional element of the lower jaw; articulation with squamosal by means of a temporo-mandibular joint; elements behind dentary no longer functioning as jaw bones but as accessory auditory elements.

*D*, dentary; *Mk*, Meckel's cartilage; *p. ang*, angular process; *Ty*, tympanic bone (probably derived from the angular of reptiles); *p. ant*, anterior process of malleus, a derm bone probably derived from the prearticular of reptiles; *Ml*, malleus, probably derived from the articular; *In*, incus, probably derived from the quadrate; *St*, stapes, probably derived from the stapes of reptiles.

clude widely diverse types of dentition, which foreshadow similar series in the mammals. Thus we have:

(a) The primitive, recurved, pointed, teeth of the more ancient cynodonts (*Cynosuchus*).

(b) The compressed, more serrate, recurved, sectorial, teeth of the specialized carnivorous *Cynognathus*.

(c) The transversely expanded oval upper molars of ***Diademodon*** and its allies, bearing regular transverse crests and low cusps. In this dentition, the small, rounded, lower, crowns fit between two upper crowns, and there is a distinct beginning of the interlocking relations of cusps and spaces that are further developed in the mammals. These transversely oval molar crowns have probably been derived by the lingual inward growth of the compressed crown of the primitive cynodonts (Watson).

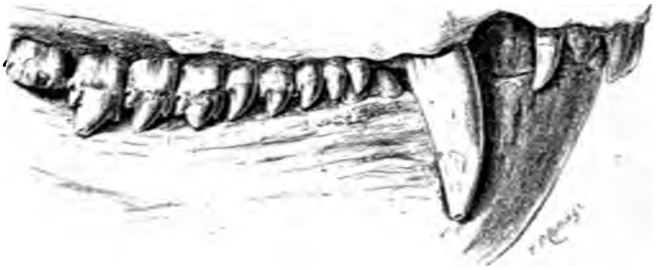

FIG. 14. DENTITION OF *Cynognathus crateronotus*, A CYNODONT FROM THE UPPER TRIASSIC OF SOUTH AFRICA. AFTER SEELEY

Showing the mammal-like differentiation of the dentition. The upper teeth overhang the lower, the lower canine being received into a deep pit in the upper jaw.

(5) The dentition is reduced to two sets, apparently corresponding to the deciduous and permanent series of mammals.

(6) The mandible of the therapsids becomes more and more mammal-like as we ascend toward the cynodonts. The dentary of the latter has a wide ascending ramus, lacking only the condyle of a mammalian jaw. The elements behind the dentary meanwhile dwindle in size and, by a readily understandable progression in the same direction, were probably carried over into the middle ear, especially as there is reason to believe that the posterior process of the angular bone was already attached to the tympanic membrane.

(7) The prearticular part of the primary lower jaw ran downward and forward, and was closely embraced by the mandibular fossa in the dentary, just as in embryonic stages of all orders of mammals, that part of the Meckelian cartilage of mammals, which becomes the anterior process of the malleus, runs downward and forward, and is embraced by the mandibular fossa of the dentary.

Although the cynodonts had many mammalian characters, including two occipital condyles, they were technically reptiles, because the quadrate and articular bones still functioned as jaw bones (at least in part), the dentary was not in contact with the squamosal,[2] the primitive postorbital and prefrontal bones were retained, and the molar teeth were each supported by an undivided root.

## IV. THE MESOZOIC MAMMALS

The wide differentiation of the dentition in the therapsid reptiles, and the steady approach of some of them toward mammalian conditions, is in harmony with the fact that, even when the mammals first appear in the geological record, they already exhibit widely diverse types of dentition. Owing to the excessive rarity of Triassic mammalian remains, we lack knowledge of the stages in the evolution of mammals from mammal-like reptiles, and consequently the beginnings of the diverse patterns of the mammalian dentition are lost to view. By Upper Triassic times we find three widely different types of dentition, which may possibly have been derived from different branches of the mammal-like reptiles.

### The Protodonta from the Upper Triassic of North Carolina

#### *Family* **Dromotheriidæ**

The first, an extremely primitive type, is represented by two lower jaws from the Upper Triassic of North Carolina, described by Emmons in 1857 and by Osborn in 1888 and 1907. Of these the first, called *Dromotherium sylvestre*, is known only from the left half of a lower jaw about 23 mm. long, seen from the lingual aspect; it is preserved in black shales along with the remains of *Rutiodon*, an extinct reptile also characteristic of the Upper Triassic. The jaw, homologous with the dentary of reptiles, is of carnivorous or insectivorous type. The

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[2] See foot-note on page 18.

dental formula is $I_3 C_1 P+M_{10}(P_{?3}M_{?7})$. The three pointed erect incisors and the single large canine are separated from each other by large diastemata, and increase regularly in size and in height from the first incisor to the canine. Between the canine and the premolars there is a wide diastema, which indicates the existence of a large upper canine. The three premolars, as figured by Osborn, are

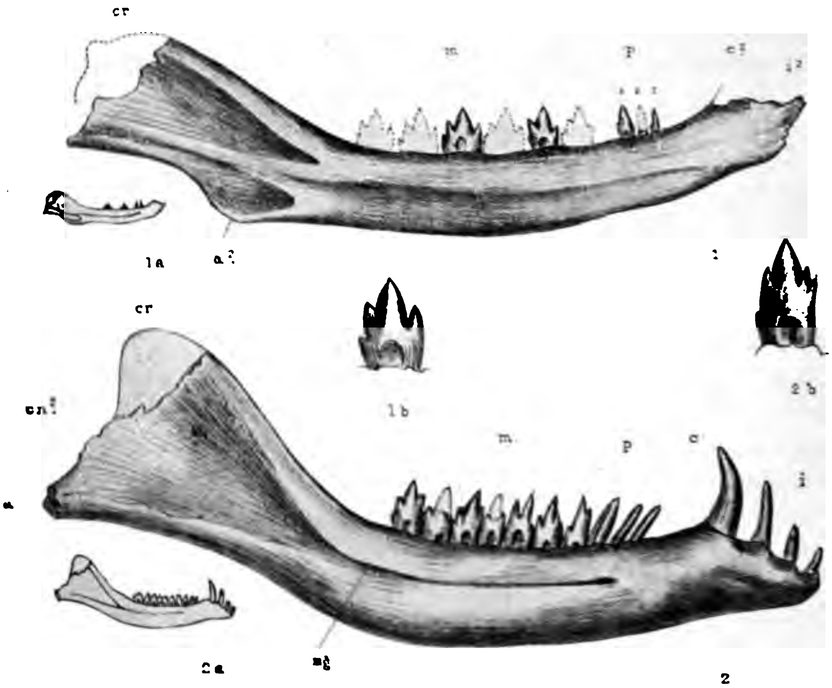


FIG. 15. LOWER JAWS OF *Dromotherium* (2) AND OF *Microconodon* (1), PROTODONT MAMMALS FROM THE UPPER TRIASSIC OF NORTH CAROLINA. AFTER OSBORN

1.—*Microconodon tenuirostris:* outer surface of right half of mandible, greatly enlarged. *1b*, the fourth or fifth molar; much enlarged. 2.—*Dromotherium sylvestre:* inner surface of left half of mandible, greatly enlarged. *2a*, the same; natural size. *2b*, the second molar. much enlarged.

styloid and forwardly inclined. The whole arrangement of the incisors, canines, and anterior premolars, is strongly suggestive of the conditions in the cynodonts, and implies a pronounced overbite of the upper incisors and canines. The chief difference from the cynodonts is the apparent lack of a chin, which is quite deep in that group.

The seven molars are compressed, with two roots[3] one behind the other, the space between the roots extending well above the level of the alveolar border. Each molar culminates above in a compressed, pointed cusp, on the anterior slope of which a second similar cusp points upward and somewhat forward. On the posterior slope there is a third cusp which, in the third molar, is relatively large, but in the posterior molars is smaller, and comes off at a lower level than the anterior cusp. The fifth molar, as figured, has a minute posterior basal spur, suggesting an incipient heel or talonid. Thus, the molars, as seen from above, would appear as compressed, pointed ovals, with a central large tip, and one anterior and one posterior smaller cusp, and sometimes a minute posterior basal spur. Although the molar teeth of this jaw are somewhat like those of *Tribolodon* and other cynodonts, they differ in having two roots instead of one. The mandible is seen from the inner side, and the surface of the dentary is deeply scored by a longitudinal "mylohyoid" groove, which is probably the fossa for Meckel's cartilage, the primary lower jaw. The mandible is curved below as in the primitive cynodonts, and the ascending ramus slopes upward at an unusually low angle, which is more like that of a cynodont than like that of a typical mammal. The condylar process, although imperfectly preserved, was apparently present, that is, the secondary or mammalian contact between the dentary and the squamosal was already established. There is no trace of an angular process on the dentary.

It was long held that the mammalian nature of this jaw was decisively shown by the fact that it consists of a single piece, whereas reptilian jaws, it was said, consist of many pieces. This argument is by no means conclusive, because the reptilian dentary consists also of only a single piece; and the cynodont dentary is, in many ways, like that of *Dromotherium*, which evidently represents the dentary alone, while the elements behind the dentary, if present, might have become separated from it. But, if the condylar process is correctly represented, it shows that there was a contact between the dentary and the squamosal, and therefore the animal is, by definition,[4] a mammal. Moreover, the cynodont molars are supported by a single root while the *Dromotherium* molars have two incompletely separated roots. Both of these may well be progressive characters derived

[3] Not yet entirely separated.

[4] See the foot-note on page 18.

from conditions in the cynodonts. The vertical position of the incisors and canines is also reminiscent of that group. The dental formula according to Osborn's figure ($I_3\ C_1 P_{?\overline{3}}\ M_{?\overline{7}}$) differs somewhat from those of Cynodonts ($I_4\ C_{\overline{1}}\ P+M_{\overline{8-12}}$).

From the same Upper Triassic beds of North Carolina is a second and somewhat similar jaw, the *Microconodon tenuirostris* of Osborn. This resembles the jaw of *Dromotherium* in general characters, but the molars, so far as preserved, approach the triconodont type, that is, the central cusp is lower and larger, and the anterior and posterior cusps are relatively higher up on the crown. The premolars also are lower and less styloid; and the posterior premolar, as figured, has an incipient division into anterior and posterior roots. The ascending ramus slopes backward at an even lower angle than in *Dromotherium* and there is a low angular process on the inferior border. The condyle is not preserved, but the flare of the lower border of the ascending ramus suggests that a condyle was present. *Microconodon* thus apparently represents a slightly more advanced stage than *Dromotherium*, pointing toward the more primitive triconodonts of a later age.

*Dromotherium* and *Microconodon*, occurring together in the Upper Triassic, are possibly a little later in age than the cynodonts, but are structurally intermediate between that group and the triconodonts of the Jurassic, and tend, so far as they go, to show that the latter have been derived from the former.

## KAROOMYS, A FORE-RUNNER OF THE TRITUBERCULATA FROM THE UPPER TRIASSIC OF SOUTH AFRICA

The second main type of Upper Triassic mammals is represented by *Karoomys browni* of Broom (1903), known from a small jaw about 20 mm. long, from the red sandstone of the Karoo series of South Africa, and assigned by Broom (1909) to the *Cynognathus* beds of Upper Triassic age. Only a single imperfectly preserved tooth remains, perhaps a part of the canine. The jaw has a mammalian look in the presence of a low condyle, a distinct corono-condylar notch and a small angular process. The condyle is only a little above the level of the alveolar border, as in many Mesozoic mammals; the angular process is, however, much larger than that of the cynodont *Dia-*

*demodon*. The ascending ramus rises at a very low angle, as it does in the cynodonts and in *Dromotherium* and *Microconodon*. The jaw is shorter than that of *Dromotherium* and of most of the Jurassic mammals except *Achyrodon* but, owing to the lack of teeth, its systematic position cannot be precisely determined. The nearest resemblance of the posterior part is perhaps with the Upper Jurassic *Diplocynodon*, as suggested by Broom. *Karoomys* thus supplies another item of evidence tending to connect the mammals with the mammal-like reptiles, and it may represent the fore-runners of the Trituberculata or "trituberculate" Jurassic mammals.

FIG. 16. LOWER JAW OF *Karoomys browni*, A SMALL MAMMAL FROM THE UPPER TRIASSIC OF SOUTH AFRICA. ×2. AFTER BROOM

## MULTITUBERCULATES FROM THE UPPER TRIASSIC OF ENGLAND AND GERMANY

### *Family* **Plagiaulacidæ**

The third and by far the most specialized group of the Upper Triassic mammals is known from a few minute teeth from the Rhaetic formations, or Upper Triassic, of Great Britain and Germany, which are the type specimens of *Microlestes antiquus* Plieninger, *Microlestes moorei* Owen, and *M. rhæticus* (Dawkins). These apparently are early, but already specialized, members of the order Multituberculata. In the typical members of this order, the dentition is of the highly specialized "diprotodont" type, with a medial pair of enlarged lower incisors; high, compressed, grooved, fourth, lower premolars; and low, crowned, multituberculate molars.

The *Microlestes antiquus* molar, in crown-view, is oval and compressed, with a long, narrow, central fossa, surrounded by lateral and medial rows of irregular cusps. This molar belongs in the lower jaw and is supported by two large fangs or roots arranged anteroposteriorly, and showing a wide space between them. The outer margin of the crown bears three tubercles of regularly increasing size, of which the first at the anterior end is the largest. The lingual border bears a single high anterior apex, the posterior slope of which bears a low cusp.

*Microlestes moorei* consists of several molars of somewhat varying character. One of them (Owen, 1871; *plate I, figs. 1–3*), supposed to be an upper molar, consists of a large, sub-oval, central basin, bordered by a nearly continuous rim which is sub-divided into three large cusps on one side, but barely divided into small cusps on the opposite side. This tooth had four roots arranged in pairs on opposite sides.

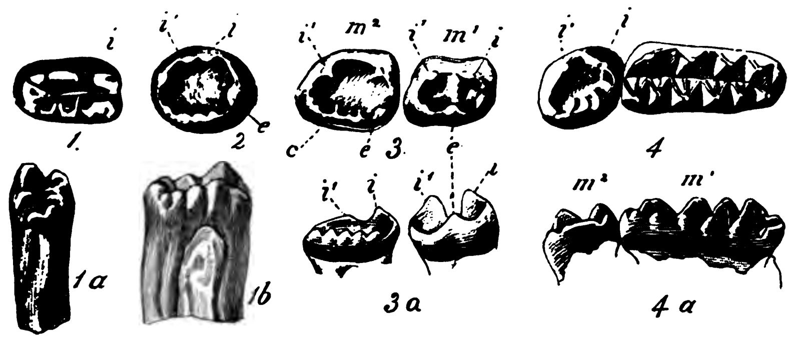


FIG. 17. LOWER MOLARS OF MULTITUBERCULATES. AFTER OSBORN

1.—*Microlestes antiquus*, crown view. *1a*, posterior face; *1b*, external face. All greatly enlarged. *2*.—*Microlestes* (*Plagiaulax*) *moorei*, crown view. 3.—*Plagiaulax minor*, crown view. *3a*, external face; ×6½. 4.—*Ptilodus trovessartianus*, crown view. *4a*, external face. i, $i^1$, internal tubercles, e, $e^1$, external tubercles.

A lower molar of this species (Owen, *plate I, fig. 6*) has a more elongate oval crown bordered by low cusps. In a third specimen the crown is considerably elongated anteroposteriorly, but not so much as in *M. antiquus*. In each case there are a number of smaller cusps on one side and three larger cusps on the opposite side.

The type of *Microlestes rhæticus* (cf. Owen, 1871, *plate I, fig. 16*) is a lower tooth with two large roots, somewhat like those of one of the *M. moorei* molars, and a compressed crown bearing numerous low cusps on one margin. Owen and Falconer recognized its resemblance to the compressed and grooved lower premolar of some of the smaller kangaroos, but in their times it was not realized that such resemblances in single teeth are often produced by convergent evolution in widely different orders.

A comparison of the lower molars of *Microlestes* with those of the Upper Jurassic genus *Plagiaulax* supports the conclusion of Falconer and of Osborn, that *Microlestes* belongs in the order Multituberculata or Allotheria. Thus, we are confronted with the apparent anomaly that one of the most specialized of mammalian dentitions is also one of the oldest, so far as the geological record is yet known; also that, even at this exceedingly early date, the multituberculate dentition was widely different from the protodont type.

## PACHYGENELEUS, A POSSIBLE ANCESTOR OF THE MULTITUBERCULATES FROM THE STORMBERG (UPPER TRIASSIC) OF SOUTH AFRICA

Numerous guesses have been made as to the origin of the multituberculate dentition. In 1910 I suggested, in a very tentative way, that it might have been derived from the primitive triconodont type, partly through the upgrowth of the basal cingulum forming a second row of cusps. But I also emphasized the extreme antiquity of the multituberculates, and considered the possibility that the order might have been derived independently from the mammal-like reptiles. Professor Bolk has also hypothetically derived the multituberculate molar from the triconodont type as a result of his peculiar theory of the origin of mammalian teeth. Until recently none of the mammal-like reptiles have afforded much evidence as to the possible mode of origin of the multituberculate dentition, but in 1913 D. M. S. Watson described the lower jaw of a new 'Cynodont' from the Stormberg (Upper Triassic) of South Africa, named *Pachygeneleus monus* which may possibly give the long sought clue. In this animal the medial incisor, $i_1$, is described as "a large tooth of oval section, which appears to be somewhat procumbent and lies close up to the symphysis. $I_2$ is a considerably smaller tooth, also of oval section, which lies close behind and outside $i_1$. The canine is a large tooth whose root, the only part preserved, is of oval section. It seems to have pointed directly upwards, and immediately follows $i_2$. Behind the canine is a long diastema, which is followed by a series of cheek teeth, six of which are preserved before the fracture which terminates the specimen."

Although the cheek teeth are described as single rooted, the figure suggests the presence of a vertical depression on the inner side which, if further deepened, would tend to divide the single root into anterior and posterior moieties. The molars are narrow from side to side. The crown of the fifth is described as "of an irregular oval shape, widest in front, where it is about three-quarters of its length. There are four cusps arranged longitudinally and forming the outer side of the tooth; the summits of the anterior three of these are broken, but it is certain that the first was much the largest and that they gradually declined in size and height to the fourth." "On the inner side," continues the describer, "is a strong cingulum, whose position will best be understood from the figures. This shows a very faint crimping, as if in the descendants of our animal it might have developed cusps."

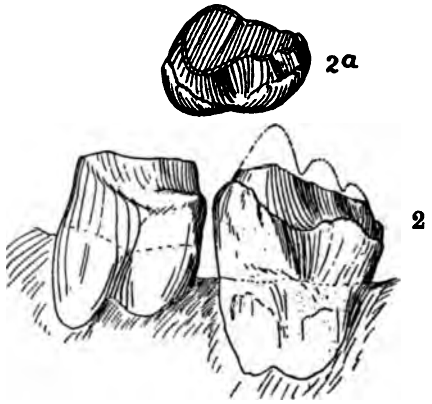


Fig. 18. Lower Molars of *Pachygeneleus monus*, a 'Cynodont' from the Upper Triassic of South Africa, Showing Characters which may be Expected in a Structural Ancestor of the Multituberculates.
×8. After Watson

2.—Inner aspect of $M_4$, $M_5$. 2a, crown view of fifth molar

This interesting specimen then foreshadows the multituberculate dentition in the following characters:

(1) There is a decided tendency for the lower front teeth, or some of them, to become procumbent.

(2) There is already developed a long postcanine diastema.

(3) The cheek teeth are narrow from side to side and the crowns are of "an irregular oval shape," with a row of four cusps arranged longitudinally and forming the outer side of the tooth, the first being the largest; while on the inner side is a strong cingulum already faintly crimped, "as if in the descendants of our animal it might have developed cusps."

Possibly Dr. Watson had the molar of *Microlestes antiquus* in mind when writing this description but was too discreet to mention it, in view of the well known tricks of convergent evolution. But the fact is that the multituberculates are evidently too highly specialized to be derived from any other *known* order of Mesozoic mammals. On the other hand, the skull structure of one of the later multituberculates shows that they were true mammals related either to the monotremes or to the marsupials, according to different authorities; hence they must at least have arisen from some family of mammal-like reptiles which was closely related to the direct ancestors of the later mammals. Although *Pachygeneleus* itself probably comes a little too late in geological time to be the immediate ancestor of the multituberculates, it shows us a structural stage through which such ancestors must have passed, as we may infer from several similar cases among later mammals with more or less multituberculate-like features of the dentition. The development of procumbent "diprotodont" front teeth, and of a long diastema, has often preceded the reduction or loss of the upper canines, and was in harmony with the development of cheek teeth, with two rows of longitudinally arranged cusps adapted finally for crushing fruits and seeds.

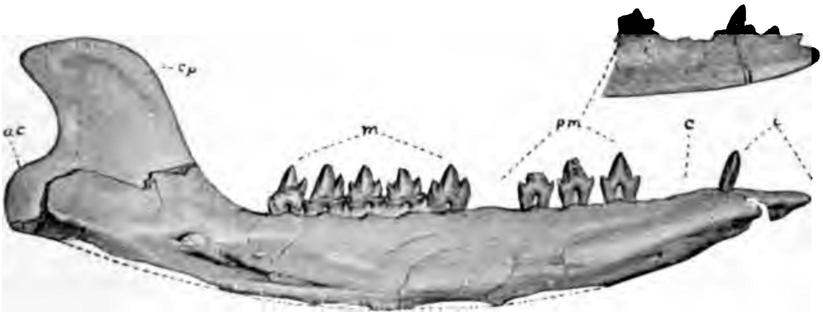
## The Mammals of the Stonesfield Slate (Lower Jurassic)

The next vista of Mesozoic mammalian life is afforded by the fauna of the Stonesfield Slate of England, of Oölitic or Lower Jurassic age. This assemblage, as described by Owen (1871), Osborn (1888) and Goodrich (1894), includes but four genera, two of them (*Amphilestes*, *Phascolotherium*) probably representing the descendants of the Protodonta; the third (*Amphitherium*) representing an extremely primitive stage of the Trituberculata; and the fourth (*Stereognathus*), of very uncertain affinities, possibly allied with the Multituberculata.

## *ORDER* TRICONODONTA

### *Family* Triconodontidæ

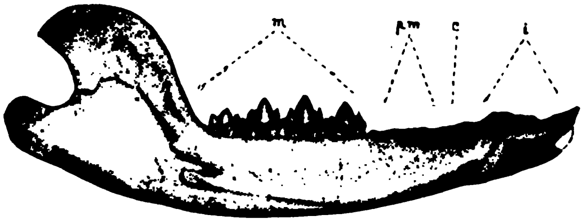
The primitive genus *Amphilestes* is of interest because it tends to connect the Order Triconodonta with the Order Protodonta and to indicate the mode of derivation of the triconodont dentition. The minute jaw of *Amphilestes Broderipii*, some 26 mm. in length, as in so many of these primitive mammals, is long and slender with a curved lower border, a low condyle near the level of the alveolar margin, and a wide coronoid process. The premolars and molars are compressed, each having two well separated roots. The four premolars have high pointed apices and incipient talonid spurs. The molars represent a distinct advance upon the above-described *Microconodon* type, as the anterior and posterior cusps are stouter, and the main central apex is wider anteroposteriorly. A strong, internal, basal cingulum appears, which is produced both in front and in the rear beyond the base of the anterior and posterior cusps. It also rises in the middle opposite the base of the central cusp. The presence of an internal cingulum has been noted above (p. 30) in the cynodont *Pachygeneleus*. It was rapidly developed to extremes in the multituberculates but, in the order Triconodonta, it did not give rise to a second series of cusps parallel to the buccal series. Its origin is obscure, but neither the Triconodonta nor any other order of Mesozoic mammals give evidence for Prof. Bolk's view that the basal cingulum represents a "deutomere," arising from the fusion of a second tooth-germ, lingual to the first. The basal cingulum is often associated with the roots rather than with the summit of the tooth, at least in early stages of evolution. The inner side of the *Amphilestes* jaw is grooved, as in other Mesozoic mammals, perhaps for the remnant of the Meckelian cartilage. Apparently, the angular region is strongly inflected, as it is in other triconodonts, and the condyle is extremely low, in line with the alveolar border. The latter fact indicates that the alveolar process (maxilla) of the upper jaw was vertically shallow and not depressed below the level of the brain case; in other words, that the basifacial and basicranial axes were nearly continuous.



Amphilestes Broderipii [York Mus.].

A. Broderipii [Oxford Mus.]

A. Broderipii [Oxford Mus.].



Phascolotherium Bucklandi [Oxford Mus.].

FIG. 19. LOWER JAWS OF TRICONODONTS FROM THE STONESFIELD SLATE (LOWER JURASSIC). ×4. AFTER GOODRICH

In *Phascolotherium Bucklandi*, the second triconodont from the Stonesfield Slate, the jaw is larger (35 mm. long) and stouter, and the molars have somewhat lower crowns, each with a lower central cusp and better (relatively) developed anterior and posterior cusps. There is a strong internal cingulum, which projects at the anterior and posterior ends of the tooth. This cingulum is clearly associated with the alveolar portion of the tooth, rather than with the coronal part.

The posterior part of the lower jaw is devoid of an angular process and is strongly inflected, while the groove for Meckel's cartilage is well defined. There are three or perhaps four small and slightly procumbent lower incisors, an erect canine and perhaps seven postcanine teeth. The premolars, as figured, are much like the molars, only smaller. Possibly, some of the submolariform premolars may belong in the deciduous series.

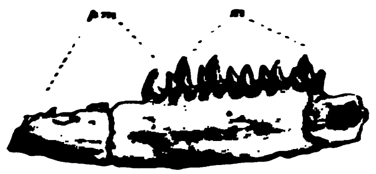
The structural series *Dromotherium*, *Microconodon*, *Amphilestes*, *Phascolotherium*, seems to be tending toward the triconodonts of a later horizon. Osborn has in fact regarded *Amphilestes* and *Phascolotherium* as ancestral to *Triconodon*, with which they agree in the general form of the jaw, inflection of the angle, and ordinal characters of the molars. They differ from *Triconodon* and its allies in the presumably much more primitive construction of the molars. They differ in many characters from the multituberculates and, although more primitive, are probably not ancestral to that group. From *Amphitherium* and the other Trituberculata they differ especially in the form of the jaw and in the construction of the molars, as will presently be shown. There is nothing definite to connect them as ancestors with any of the existing insectivores and carnivorous marsupials, or with any of the orders of placental mammals. They represent an early experiment in evolving a carnivorous type of mammalian dentition, remotely like that of certain existing seals with "triconodont" molars but of comparatively minute size. As being considerably older geologically and also much more primitive than *Triconodon*, they deserve far more attention than they have received, especially from those opponents of the Cope-Osborn "theory of trituberculy" who assume the molar pattern of *Triconodon* as the basis for rival hypotheses concerning the origin of complex mammalian molars.

## *ORDER* TRITUBERCULATA

### *Family* Amphitheriidæ

The most important mammal in the Stonesfield Slate fauna, or indeed in the whole Mesozoic history, is *Amphitherium*, since this genus represents the oldest and most primitive form of the "trituberculur" dentition. Known from several lower jaws, the dental formula as given by Goodrich is $I_4$ $C_1$ $PM_5$ $M_6$. It will be noted that this agrees with modern marsupials not only in the number of incisors, but also in the fact that the post-canine teeth (eleven in number) are much more numerous than in either placentals or marsupials of later ages. The relatively high number of post-canine teeth is thus characteristic both of the earliest triconodonts and of the primitive trituberculates, while the reduced number, seven, in typical marsupials and placentals, in all probability, has arisen through the loss of some of the posterior teeth, concomitant with an increase in the anteroposterior diameter of the remaining teeth. The *Amphitherium* jaw differs widely from the specialized marsupial and triconodont types in having a well developed and distinct angular process, as in primitive placental mammals. The areas for the temporal and masseter muscles on the outside of the jaw are clearly indicated, and likewise suggest the condition in primitive placentals. The very distinct and pedunculate condyle is raised well above the level of the alveolar border, so that the maxilla was probably deeper and the face more bent upon the cranium than in contemporary triconodonts. The coronoid process is wide, but ascends at a sharper angle than in the triconodonts and protodonts. The small incisor teeth are gently procumbent, as in insectivorous mammals. The canine appears to have two roots homologous with the two main roots of the premolars and molars. The premolars increase in size posteriorly. They have a compressed conical crown with a steeper anterior edge which appears to be deflected inward toward the base, and a more sloping posterior edge which runs into an incipient basal talonid. There are no indications of paraconids and metaconids in the lower premolars. In the true molars the main cusp on the buccal side is evidently homologous with the single tip of the molars, and, as in all primitive mammals, there is no doubt that the protoconids of the

4



Amphitherium Prevostii [Brit. Mus.].

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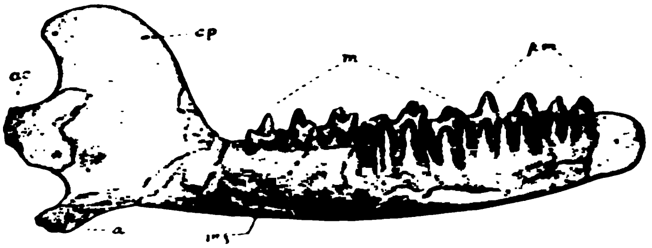
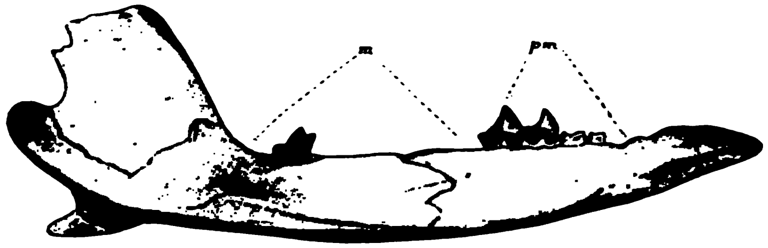


A. Prevostii [Oxford Mus].

2



A. Prevostii [Oxford Mus.].

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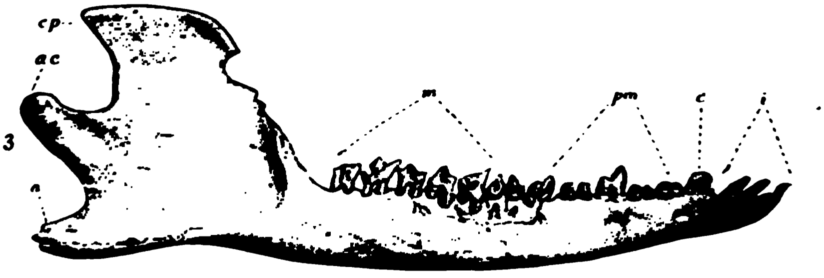

A. Oweni [Oxford Mus.].

FIG. 20. LOWER JAWS OF AMPHITHERIUM FROM THE STONESFIELD SLATE (LOWER JURASSIC)

Showing the most ancient and primitive known tritubercular lower molars, with asymmetrical trigonids and low incipient talonids. ×4. After Goodrich.

1, 2 —Inner view of left mandibular ramus. 3.—Outer view of right ramus; the outer sides of the molars, including the protoconids, have been broken off. 4.—Inner view of right ramus, showing all three cusps of the first, second and fifth molars; in the third and fourth, the protoconids have been broken off or are hidden in the matrix.

lower molars are serially homologous with the tips of the premolars. The inner side of the molars bears three cusps: (1) anteriorly, a well-developed paraconid directed upward and forward; (2) a metaconid, which is placed almost directly internal to the posterior slope of the protoconid, its tip pointing upward, on a lower level than the tip of the protoconid and level with the tip of the paraconid; and (3) a slight basal elevation on the lingual side hardly deserving to be called a distinct cusp, but representing the beginning of the talonid, or posterior heel, of future tritubercular teeth.

As thus described, *Amphitherium* has an extremely primitive pattern of the lower premolars and molars, archetypal to those of primitive placental mammals as well as of the polyprotodont marsupials.

Both the dentition and the general form of the jaw of this oldest and most primitive tritubercular mammal are in wide contrast to those of the contemporary Triconodonta, and may possibly indicate an entirely separate derivation from the mammal-like reptiles. Nevertheless, there are certain important characters in common to these two orders, as follows: (1) the presence of two main anterior and posterior roots, separated by conspicuous interspaces, on all the premolars and molars, a character distinctly mammalian and barely suggested or not found in mammal-like reptiles; (2) the obvious similarity of the compressed premolar crowns and of their protoconids in both orders; (3) the differentiation of the teeth into incisors, canines, premolars and molars; (4) the low position of the mandibular condyle, the great width of the ascending ramus, the prominence of the Meckelian groove, and the length and slenderness of the horizontal ramus.

While the lower molars of *Amphitherium* are unquestionably of the primitive tritubercular type, which thus appears for the first time in geological history, and while they are thus of great interest as being structurally archetypal to the more advanced stages of later epochs, yet this genus in itself furnishes but little evidence on the mode of origin of the tritubercular ground-plan. The three cusps on the inner side of the lower-molar crown, that is, the paraconid, the metaconid, and the low entoconid, or internal tip of the incipient talonid, might have grown out of the three similarly situated projections of the internal cingulum of the lower molars of the triconodont genera *Amphilestes* and *Phascolotherium*, but we have no convincing proof that they did so arise.

An especially significant feature of *Amphitherium* is the sharp contrast between the premolars and molars, the former lacking even a suggestion of the para- and metaconids. This contrast is more emphatic in this most ancient trituberculate genus than in the mammals of later epochs, in which the premolars tend to assume the molar pattern; so that, finally, there is a gradual passage from the anterior toward the posterior premolars, which eventually become fully molariform.

In the successors of *Amphitherium*, from the Purbeck beds, there were two sets of antemolar teeth corresponding to the deciduous and permanent series of later mammals. As the molars were not replaced the initial difference between the premolars and molars may somehow be associated with the replacement of the premolars and with the probable fact that the molars are homologous with the first or deciduous series of premolars, and that the post-deciduous molars were suppressed far back in geological time, as we have already seen to be the case in the Triassic cynodonts.

In conclusion, it is certain, from the evidence afforded by *Amphitherium*, that the primitive "tritubercular" type of molar was established as far back as the Lower Jurassic—that at that time the lower-molar crown consisted of a normal "trigonid," with a high buccally placed apex (protoconid) and a basal posterior spur or incipient talonid. The "protoconids" of the molars were evidently homologous with the compressed tips of the premolars, which lacked the para- and metaconids, but already possessed incipient talonid spurs.

Although the upper teeth of *Amphitherium* are unknown, by application of well-founded principles gained from the study of occlusal relations between the upper and lower teeth of many other mammals, it is safe to make the following inferences concerning them:

(1) The upper premolars had simple compressed apices with a low internal extension.

(2) Each upper premolar was supported by two main roots.

(3) The upper molar crowns were unevenly trigonal with high, lingually placed apices, fitting between the trigonids of the lower

molars. The triangular interdental spaces between the upper molars received the trigonids of the lower molars.

(4) The internal apices of the upper molars did not fit into the basins of the talonids as do the similarly placed but not homologous "protocones" of later mammals, for the ample reason that the talonids had not yet acquired basins or fossæ, except in an incipient degree.

(5) The internal apex of each upper molar probably, however, bore a low anterointernal basal rim, the product of the basal cingulum and the probable forerunner of the future "protocone," which articulated with the incipient talonid of the lower molars.

Thus, in *Amphitherium* of the Lower Jurassic, we have fully established the following relations which are the starting point for the more complex conditions of later types:

(1) The premolars of the adult are more simple than the molars and belong to the second or replacing series.

(2) The molars are trigonal, with the primitive apices on the lingual side in the upper teeth and on the buccal side in the lower teeth.

(3) The upper molars are received in the interdental spaces on the buccal side of the lower teeth, while the lower molars are received in the interdental spaces on the lingual side of the upper teeth.

## *ORDER* MULTITUBERCULATA?

### *Stereognathus*

The most puzzling member of the Stonesfield Slate formation is the genus *Stereognathus*, known from a fragment of a lower jaw[5]. The preserved molars exhibit two rows of more or less V-shaped cusps. The affinities of this animal are quite uncertain[5], at least it has no known bearing on the evolution of the tritubercular type except to emphasize the wide differences in molar patterns which had been evolved as far back as the Lower Jurassic.

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[5] See, however, p. xiii.

## THE SOUTH AFRICAN MAMMAL TRITYLODON (LOWER JURASSIC)

### *ORDER* MULTITUBERCULATA?

### *Family* Tritylodontidæ

In the summit of the Karoo series in South Africa, and in a horizon which Broom assigns to the Lower Jurassic, was found the skull of *Tritylodon longævus*. Owen regarded this as a mammal, but Seeley held that it was a modified cynodont reptile. An examination of the original skull by Broom led him, in 1910, to support Owen's opinion and to assign *Tritylodon* to the order Multituberculata. Its dentition is of the highly specialized rodent-like type, with a pair of enlarged pointed incisors, a wide diastema, and a row of seven molars with quadrate crowns supporting three rows of small cusps. *Tritylodon* in its molar teeth differs widely from the later multituberculates, except the Paleocene *Polymastodon* and its allies; and even these resemblances are very remote and apparently due to convergence. Possibly the "multituberculate" type of dentition was evolved more than once among the Mesozoic mammals, as we know that it was among the Tertiary mammals. The existence of this genus in the Lower Jurassic again emphasizes the extreme antiquity and independence of the multituberculate type of dentition, and strengthens the view that the Multituberculata have no near relationships with either the triconodont or the trituberculate orders.

## THE MAMMALS OF THE PURBECK AND MORRISON BEDS (UPPER JURASSIC)

In the Purbeck Beds of England, of Upper Jurassic age, described especially by Owen (1871) and by Osborn (1888), is found a relatively numerous mammalian fauna consisting mostly of the lower jaws of minute mammals of diverse types. The Morrison formation of similar age in Wyoming, which has yielded the remains of many gigantic dinosaurs, also carries a closely similar mammalian micro-fauna.

## *ORDER* MULTITUBERCULATA

### *Family* Plagiaulacidæ

In the Purbeck Beds, the multituberculates are represented chiefly by the lower jaws of the highly specialized *Plagiaulax*, which had a single pair of enlarged, procumbent, piercing incisors, followed by a short diastema; premolars, three in number, compressed and bearing many parallel, oblique ridges and grooves, the last premolar being very large and projecting far above the level of the molars; molars small, oval, with deep central fossa bordered by irregular cusps, the smaller and more numerous ones being on the buccal wall of the crown.

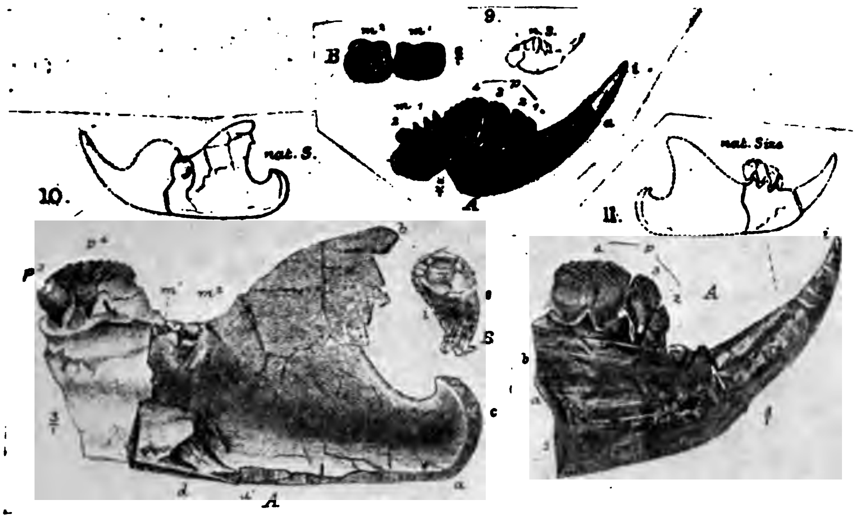

Fig. 21. Lower Jaws and Teeth of *Plagiaulax*, a Multituberculate from the Purbeck Beds (Upper Jurassic). After Owen

9.—*Plagiaulax minor*, right ramus, lateral aspect; *n. s.*, natural size. *A*, the same, × 3; *B*, the two lower molars, ×6. 10.—*Plagiaulax becklesii*, portion and impression of right ramus, ×1; *A*, the same, ×3. 11.—Counterpart impression and portion of the same ramus; natural size. *A*, the same, ×3.

As shown by Gidley (1909, p. 612), the upper dentition of *Plagiaulax* is probably represented in the type of *Bolodon crassidens* Owen. One pair of the upper incisors, possibly the second, is enlarged in opposition to the enlarged procumbent pair of lower incisors; the outermost incisors (possibly $i_3$) are small. There is a slight diastema followed by a straight row of cheek teeth, of which at least the first two have three rounded cusps with the apex on the *buccal* side, as in the Morrison genera *Ctenacodon* and *Allodon.* As shown by comparison with the Paleocene genus *Ptilodus*, these upper premolars may have served to hold the fruits or nuts in place and to assist in cracking them while the grooved lower premolars cut them.

The upper molars, as figured by Osborn, were elongate oval with two anteroposterior rows of three cusps, each separated by a median groove. Similarly in *Allodon,* from the Morrison formation, there were two rows of three cusps each separated by a long, straight central fossa. Here, again, the difference of the multituberculate type of dentition from those of the other contemporary orders is very great, and should discourage further attempts to derive it directly from the triconodont mammalian type rather than from some cynodont reptilian type, such as *Pachygeneleus* (see p. 30 above).

## *ORDER* TRICONODONTA

### *Family* Triconodontidæ

This group is now represented by numerous lower jaws of the genus *Triconodon* and the allied *Triacanthodon.* The jaw of *Triconodon mordax* is about 38 mm. in length, while that of *T. major* may have been about 55 mm. long. This was nearly twice as large as the jaw of the far more primitive *Amphilestes* of the Stonesfield Slate, and was almost gigantic in comparison with the diminutive jaw of *Stylodon pusillus* which was some 18 mm. in length. Thus, even in this micro-fauna, there was a wide variation in size; but even the largest animals were far smaller than their carnivorous analogues of later periods.

The lower molars of the Purbeck Triconodontidæ each bear three subequal, compressed, conical cusps arranged anteroposteriorly, and bordered by a stout internal cingulum. They have probably arisen through the increase in size of the anterior and posterior molar cusps of some such forms as *Amphilestes* and *Phascolotherium* of the Stones-

FIG. 22. UPPER AND LOWER JAWS OF TRICONODONTS FROM THE PURBECK BEDS (UPPER JURASSIC). AFTER OWEN

1.—*Triconodon mordax*, left mandibular ramus; natural size. *A*, the same; ×2. 11.—*Triconodon ferox*, left mandibular ramus, medial aspect; natural size. *A*, third molar; ×3. 17.—*Triconodon ferox*, portion of right maxilla, lingual aspect; natural size. *A*, the same; ×3. 2.—*Triconodon occisor*, right and left mandibular rami; natural size. 3.—*Triconodon major*, right mandibular ramus; natural size. 6.—*Triconodon minor*, right mandibular ramus; natural size. *A*, the same; ×3. 7.—*Triacanthodon serrula*, portion and impression of left mandibular ramus, natural size. *A*, the same; ×2. 8.—Counterpart impression, and portion, of the same ramus (7). *A*, the same; ×2.

field Slate fauna. As the anteroposterior diameter of each lower molar has now markedly increased, there has been a corresponding reduction in the total number of molars from five to three, or rarely four. A decrease in the number of molars, with a concomitant increase in the anteroposterior diameter of each, is also observable in comparing earlier with later members of several other phyla of mammals.

The upper molars are similar to the lower, but have the cingulum on the outer instead of on the inner side. The lower premolars, four in number, seem to have deciduous predecessors. In the lower jaw the apex of the fourth premolar is much higher than that of the first molar. The premolars have compressed protoconids and the crowns are simpler than those of the molars, but are beginning to develop the triconodont pattern. The fourth deciduous cheek tooth, as figured, is more molariform than its permanent successor, as is usually the case in all orders.

The dental formula of the adult is given as

$$I_{\overline{3}}\ C_{\overline{1}}\ P_{\overline{4}}\ M_{\overline{3-4}}$$

The lower jaw is stout, well curved below, with a prominent caniniform canine, a wide ascending ramus and fully inflected angle. The areas for the masseter and temporal muscles on the outer side, and for the pterygoid muscles on the inner side, are extensive. The condyle is in line with the lower border of the jaw, as it is also in the multituberculates. The typical triconodonts were thus evidently the aggressive carnivores of this micro-fauna, remote descendants perhaps of some of the smaller mammal-like reptiles, but already too specialized to be ancestral to the trituberculate marsupials and placentals.

In the Morrison formation of North America we find the true triconodonts represented by Marsh's genus, *Priacodon*, in which the internal cingula of the premolars and molars are strongly developed.

## *ORDER* TRICONODONTA?

### *Family* Spalacotheriidæ

Of uncertain relationships,[6] but of considerable morphological interest, are the Purbeck genera, *Spalacotherium* Owen and *Phascolestes* Owen, represented by minute lower jaws with a slender horizontal ramus and sharp, pricking, molars of insectivorous type. The sharp proto-, para-, and metaconids constitute an equilateral triangle with the protoconid at the apex. Certain characteristics of the molars of *Spalacotherium tricuspidens*, as figured by Owen (1871, plate 1) and by Osborn (1888, plate 8), have given rise to the well-known "Cope-Osborn hypothesis"[7] that the tritubercular lower molar arose through the "rotation" or circumduction of the anterior and posterior cusps toward the lingual side, so as to produce a triangular arrangement, the protoconid forming the apex on the outer or buccal side, and the main anterior and posterior cusps forming the para- and metaconids on the lingual side. The jaws of *Menacodon* Marsh and *Tinodon* Marsh, from the Morrison formation, have also given support to this suggestion because, both in the inner and outer views, their cheek teeth on the one hand recall the triconodont pattern, and on the other hand suggest that of *Spalacotherium*. Moreover, the angular region in a certain jaw referred to *Spalacotherium* appears to be strongly inflected as in the triconodont type.

It is indeed possible that, as suggested by Osborn (1888, p. 243), *Spalacotherium* and its American allies have been derived from a more primitive triconodont, such as *Phascolotherium* of the Stonesfield Slate, in which the anterior and posterior cusps were said to be slightly internal to the main cone, or protoconid.

The transition from the Spalacotheres to the true Trituberculata has not been satisfactorily established, although the lower jaws of "*Peramus*" offer some evidence in that direction, since they were referred originally to *Spalacotherium* but were subsequently shown by Osborn (1888.2, p. 295) to belong with *Peramus*. This genus has the asymmetrical trigonid of the trituberculates rather than the symmetrical trigonid of the spalacotheres.

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[6] See p. xiii.

[7] See p. vii.

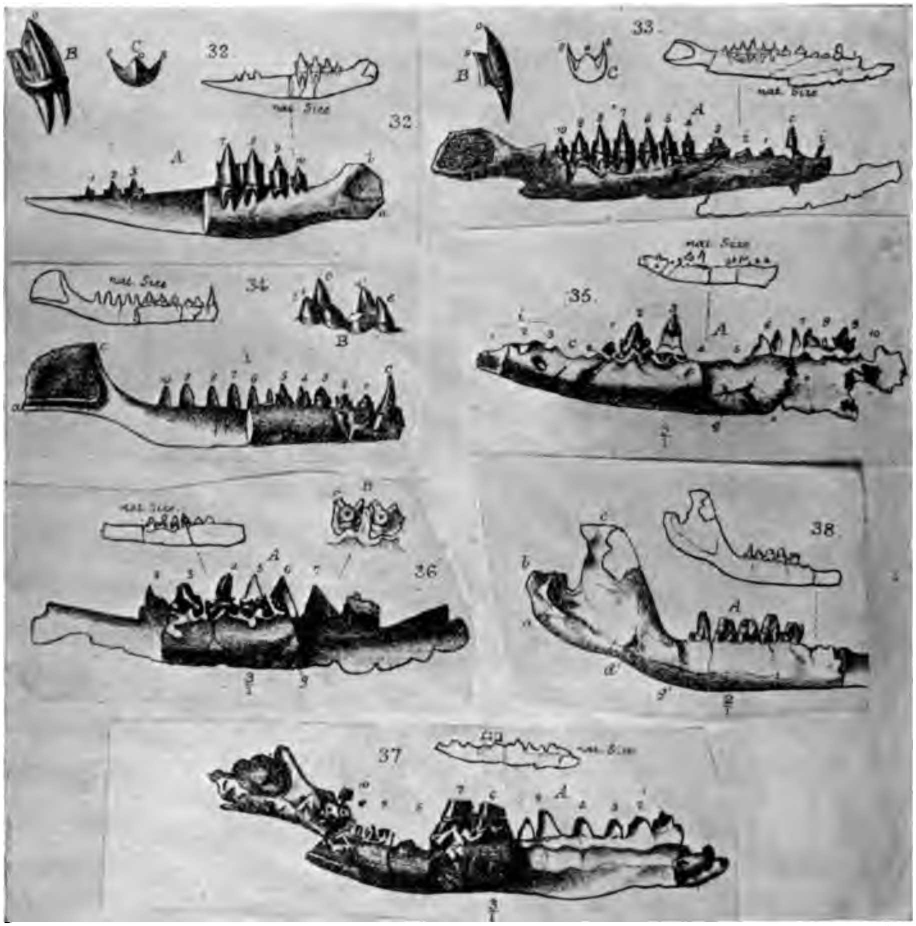

Fig. 23. Lower Jaws of *Spalacotherium tricuspidens*, from the Purbeck Formation (Upper Jurassic). After Owen

32.—Portion of left ramus; natural size. *A*, The same; ×2. *B*, oblique view of a molar tooth; ×4. *C*, the same, upper view. 33.—Part of right ramus; natural size. *A*, the same; ×2. *B*, oblique view of a molar tooth. *C*, upper view of same. 34 —Part of left ramus; natural size. *A*, the same; ×2 *B*, inner view of two molars; ×4. 35.—Part of left ramus; natural size. *A*, the same; ×3. 36.—Part and impression of right ramus; natural size. *A*, the same; ×3. *B*, upper view of two fractured molars; ×3. 37.—Part and impression of the same ramus in the counterpart slab of matrix; natural size. *A*, the same; ×3. 38.—Left ramus; natural size. *A*, the same; ×3.

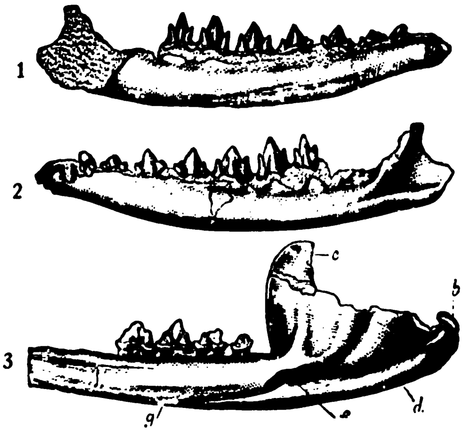

FIG. 24. LOWER JAWS OF *Menacodon rarus* AND *Tinodon bellus*, FROM THE MORRISON FORMATION (UPPER JURASSIC). AFTER MARSH

1.—***Menacodon***, left mandibular ramus, inner side. ×3. 2.—The same, outer side. ×3. 3.—***Tinodon bellus***, right mandibular ramus, inner side. ×3.

In the arrangement of the cusps of the lower molars, these genera are intermediate between the primitive triconodonts, such as *Amphilestes* and the spalacotheres, which have the three cusps arranged in a symmetrical triangle. Upon this fact was based the well known hypothesis of the origin of the tritubercular molar by the "rotation," or circumduction, of the para- and metacones toward the inner side of the lower molars.

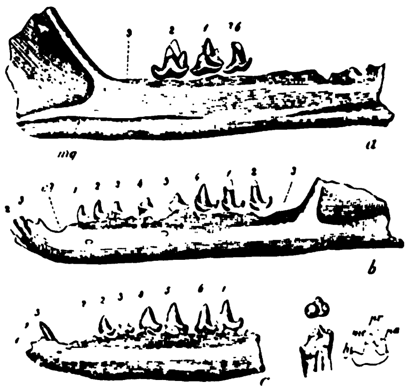

FIG. 25. LOWER JAWS OF *Peramus*, FROM THE PURBECK (UPPER JURASSIC). AFTER OSBORN. ALL MUCH ENLARGED

a.—*Peramus* (*Spalacotherium*) *minus*, left ramus, inner side. b.—*P.* (*Leptocladus*) *dubius*, left ramus, outer side. c.—*P. tenuirostris*, left ramus, outer side.

Also second lower molar of *Amphitherium prevostii*, internal view, and second molar of *Peramus minus*.

The lower molars have the asymmetrical trigonid, as in most other trituberculates and unlike the symmetrical trigonid of the spalacotheres. The presence of six premolars and three molars is peculiar.

The most important objection to the "cusp rotation" hypothesis is that, in the far older Jurassic fauna of the Stonesfield Slate, the primitive triconodont and trituberculate patterns were already widely different and were possessed by animals belonging to different orders; the primitive triconodonts, *Amphilestes* and *Phascolotherium*, apparently belonging among the Marsupialia, and having the angle of the jaw sharply inflected, while the primitive trituberculate, *Amphitherium*, represented the order Trituberculata, in which the angular process was conspicuous and not inflected. Hence, if some of the so-called trituberculates of the Purbeck fauna, such as *Spalacotherium* and its allies, were derived from the primitive triconodonts, this does not establish their status as true Trituberculata, for they may have been only Pseudo-trituberculata. Professor Osborn in 1888 (p. 245) and again in 1907 (p. 8) suggested that the trituberculate lower-molar pattern may have been derived more than once and in more than one manner, viz.: first, as an upgrowth of the internal cingulum in the true Trituberculata; secondly, as a result of the inward displacement of the anterior and posterior cusps in the Pseudo-trituberculata.

Finally, there is no evidence that these pseudo-trituberculates of the Upper Jurassic were ancestral to any of the better known mammals of the later ages.

## *ORDER* TRITUBERCULATA

### *Family* Amphitheriidæ

In the typical Purbeck trituberculates, as represented by *Amblotherium* and *Achyrodon*, the asymmetry of the trigonid is pronounced. The metaconid is now opposite the posterior slope of the protoconid while the paraconid, instead of pointing solely upward, is often directed more forward so as to make a pronounced fork with the protoconid. The incipient talonid, which is lacking in *Spalacotherium*, also now bears a rather prominent low projection, the homologue of the entoconid of later mammals. Thus in these genera the lower teeth represent an advance upon the more primitive type seen in *Amphitherium* of an older horizon. Their lower jaw agrees in essentials with that of *Amphitherium*, since it has a well-defined angular process and is therefore of the primitive placental type. In *Amblotherium mustelula* the jaw is stouter, the ascending ramus is broader, its coronoid border is more vertical, and its condyle is at a higher level above the alveolar border, recalling the conditions in *Amphitherium;* while in *Amblotherium soricinum*, the ascending ramus is narrower, its coronoid border more sloping, and the condyle set at a lower level. These differences are perhaps correlated with equal differences in food habits, *A. mustelula* possibly being carnivorous and *A. soricinum* more insectivorous. The dental formula of the latter, $I_{\overline{4}}\,C_{\overline{1}}\,P_{\overline{4}}\,M_{\overline{6}}$ is similar to that of *Amphitherium*, $I_{\overline{4}}\,C_{\overline{1}}\,P_{\overline{5}}\,M_{\overline{6}}$. The incisors are gently procumbent and slightly spatulate; the canine, erect. The premolars increase in size from the very minute $P_1$ to

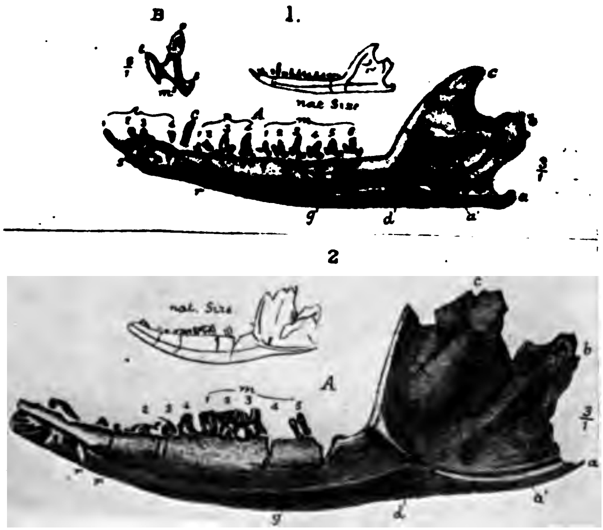

FIG. 26. LOWER JAWS OF *Amblotherium*,[8] FROM THE PURBECK FORMATION, UPPER JURASSIC. AFTER OWEN

1.—Right ramus of *Amblotherium soricinum;* natural size. *A*, the same; ×3. *B*, third molar; ×6. This view shows the paraconid (c), the high protoconid (o), the metaconid, and the low small talonid (s). 2.—Right ramus of *Amblotherium mustelula;* natural size. *A*, the same; ×3.

This jaw, as figured, differs widely from that of *Amblotherium soricinum* and, perhaps, represents a more aggressive carnivorous member of the Amphitheriidæ.

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[8] See p. xiii.

the large erect $P_4$ which has a recurved apex of piercing and pricking type. The molars increase in size posteriorly, the first being quite small. Somewhat similar but less pronounced characters may be observed in the older *Amphitherium* and in many of the contemporary trituberculates of the Purbeck beds.

For the purposes of this discussion the genera *Amphitherium*, *Achyrodon*, *Peraspalax* and perhaps *Peralestes* described below, may be referred to the family Amphitheriidæ of Owen, which, together with the Stylodontidæ, constitute the order Trituberculata of Osborn, the Pantotheria of Marsh.

In America the Amphitheriidæ appear to be represented in the Morrison formation by the genus *Paurodon* of Marsh. In this lower jaw, as figured, the molars approach those of *Peraspalax* Owen in the asymmetrical arrangement of the trigonid, in which the metaconid is opposite the posterior slope of the protoconid, and the basal spur, or talonid, is well defined. If the high, erect tooth in the anterior part of the mandible is really a canine, then *Paurodon*, as its name implies, has a reduced number of post-canine teeth, the premolars and molars being only six in number. If this is the fact, *Paurodon* would perhaps have to be made the type of a distinct family, but before this is done it should be ascertained whether the large erect tooth is not the posterior premolar ($p_4$). In this genus, as well as in the Amphitheriidæ of Europe, the para- and metaconid and the internal tip of the talonid or entoconid suggest derivation from the internal cingulum; but, as before, no decisive evidence is available.

FIG. 27. PART OF LEFT MANDIBULAR RAMUS OF *Paurodon valens*, FROM THE MORRISON FORMATION (UPPER JURASSIC) OF WYOMING. ×3. FROM OSBORN, AFTER MARSH

In this genus, as in certain other Jurassic trituberculates, (e.g., *Achyrodon*), the inner cusps (para-, meta-, and entoconids) look as if they might have grown up from the internal cingulum. The number of post-canine teeth, six, is the lowest in any Jurassic trituberculate. The jaw is remarkably short and deep.

## *ORDER* TRITUBERCULATA

### *Family* Stylodontidæ

The family Stylodontidæ is represented, in Europe, in the Purbeck Beds, by the genus *Stylodon* and, in America, by the genera *Stylacodon*, *Asthenodon* and, perhaps, by *Dryolestes* and *Laodon*. In the first three genera the molar teeth, as seen from the outside, form narrow, high, sharply-pointed columns (*Stylodon* = column tooth) which, by analogy with certain living insectivores, were adapted for piercing the shells of insects and, perhaps, for holding and piercing the writhing bodies of worms. These molars contrast with those of the Amphitheriidæ, first, in the extreme anteroposterior narrowness of their tips; secondly, in the presence of pronounced interspaces between the molars which are not interrupted by any basal expansion, or talonid,[9]

FIG. 28. LOWER JAWS OF *Stylodon*,[9] FROM THE PURBECK FORMATION. AFTER OWEN

17.—*Stylodon pusillus*, fore part of left ramus; natural size. *A*, the same; ×3. 15—*Stylodon pusillus*, hind part of left ramus; natural size. *A*, the same; ×3. 1.—*Stylodon robustus*, left ramus; natural size. *A*, the same; ×3. 2.—*Stylodon pusillus*, left ramus; natural size. *A*, the same; ×3; showing the forward inclination of molars 5, 6, 7. 3.—*Stylodon pusillus*, left ramus; natural size. *A*, the same; ×3.

This genus represents an advanced specialization for insectivorous or vermivorous habits.

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[9] See p. xiii.

but continue down between the roots to the alveolar border; thirdly, in the extreme anteroposterior shortness of the molars, which brings the anterior and posterior roots so close together that, from the outside at least, they appear to be coalesced. From the inner side, as figured, they can be barely, if at all, differentiated; while in the Amphitheriidæ, the two main roots of each molar are widely separated, especially on the inner aspect of the jaw. Fourthly, the horizontal ramus in most cases is very slender, although *Stylodon robustus* forms an exception to this rule. The dental formula $I_{\overline{4}}\ C_{\overline{1}}\ P_{\overline{4}}\ M_{\overline{7-8?}}$ differs from that of the Amphiteriidæ only in the slightly greater number of the molars, but it must be remarked that certain genera are referred to the Amphitheriidæ (*Achyrodon*, *Peraspalax*) in which there are also seven or eight molars. Significant agreement is found not only in the dental formula but also in the presence of a distinct angular process on the mandible, of a pedunculate condyle, and, especially, in the characters of the premolars, which retain the primitive two roots and increase rapidly in size from $p_1$ to $p_4$, so that the premolars of *Stylodon* and *Dryolestes* are similar to those of *Amblotherium*, *Peralestes* and *Achyrodon*. The lower molars of *Laodon* and *Dryolestes*, as figured, are essentially similar to those of *Peraspalax*, *Peralestes* and *Achyrodon* of the Amphitheriidæ. Therefore, it seems safe to infer, from the construction of the lower jaw and lower molars, that the Stylodontidæ represent a structural advance upon the Amphitheriidæ, leading towards extreme insectivorous adaptations.

Possibly some of the less specialized members of the Stylodontidæ might have given rise to the zalambdodont Insectivora of the Paleocene and later epochs, but, in the absence of real connecting links, such an inference could be at most provisional; because this high, styloid, sharply-pointed type of lower molars has apparently been evolved independently in the marsupials and placentals. The Stylodontidæ differ from the later insectivorous mammals in having a large number of molars, all of relatively small size; but this is possibly a primitive character and the reduction of the molars in the later placentals is very probably secondary. The Stylodontidæ, therefore, tell us nothing decisive about the origin of the tritubercular type of lower molar. They merely exhibit an early specialization of that type, probably derived from the more primitive conditions seen in the Amphitheriidæ.

### UPPER MOLARS OF PURBECK TRITUBERCULATA

Up to this point I have purposely omitted a discussion of the upper molars because the classification and relationships of these families must first be worked out on the lower molars, and because of the uncertain systematic position of one of the upper molar types now to be described.

### *Kurtodon*

In the Purbeck Beds there are only two types of upper molars known which may be assigned to the order Trituberculata. One of them, referred to *Stylodon* by Owen, was made the type of a new genus, *Kurtodon*, and of a new family, Kurtodontidæ, by Osborn, who, however, afterward (1888.2) recognized that *Kurtodon* belongs in the Stylodontidæ. The material consists only of a minute alveolar process and premaxilla, 13 mm. long, exposed, it is said, on the lingual side. The molars are very wide transversely and short anteroposteriorly. Thus, they consist of a narrow V-shaped crown with the high apex on the lingual side. The surface of the crown is apparently worn off, but bears a narrow low ridge running transversely from the internal apex. The dental formula includes one canine, four premolars and seven molars, and is apparently the same as in

FIG 29. LEFT PREMAXILLA AND MAXILLA OF *Stylodon pusillus* FROM THE PURBECK FORMATION (UPPER JURASSIC). AFTER OWEN

14.—Natural size. *A*, the same; ×4. *B*, crown view of sixth and seventh molars; ×3.

In this genus, as in all other trituberculates, the main tips of the molars appear to be serially homologous with those of the premolars.

*Stylodon pusillus* and in the American genus, *Dryolestes*, mentioned above. The fourth premolar is much larger than the first molar, as is usually the case in Mesozoic trituberculates. As figured, it suggests in every way the corresponding lower tooth of *S. pusillus*, as also does the third premolar. The canine is large, directed downward and somewhat backward.

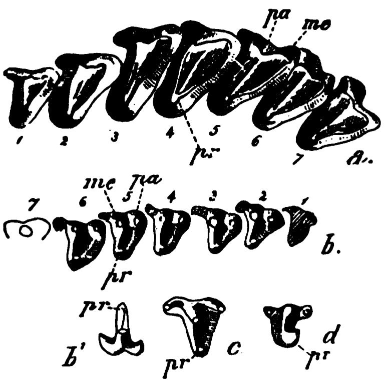

FIG. 30. UPPER AND LOWER MOLARS OF CERTAIN TRITUBERCULATES FROM THE PURBECK FORMATION (UPPER JURASSIC). AFTER OSBORN. ALL MUCH ENLARGED

a.—*Stylodon* (*Kurtodon*) *pusillus*, left upper molars, crown view. b.—Right lower molars of *Amblotherium soricinum*, crown view. $b^1$, a left lower molar of *Amblotherium* (*Peraspalax*) *talpoides*, outer side, showing the protoconid, paraconid, and entoconid c.—A right lower molar of the same species, viewed obliquely from above, showing the asymmetrical trigonid, with oblique anterior, and directly transverse, crests; and the incipient talonid bearing the low entoconid. d.—A right lower molar of *Achyrodon nanus*, crown view showing the worn transverse crest connecting the protoconid with the metaconid.

### *Dryolestes*

From the Morrison formation of America there are two sets of upper teeth of *Dryolestes* figured by Osborn which resemble Osborn's later figure of the *Kurtodon* type (1907, p. 26) in many important characters; and, as they are probably associated with lower molars referred to the Stylodontidæ, they tend strongly to support Owen's original conclusion that the *Kurtodon* upper molars belong with, or near, the *Stylodon* lower molars.

The *Dryolestes* upper molars are separated on the inner side by triangular spaces for the reception of the trigonids of the lower molars. This interlocking of the lower molars with the spaces between the upper molars is a fundamental relation in all primitive tritubercular dentitions. Attention was so long directed solely to the question of the homology and origin of the several cusps of the primitive trigon, that the importance of the interlocking relation, the trigonids fitting into the spaces between the upper molars, was not at first fully appreciated. In *Dryolestes*, as in other primitive tritubercular dentitions, no cusps of the triangular upper-molar crown could have articulated in vertical opposition with any cusps of the lower molars. The sharp sides of the upper molars sheared past the sides of the trigonids and therefore served as cutting blades. The protoconids of the lower molars certainly did not articulate with any upper cusp, but fitted into the buccal part of the triangular spaces between the upper molars. So, too, the high, pointed internal apex of the upper molars fitted chiefly into the spaces between the trigonids of the lower molars.

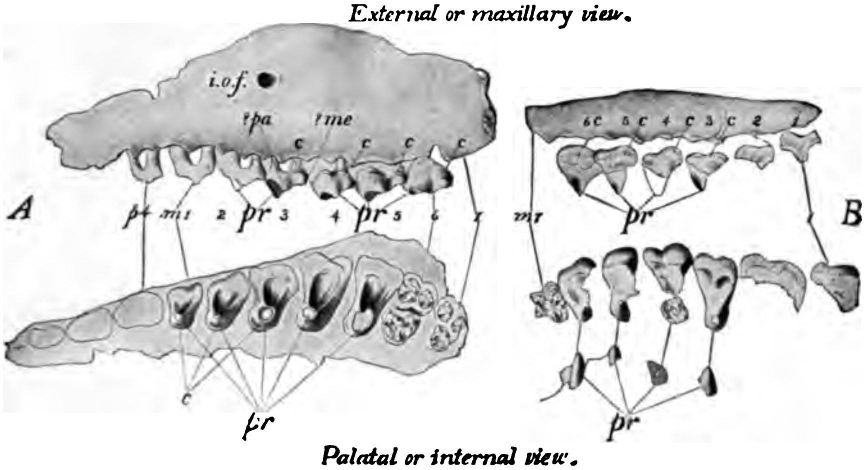

FIG. 31. UPPER MOLARS OF *Dryolestes* sp., A TRITUBERCULATE FROM THE MORRISON FORMATION (UPPER JURASSIC). GREATLY ENLARGED. AFTER OSBORN

From specimens in the Yale University Museum.

A.—Left maxilla. B.—Right maxilla. The cusps marked "pr" (protocone) are probably homologous with the tips of the premolars, and with the para- and metacones of later mammals. These molars consist only of the *primary* trigon. See p. 56.

The basin-like surface of the upper molar crowns, although worn in both *Dryolestes* and *Kurtodon*, was not so worn by articulation with any part of the lower molar crowns, but by attrition with food. It is indeed a fundamental principle deduced from the observed occlusion of upper and lower teeth of many later mammals, that, in primitive tritubercular dentitions, the upper and lower triangles (trigon[10] and trigonid) do not articulate vertically with, but shear past, each other, and that their summits are worn by attrition with food and not by articulation.

In the lower molars of *Dryolestes* there is a small talonid spur on the lingual side, the outer side of which sheared past the inner side of the apex of the upper molars. The upward movement of these talonid spurs was apparently checked by an incipient cingulum-like basal spur on the inner side of the upper molars, as figured by Osborn.

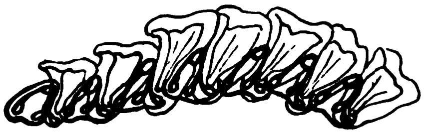

FIG. 32. PROBABLE OCCLUSAL RELATIONS OF UPPER AND LOWER MOLARS OF *Dryolestes*
The upper molar crowns comprise only the primary trigon

The homology of the internal apex of the upper molars of *Dryolestes* has been disputed. Osborn (1904, 1907, p. 217) claimed that it was homologous both with the "apex of the original reptilian cone" and with the "protocone" of later tritubercular dentitions. Gidley (1906), held that the cusp in question represented a secondary extension from the inner sides of the upper molars analogous with a similar internal extension of the premolars of later mammals. For the reasons stated below (p. 59) it now appears that the internal apex of the *Dryolestes* molars is homologous with the "apex of the original reptilian cone" but not with the "protocone" of later mammals.

### *Peralestes*

A second type of trituberculate upper molars from the Purbeck Beds is afforded by the alveolar process described by Owen as *Peralestes longirostris*. The upper molars of this genus differ widely from

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[10] The *primary* trigon (see pp. xiii and 106).

those of the *Kurtodon* and *Dryolestes* type. Instead of being very narrow, transversely extended and anteroposteriorly shortened, each upper molar in crown view shows a wide asymmetrical triangle with very high internal tip and low anteroexternal cusp connected with a

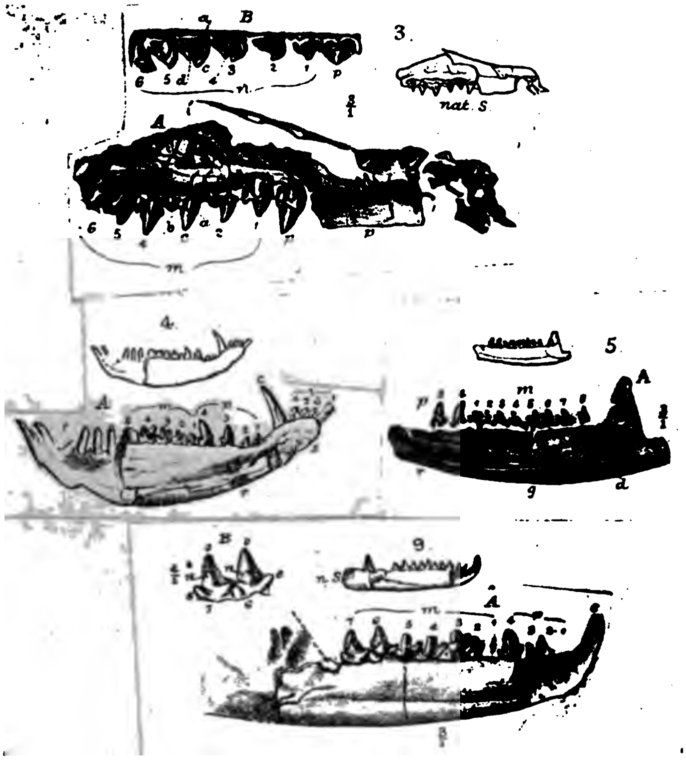

Fig. 33. Upper and Lower Molars of *Peralestes* and Other Purbeck Trituberculates. After Owen

3.—Right maxilla of *Peralestes longirostris;* natural size. *A*, the same; ×3. *B*, crown view of upper molars. 4.—Left mandibular ramus, referred by Owen to *Peralestes longirostris;* natural size. A, the same; ×3. In this drawing, only the internal cusps of the molars (para-, meta-, and entoconids) are shown the protoconids being probably hidden in the matrix. 5.—Left mandibular of *Achyrodon nanus;* natural size. A, the same; × 3. 9.—Left mandibular ramus of *Peraspalax talpoides;* natural size. A, the same; ×3. B, sixth and seventh lower molars, lingual side; ×4. *e*, paraconid; *n*, metaconid; *c*, protoconid; *s*, entoconid (incipient talonid).

The very asymmetrical trigon and high apices of the upper molars of *Peralestes* suggest that somewhat similar conditions would be found in the lower molars, as in the present specimens. (But see the note by Dr. Matthew on p. xiii.)

pronounced external cingulum, and a third prominent cusp on the posteroexternal slope of the high internal cusps. As we pass forward, the high internal cusps of the molars are certainly homologous with the still higher apex of the fourth premolar, the molars and the premolars being supported by two widely separated roots arranged anteroposteriorly, as are the roots of the lower cheek teeth in the Amphitheriidæ.

Owen (plate II, fig. 4) associated these upper teeth of *Peralestes* with a certain lower jaw which Osborn referred to *Phascolestes;* but both Owen and Osborn agree in associating the upper molars of *Peralestes* with lower molars which the present writer would refer to the Amphitheriidæ, in its wider sense, in contrast with the group here

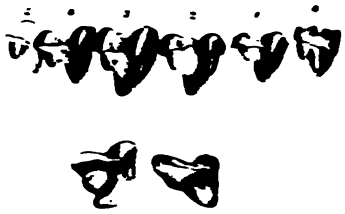

FIG. 34. UPPER MOLARS OF *Peralestes longirostris*. × 8. AFTER OSBORN

In the outer view, the apices of the molars are serially homologous with those of the premolars. The sharp blade-like edges of the molars probably sheared past equally sharp crests running from the protoconid to the metaconid in the lower molars. The lower figures show two of the molars (possibly the second and the fourth) in crown view. In general these teeth are very different from those of *Dryolestes*.

called Stylacodontidæ, which are distinguished by their very narrow molars. In his book on the "Evolution of mammalian molar teeth," however, Professor Osborn referred *Peralestes* provisionally to the Spalacotheriidæ along with the lower teeth called *Phascolestes*. After studying the various figures by Osborn and Owen, I believe that Osborn's earlier opinion was more nearly right,[1] and that *Peralestes* with its asymmetrical, wide, triangular upper crowns represents the upper dentition of some of the Amphitheriidæ, especially *Achyrodon;* or even that Owen was right in referring to *Peralestes* the lower jaw shown in his Plate II, fig. 4.

*Peralestes*, therefore, appears to be a member of the Amphitheriidæ, and it may give us some idea of the general appearance of the upper

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[1] See the note by Dr. Matthew on p. xiii.

molars of the older *Amphitherium*, but was probably somewhat more specialized. It strongly supports the view that, in the Mesozoic Trituberculata, the tips of the upper protocones were serially homologous with the tip of the posterior premolar.[12] This conclusion, in turn, is in line with the conclusions of the "premolar analogy" theory based on studies of later mammals. Assuming for the moment the correctness of this view, the tips of the upper molars of *Peralestes*, as well as those of *Dryolestes*, are to be regarded as homologous with the paracones and not with the protocones of the molars of later mammals. In 1916 I pointed out the resemblance between the upper teeth of *Peralestes* and the deciduous teeth of the polyprotodont marsupials, and suggested that the high internal cusp is homologous, not with the protocones, but with either the para- or metacones of marsupials.

## *ORDER* **TRITUBERCULATA**

### *Family* **Diplocynodontidæ**

Of the Upper Jurassic mammals there remains to be considered a peculiar and aberrant family, the Diplocynodontidæ or Dicrocynodontidæ, from the Morrison formation of Wyoming. The upper molars, as figured by Gidley, have a high, compressed, external cusp and a large, highly peculiar, internal cusp, connected with the principal external cusp by a low transverse ridge. The inner cusp is greatly expanded anteroposteriorly at the base, both its anterior and its posterior buccal surfaces bearing deep fossæ for the reception of lingual cusps of the lower molar trigonids. These strange upper molars, which might possibly be derived from a *Peralestes*-like pattern, are very doubtfully referred to the same family with lower jaws, of the type called *Docodon* by Marsh. Gidley pointed out the apparent homologies of the several parts of the upper molars of *Diplocynodon* with those of *Dryolestes;* on the other hand the supposed lower dentition of the Diplocynodonts, distinguished by the large size and oblique form of the trigonids, indicates ordinal relationships with *Peralestes* among the Amphitheriidæ. After many attempts I have failed to find a satisfactory solution of the problem of the articulating relations of the upper and lower molars of this

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[12] See p. xiv (5).

family and until this is achieved the homologies of the several parts, and the supposed association of upper and lower molars, remain in doubt.

To summarize, the upper as well as the lower molars of these upper Jurassic trituberculates already exhibit considerable diversity in form. Some, e.g., *Kurtodon*, *Dryolestes*, suggest the narrow tritubercular type of *Notoryctes* among living marsupials, but, in view of the plasticity of the mammalian dentition, it would not be safe to regard them as directly ancestral to that genus, which appears to be connected rather with the other polyprotodont marsupials. The second type of upper molars, those of *Peralestes*, in some respects foreshadows the upper-molar patterns of the opossums and other polyprotodonts, but here again there are no intermediate links tending to connect the two. The third type, *Diplocynodon*, may well represent a peculiar line of specialization, the members of which became wholly extinct.

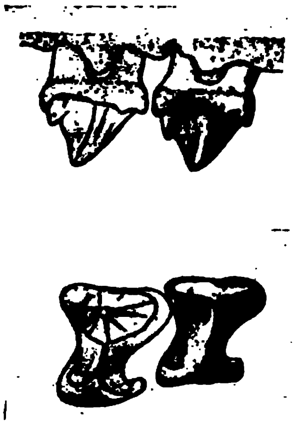

FIG. 35. TWO UPPER MOLARS OF *Dicrocynodon* sp., MORRISON FORMATION (UPPER JURASSIC). ×6. AFTER GIDLEY

These strange upper molars probably represent very aberrant relatives of the Amphitheriidæ.

## SUMMARY AND DEFENSE OF THE PRIMITIVE CHARACTERS OF THE LOWER JURASSIC AMPHITHERIUM

As a whole, both the upper and lower molars afford very strong evidence for the view that, in the Jurassic trituberculates, the main tips of the molars were homologous with those of the premolars. The Purbeck genera may all represent specializations from the primitive *Amphitherium*-like type, but by themselves they tell us little about the origin of the tritubercular type, unless one is willing to admit without evidence the hypothesis that the primitive Lower Jurassic Amphitheriidæ are descendants of unknown earlier Spalacotheriidæ, the lower-molar pattern of which was by hypothesis derived through the circumduction of the anterior and posterior cusps of a primitive *Phascolotherium*-like triconodont.

We have now to consider in conclusion a possible objection to the view that the Lower Jurassic trituberculates are really primitive and structurally ancestral to later trituberculate mammals. It is possible to argue that the known Jurassic faunæ, coming as they do from two or three extremely limited localities, represent only a fraction of the mammalian life of that epoch; that they belong only in the swamp or lowland fauna associated with the giant reptiles; and that such faunæ usually consist of the more degenerate or aberrant relatives of the more primitive faunæ of the uplands, which in this case have been entirely wiped out. From this point of view many of the characters here regarded as primitive, such as the small size of the talonid and the high number of post-canine teeth, would be under the suspicion of being secondary, not primitive. Against such an argument I would advance the following considerations:

(1) The considerable number of genera represented in the Purbeck trituberculates is favorable to the probability that some of them will be more primitive in certain characters than others, that is, will preserve more of the characters of their hypothetical ancestors of the uplands.

(2) If it be admitted that the Stylodontidæ, with high, narrow molars, are relatively specialized, it seems that *Amblotherium soricinum* is a more primitive member of the Purbeck trituberculates, which has apparently inherited many characters from a much older

form like *Amphitherium* of the Stonesfield Slate (Lower Jurassic), such as the following: lower incisors four, semiprocumbent; canine erect, caniniform, with more or less division of the fang; lower premolars four (but probably five in *Amphitherium*), with simple, conical crowns, incipient talonid and two roots; the last premolar high and projecting above the level of the molars; lower molars six, tritubercular, with incipient talonid; lower jaw with a wide coronoid process, ascending at a low angle; condyle lower than in typical later mammals, angular process of mandible hook-like, not inflected; Meckelian groove of jaw pronounced; diet prevailingly insectivorous; size much smaller than the average size of later mammals.

(3) The conclusion that at least most of the foregoing are primitive characters rests upon the direct evidence cited in the preceding pages and in the writer's opinion outweighs the negative objection noted. Although members of swamp faunas are specialized in certain features, this is often not inconsistent with their retaining many primitive characters, as in the case of certain stegocephs and primitive reptiles.

(4) Of the characters listed above as primitive for *Amblotherium* and *Amphitherium*, perhaps the only one requiring special defense is the high number of post-canine cheek teeth. In all really primitive marsupials and placentals of later ages this never exceeds seven, while in *Amphitherium* it is eleven. It has been shown above that in the very primitive triconodont *Amphilestes*, of the Stonesfield Slate, there are ten post-canine teeth, while in the specialized *Triconodon* of the Purbeck there are but seven, or at most eight. The reduction in the number of molars from five to three is at least accompanied, if not caused, by a marked increase in the anteroposterior diameter of the individual teeth. So, too, in the primitive marsupials and placentals of later ages, in which the number of lower molars is reduced to three, each of these molars is elongate anteroposteriorly, due partly to the great expansion of the talonids, so that three wide molars occupy as much space in the jaw as did the six narrow molars of *Amphitherium*. In the opposite direction, a marked increase in the length of the jaw affords opportunity for a secondarily increased number of small molars, as in *Myrmecobius* and perhaps also in the stylodonts, where the molars are sometimes as many as nine in number.

The writer's general conclusion is that although the Lower Jurassic *Amphitherium* may well be ancestral to the specialized stylodonts of the Upper Jurassic, it is at the same time an exceedingly primitive mammal, which may be assumed provisionally as structurally ancestral to the placentals and perhaps also to the marsupials of later ages. Thus, it represents a remote stage in the evolution of the human dentition.

## V. THE LATE MESOZOIC MAMMALS (UPPER CRETACEOUS)

Between the Upper Jurassic of the Purbeck-Morrison fauna and the next known mammalian fauna of the "Laramie," or Upper Cretaceous, of North America, there is a vast hiatus in the record representing millions of years of slow evolution, during which time the highly diversified reptilian orders dominate the geological record to the exclusion of the mammals.

The scarce mammals of the Upper Cretaceous, the contemporaries of the last of the dinosaurs, afford two radically different general types of dentition, which have been described by Cope, Marsh, Osborn, Gidley and Matthew: the first represents the later stages of the Multituberculata; the second, several modifications of the tritubercular type of molars.

### *ORDER* MULTITUBERCULATA

#### *Family* **Polymastodontidæ**

The multituberculates, represented by *Meniscoessus* (described by Cope and by Osborn), enter a side path of evolution in which the upper molars tend to acquire three rows of cusps. The compressed and grooved lower premolar is not so large or elongate anteroposteriorly as it is in the typical Plagiaulacidæ, a stage foreshadowing the great reduction of this tooth in the polymastodonts of the succeeding Paleocene.

## *ORDER* MARSUPIALIA, *SUBORDER* POLYPROTODONTIA

### *Family* Cimolestidæ

The tritubercular molars, according to Matthew (1916), belong to small polyprotodont marsupials, some of which (*Eodelphis browni*) are closely related, or ancestral to, the modern opossums. In the lower jaw of this animal, the dental formula, as determined by Matthew (3. 1. 3. 4), differs from that of *Didelphis* only in the presence of three rather than four incisors. It differs from that of the Jurassic trituberculates in the reduction in number both of the premolars and of the molars. But, while the teeth are fewer in number they are individually much larger in proportion to the length of the jaw, which is also heavier than that of the trituberculates. The animal itself is very much larger, the jaw being about 62 mm. long, while that of *Amphitherium* is about 25 mm. long.

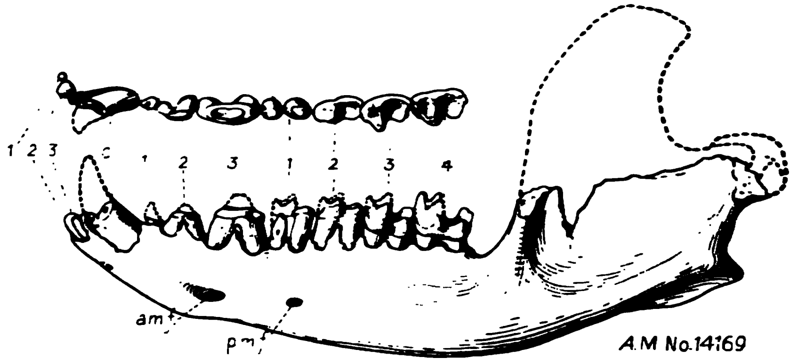

Fig. 36. Lower Jaw of *Eodelphis browni*, a Primitive Opossum from the Belly River Formation (Upper Cretaceous) of Alberta. ×3/2. After Matthew

A progressive increase in size is observable in many phyla of mammals; and, in nearly all cases in which the palæontological history is known, the earliest species of the phyla average smaller in size than the later stages. Thus this extremely primitive Upper Cretaceous marsupial *Eodelphis* is intermediate in size between the primitive Jurassic trituberculates and the largest modern polyprotodont marsupials.

*Eodelphis* agrees with the more primitive existing polyprotodonts in having three premolars and four molars, in contrast with the four premolars and three molars of primitive placentals. Opinions differ so widely on the subject of the homologies of the premolars and molars in marsupials and placentals that it would require too long a digression to discuss the subject. It is not definitely known whether the last premolar of marsupials is homologous, as it appears to be, with the last premolar of Jurassic trituberculates and with the last, or fourth, premolar of placentals. The second and third premolars of *Eodelphis*, and all the molars, are supported by two main anterior and posterior roots, which appear to be homologous with those of the Jurassic trituberculates. The premolars have simple compressed crowns with a single tip, like those of the modern opossums. In the molars, the talonids are much better developed than those of the Amphitheriidæ, occupying the posterior moiety of the tooth, being extended transversely and bearing a hypoconid or posteroexternal lower cusp in addition to the primitive entoconid. In correlation with the better development of the talonids we find that the upper molars of these Upper Cretaceous marsupials (represented perhaps by ?*Pediomys* Marsh) have widened internal cusps or protocones, which apparently now fit into the basins or fossæ of the talonids of the lower molars. This relation, which first becomes clear in these Upper Cretaceous mammals, is very characteristic of all primitive later mammals, and was apparently attained through the upgrowth of the hypoconids on the outer side of the talonid spurs overlapping the internal tip of the upper "protocones." There seems no reason to doubt that, in the lower teeth, the tips of the premolars are homologous with the protoconids of the molars; and, presumably, in the upper teeth, the tips of the premolars, if known, would be homologous with the para- and metacones of the molars, as they are apparently in living polyprotodonts.

The upper molars of *Pediomys*, another Upper Cretaceous marsupial figured by Gidley (1906), and Osborn (1907), now have two well separated cusps, corresponding to the para- and metacones of later mammals. The separation of these two cusps is correlated with the transverse widening of the talonid, and with the upgrowth of a hypoconid which articulates on the surface of the crown between the lingual slopes of the para- and metacones. There are now, also, two small intermediate V-shaped cusps, the proto- and metaconules, located respectively on the anterior and posterior slopes of the protocone. The appearance of these cusps was probably correlated both with the transverse widening of the talonid and with the shearing action of the trigonid. The protoconule fits into the reëntrant valley between the posteroexternal blade of the protoconid and the crista obliqua of the talonid. Similarly, the metaconule occludes, and has developed in, the space between the posteroexternal wall of the hypoconid and the anteroexternal wall of the paraconid of the next succeeding lower molar. The metaconule, according to Gidley, was already developed in the Upper Jurassic *Dryolestes*, where its posterior side must have been appressed to the anteroexternal side of the trigonid.

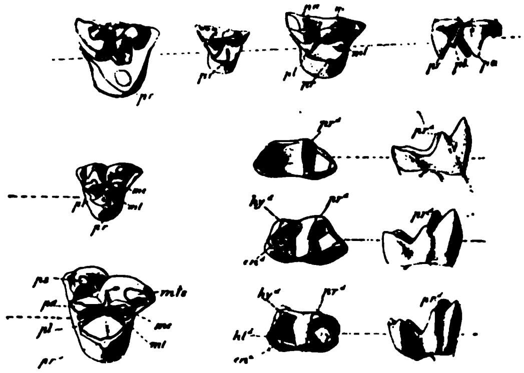

Fig 37. Upper and Lower Molars of Upper Cretaceous Marsupials. ×2
After Osborn

Upper row: upper molars, *Protolambda* (cf. *Pediomys*). Middle and lower rows: upper and lower molars of *Didelphops* (?*Thlæodon*).

In some of these Upper Cretaceous marsupials, the upper molar cusps that developed from the external cingulum attained very large size. The lower molars are of the tuberculo-sectorial type, with high trigonids and well developed talonids, which, however, are not as large as those of typical placental mammals.

The upper molars of *Pediomys* have a large internal cusp or "protocone," which is pretty surely homologous with the "protocone" of modern opossums. This, in turn, has probably arisen by a lingual extension of the base of the crown, while the original apex of the crown, homologous with the tips of the premolars, has apparently remained in the middle of the crown and is probably homologous with the para-metacone. Therefore, the direct comparison of the upper molars of *Pediomys* with those of the Jurassic trituberculates, *Dryolestes* and *Peralestes*, is probably misleading, since it would lead one at first sight to homologize the internal tip of its crown, which is probably a secondary ingrowth, with the primary apex of the molars of *Dryolestes* and *Peralestes*.

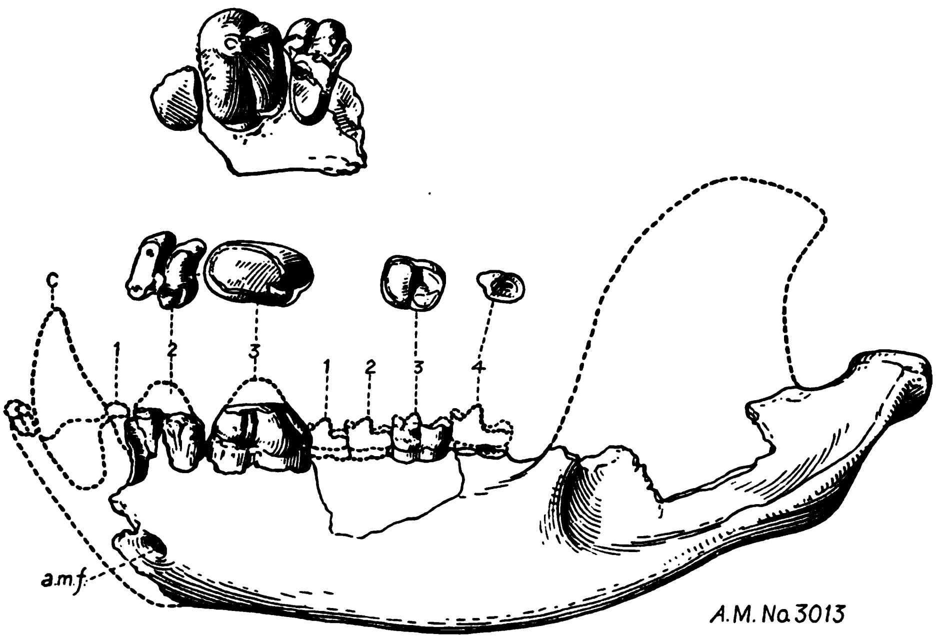

Fig. 38. *Thlæodon padanicus*, an Upper Cretaceous Marsupial. ×3/2. After Matthew

Fragment of left maxilla, with enlarged posterior premolar and first molar; crown view of lower teeth, and left mandibular ramus.

In this genus, the posterior premolars are enlarged, with swollen tips; the upper molars have swollen para- and metastyles; the lower molars are of the tuberculo-sectorial type.

The upper molars of *Pediomys* also exhibit the strong development of the external cingulum and its cusps, the para-, meso-, and metastyle, which are foreshadowed in the Jurassic mammals and become extremely developed in the related Upper Cretaceous genus *Thlæodon*.

as well as in many modern polyprotodonts. These external cingulum cusps were rightly regarded by Winge as being a very ancient part of the mammalian molar crown.

The genus *Thlæodon*, a contemporary of *Eodelphis*, is regarded by Mathew (1916) as a specialized phase of the same family (Cimolestidæ). The jaw has become much larger, attaining an estimated length of about 80 mm. The posterior premolars, both in the upper and lower jaws, have become greatly worn, and have blunt tips somewhat like the crushing molars of sea-otters and of other dentitions adapted for crushing and breaking hard substances. The upper molars exhibit an excessive increase in size of two of the external cingulum cusps, probably the para- and metastyle. The lower molars are of the modified tritubercular type with moderately well developed talonid. The angular process is inflected as it is in *Didelphys* and modern polyprotodonts.

Thus, these Upper Cretaceous polyprotodont marsupials, which, in common with the placentals, may have been derived from the Lower Jurassic Amphitheriidæ, were even in their time widely separated from the placentals and had already developed a considerable adaptive radiation in the dentition. The more primitive members (*Eodelphis*) seem to be directly ancestral to the modern Didelphiidæ of North and South America, and were also probably related to the Upper Cretaceous European and Asiatic polyprotodonts that were ancestral to the later Australian members of this group.

## VI. THE ORIGIN AND EVOLUTION OF THE MARSUPIALS (CRETACEOUS TO RECENT)

The adaptive radiation of the marsupials into many life habits, and into animals that superficially resemble placental mammals of corresponding habits, has been studied by many naturalists, especially Bensley (1903), who investigated the evolution of the dentition and of the limbs, applying the principles and results that had been gained by palæontologists concerning the evolution of the dentition and limbs of placental mammals.

Although not in the line of human ascent, the marsupials afford many beautiful examples of dental mechanics and of the coadaptation of the upper and lower teeth to diverse food habits, an understanding of which proves helpful in interpreting the evolutionary history of the human dentition.

The more primitive existing polyprotodonts are the comparatively little-changed survivors of Upper Cretaceous marsupials, and the group as a whole stands on a lower evolutionary plane than that of the placentals. In the northern hemisphere, one family, the early Tertiary opossums, which were the little-modified descendants of the Upper Cretaceous *Eodelphis* and its allies, were driven southward before the advancing hordes of placentals and found an asylum in the forests of Brazil, where, with few exceptions, they retained their primitive arboreal habits and the greater part of their ancestral heritage in dentition, skull and skeleton. One of them (*Chironectes*) became semi-aquatic in habit, but retained its primitive carnivorous dentition. Another South American family, the Borhyænidæ, which were probably also derived from arboreal ancestors, early succeeded in developing into a terrestrial and predatory line which closely paralleled the carnivorous marsupials of Australia and some of the earlier carnivorous placentals of North America, but were finally crowded out, about the middle of the Tertiary period, by the invasion of placental carnivores. According to Matthew (1916), the primitive Upper Cretaceous marsupials probably had a wide distribution in the northern continents which formed their original center of dispersal. After the ancestors of the Australian marsupials had reached that continent, possibly in the early Tertiary period, the region became severed geographically from the rest of the world, and the higher placentals, which were evolving in the northern land masses, were prevented from invading the Australian region. The marsupial stock was therefore free to branch out in many directions and take advantage of the varied environments, in that continent, without suffering severe competition from the more advanced and progressive placentals.

## *SUBORDER* POLYPROTODONTIA

Although little is known of their early history, the living Australian polyprotodonts exhibit a wide adaptive radiation in the dentition. The small Dasyuridæ, in common with the existing Didelphidæ and with the Upper Cretaceous *Eodelphis*, retain simple triangular upper molars and tuberculo-sectorial lower molars. The triangular spaces between the upper molars receive the trigonids of the lower teeth, while the "protocones," or internal cusps, of the upper molars fit into the basin of the talonids after the manner seen in *Eodelphis*. From this insectivorous-carnivorous starting-point is developed a specialized carnivorous adaptation culminating in *Thylacinus* and *Sarcophilus*, in which the posterointernal side of the upper molars becomes developed into a large shearing blade directed more antero-

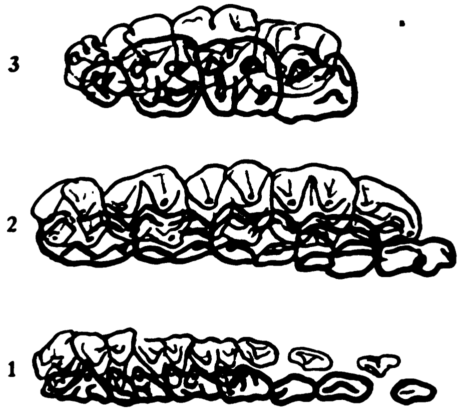

FIG. 39. OCCLUSAL RELATIONS OF UPPER AND LOWER CHEEK TEETH OF MARSUPIALS (COMPARE WITH PLATES 2, 4)

1.—*Metachirus* (a small opossum), with tritubercular upper, and tuberculo-sectorial lower, molars. The trigonds of the lower teeth fit into the interdental spaces of the upper; the central fossæ of the talonids receive the tips of the protocones of the uppers; and the hypoconid tips of the talonids fit into the central fossæ of the uppers. The oblique blades on the antero-external sides of the protoconids shear past the blades connecting the metacones with the metastyles; similarly, the transverse blades on the postero-external faces of the protoconids shear past those connecting the paracones with the parastyles. The hypoconids fit between the para- and metaconids. Cf. *fig. 47* (1).

2. *Phascolarctos* (Koala). The paraconids of the lower molars have been lost, and the remaining cusps have become more or less crescentic or V-shaped. The talonids have widened transversely, separating the para- and metacones; and the posterointernal parts of the upper molars have grown inward, filling up the interdental spaces and articulating with the talonids. Cf. *fig. 47* (2).

3. *Bettongia* (Rat-kangaroo). The quadrate upper and lower molars interlock, much as do human molars in normal occlusion. The lower molars have lost the paraconids, and consist chiefly of four main cusps arranged in two transverse pairs: protoconids, metaconids, hypoconids, and entoconids. Cf. *fig. 47* (3).

posteriorly than transversely, and shearing past the equally prominent blade formed by the enlarged para- and protoconids of the lower molars. At the same time, the talonids of the lower molars become smaller and with them the internal cusps or "protocones" of the upper molars, so that a perfected shearing action is finally developed. In South America, the Borhyænidæ go through a similar line of evolution, which is also followed even to much further lengths in two or three phyla of placental mammals. In this progressive carnivorous adaptation, the sides of the molar crowns become of predominant importance and the overlapping of the talonid upon the "protocone," or internal spur, of the molars is reduced and finally eliminated. This is the very opposite extreme from the line of evolution followed by omnivorous and herbivorous animals of all orders, in which the crowns, including especially the talonids of the lower molars, and not the sides and the interlocking parts, become dominant in function.

Primitive Australian polyprotodonts, probably of the family Dasyuridæ, also gave rise to an otherwise unknown line culminating in the highly aberrant *Myrmecobius*, or "banded anteater." In this genus the molars are more numerous (five or six on each side above and below) than in ordinary marsupials and are of very peculiar form, elongate anteroposteriorly and greatly compressed laterally. The lower molars are surmounted by three main cusps, so that they have a superficial resemblance to the triconodont type. The jaw and dentition of *Myrmecobius* have often been compared with those of Mesozoic mammals, and some have even expressed the opinion that this animal is a little-modified survivor from the Purbeck fauna. But Bensley rightly concluded that it is only an aberrantly modified dasyurid; that its molars, instead of being primitive, are peculiarly specialized; and that its apparent resemblances with the molars of Mesozoic mammals are largely secondary. In skull structure, *Myrmecobius* is plainly a specialized dasyurid, and it is noteworthy that the incisors, canines and premolars are much less aberrant than the molars; also, that the lower molars bite far to the inner side of the upper, and are directed sharply inward and upward, an anomalous adaptation to insectivorous diet (Plate 3).

In the straightness of the upper and lower tooth rows, which form nearly parallel lines, in the wide spacing between the teeth and in the flatness and length of the palate, the dentition of ***Myrmecobius*** parallels that of the armadillos.

Assuming the correctness of the conclusion, that ***Myrmecobius*** is merely a specialized dasyurid and not a close relative of the Mesozoic mammals with which it has been compared, it affords a conspicuous example of the unreliability of superficial resemblances between molar teeth of widely unrelated types.

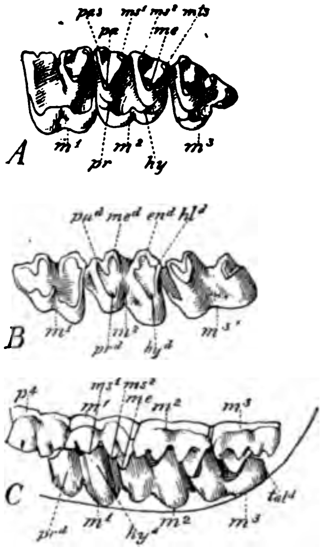

FIG. 40. UPPER AND LOWER MOLARS OF *Perameles*, REPRESENTING A SPECIALIZED DERIVATIVE OF THE TRITUBERCULAR MOLARS OF THE PRIMITIVE DASYURIDÆ AFTER OSBORN AND GREGORY

The molars are elongate anteroposteriorly and, consequently, divided into distinct anterior and posterior moieties. The enlarged V-shaped talonids fit between the widely separated V-shaped para- and metacones. The trigonid basins receive the hypocones, while the talonid basins receive the protocones.

The third offshoot of the primitive dasyurid stock is represented by the bandicoots, or Peramelidæ. These small hopping marsupials have narrow feet armed with strong claws with which they dig nests, burrows or holes in the ground. Apparently, more or less dirt must get mixed with their food, which is of the omnivorous-insectivorous kind, because their molar crowns have become hypsodont, or long-crowned, and have lost much of their primitive tritubercular heritage. The upper molar crowns are quadrangular in outline, the primitive triangle being modified through the outgrowth of the posteroexternal corner of the crown so as to produce a so-called hypocone. It is not certain whether this is a true hypocone derived as in placentals from the posterointernal cingulum, or whether it is an extension of the metaconule, but in either case it fills out the posterointernal contour of the crown and obliterates the triangular space between the adjacent upper molars. It thus fills the space formerly occupied by the trigonid of the lower molar and, consequently, the hypocone now articulates directly with the basin or fossa of the trigonid. The V-shaped para- and metacones of *Perameles* articulate between the trigonids and the talonids of the lower molars, while the "protocones" articulate with the basins of the talonids. Each lower molar consists of two narrow Vs, the higher anterior V formed by the trigonid, the lower posterior V formed by the talonid. These two Vs are well separated because of the inward position of the para- and metacones of the upper teeth. Conversely the prominent V-shaped talonid wedges in between and widely separates the para- and metacones of the upper teeth. Both the upper and the lower molars are wider anteroposteriorly than those of primitive tritubercular dentition. Thus, the pattern of the molar teeth of *Perameles* (derived according to the evidence of its skeletal structure from primitive tritubercular dasyurids) parallels similar adaptation among various other families of marsupials and placentals, and tends to confirm my view that the separation of the para- and metacones of the upper molars is correlated with the transverse widening of the talonids of the lower teeth, which push in between the lingual slopes of the para- and metacones. The upper molars of *Perameles* retain the primitive external cusps or styles which here, as in other cases, do not articulate with any part of the lower teeth but are abraded by the food which they assist in holding and pressing against the lower molars. The para- and metacones have grown so far inward that they have obliterated the proto- and metaconules, a process which may be observed in various other phyla of mammals.

Thus, the Peramelidæ afford an instructive example of incipient adaptation towards a grinding type of molars, and Bensley regarded their molar patterns as structurally intermediate between the primitive dasyurid and the primitive diprotodont molar types.

Another line of adaptation which has been derived from the primitive dasyurid is that of the "marsupial mole," *Notoryctes*. At first sight this animal appears to have almost pure tritubercular lower molars, which one might wish to derive from the primitive tritubercular lower molars of the Jurassic mammals, as *Dryolestes*, but a study of the skull and skeleton indicates that *Notoryctes* is a specialized derivative of the primitive dasyurids; and, therefore, the total lack of talonids in the lower molars, and the extremely simple tritubercular pattern of both the upper and lower molars, is probably in part secondary, as it is in similar cases among the placental insectivores. It seems very likely that the high apex of the upper-molar crowns is really the paracone, homologous with the single tips of the premolars and with the tips of the molars of *Peralestes*, and that the two large external cusps, commonly called the para- and metacones, are really the para- and metastyles, the real protocone being represented by the so-called internal cingulum (Pl. 3). An analogous condition is finally attained among placental insectivores of the zalambdodont or erinaceid group.

## *SUBORDER* DIPROTODONTIA

The Australian diprotodonts, in spite of their wide external differences in form, constitute a fairly compact group united by many peculiar common characters in the skull, limbs, brain, reproductive organs, etc. Bensley, following the suggestions of Huxley and Dollo, has shown very fully that the diprotodonts represent an evolutionary advance upon the primitive polyprotodonts. With regard to the dentition there is a considerable structural hiatus between these two groups, so that, if it were not for the strong evidence afforded by the rest of the anatomy, it would be unsafe to assume the derivation of the diprotodont molars from the primitive dasyurid type. But this evidence is so strong that there can be little doubt of such derivation of the molar patterns.

The more primitive molar patterns are preserved by some of the omnivorous-herbivorous phalangers,[13] in which the upper molar crown consists chiefly of four obtuse Vs arranged in two parallel rows and facing outward, with their apices directed inward. These apices are named protocone, paracone, metacone and hypocone. The external cingulum cusps are greatly reduced or absent. In the lower molars the trigonid and talonid, although considerably disguised, may still be recognized and consist of (a) two external Vs, representing the protoconid and hypoconid, and (b) two internal loops with the concavity directed outward, representing the metaconid and the entoconid, the paraconid being reduced or absent. This relatively primitive pattern is adapted for a combination of cutting, breaking, and grinding. The outgrowth of a hypocone having greatly reduced the spaces between the upper molars, the overlapping relations with the lower molars are correspondingly emphasized.

From this comparatively central type, Bensley derived, *first*, that of the koala (*Phascolarctos*) by the further emphasis of the V-shaped or crescentic character of the four main cusps, so that both the upper and lower molars bear four distinct Vs, or crescents, facing outward in the upper and inward in the lower molars. This crescent-shaped pattern has often been evolved among the placentals in adaptation to leaf-eating habits. The *second* line of derivation from the primitive diprotodont type leads to the molars of the kangaroos and their allies, in which the summits of the opposite cusps have been linked by prominent cross-crests developed on the slopes of the four main cusps, so that they produce a tapiroid or bilophodont type of molar. The talonid, as in all such "lophodont" types, has become greatly developed. This bilophodont pattern is paralleled not only in the tapirs and various other ungulates, but also in the monkeys of the Old World.

Perhaps the most specialized derivative of the primitive diprotodont pattern is seen in *Phascolomys*, with its beaver-like skull and dental apparatus. There is a single pair of gnawing incisors growing from persistent pulps in both the upper and lower jaws, followed by a wide diastema. The cheek teeth are hypsodont, consisting of two V-shaped columns. Many analogies with rodents are evident, but the marsupial nature of the animal is revealed not only by the brain,

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[13] See *Plate* 4.

reproductive organs, etc., but by the underlying characters of the skull and lower jaw, a long list of which agrees with those of less specialized diprotodonts.

In spite of the highly specialized dentition, *Phascolomys* and its allies are doubtless related to the koala (*Phascolarctos*), and their

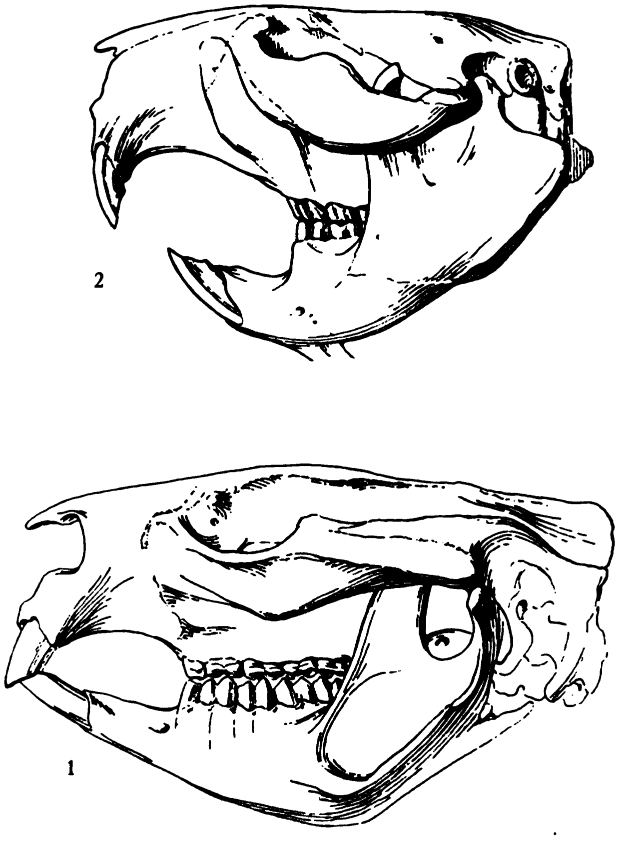

FIG. 41. SIMILAR ADAPTATIONS FOR GNAWING AND GRINDING WOODY TISSUE IN (1) THE WOMBAT (*Phascolomys*), A DIPROTODONT MARSUPIAL, AND (2) THE BEAVER (*Castor*), A RODENT PLACENTAL

The side view shows well the enlarged median pair of incisors in both upper and lower jaws, the long diastema behind them, and the long-crowned cheek teeth.

In spite of its rodent-like appearance, the skull of *Phascolomys* preserves much of its "heritage" of primitive marsupial characters, such as the strongly inflected angles of the mandible.

columnar molar teeth have probably been derived from the crescent bearing molars of the koala.

The case of *Phascolomys* is highly instructive. If we were dependent solely upon a comparison of its dentition with that of other known mammals, we could hardly infer either its real affinities or the evolutionary history of its dentition. By a study of the rest of its anatomy, however, in comparison with that of other marsupials, we determine its real relationships; and, by analogy with numerous well-established cases among the placentals, we find that the assumption of a rodent-like dentition, or of the hypsodont condition of the molars, rapidly effaces the primitive tritubercular heritage.

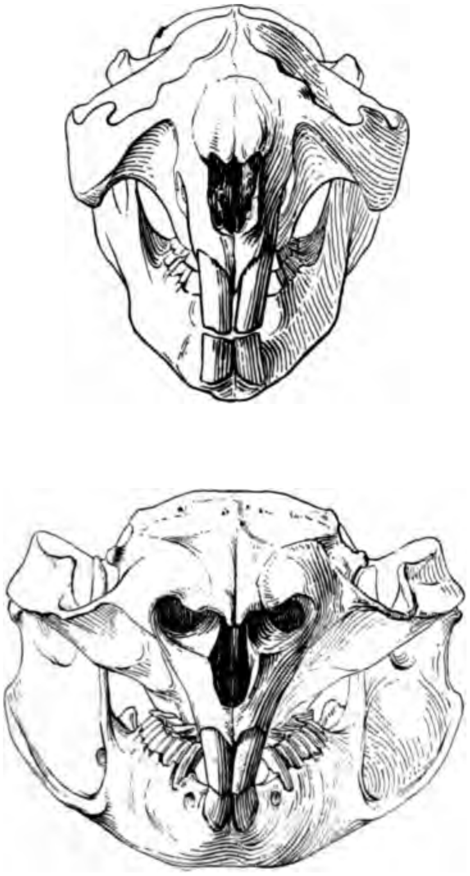

FIG. 42. FRONT VIEW OF SKULLS ILLUSTRATED IN FIGURE 41

## VII. SUMMARY AND CONCLUSIONS FOR PART I

Owing to the well-known "imperfection of the palæontological record," and to the vast chronological extent of vertebrate evolution which must be reckoned at least in tens of millions of years, the known stages of ascent are seldom in the direct relation of ancestor and descendant. Nevertheless, the broader features of the evolution of the dentition, leading eventually toward the mammalian and human types, appear to be well established.

In the earliest known stage, represented by the ostracoderms of the Upper Silurian and Devonian, the food was possibly engulfed by the capacious oral hood, or drawn in by the pumping action of the nascent branchial apparatus; but neither teeth, cartilaginous jaws, nor gill arches, had yet been evolved. These elements were first differentiated in the primitive sharks of Silurian and Devonian ages, the primary jaws (palato-quadrate and Meckel's cartilage) being merely enlarged and further modified members of the series of branchial cartilages, operated by muscles which are serially homologous with those of the branchial arches and provided with teeth derived from the infolding of the dentigerous skin around the borders of the mouth. True bony tissue had not yet been developed, but the endoskeleton was strengthened by calcific deposits in the cartilage. These primitive vertebrates were active predatory fishes of immense evolutionary potentialities, since they embody the structural ground plan of all the higher classes.

The next stage of ascent is illustrated in the primitive ganoid fishes of the Devonian age. In these the primary, or cartilaginous, jaws had become ensheathed in bony skin-plates. The teeth are now confined to the margins of the jaws and the roof of the mouth, instead of covering the whole body, as in sharks. The skin on the head gives rise to the external or dermo-cranium; and that on the body to the scales and dermal rays. True bone cells have thus invaded the skin and also extended to the cartilaginous endoskeleton, which they finally replace. Of these primitive ganoids one line, known as the Actinopterygii, becomes more and more highly ichthyized, or adapted for typical fish-like habits, and thus removes itself from the line of human ascent.

The second line, the Dipnoi, are less successful as typical fishes, but develop lungs which supplement the gills in oxygenating the blood. This group, however, is very early eliminated from the main line through the overspecialization of the dentition, which takes the form of fan-like clusters of denticles on the roof of the mouth and on the inner sides of the lower jaw. A related group, the Crossopterygii, share with the dipnoans the possession of lungs, which were naturally prerequisite for ancestors of the air-breathing tetrapods, but they avoid excessive specializations of the dentition, and, preserving their primitive predatory habits, they retained simple, unfused, teeth on the margins and inner sides of the jaws and on the roof of the mouth. Their teeth have elaborately infolded bases and are essentially identical in construction with the labyrinthodont teeth of the earliest four-footed vertebrates. Perhaps this infolding of the bases of the teeth served to strengthen the hold of the teeth upon the tough, bony, skin which bore them. A similar adaptation may be seen in the existing garpike, *Lepidosteus*. The crossopterygians also possess the right kind of pectoral and pelvic paddles to give rise to the paired limbs of the primitive tetrapods.

The greatest advances in evolution have always accompanied revolutionary changes in habits and the passage from one life zone to another. The emergence of the primitive tetrapods from the stem of the crossopterygians involved the most profound alterations in the locomotor apparatus, since the adventurous pioneers had to sacrifice the hard won adaptations for a fish-like mode of life, and to learn to support the entire weight of the body in a new medium which gave no aid through its buoyant properties. But, while the changes in locomotor and respiratory apparatus were truly revolutionary, the organs of ingestion and digestion preserved much of their piscine heritage.

As we pass from lower to higher vertebrates there is a steady reduction in the number of different parts, sometimes accompanied by the multiplication of single parts. So, too, in the passage from the crossopterygian to the tetrapod, there is a marked reduction in the number of bony plates covering the skull and lower jaws, the former losing the opercular series and the latter losing many of the plates on the under side, especially the gular and infradentary series.

The earliest tetrapods still went through a fish-like or tadpole stage of development, which has been retained in modernized amphibians. The latter early removed themselves from the direct line of human ascent by becoming secondarily adapted for living in the water, even in the adult stage and after the development of complete limbs. In these forms, the head becomes broad and depressed through the lateral spreading of the jaws and the failure of the middle part of the skull to increase in vertical depth. At the same time, the primitive tripartite occipital condyle loses its medial portion and becomes confined to the exoccipital bones. The palate, at first closed-over in the midline, opens out and the epiphyses of the limb-bones fail to ossify.

In the primitive reptiles, on the other hand, which were the ancestors of all the higher types of vertebrates, the tadpole stage was early eliminated, the adaptations for quadrupedal progression on land were progressively developed, and the easy descent to secondary aquatic habits, which has tempted many lines away from the upward path, was avoided. The skull, as a whole, became compressed rather than flattened, the brain-case and upper and lower jaws being vertically deepened. The labyrinthodont pattern of the bases of the teeth was gradually lost as the teeth became implanted in distinct sockets.

In the stem reptiles (Cotylosauria) the occipital condyle retains its primitive centrum-like character, and the primitive roofing bones on the occiput and temporal region are preserved intact. Most of the better known cotylosaurs are already too specialized in dentition to be directly ancestral to the higher reptiles, which must have been derived from primitive insectivorous members of the order, perhaps allied with the Captorhinids. The various lines leading to modern reptiles diverged from the primitive stock and from their remote relatives, the mammal-like reptiles, at an exceedingly early period, certainly not later than the Lower Permian. In so doing, they lost many primitive reptilian characters, and acquired new specializations which have often deceived those who expect to find in modern reptiles the clues to the early history of the human dentition.

The earliest stages of the mammal-like series of reptiles are represented in the smaller and less specialized pelycosaurs, or Theromorpha, of the Upper Carboniferous and Lower Permian of North America. In these the temporal region is perforated by the lateral temporal fenestra, lying beneath the junction of the postorbital and squamosal bones and above the jugal. This opening was apparently developed in connection with the activity of the muscles of mastication, the bone being strengthened and reinforced around the borders of insertion of the temporal muscle and weakened or removed in the middle of this area. The effectiveness of such an arrangement is seen by opening and closing the jaws of the modern *Sphenodon;* the bony strips that remain around the lateral temporal fenestræ afford adequate supports for the temporal muscles, while the openings permit the free expansion and contraction of these muscles. In the pelycosaurs, the stout bar of bone below the lateral temporal fenestra, composed of branches of the jugal and squamosal, is the forerunner of the zygomatic arch of mammals.

In the true mammal-like reptiles (Therapsida), at present known only from the Permian of South Africa and Russia, and from the Triassic of South Africa, we observe a great advance toward the mammalian grade of organization involving especially the following changes: (1) a progressive improvement in the respiratory system, as indicated by the final development of a sub-mammalian type of palate, and by the differentiation of the ribs into dorsal and lumbar regions; (2) equal improvement in the locomotor apparatus, pointing towards mammalian conditions, and (3) a progressive evolution of the dentition, beginning with the compressed, simple, recurved teeth of the gorgonopsians and culminating in the diverse and almost mammal-like dentition of the cynodonts. In the Therapsid series, the multiple succession of teeth, characteristic of later reptiles, is not found, as there are but two sets, corresponding to the deciduous and permanent series of mammals. The incisors, canines, and premolars, were replaced by permanent successors, but the molars, although apparently never replaced, are serially homologous with the deciduous series, or exostichos. Replacement was vertical, as in mammals, the permanent teeth pushing out their deciduous predecessors from below, but not becoming intercalated between them as in recent reptiles.

In this group of mammal-like reptiles we find, foreshadowed, many of the fundamental inter-relations of the upper and lower teeth that are preserved in primitive mammals: thus, the upper set bite outside of the lower set and. at least in the more advanced types each lower tooth articulates with two uppers. In the primitive cynodonts the cheek teeth are compressed and serrate, remotely suggesting the triconodont type, but differing in that each tooth is supported by only one root. In the nearly related *Diademodon* and its allies, the upper cheek teeth become widened transversely through the inward growth of the basal portion of the crown and root. At the same time the crowns of the lower molars exhibit a tendency to be divided into an anterior moiety, foreshadowing the trigonid of mammals, and a posterior moiety, possibly homologous with the talonid. Thus, in this very early stage, the upper and lower teeth are very unlike each other in form. Nevertheless, it is probable that *Diademodon* and its allies were not directly ancestral to any of the mammals, as their dentition does not appear to lead to any of the later types.

All the cynodonts are very progressive toward mammalian conditions in the construction of the lower jaw, since they have a mammal-like dentary with a wide ascending ramus, although they had not yet established a secondary contact between the dentary and squamosal,[14] while the posterior jaw elements (quadrate, articular, etc.) still functioned for the support of the jaw and for the attachment of the reptilian pterygoid muscles. They were also connected with the auditory apparatus, since the stapes is known to have been in contact with the quadrate, while the tympanic membrane was probably stretched upon the posteriorly forked angular bone (Watson, Palmer). The inner side of the dentary was deeply grooved for the reception of the primary lower jaw, consisting chiefly of the articular bone. The main jaw muscles, as shown by the form of the temporal fossa, and by the shape of the dentary bone and of the zygomatic arch, were of submammalian type. The zygomatic arch differed from that of mammals chiefly in retaining the primitive postorbital bone at its anterosuperior end. Some of the more primitive cynodonts, such as *Ictidopsis* (fig. 9), may have been closely related to the direct ancestors of the Protodonta and Triconodonta of the mammals. *Pachygenelus*, which is possibly related to *Diademodon*, affords several characters which must be looked for in the ancestors of the mammalian order of Multituberculata.

The fragmentary paleontological record does not reveal the transitional stages between the mammals and the mammal-like reptiles.

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[14] See the foot-note on page 18.

and the wide differentiation of the dentition in the few known mammals of the Upper Triassic indicates that the protodonts and the multituberculates were derived from different members of the cynodont reptiles. The protodonts emphasize the characters foreshadowed in the cynodonts with compressed teeth, but differ in the subdivision of the single fang of the cheek teeth into two distinct roots, at least in the molars. The incisors and canines of these animals retain much of their cynodont character and so does the whole dentary bone. Now, however, a secondary contact has apparently been established between the dentary and squamosal, since there are indications of a condylar process on the dentary.

The contemporary multituberculates, on the other hand, had already attained a high degree of specialization, since the lower molars had become "basin-shaped" (*Microlestes*), possibly through the upgrowth of the internal cingulum parallel to the primitive row of low cusps on the buccal side of the tooth. Apparently the posterior premolars had already become enlarged and grooved (*Microlestes rhæticus*). Although the front teeth of *Microlestes* remain unknown, they were probably not dissimilar to those of the later multituberculates, and were thus already enlarged, procumbent, and separated from the cheek teeth by a diastema.

About this time (Upper Triassic), or perhaps somewhat later, the order Trituberculata may already have been differentiated from primitive cynodonts, as it appears to be represented by an imperfect lower jaw (*Karoomys*) from the summit of the Karoo series in South Africa.

In the fauna of the Stonesfield Slate (Lower Jurassic of Great Britain) we find three very distinct orders of mammals, the *first* type of dentition including the primitive triconodonts, *Amphilestes* and *Phascolotherium*, in which each lower molar tooth had a compressed crown with a central apex, and two low cusps on its anterior and posterior slopes. The *second* type is represented by *Amphitherium*, the oldest and most primitive of the order Trituberculata, which exhibits the tritubercular lower molar in its archetypal form. In this genus the incisors, canines, and anterior premolars, are not dissimilar to those of the triconodonts. All the cheek teeth, likewise, are supported by two roots, and the number of post-canine teeth (eleven) is higher than in primitive placentals and marsupials of later ages. The molar teeth, however, are tritubercular instead of triconodont, and there is no evidence that, in this early stage (Lower Jurassic), the tritubercular pattern had been derived from the triconodont. On the contrary, it seems probable that the paraconid, metaconid, and entoconid, arose *in situ* on the slopes of the protoconid, and were not derived through the "rotation," or circumduction, of the lateral smaller cusps of a triconodont crown. Moreover, the jaw differs considerably from that of the triconodonts, inasmuch as it has a primitive uninflected angular process like that of the earliest placentals. Hence, this earliest known and most primitive trituberculate affords no support for the famous Cope-Osborn hypothesis of the origin of the tritubercular molar pattern, which was based on conditions observed in mammals of a later period. The *third* order (?Multituberculata) is obscurely represented in this fauna by the fragmentary jaw called *Stereognathus*.

From the Lower Jurassic of South Africa the genus *Tritylodon* is literally multituberculate, since each upper molar tooth bears three rows of cusps, but this form is very unlike any other member of the order to which it doubtfully belongs. It serves to emphasize the extremely early differentiation of the multituberculate type of teeth, and to indicate the wide separation of this group from the tritubercular and triconodont mammals.

In the Purbeck and Morrison faunas of Upper Jurassic age we find the same three orders, Multituberculata, Triconodonta, and Trituberculata, but in a more advanced stage of evolution. The multituberculates are now represented by the family Plagiaulacidæ, which are differentiated by the great development of the compressed, grooved, lower premolars and the small size of the lower molars.

At that time (Upper Jurassic) the normal triconodonts apparently reached the end of their evolutionary span. They exhibit, first, a reduction in the number of true molars, concomitant with an increase in the anteroposterior diameter of each molar and, secondly, the final stage in the production of a pure triconodont crown, with three equal cusps placed in a single fore-and-aft line. In certain aberrant triconodonts (*Menacodon*, *Tinodon*), the accessory cusps on the slopes of the protoconid are displaced toward the inner side of the crown, and it is possible that this line gave rise to the Spalacotheriidæ, in which the three primitive cusps are finally arranged in an equilateral triangle with the apex (protoconid) on the buccal side. It is also possible that, in some of these, the triad of cusps became asymmetrical, giving rise to the conditions, in *Leptocladus* (*Peramus*) and related genera, which have been referred to the Trituberculata. Here, in substance, is the whole evidence for the Cope-Osborn hypothesis of the origin of the trigonid through the rotation or circumduction of the accessory cusps toward the inner side of the protoconid. But, as we have seen, this would only account for the origin of the trigonid in certain genera which may well be pseudotrituberculates, and its force is lessened by the wide difference between the trituberculates and the triconodonts in the earlier Stonesfield Slate fauna. It was definitely recognized by Osborn, in 1888, that the tritubercular type may have been derived more than once and in different ways, but his opponents have forgotten this; and, by endeavoring to overthrow the "cusp-rotation" hypothesis, have imagined that they have undermined the whole theory of trituberculy.

The true Trituberculata of the Purbeck and Morrison faunas include a considerable variety of forms ranging from the more primitive *Amblotherium*, possibly a descendant of *Amphitherium*, with more normal tritubercular molars, to the stylodonts, which have high, styloid, molars with three sharp pricking cusps, and with an apparently secondary reduction of the talonid and more or less coalescence of the two main roots. In *Amblotherium* the incisors, canines, and premolars, remain very primitive, the latter having high compressed crowns, the apices of which are undoubtedly homologous with the protoconids of the molars. The lower jaw closely resembles that of *Amphitherium* and has a distinct angular process of primitive placental type.

There are several types of upper molars among the Purbeck trituberculates, of which the association with the lower molars has been more or less in doubt. A conclusion reached in this paper is that Owen was right in associating the upper teeth of the animal named *Peralestes* with a lower jaw having teeth resembling, in many respects, those of *Amblotherium*, *Achyrodon*, and *Peraspalax;* in other words, that *Peralestes* represents the upper dentition of the Purbeck successors of *Amphitherium*. In this genus, with its irregularly trigonal upper molars, the high apices of the molars are evidently homologous with those of the premolars. The upper molars of the stylodonts (*Kurtodon*, *Dryolestes*) are very narrow transversely and unlike those of *Peralestes* in appearance, yet they also have the high internal apex serially homologous with that of the premolars. A third type of upper molars, seen in *Diplocynodon*, is very aberrant. The internal apices are greatly expanded anteroposteriorly and connect with the external apices by low transverse crests. The homologies of the parts in this type of molar are doubtful. In the more normal trigonal upper molars of *Peralestes* and *Kurtodon*, there are interdental spaces for the reception of the trigonids of the lower teeth. On the inner side of the upper molars of *Dryolestes*, an internal cingulum at the base of the crown may foreshadow the lingual process which becomes highly developed in the molars of later types and gives rise to the so-called protocones.

In the typical Amphitheriidæ there are eleven post-canine teeth, which are short in the anteroposterior diameter. In typical later mammals (marsupials and placentals) the number of post-canine teeth is reduced to seven, but each molar has its anteroposterior diameter considerably increased through the great development of the talonid. Apparently, this process occurred in the later part of the Age of Reptiles, because the opossum-like marsupials of the Upper Cretaceous already have well developed talonids which receive the expanded protocones of the upper molars. The latter appear to be homologous with the internal extensions from the base of the crowns of the premolars, and likewise the para- and metacones have every appearance of serial homology with the tips of the premolars. The transverse expansion of the talonid of the lower molars presses the hypoconid against the lingual slope of the original apex of the crown and apparently conditions its division into two cusps, para- and metacone, which moved apart anteroposteriorly in proportion to the buccal growth of the hypoconid. The V-shaped proto- and metaconules are developed on the anterior and posterior slopes of the protocones, shear past the external faces of the trigonids, and fit into the V-shaped reëntrant valleys left between the trigonids for the fully developed talonids of the lower teeth.

The primitive marsupials of the Upper Cretaceous exhibited a considerable adaptive radiation in the dentition, ranging from tritubercular forms, adapted for a carnivorous diet, to animals in which the molar and premolar crowns were surmounted by massive, swollen and blunt cusps, possibly adapted for breaking and crushing the shells of invertebrates. The modern marsupials of Australia and South America are probably specialized descendants of the Upper Cretaceous "opossums," which were contemporaries of the last of the great reptiles.

The adaptive radiation of the dentition of marsupials was first fully worked out by Bensley, by applying the principles of dental evolution deduced from the better known palæontological record of the placentals. It also affords an illuminating example of the diverse inter-relations of the upper and lower teeth in carnivorous, omnivorous, and herbivorous, types of dentition. In the carnivorous types, the shearing blades on the sides of the upper and lower crowns become greatly emphasized and are shifted from a transverse to a more anteroposterior position. At the same time, the talonids of the lower molars and the so-called protocones of the upper molars become progressively reduced and the para- and metaconids approximated. In the herbivorous types, on the contrary, the talonids are progressively developed, overlapping broadly on the crowns of the upper teeth; by the development of crests on the crowns of the upper and lower molars various effective combinations for cutting and crushing are produced. The filling out of the quadrate contour of the crown, through the upgrowth of the hypocone, accompanies the anteroposterior elongation of the tooth, and, obliterating the interdental spaces, effects an overlapping of the hypocones of the upper molars into the basins of the trigonids of the lower molars.

Thus, the marsupials parallel the placentals in dental evolution as well as in body form and habits, and a clear understanding of the mechanical relations of the parts of their upper and lower teeth will be helpful to students of the human dentition.

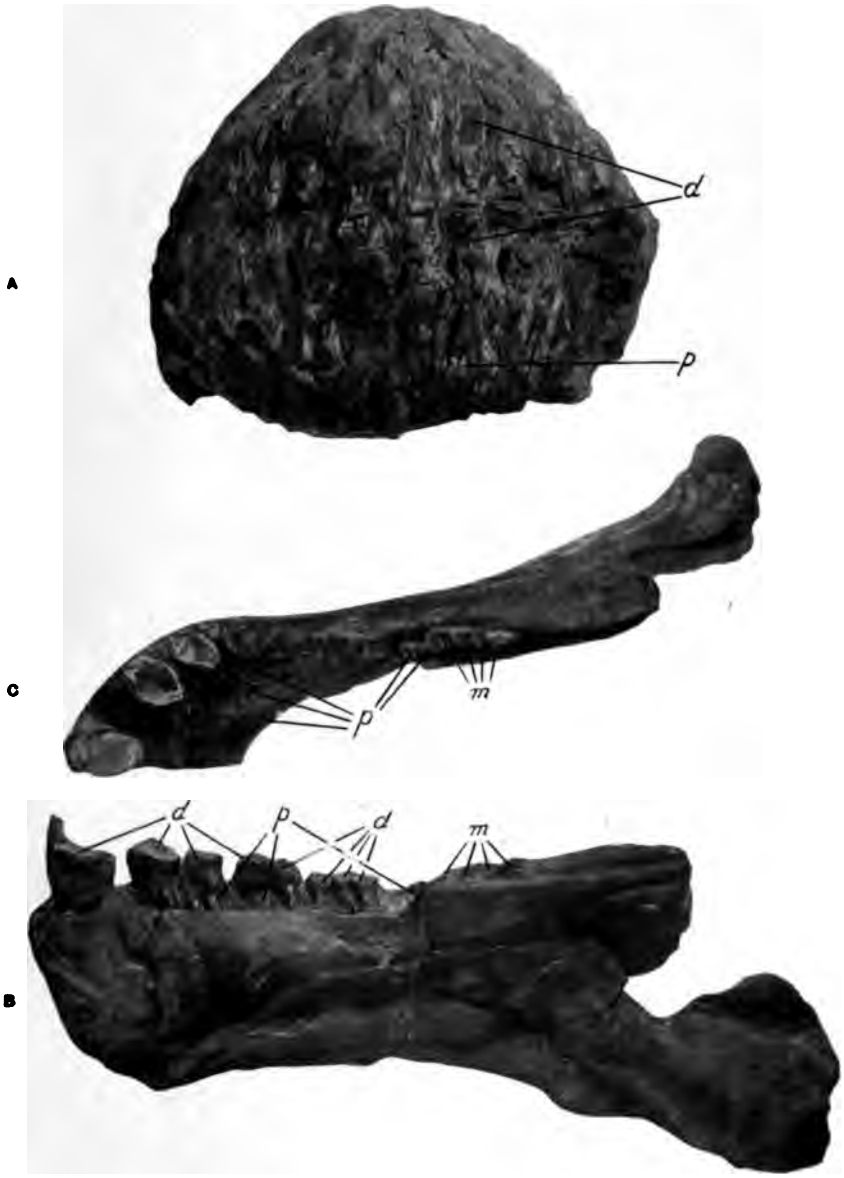
## PLATE 1

Upper and lower jaws of mammal-like reptiles from the Permian of South Africa, showing deciduous and permanent teeth.

A.—Front view of upper and lower jaws of *Taurops macrodon* Broom (Amer. Mus. Nat. Hist., no. 5,610), showing the deciduous upper and lower teeth (*d*) in occlusion, and, in the lower jaw, the unerupted permanent teeth (*p*) beneath the deciduous series.

B.—Right mandibular ramus of *Moscognathus whaitsi* Broom (Amer. Mus. Nat. Hist., no. 5,602), showing the deciduous series (*d*) in place and some of the permanent teeth (*p*) directly beneath them. The molars (*m*), in the back part of the jaw, belong to the exostichos, as do also the deciduous teeth, but apparently were never replaced.

C.—The same (B), seen from above.


A
d
p
C
p
m
B
d
p
d
m

# PLATE 2

Teeth of insectivorous and carnivorous polyprotodont marsupials, arranged to indicate the functional relations of the parts of the upper and lower molars (cf. *fig. 39*). Specimens in the American Museum of Natural History.

1.—*Metachirus*, × 2. 2.—*Phascogale*, × 6. 3.—*Dasyurus*, × 2. 4.—*Thylacinus* × 1. 5.—*Sarcophilus*, × 3/2.

In the most specialized carnivorous type (5), the shearing action of the anterior blades of the trigonids is greatly emphasized; while the talonids of the lower, and the "protocones" of the uppers, are correspondingly reduced.

In any dentition the upper teeth, in occlusion, face downward and the lower teeth upward. Therefore, their images, if projected onto the plane of the paper, would fall on opposite sides of it. As the paper is opaque and we wish, nevertheless, to represent both upper and lower teeth on one side of it, and at the same time to indicate the occlusal relations, we must present a direct image of, say, the left uppers in association with an inverted image of the left lowers. In practice we may obtain this effect, as in *plates 2–4*, by using a direct image of the left uppers in association with a direct image of the right lowers, since the crown view of the right lowers gives substantially an inverted image of that of the left.

1

2

3

4

5

## PLATE 3

Aberrant types of dentition among the polyprotodonts, derived apparently from the primitive dasyurid type. Specimens in the American Museum of Natural History.

1.—*Myrmecobius*, "banded anteater." The teeth are modified in connection with anteating habits. The molars have increased in number and, becoming elongate, have lost their primitive tritubercular character.

2.—*Notoryctes*, the "marsupial mole." The teeth are modified, perhaps, in connection with worm-eating habits. The "tritubercular" form of the teeth is probably secondary, and may have arisen, as in the last molars of *Dasyurus* and *Phascogale* (*plate 2, fig. 2, 3*), through the reduction of the talonids and the loss of the paracones.

2

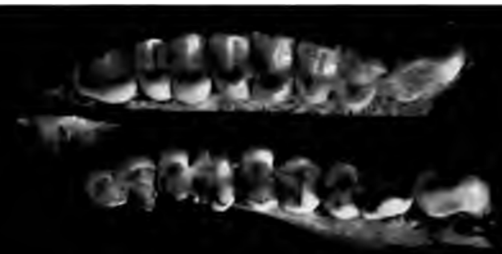
## PLATE 4

Teeth of omnivorous, herbivorous, and leaf eating diprotodont marsupials. Specimens in the American Museum of Natural History. See remarks under *plate 2.*

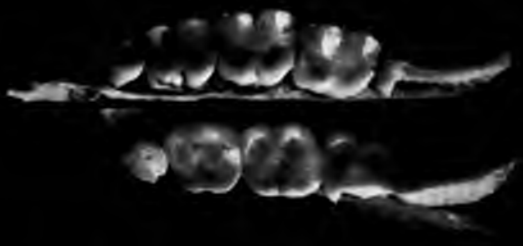
1.—*Phalangista*, phalanger, × 2. 2.—*Bettongia*, rat-kangaroo, × 3. 3.—*Macropus*, kangaroo, × 3/2. 4.—*Phascolarctos*, koala, × 3/2.

The upper molars are now elongate anteroposteriorly, and divided into subequal anterior and posterior moieties, each bearing either a transverse crest or a V. The interdental spaces are now filled out and the surfaces of the crowns articulate with each other the crests of the upper and lower alternating.

1



2



3

4

# PART II

## Stages of Ascent from the Paleocene Placental Mammals to the Lower Primates

# I. THE PRIMITIVE PLACENTAL MAMMALS OF THE PALEOCENE AND EOCENE EPOCHS, AND THE ORIGIN OF THEIR MOLAR TYPES

## Origin of the Placentals

During the millions of years of the Age of Reptiles, when the dinosaurs were the "lords of the swamps and forests," the mammals, so far as the imperfect palæontological records show, remained small and inconspicuous. The multituberculates went on specializing to their extinction in the Paleocene epoch, but were never a prominent element of the Mesozoic fauna. The triconodonts apparently became wholly extinct in the Upper Jurassic and were not ancestral to any of the Cretaceous or existing marsupials. Most of the diversely specialized Jurassic trituberculates probably also died out, but some of the more primitive ones, such as *Amphitherium*, may have given rise, first, to the marsupials of the Upper Cretaceous and, secondly, to the placentals of the Age of Mammals.

The great series of placental orders is conspicuously absent from the record of the Age of Reptiles as it stands. Possibly they may have been evolving somewhere in the uplands, out of reach of the swarming reptiles of the swamps, and thus may have left their remains in upland deposits which, during the many millions of years since Mesozoic time, have all been completely eroded away (W. D. Matthew).

At the close of the Cretaceous, or soon afterward, the dinosaurs disappear from the record and, after a relatively brief interval, archaic placental mammals of several orders appear in the Paleocene of western North America and Europe. As they are already typical placentals and sharply differentiated from the Upper Cretaceous marsupials, they must have been evolving in some palæontologically unknown region from which they migrated into the known localities, chiefly in New Mexico and Montana; unless, by a highly improbable evolutionary miracle, they suddenly sprang into being from the more primitive marsupials.

In this connection it is necessary to consider whether the placental orders constitute a natural group, derived from a single family, or from closely related families, of pre-placentals, or whether the placental grade of organization has arisen independently and at different times from widely different sources. Wortman, in 1904, expressed the view that some of the placental orders, especially the Carnivora, had been derived directly from Cretaceous Metatheria, and an inspection of his context indicates that he had in mind particularly the group here classed as polyprotodont marsupials. Gidley, in 1919, suggested that "there is some evidence that the primates, and probably some other orders as well, have been derived independently from different though probably more or less closely related *pre-mammalian*[2] ancestral groups." Gidley did not specify what the evidence was for this view, which is a fine expression of his favorite "polyphyletic theory" applied on a large scale. The general problem of the origin of the placentals will be fully discussed by Matthew in his forthcoming memoir on the Paleocene faunas; so that it need only be stated here, that the present writer thoroughly accords with him in the opinion that most of, or probably all, the orders of placental mammals have been derived from related families of pre-placental mammals, which were in turn remotely allied with the ancestors of the Upper Cretaceous marsupials. At least it is a fact that, as we trace backward the history of various placental orders during Tertiary times, in all cases in which the record is adequate, the earlier forms tend toward or actually exhibit the following characters:

(1) Dental formula of adults: $I\frac{3}{3}$ $C\frac{1}{1}$ $P\frac{4}{4}$ $M\frac{3}{3}$; deciduous dental formula: $Di\frac{3}{3}$ $Dc\frac{1}{1}$ $Dp\frac{4}{4}$.

(2) Upper molars narrow anteroposteriorly, evenly trigonal, with moderate development of the external cingula.

(3) Lower molars have a well developed talonid, bearing a distinct hypoconid and entoconid.

(4) Angle of mandible not inflected; postglenoid process of squamosal not modified into an auditory bulla.

(5) General construction and foramina of the skull essentially as in the *Deltatherium*[3] type and differing in numerous points from the primitive marsupial type.

(6) Skeleton extremely primitive, lacking the pronounced arboreal specializations of the primitive marsupials.

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[2] The italics are mine.—W. K. G.

[3] To be described by Matthew.

The placental mammals of the Paleocene formations of New Mexico belong to two successive faunas, the Puerco and Torrejon, which include, besides the last multituberculates, representatives of several archaic placental orders. The latter, for the most part, did not give rise to the modernized placental orders, but belonged to groups that died out in the Eocene. Nevertheless, these numerous archaic Paleocene mammals, such as the mesonychid creodonts, the condylarths, periptychids, tæniodonts and zalambdodont insectivores, are of immense value and importance, partly because they reveal the ways in which primitive dentitions with tritubercular upper molars evolved, on the one hand into the elaborate grinding mechanisms of herbivorous mammals and on the other hand into the efficient shearing and crushing dentitions of the creodonts; they also furnish invaluable collateral evidence on the origin of the dental construction of the later placental orders, such as the perissodactyls, artiodactyls, rodents and primates, which come into view either at the summit of the Paleocene (Tiffany formation) or at the base of the Lower Eocene. The Paleocene and Eocene placental mammals are represented in the American Museum of Natural History by great collections, numbering thousands of specimens, which deserve far more attention from odontologists than they have received, since they afford convincing proof of the enduring portion of the "Cope-Osborn theory"—that the diverse molar patterns of late mammals have been derived from the primitive tritubercular molar types of the Paleocene.

## ORIGIN OF THE "TRITUBERCULAR" UPPER MOLARS OF PRIMITIVE PLACENTALS

Of the many known Paleocene mammals, *Palæoryctes* (described by Matthew in 1913), at first sight looks most like a direct descendant of one of the Jurassic trituberculates. The lower molars have the high, pricking, type of trigonid and the low, small, talonid, while its upper molars also have a narrow trigonal form suggesting the Jurassic Stylodontidæ; but, as Matthew has shown, the upper and lower molar patterns of this animal are apparently homologous with those of more normal tritubercular dentitions, such as that of *Didelphodus* (*fig. 45*) of the Lower Eocene. It also appears probable that, as *Palæoryctes* represents the zalambdodont, or centetoid, division of the insectivores, it is already tending toward the secondarily simplified, V-shaped, upper molar of *Centetes* (*plate 5*, *figs. A–D*).

As may be seen by comparing the upper molars of *Palæoryctes* with its premolars, it is also highly probable that the para- and metacones of the molars are homologous with the tips of the premolars, and with the apices of the molars, of Jurassic trituberculates, while its protocones, or basal internal cusps, appear to be outgrowths from the base of the crown, homologous with that of the fourth premolar.

Fig. 43. Dentition of *Palæorcytes puercensis*. Upper Teeth, ×5; Lower Teeth, ×6 After Matthew

The molar teeth of this minute Paleocene insectivore resemble those of the Jurassic trituberculates in some respects. (Compare Part I, p. 143.)

Here, then, is an example of a fact observed in very many phyla of Paleocene and Eocene placental mammals, namely, that, *as we pass backward from the anterior premolars through the fourth premolar to the molars, the main tip of the premolar crown appears to be homologous with the paracone + metacone of the molars, while the internal basal spur of the premolars appears to be homologous with the so-called "protocones" of the molars.* It is highly unfortunate that this cardinal fact was long obscured by the unproved assumptions that the resemblance between $p^4$ and $m^1$ is largely secondary, and that the main tip of $p^4$ is homologous with the internal apex, or "protocone," of the first molar rather than with the paracone + metacone. This conclusion, now believed to be erroneous by nearly all investigators, arose from the circumstance that, according to the Cope-Osborn theory, the para- and metacones of the *upper*, as well as of the lower, molars had arisen, during the Mezozoic era, by the circumduction of the accessory cusps of an original triconodont tooth, although no upper molars were ever found in an intermediate stage of evolution.

So firmly was this hypothesis established in the literature, that the contradictory evidence afforded by the premolars of Eocene and later mammals was discarded, and a separate system of nomenclature was early invented by Scott for the cusps of the premolars, in which the name protocone was applied to the main apex of the upper premolars. Thus arose the anomaly that, in the lower premolar-molar series, the protoconids, or apices, of the trigonids were rightly regarded as homologous with the apices or protoconids of the premolars; so that, as we pass backward, the protoconids of the premolars and molars were arranged one behind the other in an anteroposterior series on the buccal side of the crowns; while in the upper dentition, according to the Cope-Osborn nomenclature, as we pass backward from the premolars to the molars, the protocone suddenly shifts from the buccal side of the premolars to the lingual side of the molars! This inconsistency was challenged on embryological grounds by Röse, Kukenthal, Leche, Taeker, Marett-Tims and M. F. Woodward; while Winge, as far back as 1882, had held that the anterior external cone, or paracone, above, and the protoconid below, represent the "reptilian cone" both in molars and premolars. This conclusion was also supported on palæontological and comparative anatomical grounds by Schlosser (1891) and Scott. Wortman (1903) and Gidley (1906) renewed the attack on this fundamental inconsistency of the Cope-

Osborn theory. Wortman emphasized the insufficiency of the evidence for the "cusp-rotation" hypothesis and clearly formulated the "premolar analogy theory," the main point of which is that the evolution of the molars during pre-Tertiary times probably followed the same general lines as the observed evolution of the premolars in many phyla during the Tertiary.

Osborn (1907, pp. 216–217) was greatly impressed by the evidence against the Cope-Osborn view that the so-called "protocone" of the molars of primitive placental mammals represents the original reptilian cone and, in collaboration with the present writer, gave an impartial review of the whole problem. But he brought to the support of the original identification of the "protocone," or "anterointernal" molar cusp of later mammals, with the original apex of the crown, his later observations on the superior molars of the Upper Jurassic trituberculate *Dryolestes*. In this animal the internal apices of the upper molars have the appearance of being homologous with the so-called "protocones" of Tertiary mammals and Osborn took it for granted that they were so. But, as shown in Part I of this paper, a comparison of the upper teeth of *Dryolestes* and of *Kurtodon*, with those of their contemporary, *Peralestes*, affords convincing evidence that, in all three genera, the protocones or apices of the upper molars are serially homologous with the apex of the last upper premolar. Now, in *Palæoryctes*, *Didelphodus*, and many other Paleocene and later mammals, the apex of the last upper premolars is apparently the serial homologue of the paracone + metacone of the molars, not of the so-called "protocone." Hence it appears that the apices of the *Dryolestes* upper molars and premolars are not homologous with the "protocones" of molars of later mammals but with the tips of their premolars, and with the para- and metacones.

On the inner side of these internal tips of the premolars and molars of *Dryolestes*, Osborn figured the beginnings of a basal cingulum (compare *plate 5E*). A similarly situated, but better developed, basal cingulum in later mammals may be traced from the premolars, where it gives rise to the so-called "deuterocone" or internal spur, backward to the "protocone" of the molars.

To return to *Palæoryctes:* (1) The lower molars of this animal have low and small talonids; and, in correlation with this fact, we find that the protocones or internal cusps of the upper molars, as well as the internal spur of the fourth premolar, are small and unexpanded, because the protocones of the upper molar fit into the basins of the talonids of the lower molars—and if one is small, the other must also be small. (2) The para- and metacones of *Palæoryctes* are small and closely appressed, one to the other, and located well toward the lingual side of the tooth. This is correlated with the small size, and especially with the narrow transverse diameter, of the hypoconid or posteroexternal cusp of the talonid, because, when this cusp is expanded transversely, as I have already shown, it pushes the para- and metacone apart, and tends to increase the anteroposterior diameter of the tooth. (3) The external cingulum and its cusps are well developed in *Palæoryctes*, and this is usually the case among mammals in which the para- and metacones are located well toward the lingual side of the crown. (4) The triangular interdental spaces of the upper molars are relatively large, because the primitive high trigonids fit solely into these interdental spaces and do not overlap on the crowns of the upper molars. All these characters, which recall the conditions in Jurassic trituberculates, may well be secondary in *Palæoryctes*, because this genus was evidently tending toward the modern zalambdodont insectivores, which are in many ways degenerate and specialized, and in which the para- and metacones become entirely confluent and widely displaced toward the lingual side of the crown, the internal ledges, or protocones, finally becoming vestigial, as shown by Leche, by Gidley (1906), and by Matthew (1913).

(5) All the elements of the *Palæorycytes* premolars and molars are evidently homologous with the more normal conditions retained in *Didelphodus*, which, together with the primitive Oxyclænidæ, are far more central types.

The vast time-interval between the Paleocene *Palæoryctes* and the Jurassic trituberculates warns us against deriving the former directly from the latter; and the frequency with which similar dental patterns are brought about by convergent evolution, in widely different orders of mammals, inspires further caution. Nevertheless, *Palæoryctes*, *Didelphodus*, *Apternodus*, and various other early placental mammals, in which the paracones are more lingually placed and the external cingulum cusps are strongly developed, aid us in recognizing the following fact, which has never before been clearly formulated, namely, *that the homologue of the trigonid of the lower molars is not the so-called "trigon" of the upper molars, formed by the tips of the proto-, para-, and metacones, but it is the triangle formed by the tips of the paracone, para-*

*style and metastyle.* These original trigons of the upper molars alternate with the interdental spaces, which are filled in occlusion by the trigonids of the lower articulating molars, the apex of the primary trigon being on the lingual side while that of the trigonid is on the buccal side.

The secondary trigon, long confused with the primary trigon, later arose through the lingual growth of the internal basal cingulum, correlated with the overlapping of the lower molar talonid upon the inner side of the upper tooth. The primary trigon lost its triangular character through the separation of its para- and metacones, correlated with the transverse widening of the talonids, and the consequent development of large hypoconids, which wedge between the para- and metacones.

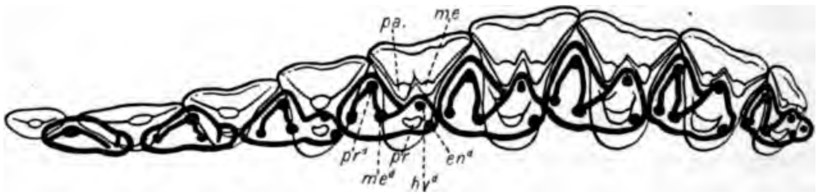

FIG. 44. DIAGRAM ILLUSTRATING (1) THE PROBABLE MODE OF ORIGIN OF THE MOLARIFORM PATTERNS OF PRIMITIVE PLACENTALS, AND (2) THE CORRELATED EVOLUTION OF UPPER AND LOWER TEETH

Successive stages are shown in passing from the simple anterior premolars, which have only the primary trigon, backward to the molars, in which the secondary trigon arises through the inward growth of the "protocones" and the division of the primitive apex into two cusps, the para- and the metacones. This hypothesis is based on indirect evidence and awaits direct palæontological confirmation, as the upper molars of the oldest known placental mammals of the Paleocene had already acquired the secondary trigon in the upper, and the expanded talonid of the lower, molars. *pr*, protocone; *pa*, paracone; *me*, metacone; $pr^d$, protoconid; $me^d$, metaconid; $hy^d$, hypoconid, $en^d$, entoconid.

In the majority of placentals the talonids, rapidly increased in transverse diameter. This not only caused the anteroposterior separation of the para- and metacones, but often tended to push them toward the buccal side of the crown, as in many carnivores and primates, where the para- and metacones finally lie on the buccal side of the crown, and the external cingulum, primitively forming a large part of the outer side of the crown, becomes reduced or obsolete. *By these stages the primary trigon is almost completely effaced and a secondary trigon, consisting of the proto-, para-, and metacones, stands in its place.*

If this has been a universal rule, as I think it has, then many phyla of placental mammals were well advanced toward this stage when they first become known in the Paleocene and Eocene, but only the final stages of the transition, namely, the further development of the talonid, the separation of the para- and metacones, and the reduction of the external cingulum cusps, are actually known. This would explain the failure to recognize the differences between the primary trigon and the secondary trigon, which has given rise to so much confusion in the nomenclature. Meanwhile, the primary trigonids of the lower molars were often retained for the reason that they continued to wedge between successive upper molars, while a secondary or posterior trigonid, including the hypoconid, the crista obliqua, and the entoconid, was developed on the crown of the talonid.

*The obliteration of the primary trigon, and the development of a secondary trigon and a secondary trigonid, is the opposite specialization from that in the zalambdodont insectivores, in which the para- and metacones are displaced toward the lingual side, while the talonids become reduced and the outer or stylar cusps become very conspicuous* (see Matthew, 1913). Possibly, *Apternodus* Matthew of the Lower Oligocene, and the existing *Chrysochloris*, represent a stage in which the primary trigon has been retained, while the secondary trigon has never progressed beyond the first stage, through the budding off of the basal internal cusp of the upper molars to give rise to the low protocones. (*Plate 5, figs. F* and *G.*)

## ORIGIN OF OMNIVOROUS AND HERBIVOROUS TYPES OF MOLARS IN THE EARLY PLACENTALS

Up to this time we have been dealing, in the placental mammals, with teeth that were trigonal in form, whether exhibiting the primary trigon or the secondary trigon, or a combination of the two. In all such teeth, the interdental spaces between the upper molars are conspicuous and receive the whole of the trigonids of the lower teeth. But, with the great expansion of the talonid, which in many lines had begun even before the Paleocene, there was a corresponding widening anteroposteriorly of the protocone; and, as we pass upward toward omnivorous and herbivorous types of later ages, there is a steady increase in the anteroposterior diameter of the whole tooth, correlated not only with the expansion of the protocones and talonids but also with the separation of the para- and metacones.

*While the progressive overlapping of the talonids conditioned the development of the protocones of the upper molars, the later expansion of*

***the trigonids, overlapping the posterointernal sides of the upper molars, conditioned the development of the hypocones, or posterointernal cusps.*** A similar development in the dentition of the marsupials has been described in Part I of this work. The typical hypocones of placental

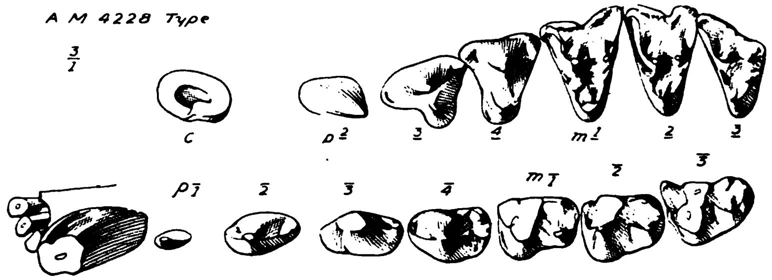

Fig. 45. Left Upper and Lower Teeth of a Primitive Insectivore, *Didelphodus absarokæ*, from the Lower Eocene of Wyoming. ×3/1
After Matthew. (Compare *fig.* 47)

The sharp blades of the trigonids of the lower molars shear past the blades of the uppers. The narrowness of the protocones, and the nearly central position of the para- and metacones, are correlated with the transverse narrowness of the talonids. See *fig.* 47, *A*.

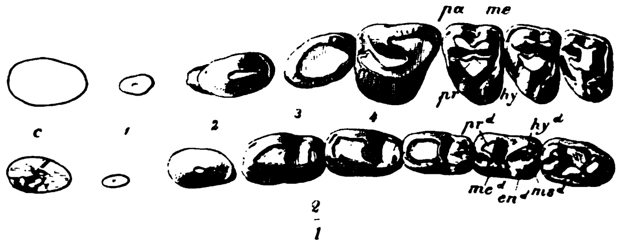

Fig. 46. Left Upper and Lower Cheek-Teeth of *Haploconus lineatus*, a Primitive Placental Mammal with Tritubercular Upper Molars, from the Paleocene of New Mexico. ×2. After Osborn

By the beginning of the Paleocene, the tritubercular molar type had been fully attained in most phyla of placental mammals; and was already undergoing diverse modifications tending toward the highly specialized molar patterns of later ages. *pa*, paracone; *me*, metacone; *pr*, protocone; *hy*, hopocone; $pr^d$, protoconid; $me^d$, metaconid; $hy^d$, hypoconid; $en^d$, entoconid; $ms^d$, hypoconulid (mesoconid).

mammals arose as upgrowths from the posterointernal cingulum of the upper molars, which overlapped into the basins of the trigonids of the lower molars. As the hypocones develop the interdental spaces between the upper molars gradually become smaller and are finally crowded out.

When this stage is attained, the trigonids no longer fit into the interdental spaces but they now articulate with the expanded surfaces of the upper molar crowns. The anteroexternal sides of the trigonids now shear past the expanded metaconules. The basins of the trigonids receive the hypocones of the upper molars, while the paraconids, if retained, very often articulate between the protocones and the hypocones. The posteroexternal slopes of the protoconids now shear past the anterior slopes of the protoconules, while the protoconids thus articulate between the paracone of one upper molar and the metacone of the next.

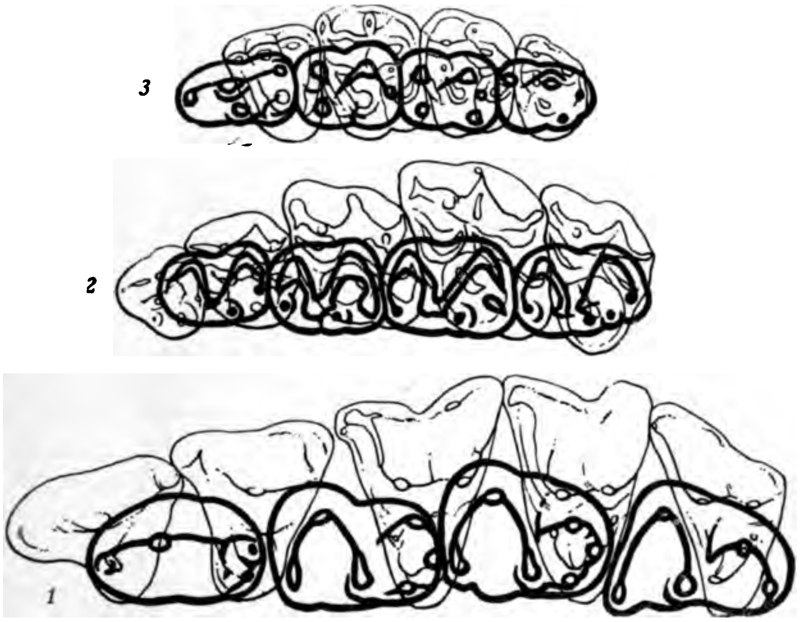

FIG. 47. OCCLUSAL RELATIONS OF THE UPPER AND LOWER CHEEK-TEETH IN EOCENE MAMMALS. (COMPARE *fig. 48*)

1.—***Didelphodus absarokæ***, a primitive insectivore with tuberculo-sectorial lower, and trigonal upper, molars. The interdental spaces are still widely open and the talonids are not expanded. ×6

2.—***Meniscotherium chamense***, an herbivorous mammal (Order Condylarthra) with relatively complex upper molar pattern. The paracone and metacone are V-shaped, and so is the protoconule; the metaconule bears an oblique straight crest; the hypocones are prominent, acuminate. The protocone is conical. In the lower molars the trigonid is V-shaped, with reduced paraconid, and the talonid-V is wide. Enlarged.

3.—***Phenacodus brachypternus***, a primitive condylarth with conical upper molar cusps and well developed hypocones. In the lower molars, the paraconid is absent and the principal cusps are arranged in two pairs which fit between corresponding pairs on the upper molars.

*Since the old shearing and interlocking relations have now been largely superseded through the anteroposterior spreading of the upper molars, new and diverse shearing adaptations are often developed by the elaboration of sharp crests on the surfaces of the crowns.* These higher stages are attained in various ways, such as (1) by the emphasis of one or the other slopes of the proto- and metaconules; (2) by the subsequent connection of these intermediate ridges with the four main cusps; (3) by the development of a large V or crescent on one or all of the cusps; (4) by the confluence of the para- and metacones into an ectoloph.

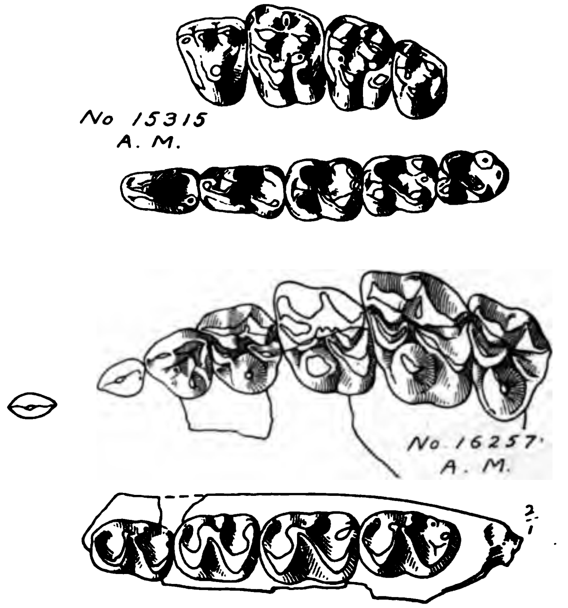

FIG. 48. LEFT UPPER AND LOWER MOLARS OF *Phenacodus brachypternus* AND *Meniscotherium chamense*. AFTER GRANGER

Given the four main cusps, protocone, paracone, metacone, and hypocone, and the two intermediate cusps, the proto- and the metaconule, there is a wide range of possibilities in the manner in which these may be connected one with the other to form effective shearing and crushing relations with the homologous elements of the lower teeth. In the great series of ungulate orders, we find remarkably diverse developments of these possibilities, which have been set forth by Osborn and others, and which afford diagnostic patterns of the molars in the multitudinous families of this group.

The underlying tritubercular pattern is obscured not only by these secondary complications, but is often more or less completely effaced as a result of the rapid vertical deepening of the crown and the further folding and twisting of its crests. This "hypsodont" transformation, which is very prevalent in the numerous families of ungulates and rodents, compensates for the rapid grinding down of the crown by silicious and woody material in the food.

## II. INTRODUCTION TO THE STUDY OF THE EVOLUTION OF THE TEETH IN THE PRIMATES. DEPENDENCE OF ODONTOLOGY UPON PALAEONTOLOGY AND TAXONOMY, OR CLASSIFICATION ACCORDING TO KINSHIP

The lines of evolution of the molar patterns described above have not been discovered through an exclusive examination of the dentition. They are rather a by-product of innumerable studies, by palæontologists and systematists, on the anatomy and classification of recent and fossil mammals. Even studies on the chronological succession, geographic distribution and centers of dispersal of animals, and upon the palæogeographic histories of the countries in which they are found, have had an indirect bearing upon our knowledge of the evolution of the teeth of mammals, since such investigations, supplementing the morphological and taxonomic data, have brought to light many cases where more or less similar dental patterns have been produced at different times, in different places, and among widely different stocks. Accordingly, modern palæontologists are cautious about basing phylogenetic or evolutionary hypotheses on the evidence of similarities in teeth alone, unless the dental patterns compared be either very complicated or exceptionally peculiar and characteristic. It was formerly thought, for example, that the Eocene creodonts of North America were more or less intermediate between the carnivorous marsupials and the typical placental carnivores, but it is now recognized that quite similar adaptations to the shearing of flesh were independently produced at different times and in different places in all three groups.

*It has not always been realized that, to be well-founded, theories of the evolution of the dentition must rest upon a broad palæontological and morphological base, and that the study of taxonomy, or classification* *according to phyletic relationships, is the very cornerstone of such a base.* For, without a full understanding of the taxonomic position and relationships of the organisms studied, it is easy to put too high a value upon random comparisons of structures in members of widely separated groups. *A considerable part of anatomical literature seems, indeed, to be filled with scattered comparisons of a few terminal and widely separated twigs on different boughs and stems of the vast phylogenetic tree of the vertebrates.* For example, the advocates of the concrescence theory, in its cruder form, point to the concrescence of teeth in the elasmobranchs in support of their view that mammalian molars have arisen through the concrescence of separate teeth, or of separate tooth germs, not realizing the tremendous taxonomic and chronological

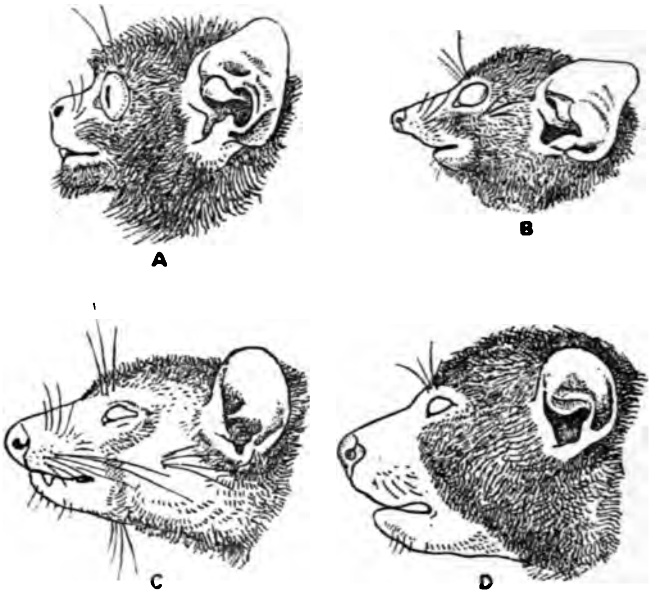

FIG. 49. HEADS OF *Tarsius* AND OF REPRESENTATIVE LEMUROIDS. × ¾. AFTER POCOCK. (DRAWN FROM SPIRIT SPECIMENS)

*A.—Tarsius.* Suborder Tarsioidea. Family Tarsiidæ. *B.—Hemigalago demidoffi.* Suborder Lemuroidea, Series Lorisiformes, Family Galagidæ. *C.—Chirogaleus major.* Suborder Lemuroidea, Series Lemuriformes, Family Lemuridæ, Sub-family Chirogaleinæ. *D.—Perodicticus.* Suborder Lemuroidea, Series Lorisiformes, Family Lorisidæ (Nycticebidæ).

gap between man and the elasmobranchs, or the fallacy of passing from one to the other without considering the intervening stages. Even at the present day there are those who point to chance cases of concrescence between adjacent teeth of modern mammals as evidence for the baseless hypothesis that mammalian molars originally arose in this manner millions of years ago in the prototherian ancestors of the mammals.

*In considering the evolution of the human dentition we must constantly take into account the taxonomic relations of man to other primates.* For the proper understanding of the subject it will naturally make a great difference whether man is an offshoot of the Old World series, whether he has been derived from some South American monkey, whether the human stem is remotely related to *Tarsius*, or is an entirely distinct family tracing its independent line back to the stem of the primates in pre-Tertiary times. It will therefore be worth while to summarize, briefly at this point, the history of the classification of the Primates in so far as it relates to the taxonomic position of man.

Even before the time of Linnæus various observers noted the marked structural similarities between man and the apes, which were especially evident in Tyson's classic studies on the anatomy of the chimpanzee (1699); but the doctrine of special creation had so firm a hold that it long inhibited recognition of the significance of such facts. One of the greatest discoveries of Linnæus was his clear recognition that man is anatomically a member of the class Mammalia and that among all living animals his nearest relatives are the apes and monkeys. Therefore Linnæus, in 1759, grouped them with man under the order Primates, which he placed, in his Systema Naturæ, at the head of the animal kingdom. The recognition of this cardinal taxonomic fact prepared the way for the subsequent discovery that man had evolved out of some primitive primate stock.

As anatomical and taxonomic research progressed, it became evident to the majority of investigators that man belonged among the Old World series of primates, and that the surviving representatives of the order may be distributed as follows:

Primates
- Suborder Lemuroidea
  - Lemurs of Madagascar
  - Lorises, galagos, etc., of Asia and Africa
  - *Tarsius* of Borneo and other Malayan islands
- Suborder Anthropoidea
  - Platyrrhinæ (New World monkeys)
    - Cebidæ: capuchins, howlers, etc.
    - Hapalidæ: marmosets
  - Catarrhinæ (Old World series)
    - Cercopithecidæ: monkeys of Asia and Africa
    - Simiidæ: anthropoid apes
    - Hominidæ: men

Recent researches by Pocock and others make it advisable to separate *Tarsius* and its allies from the lemurs, as a distinct suborder, Tarsioidea, combining features of the other two suborders. Wood-Jones, the prosector of the Zoological Society of London, will not admit that the lemurs are primates at all and regards man as a special branch from the stem of the Tarsioidea, thus removing him entirely from the suborder Anthropoidea. This proposed new alignment will be discussed below, and also more fully in other papers, but, for the purposes of the present article, the groups given above will be accepted as practically established through the long and world-wide process of research and criticism to which the problem of the relationship of man has been subjected.

## III. THE LEMUROID PRIMATES (EOCENE TO RECENT)

### Are the Lemurs True Primates or Pseudo-Primates?

Before taking up the palæontological history of the dentition of the Primates, it is necessary to consider briefly the relationships of the Lemuroidea to the remaining Primates and to other orders of mammals. Wood-Jones (1918, p. 26) is not willing to admit that the lemurs are true primates at all, and therefore ascribes all their resemblances to the primates to a retention of primitive arboreal characters and to convergent evolution. If this were true, it would render nugatory the subsequent comparisons of the dentition of recent and fossil lemurs with those of the higher primates.

In a recent memoir (1920) on the American Eocene lemurs I have discussed the relations of the lemuroids to the higher primates and have concluded that the evidence is all against their proposed separation under a distinct order. It is true that the method of placentation in typical lemurs, so far as known, is radically different from that of *Tarsius* and the higher primates, and that every one of the modern lemurs has in many respects become specialized away from the primitive primate conditions. But most investigators have recognized that in the totality of their organization even the existing lemurs are at least the nearest relatives of the primates among all the orders of mammals.

The suborder Lemuroidea embraces a very wide range of forms. The more primitive Eocene lemuroids retain a number of primitive mammalian characters, especially in the skull and dentition, while the later and more advanced forms closely parallel the higher primates, so that the systematic position of some of them was once in doubt, on account of the very progressive and monkey-like appearance of their cranium and face. But, as shown by Forsyth Major and others, (1) it is now well established that these monkey-like lemurs (*Archæolemur*, *Nesopithecus*) are true lemuroids and in no sense transitional to the higher primates, and that their resemblances to the monkeys are an expression of parallel or homoplastic evolution. Nevertheless, this fact in itself considerably strengthens the claims of the Lemuroidea as a whole to be considered as true primates, *because it has frequently been observed by palæontologists that parallelism is more complete and detailed in nearly related than in widely removed stocks.* (2) Some of the recent and fossil Lorisidæ (Nycticebidæ) closely parallel the tarsioids in skull, dentition and limbs, so that formerly I had difficulty in deciding what characters are due merely to parallelism and what may indicate a closer relationship. The resemblances between some of the galagos and *Tarsius* are so numerous and detailed that, even after parallelism has been well discounted, a substantial agreement in stem characters is surely indicated. (3) While some of the lemuroids appear to be remotely connected by numerous stem characters with the tarsioids, others, especially among the American Eocene forms, appear to be evolving toward the South American monkeys.

In brief, and without setting forth the full evidence in this place, it may be stated that *the right of the Lemuroidea to be included under the order of Primates seems much clearer at the present time than it was to Mivart and to Milne-Edwards.*

## ORIGIN OF THE PRIMATES

From the Paleocene formations of the west no undoubted primates are known, although very possibly *Indrodon*, of the family Mixodectidæ, a genus with primitive molars but somewhat specialized procumbent incisors, may be related more remotely to the Primates and more closely to the Menotyphla. The latter group is represented at the present day by the Tupaiidæ, or tree-shrews, and the Macroscelididæ, or jumping shrews. The recent Tupaiidæ are more or less lemur-like in general appearance as well as in many anatomical and osteological details, so that they are probably the nearest living relatives of the pre-Tertiary ancestors of the Primates. Their feet and limbs are less specialized for arboricolous habits, but seem to be of sub-Primate type.

A second Paleocene and Eocene family, having claims to be included in the order of Primates, is the Plesiadapidæ, which, in the Tiffany formation at the summit of the Paleocene, is represented by *Nothodectes* (Fig. 54), a genus with enlarged and shrew-like front teeth, and with molars recalling those of *Pelycodus* and other Eocene primates. The skeleton of *Nothodectes* shows many significant resemblances to the Tupaiid type, but is more primitive and at the same time recalls that of the Eocene lemuroids, especially the Notharctidæ. In the Lower Eocene of Europe a related genus, *Plesiadapis*, also has enlarged front teeth and primate-like molars, and is referred to the order Primates by Stehlin, the leading authority on the Eocene Primates of Europe. In 1910, I argued that the existing tree-shrews have preserved many intermediate conditions tending to connect the Primates

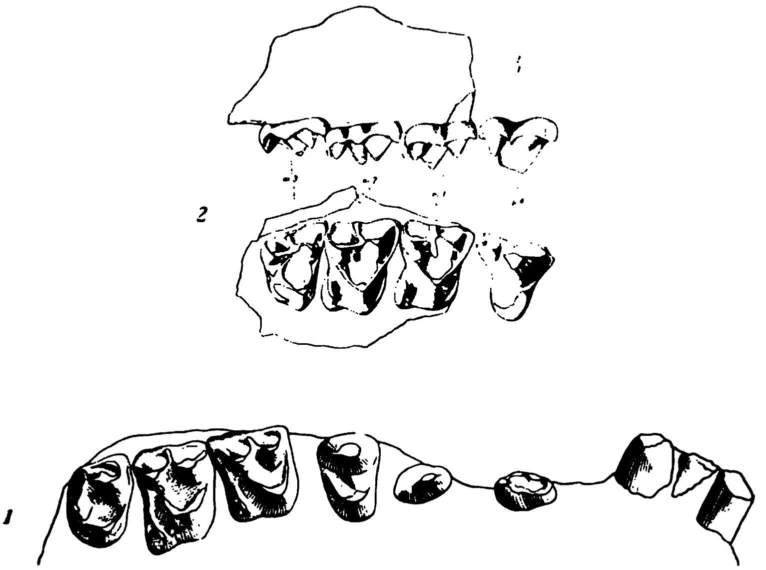

Fig. 50. Upper Teeth of Possible Relatives of the Existing Tree-Shrews, from the Paleocene of New Mexico. After Osborn

1.—*Indrodon malaris*. Amer. Mus., no. 3080. ×3. (See note on p. xiv )
2.—*Mixodectes* sp. Amer. Mus., no. 833. ×3.

Fig. 51. Upper Teeth of Existing Tree-Shrews. ×3

1.—*Tupaia.*
2.—*Ptilocercus.*

with unknown Mesozoic Insectivora of arboricolous habits. All recent evidence tends to confirm this view.

The American Eocene family of Hyopsodontidæ, which were formerly referred to the Primates and which resemble the Notharctidæ in many characters of the molars, have been removed from the order by Wortman; and were later shown, by Matthew, to belong with the

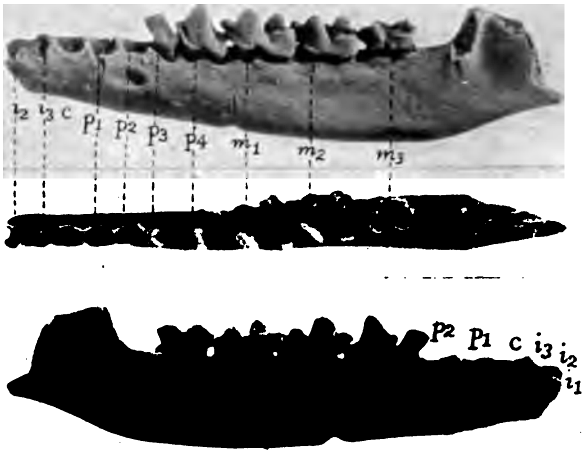

FIG. 52. LOWER JAW (LEFT SIDE) OF *Entomolestes grangeri*, A POSSIBLE RELATIVE OF THE TREE-SHREWS. AMER. MUS., NO. 11,485. MIDDLE EOCENE, WYOMING. ×6. AFTER MATTHEW

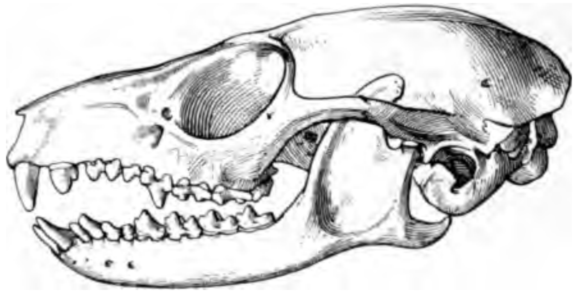

FIG. 53. SKULL AND MANDIBLE OF THE PEN-TAILED TREE-SHREW, *Ptilocercus lowii.* U. S. NAT. MUS., NO. 112,611. ×2

The skull and dentition present many points of resemblance to those of primitive primates.

Condylarthra, or primitive ungulates. Their resemblances to the Primates (*fig. 55*) afford a good example of the parallelism that is often developed in the dentition of animals that are shown by the construction of the limbs to belong in different but related orders.

FIG. 54. UPPER AND LOWER TEETH OF *Nothodectes gidleyi*, FROM THE TIFFANY FORMATION (SUMMIT OF PALEOCENE) OF COLORADO. ×3. AFTER MATTHEW. AMER. MUS., NOS. 17,171 (UPPER), 17,174 (LOWER)

An American representative of the extinct European family, Plesiadapidæ. As shown by the construction of the limbs, this animal is probably related to the tree-shrews and, more remotely, to the Primates.

## The Primitive Lemuroids (Notharctidæ) of the American Eocene

Thanks chiefly to the intensive work of American Museum explorations under Granger, we can follow the evolution of the dentition of the Notharctidæ through a long series of ascending forms. The oldest members, from the base of the Lower Eocene, are very small, the lower molar series measuring only 11–14 mm. in length. As we pass upward, the size gradually increases until, at the summit of the Middle Eocene, *Notharctus crassus* is an animal about as large as a howler monkey and its lower molars measure 20–23 mm. in length. (Cf. Plate 6.)

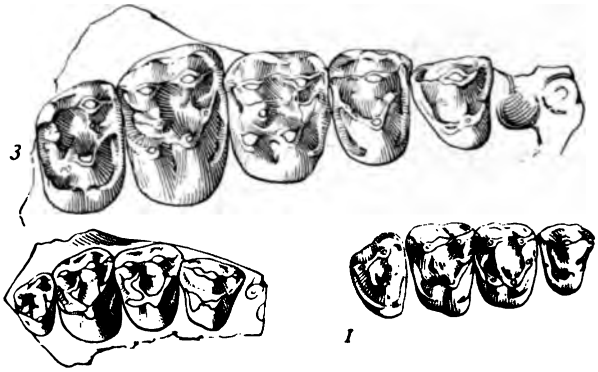

Fig. 55. Comparison of the Upper Molars of Primitive Primates (*1*) and Condylarths (*2*, *3*.)

*1.—Pelycodus trigonodus.* After Matthew. ×2. *2.—Haplomylus speirianus.* After Matthew. ×2. *3.—Hyopsodus mentalis.* After Matthew. × 10/3.

Similarly, among the Eocene tarsioid series, the older and more primitive members are very small. There is, in brief, strong evidence for the view that the stem primates were quite small animals, even smaller then the existing tree-shrews, and of primitive insectivorous habits. That they were also arboricolous is shown by the relatively high degree of adaptations for such habits exhibited in the skeleton of their descendants, the Eocene primates. The skull in the older Lower Eocene species of the Notharctidæ is known from fragments which indicate that the orbits were relatively a little larger, and the zygomatic arches and temporal crests less well developed, than in the later and larger species, especially *Notharctus crassus*. The skull of the Middle Eocene *Notharctus osborni* is shown in *fig. 56*.

The systematic position and relationships of the Notharctidæ are largely determined by the lemuroid characters of the skull and skeleton. The orbit, as in lemurs, was not separated from the temporal fossa by a bony partition but merely by a post-orbital process of the frontal, connected on the orbital rim with a similar upgrowing process of the malar. The whole construction of the skull closely resembles that of modern lemurs, with the important exception that the brain-case and the brain itself were much less expanded, and consequently more primitive and more like those of other Eocene mammals. Even the minute characters of the bony cochlea, the bony canals for the internal carotid and stapedial arteries, the construction of the auditory bullæ and surrounding parts, and the form of the auditory ossicles, were all of lemuroid type. The same is true of the characters of the backbone, pectoral and pelvic girdles, and the limbs. The Notharctidæ, so far as our evidence goes, were confined to the New World and may well have given rise to the New World monkeys, as suggested by Leidy and by Wortman. But they are also rather closely related to the Adapidæ of the Eocene of Europe and may even be placed in the same family with them. The dental formula of the Notharctidæ ($I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{4}{4}$ $M\frac{3}{3}$) lacks but one incisor, on each side

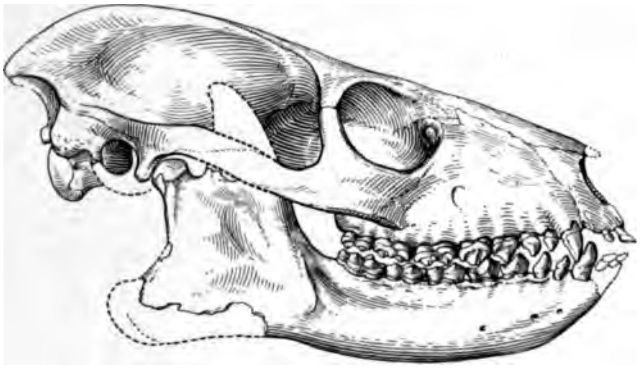

FIG. 56. SKULL AND LOWER JAW OF *Notharctus osborni*, A LEMUROID PRIMATE FROM THE MIDDLE EOCENE OF WYOMING. ×1. AMER. MUS., NO. 11,466

Fig. 57. Under Side of the Skull Shown in Fig. 56. ×2

above and below, of the formula of the stem placental mammals ($I\frac{3}{3}$ $C\frac{1}{1}$ $P\frac{4}{4}$ $M\frac{3}{3}$), and all the teeth are in a very primitive and characteristic Lower Eocene stage of evolution. The upper and lower dental arches are also very primitive. The lower incisors and canines totally lack the specialization seen in modern lemurs, by which all the incisors become transformed into small, procumbent, or porrect, compressed teeth, the lower canines are taken over into the incisor series, and the second lower premolar is modified into an erect, almost caniniform, tooth. In the Eocene Notharctidæ, on the contrary, the lower incisors and canines were not notably different from those of other primitive mammals. Partly because the lower incisors and canines of the Notharctidæ had not assumed the lemurine specialization, the family has been excluded, by Wortman, from the Lemuroidea; but, as fully shown elsewhere (*Memoirs of the American Museum of*

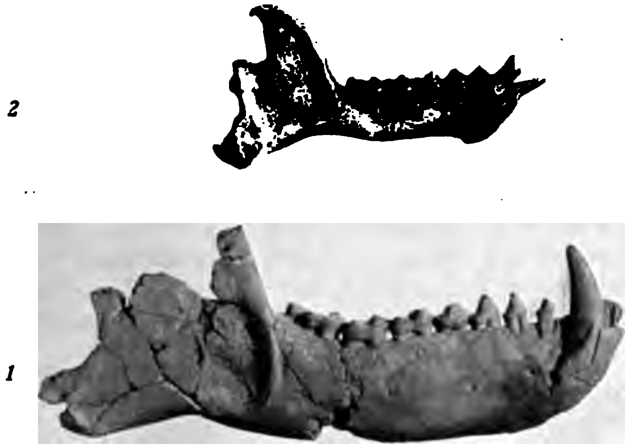

Fig. 58. Lower Jaw (Right Ramus) of (1) an Eocene Lemuroid *Notharctus venticolus* (Amer. Mus, no. 14,655) and of (2) a Modern Lemur, *Lepilemur mustelinus* (Amer. Mus., no. 4,659). Natural Size

In the ancient lemuroid the incisors (here represented by their alveoli), canines and four premolars, are primitive, both in form and in position; but, in the modern lemur, the front teeth are specialized, the incisors and canines being much alike, reduced in size and directed sharply forward. The prominent projecting tooth, in the front end of the tooth row, represents the second lower premolar of more primitive mammals, the first having been lost.

*Natural History*, 1920), the characters of the dentition, skull, and skeleton are unquestionably lemuroid.

The lateral upper incisors were already beginning to assume somewhat the compressed shape which is retained in certain modern lemurs (*Chirogaleus*). Stehlin (1916, p. 1530) argues that the canines of the original primates must have been small and more or less intermediate between the incisors and the premolars. But in all known Palæozoic, Mesozoic, Paleocene, and Eocene orders, except the multituberculates, the canines are usually more or less enlarged, and well differentiated both from the incisors and the premolars. Stehlin boldly meets this difficulty by assuming that such cases are already specialized away from the hypothetical condition conceived by him to be primitive, but I prefer not to set aside so lightly the direct palæontological and comparative anatomical evidence.

In brief, these primitive Lower Eocene lemuroids indicate *that in the stem primates the canines were well differentiated from both the incisors and the premolars, and that the lower canines occluded in front of the upper with their tips directed slightly outward.* Very probably in a premammalian stage of evolution the lower canines had occluded inside of the uppers and their tips were received in sockets in the upper jaw, as may be observed in the cynodont reptiles. But even in the oldest mammals the tips of the lower canines had become directed slightly outward, so that they occluded chiefly in front of the uppers, with their tips pointing buccally. This condition is preserved in a great majority of the primates; and it is only in the lemurs on the one hand, and in man, on the other, that the lower canines, as a result of reduction, come to occupy entirely new and anomalous positions.

*The evolution of the premolar series in the Notharctidæ, as shown in the species from ascending levels, parallels that in many other Eocene phyla of placental mammals and lends further support to the "premolar analogy theory" of the origin of the tritubercular molar.* First, as we pass backward, from the simple pointed tip of the first lower premolar ($p_1$) to the submolariform crown of $p_4$, there can be no doubt that the real protoconid, or original tip, is on the buccal side of the crown; but in the upper molars, if we were to accept the Cope-Osborn view, we should have to pass suddenly from the buccal tip of $p^4$ to the lingual tip of $m^1$. Secondly, the lower premolars show also the most detailed steps in the evolution of a submolariform pattern, starting with the simple, compressed, protoconid of the first premolars. The posterior slope of the first lower premolar, and still more that of the second premolar, shows faintly the very beginnings of a talonid, which becomes larger and more distinctly modelled as we pass backward towards the third and fourth premolars. The third lower premolar of the later species shows also the incipient separation of the paraconid and metaconid from the anterior and posterior slopes, respectively, of the protoconid. The lower molars also illustrate the progressive development of the trigonid, which becomes subtriangular in $p_4$ and fits into the interdental space between the third and fourth upper premolars. *In this progressive modelling of the lower premolars, the internal cingulum plays a prominent part, since it gives rise to the incipient paraconid, to the basin of the talonid, and to the incipient hypoconid (plate 6).*

In correlation with these changes in the lower premolars, the upper premolars also gradually attain a submolariform type, both as we pass backward from the compressed tip of $p^1$ and as we follow the course of evolution in successive species. In the more anterior upper premolars, the apices bite outside of the protoconids of the lower teeth. The internal ledges, which are progressively developed on $p^2 - p^4$, at first engage with the progressively developed talonids of the lower premolars. In the older members, even the fourth upper premolar has only a single external apex; but, with the progressive widening of the talonids and the buccal growth of the hypoconids, the single apex gradually divides into two, so that in the latest stage there are two cusps on the outer side of $p^4$. These, however, are still close together because the hypoconid of the lower premolars never becomes as large as that of the molars. Also, the anteroposterior diameter of $p^4$ is much less than that of the molars because the anteroposterior diameter of $p_4$ is also relatively small (*plate 7*).

The upper premolars of the earlier forms have a very distinct external cingulum, representing the reduced outer part of the primitive upper premolar crown. In the premolars of the later members of the series, this external cingulum, although somewhat less pronounced, is still evident. On the posterior premolars of the earlier stages there are small stylar cusps, corresponding to the parastyle and metastyle.

Fig. 59. Right Upper Cheek-Teeth of *Notharctus osborni*, a Lemuroid from the Middle Eocene of Wyoming. Amer. Mus., no. 11,466. ×3.

The first upper premolar is represented by its alveolus; the second has a simple compressed crown which, however, shows the beginning of structures which attain a fuller development in the third and fourth premolars.

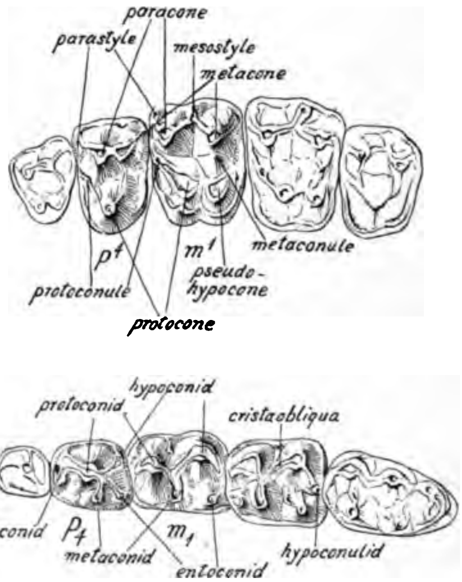

Fig. 60. Upper and Lower Cheek-Teeth of *Notharctus crassus*, an Eocene Lemuroid

Illustrating the names of the principal cusps, etc., of the premolar and molar crowns. Osborn's names for the parts of the molars are used also for the similarly placed parts of the premolars.

FIG. 61. UPPER AND LOWER TEETH, IN OCCLUSION, OF (1) *Pelycodus trigonodus* (AMER. MUS., NO. 15017, LOWER EOCENE, WYOMING) AND (2) *Notharctus crassus*, (AMER. MUS., NO. 11,982, MIDDLE EOCENE, WYOMING). X3. (INNER SIDE)

In the older and more primitive species, *Pelycodus trigonodus*, the pseudo-hypocones, or postero-internal cusps of the upper molars, are but poorly developed; thus, the interdental spaces are not restricted and receive the greater part of the trigonids of the lower teeth. In the later species, *Notharctus crassus*, the pseudo-hypocones are fully developed, encroaching on the interdental spaces and articulating with the paraconids of the lower molars.

These retain their distinctness in the later members. They did not articulate with any part of the lower teeth, but assisted in pressing the food against the lower teeth and in increasing the hold of the teeth upon the food.

The inner side of the upper premolars terminates in the low cusp, apparently homologous with the socalled "protocone" of the molars; it arose, as already stated, in correlation with the expansion of the talonids of the lower premolars. At first, this internal spur lacks all trace of a posterointernal division; but, in the fourth upper premolar of the latest stage, there is an incipient cusp which is beginning to separate from the posterior slope of the internal spur of $p^4$. This low postero-internal cusp, called the tetartocone in Scott's nomenclature, articulates with the paraconid of the first lower molar.

*Thus, both on the outer and on the inner side of the crown, the fourth upper premolar of the Notharctidæ exhibits an incipient tendency to divide into anterior and posterior moieties; in other words, to assume the molariform pattern which is more fully realized in the last deciduous premolar.* In this respect the posterior upper and lower premolars thus parallel the conditions in many other Eocene phyla, but in this series the transformation is slower and less complete; and in many of the higher primates the posterior premolars are less molariform than in the later species of Notharctidæ.[4]

The difference in pattern in $p^4$ and $p^3$ in the Notharctidæ is always pronounced, while in many other primates $p^4$ and $p^3$ become very much alike. Here again the Notharctidæ are more like other phyla of Eocene mammals, and the conditions of the premolars in the higher primates are in all probability less primitive, although more simple in appearance.

The first and second lower molars of the earliest Notharctidæ have all the elements of the primitive tuberculo-sectorial tooth; that is, the trigonid bears all three primitive cusps, and the talonid already has a high hypoconid and a low entoconid. Moreover, the trigonid is on a considerably higher level than that of the talonid, while the hypoconid is connected with the posterior wall of the trigonid by a prominent "crista obliqua." Thus, the lower molar is surmounted by

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[4] By this I mean that the relative simplicity of the bicuspid premolars of later primates may be due to arrest of the tendency to become molariform and to divergence in function of premolars and molars.

two Vs—the smaller V, formed by the cusps of the trigonid; the much wider posterior V, formed by the crista obliqua, the hypoconid and the entoconid (*fig. 62*). Such a pattern is seen in many other Eocene phyla.

As we pass upward from the lower and more primitive species of Notharctidæ, the paraconids of the lower molars disappear or are retained only in a reduced condition Meanwhile, the crest connecting the protoconid with the metaconid assumes a more anterior posi-

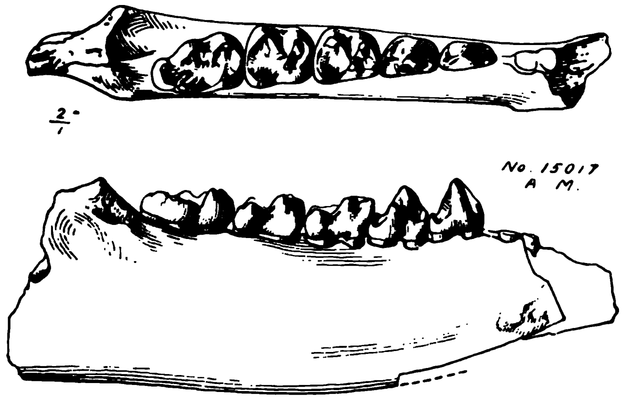


Fig. 62. Left Mandibular Ramus of *Pelycodus trigonodus*, a Primitive Notharctid from the Lower Eocene of Wyoming. Amer. Mus., no. 15,017. X2. After Matthew

In the fourth lower premolar, the trigonid and talonid of the molars are foreshadowed, but the third lower premolar retains its simple conical shape, with only an incipient paraconid and a very small talonid. In the molars, the trigonid is still on a higher level than the talonid—the paraconid, especially on $m_1$, is retained; the talonid of $m_1$,$m_2$ has already surpassed the trigonid in width.

tion, while the whole talonid and its V-shaped hypoconid become larger. At the same time, the trigonid becomes relatively lower and the talonid higher, so that the general level of the talonid is only a little below that of the trigonid. *This expansion of the whole talonid, including the hypoconid, as in so many other cases, is associated with the reduction of the interdental spaces between the upper molars, with the lengthening of the anteroposterior diameter of both upper and lower molars, with the further increase of the protocones which fit into the talonids; finally, with the progressive separation of the para- and meta-*

*styles, and with the filling out of the postero-internal corner of the tooth, so that the hypocones occupy much of the space formerly filled by the trigonids of the lower molars* (*fig. 61*).

In most phyla of mammals the true hypocones, or postero-internal cusps of the upper molars, arise as upgrowths of the cingulum, and progressively articulate with the basins of the trigonids of the lower molars. In the Notharctidæ, on the other hand, the postero-internal cusps arise as a budding or outgrowth from the posterior slope of the protocones, and they articulate rather with the paraconids of the lower molars. In the lower, older species of the family (*plate* 7), this process is just beginning on the first and second molars, and has not yet begun on the third molar. In later members this cusp becomes larger and larger, until, in the first upper molar of the highly progressive *Notharctus crassus*, the postero-internal cusp is even larger than the protocone itself. All the while the internal cingulum, which in other mammals gives rise to the hypocone, remains distinct and fails to produce a normal hypocone. *The budding off of the postero-internal cusp or pseudohypocone in the Notharctidæ has probably been conditioned by the attrition of the upgrowing entoconid of the lower molar.* When the mandible is moved obliquely, this cusp shears transversely across the posterior slope of the protocone just in front of the pseudohypocone; the latter also articulates directly with the paraconid of the next lower molar. In the titanotheres and other perissodactyls, a somewhat similar process in the premolars conditions the origin of the so-called tetartocone, which buds off from the posterior slope of the main internal cusp immediately behind the place where that cusp is worn by the upgrowing entoconid of the lower molar. The same process occurs also in the Equidæ and other perissodactyls.

In correlation with the more rapid development of the postero-internal cusp of the first upper molar of the Notharctidæ, we find that the level of the talonid of the first molar is higher than that of the second molar. The former tooth is also more conservative in the retention of the paraconid, which tends toward reduction or disappearance in the second and third molars of later species. When present, the paraconid articulates with the pseudohypocone of the preceding upper molar (*figs. 61, 63*).

The progressive development of a mesostyle on the upper molars is another specialization in which the Notharctidæ parallel many

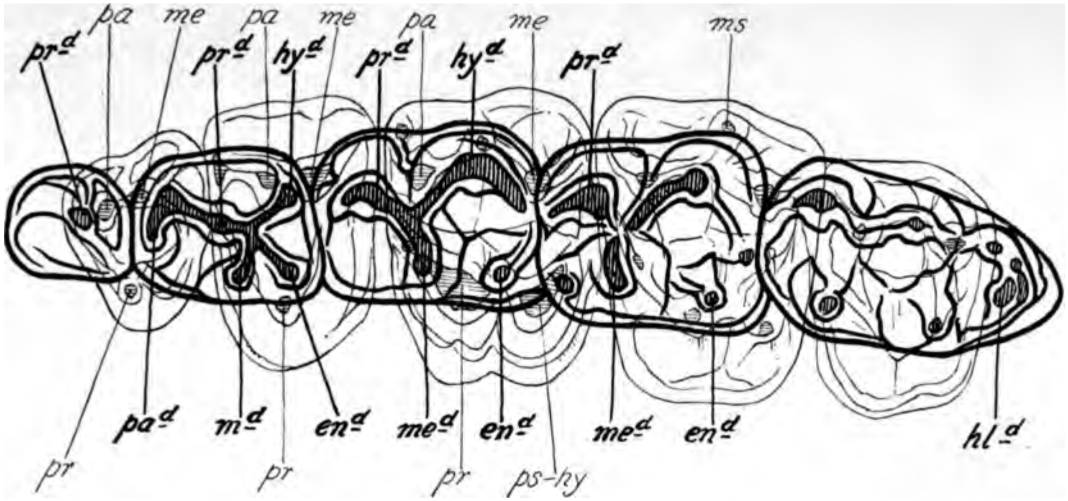


FIG. 63. PROJECTION OF THE LOWER UPON THE UPPER CHEEK-TEETH OF *Notharctus crassus*

Illustrating the articular relations of the upper and lower teeth when the mandible has been shifted toward the outer side. The protoconids of the lower teeth fit between two upper teeth.

other phyla of Eocene and later mammals. In the earlier members of the family, the mesostyle is barely indicated by a very slight wrinkle in the external cingulum between the para- and metacones. This steadily becomes larger, culminating in the robust mesostyle of *Notharctus crassus*. *As in so many other cases, these cusps do not articulate with the lower teeth, except when the lower jaw is swung far to one side so as to bring the hypoconids opposite the mesostyles, but they assist chiefly in pressing the food against the lower molars.* The mesostyle is connected with the slopes of the para- and metacones and, finally, coöperates with them in the formation of two well developed external Vs, or crescents, on the outer side of the tooth. These two Vs open outward, while the Vs of the lower molars open inward, a device frequently adopted among herbivorous dentitions and apparently efficient in the subdivision of a vegetable or mixed diet.

The third molars, both in the upper and lower jaw of the Notharctidæ, are narrower transversely, and in all respects less progressive, than the second molars. The third upper molars fail to develop a pseudo-hypocone, or postero-internal cusp, and the mesostyle is also smaller than in $m^2$. The third lower molar, even in the oldest forms, has a hypoconulid, or median posterior spur, which articulates just behind the posterior border of the third upper molar, and assists in a pivoting action when the jaw swings from side to side.

As shown by a careful study of the articulating relations of the upper and lower teeth in various species of Notharctidæ, and also by the mandibular condyles and glenoid fossæ, the lower jaw in the earlier forms had a somewhat more vertical movement, while in the later forms with crescentic molars there was a considerable transverse swing of the mandible (*fig. 67*). This ruminant-like action of the lower jaw is developed also in the howler monkeys of the New World series, and in *Propithecus* among the indrisine lemurs of Madagascar. *Probably the increasingly transverse component of the movement of the lower jaw conditioned, or was associated with, the development of both the pseudo-hypocones and the mesostyles in the upper molars, since the entoconids of the lower teeth sweep across the isthmus connecting the two internal cusps of the upper molars, while the hypoconids sweep across the region from the inner side of the mesostyle to the inner side of the protoconule (fig. 63).*

The deciduous dentition of *Notharctus* agrees with that of the European *Adapis* in the fact that all the molars erupt early, while the deciduous teeth are still in use. This is also the condition in the modern lemurs. In the higher primates, on the contrary, the eruption of the second and third molars is delayed until the close of the replacement period. As in many other mammalian phyla, the last

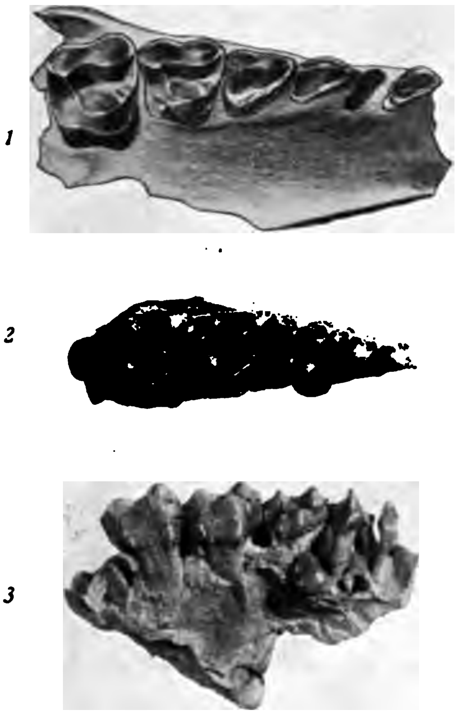


FIG. 64. DECIDUOUS AND PERMANENT UPPER TEETH OF *Adapis magnus* AND *Notharctus tyrannus*

1.—*Adapis magnus*. Eocene of Europe. ×2. After Stehlin. From left to right the teeth in place are $m^1$, $dp^4$, $dp^3$, $dp^2$, alveolus of $p^1$, dc.

2, 3.—*Notharctus tyrannus*. Amer. Mus., no. 13,025; Middle Eocene of America. ×2. The third molar has barely begun to erupt; $m^2$, $m^1$ and three deciduous premolars are in place, with the permanent $p^4$, $p^3$, and space for $p^2$ beneath them. As in most other mammals, the posterior deciduous teeth are more molariform than the permanent teeth that succeed them. In these Eocene lemurs the true molars are in use along with the deciduous teeth.

deciduous premolars are molariform in general pattern, while their successors, the fourth premolars, are much simpler.

We may summarize the morphology and evolution of the dentition of the Notharctidæ as follows:

(1) Dental formula: the primitive one for Primates; differs from the primitive placental formula only in the loss of one incisor on each side above and below. Same formula retained in the Adapidæ, but variously reduced in later primates.

(2) Dentition: increases in size from the Lower, through the Middle, Eocene; the length of the three lower molars rises from 11 to 23 mm.

FIG. 65. LOWER JAWS OF *Notharctus tyrannus*. AMER. MUS., NOS. 13,029 AND 12,578. ×2

All the true molars were in place before the deciduous molars were shed

(3) Lower incisors and canines: of primitive placental type; not specialized as in lemurs, but not very different from those of the more primitive South American monkeys.

(4) Evolution of the premolar series: parallels that in other Eocene placental mammals and lends support to the "premolar analogy" theory of the origin of the tritubercular molar.

(5) Evolution of the upper molars: from the trigonal to the quadrangular type, with consequent reduction of the interdental spaces

correlated with an increase in the anteroposterior diameter of the crowns, and with the expansion of both the protocones and the talonids that receive them.

(6) Budding off of the postero-internal cusps, or pseudo-hypocones from the posterior slopes of the protocone: conditioned by, or associated with, the attrition of the entoconids of the lower molars; the pseudo-hypocones articulate with the reduced paraconids.

(7) Progressive development of mesostyles on upper molars: correlated with obliquely transverse movements of the mandible in mastication.

## THE ADAPIDÆ OF THE EOCENE OF EUROPE

These European relatives of the Notharctidæ resemble the latter in so many fundamental characters of the dentition, skull and limbs, that they may well be united with them in a single family, for which the prior name, Adapidæ, has often been used. But the American and European representatives of this group are, on the other hand, separated by a number of minor but trenchant differences, which make it desirable to class them as either distinct families, as Stehlin does; or, at least, as very distinct subfamilies, Notharctinæ, Adapinæ, as I have done in the memoir already cited. Stehlin has emphasized the fact that, in the American family (or subfamily), the so-called hypocones, or postero-internal cusps, of the upper molars are really pseudo-hypocones, formed by budding off from the antero-internal cusps or protocones; while, in the European series, the hypocones are formed by the upgrowth of the postero-internal cingulum in the more usual mammalian fashion. He also noted that, in the Notharctidæ, the upper molars develop mesostyles, which are entirely absent in the Adapidæ. But I have shown (1920) that, although these and other differences demonstrate a divergence in evolutionary trend, they do not disprove a common origin of the two groups, as evidenced by the long list of primitive lemuroid characters which they have in common.

The differences in the molars noted above are associated with corresponding differences in the normal paths of the mandibular excursion during mastication. In the Notharctidæ, as already noted, the excursion of the mandible became increasingly lateral, so that the lower grinding teeth were swept part way across the crowns of the upper teeth, and the incipient mesostyles pressed the food against the hypoconids; while the pseudo-hypoconids grew out just behind

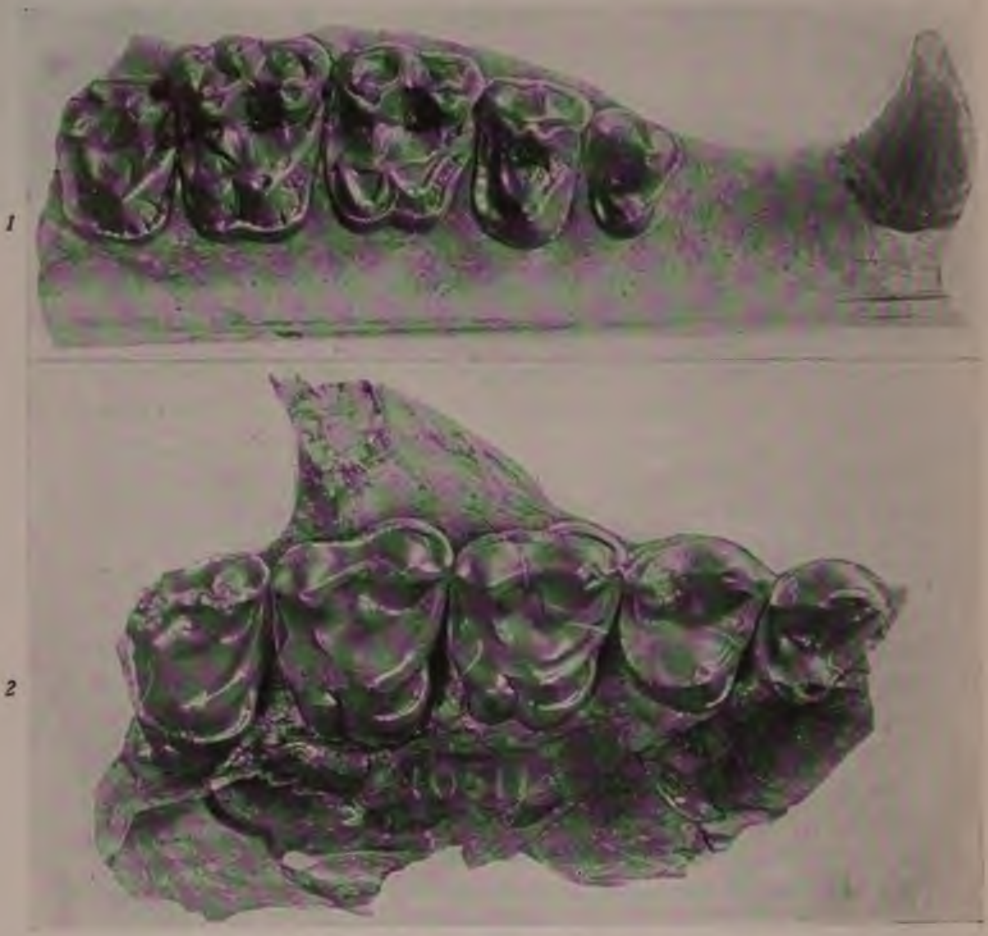


Fig. 66. Upper Cheek-Teeth of *Notharctus* and *Adapis*

1.—*Notharctus crassus*. Amer. Mus., no. 11,982; Middle Eocene, Wyoming. ×3.
2.—*Adapis magnus*. Amer. Mus., no. 10,511; Eocene, France. ×3.

Shows, in *Notharctus*, the presence of mesostyles and of pseudohypocones; in *Adapis*, the absence of mesostyles and the presence of true hypocones, connected with the internal cingulum.

the points where the entoconids swept across the posterior ridge of the protocones, and also came into contact with the reduced paraconids of the lower molars. In the Adapidæ, on the other hand, the excursion of the mandible remained more vertical, no mesostyles were developed and the true hypocones finally came to articulate with the basin of the trigonids, as in many carnivorous mammals, with a chiefly vertical excursion of the mandible. So also, in association with the vertical movement, the protoconule crest of the Adapidæ became well developed (*fig. 66*), foreshadowing the conditions in the modern Lemuridæ (*fig. 70*). These differences in the excursion of the mandible are associated with corresponding differences in the mandib-

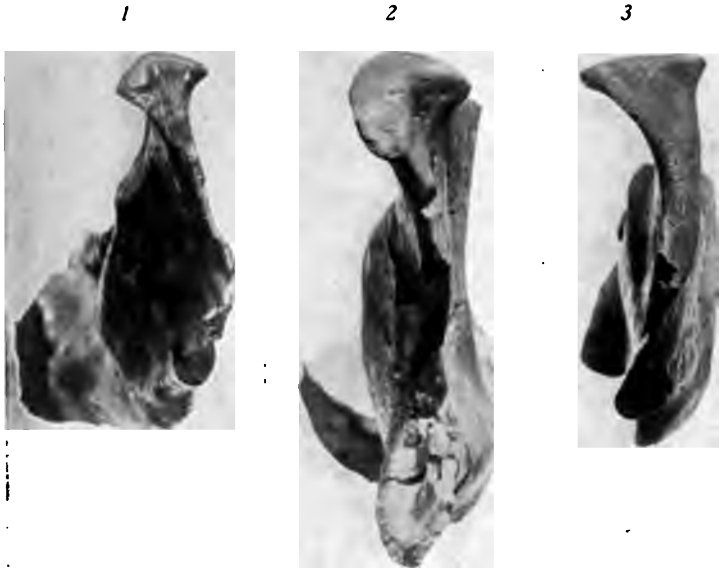


FIG. 67. REGION OF THE MANDIBULAR CONDYLE OF *Notharctus* AND OF *Adapis*. VIEWED FROM THE REAR. ×2

1.—*Notharctus osborni*. Amer. Mus., no. 11,466.
2.—*Notharctus crassus*. Amer. Mus., no. 12,588.
3.—*Adapis parisiensis*. Amer. Mus., no. 10,007.

The more convex condyles of *Notharctus* permitted freer movements of the mandible, while the flatter and more transversely extended condyle of *Adapis* implies a more orthal (vertical) movement.

ular condyles, those of *Notharctus* being rounder and permitting freer movements; those of *Adapis* being flatter and suggestive of the condyles of carnivores (*fig. 67*).

FIG. 68. SKULL AND LOWER JAW OF *Adapis magnus*. × 1. AFTER GRANDIDIER

**The skull in general resembles that of the larger species of *Notharctus*, but is distinguished by the heavier jaw and stouter zygomatic arch. The orbit, as in other lemuroids, opens beneath the postorbital bar into the temporal fossa.**

Setting aside the differences in the dentition noted above, the whole construction of the skull in the Adapidæ, including the detailed characters of the bony face, brain case, auditory region, etc., on the one hand represents an advance upon the conditions exhibited in the Notharctidæ; on the other hand foreshadows the Lemuridæ.

## ORIGIN OF THE LEMURIDÆ

Forsyth Major, after extensive comparisons of the auditory and lacrymal regions of the skulls of primates, came to the conclusion that the modern Lemuridæ had been derived from the Adapidæ. This is the view I have endeavored to defend in the memoir cited above. But Stehlin, the leading authority on the Eocene primates of Europe, would exclude at least the typical Adapidæ from such a connection, on the ground that they are already too specialized in certain characters of the dentition and of the skull to be ancestral to the Lemuridæ. I have argued, on the contrary, that *it is of the greatest importance to realize that Eocene ancestors may be expected to resemble or foreshadow their modern descendants only in respect of those characters the function of which has either remained the same or has become intensified in a positive sense; and that, on the other hand, the Eocene ancestors will differ from their descendants in proportion as their adaptive characters have suffered a radical change of function.* Accordingly, I have endeavored to show that the chief differences in the dentition and skull between *Adapis* and the Lemuridæ (which have been cited by Stehlin as excluding the former from ancestry to the latter), may rather be interpreted as signs either of changes of function and structure or, in some cases, of marked intensification of function of the given parts.

In the most primitive Adapidæ the dentition (*fig. 71*) approaches the normal primitive form exhibited in other placental orders. Consequently the aberrant specialization of the incisors, canines, and anterior premolars, which is characteristic of the Lemuridæ and other lemuroid families, is surely a later acquisition, and the lack of it in the Eocene Adapidæ by no means excludes that family from ancestry to the Lemuridæ. In modern lemurs the specialization in question is connected with the habit of combing and cleaning the fur with the lower front teeth, and is associated with a thickening and enlargement of the tongue, as well as of the sublingua, so that the minute and procumbent lower incisors, and canines, fit beneath the overlapping and more or less protrusile tongue. This peculiar modification in the several families of modern lemuroids has very probably been acquired independently, starting from the more primitive conditions illustrated in *Adapis priscus* and the more primitive Notharctidæ.

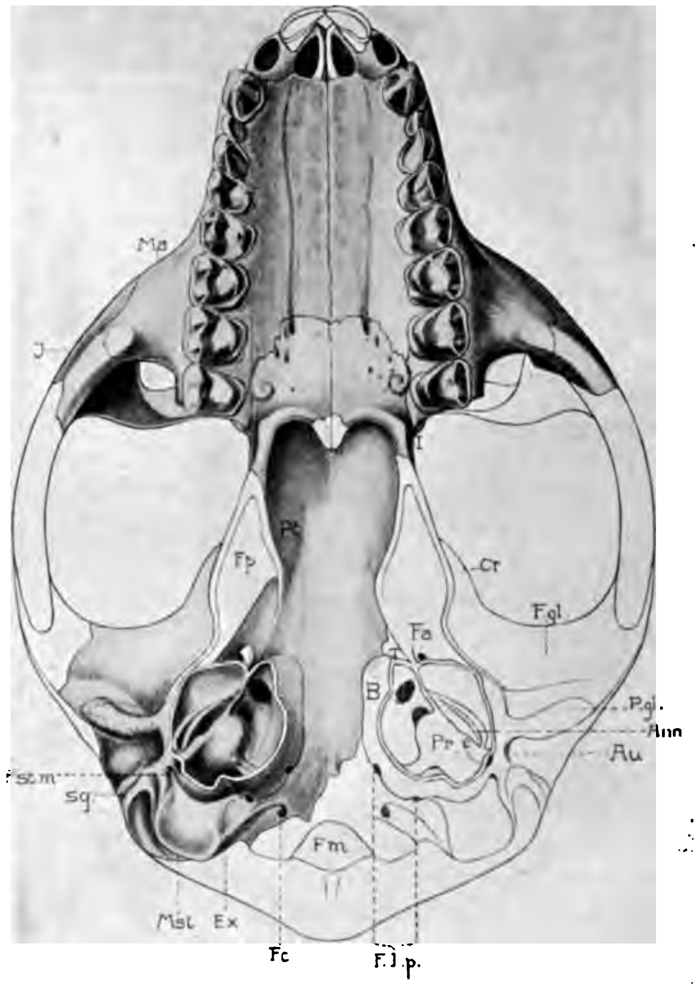


FIG. 69. UNDER SIDE OF THE SKULL OF *Adapis magnus*. ×1. AFTER STEHLIN

In the construction of the auditory region and many other parts, the European Adapidæ are closely related to the American Notharctidæ. In another direction they foreshadow the modern Lemuridæ in skull and dentition.

FIG. 70. UNDER SIDE OF THE SKULL OF A RECENT LEMUR, *Lepilemur mustelinus*. ×2

Shows numerous points of resemblance to *Adapis*, but differs in the more specialized form of the front teeth.

Here we have an excellent example of the phenomenon *that numerous similar specializations are often independently developed in families that have been derived from a common stock.* The opposite principle, that *wide differences may also be evolved in closely related stocks,* is well illustrated by the wide adaptive radiation of the molar patterns in the various families of Lemuroidea.

Fig. 71. Left Mandibular Ramus of *Adapis sciureus*. ×4. After Stehlin. Lower Eocene, Europe

Shows the relatively primitive form of the teeth and the primitive dental formula: $I_2 C_1 P_4 M_3$. The molars, however, have lost the paraconids and have wide talonids.

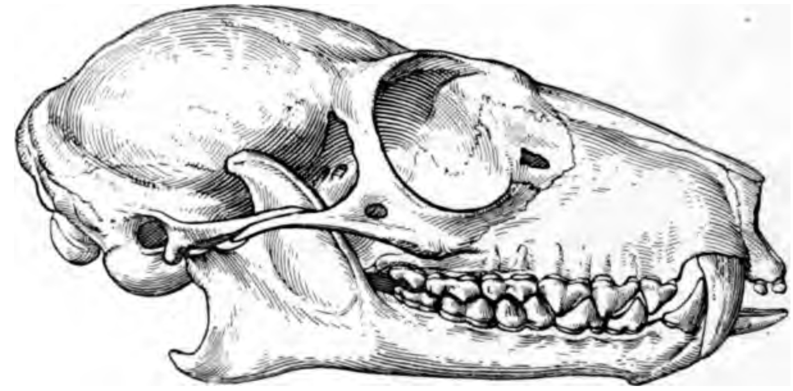


Fig. 72. Side View of the Skull of a Modern Lemur (*Lemur varius*). ×1

Shows particularly the specialized character of the lower front teeth, the enlargement and subcaniniform shape of the anterior lower premolar, the lengthening of the lower jaw, and the expansion of the lacrymal bone and brain-case.

## ADAPTIVE RADIATION OF THE DENTITION IN THE HIGHER LEMURS OF MADAGASCAR. "HABITUS" AND "HERITAGE"

There can be no reasonable doubt that the Archæolemuridæ, an extinct family of Madagascar lemurs, were true lemuroids; and yet, in some of them, the upper molar teeth became bilophodont, so as to suggest at first sight the bilophodont molars of the Cercopithecidæ. The same genera also acquired a short face and expanded brain-case so that they were erroneously regarded by some as transitional between monkeys and lemurs. But their true status as lemurs is revealed by the retention of many highly significant lemuroid features in the skull and skeleton (*fig. 73*).

***More recently acquired characters and special adaptations to the final life habits constitute what I call the "habitus," or adaptive form of the animal, while characters which it has inherited from ancestors in an earlier stage of evolution, and before the assumption of its present life habits, make up its "heritage." Both sets of characters are adaptive, but the first set are adapted to its present life habits; and the second set were adapted to the different life habits of its ancestors, and have been retained either because they are still useful, or because they have not yet been eliminated by later adaptations.*** This cardinal principle is of the utmost importance in the study of the evolution of the human dentition and of the whole question of man's relationship with other primates.

While the Archæolemuridæ tend to evolve bilophodont molars, ***Propithecus*** of the Indrisidæ has selenodont molars, that is, the molar patterns consist of Vs or crescents, which recall the conditions in the Eocene Notharctidæ but are more specialized. In *Indris* itself, the crescentic pattern of the upper molars is more or less effaced, the cusps losing much of their crescentic shape and the crowns tending to be divided into subequal anterior and posterior moieties (*figs. 74, 75*).

The Indrisidæ also afford an instructive example of the reduction in the number of premolars from four to two, a reduction which has occurred independently in many other groups of primates. Even in the Notharctidæ, the first and second premolars, both in the upper and lower jaw, remained retarded in development, while the third and fourth premolars were more progressive. This tendency, for

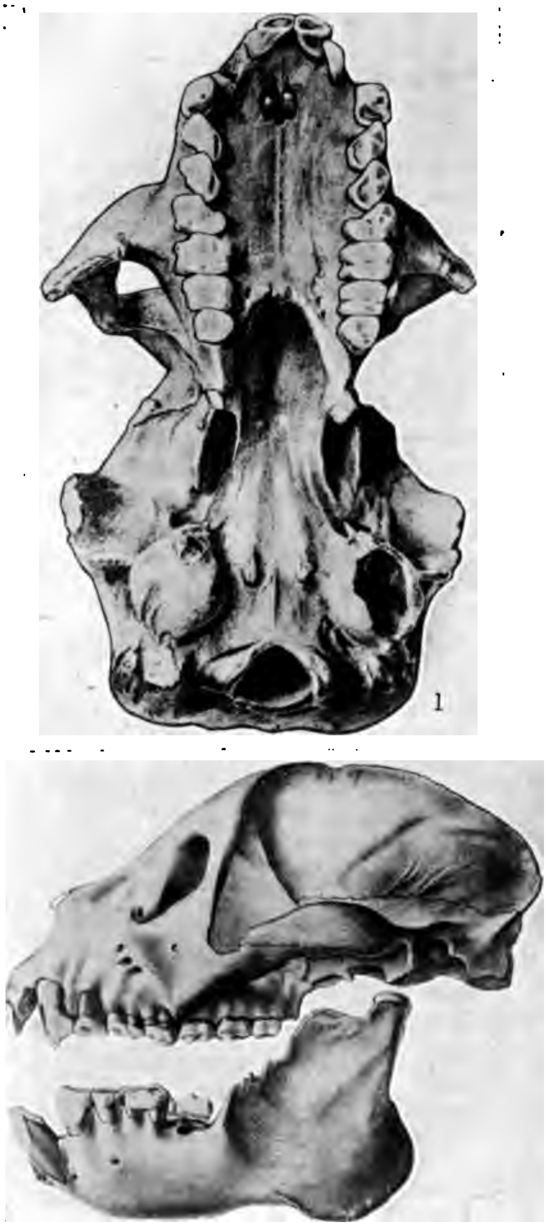


Fig. 73 Skull and Lower Jaw of *Archæolemur edwardsi*, an Extinct Monkey-like Lemur from Madagascar. ×½. After Standing

FIG. 74. UNDER SIDE OF THE SKULLS OF TWO MODERN INDRISINE LEMURS, *Propithecus* (1) AND *Indris* (2)

1.—*Propithecus diadema.* Amer. Mus., no. 31,253. ×1.

2.—*Indris indris.* Brit. Mus., 48.10.28.1. ×1.

In *Propithecus*, the first and second upper-molars bear two rows of W-shaped crests. In *Indris*, the W-shaped pattern is becoming obsolete and the cusps are more conical.

the premolar series to differentiate into two contrasting parts, the anterior part consisting of the small or reduced $p^1$ and $p^2$, and the posterior part consisting of the progressive $p^3$ and $p^4$, is highly developed, not only in the Indrisidæ, but also in several other groups, such as the Old World primates, including man. In the final stage of this evolution, the first and second premolars disappear entirely and the remaining premolars are homologous with the third and fourth of the primitive placental dentition. *This important fact seems to be little appreciated by those odontologists who do not recognize the fact that the tooth immediately in front of the molars, in all primates, is the homologue of the fourth premolar of primitive placental mammals.*

In all primates the elimination of the two anterior premolars is probably correlated with the shortening of the face, with the marked increase in size of $p^3$ and $p^4$, and often with the anteroposterior lengthening of the molars. When, as in the Indrisidæ and many apes, the upper canine becomes considerably enlarged, its posterolingual side comes into secondary articulation with the anteroexternal side of the anterior premolar, which is the second of the primitive series. This lower premolar thus becomes more or less enlarged. Up to this point, its tendency was to become like $p_4$, which in turn was tending toward the molar pattern; but, when $p_2$ comes into relation with the upper canine, its protoconid becomes enlarged and pointed, so that in *Propithecus diadema*, of the Indrisidæ, this tooth is almost caniniform in appearance. *This illustrates the general principle that individual teeth, like other parts of the skeleton, tend to assume the form required of them by their topographic position and functional relations to the surrounding parts.*

In the Indrisidæ and, more particularly, in the Archæolemuridæ, the true canines are taken over into the incisor series; and, in the latter, they tend to become enlarged, procumbent, and opposed by both the central and the lateral incisors. The tendency for the lower canines to become incisiform, and to oppose the upper incisors, is carried to an extreme in *Chiromys*, the Aye-aye, in which a single pair of upper incisors have become enormously enlarged and compressed, and opposed to a similar pair of pointed and enlarged lower teeth. The lower pair have often been regarded as incisors, but it is far more probable that they are enlarged canines. The almost rodent-like

Fig. 75. Skulls of Two Divergent Members of the Indrisidæ

1.—A dolichocephalic, dolichopic, type: *Indris indris*. Brit. Mus., 48.10.28.1. ×1.
2.—A brachycephalic, brachyopic, type: *Avahis*. ×2.

FIG. 76. SKULL OF THE AYE-AYE, *Chiromys madagascariensis*, A HIGHLY SPECIALIZED LEMUROID. COLLEGE OF PHYSICIANS AND SURGEONS, LONDON. ×1

The rodent-like front teeth are used to pierce the bark of trees; in the incisions thus made, the animal inserts its extremely attenuated, elongate, third finger to extract the grubs upon which it feeds. In correlation, perhaps, with the soft character of the food, the molar teeth are of degenerate type.

front teeth of the Aye-aye, and the correlated modifications in the form of the lower jaw, zygomatic arch and alveolar process, deceived some of the early investigators into grouping this animal with the rodents, but thorough comparisons of its osteology and anatomy soon indicated its proper place in the system. Its rodent-like appearance is found, on analysis, to be extremely superficial and to be manifested in characters which have been independently acquired in many widely removed phyla of mammals. In correlation with its habit of eating soft bodied grubs, its molar teeth are small in size and degenerate in pattern.

## IV. SUMMARY AND CONCLUSIONS FOR PART II

After the evolution of mammals from mammal-like reptiles, in the early part of the Age of Reptiles, and after the subsequent origin of the tritubercular type of molars (as discussed in Part I of this work), the primitive mammals, represented perhaps by *Amphitherium* of the Middle Jurassic of England, probably gave rise (in the latter half of the Age of Reptiles) to two great series: the "marsupials" and the "placentals." The evolution of the molar patterns in the marsupials closely paralleled that in the placentals; and, likewise, has been traced by several investigators from a primitive triangular type, still largely preserved in the opossums, into the diverse shearing, cutting, crushing and grinding molars of the existing marsupials.

In Part I a study of the occlusal relations of the upper and lower teeth of the marsupials was shown to be requisite for an adequate understanding of the function and evolution of the several parts of the teeth. The same method has been followed in studying the evolution of the dentition of the Paleocene and later placentals. Emphasis was also laid upon the importance of not confining attention exclusively to the dentition, but of taking into consideration the evolution of other parts of the organization; and of keeping constantly in mind the taxonomic position, relationships, and evolution, of the organisms whose dentitions are studied; on the ground that when only one or two terminal and widely separated twigs of the great phylogenetic tree are compared, the observer is likely to be deceived into mistaking both fortuitous and convergent resemblances for genuine homologies.

The extinction of the giant reptiles at the close of the Cretaceous was then noted; also, the apparently sudden immigration into the known collecting fields of the archaic placental orders in the Paleocene epoch. With regard to the origin of the placentals, some of the cranial and dental characters which may be safely assigned to the (as yet) undiscovered common ancestors of all the placental orders were enumerated. The great collections of Paleocene and Eocene mammals in the American Museum of Natural History are, it was suggested, of signal importance to odontological science, because they afford cumulative evidence for the truth of the central proposition of the "Cope-Osborn theory of trituberculy," namely, that all the highly diverse molar patterns of later placental mammals may be traced back to primitive tritubercular types.

In connection with the time honored problem of the origin of the tritubercular molar patterns of Paleocene and Eocene placentals, the writer, in common with many earlier authors, regards as erroneous the view that in the upper molars the true or original protocone is the internal apex of the trigon, while in the premolars it is the main external cusp; because, as pointed out by Wortman and others, the evidence tends to show that, as we pass backward from the anterior premolars through the fourth premolars to the true molars, the main tips of the premolar crown are homologous with the paracones + metacones of the molars; and, further, because the so-called "protocones" of the molars seem to have arisen as outgrowths from the internal basal cingulum, correlated with the development of the talonids or heels of the lower molars.

A further conclusion (p. 105), in line with the foregoing, is that in the upper molars of primitive mammals there are two trigons: (1) a primary or anterior trigon, consisting of the outer side of the tooth as a base and the tip of the paracone as its apex, and (2) a secondary or inner trigon, consisting of the para- and metacones as its base and the inwardly grown "protocone" as its apex. The primary trigon, it was argued (p. 106), was afterward often effaced in correlation with the transverse expansion of the hypoconid of the lower molar, because the hypoconid grew toward the buccal side, separating the para- and metacones, and also, as it were, pushing them toward the outer side of the crown, which often became reduced in width. In the placental series, just as in the marsupials, the expansion of the talonid accompanied the (1) anteroposterior widening of the molars, their (2) division into anterior and posterior moieties, and the (3) reduction of the interdental spaces through the development of a postero-internal cusp or hypocone. Thus, while the "protocones," or internal spurs, were received into the basin of the talonids of the lower molars, the hypocones overlapped into the trigonid basins of the molars.

As the primary shearing and interlocking relations of the primitive trigonal upper and lower teeth were more or less superseded, new and diverse cutting and crushing adaptations were often developed by the elaboration of crests upon the surface of the crown (p. 108). The subsequent history of the molar patterns in the highly specialized ungulates and rodents demonstrates the high potentialities for subsequent modification of the primitive tritubercular type, and affords so many examples of the methods by which these complex patterns have been attained that the more simple results of molar evolution in the primates become readily discernible.

Coming nearer to the latter subject, I again (p. 112) suggested the futility of basing evolutionary conclusions on comparisons of conditions in widely unrelated groups, as when authors point to concrescence of teeth in elasmobranchs as evidence that in mammals each tooth represents the fused germs of a "dental family;" and I emphasized the importance of systematic comparisons according to the taxonomic or phyletic relationships of large groups. An outline of the history of the classification of the primates was then given (p. 113), culminating in the allocation by Linnæus, of man, the apes, monkeys, and bats, to the order Primates; and the subsequent improvement of this classification down to the present time was noted.

Although the direct line of human ascent is but imperfectly known, synthetic studies on living and extinct primates, in the light of the palæontological history of other mammalian phyla, have yielded definite evidences as to the evolution of many human structures, such as the dentition. In this connection I find much that is true and enduring in the teachings of Huxley and other pioneers concerning human evolution, notwithstanding the fact that their results have recently been thrown lightly into the discard by Wood-Jones, a polemic author with a strong bias for iconoclastic methods. To judge by his book on "Arboreal man" and by his brochure on "The problem of man's ancestry," Wood-Jones may fairly be classed with those anatomists who have, at most, a superficial acquaintance with vertebrate palæontology and yet do not hesitate to give judgment on phylogenetic problems, for the proper understanding of which long and wide experience with palæontological facts and principles is prerequisite.

I hope to show in Part IV of this paper, and in other publications, that Wood-Jones's leading thought as to "the basal mammalian primitiveness" of human anatomy has even less foundation in fact than his pronouncement that the lemurs certainly do not belong to the Primate stem (1918, p 27). In the present section (p. 114) and in my memoir on the American Eocene Primates, I have defended the older view that the lemurs are true primates; and have shown that a study of the evolution and adaptive radiation of their skull and dentition has yielded some important facts and principles bearing on the early stages of the evolution of the skull and dentition of man.

Concerning the origin of the primates it is held (p. 116) that the existing Menotyphla (a group of insectivores including the Tupaiidæ and Macroscelididæ) represent the comparatively little modified Cretaceous ancestors of the Primates; and the dentition of several Paleocene and Eocene "Insectivores," that probably represent more or less specialized survivors of this primitive ancestral group, are described and figured. Even in the existing Tupaiidæ, the molars are of primitive tritubercular type with small hypocones in the upper, and relatively narrow talonids in the lower, molars.

The evolution of the dentition in the primitive American Eocene lemuroids of the family Notharctidæ was then reviewed (p. 121). It was shown that, when first known, near the base of the Lower Eocene, these animals were of very small size, with insectivorous-frugivorous dentition; and that as we pass through ascending levels they steadily increase in size, culminating in *Notharctus crassus* at the summit of the Middle Eocene, the adults of which were about as large as a howler monkey. The lemur-like skulls and jaws in this family assuredly afford an early stage of primate evolution, tending to connect the higher primates with primitive placental mammals.

The same is true of their dental formula ($I\frac{2}{2}\ C\frac{1}{1}\ P\frac{4}{4}\ M\frac{3}{3}$) and of the construction of all their teeth. The incisors and canines are of primitive type—not modified as they are in modern lemurs—and are fitted to give rise on the one hand to the procumbent incisors and canines of the lemurs, and on the other to the widened incisors and stout canines of the higher primates.

The evolution of the premolar series in the Notharctidæ, it was shown (p. 124), parallels that in many other Eocene phyla of placental mammals, and lends further support to the "premolar analogy" theory of the origin of the tritubercular molar. It was noted that the fourth upper molar, as in many other Eocene phyla, exhibits a tendency to divide into anterior and posterior moieties, that is, to assume the molariform pattern which is more fully realized in the last deciduous premolars. It was also observed that, in the Eocene primates, the ultimate and the penultimate premolars always differ considerably in pattern; whereas, in later or modern primates, these two adjacent teeth tend to become bicuspid and quite like each other, and unlike the molars. It was also held that, in later primates, where only two premolars on each side are present, the missing ones are the first and second of the primitive four. In the evolution of the lower molars were noted the gradual disappearance of the paraconid, correlated with the development of the hypocone and the reduction of the interdental spaces in the upper molars. We also noted the transverse widening of the talonid and the buccal growth of the hypoconid, this, as in other phyla, conditioning the anteroposterior elongation of the upper molars and the wider separation of the para- and metacones.

The Notharctidæ are distinguished from their cousins, the European Adapidæ, especially by the progressive development of the mesostyles and V-shaped para- and metacones; and by the origin of the postero-internal cusps by budding or fission from the antero-internal cusps; whereas, in the Adapidæ, the upper molars never develop mesostyles, and the postero-internal cusps arise as normal hypocones by the upgrowth of the posterior basal cingulum. These differences, we saw (p. 135), were associated with differences in the articular relations of the parts of the upper and lower teeth, and in the normal paths followed by the mandible in mastication. In the Notharctidæ, the movement of the mandible progressively developed a more transverse component, the lower teeth engaging first on the outer side of the upper and passing obliquely across them toward the inner side; whereas, in the Adapidæ, the motion of the mandible was more vertical. There was therefore, in the latter family, no functional need of mesostyles; but, on the other hand, the transverse crests on the protoconules became emphasized, as in the Lemuridæ.

Forsyth Major's view, that the Lemuridæ have been derived from or are closely related to the Adapidæ, was adopted in preference to that of Stehlin, who holds that the Adapidæ have no near relations with the Lemuridæ. It was held that the observed conditions of the front teeth in the Lemuridæ have been derived from the primitive conditions seen in the primitive *Adapis sciureus* through a profound change of function, because the modern lemurs use their curiously specialized comb-like front teeth in cleaning their fur (*figs. 71, 72*).

The Adapidæ have sometimes been regarded as standing in, or near, the line of ascent leading to the higher Primates; but this view is held to be erroneous on account of their resemblances with the Lemuridæ and partly because, as suggested by Leidy and by Wortman, the South American monkeys may have been derived from the Notharctidæ, as indicated by many resemblances in the skull and dentition. The peculiar procumbent, comb-like arrangement of the front teeth has been assumed independently in the Lemuridæ, Indrisidæ and Lorisidæ. It affords an example of the phenomenon that quite similar specializations are often independently evolved in families that have been derived from a common stock.

The opposite principle, that very wide differences may also be evolved in closely related stocks, is then illustrated by a brief review of the adaptive radiation of the dentition in the higher lemurs of Madagascar. Some of these animals became so monkey-like in appearance as to have led certain authors to the conclusion that they were really intermediate between monkeys and lemurs. The fact is, however, that they were monkey-like only in their "habitus" of recently adapted features, while they retained the old lemuroid "heritage" in many less conspicuous characters. This family (the Archæolemuridæ) further parallels some of the higher primates in the bilophodont specialization of the upper molars.

The indrisine lemurs (Indrisidæ) afford an instructive example of the reduction in the number of the premolars from four to two on each side, by the loss of the anterior two, probably conditioned by the shortening of the face and by the crowding of the dentition due to the increase in the anteroposterior diameter of the remaining cheek-teeth. The molars bear W-shaped crests on the para- and metacones, and thus parallel those of the Notharctidæ and other leaf-eating mammals.

In all the modern lemuriform primates, the lower canine is taken over into the incisor series; and the second or third lower premolar becomes more or less caniniform and opposes the upper canine. This illustrates the important general principle that individual teeth, like other parts of the skeleton, tend to assume the form required of them by their topographic position and functional relations to the surrounding parts.

The case of *Chiromys* (p. 146), which was regarded by early zoölogists as a rodent but was soon shown to belong with the lemuroid primates, illustrates a fact bearing on the taxonomic history and relationships of man, namely, that the taxonomic system of the present time is the end-result of innumerable detailed studies on the anatomy and palæontological history of the vertebrates; and, in consequence, the status of the vast majority of known mammals has been closely scrutinized, and many erroneous allocations, due to deceptive resemblances brought about by convergent evolution, have been detected and the intruding forms transferred to their proper places in the system.

## PLATE 5

Homologies of the external, middle, and internal row of cusps in the premolar-molar series of primitive placentals and marsupials. The figures are arranged according to the geological horizon of the genera.

The *red* series includes the main tips of the premolars, and the para- and metacones of the molars.

The *green* series includes the primitive outer row, which gives rise in later forms to the external cingulum and its cusps.

The *yellow* series includes the internal spur of the premolars and the so-called protocones of the molars.

*A–D.*—Zalambdodont insectivores. In these, the red series becomes predominant, growing inward, as the yellow series is reduced to a vestigial condition associated with a secondary reduction of the talonid.

*E.*—*Dryolestes.* The main tips of the molars appear to be homologous with the apices of the premolars and, therefore, to belong to the red series. The yellow series is possibly represented by the internal cingulum of the molars.

*F.*—*Apternodus*, an Oligocene forerunner of the modern Cape Golden Mole (*G*). Here we seem to have the primary trigon with its apex (red) still undivided, but this is possibly secondary. It is surely correlated with the lack of a talonid in the lower molars.

*H.*—*Didelphodus.* A primitive Eocene insectivore, in which the three series of cusps are all well developed. The para- and metacones are moderately separated in correlation with the moderate transverse diameter of the talonid (Compare *fig. 47*).

*I.*—*Proscalops.* A highly specialized insectivore, in which the para- and metacones are widely separated and the talonid is wide.

*J.*—*Tricentes.* A primitive carnivore with reduced outer cusps (green row) and well developed inner row (yellow). The secondary trigon has replaced the primary trigon.

*K.*—*Peralestes.* In this Jurassic trituberculate only the primary trigon is developed.

*L, M.*—Modern polyprotodont marsupials (survivors of the Upper Cretaceous marsupials), in which the outer (green) row is strongly developed.

*N.*—Primitive Eocene condylarth, with reduced outer row and large inner row.

*O.*—Primitive tarsioid primate.

*P, Q, R.*—Primitive leptictid insectivores.

## PLATE 6

Medial aspect of the right mandibular ramus in three species of Eocene Notharctidæ from successive horizons, showing a rapid increase in size of jaw and a slow evolution of the third lower premolar. × 3.

1.—*Pelycodus trigonodus*. Lower Eocene, Gray Bull formation, Wyoming. Amer. Mus. Nat. Hist., no. 16,843.

2.—*Pelycodus jarovii*. Lower Eocene, Lysite formation, Wyoming. Amer. Mus. Nat. Hist., no. 15,624.

3.—*Notharctus osborni*. Middle Eocene, Lower Bridger formation, Wyoming. Amer. Mus. Nat. Hist., no. 11,466.

3

2

1

## PLATE 7

Evolution of the upper premolar-molar series in species of Eocene Notharctidæ from successive geological horizons.

1.—*Pelycodus ralstoni.* Lower Eocene, Sand Coulée formation, Wyoming. Amer. Mus. Nat. Hist., no. 16,089.

2.—*Pelycodus frugivorus.* Lower Eocene, Gray Bull formation, Wyoming. Amer. Mus. Nat. Hist., no. 15,022.

3.—*Notharctus nunienus.* Lower Eocene, Lost Cabin formation, Wyoming. Amer. Mus. Nat. Hist., no. 4,735.

4.—*Notharctus crassus.* Middle Eocene, Upper Bridger formation, Wyoming. Amer. Mus. Nat. Hist., no. 11,982.

4

3

2

1

# PART III

## Nature's Earlier Experiments in Evolving Large-eyed and Short-jawed Primates

# I. THE LORISES (LORISIDÆ)

The existing lorises, of Asia and Africa, and the galagos, of Africa, represent some of nature's experiments in evolving large-brained and short-jawed primates from a primitive lemuroid stock. Although they closely parallel the tarsioids in these features, as well as in the enlargement of the eyes and internal ears, their status as true lemuroids is established by the following characters: (1) their lower front teeth have assumed the peculiar lemurine specializations described in Part II of this review; (2) they still retain the primitive pointed and projecting rhinarium, or snout, of the lemurs, which is replaced by a true nose in *Tarsius* and the higher primates (Pocock, 1918); (3) their hands and feet and (4) their reproductive organs (Pocock, *op. cit.*) are much like those of typical lemurs, only further evolved in the same direction.

The chief lines of specialization in the skull and dentition of the Lorisidæ (*figs. 78–93*) have apparently been as follows: in connection with nocturnal habits the orbits in the more typical forms have become greatly enlarged and their outer rims have grown forward, so that the eyes look partly forward and protrude widely from their sockets. Thus the orbits closely approach each other in the mid line, finally producing an extreme constriction of the interorbital region as in *Loris* (*figs. 79–91*). In correlation with the bulging and forward shifting of the eyes and the restriction of the interorbital space, the lacrymal bones become greatly reduced in size and the lacrymal ducts are displaced forward in front of the orbits. In spite of these specializations the whole bony face, instead of being greatly retracted and bent down beneath the braincase, as in some higher primates, retains much of its primitive lemuroid appearance in which the face is wholly anterior to the low braincase, and the pointed insectivore-like snout projects strongly in front of the orbits.

Perhaps in correlation with the enlargement of the eyes and of the auditory parts of the brain, the cranium has become expanded laterally, especially in the occipital region (*figs. 86–93*). The middle part of the cranium between the posterior molars and the auditory bullæ appears relatively long, possibly in part because the orbits, in shifting forward, have carried with them the alveolar processes of the maxillæ. As the muzzle is produced anteriorly there is little evidence of crowding in the front part of the dental arch except when the upper

FIG. 77. THE SLOW LORIS (*Nycticebus coucang*). AFTER D. G. ELLIOT, FROM A SPECIMEN IN THE NEW YORK ZOÖLOGICAL PARK

Habitat: Bengal, Burma. Suborder Lemuroidea, family Lorisidæ. One of nature's experiments in evolving large-eyed, short-jawed primates.

canines are considerably enlarged, as in *Nycticebus natunæ* (*fig. 86*). The molar series in *Nycticebus* is restricted posteriorly, the third molars being small, a tendency shown in other groups of primates.

The loss of $p^1$ in the upper jaw and $p_1$ in the lower jaw, on the other hand, was probably coincident with the transformation in the lower front teeth by which the canine was taken over into the incisor series, and the second lower premolar became enlarged and subcaniniform.

FIG. 79. *Loris tardigradus*, × 3 / 2

FIG. 81. *Perodicticus potto*, × 1

FIG. 78. *Nycticebus natunæ*, × 3 / 2

FIG. 80. *Arctocebus calabarenssi*, × 3/ 2

FIGS. 78 TO 93, INCLUSIVE. COMPARATIVE SERIES: SKULLS OF RECENT LORISIDÆ

**Photographs by A. E. Anderson, figures rearranged from D. G. Elliot's monograph on the Primates. Plates loaned by the American Museum of Natural History.**

This, in turn, may have been conditioned by the lemurid habit of cleaning the fur with the thick tongue and the lower front teeth. The

FIG. 83. *Loris tardigradus*, × 3 / 2

FIG. 82. *Nycticebus natunæ*, × 3/2

lorises are said to feed upon leaves and young shoots, fruits, insects, birds and bird eggs, and for this mixed diet their sharp piercing canines and low-cusped cheek teeth appear well adapted.

The genera *Nycticebus*, *Loris*, *Arctocebus* and *Perodicticus* appear to form a structural series (*figs. 86–89*), showing a gradual loss of more primitive characters in the cheek teeth.

FIG. 85. *Perodicticus potto*, × 1

FIG. 84. *Arctocebus calabarensis*, × 3/2

Fig. 87. *Loris tardigradus*, × 3/2

Fig. 86. *Nycticebus natuna*, × 3/2

FIG. 89. *Perodicticus potto*, × 1

FIG. 88. *Arctocebus calabarensis*, × 3/2

Fig. 91. *Loris tardigradus*, × 3/2

Fig. 90 *Nycticebus natuna* × 3/2

FIG 92. *Arctocebus calabarensis*, × 3/2

FIG. 93. *Perodicticus potto*, × 1

*Nycticebus.* The dentition of *Nycticebus natunæ* is relatively primitive in the fact that $p^3$ has a well-developed internal cusp like that in the Eocene lemurs, while $p^4$ likewise retains a well developed postero-internal cingulum and sharp external cingulum, parastyle and metastyle. The molars also retain some of the crescentic or V-shaped form of the principal cusps usually found in Eocene primates. The proto- and metaconules are also distinct, and except on $m^3$ they have a well-developed cingulum-hypocone. The upper incisors, on the other hand, are often quite small. The canines are large and dagger-like with a pronounced worn surface on the postero-lingual face for articulation with the high, caniniform lower premolar ($p_2$).

*Arctocebus.* This genus is more or less intermediate in skull and dental characters between *Nycticebus* and *Loris*, on the one hand, and *Perodicticus* on the other.

*Perodicticus.* As compared with other lorises this retrogressively specialized genus has comparatively small orbits, a coarse, wider muzzle, stouter zygomatic arches and lower jaw, and a less voluminous brain case. The incisors and canines exhibit the typical lemuroid specializations, being procumbent and styloid. The lower anterior premolar ($p_2$) is enlarged and more or less caniniform. In the upper dentition there are three premolars, only the first of the primitive placental series being absent. The upper canine is considerably enlarged and dagger-like, directed vertically downward, and adapted perhaps to piercing fruit and to killing insects and small animals. The first functional upper premolar (homologous with $p^2$) is somewhat large and partly resembles the canine, since its border articulated with the subcaniniform $p_2$. $P^3$ is quite small, with very simple rounded crown, which may safely be regarded as degenerate in form. The rounded fourth upper premolar is bicuspid, so that $p^4$ and $p^3$ are very unlike. The first and second upper molars are tritubercular, with rounded cusps lacking external cingula and with very feeble hypocones.

The rounded form of all the cheek teeth is certainly a degenerate and secondary character. It has been paralleled in other phyla of mammals, as among the Viverridæ, Procyonidæ, Lemuridæ (*Chirogale, Attililemur*), Cebidæ, Hapalidæ. Similarly in the lower teeth of *Perodicticus* the cusps are for the most part blunt and rounded. This retrogressive rounding of the teeth is also observed in modern man and to a certain extent in the chimpanzee, and is often connected with omnivorous habits. In *Perodicticus* the thickened form of the zygomatic arch, the widening of the muzzle, and the relatively small size of the orbits and braincase are probably all degenerative specializations, derived, through the conditions preserved in *Arctocebus*, from the more primitive conditions of *Nycticebus*.

Thus, careful and repeated studies of the skulls and dentitions of recent lorises and galagos lead to the provisional conclusion that on the whole the least specialized dentition is that of *Nycticebus*. Considering the dentition of the whole group, degeneration, or the loss of primitive characters, in this case, as in many others, has brought about an apparent simplicity or primitiveness in the end stages, which is at first sight very deceptive and likely to lead to erroneous phylogenetic conclusions.

Unfortunately but little or nothing is known of the palaeontological history of the Lorisidæ. *Pronycticebus*, of the Bartonian or Middle Eocene of France, represented by a skull (*fig. 133*) with well preserved cheek teeth, was regarded by its discoverer, Grandidier (1905), as at least structurally ancestral to the existing *Nycticebus*; in many respects it is certainly more primitive than that animal and stands on a lower stage of evolution. Stehlin, on the other hand, in his great work on the primates of the Swiss Eocene (1916, pp. 1421–1423), shows that *Pronycticebus* (*fig. 132*) resembles *Anchomomys* (*figs. 128, 129, 130*) in many characters of the dentition; and thus it may be connected with the stem of the tarsioid series (see below, page 393). *Pseudoloris* (*figs. 126, 127*), another primate of Bartonian age, also appears to be related to the Eocene tarsioids rather than to the lorises (Stehlin, *op. cit.*, pp. 1396–1400).

***In conclusion, the Lorisidæ in their cranial and dental construction carry further the normal line of lemuroid evolution indicated in some of the smaller Lemuridæ, such as Microcebus and Chirogale, which they closely resemble in many characters. Their evolutionary trends contrast widely with those of many of the higher primates, in which the shortening of the face and its retraction beneath the braincase foreshadow the human conditions. So, too, the dentition of the Lorisidæ as a whole, although***

*sometimes retrogressive in the molar region, parallels that of the smaller lemurs and to a certain extent that of the tarsioids, but contains no promise of human possibilities.*

## II. THE GALAGOS (GALAGIDÆ)

The galagos were formerly united with the lorises in the family Lorisidæ, but they differ very widely from them in the elongation of the tarsus and in the more *Tarsius*-like general appearance (*fig. 94*), so that they have lately been set apart as a separate family (Pocock, 1918). Their fossil history is entirely unknown.

FIG. 94. HEMIGALAGO DEMIDOFFI. WEST AND CENTRAL AFRICA. AFTER ELLIOT
Suborder Lemuroidea, family Galagidæ

FIG. 95. *Hemigalago demidoffi*, × 2

FIG. 96. *Galago alleni*, × 3 / 2

FIG. 97. *Galago crassicaudatus*, × 1

FIG. 98. *Galago elegantulus*, × 3 / 2

FIGS. 95 TO 110, INCLUSIVE. COMPARATIVE SERIES: SKULLS OF RECENT GALAGIDÆ
Photographs by A. E. Anderson; skulls after Elliot, rearranged. Plates loaned by the American Museum of Natural History.

FIG. 99. *Hemigalago demidoffi*, × 2

FIG. 100. *Galago alleni*, × 3/2

FIG. 101. *Galago crassicaudatus*, × 1

FIG. 102. *Galago elegantulus*, × 3/2

FIG. 103. *Hemigalago demidoffi*, × 2

FIG. 104. *Galago alleni*, × 3 / 2

FIG. 105. *Galago crassicaudatus*, × 1

FIG. 106. *Galago elegantulus*, × 3 / 2

FIG. 107. *Hemigalago demidoffi*, × 2

FIG. 108. *Galago alleni*, × 3/2

FIG. 109. *Galago crassicaudatus*, × 1

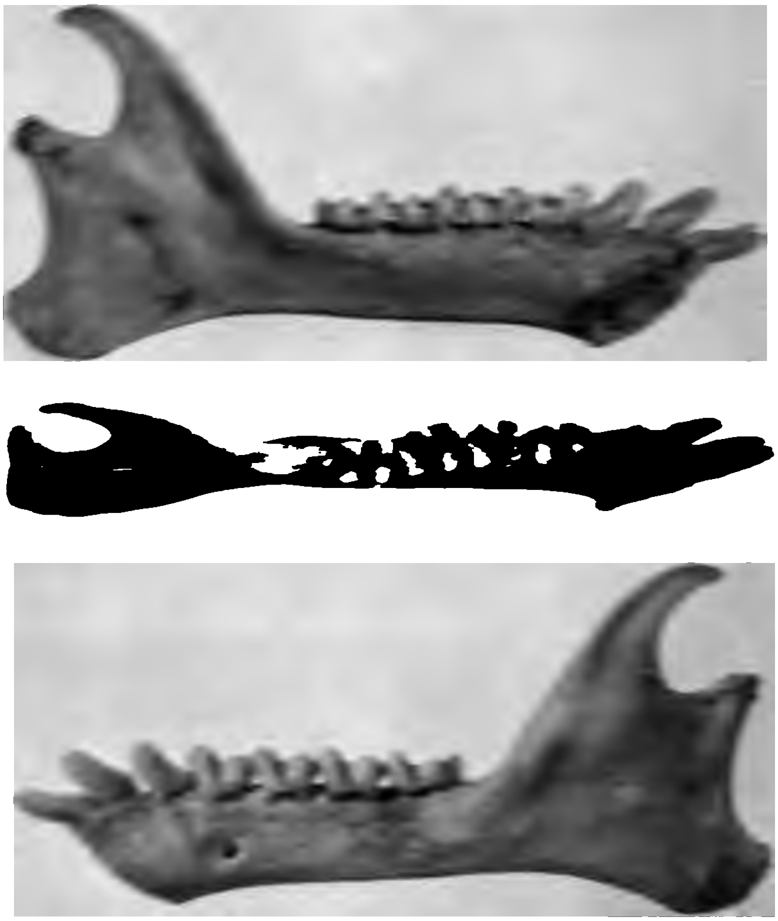
FIG. 110. *Galago elegantulus*, × 3/2

They are essentially nocturnal in habits and accordingly they parallel the Lorisidæ and Tarsiidæ in the enlargement of the orbits, in the restriction of the interorbital region, in the pointed elongate form of the muzzle, and in the transverse expansion of the braincase. But they differ from the typical Lorisidæ in the following skull characters: (1) the orbits (*figs. 107–110*) are directed more outward and are usually even larger than in the Lorisidæ; (2) the orbital rims and zygomatic arches are extremely delicate; (3) the cranium is not flattened posteriorly but is decidedly rounded across the occiput, and the mastoids, although inflated, do not project laterally; (4) the basicranial region (*figs. 102–105*) is often longer and the midcranial region relatively shorter; (5) the palate and dental arch are often narrower; (6) the mandible (*figs. 99–102*) is longer and much more slender and the ascending ramus is narrower. The skull as a whole is longer and narrower, with a more elongate muzzle and with the face even more produced in front of the cranium.

There are no very important differences between the galagos and the lorises in their lemur-like incisors and canines (*fig. 111*), but the fourth premolars of the galagos are submolariform, with a well developed cingulum-hypocone and two external cusps. Similarly, the fourth lower premolars are more advanced and submolariform, with well developed talonids, while those in the Lorisidæ are compressed anteroposteriorly, with reduced talonids. The upper molars are of the narrow tritubercular type, often with conspicuous posterior projections in the region of the metastyles and the upper molars with prominent cingulum-hypocones. They feed upon a mixed diet including fruits, insects, and small birds and their eggs (Lydekker).

*Galago elegantulus* (*figs. 98, 102, 106*) and *Hemigalago* (*figs. 95, 99, 103*) have extremely large eyes and well rounded crania, so that they especially suggest the tarsioids, but they retain the projecting nose and many other lemuroid characters (Pocock, 1918).

Thus the galagos are unquestionably true lemuroids, which parallel the *Tarsius* group, but are not ancestral to it. Nevertheless they illustrate, in certain characters, some of the structural stages by which the tarsioid grade of evolution was derived from that of the primitive lemuroids.



[illegible] U. S.
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[illegible] shows the comb-like specialization of the lower front teeth [illegible] and the relatively advanced stage of the [illegible].

## III. THE TARSIOIDS (TARSIOIDEA)

### NORTH AMERICAN EOCENE TARSIOIDS

The Eocene tarsioids of North America have been described especially by Cope (1885), Osborn (1902), Wortman (1904), and Matthew (1915). They include a number of early specialized side lines of the Lower and Middle Eocene, such as *Tetonius*, *Absarokius*, *Anaptomorphus*, *Uintanius*, together with somewhat less specialized and more central but on the whole later genera of the Middle Eocene, especially *Omomys* and *Hemiacodon*. They are not known in later formations. On account of their various specializations none of them seems to be directly ancestral to the modern *Tarsius*, which is more probably derived from some Eurasiatic Eocene member of the group. They are all small and some are very minute in size, one of them (*Tetonius musculus* Matthew) having the three lower molars not more than 5 mm. in length. From the fairly well preserved skull of *Tetonius homunculus*, noted below (*fig. 118*), and from fragmentary remains of the skull in other genera, it appears that the American Eocene tarsioids, like their contemporary relatives in Europe, had very large orbits and were possibly nocturnal in habits, like the existing lorises, galagos and *Tarsius;* also that the braincase was widely expanded transversely, with slight or no sagittal crest. The jaws were slender (*fig. 112*) to deep (*fig. 119*) in front, the latter in those with enlarged front teeth; lower front teeth variously modified, but often with a pair of enlarged proclivous lower canines or incisors (*fig. 118*); premolar series reduced, the third and fourth upper premolars (*figs. 112, 116, 117, 119, 125*) tending to become bicuspid, the fourth lower premolar (*figs. 112, 118, 125*) often with high compressed crown; upper molars triangular (*figs. 112, 113, 116, 117, 119, 125*), wide transversely, in correlation with transverse widening of the talonids of the lower molars (*figs. 119, 124*); trigonids small, high; talonids low and large. Olfactory parts of skull much restricted; optic and auditory parts greatly enlarged (*fig. 123*). Limbs, so far as known, adapted for leaping in the trees, as in the modern *Tarsius*. This animal is said to feed upon insects and small reptiles, but apparently not upon fruits (Lydekker).

The known American Eocene tarsioids were rather widely separated from the contemporary lemuroids, both in dentition and in skull characters.

*Omomys*. Apparently the least specialized of the American forms is the genus *Omomys* Leidy (*fig. 112*), from the Lower and Middle Eocene of Wyoming. As described by Wortman (1904) and by Matthew (1915), the dental formula is $I\frac{?}{2}\,C\frac{?}{1}\,P\frac{3}{3}\,M\frac{3}{3}$ which, so far as known, is identical with that of the South American monkeys. The lower incisors are procumbent and the medial pair somewhat enlarged, the second small. The lower canine also is semi-procumbent, tending to become like the incisors. Thus even in this early genus there is already a tendency toward the enlargement and procumbency of the medial and lower front teeth, a feature which in some tarsioids finally results in an almost rodent-like condition.

The first lower premolar of the primitive primates has already been eliminated. The second has a pointed conical tip, the third ($p_3$) has a high, pointed protoconid, a triangular base, with an incipient metaconid; it also has a very small and crowded talonid overlapped by the front part of $p_4$. In $p_4$ the crown is submolariform, as there is a trigonid with an incipient paraconid and well developed metaconid in addition to the high protoconid; but the talonid is very small and crowded, and is widely overlapped by $m_1$, in correlation with the anteroposterior elongation of the lower molars. Thus there is a greater contrast between $p_4$ and $m_1$ than there is in the more primitive contemporary primates of the family Notharctidæ (described in Part II), and very possibly the abbreviation of the talonid of $p_4$ is partly secondary in this family.

The lower molars are fairly primitive, with a high, well defined trigonid and a comparatively low talonid. But the hypoconid is unusually large and projects buccally. This is correlated with the transverse widening of the upper molars and with the displacement of the para- and metacones toward the buccal margin of the crown. (Analogous instances have been cited in Part II of this work.) The third lower molar has a reduced trigonid and a fairly large median cusp, or hypoconulid. In general the lower dentition, even of this relatively primitive member of the tarsioid series, is probably more specialized than that of the oldest Notharctidæ, described in Part II.

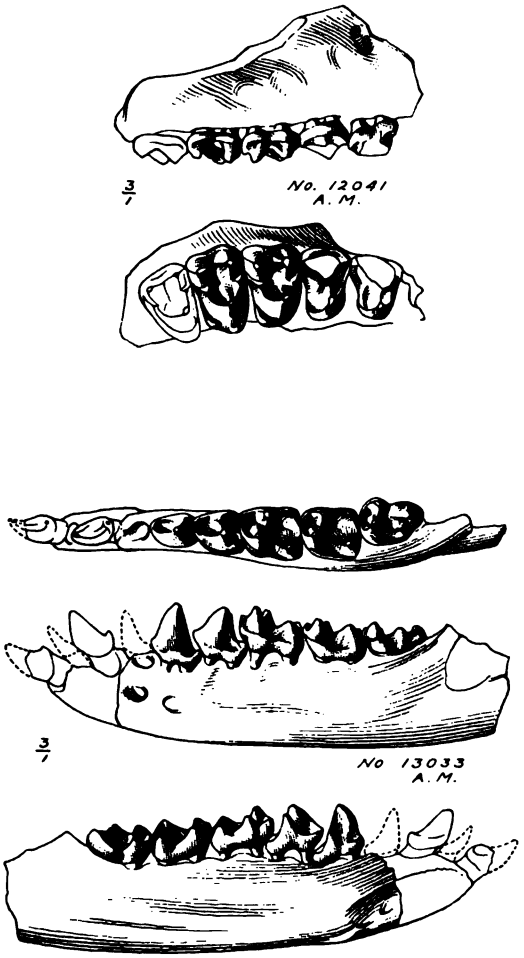


**Fig. 112.** *Omomys* sp. Upper and Lower Jaws. × 3. After W. D. Matthew

Upper jaw, outer and crown views. Upper Bridger beds (Middle Eocene), Bridger basin, Wyoming. Lower jaw, inner, outer and crown views. Lower Bridger beds (Middle Eocene), Bridger basin, Wyoming. Front teeth restored from Amer. Mus. no. 12,600. Suborder Tarsioidea, family Tarsiidæ.

The upper incisors and canines of *Omomys* are not known. The first premolar was probably wanting and $p^2$ was certainly small, as shown by its alveolus. $P^3$ is bicuspid and like $p^4$, but less advanced. It has a high, pointed apex on the outer side of the crown and a low lingual cusp continuous with the internal cingulum. $P^4$ is fully bicuspid, with a very prominent piercing external apex. Thus the tendency for $p^3$ and $p^4$ to become closely alike is evident even in the most primitive of this family.

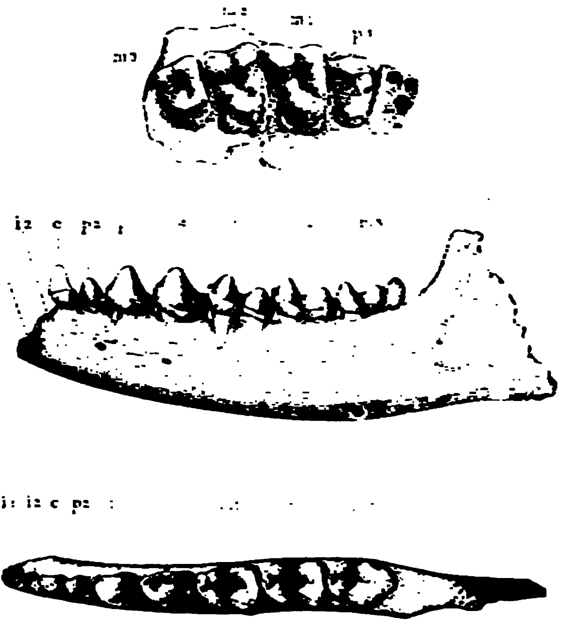


FIG. 113. *Hemiacodon gracilis.* LOWER JAW (LEFT RAMUS) AND RIGHT UPPER CHEEK TEETH. × 5/2. AFTER WORTMAN

Upper Bridger beds (Middle Eocene), Bridger basin, Wyoming. Suborder Tarsioidea, family Tarsiidæ.

The upper molars of *Omomys* are wide, in correlation with the width of the talonid. The external cingulum is reduced and the para- and metacones are more or less rounded, all relatively advanced characters. Well defined V-shaped proto- and metaconules are present on the sharp slopes of the protocones and have the usual relations with the parts of the lower molars. The interdental spaces are well marked, in correlation with the comparatively primitive condition of the trigonids and the feeble development of the hypocones. They are retained throughout the family and even in the modern *Tarsius*.

*Hemiacodon*. This genus, from the Middle Eocene of Wyoming, is closely related to *Omomys* and may be regarded as a derivative of it (Matthew, 1915, p. 451). The wide upper molars (*fig. 113*) have large rounded proto- and metaconules and two small accessory cusps (proto- and hypostyles) on the internal cingulum of $m^1$, $m^2$. The third upper molar is much smaller than the others; the enamel surface of the crowns is wrinkled. The lower premolars, $p_4$, $p_3$, are somewhat but not greatly enlarged, and the lower front teeth are gently procumbent (*fig. 114*). The lower molars $m_1$, $m_2$ (*figs. 113, 114*) have

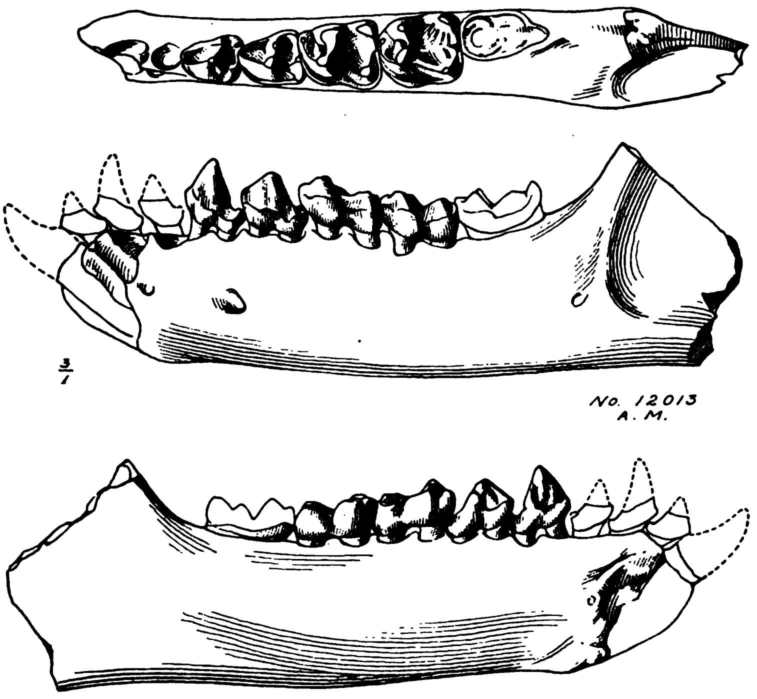


**Fig. 114.** ***Hemiacodon gracilis*****.** LOWER JAW (LEFT RAMUS). × 3. AFTER MATTHEW

**Upper Bridger beds (Middle Eocene), Bridger basin, Wyoming. Front teeth restored from Amer. Mus. no. 12,037. Suborder Tarsioidea, family Tarsiidæ.**

the wide talonids, characteristic of the group, and correlated with the great width of the upper molars. The lower front teeth, or central incisors, are semi-procumbent and considerably enlarged; the canines are small (*fig. 114*).

With regard to skull characters Wortman states (1904, p. 137) that in the fragment of a maxillary which he figures (*fig. 113*), "the anterior limits of the malar can be easily made out. It is thus shown that it does not reach forward to the lachrymal, but leaves the maxillary a considerable share in the anterior boundary of the orbit, as in the monkeys. The rather small, single, infraorbital foramen is situated above and opposite the posterior edge of the third premolar, about in the same relative position as that of the squirrel monkey. The maxillary gives further evidence of proportionately large orbits, and if the superior dental formula was the same as that for the lower jaw, the muzzle must have been considerably abbreviated. The whole aspect is, in fact, not only characteristically Primate, but one considerably advanced."

*Washakius.* As described by Leidy (1873), Wortman (1904), and Matthew (1915), *Washakius* (*figs. 115, 116*) is another very small tarsioid from the Middle Eocene of Wyoming, which has the dental formula $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{3}{3}$ $M\frac{3}{3}$. *Washakius* is distinguished especially by the presence of metastylids (accessory cusps posterolingual to the metaconids of the lower molars), and by the coarse wrinkling of the enamel in the upper molars. The latter have the main cusps well rounded rather than angulate, and the first and second upper molars have small but rounded hypocones. The lower incisors were small, much less procumbent than in *Hemiacodon;* the lower canine was small, not procumbent. From the shape of the superior maxilla, figured by Wortman (1904, p. 210), it seems very likely that the orbit was large, as it was in *Hemiacodon* and in the older related genus *Shoshonius* (*fig. 117*), which is distinguished especially by its large mesostyles and by the feeble development of the internal cingulum cusps.

*Tetonius.* That the tarsioid group very early became separated from the lower lemuroid primates is indicated by the fact that even in the Lower Eocene it is already represented by a relatively specialized member, *Tetonius homunculus* (*figs. 118, 119, 121, 123*), the "*Anaptomorphus*" *homunculus* of Cope. In this animal, as lately

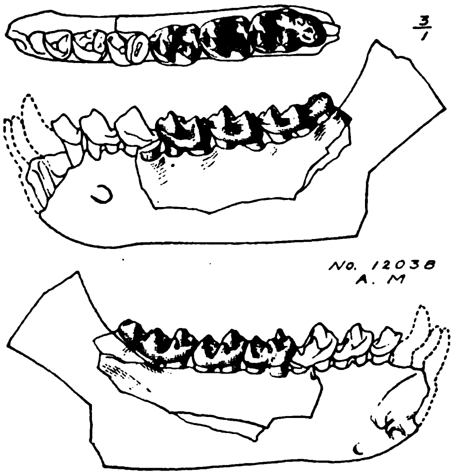
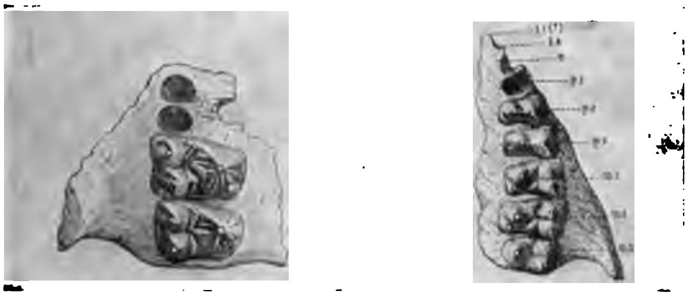


FIG. 115. *Washakius insignis*. LOWER JAW (LEFT RAMUS). × 3. AFTER MATTHEW

**Upper Bridger beds (Middle Eocene), Bridger basin, Wyoming. Suborder Tarsioidea, family Tarsiidæ.**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146

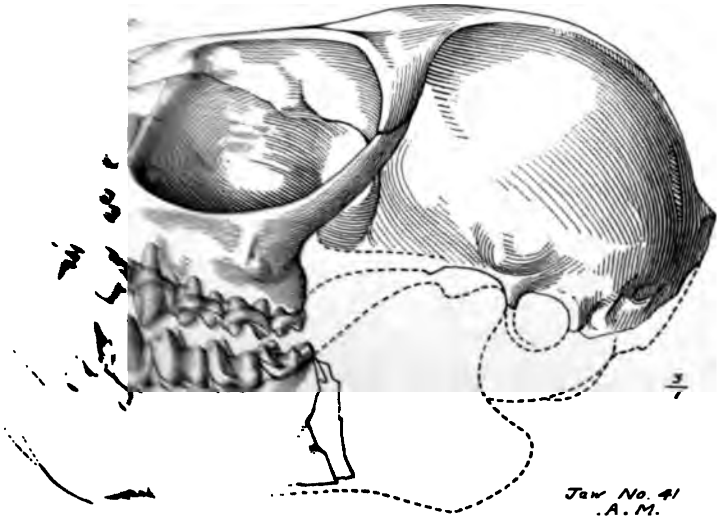
FIG. 116. *Washakius insignis*. UPPER PREMOLARS AND MOLARS. AFTER WORTMAN

**145.**—Second and third right upper molars and fragment of maxilla. × 4.

**146.**—Left upper jaw with $p^3$–$m^3$. × 3 / 2. Upper Bridger beds (Middle Eocene), **Bridger basin**, Wyoming. Suborder Tarsioidea, family Tarsiidæ.

[illegible] Right Maxilla. × 4. After Granger

[illegible] near Lost Cabin, Wyoming. Suborder Tarsioidea,



[illegible] homunculus. Skull and Lower Jaw. × 3. After Matthew

[illegible] of skull restored. Gray Bull beds (Lower Eocene), Bighorn basin, Wyoming. Lower jaw from no. 41, same horizon and locality. Suborder Tarsioidea, family Tarsiidae.

redescribed by Matthew (1915), one pair of the lower front teeth, possibly the opposite canines, is greatly enlarged and procumbent, and produced in rodent-like or diprotodont fashion, the dental formula being $\mathrm{I}\frac{?}{0}\ \mathrm{C}\frac{1}{1}\ \mathrm{P}\frac{2}{2}\ \mathrm{M}\frac{3}{3}$ (Matthew). The enlargement of the lower front teeth has conditioned the loss of the lower incisors, the development of a diastema behind the large procumbent tooth, the deepening of the front part of the mandible, the crowding of the premolar series and the consequent enlargement and strengthening of the insertion

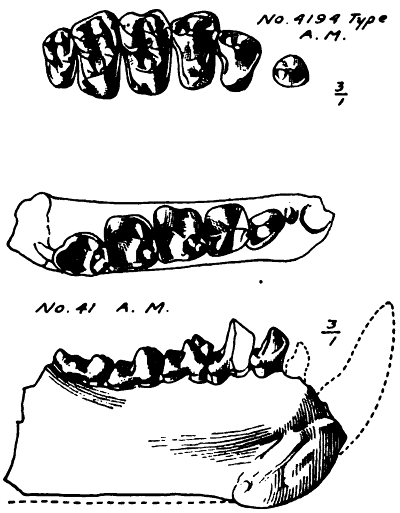


FIG. 119. *Tetonius homunculus.* UPPER TEETH AND LOWER JAW, PART OF RIGHT RAMUS. × 3. AFTER MATTHEW

Gray Bull beds (Lower Eocene), Bighorn basin, Wyoming. Suborder Tarsioidea, family Tarsiidæ.

areas of the jaw muscles, both of the skull and mandible. The fourth lower and the fourth upper premolars have large piercing apices, and the first and second lower molars are much widened across the talonids. The upper molars are very wide transversely and narrow anteroposteriorly, with rounded para- and metacones. The third molars are small. These modifications are perhaps adapted either for piercing and breaking the hard bodies of insects or for extracting and crushing seeds from fruits.

Fig. 120. *Tarsius spectrum*

Fig. 121. *Tetonius homunculus*. Amer. Mus., no. 4,194. Gray Bull beds (Lower Eocene), Bighorn basin, Wyoming.

Figs. 120 to 123, inclusive. Comparative Series: Skulls of Recent Tarsius and of Eocene Tetonius. × 3

Suborder Tarsioidea, family Tarsiidae.

FIG. 122. *Tarsius spectrum*

FIG. 123. *Tetonius homunculus*

The orbits (*fig. 123*) are much enlarged, the braincase expanded and the muzzle narrow, so that the general appearance of the skull approaches that of *Tarsius*. Even the construction of the auditory region points in the same direction, since the bullæ were expanded and pressed forward against the lower part of the braincase.

A more detailed examination of the type skull of *Tetonius homunculus* supports the generally accepted view that this animal was a tarsioid, although already too specialized in the dentition to be directly ancestral to the modern *Tarsius*.

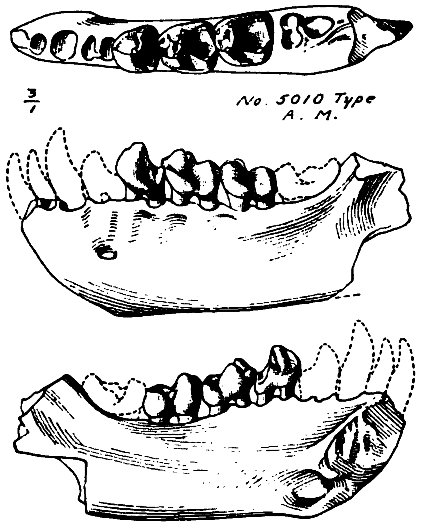


FIG. 124. *Anaptomorphus æmulus*. LOWER JAW (RIGHT RAMUS). × 3. AFTER MATTHEW

Lower Bridger beds (Middle Eocene), Bridger basin, Wyoming. Suborder Tarsioidea, family Tarsiidæ.

*Anaptomorphus*. This genus (*fig. 124*) has the dental formula $I_{\bar{2}}\ C_{\bar{1}}\ P_{\bar{2}}\ M_{\bar{3}}$, the same as for the Old World series of Primates, but it is a true tarsioid in the form of its lower molars and premolars, and widely different from *Parapithecus*, the oldest and most tarsioid primate of the Old World. Its lower front teeth are not enlarged nor strongly procumbent; the jaw is stout and deep anteriorly The fourth lower premolar is not as large as in the more specialized genera *Uintanius* (*fig. 125*) and *Absarokius*. These specializations of the fourth premolars surely remove these genera from ancestral relationships with any of the higher primates.

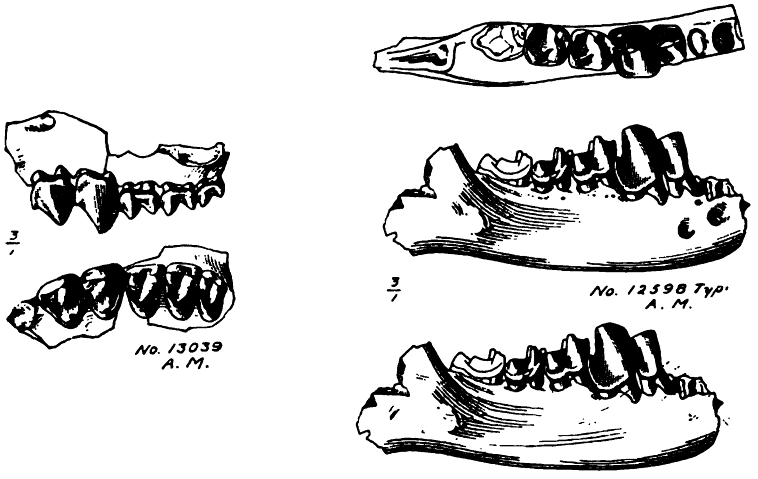


FIG. 125. *Uintanius turriculorum*. LOWER JAW (RIGHT RAMUS) AND LEFT UPPER CHEEK TEETH. × 3. AFTER MATTHEW

Lower jaw, Lower Bridger beds (Middle Eocene), Bridger basin, Wyoming. Upper teeth, Upper Bridger beds (Middle Eocene), Bridger basin, Wyoming. Suborder Tarsioidea, family Tarsiidæ.

## EUROPEAN EOCENE TARSIOIDS

In the European Eocene the tarsioid group is represented by seven genera, mostly known from teeth and jaws, except *Pronycticebus* and *Necrolemur*, which are known from well preserved skulls. All have recently been carefully described and figured by Stehlin (1916). The group first appears in the Lower and Middle Lutetian beds, in the second half of the Lower Eocene; and after passing through the Upper Lutetian, Bartonian and Lower Ludian beds, disappears during the Upper Ludian of Upper Eocene age. Its range in Europe is thus nearly contemporaneous with the range of the related genera in America, although not extending so far down into the Lower Eocene as do the latter. No known genera of tarsioids are common to Europe and America; and thus there is evidence that, although derived from a common stock, perhaps of Lower Eocene age, the tarsioids of the two continents followed independent lines of evolution without faunal interchange (Stehlin). Both the American and European groups are "polyphyletic," and although we know only fragments of different phyla, they afford strong evidence of the evolution of the upper molars from the triangular to the quadrangular stage, in the normal mammalian manner described in earlier parts of this work.

*Pseudoloris.* Perhaps the most primitive of the European genera is *Pseudoloris* (*figs. 126, 127*), from the Bartonian (Middle Eocene) of France, which has tritubercular upper molars with well developed proto- and metaconules, small cingulum-hypocones and very small protostyles, or projections of the anterointernal cingula. The general form of the upper molars suggests those of the recent lorises and galagos, as noted by Stehlin (1916, p. 1396), but, as he also suggests, the resemblances are not sufficiently close to prove a near relationship, and it is far more probable that *Pseudoloris* is a true tarsioid, only remotely related to the Lorisidæ, which appear to be *Tarsius*-like derivatives of some primitive Eocene lemuroids. *Pseudoloris* is probably related, by descent from a common ancestor, to the American tarsioids. As it had a pair of enlarged lower front teeth, which are regarded by Stehlin as canines, it resembles rather *Tetonius* in this character; on the other hand, its molars recall those of *Omomys*, except for the large size of the metaconules of the upper molars and the loss of the paraconids of the second and third lower molars.

*Anchomomys.* This genus is known from two species: one in the Lutetian or summit of the Lower Eocene of France and Switzerland, the other in the Bartonian or Middle Eocene of France. It differs from *Pseudoloris* especially in the reduction or absence of the metaconules. In *Anchomomys quercyi* (*fig. 130*) the first and second upper molars are less wide transversely and relatively wider anteroposteriorly than in *Pseudoloris;* the posterointernal corners of the crown are developing, so that the contour is becoming more quadrate. The orbit in this genus was certainly large, as shown by the form of its floor and border, above the maxilla. The mandible of *Anchomomys* cfr. *Gaillardi*, figured by Stehlin (*op. cit.* p. 1412), shows that the dental formula was probably $I_{\overline{2}}\ C_{\overline{1}}\ P_{\overline{3}}\ M_{\overline{3}}$, as in the American *Anaptomorphus*. The two incisors were small and gently proclivous, the canine large and erect.

Fig. 126. *Pseudoloris parvulus.* Left maxilla, with $p^4$–$m^3$. × 8. Phosphorites near Caylux.

Fig. 128. *Anchomomys gaillardi.* Fragment of left maxilla, with $m^1$-$m^3$. From Lissieu near Lyon. × 6.

Fig. 127. *Pseudoloris parvulus.* Left mandible, with $p_4$–$m_3$. Phosphorites near Caylux.

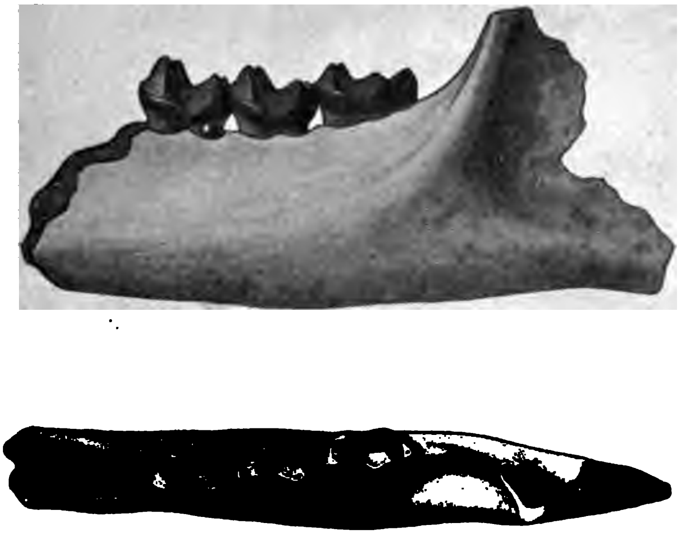


Fig. 129. *Anchomomys gaillardi.* Fragment of left mandible, with $m_1$-$m_3$. From Lissieu, near Lyon. × 6.

Figs. 126 to 129, inclusive. European Eocene Tarsioids. Lower and Upper Cheek Teeth. After Stehlin

**Suborder Tarsioidea,** family Tarsiidæ.

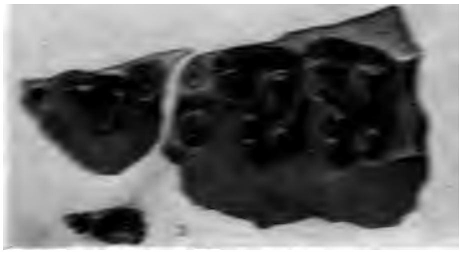


Fig. 151. *Periconodon helveticus*. Left Maxilla with p³–m³. × [illegible]. After Stehlin.

From Egerkingen, Switzerland.

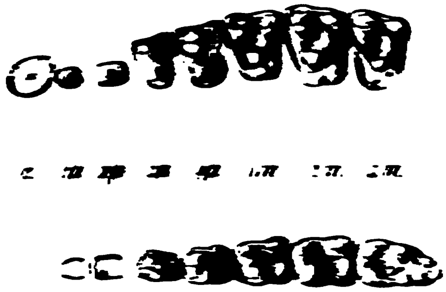


Fig. 152. *Pronycticebus gaudryi*. Left Upper and Right Lower Cheek Teeth. × 2. After Grandidier.

From Memerlein, Lot, France.

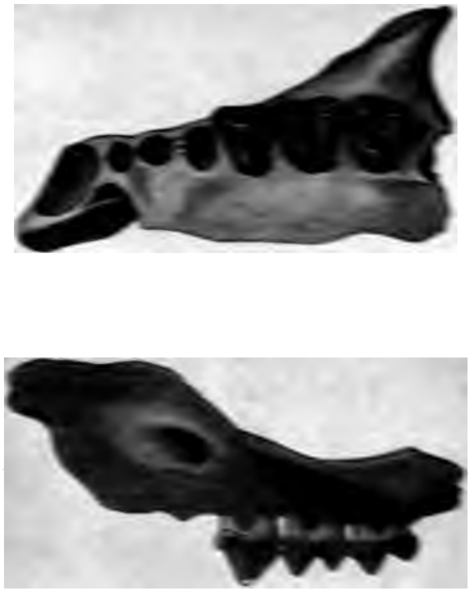


Fig. 150. *Anchomomys quercyi*. Fragment of Left Maxilla with p⁴–m³. × 6. After Stehlin.

From Phosphorites of Quercy, France.

Figs. 150 to 152 inclusive. European Eocene Tarsioids. Upper and Lower Teeth. After Stehlin, Grandidier.

Suborder Tarsioidea. Family Tarsiidae.

***Periconodon.*** In this more specialized relative of *Anchomomys* from the Lower or Middle Lutetian of Switzerland, the metaconules of the upper molars (*fig. 131*) have been suppressed and the cingulum-hypocones and protostyles have become quite prominent. Stehlin (*op. cit.*, p. 1432) notes the striking resemblances of these teetb to the molars of the recent South American monkeys *Chrysothrix* and *Cebus*, but concludes that the hiatus in geological time between the recent and the Eocene primates is far too great to permit us to regard the resemblance in question as indicating close relationship.

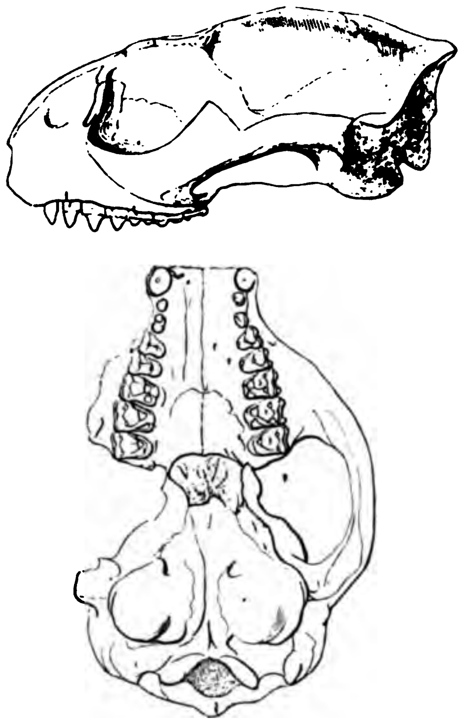


FIG. 133. *Pronycticebus gaudryi.* SKULL, × 1. AFTER GRANDIDIER

Phosphorites (Middle Eocene), of Mermelein (Lot), France. Suborder Tarsioidea, family Tarsiidæ (?).

***Pronycticebus.*** This animal was regarded by its discoverer, Grandidier (1905), as a forerunner of the modern loris, but Stehlin has shown (1916, p. 1422) that its dentition (*figs. 132, 133*) rather indicates relationship with *Anchomomys*. The upper canine was relatively large with a rounded rather than compressed base. All four premolars are retained in both the upper and lower jaws. The first upper premolar is very small and peglike; the second, larger and slightly more advanced but widely different from the third premolar, which is approaching the condition of $p^4$. The latter is bicuspid and quite different in form from $m^1$. The first and second upper molars are of primitive tritubercular type with V-shaped cusps, well developed external cingula, complete proto- and metaconules, and hypocones connected with the cingulum. The third molar is tritubercular with a well developed internal cingulum not rising into a distinct hypocone. The lower cheek teeth are correspondingly primitive and approach the common plan of the primitive Lemuroidea. The skull is also more primitive, more like that of the primitive Notharctidæ, than is that of any other known tarsioid, the face being less reduced than in the known tarsioids, while the braincase, orbits and auditory bullæ are less expanded.

*Nannopithex.* The curious type called *Nannopithex polycarus* by Stehlin (*op. cit.* p. 1392) is represented by a fragment of the right maxilla containing three upper molars (*fig. 134*). The tritubercular first and second upper molars recall those of the American *Hemiacodon* in the unusually large size of the circular metaconules and in the strong development of the cingulum-hypocone. On the other hand, they foreshadow the upper molars of *Necrolemur* cfr. *Zitteli* (*fig. 135*) in the peculiar relations of the protoconule fossa to the anterior slope of the paracone and in the appearance of the large, conspicuous, conical metaconule. The most striking difference is that the cingulum-hypocone is distinct from the posterior slope of the protocone, whereas in *Necrolemur* it is connected with it. However, in the third molar ($m^3$) the cingulum lacks a distinct hypocone and is connected with the posterior slope of the protocone, as in *N. zitteli*. *Nannopithex* also lacks the small accessory cusp between the metaconule and the protocone which is incipient in some specimens of *N. antiquus* (*fig. 136*). Nevertheless the anterior slope of the metaconule of *Nannopithex* is conspicuous and could readily give rise to the conditions in *Necrolemur*.

Stehlin has noted these and other resemblances. but refers to them only as analogies (p. 1393) and doubts the relationship (p. 1395), as he ascribes great importance to the differences in the postero-internal cusp; but he suggests a possible relationship between *Nannopithex* and the American *Washakius*.

But, even if *Nannopithex* be not directly ancestral to *Necrolemur*, it illustrates a stage of molar evolution tending to connect the highly specialized conditions of the upper molars of *Necrolemur* with the more primitive tarsioid stage preserved in *Hemiacodon* and *Washakius*.

FIG. 134. *Nannopithex pollicaris.* $m^{1-3}$ RIGHT. × 8

From the lower Eocene of Egerkingen, Switzerland. Suborder Tarsioidea, family (?) Microchœridæ.

FIG. 135. *Necrolemur* CFR. *Zitteli.* LEFT MAXILLA, WITH $p^3$–$m^3$. × 4

From the Lower Eocene of Egerkingen, Switzerland. Suborder Tarsioidea, family Microchœridæ.

FIGS. 134, 135. COMPARISON OF NANNOPITHEX POLLICARIS AND NECROLEMUR CFR. ZITTELI. AFTER STEHLIN

*Necrolemur and Microchœrus. Necrolemur antiquus* (*fig. 136*) is characterized by the elaborate pattern of the upper molar crowns in which there was a strong tendency toward the development of extra conules and the division of the upper molar crown into anterior and posterior moieties.

According to Stehlin (*op. cit.*, p. 1329) the dental formula was $I\frac{2}{0}C\frac{1}{1}\ P\frac{3}{4}\ M\frac{3}{3}$. There was a pair of enlarged proclivous lower front teeth(*fig.137*), which Stehlin regards as canines. This specialization, with others, removes *Necrolemur* from the line of ascent either to *Tarsius* or to any of the higher primates.

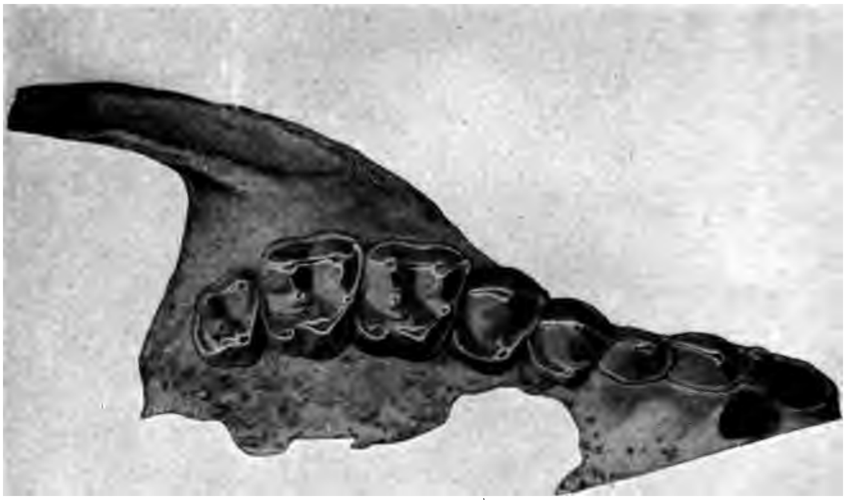


FIG. 136. *Necrolemur antiquus*. RIGHT MAXILLA, WITH LATERAL INCISOR, CANINE AND CHEEK TEETH. × 5. AFTER STEHLIN

From the Phosphorites of Largnol, France. Suborder Tarsioidea, family Micro-Chœridæ.

The skull of *Necrolemur* (*figs. 137, 138, 139, 141*), as known from beautifully preserved specimens, is of a highly modified tarsioid type, with convergent upper dental arches and excessive enlargement of the auditory bullæ, which press forward into the braincase in front of them and are provided with bony external auditory tubes, as in *Tarsius*. The obits are much enlarged, the interorbital portion of the

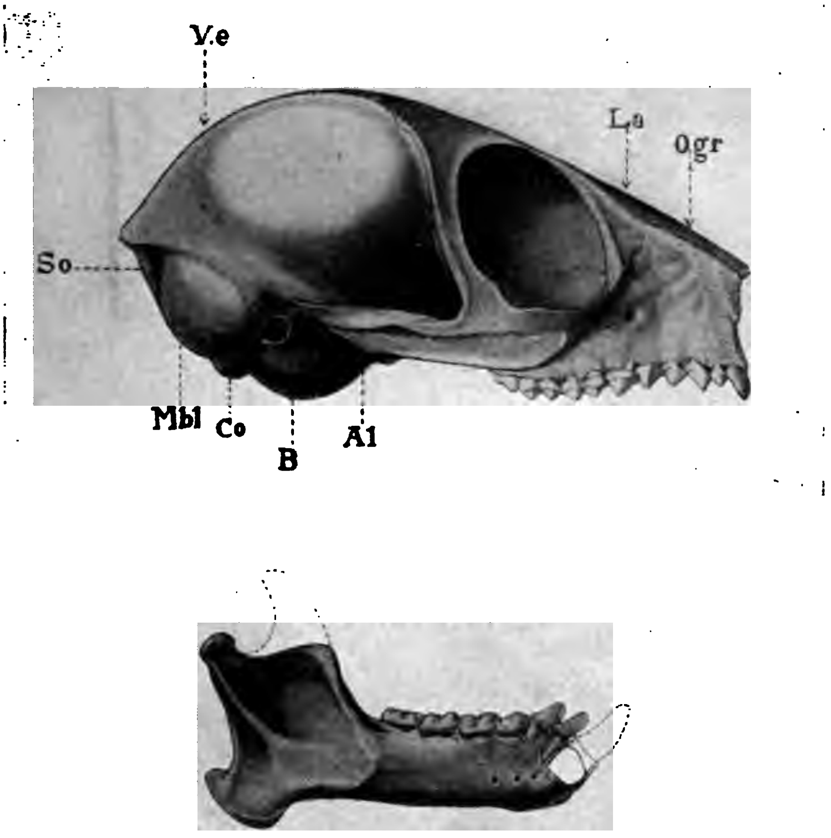


**Fig. 137.** *Necrolemur antiquus.* Reconstruction of Skull and Lower Jaw. × 2. After Stehlin

From the Phosphorites (Middle Eocene) of France. Suborder Tarsioidea, family Microchœridæ.

**Fig. 138.** *Necrolemur antiquus.* Skull in the Princeton University Palæontological Collection. × 2

Courtesy of Dr. W. J. Sinclair.

braincase is reduced to a thin septum; the construction of the lacrymal region is also of tarsioid type. On the other hand, the great inflation of the mastoid region heightens the general resemblance to the skull of *Galago* (*fig. 140*).

The tendency toward a multiplication of small cusps on the surface of the upper molar crowns culminates in the *Microchœrus ornatus* of Stehlin, in which the molar crown of m$^2$ (*fig. 142*) is surmounted by no less than eleven cusps and cuspules. Both the proto- and the metaconule appear to be double. There is a large mesostyle and an accessory stylar cusp on the cingulum-hypocone. The contours of the


FIG. 139


FIG. 140

FIGS. 139, 140. COMPARATIVE SERIES: SKULLS OF NECROLEMUR ANTIQUUS AND GALAGO CRASSICAUDATUS. × 2

**Specimens in the Peabody Museum of Comparative Zoölogy, Harvard University. Courtesy of Dr. Samuel Henshaw. Illustrating the close convergence in skull form between these two genera, which belong respectively in the suborders Tarsioidea and Lemuroidea.**

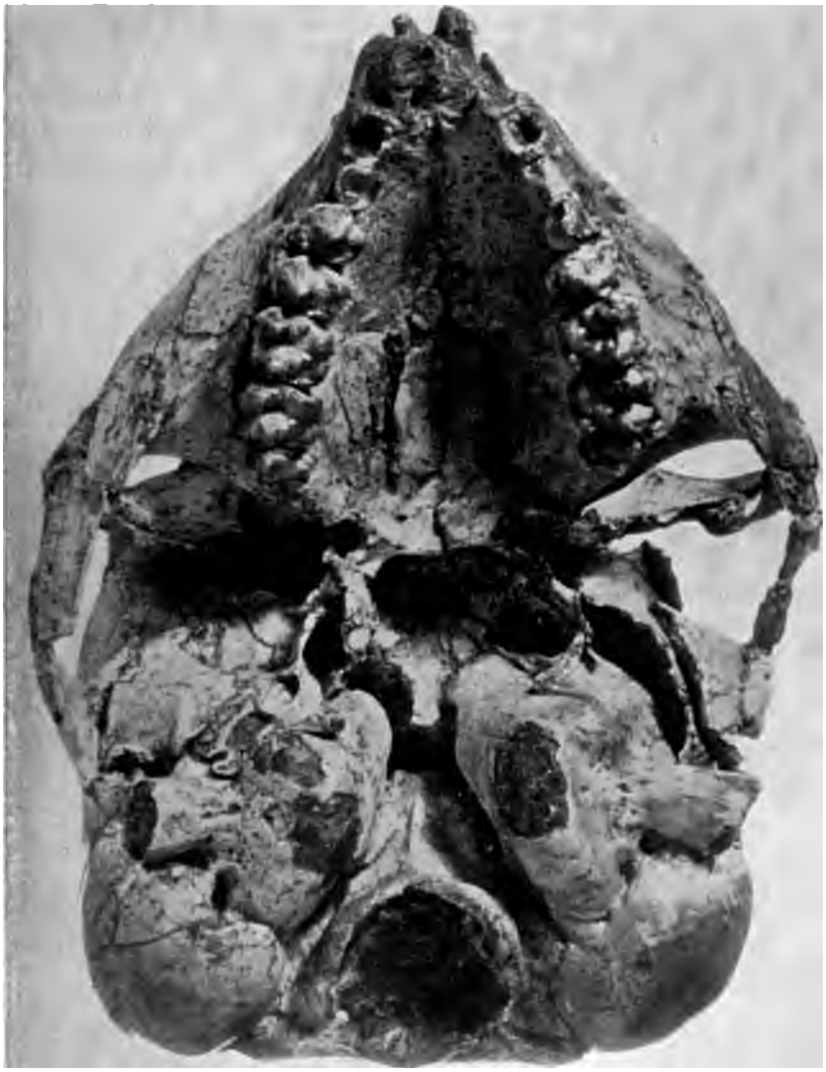


FIG. 141. *Necrolemur antiquus.* PALATAL VIEW OF SKULL. × 3

Specimen in the Museum of Comparative Zoölogy, Harvard University. Courtesy of Dr. Samuel Henshaw. Suborder Tarsioidea, family Microchœridæ.

upper molars are subquadrate and the interdental spaces are practically obliterated. This pseudo-multituberculate specialization evidently preceded the extinction of the family.

The differences separating *Necrolemur* and *Microchœrus* from any of the New World or Old World monkeys are numerous and important, and there is no evidence for deriving any of the higher types directly from this source. Nevertheless these genera exhibit certain important advances in the direction of the Old World primates, among which may be noted the development of quadrate upper molars with subequal anterior and posterior moieties, the development of hypoconulids in the lower molars (*fig. 143*), the final loss of the paraconids in the lower molars and the tendency for the reduction of the trigonid basins, the tendency for $p^4$ and $p^3$, and the corresponding lower teeth, to

FIG. 142. *Microchœrus ornatus*. RIGHT MAXILLA, WITH $p^2$–$m^3$. × 6. AFTER STEHLIN

Upper Eocene of France.

FIG. 143. *Microchœrus ornatus*. RIGHT LOWER CHEEK TEETH, $p_3$–$m_3$, THE FIRST TOOTH DISPLACED. × 4. AFTER STEHLIN

Suborder Tarsioidea, family Microchœridæ.

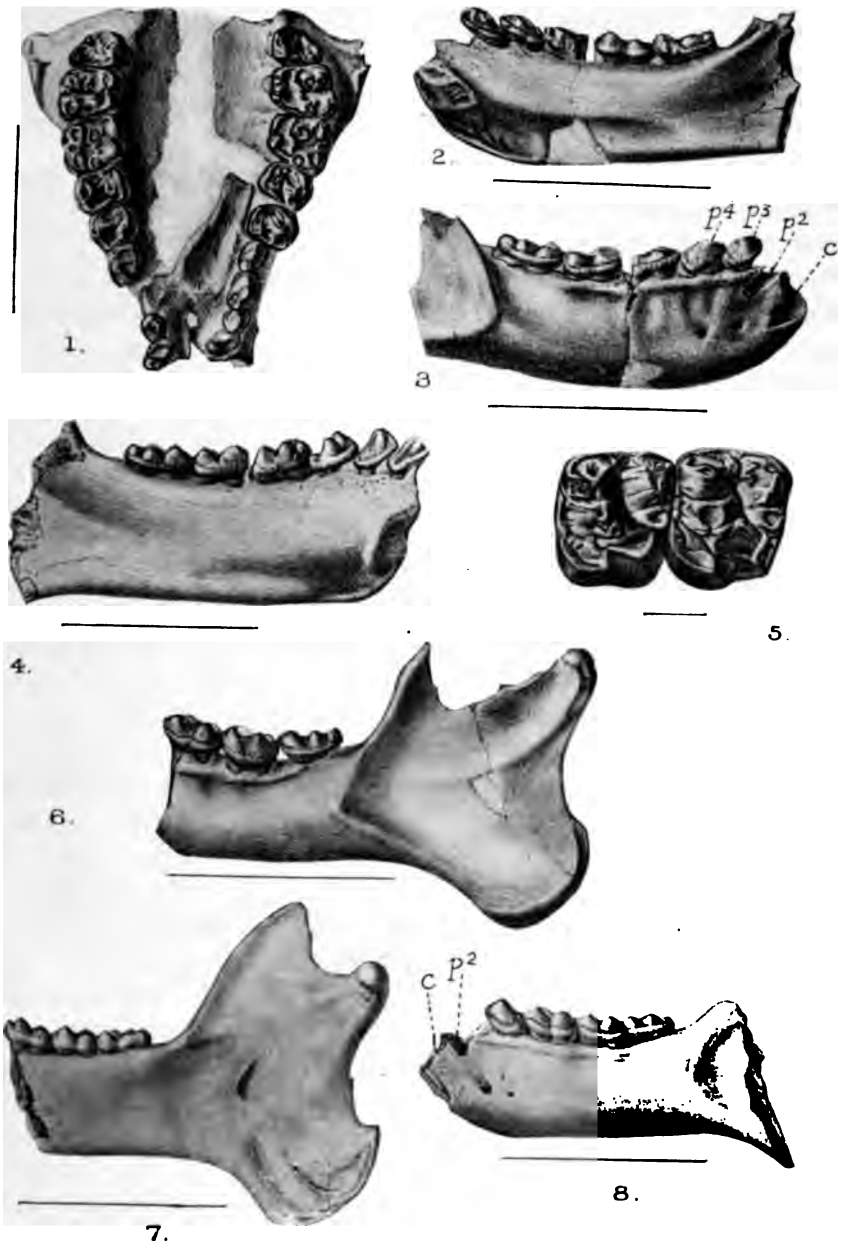


FIG. 144. *Microchœrus* AND *Necrolemur*. ENLARGED. AFTER FORSTER-COOPER

1.—***Microchœrus erinaceus.*** Palate. British Museum. Upper Eocene, Hardwell, Isle of Wight.

2.—Ditto. Right lower ramus, inner side (Cambridge).

3.—Ditto. Right lower ramus, outer side (British Museum). The small socket for the second tooth can be made out as a small black dot at the upper point of the large socket.

4.—Ditto. Right lower ramus, inner side (Cambridge).

5.—Ditto. Upper molars (British Museum).

6.—Ditto. Hind part of left ramus (Cambridge).

7.—***Necrolemur edwardsii.*** Hind part of left ramus (British Museum).

8.—Ditto. Front part of left ramus (British Museum).

The small black lines show the actual sizes of the specimens.

become bicuspid, the incipient development of a bony postorbital partition, the lateral expansion of the base of the braincase, the development of a tubular external auditory meatus, and the tendency for the angle of the mandible to be expanded and for its posterior border to become very large and rounded. Thus *Necrolemur* and *Microchœrus* have advanced far from the primitive tarsioid type and indicate some of the structural stages through which the actual ancestors of the Old World series probably passed.

### THE MODERN TARSIUS

The systematic position and relationships of the Spectral Tarsier, of Borneo and other Malayan islands, including the Philippines, have constituted a long debated question that has a direct bearing upon the problem of man's ancestry. As noted in Part II of this work, *Tarsius* was formerly classed among the Lemuroidea, but all recent investigation has tended to confirm its right to be assigned, together with its Eocene relatives, to a distinct suborder Tarsioidea, coördinate with the other two suborders, Lemuroidea and Anthropoidea. Neither *Tarsius* itself nor its known Eocene relatives, described above, appear to be directly ancestral either to the platyrrhine or to the catarrhine divisions of the Anthropoidea. Nevertheless *Tarsius* parallels the higher primates in so many characters of the brain, skull, reproductive organs and other parts, that a very remote common ancestry of the three suborders seems highly probable.[2] Moreover the earliest known and by far the most primitive representatives of the Anthropoidea, namely, the genus *Parapithecus* from the Lower Oligocene of Egypt, carries that group well back toward a short-jawed and probably large-brained stem, which might be described as tarsioid in a broad sense; while, as will presently be shown, the various Platyrrhinæ appear also to have been derived from another short-jawed and large-brained stock, belonging perhaps to a quite different family of the ancestral tarsioid primates.

With regard to the derivation of *Tarsius*, very possibly *Anchomomys* was more or less closely related to its Eocene ancestors, but

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[2] In this connection see the recent "Discussion on the zoological position and affinities of *Tarsius*:" *Proceedings of the Zoölogical Society of London*, 1920 (Feb.), p. 465.

the loss of the paraconids in the lower molars (*fig. 127*) appears to remove ***Anchomomys*** from the direct line of ascent (Stehlin, p. 1426). The modern genus, although retaining much of its Eocene heritage, has reduced metaconules in the upper molars (*fig. 120*), and it has become further specialized in the extreme enlargement of the orbits (*fig. 122*). Its front teeth are moderately specialized by the reduction of the lower incisors to one on each side. This nocturnal and arboricolous animal is said to feed largely upon insects and small reptiles (Lydekker).

FIG. 145. THE SPECTRAL TARSIER (*Tarsius spectrum*). AFTER DUCKWORTH
Suborder Tarsioidea, family Tarsiidæ.

The palæontological evidence reviewed in this work is surely against Wood-Jones's view that the existing *Tarsius* is the nearest living relative of man. *Tarsius* may well parallel the human condition in the construction of the placenta, and in a few other points noted by Wood-Jones (to all of which I have given careful consideration), but its relationships to man are plainly very indirect and must be traced backward along gradually converging lines to the primitive tarsioid stocks which gave rise at different times and at different places to the higher groups of primates.

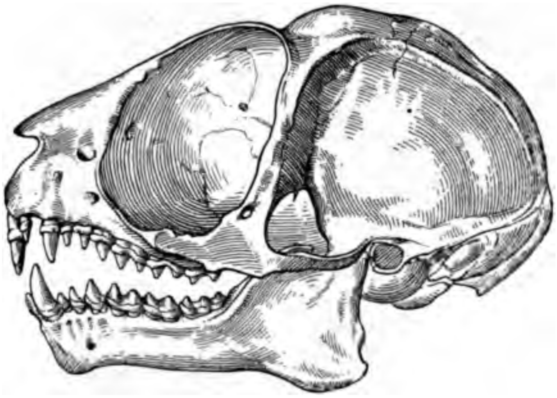

FIG. 146. *Tarsius spectrum*. SKULL. × 2
Suborder Tarsioidea, family Tarsiidæ.

## IV. THE SOUTH AMERICAN MONKEYS (PLATYRRHINAE)

### TERTIARY FOSSIL PLATYRRHINÆ

Of the few South American Tertiary genera which have been attributed to this group, only one of them, the *Homunculus patagonicus* (*fig. 147*) of Ameghino, from the Santa Cruz Miocene of Patagonia, is known from a well preserved jaw and the fore part of the skull. Although this genus was already a true platyrrhine monkey, it does carry us back a short way toward the stem of the group. According to Bluntschli (1913), who has carefully studied the original specimens, the closest resemblances of *Homunculus* are with the smaller Cebidæ, especially "*Nyctipithecus*" (*Aotus*) and "*Callithrix*" (*Callicebus*); genera which, for reasons set forth below, appear to have retained many primitive or stem characters.

Another Santa Cruzian form, *Anthropops perfectus* (*fig. 148*) of Ameghino, based on the front end of a lower jaw, has a deep chin that is even better developed than that of *Cebus*. Its dental formula was $I_2\, C_1\, P_3\, M_?$; the first two premolars ($p_2$, $p_3$) were small. Bluntschli states that very probably "*Anthropops*" is identical with *Homunculus*. Still another Santa Cruz type, referred to the primates by Ameghino and by Abel, is *Eudiastatus lingulatus* Ameghino (*fig. 148*), based on the front end of a small jaw; this bears on the inner and ventral side of the symphysis a very large median tubercle in place of the usual paired pits for the tendons of the geniohyoid muscles. A faint suggestion of this condition may be seen in some jaws of *Cebus* and *Alouatta*. The dentition is very poorly preserved. According to Bluntschli (*op. cit.* p. 38) *Eudiastatus* is not a primate at all but may be a bat.

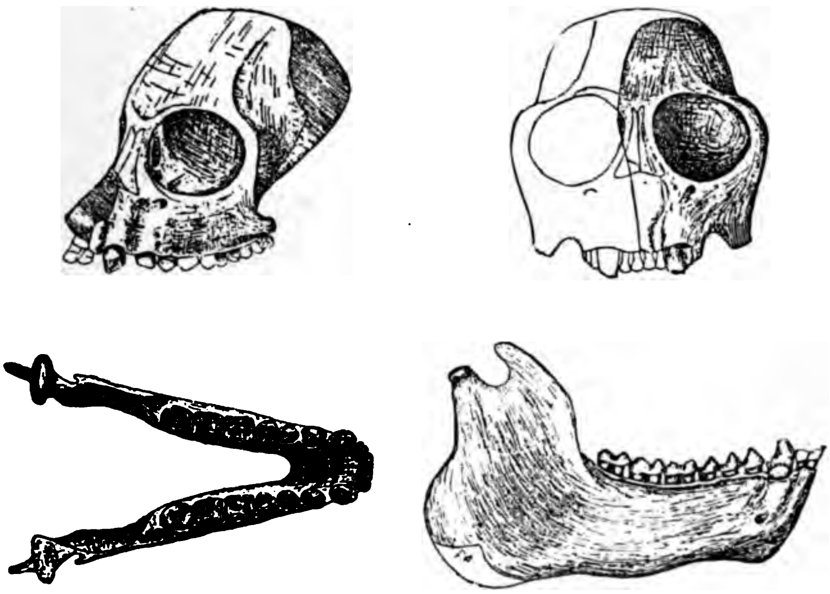

FIG. 147. *Homunculus patagonicus*. SKULL AND JAW. × 1. AFTER F. AMEGHINO

Santa Cruz (Lower Miocene), Patagonia. Suborder Anthropoidea, section Platyrrhinæ, family Cebidæ.

Neither the "chin" of *Anthropops* nor the "genial tubercle" of *Eudiastatus* afford the least evidence of special relationship with Man.

It is therefore apparent that the direct palæontological record of the evolution of the Platyrrhinæ does not extend below the Miocene, and we are therefore limited to indirect evidence as to the earlier course of evolution and derivation of the group.

FIG. 148. *Anthropops perfectus* (A) AND *Eudiastatus lingulatus* (B). LOWER JAW FRAGMENTS. × 1. AFTER F. AMEGHINO

Santa Cruz (Lower Miocene), Patagonia.

Bluntschli (1913, p. 38), who has examined these remains, states that the lower jaw of "*Anthropops*" probably belongs to *Homunculus*, while "*Eudiastatus*" is not a primate at all, but probably a bat.

### WERE THE PLATYRRHINÆ DERIVED FROM NOTHARCTUS?

In 1904 Wortman's investigations led him to conclude that while the American Eocene tarsioids were related to the modern *Tarsius*, they were also related to the ancestors of the higher primates, so that he transferred all the known tarsioids under the group name Paleopithecini to the suborder Anthropoidea. He also suggested that *Omomys* and *Washakius* (described above), "as far at least as we are permitted to judge from their scant remains, are closely related to *Adapis* and *Notharctus*, but had made greater progress in the reduction of the premolars. This gives an especially monkey-like appearance, pointing particularly in the direction of certain living Cebidæ." He also concluded that "it is in just such a group as that which includes *Adapis*, *Notharctus* and *Limnotherium*, that we must seek for the beginnings of the higher monkeys and apes which follow; and while these species may not have been in the direct line of descent, they cannot at the same time have been far removed from it (1904, pp. 172, 173)."

This concept unquestionably overemphasizes the nearness of the tarsioids to the Adapidæ. At least as far back as the Lower Eocene the tarsioids and the Adapidæ were wholly distinct families. As I have elsewhere shown (1920), the Adapidæ were still in a primitive lemuroid stage of evolution in the great majority of their cranial, dental and skeletal characters, while the tarsioids (as Wortman himself recognized) were precociously specialized in many respects. Nevertheless it is possible that Wortman may have been right in his general conclusion, and that the platyrrhine series have been derived from the Notharctidæ. This subject has a bearing upon the origin of man and the evolution of the human dentition, and it therefore calls for fairly detailed consideration at this point.

If the South American monkeys have been derived from large and progressive Notharctidæ, such as *Notharctus crassus* (see Part II), then very probably the most primitive dentition of the series is that of the Howler monkeys, *Mycetes* (= *Alouatta*). Unfortunately, however, we have but little means for judging whether the resemblance in the cheek teeth (*fig. 149*), which is by no means close, is a direct heritage from the later Notharctidæ, or whether it is due largely to homoplastic evolution. *Alouatta* (*fig. 151*) differs from *Notharctus* (*fig. 150*) in the marked shortening of the bony face, and it is in every important character a true platyrrhine monkey. The resemblances to *Notharctus crassus* are accompanied by an obviously high degree of specialization of the basihyal bone, which is of enormous size and greatly inflated. The lower jaw is also deepened and expanded in such a way as to provide sufficient room in the throat for this great resonating pouch. This expansion of the jaw has not only provided opportunity for great increase in the jaw muscles, but is also accompanied by a very pronounced upward tilting of the braincase.

Possibly the curious characters of the lower jaw and skull may have been partly developed before the great expansion of the resonating pouch in the throat, because they are partly foreshadowed in the genera *Callicebus*, *Aotus* (*Nyctipithecus*), *Brachyteles* (*pl. 8–9*). These forms are also the ones in which the molar patterns appear to

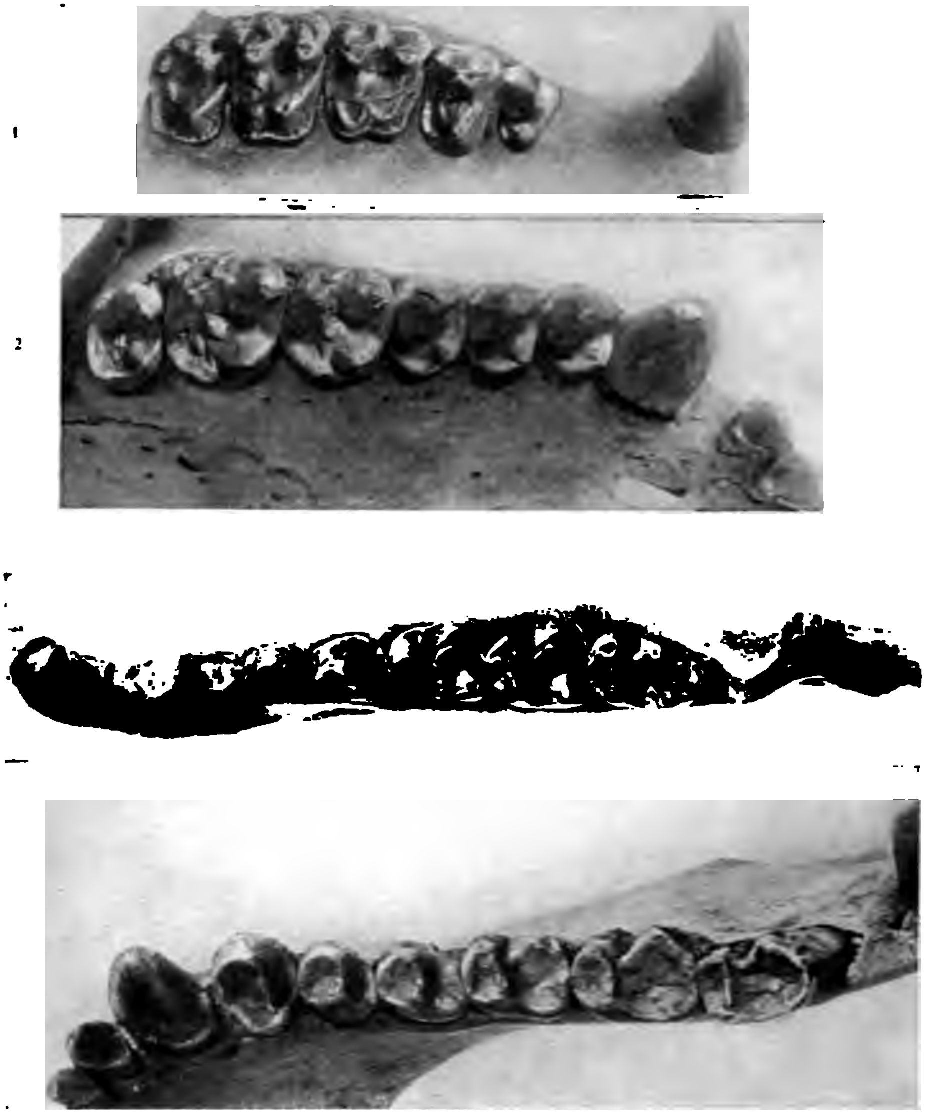

Fig. 149. Comparison of Teeth of American Eocene Primate *Notharctus* and Recent Platyrrhine Monkey *Alouatta*

1.—*Notharctus crassus.* Right upper cheek teeth (p$^1$, p$^2$ not preserved). × 2. Amer. Mus. no. 11,689. Upper Bridger beds (Middle Eocene). Wyoming. Suborder Lemuroidea, family Notharctidæ.

2.—*Alouatta* sp. Howler Monkey. Right upper jaw. × 2. Recent, South America. Suborder Anthropoidea, family Cebidæ.

3.—*Notharctus crassus.* Right lower jaw. × 2. Amer. Mus. no. 11,689. Upper Bridger beds (Middle Eocene), Wyoming. × 2.

4.—*Alouatta* sp. Amer. Mus. no. 14,660. × 2.

**Fig. 150.** *Notharctus osborni.* × 1. Amer. Mus. no. 11,466. Lower Bridger beds (Middle Eocene), Bridger basin, Wyoming.

Fig. 151. *Alouatta beelzebul.* × 3/4

**Figs. 150, 151.** Comparisons of Skulls of Eocene Lemuroid *Notharctus* and Modern Platyrrhine Monkey, *Alouatta* be fairly primitive, and *Callicebus* seems to be on the whole the most primitive and also the most "tarsioid" (in a broad sense) of the entire platyrrhine series. In this genus the molars (*pl. 11*) are of comparatively primitive tritubercular type with distinct remnants of the V-shaped form of the para- and metacones, and sharp crests on the anterior slopes of the protocones. The hypocones are connected with the posterior slopes of the protocones and are therefore apparently pseudohypocones like those of the Notharctidæ. This is especially evident in the specimen of this genus figured by Winge (1895). In *Aotus* (*Nyctipithecus*) on the other hand, the hypocones are quite prominent and appear to be connected with the cingulum (*pl. 11*). In *Alouatta* (*pl. 11*) they are connected both with the cingulum and with the crest of the protocone; in many or perhaps all of the remaining Cebidæ (*pl. 11*) and Hapalidæ (*pl. 13*), the hypocones are widely connected with the cingula and well separated from the protocones by a deep cleft. Thus the more primitive genera approach the conditions in the Notharctidæ, while the more specialized have lost them. But instead of postulating a direct derivation of the modern *Alouatta* from the Eocene *Notharctus crassus*, it seems safer to regard the Notharctus-like characters of the *Alouatta* molars as partly homoplastic and secondary, partly because they are associated with so many obviously peculiar specializations in the rest of the skull and skeleton, partly because they are adapted to the leaf-eating habits of the animal—an exceptional diet for a member of the Platyrrhinæ, which feed typically on fruits and insects.

For the present, therefore, the available evidence indicates that the stem Platyrrhinæ had many characters of the Notharctidæ, together with others like those of certain Eocene tarsioids. The auditory region of the skull (*plates 11, 13*), which usually furnishes important evidence as to the relationships of groups, points in the same direction, that is, the conditions in the Platyrrhinæ are far more advanced than those in the Notharctidæ, but might be derived eventually from them.[3]

Unfortunately in the absence of annectant forms from intermediate horizons, we cannot assert that the Notharctidæ are the direct

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[3] A more detailed discussion of this subject is given in my memoir on Notharctus (1920, p. 220).

ancestors as well as the remote structural ancestors of the Platyrrhinæ. The American Eocene genus *Aphanolemur* (*fig. 152*) of Granger and Gregory (1915) has a more expanded braincase and a shorter face than the typical Notharctidæ, and possibly it is sufficiently like the tarsioids to be a direct ancestor of the Platyrrhinæ.

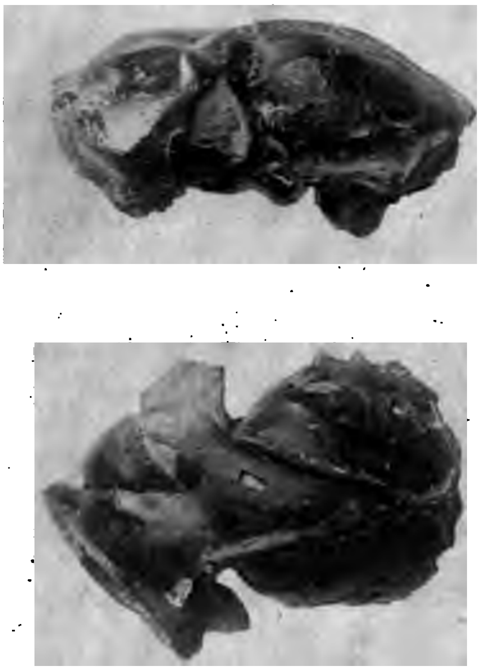

Fig. 152. *Aphanolemur gibbosus*. Imperfect Skull. × 1. After Granger and Gregory

Yale University Museum. Lower Bridger beds (Middle Eocene). Suborder Lemuroidea, family uncertain.

Of considerable importance are the characters of the incisors and canines, which in the South American series (*plates 8, 9, 11, 12, 13*) avoid all the peculiar specializations observed in the lemuroids and in most known tarsioids, and are closely comparable with the conditions in the Notharctidæ described in Part II of this review. The diverse specializations of the front teeth in these other families are such as to remove most of the known genera definitely from direct ancestry to the Platyrrhinæ, and therefore they serve to enhance the value of the relatively close agreement in this region between the platyrrhines and the Notharctidæ.

## ADAPTIVE RADIATION OF THE CEBIDÆ

The existing South American monkeys exhibit a considerable adaptive radiation (*plates 9–13*) in the dentition and skull, but in view of the poverty of palæontological evidence it was for a long time difficult to decide which are the more primitive species. After repeated comparisons of the skulls and dentitions of the recent platyrrhine genera, during several years past, I have now adopted the provisional conclusion that in the construction of the skull and in the characters of the dentition the genera *Callicebus* and *Aotus* ("*Nyctipithecus*") are on the whole the most primitive and "tarsioid" living cebids, while *Cebus* and *Chrysothrix* (*Saimiri*) are the most advanced and pithecoid.

From or near *Callicebus* (*pl. 8*) as a starting point we may trace "an adaptive radiation" in skulls and dentitions, one morphological series leading through *Brachyteles*, *Ateles* and *Homunculus* to *Lagothrix*, *Cebus* and *Saimiri*. In this line the back part of the jaw becomes shallower, the upper and lower canines increase in size, and a bony chin and wide intercanine diameters are finally developed. Meanwhile the tooth rows (*plates 11, 13*) become straight or slightly divergent and the molars vary from the subtriangular to the subbilophodont condition. The anterior premolars, at first small, finally become quite large (*Cebus*); the face (*plates 8, 9*) becomes shallower and more protruded below the orbits; and the zygomatic arches, originally stout and inclined downward, become slender and horizontal; the cranium (*plate 10*) finally bulges greatly behind the foramen magnum, and is very dolichocephalic; the outer borders of the orbits meanwhile grow forward so that the eyes finally look more directly forward instead of partly outward, and they have also become separated from the temporal fossæ by bony partitions.

More in detail, the steps by which the platyrrhine skull became modernized from a tarsioid to a pithecoid stage may be visualized as follows: First, in correlation with the rapid expansion of the brain there has been a steady and moderate increase in the breadth of the braincase across the parietal, a rapid increase in the frontal region just behind the orbit, accompanied by a rapid increase in antero-posterior diameter, so that in the higher Platyrrhinæ (*Cebus*, *Chrysothrix*) the general form of the cranium as seen from above finally becomes like a stout, wide-necked vase (*pl. 10*). Secondly, the outer rim of the orbits has grown forward, while the inner borders have been brought nearer to the midline, greatly restricting the interorbital, nasal and lacrymal regions, the end result being that the axis of the eyes point forward rather than sideways. This has been associated with a shortening and a retraction of the face beneath the orbit, and with a progressive separation of the orbits from the temporal fossæ by bony partitions developed chiefly on the frontals and malars, and partly on the sphenoid. Possibly the first development of this partition may have been in response to an enlargement of the orbits connected with nocturnal habits. Indeed the available evidence suggests that in many phyla of Platyrrhinæ, such as the marmosets and the squirrel monkeys, the relatively small size of the orbits is secondary.

The skull of *Aotus* (*Nyctipithecus*) is near to the primitive *Callicebus*-like type, differing in the large size of the orbits (*plates 8, 10*). The orbito-temporal fissure (*pl. 11*) is unusually large in this form, which may indicate that the incomplete condition of the postorbital septum is a primitive inheritance from remote tarsioid ancestors. The short, wide cranium (*pl. 10*) seems much more primitive than the excessively elongate cranium of the squirrel monkeys.

The early shortening of the face and the transverse expansion of the braincase, which increased the intercondylar diameter of the jaw, together with the relatively small size of the incisors and canines, were at first concomitant with a marked convergence of the opposite dental arches, which were more or less pointed in front, both in the upper and lower jaws. These primitive conditions are largely retained in the existing *Callicebus*, but in the more specialized genera the upper canines become enlarged and the inter-canine diameter much increased, so that the canines protrude at the side and the rows of opposite cheek teeth become parallel or even slightly divergent anteriorly. Meanwhile the lower jaw, at first deep posteriorly and shallow anteriorly, becomes wider and flatter across the symphyses; a bony chin is finally developed and the center of power moves forward from the back part of the jaw, the angular region becoming smaller and the vertical depth of the body of the jaw decreasing.

The shortening of the bony face perhaps conditioned the crowding out of the first premolar, both in the upper and lower jaws, but the remaining three premolars stoutly asserted themselves against further encroachment, and indeed in several cases, *e.g.*, *Cebus*, *Lagothrix*, and *Saimiri* (*pl. 11*), became larger than the molars.

In the Notharctidæ, which in general are far older and more primitive than the Platyrrhinæ, there was a progressive development of the premolars as we pass from $p^1$ to $p^4$; but in the typical Platyrrhinæ all three premolars tend to become bicuspid with oval crowns and low rounded cusps. It is chiefly in *Brachyteles*, *Alouatta* and *Callicebus* that vestiges of more primitive conditions may be observed. Perhaps the most extreme advancement in the premolars is seen in *Cebus*, in which the anterior upper premolars have shared in the enlargement of the canines and are wide, completely bicuspid teeth (*pl. 11*). This bicuspid form of the upper premolars has probably contributed to the erroneous idea of some authors that the Hominidæ have been derived from some platyrrhine with an expanded braincase. In *Alouatta* the fourth lower premolar (*fig. 149*) especially shows vestiges of the conditions seen in *Notharctus crassus* in the form and arrangement of the cusps both of the trigonid and of the talonid.

In general the Cebidæ feed upon a mixed diet of fruit and insects; except *Alouatta*, which is said to limit its diet to leaves. Probably if we had fuller information we should find a closer correlation between the particular kinds of insects fed upon by the different genera and the detailed characters of the dentition.

Besides the main morphological series of skulls and dentitions described above, there are several aberrant side branches. First that of *Alouatta*, which may be derived from that of *Callicebus* by a great increase in size, inflation of the larynx, consequent upturning of the cranium posteriorly and marked anteroposterior expansion of the first and second upper molars (*fig. 149*), involving the development of mesostyles and V-shaped para- and metacones. A parallel adaptation to leaf-eating habits occurs in the Indrisidæ.

If, as seems improbable, the V-shaped cusps and well developed mesostyles of the *Alouatta* molars were primitive, that is, by direct derivation from the conditions in *Notharctus crassus*, then the lack of a mesostyle and the low condition of the hypocone in the upper molars of the other genera would be secondary. However, the antero-posterior expansion of the molars in *Alouatta* may rather be dependent upon the greatly increased size of the animal, while the expansion of the whole jaw region may have afforded opportunity for the exceptional development of the hypocones and of the mesostyles, and thus have brought about a secondary resemblance to the molar pattern of *Notharctus crassus* (*fig. 149*). It has already been noted that, as *Alouatta* is only a single and probably specialized type of this family, it is safer to assume that the more tritubercular molars of *Callicebus* (*pl. 11*) are relatively primitive and that the line of molar evolution passes through stages represented in *Callicebus* and *Brachyteles* toward that of *Alouatta*. The other Cebidæ depart further and further from the primitive molar patterns of *Callicebus*. In some of them (e.g., *Cebus*) the first and second upper molars tend to become divided into anterior and posterior moieties through the slight antero-posterior widening of the upper molars and the marked separation of the hypocones. Thus an incipiently bilophodont condition may be produced, which may be a progressive adaptation to insectivorous and frugivorous habits. In *Cacajao* and *Pithecia* the molar cusps tend to lose their sharp relief and distinctness (*pl. 11*). The upper molar crowns become concave transversely and a somewhat squirrel-like molar pattern is produced. This is associated with a marked grinding action of the mandible, and with the development of semi-procumbent upper and lower incisors. Thus these genera have departed very widely from the primitive conditions, and there is no doubt that the observed conditions are secondary and not primitive platyrrhine characters.

The third upper molars of the Platyrrhinæ are relatively small, sometimes dwindling greatly, as in *Saimiri*, *Cebus* and *Aotus*, and foreshadowing the loss of these teeth in the Hapalidæ (*pl. 13*). But this reduction of the third molar was already foreshadowed in the Notharctidæ and is in fact a primitive primate character.

Rather primitive lower molars are preserved in *Alouatta* (*fig. 149*), while fundamentally similar lower molar patterns were present in the Miocene genus *Homunculus* (*fig. 147*). In *Alouatta* the trigonids are distinctly primitive, lacking only the paraconids of the *Notharctus* molars. The hypoconids are larger than in the Notharctidæ and the entoconids have become well defined. The talonid basin is moderately expanded to receive the tip of the large protocones of the upper molars, but there is no excessive transverse widening of the talonid in any of the Platyrrhinæ such as occurs in many tarsioids. In the more advanced platyrrhines (e.g., *Cebus*) the paraconids are lost, and the posterior wall of the trigonid connecting the protoconid and the metaconid is near the anterior border of the tooth, while the talonid fossa is expanded. This parallels the conditions observed in the Old World monkeys and is associated with the obliteration of the interdental spaces through the filling out of the hypocones. The hypoconids are often connected with the entoconids by a low narrow crest homologous with the posterior limb of the talonid-V of Notharctus. The third lower molars of *Alouatta* (*fig. 149*) and of all the other Cebidæ have lost the hypoconulids, but are readily derivable from the primitive notharctid type.

## STEM CHARACTERS AND ORIGIN OF THE PLATYRRHINÆ

We are now in a position where we can reconstruct provisionally the stem characters of the platyrrhine skull and dentition. I conceive the stem Platyrrhinæ as small primates in a somewhat tarsioid stage of skull evolution, having the following characters: dental formula, $I\frac{2}{2}\,C\frac{1}{1}\,P\frac{3}{3}\,M\frac{3}{3}$; face short; braincase expanded; orbits relatively small, well-rimmed, directed partly forward; lacrymal mostly within orbits; nose wide, flat; auditory bullæ expanded; tympanic bones large, ring-like; front teeth not rodent-like, but "normal;" dental arches pointed; lower jaw short, deep; canines small, no bony chin; zygomatic arches stout, pitching sharply downward in front; all three upper premolars bicuspid; upper molars tritubercular, with small hypocones and reduced proto- and metaconules; lower molars with trigonid but little elevated above talonid, the latter large but not excessively widened, paraconids reduced or absent, hypoconulids present.

These characters, which are largely retained in some of the more primitive existing Cebidæ, as a whole exclude the Platyrrhinæ from ancestry to the Old World series; so that the two series appear to be parallel and independent branches from a more primitive and more tarsioid ancestral stock.

When and where these hypothetical ancestral tarsioids lived are questions outside the scope of the present inquiry. Those who believe in a lost mid-Atlantic land-bridge, or archipelago, would doubtless put them there, in Upper Cretaceous times, along with many other lost mammalian types that are supposed to have spread eastward and westward into the palæontologically known Eocene regions of Europe and America. The existence of the hypothetical mid-Atlantic land, at least during the Tertiary, is denied, however, on strong palæontological evidence by Dr. W. D. Matthew (1904), who holds that the Paleocene and Eocene faunas of Europe and North America were derived from older centers of dispersal (probably Upper Cretaceous) in the northern circumpolar land mass.

One may therefore assume as a working hypothesis that in this Upper Cretaceous northern hemisphere (the climate of which is known to have been temperate) there was a widely distributed and considerably differentiated pro-tarsioid group, derived eventually from more primitive lemuroids of the Paleocene or of the Upper Cretaceous, and that different families of the pro-tarsioid group spread southward to give rise first to the known tarsioids of Eocene Europe and North America; and somewhat later and at different times, to both the New World and the Old World series.

### THE MARMOSETS (HAPALIDÆ)

The taxonomic position and relationships of the Hapalidæ, or marmosets, have in several ways an important bearing on the problem of the origin of man, first, because certain observers are inclined to regard these little animals as very primitive primates, tending to connect this order with unguiculate mammals; and secondly, because Bolk (1916) has found in the dentition of the Hapalidæ a supposed solution of the origin of certain phenomena of the human dentition.

It may be stated at the outset that in the writer's opinion both these conclusions are very far from the truth; that the Hapalidæ are is really less primitive than some of the Cebidæ, that they are widely remote from the origin of any of the Old World series, including man, and that Bolk's comparisons are largely based upon independently acquired features.

Repeated comparisons of the skulls of the Hapalidæ (*plates 12, 13*) with those of the Cebidæ have finally led to the conclusion that the former have been derived from the ancestors of *Aotus* (“*Nyctipithecus*”) and *Callicebus*, of the Cebidæ, from which genera they differ chiefly in the enfeeblement of the lower jaw and zygomatic arch, the loss of the upper and lower third molars, the reduced size of the orbits, the varying anteroposterior elongation of the cranium and the enlargement of the canines. The molar series (*pl. 13*) both upper and lower, are more or less retrogressive in size and probably also in the form of the crown. Starting with *Aotus*, of the Cebidæ, and passing to *Tamarin* (*Seniocebus*) and the other genera of the Hapalidæ, we may observe the traces of this retrogressive process. In *Aotus* the first upper molar, which in most mammals is conservative, in form, retains the subquadrate contour which is characteristic of this tooth in other Cebidæ; but the second upper molar is reduced in size and subtriangular in form, through the partial suppression of the postero-internal corner. The third upper molar is very retrogressive, only the anterior moiety remaining, the posterior moiety being barely, if at all, represented. The Hapalidæ have carried this process much further, suppressing the third molars entirely and often reducing the second molars to a form quite like that of the third molars of *Aotus*. Even the first molars of the Hapalidæ apparently have shared in this general retrogressive evolution, for in *Midas* the metacones of the first molars are reduced in size, and the hypocones are vestigial, a condition which, in view of the generally high grade of organization of the skull of this animal and of the advanced development of the molars in many Eocene primates, we may not safely regard as primitive. The roundness of the molar cusps and of the whole crowns is also a retrogressive character in certain other phyla of primates, including the human phylum.

The Hapalidæ, having certain peculiar specializations, also parallel different members of the Cebidæ in different characters. In the extreme lengthening of the cranium, as seen from above, *Midas* (*pl. 13*) of the Hapalidæ parallels and even surpasses *Ateles*, *Cacajao* and *Pithecia*, and approaches *Saimiri* (*Chrysothrix*) of the Cebidæ. In the sharp protrusion of the interorbital and nasal region they go beyond *Aotus* and *Callicebus*, as also in the retraction of the face beneath the cranium (*pl. 12*). As in these genera, the malar walls of the orbits are broadly convex and have much the same relations with the zygomatic arches. It is quite possible that the Hapalidæ may have been derived from nocturnal or seminocturnal ancestors with enlarged orbits, much like those of *Aotus*, and that their still protruding orbits have become secondarily reduced in size. The ramus of the lower jaw (*pl. 12*) is much more slender and the angular process more distinct, than in *Aotus* and secondarily suggests the conditions in *Chrysothrix*, which genus the Hapalidæ also approach in the enlargement of the canines and of the premolar series.

As noted above the Hapalidæ have but two upper molars, the third having been lost and even the second greatly reduced. The small size of the third molar is suggested in various genera of the Cebidæ, especially *Saimiri;* but as the other resemblances with the latter are not very close, the reduction of the third molar may be regarded as a parallel adaptation to the extreme lengthening of the braincase and the forward crowding of the whole dental arch. It is as if the center of maximum growth had shifted forward from the molar to the antemolar region. The three upper premolars (*pl. 13*) are wide and bicuspid, and the tritubercular upper molars have low rounded cusps, the dentition as a whole being adapted, as in so many other small primates, to a mixed diet of fruit and insects.

In brief, the skull and dentition of the Hapalidæ appear to indicate that its nearest relatives are *Callicebus* and *Aotus* of the Cebidæ and that it has paralleled the other Cebidæ in various ways.

The question of the derivation and relationships of the Hapalidæ has such a direct bearing upon the problem of the evolution of the human dentition that it seems necessary to consider briefly some pertinent morphological evidence other than that which is to be found in the characters of the skull and of the dentition. Gidley, following Wortman, is inclined to regard the Hapalidæ as a "rather primitive and generalized group," partly because their pollex is said to lack the usual opposability typical of the primate thumb, and he concludes

(1919, p. 276) that these "small, lighter-bodied animals seem never to have acquired the function of grasping a limb, but depend rather on their sharp, widely-spread claws for support in progressing among the treetops." If this conclusion were correct the Hapalidæ would be a structural link between the primates and more primitive clawed mammals. But a comparison of their hands and feet leads me to the opposite conclusion that their "claws" are merely bent up nails, such as are already foreshadowed in less extreme condition in the smaller Cebidæ (including *Callicebus* and *Aotus*), and that the lack of opposability is a degenerate and secondary character.

The first consideration is that true unguiculates that climb have short proximal phalanges and powerful flexors of the digits, by means of which they are able to dig their claws into the bark of trees; while the Hapalidæ have the longer and more slender metatarsals and phalanges, and the feeble flexors, of the primates, which depend rather on grasping the branches with the friction pads on their digits.

Secondly, the hallux of the Hapalidæ is characteristically primate in form, bearing the flattened nail which is found even in Eocene primates.

Thirdly, the fibula of the Hapalidæ shows a tendency to be immovably jointed or partly coalesced with the tibia at the lower end, a condition which no morphologist could safely regard as primitive.

Fourthly, the backbone and pelvis of the Hapalidæ are in many respects more or less intermediate in form between those of the primitive Eocene Notharctidæ, on the one hand, and of the larger Cebidæ on the other, a fact indicating the essentially primate character of their whole locomotor apparatus, and strengthening the conclusion that the clawed condition of their digits is entirely secondary.

This digression seems necessary in order to establish the true position of the Hapalidæ as aberrant members of the New World series. Their very small size is possibly secondary and they have suffered a serious impairment of the typical primate method of locomotion. But they are extremely progressive in the great enlargement of the braincase and in the shortening of the dental arch posteriorly, in the consequent loss of the third molars, and in the reduction of the second; also in the progressive development of the upper canines, which are large and widely separated and well able to pierce the bodies of still smaller or more helpless animals, such as young birds and insects.

Bolk apparently leaves out of consideration the wide differences in skull and skeleton between the Hapalidæ and any of the Old World series, including man. The Hapalidæ, like the Cebidæ, have:

(1) The bony auditory meatus (*pl. 13*) in the form of a large ring, which is short in its transverse diameter, widely open at the outer end and greatly expanded anteriorly on the inner end, so as to overlap the inflated bulla. Behind the ring, between it and the underlying bulla, is a conspicuous foramen for the internal carotid artery. In all the Old World series, on the contrary, the tympanic bone forms a narrow tube, projecting transversely and more or less overlapped between the postglenoid and the post-tympanic processes. Its inner end is not greatly extended anteriorly where it overlaps the bulla.

(2) The skull as seen from above in the Hapalidæ (*pl. 13*) and the rest of the New World series (*plate 10*) is very long and narrow, with a marked posterior prolongation. In the Old World series, on the contrary, the cranium is primitively short and wide, not bulging backward in the occipital region except in the Hominidæ, where a similar condition is likewise correlated with the secondary overlapping of the cerebellum by the cerebrum.

(3) The eyes in the Hapalidæ (*pl. 13*) and most other New World monkeys (*plate 10*) are directed outward and forward, whereas in the Old World series they are directed forward, and the crests above the orbits tend to be arranged at right angles to the long axis of the skull.

(4) In the New World series the top of the braincase typically lies considerably above the dorsal rim of the orbits (*plates 8*, *12*), while in the Old World series this dorsal rim is usually nearer the level of the top of the cranium except in obviously specialized end members, such as the orang, and still more, man, where there has been a rapid increase in the vertical diameter of the braincase.

(5) In the Hapalidæ, as in the less specialized Cebidæ (*e.g.*, *Callicebus*), the maxilla (*pl. 12*) beneath the orbit is shallow, while in all the Old World series, including man, it is much produced forward and downward below the level of the orbits.

(6) The nasal region of the Hapalidæ is of the platyrrhine type, with the nasals widely separated at the base and tending to face outward ("narines éloignées," De Blainville); whereas in the Old World,

or catarrhine, series the opposite nostrils tend to be drawn together toward the midline so as to form a narrow V ("narines rapprochées").

Further, the anatomy of the Hapalidæ as described, for example, by Weber (1904, p. 784), leaves no doubt that they belong in the platyrrhine series, and affords no evidence either for any annectant position between primates and unguiculates, or for the view that they represent a structural starting-point of the Old World series.

## DO THE CEBIDÆ AND HAPALIDÆ AFFORD STRUCTURAL STAGES IN THE EVOLUTION OF THE HUMAN DENTITION?

The important evidence derived from taxonomic considerations wholly fails to support Bolk's view that the loss of the third molar in the Hapalidæ is peculiarly significant in the problem of the origin of the human dentition. Bolk (1916, p. 139) supposes that man, and presumably the whole Old World series, passed through a stage still represented in the Hapalidæ, in which the last molar, both in the upper and lower jaws, was normally suppressed and in which the last deciduous molar became retained as the first permanent molar of the human dentition. The occasional appearance of a fourth molar would therefore be explained as a reversion to a pre-hapalid stage and as a reappearance of the suppressed $m^3$ and $m_3$.

That the first permanent molar of typical placental mammals is serially homologous with their last deciduous molar has long been believed by Matthew and others, and is supported by the fact that in very numerous phyla of mammals the first permanent molar erupts early, is closely associated with the last deciduous molar, and resembles it so closely that a pure convergence in origin and pattern seems highly improbable. But we assuredly do not need to cite the Hapalidæ in this comparison, which holds true apparently in all phyla of placental mammals that retain a normal replacement of the dentition.[4] The conditions presented in the Eocene and modern lemurs, as well as in many other phyla of mammals, tend to indicate, in the opinion of the writer, that not only the first permanent molar but also the second and third are serially homologous with the deciduous molars, and

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[4] Evidence for this statement is cited in my "Studies on the evolution of the Primates." 1916, pp. 243–246.

that the replacing teeth of the molar series were eliminated as far back as the cynodont reptilian stage;[5] first, because an examination of available material indicates that as far back as the cynodont stage there was but a single set of molars without successors; secondly, the nearness of the first molar with the last deciduous molar in time of eruption is not significant of any special homology which would not also apply to the remaining molars, for the reason that in both Eocene and modern lemurs the second and third molars appear shortly after the first molar, and the great delay in the appearance of these teeth in later forms is perhaps secondary, conditioned often by their bulk, which is too great to be accommodated in the infantile jaws.

According to Bolk's view the third molars of the catarrhine series are not homologous as a whole with those of the Platyrrhinæ; consequently the third lower molar in all the Tertiary Old World primates as far back as the primitive *Propliopithecus* and *Parapithecus* are not homologous with the third molars of existing Cebidæ. On palæontological grounds this must be considered a wholly unproved assumption, since there is nothing to indicate that the third lower molar of the ancient *Parapithecus* and *Propliopithecus*—Old World genera of extreme primitiveness—is not homologous with that of other primates, which it resembles in essentials.

How, then, are we to regard the fourth molar of man and other primates, and what is its origin? Is it, as Bolk supposes, a reversion to a pre-Hapalid stage, before the loss of the true third molar? A fourth molar, especially in the lower jaw, is not infrequently recorded in the orang and even in the gorilla and other anthropoids.[6] It is also recorded in *Otocyon*, among the Canidæ, and in the lemurs, and I have before me a lower jaw of the platyrrhine genus *Ateles* (Amer. Mus. no. 17,218), with a small but well developed fourth molar on each side, directly behind the third molar.

It is by no means necessary to regard these fourth molars as reversions to a pre-placental or marsupial condition. Granger, of the American Museum of Natural History, has collected, examined and catalogued thousands of specimens of American Paleocene and Eocene placental mammals, belonging to all the known orders and fami-

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[5] See Part I.

[6] Even a fifth lower molar has been observed by Hellman (1918) in the orang.

lies, but he has never, he informs me, observed a single instance of the presence of a fourth molar in these very early placental mammals. Matthew testifies to the same effect, and so far as I am aware the extensive literature of the Eocene placental mammals of America and Europe affords no record of a fourth molar.

The presence of a fourth molar in modern mammals may be ascribed to a specialized or relatively new tendency of the dental lamina to bud off more than the normal number of teeth. This tendency is very obvious in certain phyla of mammals, such as the Sirenia and armadillos, where the number of molar teeth is considerably increased, and in certain odontocete Cetacea where the primitive number of cheek teeth is multiplied.

## V. SUMMARY AND CONCLUSIONS FOR PART III

In spite of the fact that probably none of the animals studied in Part III lie in or near the direct line of human ascent, yet they show us successive improvements in the skull and in the dentition which mark a general advance from the lemuroid toward the anthropoid grade of evolution.

The lorises and galagos represent an early attempt to evolve a large-brained large-eyed primate out of the primitive lemuroid stock, but they still retain the lemuroid face and their cheek teeth do not advance much beyond the primitive lemuroid types with tritubercular upper molars. At the same time they parallel the true lemurs in the specialization of the incisors and canines for combing their fur, and thus they remove themselves from the line of human ascent.

The tarsioids as a group equal or excel the lorises and galagos in the enlargement of the eyes and braincase, and some of them foreshadow the Platyrrhinæ in the reduction of the dental formula to $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{2}{2}\ M\frac{3}{3}$. They finally attain a high and almost pithecoid grade of organization in the construction of the orbits, auditory, and basicranial regions; their upper molar crowns tend to pass from a wide trigonal to a subquadrate form, divided into subequal anterior and posterior moieties as in the Old World stock; while their lower molars, at first with small trigonids and wide talonids, often lose the paraconid and tend to develop a hypoconulid (as in *Microchœrus*). But, as a group, they carry too far the enlargement of the orbits and internal ears, and mostly acquire specialized conditions of the front teeth which rule them out of the line of ascent either to the Platyrrhinæ or to the Catarrhinæ.

The platyrrhine or New World series seem to have started from small primates which had a tarsioid form of skull, but with certain marked differences in the front teeth and in the region of the auditory bullæ, which are more compatible with derivation from primitive members of the Notharctidæ. These presumably primitive and "tarsioid" ancestors seem to be most nearly represented in the present fauna by the genus *Callicebus*, a small cebid monkey once classed with the marmosets, but much more primitive in many characters of the skull and dentition. From this primitive type we traced an "adaptive radiation" (illustrated in *plates 8–11*) along several lines:

The first line, represented by the large-eyed and nocturnal douroucolis, or owl-faced monkeys (*Aotus*, "*Nyctipithecus*") and possibly also by the marmosets (*plates 12*, *13*) which appear to be more closely related to the douroucolis than to other Cebidæ;

The second line, represented by the relatively large and in certain respects highly specialized "howlers" (*Alouatta*);

A third line leading through or near the woolly spider monkeys (*Brachyteles*) and culminating in the true spider monkeys (*Ateles*);

A fourth and a fifth line represented by the aberrant uakaris (*Cacajao*) and sakis (*Pithecia*), which have procumbent front teeth but somewhat different types of grinding teeth;

The sixth and seventh lines, including the large-brained sapajous (*Cebus*) and the squirrel monkeys (*Saimiri* = "*Chrysothrix*"), which are by far the most advanced and pithecoid of all the Platyrrhinæ. The latter two genera have contributed to the wholly erroneous view of some authors (Ameghino, Sera, et al.) that the remote origin of the Old World series (including man) must be sought in the New World Platyrrhinæ. Nevertheless they afford an instructive example of the manner in which a pithecoid type of skull and dentition may have been derived from a more primitive tarsioid stage.

The marmosets (Hapalidæ), it was shown, are dwarfed Platyrrhinæ, derived perhaps from the ancestors of the douroucolis (*Aotus*), which have probably suffered retrogressive modifications of their locomotor apparatus and have become pseudo-unguiculates, climbing by means of their claw-like, bent-up nails, and tending to lose the typical platyrrhine grasping adaptations of the hands and feet. At the same time they have lost the posterior or third upper and lower molars, a peculiar specialization which, together with many others, wholly unfits them to be structurally ancestral to the Old World primates. And yet Bolk bases an elaborate theory of the origin of the human dentition partly upon the conditions observed in the Hapalidæ!

The Platyrrhinæ as a whole afford a beautiful illustration of a natural group, the members of which show markedly diverse specializations, which have, however, not gone far enough to obliterate an underlying heritage received from the stem forms of the whole group. Unless one chooses to believe in the special creation of each genus of Cebidæ and Hapalidæ, the evidence is decisive that the "heritage" which they all have in common proves their descent from a common ancestral stock. This conclusion is evidently valid in spite of the almost complete absence of palæontological proof. Thus, when we have satisfied ourselves that we are dealing with a natural group, we thereby postulate the existence of a common ancestral species or genus, bearing distinctly primitive characters which have been lost by its diverse descendants, and other primitive characters which have been preserved by them. Now, the determination of these characters requires close and repeated examination of all the existing genera of the group. Thus we again perceive the indispensability of thorough taxonomic study in close connection with all investigations of the evolution of particular structures, such as the dentition.

Two of the most easily recognizable items of the platyrrhine heritage are the presence of three more or less bicuspid premolars on each side both in the upper and in the lower jaws, and the peculiar relations of the tympanic ring to the auditory bullæ (see above, p. 231). These characters, along with many others, separate all the Platyrrhinæ from the whole Old World series and should have been taken more fully into account by those who have sought to find the remote ancestors of man, and the ancestral conditions of the human dentition, among large-brained Platyrrhinæ.

# PLATES 8–13

(GREGORY: EVOLUTION OF THE HUMAN DENTITION)

FIG. 194. *C*

FIG. 193.

# PART IV

## The Dentition of the Higher Primates and Their Relationships with Man

# 1. ORIGIN AND RISE OF THE "OLD WORLD" MONKEYS (SERIES CATARRHINÆ, FAMILY CERCOPITHECIDÆ)

## INTRODUCTION: PHYLOGENETIC RELATIONSHIPS OF THE TARSIOID, PLATYRRHINE AND CATARRHINE SERIES

In Part II of this review we have seen that, so far as is known, the true primates of the Lower Eocene were already thoroughly arboricolous in habit, as is shown by the quadrumanous form of their extremities; and that consequently their dentition was adapted to the food that may be found in trees, such as fruits, leaves, insects, and the eggs and young of small birds. The existing tree-shrews, or Tupaiidæ, and their Paleocene relatives the Plesiadapidæ, as we saw, are very probably more or less specialized side branches from the very base of the primate stem; indeed in many respects they are intermediate between the primates and some still more primitive but as yet undiscovered clawed, insectivorous, ancestral, placental mammals of the Paleocene and Upper Cretaceous epochs. Whether or not the Menotyphla, comprising the Plesiadapidæ, Tupaiidæ and Macroscelididæ, are to be included within the order Primates, seems, from present evidence, to be largely a matter of definition. The oldest known Menotyphla, the Plesiadapidæ, were apparently excluded from direct ancestry to the typical primates by the specialized characters of their front teeth, while, on the other hand, their extremities, so far as known, had not yet attained such a high grade of adaptation to grasping the limbs of trees as is exhibited by the oldest typical primates of the families Notharctidæ and Tarsiidæ.

The last two families are first definitely known, or generally admitted to be present, in the Lower Eocene of North America and of Europe, but they may have been partly differentiated in the Paleocene both from each other and from the Menotyphla, the Condylarthra and other placental orders.

The Notharctidæ, it was shown, were a comparatively conservative and slowly evolving group. They had the remarkably primitive dental formula of $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{4}{4}$ $M\frac{3}{3}$, and at first their dentition differed but little from that of the most primitive families (Mioclænidæ, Hyopsodontidæ) of the contemporary Condylarthra, or "proto-ungulates." The earliest species of Notharctidæ, and indeed of all other primates, had tritubercular upper molars and well marked interdental spaces; but, as we pass upward through ascending geological levels, the upper molars gradually become more quadrangular by the outgrowth of the postero-internal (disto-lingual) cusp. This arises either from the cingulum (Adapidæ, Tarsiidæ), or by budding from the main internal cusp, or "protocone" (Notharctidæ). The Notharctidæ, as well as their relatives, the European Adapidæ, retained a relatively primitive type of skull structure, with unreduced muzzle, orbits of moderate size, and braincase not greaty expanded.

The Adapidæ were in a distinctly sub-lemuroid stage of evolution, and some of them transmitted many of their primitive dental and cranial characters to the modern Lemuridæ and related families, all of which, however, have progressed in the further enlargement of the brain case and in the peculiar specialization of the lower incisors and canines.

The Notharctidæ increased gradually in size until the close of the Middle Eocene, when the largest of them was nearly as large as a modern howler monkey (*Alouatta*). The family may perhaps be represented in the Upper Eocene by a fragment of a lower jaw, the type of *Notharctus (?) uintensis*, the last known member of the family.

As was suggested by Leidy and by Wortman, it is possible that the Notharctidæ gave rise to the "New World" monkeys, or Platyrrhinæ; but, after considering the available evidence, it was suggested that the Platyrrhinæ may rather have been derived from some genera of Eocene or Paleocene primates that combined the more primitive front teeth of the Notharctidæ with the more advanced skull characters of the Tarsiidæ.

The known Eocene Tarsiidæ, as described in Part III, are precociously specialized forms, which rapidly develop many of the higher characters of an expanded braincase, large orbits, a shortened face, large auditory bullæ, etc. But most of them yielded too readily to the tendency to acquire enlarged and specialized lower front teeth and many also seem to have overdone, as it were, the progressive skull characters named above. Thus many of them remove themselves from the lines of ascent leading respectively to the New World and to the Old World series of higher primates. Some of the tarsioids by eliminating the first premolar of the original four, both in the upper and lower jaws, reduced the dental formula to $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{3}{3}$ $M\frac{3}{3}$, as in the Platyrrhinæ, while some others went further and eliminated also the second upper and lower premolars, thus reducing the formula to $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{2}{2}$ $M\frac{3}{3}$ as in the Catarrhinæ.

The later Eocene European tarsioids (*Necrolemur*, *Microchœrus*) have advanced toward the pithecoid grade of organization in the construction of their orbits, auditory region, and dental arch, and they have likewise succeeded in differentiating the quadrate first and second upper molar crowns into subequal anterior and posterior moieties, without, however, obliterating the tritubercular ground plan; while the crown patterns of their lower molars are more or less transitional between the more primitive VV-shaped tuberculosectorial and the more advanced five-cusped bunodont type of the stem Catarrhinæ. The crown patterns of the third and fourth upper and lower premolars of *Microchœrus erinaceus* are likewise more or less intermediate between those of lower, more primitive, tarsioids and those of *Oreopithecus*, *Parapithecus* and other relatively primitive Catarrhinæ to be described below. It will also be recalled that in *Necrolemur* and *Microchœrus*, the angular process of the mandible becomes expanded into a form which foreshadows the still more expanded condition of this part in the "Old World" group.

The phylogenetic significance of these pro-pithecoid characters attained by later Eocene tarsioids of Europe, becomes greater in consideration of the fact that their modern relative, *Tarsius*, possesses many clear marks of remote kinship with both main divisions of the higher primates, so that some authors have even proposed to brigade *Tarsius* and its relatives with the Platyrrhinæ and the Catarrhinæ in a single suborder.

Although the Platyrrhinæ and the Catarrhinæ may have been derived from Eocene primates that might fall under a broad definition of the Tarsioidea, it is not probable that they both started from the same genus of tarsioids or even from closely allied genera. In view of the remarkable constancy of the cranial, dental, and other characters that separate the Platyrrhinæ and the Catarrhinæ, and also of the marked differences in the jaws and dentition between the oldest members of each series, it seems far more probable that the New World series has been derived from some relatively primitive American tarsioid genus having the dental formula, $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{3}{3}$ $M\frac{3}{3}$; and

FIG. 213. *Cebus capucinus*, REPRESENTING THE PLATYRRHINÆ. AFTER ELLIOT

that the Old World group was derived from a much more advanced and later Eurasiatic tarsioid genus having the dental formula, $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{2}{2}$ $M\frac{3}{3}$, and many but not all dental and cranial characters in common with *Necrolemur* and *Microchœrus*.

## PARAPITHECUS, OF THE LOWER OLIGOCENE OF EGYPT, AND THE TRANSITION FROM THE TARSIOID TO THE CATARRHINE GRADE OF ORGANIZATION

That the higher primates have been derived from Tarsioids of some sort, although not necessarily from any known genera, has also been maintained on palæontological grounds by Schlosser, who in 1911 described and figured the mandible of *Parapithecus fraasi*, a small primate from the Lower Oligocene of Egypt. The dental formula of this highly important genus was provisionally given by Schlosser (*op. cit.*, p. 58) as $I\frac{1}{1}$ $C\frac{1}{1}$ $P\frac{3}{3}$ $M\frac{3}{3}$, but he noted that the identification of the second lower tooth as a canine was doubtful. The anthropologist Schwalbe (1915, pp. 234, 235), after examining a cast of this specimen, rightly concluded that the second tooth was the lateral incisor and that the dental formula was $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{2}{2}$ $M\frac{3}{3}$, as in the other "Old World" primates. The same interpretation was independently reached and defended in detail in my "Studies on the evolution of the

FIG. 214. *Lasiopyga (Cercopithecus) pygerythrus*, REPRESENTING THE CATARRHINÆ. AFTER ELLIOT

primates" (1916, p. 281). In 1919 E. Werth published his valuable paper entitled "*Parapithecus*, ein primitiver Menschenaffe," in which he gives (p. 329) a medial view of the lower incisors, canine, and premolars of this animal, which should set at rest all doubt as to the correctness of the dental formula as interpreted by Schwalbe, Werth, and the present writer.

*Parapithecus* is by far the most primitive of all known Old World monkeys and apes, and with regard to its known characters it may well be regarded as standing in or quite near to the line of ascent leading to the anthropoid apes and eventually to man. Unlike most or all of the known tarsioids it does not appear to be excluded from this important position by any pronounced aberrant specializations of the dentition, except possibly the too conic form of the lower molar cusps. *Parapithecus* is the smallest of all known Catarrhinæ, its interesting size-relations being suggested in the following comparative measurements:

| | SUBORDER TARSIOIDEA | | SUBORDER ANTHROPOIDEA, SERIES CATARRHINÆ | | | |
|---|---|---|---|---|---|---|
| | *Necrolemur antiquus*, Upper Eocene, Europe | *Microchœrus erinaceus*, Upper Eocene, Europe | *Parapithecus fraasi*, Lower Oligocene, Egypt | *Propliopithecus haeckeli*, Lower Oligocene, Egypt | *Pliopithecus antiquus*, Pliocene, Europe | *Hylobates (Symphalangus) syndactylus*, Recent |
| | *mm.* | *mm.* | *mm.* | *mm.* | *mm.* | *mm.* |
| Length of whole tooth row ($I_1$–$M_3$).................. | 16 | — | 25 | 30 | 43 | 51 |
| Length of three lower molars. | 8 | 11 | 12.5 | 15 | 20 | 24 |
| Length from mandibular condyle to tip of lower front teeth.................... | 28 | — | 36.5 | — | — | 86 |

The opposite rami of the lower jaw of *Parapithecus* converged rapidly toward the narrow chin, which sloped sharply backward. This configuration is partly correlated with the small size of the lower canines, which had not yet become enlarged as they are in later anthropoids. The marked divergence posteriorly of the mandibular rami and the relative anteroposterior shortening of the jaw indicate that the skull was correspondingly wide across the glenoid surfaces, this character being frequently correlated with a transverse expansion of the brain. The absence of $p_1$, $p_2$ and the consequent reduction of the lower premolars to two on each side imply an early shortening of the face, perhaps not unlike that seen in *Necrolemur*. The relatively low position of the mandibular condyle, together with the backward inclination of the whole ascending ramus and the relative shallowness of the horizontal ramus, indicate that the face was less bent down upon the cranium than it is in the higher apes.

As to the probable nature of the food of *Parapithecus*: the small size and lack of laniary modification of the canines, and the blunt non-sectorial form of the premolars and molars, would exclude specialized carnivorous habits, while the gently procumbent incisors and low-cusped cheek teeth seem to indicate a mixed diet, possibly of insects, fruits, bird eggs, and small reptiles. From the pointed form of the lower dental arch it is legitimate to infer that the upper dental arch was also convergent in front and, from this fact and other considerations, it is apparent that the upper canines were not laniariform. The two upper premolars must have been more or less bicuspid in order to articulate properly with the lower premolars; while from the elongation of the first and second lower molars, and from the

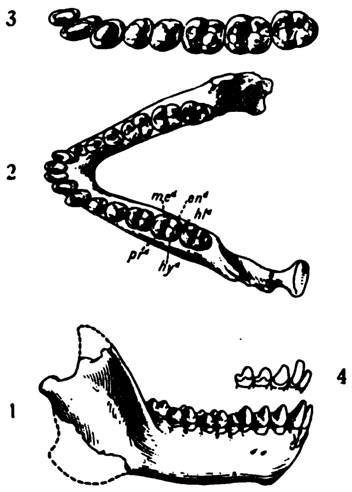

FIG. 215. *Parapithecus fraasi.* LOWER OLIGOCENE, FAYÛM, EGYPT

1, 2.—Lower jaw. × 1. Modified from Schlosser.
3.—Lower teeth, crown view. × 3/2. After Schlosser.
4.—Medial view of incisors, canines, and premolars. × 1. After Werth.

arrangement of their five cusps, it is perfectly safe to infer that the first and second upper molars were more or less quadrate in form, with well-developed posterointernal cusps or hypocones. The five-cusped bunodont lower molars had already advanced far from the primitive primate types represented in the Lower Eocene tarsioids and lemuroids. The trigonid is now depressed to the level of the talonid, the paraconid has been lost, and the primitive V-shaped cusps have become low and conical and have almost lost their crests. The potentially bicuspid premolars are widely unlike the molars, whereas in more primitive mammals the contrast between the posterior premolars and the molars is not so great

In view of the foregoing considerations, taken in connection with the fact that there are many special resemblances between the lower dentition of *Parapithecus* and that of the contemporary *Propliopithecus*, the oldest known true anthropoid, there is good reason to infer that the skull of *Parapithecus*, when discovered, will be found to exhibit a mixture of characters, some recalling tarsioid conditions and others foreshadowing the catarrhine or primitive anthropoid grade of organization, but none of extreme or aberrant specialization.

## APIDIUM, OF THE LOWER OLIGOCENE OF EGYPT, A STRUCTURAL ANCESTOR OF THE CERCOPITHECOID TYPE OF DENTITION

This interesting fragment of a small lower jaw, containing the fourth premolar and the three lower molars, was found in the Lower Oligocene of Egypt and described in 1908 by Professor Osborn, who showed that the animal differed from the small contemporary artiodactyls, especially in the form of its premolars. He noted that it differed also from all hitherto described genera of Primates and stated that its ordinal position would remain uncertain until the front teeth are discovered. Schlosser, in his memoir on the Lower Oligocene mammals of the Fayûm (1911, pp. 67–68), inclined to the opinion that *Apidium* was a primate and possibly a forerunner of the Cercopithecidæ. This determination is somewhat strengthened by the following considerations.

(1) As compared with the contemporary *Parapithecus*, which is admittedly a primate, *Apidium* presents a fundamental agreement in the ground plan of its fourth lower premolar and three lower molars. In both cases the fourth lower premolars are potentially more or less

bicuspid and sharply differentiated from the molars; the molars are elongate anteroposteriorly and bear five principal subconical cusps, arranged in two pairs, with a median hypoconulid. These resemblances alone would not be sufficient to demonstrate an ordinal affinity of *Apidium* with *Parapithecus*, but they gain in value when considered in connection with other evidence.

(2) From an inspection of Figs. 216 and 217, it will be evident that the lower teeth of *Apidium*, so far as known, have the same ground plan as do those of *Oreopithecus* (a peculiar catarrhine ape from the Lower Miocene of Italy), but that they are far more primitive and are nearer to a still older, more tarsioid stage. Thus in *Apidium*, while $p_4$ is at most incipiently bicuspid, in *Oreopithecus* the corresponding tooth is fully bicuspid and has the posterior cingulum and talonid fossa further developed. The lower molars of *Apidium* retain much that is reminiscent of a lower primate stage, the talonids of $m_1$, $m_2$ being notably wider than the trigonids. On the other hand they foreshadow the conditions in *Oreopithecus* in the facts (a) that the molars are elongate anteroposteriorly, (b) that the third molar is longer than the second, and (c) that the crista obliqua bears a new

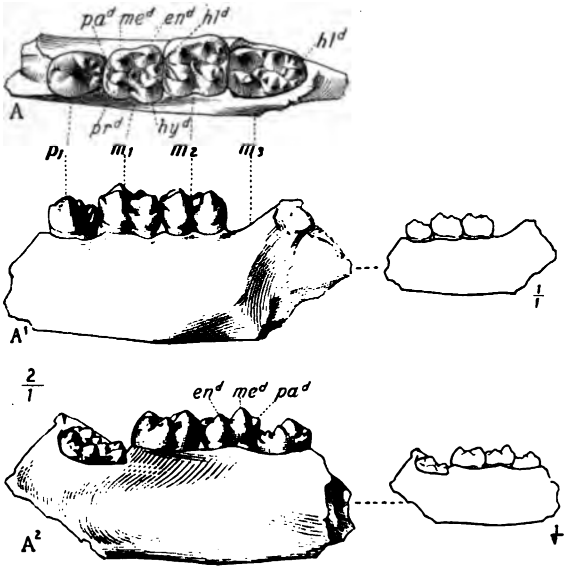

FIG. 216. *Apidium phiomensis.* LOWER OLIGOCENE, FAYÛM, EGYPT. AFTER OSBORN Type, Amer. Mus., no. 13,370. A, superior; A$^1$, lateral; A$^2$, medial view. Outline figures, × 1; shaded figures, × 2.

cusp at its anterior end immediately behind the posterior slope of the talonid. The hypoconulids, unusually prominent, at least on $m_1$, $m_2$ in *Apidium*, are well developed in *Oreopithecus*.

(3) The lower molars of *Apidium* remotely resemble those of *Cebochœrus*, a relatively primitive member of the Suidæ from the Eocene of Europe, but Schlosser (*op. cit.*, p. 68) pointed out that this general resemblance does not extend to the more significant details and that *Apidium* differs widely from *Cebochœrus* and other early artiodactyls which have compressed lower premolars. Although the status of *Apidium* as a primate is not fully established, no Eocene artiodactyl, hyracoid, or other mammal with which I have compared it, affords so favorable a comparison of the patterns of $p_4$, $m_1$, $m_2$, $m_3$, with those of *Oreopithecus*. We have also seen that, so far as known, the lower teeth of *Apidium* are more or less intermediate in pattern between an Upper Eocene, *Necrolemur*-like stage and a Lower Miocene cercopithecoid stage.

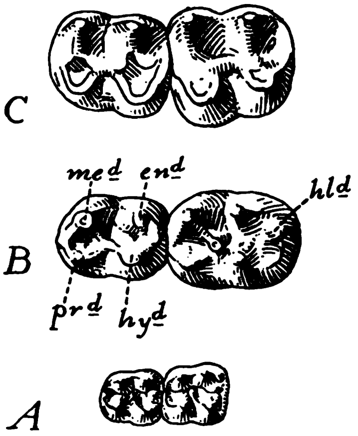

Fig. 217. Comparative Series: First and Second Lower Molars of *Apidium*, *Oreopithecus*, *Dolichopithecus*.

A. *Apidium phiomensis*. × 2. After Osborn. B. *Oreopithecus bamboli*. × 3/2. From a cast. C. *Dolichopithecus ruscinensis*. × 3/2. From a cast.

(4) From the relatively high stage of evolution attained by *Oreopithecus* in the Lower Miocene, it is to be expected that in the Lower Oligocene the cercopithecoid group had already begun to separate from the related anthropoid stock. *Apidium*, so far as known, appears to conform with reasonable expectations of what such a Lower Oligocene stage should be like.

(5) That ancestors or relatives of the later Cercopithecidæ were present in the Lower Oligocene of Egypt is also extremely probable from the fact that the American Museum expedition in 1907 discovered there a frontal portion of a skull which resembles closely the corresponding part of some of the smaller Cercopithecinæ.

### OREOPITHECUS, A PRIMITIVE CERCOPITHECOID OF THE LOWER MIOCENE OF ITALY

In Lower Miocene (Vindobonian) times there was a more or less continuous tract of land extending from northern Italy eastward to and beyond India. Primitive anthropoid apes, cercopithecoid monkeys and other mammals, all originating, it is believed, in Asia, spread westward and are found in Miocene and Pliocene deposits of Europe and Asia (Osborn, 1910, p. 255). The genus *Oreopithecus*, already mentioned as occurring in the Lower Miocene of Italy, differs in so many details of its dentition from the typical Cercopithecidæ that it was set apart as a distinct family, "Oreopithecidæ," by Schwalbe (1915), who has described the jaws and dentition of this animal in great detail. Its dentition on the whole appears to be more primitive than that of the Cercopithecidæ in the fact that the molars, although having the principal cusps arranged in pairs, do not have the opposite cusps connected by high transverse crests. The upper molars are quadrate with four principal conical cusps. They differ from the molars of anthropoids especially in having a prominent crest running obliquely from the base of the metacone forward and inward toward the protocone, and meeting another oblique crest running forward and outward from the hypocone. The mode of derivation of this rather peculiar arrangement is unknown. The upper canines are not enlarged as they are in most other monkeys and apes, but end in a bluntly conical tip, which does not project below the level of the premolars. Partly in correlation with the lack of a tusk-like specialization of the canines the upper dental arch is convergent in front. As noted above (p. 288), the lower molars differ from those of the more typical Cercopithecidæ in having a rather prominent cuspule located at the anterior end of the crista obliqua of the hypoconid. On the whole the affinities of *Oreopithecus* seem to be clearly with the Cercopithecidæ rather than with the anthropoid apes, and its peculiar generic characters do not seem sufficiently important to necessitate placing it apart in a distinct family.

### THE SEMNOPITHECINE MONKEYS OF MIOCENE AND LATER EPOCHS

The semnopithecine monkeys (including the well-known "Entellus" monkey of India and many other Asiatic and African forms) represent an herbivorous specialization of the primitive catarrhine stock. As is well known, the cœcum is enormously developed for the digestion of vegetable food, while the two-crested molars, which in the Lower Pliocene genus, *Dolichopithecus*, were remarkably like those of tapirs and kangaroos, are also adapted for the cutting of leaves and tender shoots. The laniariform canines, which have doubtless become specialized from the smaller canines of more ancient primates, are useful in fighting and possibly in piercing the tough rinds of large fruits.

The Semnopithecinæ exhibit some interesting variations in the length and proportions of the jaws and cranium, and in the form of the upper dental arch. The most primitive genera, *Dolichopithecus*, *Mesopithecus*, had a rather large muzzle and a comparatively low braincase. In some species of *Semnopithecus* (*Pygathrix*) and *Colobus* (*fig. 218*), the face and the cranium both become short, with consequent anteroposterior shortening of the dental arches, molars and lower jaw. The upper dental arch in *Colobus* males diverges anteriorly in correlation with the tusk-like form of the canines, while in females with small canines the dental arch becomes convergent in front. In *Nasalis* (*fig. 222*) there has apparently been a marked oblique downward growth of the upper jaw and a secondary anteroposterior elongation of the molars. In *Rhinopithecus* (*fig. 220*) the lower jaw becomes very stout and deep and acquires a sort of anthropoid appearance.

### THE CERCOPITHECINE MONKEYS

This division of the family Cercopithecidæ first appears in the Lower Pliocene of India, from which isolated molars not differing greatly from those of modern cercopithecine monkeys have been described by Lydekker and by Pilgrim (1915). The primitive cercopithecine monkeys (macaques, baboons, and related genera) apparently had a rather short face. There are many species still existing, the skulls of which may be arranged in a structural series beginning with the short-faced macaques (*fig. 227*) and culminating in the mandril among the dog-faced baboons (*fig. 229*). The molars share a little of this anteroposterior elongation (*fig. 234*) but not nearly so much as in many lines of long-faced ungulates.

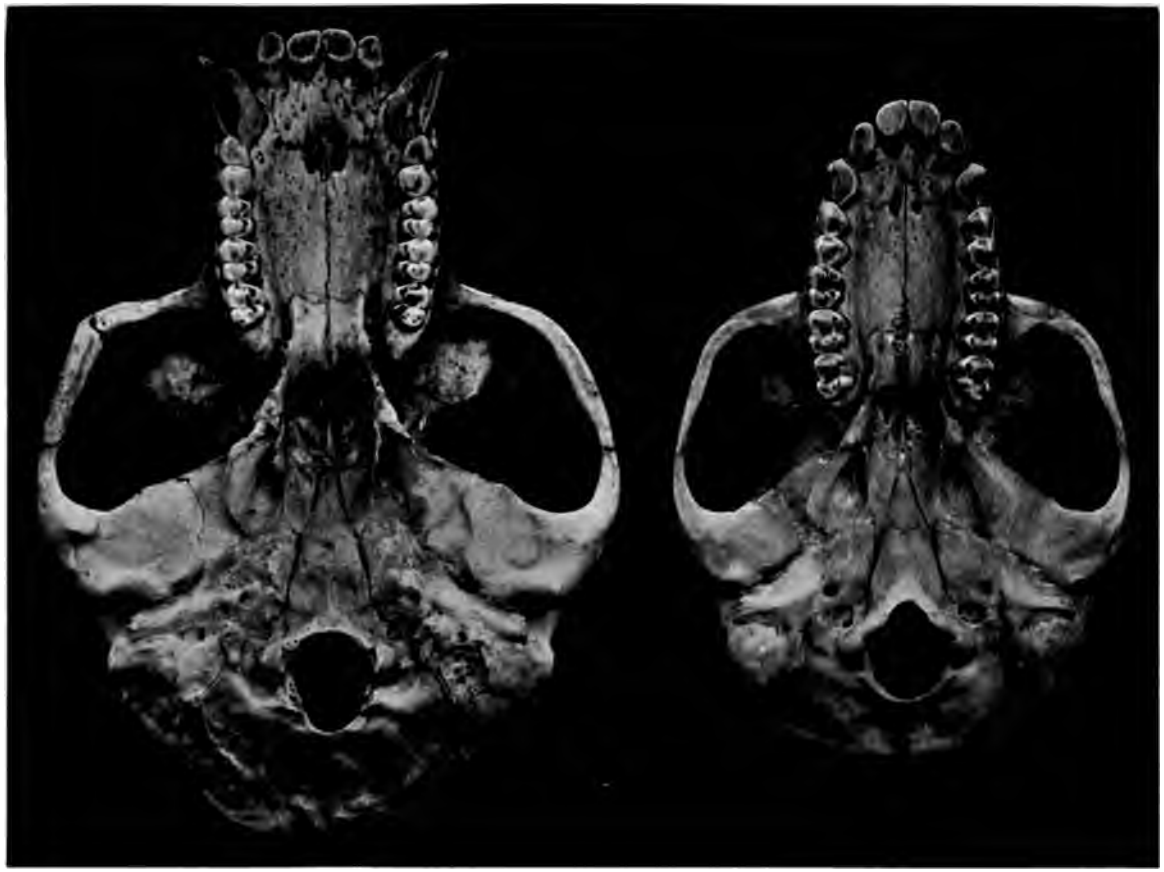

FIG. 218. *Colobus brunneus.* UNDER SIDE OF MALE (LEFT) AND FEMALE SKULLS SHOWING WIDE DIFFERENCES IN DENTAL ARCHES, ASSOCIATED WITH DIFFERENCES IN FORM OF CANINES

Courtesy of Dr. J. A. Allen and Mr. H. Lang, American Museum of Natural History.

FIG. 219. *Pygathrix (Semnopithecus) entellus.* × 4/5

FIG. 220. *Rhinopithecus bieti.* × 4/5

FIGS. 219 to 226, INCLUSIVE. COMPARATIVE SERIES: SKULLS OF SEMNOPITHECINÆ. SKULLS AFTER ELLIOT, REARRANGED

FIG. 221. *Colobus verus.* × 4/5

FIG. 222. *Nasalis larvatus.* × 4/5

FIG. 223. *Pygathrix entellus.* × 4/5

FIG. 224. *Rhinopithecus roxellanæ.* × 4/5

Fig. 225. *Colobus verus.* × 4/5

Fig. 226. *Nasalis larvatus.* × 4/5

Fig. 227. *Pithecus brevicaudus.* × 4/5

Fig. 228. *Theropithecus obscurus.* × 3/4

Figs. 227 to 229, Inclusive. Comparative Series: Skulls of Cercopithecinæ.
Skulls after Elliot, Rearranged

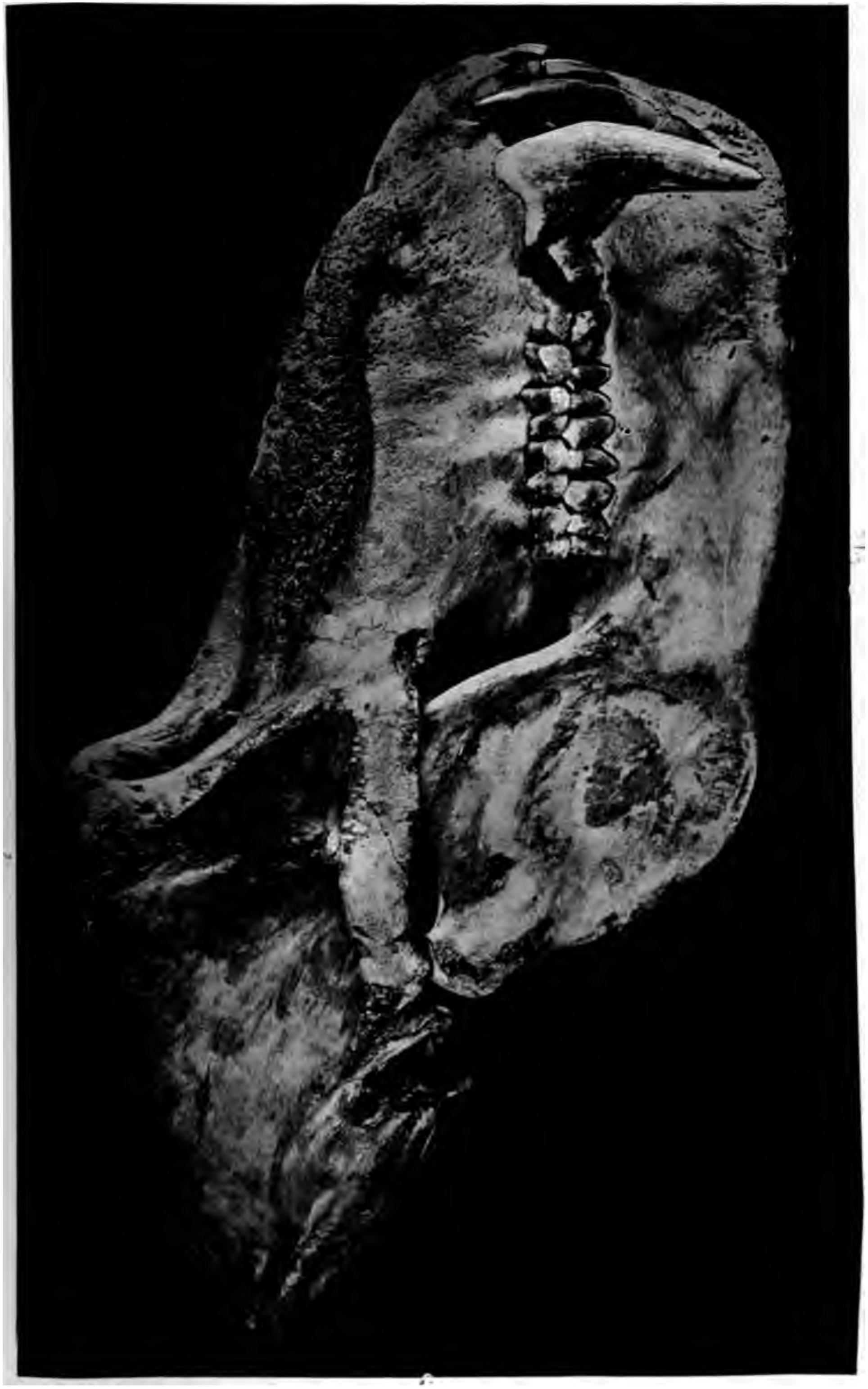

Fig. 229. *Papio sphinx.* × 3/4

In another direction we may pass by way of the Gibraltar ape (*Macacus inuus*) to the deep-faced gelada baboon (*Theropithecus, fig. 228*). There is a group of African genera centered around *Cercocebus*, which likewise exhibits some interesting variations in head form. One of them (*Erythrocebus*) has a relatively long cranium and face, while a related genus, *Miopithecus*, has an expanded braincase and short mandible (*figs. 230–232*). The former is a plains-living quadrupedal monkey, while the latter lives in the trees.

Notwithstanding the variations in length of face among the Cercopithecidæ, the first and second upper and lower molars always present two distinct and subequal anterior and posterior moieties, which often bear high transverse crests; and this character is so deeply impressed upon all known members of both divisions of the family that it probably was acquired at a relatively early date. And, if the above-described genus, *Apidium*, really be a forerunner of the Cercopithecidæ, it will be seen that an earlier stage in the development of this condition had been attained as far back as the Lower Oligocene.

In the existing cercopithecoid genera the steps by which these "bilophodont" molars have been derived are wholly wanting, but we know many analogous cases of the development of bilophodont molars from more primitive quadritubercular stages among the perissodactyls (tapirs, etc.), Eocene artiodactyls (*Tapirulus*), kangaroos and other groups, so that merely by analogy with these other cases we may infer that the bilophodont pattern of the upper molars in the Cercopithecidæ has been attained as follows:

(1) After the development of the secondary trigon and the obliteration of the primary trigon, as described in Part II, and after

(2) the progressive widening of the talonids and the correlated expansion of the "protocones," we have

(3) a lowering of the trigonid to the level of the talonid, and

(4) a secondary transverse widening of the trigonid, so that the trigonid and talonid become subequal in width; there is also

(5) a loss of the paraconid and

(6) a correlated outgrowth of the hypocone which articulates with the basin of the trigonid; meanwhile we have

(7) a coupling of protoconid and metaconid, of hypo- and entoconid, the latter pair articulating in the middle of the upper molars, which

have now become quadrate in form and more elongate anteroposteriorly. The palæontological record, although incomplete, supports this interpretation since it affords the following structural stages:

(1) Lower Jurassic Trituberculata (especially *Amphitherium*): Early stage in the evolution of the talonid, upper molars with primary trigon retained, secondary trigon in early stage (see Part II).

(2) Paleocene insectivores: Primary trigon modified, secondary trigon developing, upper molars tritubercular, lower molars tuberculo-sectorial.

(3) Lower Eocene tarsioids: Primary trigon obliterated by wide separation of para- and metacones and great expansion of "protocones;" lower molars with wide but low talonids and small high trigonids.

(4) Upper Eocene tarsioids (e.g., *Microchœrus*): Upper molars more or less quadritubercular through upgrowth of hypocone, but tritubercular ground plan still evident; second lower molars with subequal trigonid and talonid; a hypoconulid.

(5) Lower Oligocene *Apidium*: Upper molars unknown, but (as shown by the structure of the lower molars) necessarily quadrate, elongate anteroposteriorly, and with incipient pairing of the four main cusps, dividing the crown into anterior and posterior moieties; second lower molars elongate, $m_2$ with trigonid and talonid subequal in width, four main cusps conical, paired but not joined by transverse crests; paraconids reduced, hypoconulids prominent, double on $m_3$, an accessory cusp at the anterior end of the crista obliqua on all three molars.

(6) Lower Miocene *Oreopithecus*: Upper molars anteroposteriorly elongate; four main cusps conic, paired but not connected by transverse crests; lower molars fundamentally as in (5) but opposite cusps more distinctly paired.

(7) Lower Pliocene *Dolichopithecus*: Fundamentally as in (6), but paired cusps in both upper and lower molars bearing high transverse crests; reduction of the hypoconulid, except on $m_3$.

*The early pairing of the molar cusps in groups of two, together with the relative unimportance of the hypoconulid, are conspicuous characters which definitely rule all cercopithecoid monkeys out of the line of ascent leading to the anthropoid apes and man.*

Fig. 232. *Erythrocebus albigenis.* × 4/5

Fig. 231. *Miopithecus talapoin.* × 4/5

Fig. 230. *Miopithecus talapoin.* × 4/5

Fig. 233. *Pithecus brevicaudus.* × 4/5

Figs. 230 to 234, Inclusive. Comparative Series: Skulls of Semnopithecinæ and of Cercopithecinæ. Skulls after Elliot, Rearranged

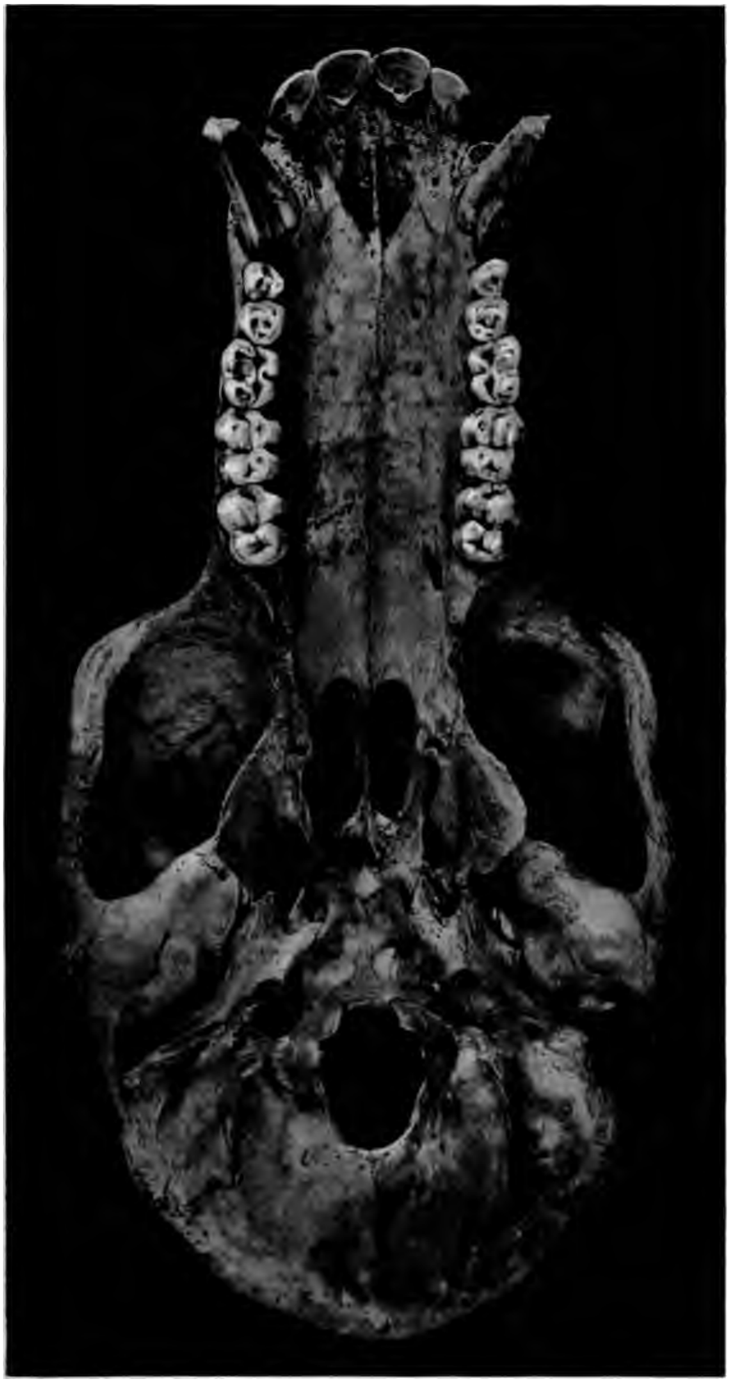

FIG. 234. *Papio cynocephalus.* × 3/4

## II. ORIGIN AND RISE OF THE ANTHROPOID APES (SERIES CATARRHINÆ, FAMILY SIMIIDÆ)

### PROPLIOPITHECUS, FROM THE LOWER OLIGOCENE OF EGYPT, AND THE ANCESTRY OF THE GIBBONS (SUBFAMILY HYLOBATINÆ)

*Propliopithecus.* This important stage of evolution is so far known only from an incomplete lower jaw from the Lower Oligocene of Egypt, which was appropriately named *Propliopithecus haeckeli* by Schlosser in 1911. Fortunately the teeth are so highly characteristic and so much like those of the later *Pliopithecus* in general plan that there can be no question that *Propliopithecus* is an early and relatively primitive representative of the anthropoid stock. As compared with the jaws of modern gibbons that of *Propliopithecus* is much more primitive in respect of the following characters:

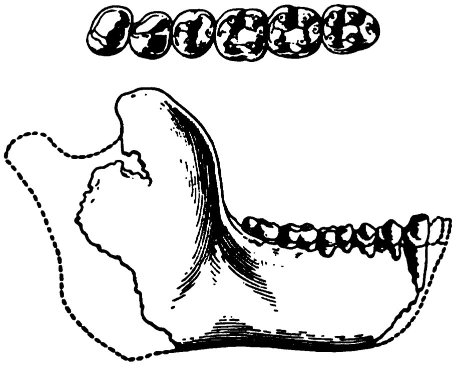

FIG. 235. *Propliopithecus haeckeli.* LOWER OLIGOCENE, FAYÛM, EGYPT. AFTER SCHLOSSER

Lower jaw. × 1. Left lower teeth (canine to $m_3$, inclusive). × 3/2

(1) The lower canines were not much enlarged and the anterior lower premolars were not compressed, elongate or sectorial, but anteroposteriorly shorter, more like those of the contemporary *Parapithecus*. Hence (although such an inference may appear unscientific to skeptics who insist on waiting for "more fossils"), it is safe to infer that the upper canines were of relatively small size, not greatly enlarged and sabre-like as they are in the modern gibbons and siamangs.

(2) As the whole jaw is shorter and relatively deeper than those of gibbons and siamangs, and as the upper canines were evidently not tusk-like, it is extremely probable that the dental arches were shorter, and more convergent in front.

(3) The relatively small size and vertical position of the lower canine, and the shorter, more convergent dental arches, indicate a correspondingly shorter face and probably less pronounced prognathism than is common among recent gibbons. From these and other considerations it seems highly probable that the primitive anthropoids were less prognathous than their modern descendants, and that prognathism has increased *pari passu* with the enlargement of the canines, and (except in the gibbons) with the widening of the central incisors.

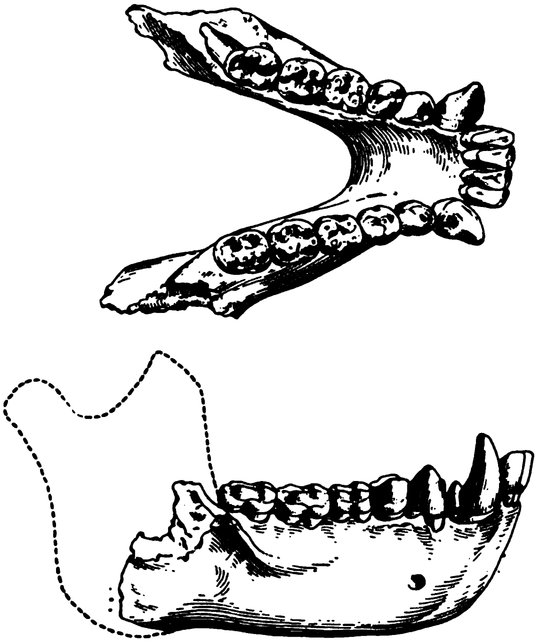

Fig. 236. *Pliopithecus antiquus.* Lower Pliocene, Germany. Lower Jaw and Dentition. × 1. From a Cast

As noted by Schlosser, *Propliopithecus* is structurally allied with and probably ancestral to *Pliopithecus* of the Upper Miocene and

Lower Pliocene of Europe, which in turn leads to the modern gibbons. The conclusion supported by the writer is that *Propliopithecus*, standing in or near the base of the gibbon line, also affords an early stage of the dentition that is structurally intermediate between the lower, more tarsioid *Parapithecus* and some primitive *Dryopithecus*-like stage, which would be the common starting-point for the main branch leading to the anthropoids and to man.

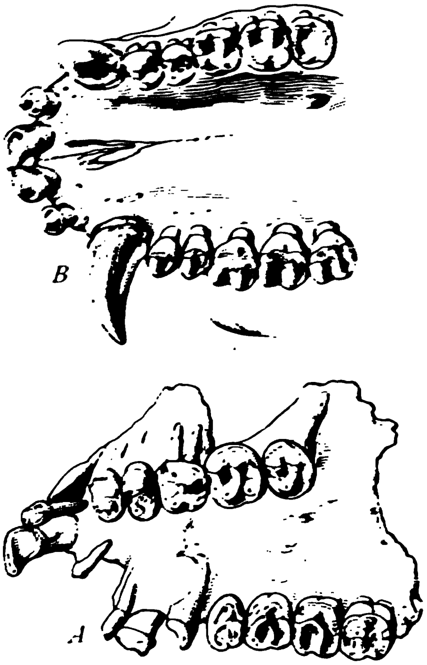

FIG. 237. COMPARISON OF (A) *Pliopithecus antiquus*, AFTER HOFFMANN, AND (B) *Hylobates lar*. × 1.

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.

*Pliopithecus*. The dentition and relationships of this important form are discussed in the following passages quoted from my "Studies on the evolution of the primates" (1916, pp. 301–305):

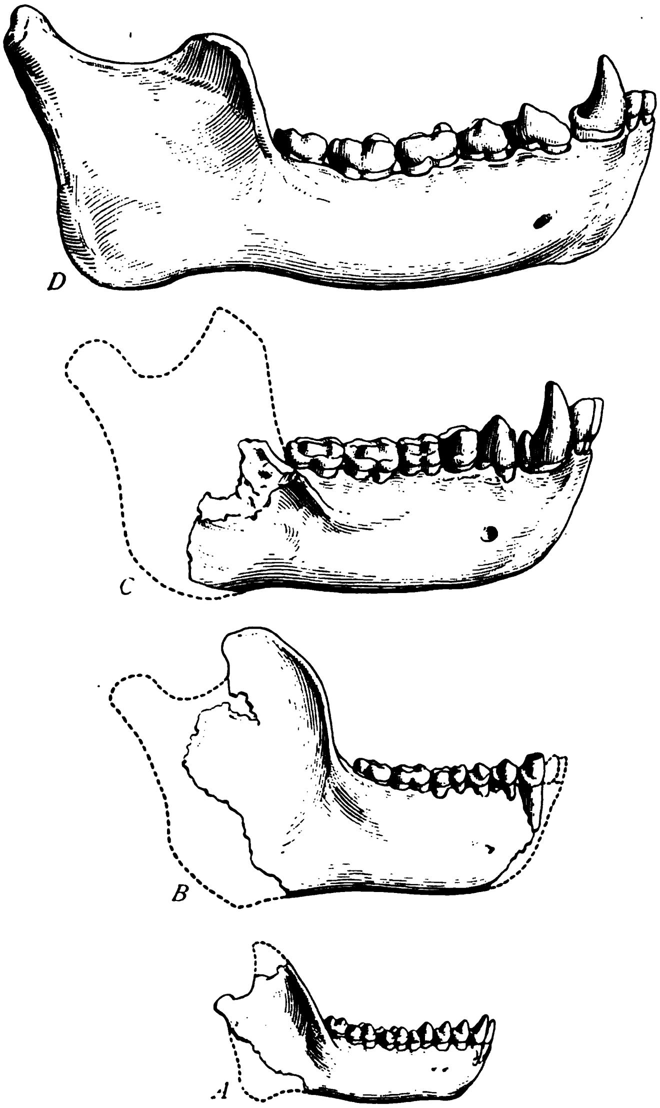

FIG. 238. COMPARATIVE SERIES: LOWER JAWS OF *Parapithecus* AND HYLOBATINÆ. × 1

A.—*Parapithecus fraasi.* Lower Oligocene, Fayûm, Egypt. After Schlosser.

B.—*Propliopithecus haeckli.* Lower Oligocene, Fayûm, Egypt. After Schlosser.

C.—*Pliopithecus antiquus.* Lower Pliocene, Germany. From a cast.

D.—*Symphalangus syndactylus.* Recent, Asia. After De Blainville, modified from specimens.

Missing parts restored hypothecially in broken lines.

"This Upper Miocene and Lower Plicocene 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 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 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 Anthropoidea, 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 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 anteroposterior 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 in 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 that there are marked changes and even reversals in the trend of evolution as we follow the lines onward—of which many fairly well attested 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 of length 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*, *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."

*The modern gibbons.* The following discussion of the cranial and dental characters of the modern gibbons (*Hylobates*, *Symphalangus*) is quoted from "Studies on the evolution of the primates" (1916, pp. 272–273):

"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 braincase,
the backward growth of the occipital portion of the braincase,
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 orbits 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 braincase. This voluminous anterior extension of the temporal insertion-area, together with the forward pushing of the braincase, 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.[2] 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

---

[2] No doubt the forward shifting of the orbits has also been in correlation with the approach toward, and final attainment of, the ability to focus both eyes on a nearby object.

FIG. 239A. SKULL OF *Hylobates lar*. × 4/5. AFTER ELLIOT

Fig. 239B. Skull of *Symphalangus syndactylus*. × 4/5. After Elliot

FIG. 240A. SKULL OF *Hylobates lar*. × 4/5. AFTER ELLIOT

Fig. 240B. Skull of *Symphalangus syndactylus*. × 4/5. After Elliot of the crown still being narrow and supported by an undivided root. All the molars lack the folds and wrinklings that are seen in the higher anthropoids. 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 bicuspids, 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.

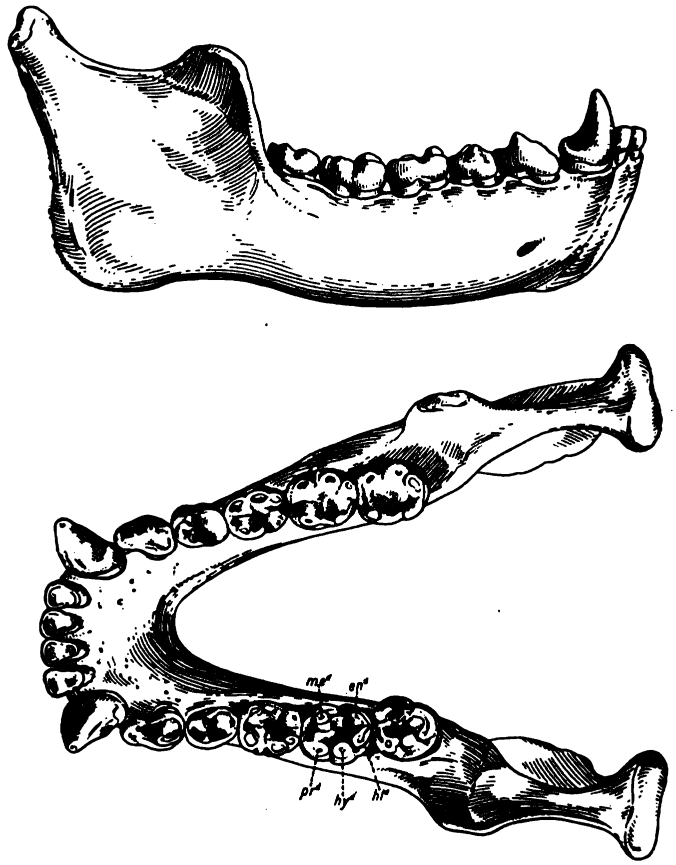

FIG. 241. *Symphalangus syndactylus.* LOWER JAW. × 1

The very large sabre-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."

*An important conclusion of the foregoing discussion is that the sabre-like form of the upper canines and the sectorial form of the anterior lower premolars of the gibbons are relatively late specializations.*

The gibbons are intermediate between the cercopithecoid monkeys on the one hand and the true Simiidæ or anthropoids on the other, so that they are often set apart as a distinct family, Hylobatidæ. Thus they agree with the Cercopithecidæ in many significant characters of the brain (Keith), in the lack of a frontal sinus, in the possession of large ischial tuberosities, in the persistence of the fossa subarcuata in the periotic bone of the adult, and in many other features of the anatomy, so that Keith (1896, p. 396) regards them as essentially cynomorph monkeys. But these are all primitive characters; and in the other direction the gibbons are widely removed from the cynomorphs and definitely allied with the anthropoids by the characters of the dentition, by the brachiating adaptations of the skeleton, and by the erect mode of progression on the ground. Also the palæontological evidence reinforces the conclusion that the gibbons, by derivation from *Propliopithecus* or some closely allied genus, are also related with *Dryopithecus chinjiensis*, and the other anthropoids and widely removed from the cynomorphs. The suggestion of various authors, especially Pilgrim (1915), that the gibbons and their predecessors stand relatively near the line of human ascent is discussed below (p. 363).

## ZOÖGEOGRAPHIC RELATIONS OF EUROPE, ASIA, AND AFRICA, DURING THE EOCENE AND MIDDLE TERTIARY EPOCHS

Before taking up the dentition of the Miocene and Pliocene anthropoids it may be well to consider briefly some of the probable zoögeographic relations of Europe, North Africa, Western Asia, and India, during middle and later Tertiary ages, as described especially by Osborn (1910), Matthew (1912), and Andrews (1906).

During the long Eocene epoch numerous genera and species of primates flourished in central Europe, including various lemuroids and tarsioids, but the whole catarrhine division of the primates is conspicuous by its absence. North Africa at some very early time must have been connected by land either with Europe or western Asia, for in the Lower Oligocene of Egypt we find various mammals that are rather closely related to their European contemporaries (e.g., primitive artiodactyls, hyænodont carnivores, etc.) along with other groups that had apparently been evolving in Africa for many ages (arsinoitheres, hyracoids, etc.). Among these are the catarrhine primates, including *Parapithecus*, *Prŏpliopithecus*, *Mœripithecus* and probably *Apidium*. Although perhaps remotely related to the *Necrolemur*-like tarsioids of the Upper Eocene of Europe, these Egyptian primates represent a very distinct family, not known from any other region, and probably derived from some early Eocene immigrants from Europe or possibly from southern Asia. Fortunately the genera named above afford clues, first as to the origin of the whole series from some unknown genera of tarsioids, and secondly as to the divergence of the cercopithecoid and anthropoid-man stocks; although it may well be that there were other genera in existence at that time which would supplement our knowledge of the more precise interrelationships and detailed stages in the evolution of the dentition.

Europe, North Africa and Eastern Asia were more than once in contact during the long mid-Tertiary ages; for we find such faunas as the *Hipparion* fauna of the Miocene spreading over this immense region so widely that it is often impossible to be sure in what part of the range a particular group originated. Hence there has been some doubt whether the primitive proboscideans, for example, which are found along with the above-named primates in the Lower Oligocene of Egypt, originated in North Africa or in western Asia, where somewhat more advanced forms are found in the succeeding ages. The proboscideans may have reached India from North Africa by way of Baluchistan, where successors of the Egyptian *Palæomastodon* have been reported by Pilgrim and by Forster-Cooper (1915, pp. 409, 410), and the primitive anthropoids may have followed the same path. On the other hand the Indian primates about to be described may have been derived from some Upper Eocene distribution center other than North Africa, such as Burma, where a characteristic Upper Eocene fauna of hoofed mammals has lately been discovered (Pilgrim and Cotter, 1916). At any rate the Middle Miocene beds of the Siwalik Hills in northern India contain teeth and fragments of jaws of three genera and four species of anthropoid apes, described originally by Pilgrim (1915), which are of the greatest importance in the problem of the origin of the modern anthropoids and even of man himself.

## THE MIOCENE AND PLIOCENE ANTHROPOIDS AND THEIR MODERN DESCENDANTS

The following general remarks on the fossil primates of India are quoted from "Studies on the evolution of the primates" (1916, pp. 285–286):

"As described by Lydekker in 1886, the fossil primates of India included extinct species of macaques, baboons and semnopitheques, 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.'

"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.

"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 semnopitheques.

"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."

As the Middle Miocene anthropoids are more than a whole geological epoch later than the Lower Oligocene apes of Egypt, they are naturally far advanced in structure towards their modern relatives and descendants, the orangs, chimpanzees, gorillas and possibly man. As compared with *Propliopithecus* they are already "giant apes," and unlike that genus none of them seems to be closely related either to *Pliopithecus* or to the modern gibbons. In the Upper Miocene and Pliocene of Europe we find fragmentary specimens of anthropoids, some of which (*Pliopithecus*) may be descended from the Lower Oligocene genus *Propliopithecus* of North Africa, while others (*Dryopithecus*) are more closely related to the anthropoids of India.

*Palæosimia.* Of the Middle Miocene Indian anthropoids, *Palæosimia* is known only from a third upper molar (*fig. 242*) which, as noted by Pilgrim, shows significant agreement with that of the orang, but is much more primitive and is related also to the contemporary genus *Dryopithecus*. The following is quoted from "Studies on the evolution of the primates" (p. 287):

> "This anthropoid is represented only by the third upper molar of the right side. 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.

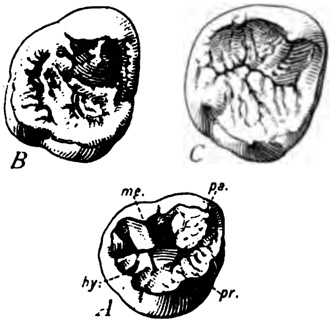

FIG. 242. COMPARISON OF RIGHT UPPER THIRD MOLAR OF (A) *Palæosimia*, WITH (B, C) MODERN ORANGS

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

In *Palæosimia* the third upper molar is of relatively primitive form, showing affinities with *Dryopithecus*. In the modern orangs, $m^3$ is variable in form and the surface is much wrinkled.

> 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'."

*The orang-utan.* The orang line is represented in the Upper Pliocene Siwalik series of India by a lower jaw. Thus the orangs probably became differentiated in the lower Miocene from the primitive giant ape stock in the region of northern India, but during later times were pressed southward to their present habitat in Borneo and Sumatra. During the vast time since the Miocene, the orangs have become highly specialized for arboreal life and for feeding upon fruits with heavy rinds, which they are able to pierce with their heavy jaws and large front teeth. No doubt the brain and braincase have also increased in size during the same period. In many respects they have become remarkably specialized and highly variable in structure. They are specialized in the deepening and rounding of the head and flattening of the face, close approximation of the orbits, extreme concavity of the facial profile, excessive wrinkling of the enamel on the molars, etc. They are extremely variable in the contour of the face, degree of prognathism, form of dental arches, overbite, and other characters noted by Selenka (1898–1903), Elliot (1912), and Hellman (1918).

FIG. 243. HEAD OF BORNEAN ORANG, *Pongo* (*Simia*) *pygmæus*. AFTER ELLIOT

FIG. 244. SKULL OF BORNEAN ORANG, *Pongo* SP. × 2/3

In this specimen the upper dental arch somewhat resembles the supposed prehuman type. The excessive wrinkling of the enamel on the molars is well shown.

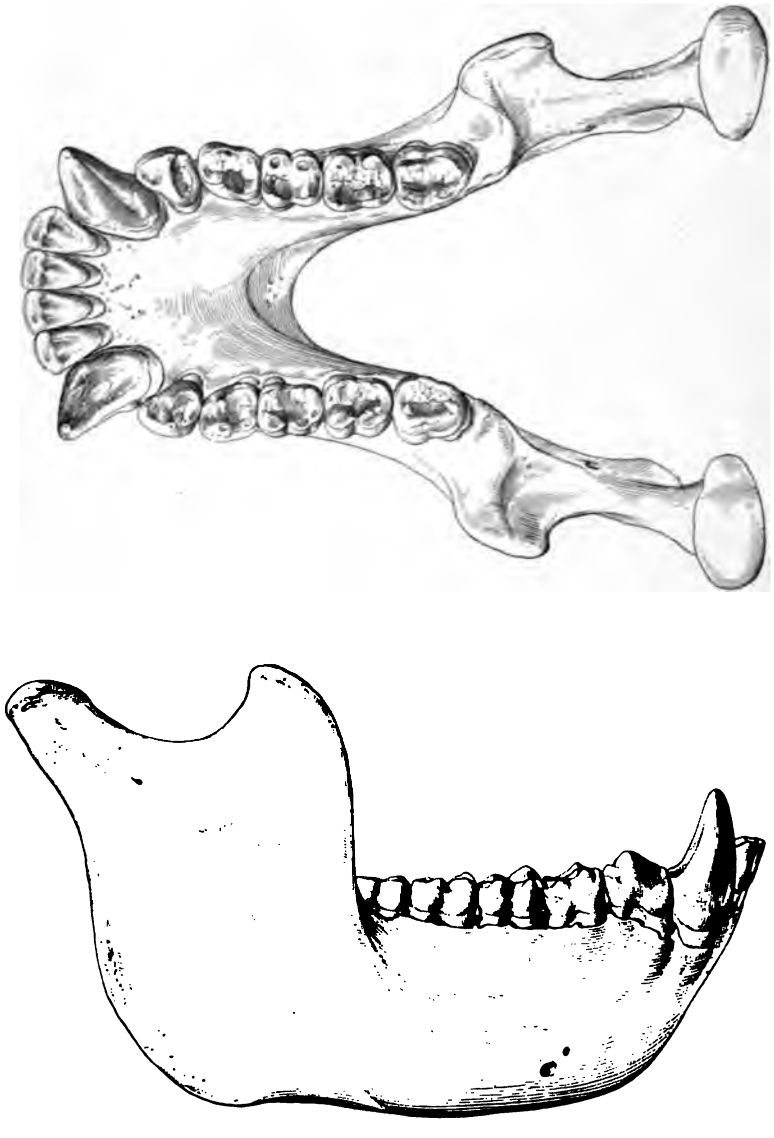

Fig. 245. Lower Jaw of Orang. *Pongo (Simia)* sp. × 2/3

The following description of the jaws and dentition of the orang is quoted from "Studies on the evolution of the primates" (p. 274):

> "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 quadritubercular with four-sided rather than triangular crowns. The surface of the crowns is low and flat with very numerous fine wrinklings 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 braincase 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 wide separation of the opposite canines at this point."

Although the orang skull may be described as a sort of caricature of an excessively brachycephalic, wide-faced human skull, these very superficial resemblances, mingled with many primitive characters common to the anthropoid-man stock, have never deceived competent students of the subject, who have always recognized that of the three modern giant apes the orang is in many respects the furthest removed from man. For reasons which will be developed later it seems highly probable that the orang line separated from the giant ape-man stock *before* its subdivision into chimpanzee, gorilla and human lines. Nevertheless the orang affords some interesting par-

FIG. 246. SKULL OF ORANG, *Pongo* (*Simia*) *pygmæus*. × 1/2. AFTER ELLIOT

allels to human conditions in the variable occlusal relations of the upper and lower incisors (edge-to-edge or extreme overbite) and in the wide variability in the upper and lower dental arches (Hellman, 1918).

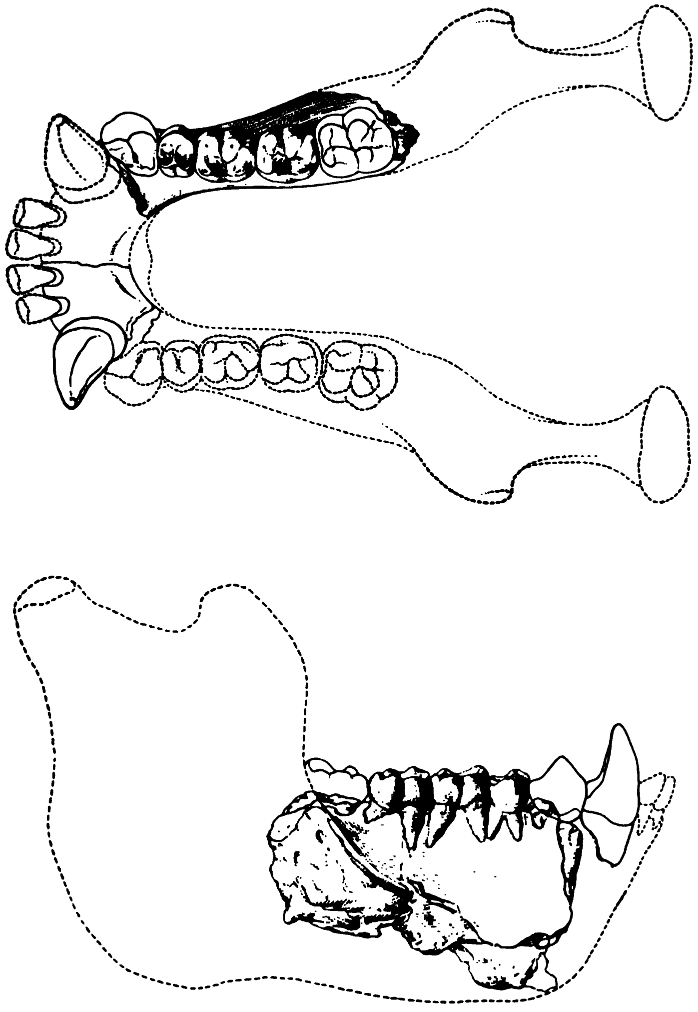

Fig. 247. *Sivapithecus indicus.* Reconstruction of Lower Jaw, Based on Casts of Type and Referred Specimens. × 2/3

Hypothetical parts in broken line

*Sivapithecus indicus.* In my "Studies on the evolution of the primates" (1916, pp. 287–292) this interesting form was discussed as follows:

> "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 containing the left canine and parts of the roots and alveoli of the incisors and front premolar; (b) a front lower premolar; (c) a lower third molar. An upper canine from the Lower Siwaliks of Chinji is provisionally referred to the same genus, while a fragment of the right maxilla containing the much worn first and second 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 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 man. 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:

| | SIVAPITHECUS | MAN |
|---|---|---|
| $m_3$ | 93.7 | 91.6 |
| $m_2$ | 94.6 | 94.4 |
| $m_1$ | 92.1 | 92.0 |
| $pm_4$ | 116.5 | 112.7 |
| $pm_3$ | 110.1 | 111.6 |

"The premolars also approach the human type in fundamental pattern.

. . . .

"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.* This genus, including three species from the Miocene of India and three from the Upper Miocene and Pliocene of Europe, was discussed as follows in "Studies on the evolution of the primates" (1916, pp. 293–298):

"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 (hypoconulid). 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 (Λ), the narrow end of which is at the center 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 Dr. Pilgrim regards as ancestral to *Homo sapiens*. The *Dryopithecus* lower molar without doubt also reveals the fundamental ancestral pattern 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 *Propliopithecus*-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

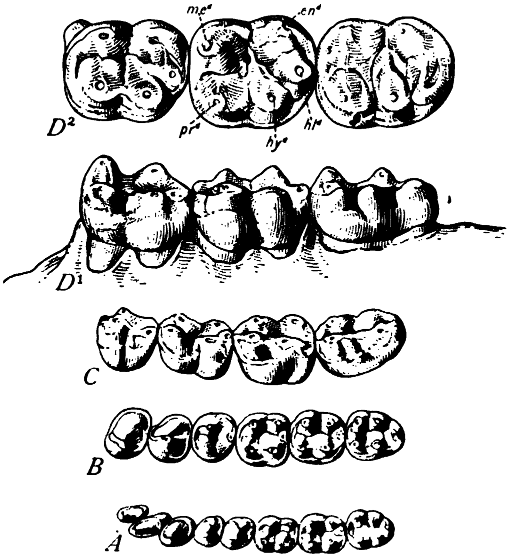

FIG. 248. COMPARISON OF LOWER TEETH OF *Parapithecus*, *Propliopithecus*, *Pliopithecus*, *Dryopithecus*. × 3/2

A.—*Parapithecus fraasi.* Lower Oligocene, Fayûm, Egypt.

B.—*Propliopithecus haeckeli.* Lower Oligocene, Fayûm, Egypt.

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.

*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 $m_3$, 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.

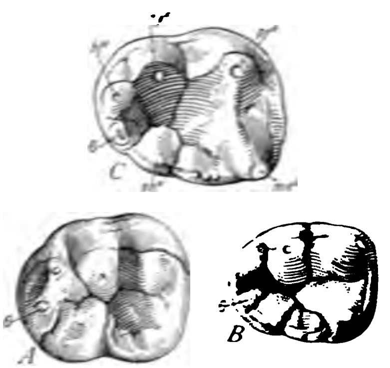

FIG. 249. COMPARISON OF THE LEFT LOWER THIRD MOLAR OF (A) *Dryopithecus chinjiensis*, (B) *D. punjabicus*, AND (C) *Gorilla* SP. × 3/2
A and B after Pilgrim

"*Dryopithecus chinjiensis* Pilgrim. The type consists of an isolated third lower molar 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 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 resemblances to the corresponding teeth of the gorilla, the differences being all apparently primitive characters.

"*Dryopithecus punjabicus* Pilgrim. 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 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.)

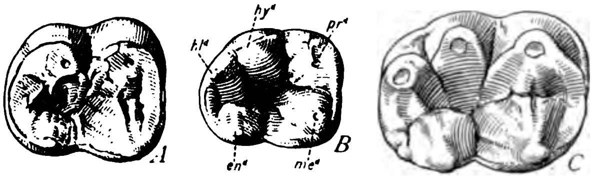

FIG. 250. COMPARISON OF THE LEFT LOWER SECOND MOLAR OF (B) *Dryopithecus punjabicus*, (A) ORANG, AND (C) GORILLA. × 3/2

B after Pilgrim

"The author refers to this species a specimen from the Nagri horizon of the Simla Hills, which is highly important, since it is a maxilla containing both premolars and the first and second molars in excellent preservation. 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. 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

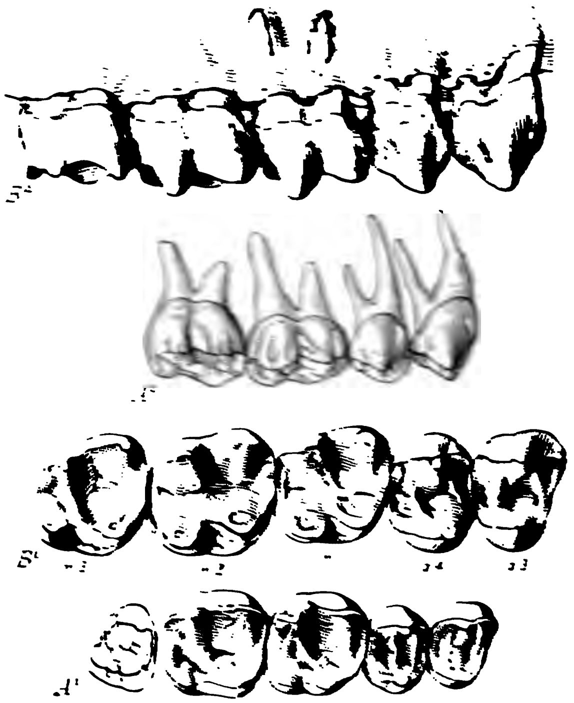

FIG. 251. COMPARISON OF UPPER CHEEK TEETH OF A¹, A² *Dryopithecus punjabicus*, AND B¹, B² GORILLA. × 1
A¹, A², after Pilgrim

much larger than that of any other species of the genus but also larger than that of the chimpanzee, in 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.

"*Dryopithecus darwini* Abel. 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 center of the crown than in *D. fontani*.

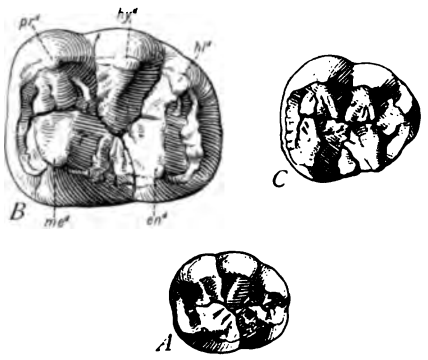

FIG. 252. COMPARISON OF RIGHT LOWER THIRD MOLAR OF (A) *Dryopithecus rhenanus*, (B) *D. giganteus*, AND (C) CHIMPANZEE. × 3/2

A, from a cast of a specimen figured by Branco; B, from a cast of the type

"*D. Darwini* is undoubtedly widely different from Abel's 'second type' of *D. fontani*, in which $m_3$ is elongate with a weak cingulum and externally placed hypoconulid; but it approaches Abel's 'first 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 distinguished, 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. This species (*fig. 248*) 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 age 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.

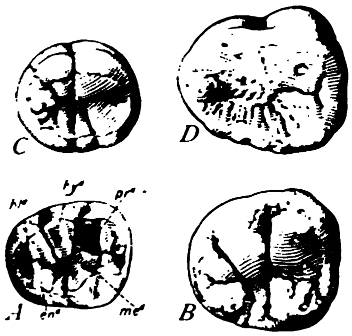

FIG 253. COMPARISON OF THE LEFT LOWER THIRD MOLAR OF (A) *Dryopithecus rhenanus*, (B) *D. darwini*, (C) STRANDLOOPER BUSHMAN, (D) ORANG. All × 3/2

A and B from photographs by Abel. Note the secondary furrows between the metaconid and the entoconid.

"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 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 primitve 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 no 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.

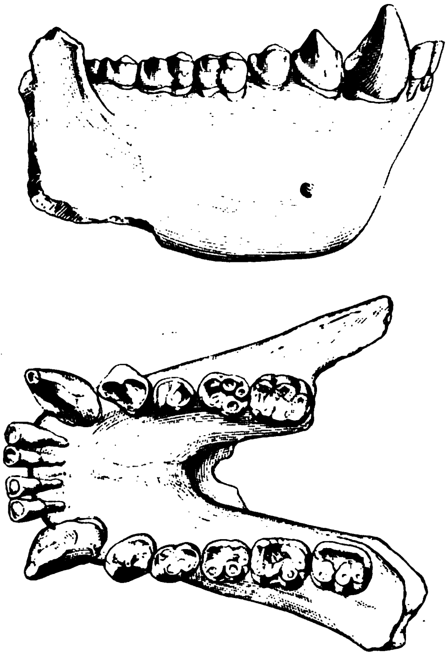

FIG. 254. *Dryopithecus fontani.* LOWER JAW. × 2/3. AFTER BRANCA

"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 *Propliopithecus* 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 in *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 of 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 of 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 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 of 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). While *D. fontani* is of Upper Miocene age, *D. rhenanus* comes from the Lower Pliocene (Swabian Bohnerz). 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 *Paidopithex 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 center. Basal cingulum as a rule not present, except on the last lower deciduous molar.

"The trigonid basin is represented by a transversely oval pit (fovea anterior) at the front end of the crown, while a similar pit (fovea posterior) 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. 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 seems 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 quadrangular; 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."

FIG. 255. COMPARISON OF LEFT UPPER MOLARS. × 3/2

A.—*Griphopithecus 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, $m^1$. Amer. Mus. Nat. Hist., no. 35,550.
E.—Orang, $m^1$. Amer. Mus. Nat. Hist., no. 35,549.

*Neopithecus*. (From "Studies on the evolution of the primates," 1916, pp. 310–311.)

"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. 162), 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 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 gibbons, its presence in a fossil anthropoid, says Schlosser, is not surprising.

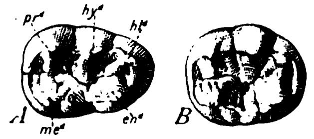

FIG. 256. COMPARISON OF LOWER THIRD MOLARS OF (A) *Neopithecus brancoi* AND (B) *Dryopithecus rhenanus*

A.—Lower third molar of *Neopithecus* (*Anthropodus*) *brancoi* Schlosser. × 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*. × 3/1. From a cast of a specimen figured by Branco.

"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 insinking 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."

*Palæopithecus sivalensis* Lydekker. (From "Studies on the evolution of the primates," 1916, pp. 299–301.)

"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) 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 Simiidæ and the Hominidæ. In the inclination of the two series of cheek teeth and the relative lateral position

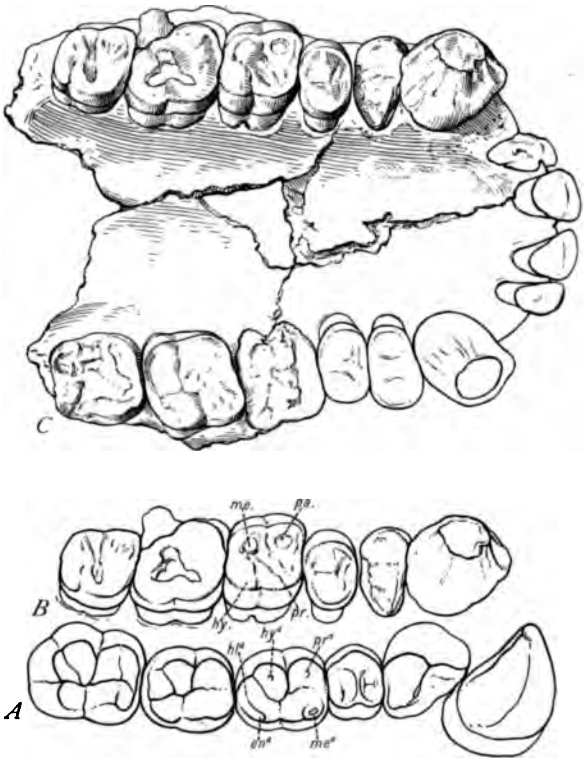

FIG. 257. TEETH OF *Palæopithecus* AND OF *Sivapithecus*

C.—Upper teeth and palate of *Palæopithecus sivalensis.* After Dubois. × 1.
B.—Upper teeth of *Palæopithecus.*
A.—Lower teeth of *Sivapithecus.*

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.

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 Simiidæ, 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 Simiidæ lower than that of any of the four living genera (p. 90); also 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 Simiidæ. 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."

*The chimpanzee.* (From "Studies on the evolution of the primates," 1916, p. 275.)

"The head of the chimpanzee is considerably longer than that of the orang; the most prominent feature in the top view (*fig. 259*) 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 (*figs. 255, 259*) 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 (*figs. 252 (C) and 280*) 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 anteroposterior 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 (*fig. 258*) 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."

FIG. 258. SKULL OF CHIMPANZEE, *Pan vellerosus*. × 4/5. AFTER ELLIOT

FIG. 259. SKULL OF CHIMPANZEE, *Pan vellerosus*. × 4/5. AFTER ELLIOT

FIG. 260. *Gorilla gorilla.* × 2/5. AFTER ELLIOT

*The gorilla.* (From "Studies on the evolution of the primates," 1916, pp. 276–277.)

"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 are parallel or 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. The lower molars 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. 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 braincase, and in the details of the tympano-petrosal region."

Fig. 261. *Pseudogorilla mayema* ♀. × 1/2 After Elliot

FIG. 262. *Pseudogorilla mayema* ♀. × 1/2 AFTER ELLIOT

*Relationship of the chimpanzee and the gorilla.* The prolonged and thorough anatomical investigations of Keith (1915) have demonstrated the relatively close relationship to each other of these two genera (*Pan*, *Gorilla*), which were formerly placed in a single genus, *Troglodytes*. But although certain species of chimpanzee approach the gorillas in some characters it is probable that the two genera have been separated since Miocene times, because one species of *Dryopithecus*, *D. chinjiensis*, seems to be tending in the direction of the gorilla, while another, *D. giganteus*, as well as *D. rhenanus*, appear to be more nearly related to the chimpanzee.

## THE PILTDOWN PROBLEM

Stated in the briefest terms this problem is as follows: In 1911, Sir Charles Dawson discovered some fragmentary human and other ancient animal remains in a gravel pit on Piltdown Common, Fletching, in Sussex, England, the human remains being described by Smith Woodward (1913) under the name of *Eoanthropus dawsoni*. The age of the gravel bed has been much disputed, some holding that it was of Upper Pliocene age, but the majority regard it as of Pleistocene age.

The fragmentary pieces of the skull are admitted by all to be of human type. The lower jaw fragment found near the skull in many respects resembles that of a chimpanzee, so that several investigators deny that it belongs with the human skull. Gerrit S. Miller (1915), who has made a very careful study of the subject, concludes that the lower jaw represents a Pleistocene species of chimpanzee which he has named *Pan vetus*. Subsequently a canine tooth was found in the same locality, but opinion is divided whether it is an upper or a lower canine, the writer and Miller holding that it is an upper. Smith Woodward, Pycraft (1917), Elliot Smith, Keith, and most British authors, adhere to the view that the jaw belongs with the skull, while Miller has published a second paper (1918) supporting his contention (which is accepted by many Americans, including the writer) that the weight of evidence up to the present time favors the conclusion that the jaw belonged to a chimpanzee. Smith Woodward (1917) has discovered in another locality, but in the same geological formation, a couple of fragments of another skull and a lower molar, and he regards these remains as affording decisive evidence in favor of the original association of the Piltdown jaw with the skull. But others doubt whether the new lower molar is really conspecific with the original Piltdown jaw, as it is of definitely human type. (See, however, p. x, line 29.)

In my "Studies on the evolution of the primates," 1916, pp. 313–320, the Piltdown problem was discussed as follows:

> "In an earlier paper (1914) I have reviewed the controversy over the Piltdown remains (*Eoanthropus dawsoni*), emphasizing the entirely human character of the braincase, the essentially ape-like character of the lower jaw and teeth and the doubt as to their association already expressed by several authors. With some doubts, which were even more strongly felt 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 Miller (1915) has practically demonstrated that the Piltdown lower jaw represents a Pleistocene species of chimpanzee and that it did not belong with the associated braincase.
>
> "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 (1915, pls. 1, 2). 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 symphysial 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.

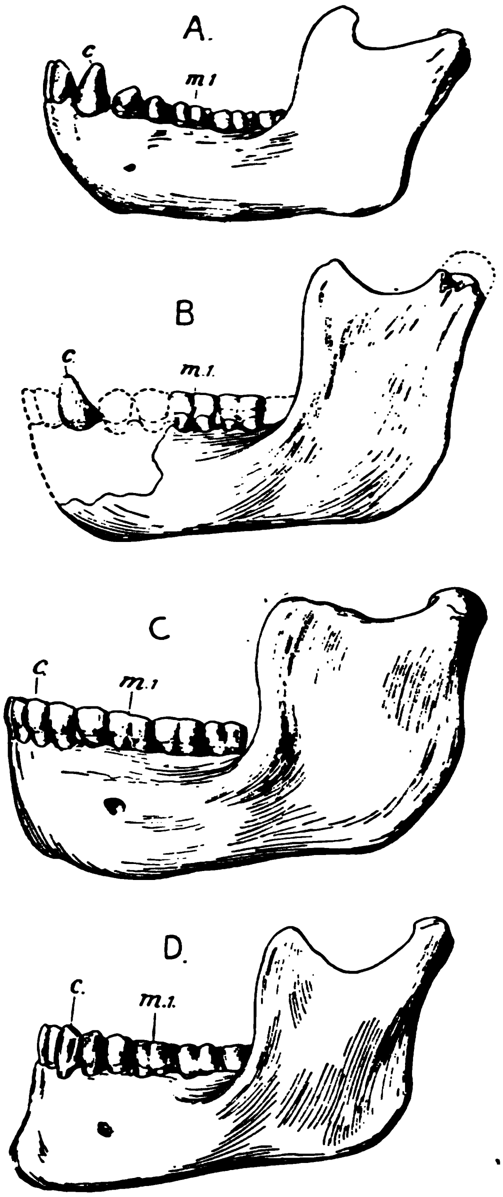

FIG. 263. COMPARATIVE SERIES: LOWER JAWS. × 1/2. AFTER SMITH WOODWARD

| | |
|---|---|
| A.—Modern chimpanzee. | C.—Heidelberg jaw. |
| B.—Piltdown jaw. | D.—Modern man |

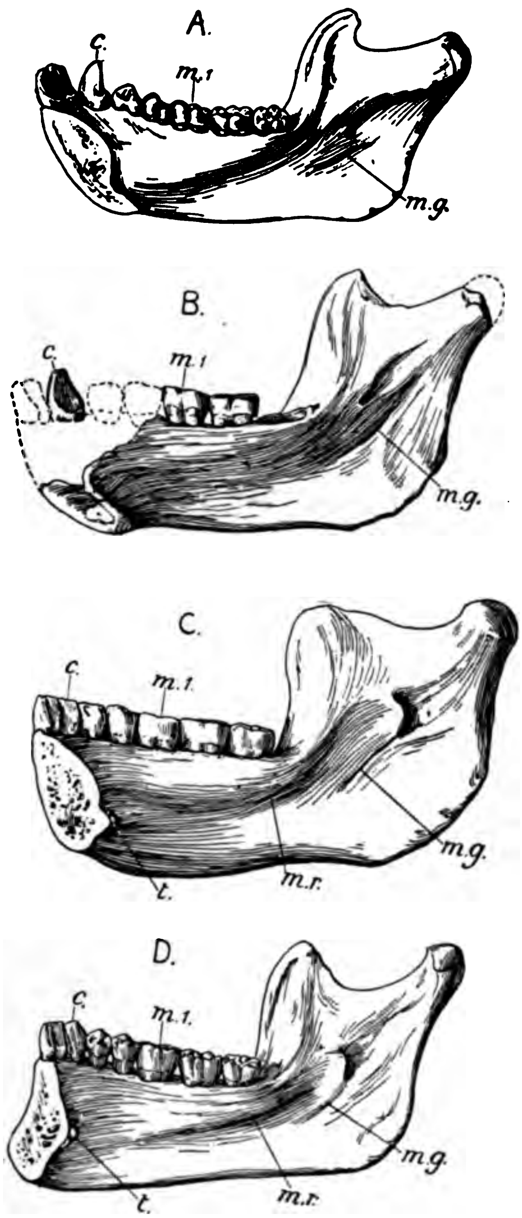

Fig. 264. Comparative Series: Lower Jaws, Medial View of Right Half. × 1/2
After Smith Woodward

*t.*, genial tubercles; *m.g.*, mylohyoid groove; *m.r.*, mylohyoid ridge

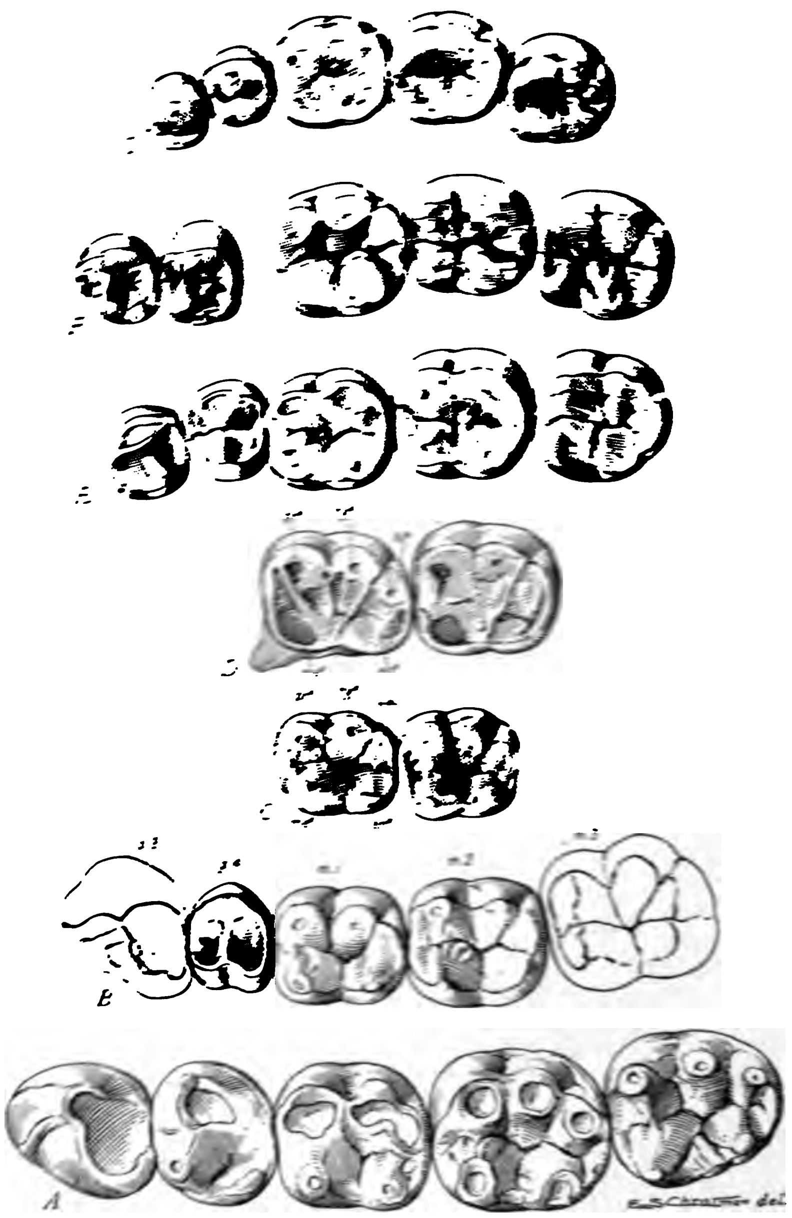

FIG. 265. COMPARATIVE SERIES: RIGHT LOWER PREMOLAR-MOLAR SERIES OF PRIMITIVE MEN AND OF ANTHROPOIDS. CROWN VIEWS. × *circa* 3, 2

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 (× 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 Miller is well warranted in stating that the Piltdown molars are generically referable to *Pan* rather than to *Homo.*

"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*

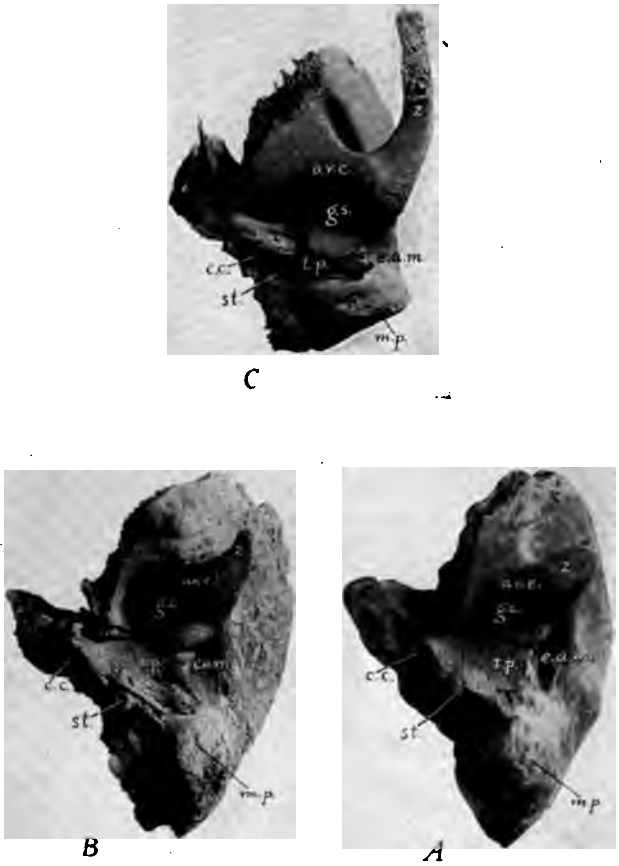

FIG. 266. COMPARATIVE SERIES: TEMPORAL BONES OF (A) THE PILTDOWN SKULL, (B) A NEGRO, AND (C) A FEMALE ORANG. × 2/3

*ar.e.*, articular eminence (for lower jaw); *c.c.*, carotid canal; *e.a.m.*, external auditory meatus; *g.s.*, glenoid socket; *pet.*, petrous bone; *st.*, pit for styloid process; *t.p.*, tympanic plate; *z*, root of zygomatic arch.

*heidelbergensis* they differ in the same characters, although in somewhat less degree. Also $m_1$ 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, 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 Dr. Miller (*op. cit.*, pp. 14–18), the whole conformation of this region in the Piltdown skull demands a human or subhuman lower jaw, while the anthropoid jaw demands anthropoid glenoid and temporal regions.

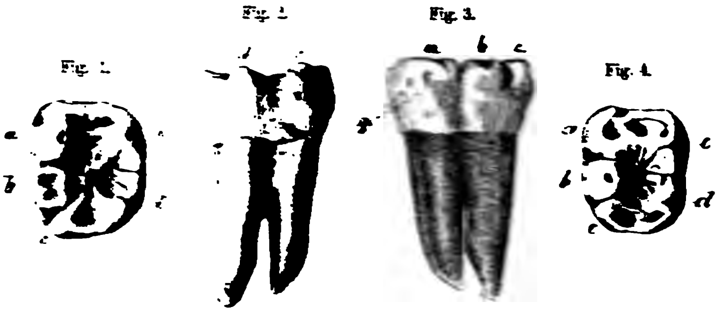

FIG. 267. LOWER LEFT FIRST MOLAR (*figs. 1–3*) FROM THE DILUVIUM AT TAUBACH NEAR WEIMAR. AFTER NEHRING. ABOUT 3/2 NATURAL SIZE

1. crown view; 2. lingual side; 3. labial side. 4. crown view of $m_1$ of a modern chimpanzee

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*.

"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 dawsoni* and *Homo* far back into the Lower Pliocene, as in Professor Keith's diagram (1915, p. 509).

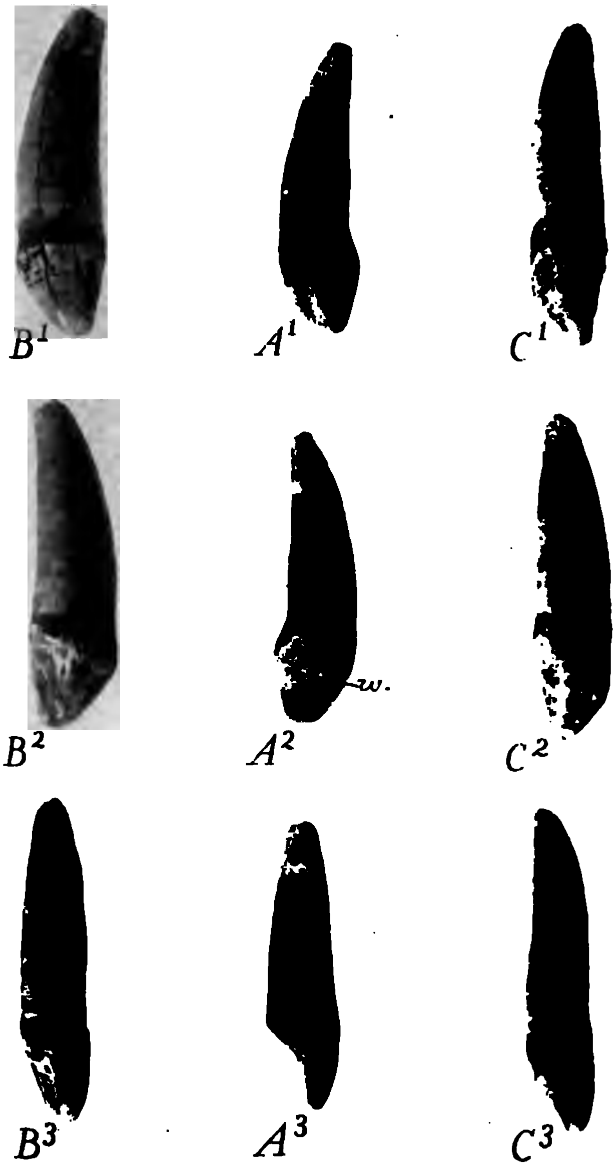

FIG. 268. COMPARATIVE SERIES: (A) CANINE TOOTH (CAST) FOUND AT PILTDOWN IN COMPARISON WITH (B) THE LEFT UPPER CANINE AND (C) THE RIGHT LOWER CANINE OF A FEMALE ORANG. × 1

The lower canine is turned upside down to facilitate comparison with the others. In A the tip of the root is restored.

$A^1$, $B^1$, $C^1$, seen from the outer or labial side

$A^2$, $B^2$, $C^2$, seen from the inner or lingual side; *w*, worn surface.

$A^3$, $B^3$, $C^3$. seen from the front, or antero-internally

"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 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.

"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 Dr. Miller (1915, 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."

It is not practicable, within the limits of this review, to follow the subsequent development of the Piltdown problem in its numerous ramifications and detailed discussion. The reader is referred to the recent papers by Pycraft (1917) and by Miller (1918), the latter containing an annotated bibliography of the subject.

The Piltdown problem has bearing on the general subject of the evolution of the human dentition in so far as it raises the question whether the human brain and braincase assumed its distinctive characters at a relatively early period when the jaws and dentition were still ape-like, as maintained by Elliot Smith (1913). Whether or not the Piltdown jaw belongs with the skull, the fact remains that its contained lower molars are in many respects extremely like those of chimpanzees. But these, in turn, are closely related in pattern to primitive human molars; and the whole Piltdown controversy serves to emphasize not only the fundamental agreements but even the numerous special resemblances in structure of the jaws and teeth of chimpanzees and men.

### THE PITHECANTHROPUS PROBLEM

The celebrated fossils discovered in Java by Dubois were described by him in 1892 under the name of *Pithecanthropus erectus*. **The** remains were not all found in one spot but were scattered along the course of an ancient stream bed. Although some authorities have doubted the association of skull-top, femur and molars, the majority have accepted Dubois's view that all the remains belonged to one skeleton which had become broken up and distributed by stream action. The geological horizon is uncertain. It was originally thought to be Upper Pliocene from the character of the fossil mammals found in the same formation, but later investigators incline to regard it as of Pleistocene age. The skull-top resembles in general that of a gibbon but it is of human size and the braincase was more voluminous than that of any other known anthropoid. The femur much resembles that of modern men and its form implies an upright gait.[8]

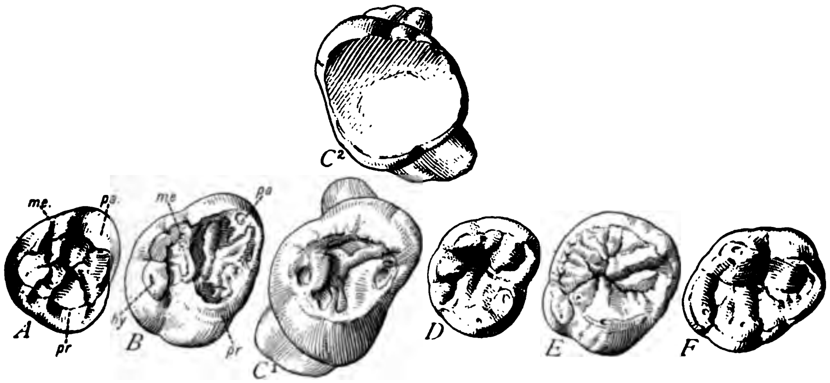

FIG. 269. COMPARATIVE SERIES: RIGHT UPPER THIRD MOLAR REFERRED BY DUBOIS TO *Pithecanthropus* ($C^1$) IN COMPARISON WITH VARIOUS HUMAN AND ANTHROPOID TYPES. ALL FIGURES × 3/2

A.—*Dryopithecus punjabicus*, referred specimen. After Pilgrim.
B.—Modern orang.
$C^1$.—*Pithecanthropus erectus*. Cast of referred specimen ($m^3$, right).
$C^2$.—*Pithecanthropus erectus*. Cast of a second referred specimen ($m^2$, left).
D.—*Homo sapiens*. Australian black (♀).
E.—*Homo sapiens*. Kaffir.
F.—*Homo sapiens*. Brachycephalic Caucasian.

The upper molars represent $m^2$ of the left and $m^3$ of the right side. They are distinguished by their very large size and strongly divergent roots. The third upper molar looks as if it might be an enlarged

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[8] It is possible that the upright gait was early acquired by the pre-human stock. See Part V.

derivative of a third molar of *Dryopithecus* type (*fig. 269*). It is distinguished by the weak development or absence of the metacone, which is confluent with the general outer rim of the crown. A cast of the second upper molar was erroneously identified by me (1916, p. 320) as a third, but Dr. Dubois has kindly informed me that the original bears a distinct pressure scar on its posterior border which shows that there was a tooth behind it. Moreover this tooth is somewhat more quadrate than the third molar of the opposite side and is far from being a reversed duplicate of that tooth. As a second upper molar it is remarkable for the pronounced reduction in size of the posterior moiety of the crown, including the metacone and the hypocone; the reduction of the metacone is concomitant with a buccal protrusion of the large paracone and a pronounced bucco-lingual slope of the outer border of the crown. The reduction of the hypocone and metacone are a result of degenerative processes in the dentition of the most advanced and presumably late races of man, and their presence at this relatively early period in *Pithecanthropus* tends to remove that genus from the line of ascent leading to later human races. The molar teeth, while of subhuman type, differ in their details from any others known to me.

The association of gibbon-like skull-top, modernized human femur and subhuman upper molars with reduced posterior moiety, if correctly assigned to one animal, may perhaps define *Pithecanthropus* as an early side branch of the Hominidæ, which had already been driven southward away from the primitive center of dispersal in Central Asia, by the pressure of higher races. But whatever its more precise systematic and phylogenetic position, *Pithecanthropus*, or even its constituent parts, the skull-top, the femur and the molars, severally and collectively testify to the close relationship of the late Tertiary anthropoids with the Pleistocene Hominidæ.

## III. SUMMARIES AND CONCLUSIONS FOR PART IV

### SUMMARY, BASED CHIEFLY ON DENTAL CHARACTERS, OF THE RISE AND EVOLUTION OF THE ANTHROPOID APES

The accompanying diagram (*fig. 270*), taken from my "Studies on the evolution of the primates," expresses the phylogenetic relationships of the higher primates in so far as I was able to conceive them in 1916. After a careful and as far as possible impartial review of the whole subject, and in the light of recent criticisms and developments, I have to confess that I find but little or nothing to change in this diagram at the present time. In so far as it relates to the origin and rise of the whole catarrhine series, except man, whose origin and divergence will be discussed below, the conception thus symbolized is outlined in the following pages.

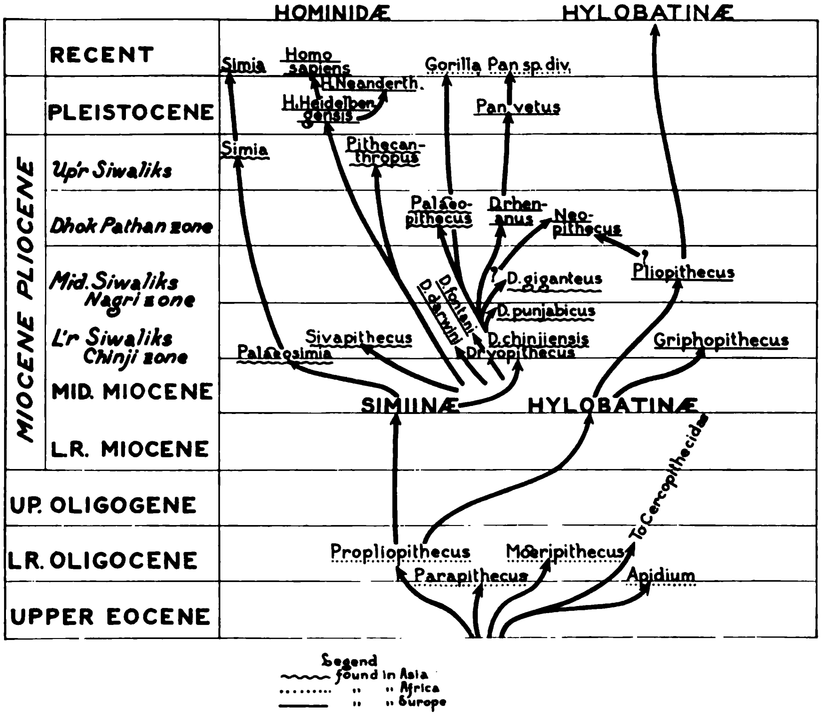


FIG. 270. GEOLOGICAL SUCCESSION AND PROVISIONAL PHYLOGENY OF THE HOMINIDÆ AND SIMIIDÆ, AS INTERPRETED FROM AVAILABLE EVIDENCE BY THE AUTHOR IN 1916

The ancestral stock of the Catarrhinæ may be supposed to have separated from some still undiscovered family of tarsioids at a time considerably before the Lower Oligocene, perhaps the Middle Eocene. The dentition of the ancestral Catarrhinæ, as here conceived, resembled in many respects that of *Necrolemur*, described in Part III, save that there was no undue specialization of the middle pair of lower incisors.

*Parapithecus* (*fig. 215*), of the Lower Oligocene of Egypt, may be regarded as a "left-over," or persistently primitive survivor of the ancestral catarrhine stock.

*Apidium* (*fig. 216*), of the same formation so far as known, appears to represent a similar left-over that gives us a structural stage in the origin of the lower molars of the cercopithecoid branch (family Cercopithecidæ) of the series. These very early entered upon a side path of evolution leading to the specialization of bilophodont upper and lower molars, normally adapted to frugivorous diet; but they retained the more primitive, more quadrupedal mode of progression both in the trees and upon the ground.

The anthropoid-man group of the Catarrhinæ, while early acquiring a new mode of locomotion called brachiation, which will be discussed later, avoided a too early specialization of the dentition, conserving the tritubercular ground plan of the upper molars even after the filling out of the postero-internal corner of the crown (by the development of a prominent hypocone) and retaining the prominent hypoconulid in the lower molars, which is of very subordinate value in the cercopithecoids. The upper molars are, then, essentially four-cusped, while the lower molars have five cusps, namely, the proto-, meta-, hypo-, and entoconids, and the prominent hypoconulid, or mesoconid. The latter is at first medial in position on the crown of the tooth, but early tends to shift toward the outer or buccal side. The posterior lower premolars tend to attain the fully bicuspid type, but the anterior premolars, in all the lines in which the upper canines become large, acquired an oblique, sloping, antero-external sectorial face, which articulates with the postero-internal face of the upper canine. The upper canines usually become enlarged and tusk-like, especially in males, but the lower canines are always smaller. The central upper incisors are more or less widened, with a sharp cutting edge, and often with a posterior central ridge and basal cingulum. The upper incisor crowns are often more or less curved or bent upon the roots in accordance with the degree of prognathism and of overbite. The dental arches, while extremely variable in form, tend to be wide in front, especially in forms with much enlarged canines.

The characters of the dentition in anthropoids appear to be adapted to a mixed diet, large fruits being the principal staple, but insects, young birds, etc., being devoured as opportunity affords. A chiefly frugivorous diet, more or less skill in brachiation, and the habit of sitting upright, are not only characteristic of recent anthropoids but may well be ascribed to their Tertiary ancestors, whose scant remains indicate a fundamental similarity to the surviving members of the family.

The oldest known true anthropoid, as we have seen, is *Propliopithecus*, (*fig. 235*), from the Lower Oligocene of Egypt. Although the type and only known specimen consists merely of a part of the left side of the lower jaw containing the canine and complete cheek teeth, its right to be regarded as a true anthropoid is established by its very characteristic dentition, which shows many strong points of resemblance with that of the Pliocene genus, *Pliopithecus* (*fig. 236*). It is thus connected with the ancestry of the modern gibbons and may also stand in the direct line of ascent leading to the higher anthropoids, as suggested by Schlosser. *Propliopithecus* is much more primitive than any other known anthropoid in its very small size, in the lack of furrows and wrinkles on its molar crowns, in the non-laniary form of the canines, and the non-sectorial form of the anterior lower premolars. On these accounts it might even be conceived as an immediate ancestor of man were it not for much other evidence that tends to connect man closely with the later *Dryopithecus* group, especially with the chimpanzee-gorilla branch.

The modern gibbons (*figs. 237–241*), as we saw, are the smallest and in some ways the most primitive of the anthropoids, retaining many characters of a lower grade of organization and thereby structurally allied with the cercopithecoid group, but nevertheless true anthropoids in the form of the molar teeth; specialized in the laniary development of the upper canines, in the sectorial form of the lower premolars and in the elongation and shallowness of the body of the mandible.

There is a long hiatus in our knowledge of the evolution of the anthropoids, extending between the Lower Oligocene and the second half of the Middle Miocene. When therefore we next meet the group, in the Middle Miocene of India and Europe, we find a great advance toward the modern genera. The three genera and six species so far known from this age are all very much larger than *Propliopithecus*, one of them, *Dryopithecus giganteus* (*fig. 252*), being truly gigantic in size.

Among the Miocene Indian anthropoids, *Palæosimia* (*fig. 242*) is known only from a third upper molar, which, while structurally related to that of *Dryopithecus*, foreshadows the orangs in some respects. As the orangs are in many respects the most specialized members of the family, it seems highly probable that they were among the first to be differentiated from the *Dryopithecus* stem, and *Palæosimia*, although known only from a single tooth, appears to indicate that this separation took place considerably before the Middle Miocene.

The orangs (*figs. 243–246*) have become excessively specialized for arboreal life and have thereby removed themselves widely from the line of human ascent. Their dentition is specialized in the extreme wrinkling of the enamel (which even obscures the primary cusps of the molar crowns) and often in the excessive prognathism of the upper incisors. The living orangs are extremely variable in dental and cranial characters; for example, the central upper incisors of males vary from 8.5 to 16 mm. in width (Hellman, 1920, p. 27).

*Sivapithecus* (*fig. 247*). This Upper Miocene Indian genus was regarded by its describer, Pilgrim, as standing near to the line of human ascent, a view which possibly may yet be confirmed by future discoveries. Its lower molars have the "*Dryopithecus* pattern," but are relatively short and wide and in that respect approach the human type. The same is also true of the lower premolars. If the lower canine and incisors are rightly associated with it, it is probable that the general form of the jaw and arrangement of the dental arches were not dissimilar in essentials from those of *Dryopithecus*, from some primitive species of which *Sivapithecus* may be regarded as an offshoot.

*Sivapithecus* is perhaps more progressive than *Dryopithecus* in the loss of the external cingulum on the lower molars, in their greater breadth-index, in the strong divergence of the molar roots, in the probably greater depth of the mandible and in its shorter symphysis; in the marked advance toward the bicuspid type in the posterior lower premolar, and in the nearer approach toward the bicuspid type in the anterior lower premolar. The third lower molars lack the "sixth cusp," between the hypoconulid and the entoconid, which occurs in certain orangs, in *Dryopithecus chinjiensis*, in *D. punjabicus*, and in many primitive human jaws. In the phylogenetic diagram (*fig. 270*) *Sivapithecus* is provisionally placed as an early offshoot from the *Dryopithecus* stem, intermediate between the *Dryopithecus*-man group and the *Palæosimia*-orang line.

*Dryopithecus* (*figs. 248–256*). The six species assigned to this genus differ greatly in size and considerably in details, one of them, *D. darwini*, having such a wide and wrinkled $m_3$ that it may eventually deserve to be set apart as a distinct but related genus. Abel (1902) has noted that this tooth in its whole appearance and size, and in the arrangement and abundant branching of the furrows, suggests the corresponding characters in the men of Krapina, but that it differs from them in the narrowness of the posterior moiety of the crown, a primitive character. These resemblances are naturally not very close or detailed, because *Dryopithecus darwini* (*fig. 253*) is separated from the Krapina men by the vast time interval between the Upper Miocene and the late Pleistocene; nevertheless it affords one of a number of instances in which the jaws and dentition of the Miocene anthropoids were assuming characters favorable for the starting point of lines of evolution tending toward the human grade.

Of the remaining species of *Dryopithecus*, *D. fontani* (*fig. 254*) of Europe is possibly the most primitive, since its lower molars are (a) relatively narrow, (b) increase in antero-posterior length from $m_1$ to $m_3$, and (c) retain the external cingulum seen in *Propliopithecus* and *Pliopithecus*. It is the only species in which the lower jaw and all the lower teeth are known. It is evidently much less specialized than the existing organs, chimpanzees and gorillas: the lower incisors and canines are of moderate size, the lower molars exhibit the typical "*Dryopithecus* pattern," with little or no wrinkling of the enamel and with sharp definition of the cusps; the hypoconulid is more central, less lateral in position than in *D. rhenanus* or in *D. giganteus;* and, as Smith Woodward (1914) has shown, it is also more primitive than existing chimpanzees and gorillas in the shortness of the symphyseal ledge of the mandible. For these reasons I have placed *D. fontani* near the base of the *Dryopithecus* series (*fig. 270*).

*Dryopithecus chinjiensis* (*fig. 249*), from the Middle Miocene of India, is represented by the type, a third lower molar which resembles that of the gorilla, except that it is more primitive in certain respects. It exhibits the "sixth cusp" which is also found in *D. punjabicus*, the gorilla and certain human molars. The species may stand in or near the gorilla line. A referred first lower molar (*fig. 285*) shows the *Dryopithecus* pattern; it is unusually wide across the posterior moiety, thus suggesting a human tooth.

*Dryopithecus punjabicus*. In this Miocene Indian species the third lower molar (*fig. 250*) is much smaller than that of *D. chinjiensis*, but it nevertheless approaches even more closely the corresponding tooth of the gorilla in the detailed pattern of the crown. The upper molars and premolars (*fig. 251*) referred to this species by Pilgrim are highly important; first, because they afford knowledge of these parts in an Indian species of *Dryopithecus;* secondly, because they resemble the isolated upper molars of the European *D. rhenanus* well enough to make the generic reference of all the Indian species more certain; and finally, because they show a highly significant resemblance to the upper teeth of gorillas and chimpanzees and more remotely to those of primitive men.

*Dryopithecus giganteus* (*fig. 252*). This relatively enormous third lower molar from the Indian Miocene resembles those of modern chimpanzees except in its more primitive, less wrinkled character.

*Dryopithecus rhenanus*. The upper (*fig. 255*) and lower molars, (*fig. 256*), and the deciduous last lower molar (*fig. 287*), of this Lower Pliocene species of Europe closely approach those of modern chimpanzees. The third lower molar shows the "fovea anterior" and the "fovea posterior," which are found in some of the Krapina molars; the fovea anterior being merely the vestigial basin of the trigonid and the fovea posterior being the space between the posterior cingulum, the hypoconulid and the entoconid (cf. *D. giganteus*, *fig. 252*). As shown in *fig. 265*, it is possible that *D. rhenanus* stands in or quite near to the line of ascent leading on the one hand to the "Piltdown jaw" (*Pan vetus*) and on the other to the modern chimpanzees of Africa.

*Pan vetus* (*figs. 263-265*). Assuming provisionally the correctness of Miller's conclusions, the Piltdown jaw represents the survival of a species of chimpanzee in England, probably in late Pleistocene times, existing there along with other mammals, including man, which had invaded Great Britain by way of a broad land bridge from the continent, and which were related to modern species now inhabiting more southern countries, such as elephants, hippopotami, rhinoceroses, hyenas, lions, etc. To the same or to an allied species of chimpanzee, Miller also provisionally referred the "human" lower molar (*fig. 267*) found in a Pleistocene deposit near Weimar in Germany and described by Nehring in 1895.

*Neopithecus* (*fig. 256*). The exact systematic and phylogenetic relations of this third lower molar from the Lower Pliocene of Europe remain uncertain. It is remarkably long in proportion to its breadth, thereby differing from all the known species of *Dryopithecus* and *Pliopithecus*, but the crown pattern looks like an elongated derivative of that of $m_3$ of *Dryopithecus rhenanus*. It shows the "fovea anterior" and "fovea posterior" of that species and other offshoots of the *Dryopithecus* stock. The remarkable contrasts in proportions between the narrow $m_3$ of *Neopithecus* and the very wide $m_3$ of *Dryopithecus darwini*, suggest that we may find corresponding differences in the proportions of the entire jaws of these forms; and the further differences in the "*Dryopithecus* pattern" of the lower molars show that there was a wide adaptive radiation of the *Dryopithecus* stock in mid-Tertiary Europe and Asia, of which we have so far obtained only a preliminary suggestion. Notwithstanding the narrowness of the $m_3$ of *Neopithecus*, it resembles a human tooth to such a degree that Schlosser, a high authority on extinct primates, at first named it "*Anthropodus*," in allusion to its human appearance.

*Palæopithecus* (*fig. 257*). In this Upper Pliocene descendant of the *Dryopithecus* group (which is known from an imperfect palate with much worn cheek teeth), the upper teeth approach those of the gorilla but are smaller and more primitive in some respects. The premolars and the molars are also fundamentally similar to those of primitive races of men, the most conspicuous difference being that the upper canine is much larger than in man and its apex extends much below the level of the premolars. The canine is also separated from the lateral incisor by a wide diastema for the reception of the lower canine.

*Pithecanthropus (fig. 269).* As noted above, the association of gibbon-like skull top, modernized human femur, and subhuman upper molars with reduced posterior moiety, if all correctly assigned to one animal, may perhaps define *Pithecanthropus* as an early side branch of the Hominidæ, an offshoot of the *Dryopithecus* group, which had early been driven southward away from the primitive dispersal center, in west-central Asia, by the pressure of higher races.

In conclusion, the Tertiary anthropoids are of interest in the present connection because they assuredly afford prehuman stages in the evolution of the dentition. It is true that certain investigators have not recognized their importance, partly because they are so fragmentary; but it must be remembered that the various fragmentary specimens supplement each other in giving us a general idea of the characters of the dentition and jaws. Thus the lower incisors are known in *Parapithecus*, *Pliopithecus*, *Dryopithecus fontani*, and partly in *Sivapithecus;* the upper incisors are known in *Pliopithecus* and partly in *Palæopithecus*. The lower canines are known in *Parapithecus*, *Propliopithecus*, *Pliopithecus*, *Sivapithecus*, *Dryopithecus fontani;* the upper canines only in *Pliopithecus* and *Palæopithecus*. The lower premolars are known in representatives of all the genera except *Palæopithecus*. All three lower molars are known in all the genera except *Palæosimia*. The upper molars are known in *Pliopithecus*, *Dryopithecus*, *Palæopithecus*, and possibly in *Sivapithecus* and *Pithecanthropus*. More or less of the body of the mandible, sometimes with part of the ascending ramus, is known in *Parapithecus*, *Propliopithecus*, *Pliopithecus*, *Sivapithecus*, and *Dryopithecus fontani*. The third lower molar, which is well guarded from disruptive post-mortem agencies by the surrounding bone, is preserved in five of the genera and in all the six species of *Dryopithecus*.

Notwithstanding the warnings of those who cite the principle of "non-correlative evolution" (see Part V), palæontologists have been well repaid by most diligent and minute comparisons of these extinct anthropoid remains with each other and with the corresponding parts of surviving members of the group. From such comparisons the conclusions may be gained, first, *that the mid-Tertiary anthropoids in dental structure fall well within the limits of specialization set by the modern orangs, chimpanzees, and gorillas; secondly,* *that they afford several successive stages of dental evolution, represented especially by Parapithecus, Propliopithecus, and Dryopithecus, beginning with a relatively low, almost tarsioid stage and culminating in the diverse genera of modern anthropoids. The third and most important conclusion, and the one which will encounter the most opposition, is that the same series also lies in or near the line of human ascent.* Because these mid-Tertiary primates are named and generally recognized as anthropoids, Wood Jones (1918, p. 40) insists that none of them can be ancestral to man, partly because he, in common with many others, apparently expects the mid-Tertiary ancestors of man to have only recognizably human characters. This matter is so important and so critical a part of our general problem that it must be reserved for special discussion in the succeeding parts of this work. But before this can be done effectively it seems necessary to make a final review and summary of the chief characteristics of the anthropoid dentition, as a whole and in its several parts, bearing in mind the phylogenetic concept outlined in the preceding pages, and setting forth at the same time the broad resemblances and contrasts in dental characters between anthropoids and man.

## SUMMARY OF ANTHROPOID DENTAL CHARACTERS, RESEMBLANCES AND CONTRASTS WITH HUMAN CONDITIONS

(1) The dental formulæ, $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{2}{2}\ M\frac{3}{3}$ and $DI\frac{2}{2}\ DC\frac{2}{2}\ DP\frac{2}{2}$, are characteristic of all anthropoids and primitive men; but a fourth molar rather frequently occurs in anthropoids and occasionally in man.

(2) The incisors, excepting the central uppers, are primitively simple pointed teeth, with a basal cingulum. The central upper incisors, both in anthropoids and in men, tend to become wide, and in certain orangs and chimpanzees they finally become excessively large and wide, with crenate or denticulate edges. They often have on the lingual surface a central tubercle confluent with the cingulum. The lower incisors are relatively simple, primitively rather narrow, not greatly expanded or crowded, gently inclined; becoming vertical or even slightly recurved in man. The incisor crowns are often more or less curved or bent upon the roots in accordance with the degree of prognathism and of overbite. Adjacent incisors are primitively

separated from each other, at the base of the crown, and in anthropoids the upper incisors are also usually separated by diastemata from the canines. Diastemata are lost in man, probably in correlation with reduction of canines and increasing verticality of incisors. While their crowns are often in contact at the inner and outer borders, the incisors of anthropoids are not so crowded as to derange the even curve of the incisor arch, as they often are in man.

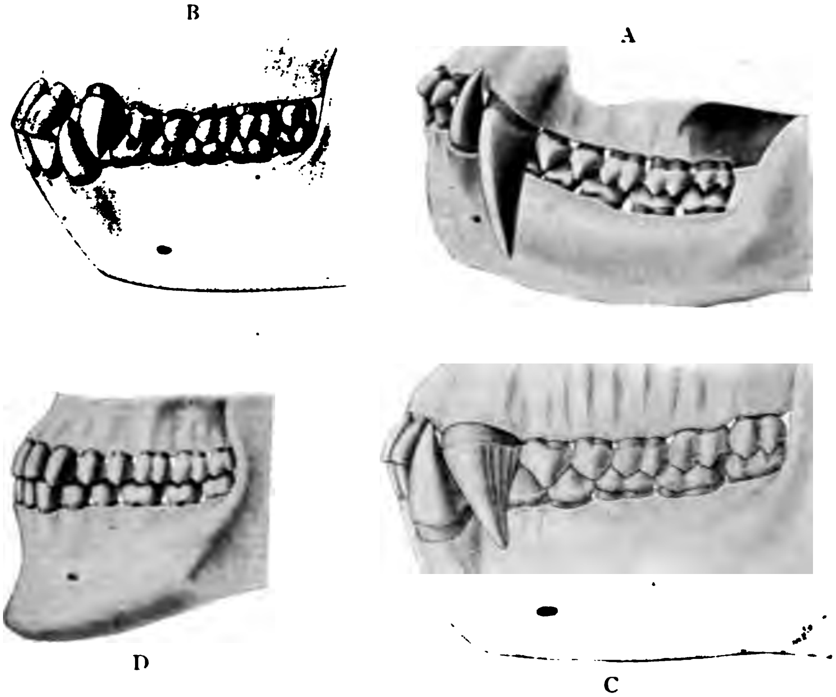


FIG. 271. COMPARATIVE SERIES: UPPER AND LOWER TEETH IN OCCLUSION OF ANTHROPOIDS AND MAN. FROM SALENSKY, AFTER RÖSE

Fig. *A*—Gibbon, *B*—Chimpanzee, *C*—Gorilla, *D*—Man

(3) The canines of males, originally small, are progressively enlarged in all phyla of anthropoids, the upper canines finally becoming sabre-like in the gibbons and tusk-like in the gorilla. Female canines smaller, with lower crowns. The small size and low crown of normal human canines are very probably to some extent retrogressive. Lower canines biting partly in front of uppers, their tips originally received

by diastemata between the lateral upper incisors and the upper canines. The upper canines tend to align themselves with the premolars, while the lower canines are rather associated with the lower incisors (*figs. 273, etc.*).

(4) Anterior lower premolars ($p_3$) originally with simple convex crown and strong internal cingulum; in forms with progressively enlarged upper canines the antero-external face tends to become enlarged and more or less sectorial. The stages *Parapithecus*, *Propliopithecus*, *Pliopithecus*, *Hylobates*, show the evolution of the sectorial premolars in the Hylobatinæ (p. 305), while the first two genera and *Dryopithecus* give the origin of the same structure in the higher anthropoids. In *Sivapithecus* (*fig. 247*) the anterior lower premolar,

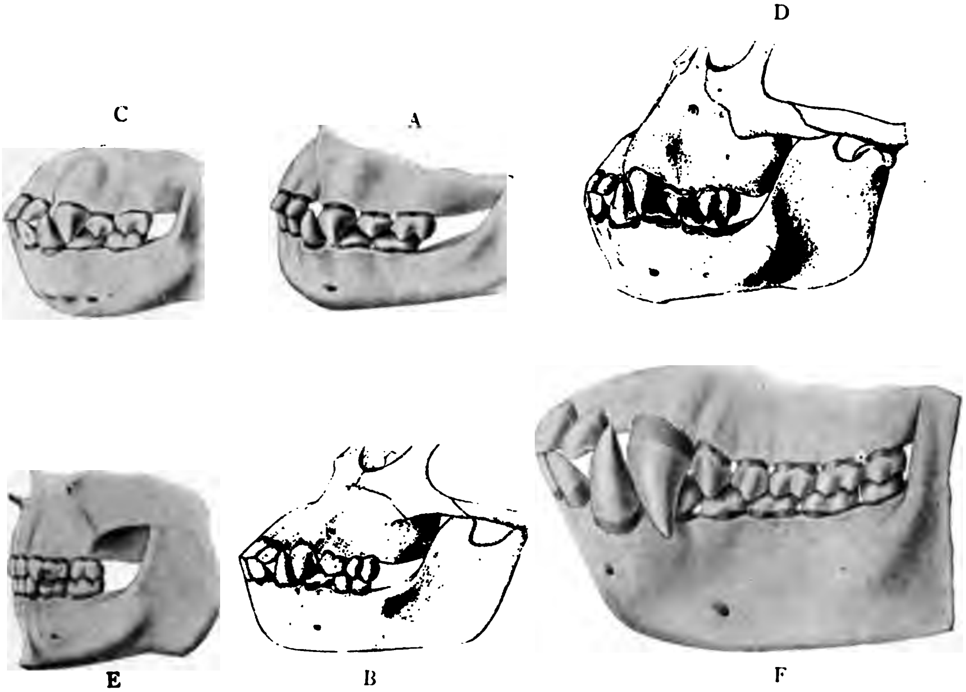


FIG. 272. COMPARATIVE SERIES: UPPER AND LOWER TEETH, IN OCCLUSION, OF ANTHROPOIDS AND MAN. FROM SALENSKY, AFTER RÖSE

*A*—Gibbon, *B*—Orang, *C*—Chimpanzee, *D*—Gorilla, *E*—Man, *F*—Orang (adult)
All except *fig. F* represent the deciduous dentition.

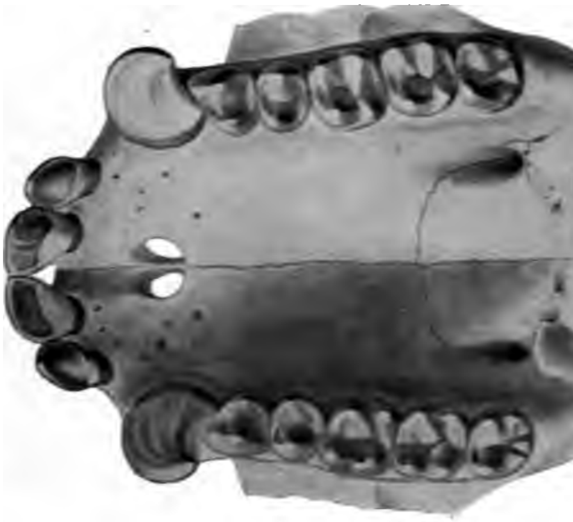


FIG. 273. GIBBON

FIG. 277. MAN.

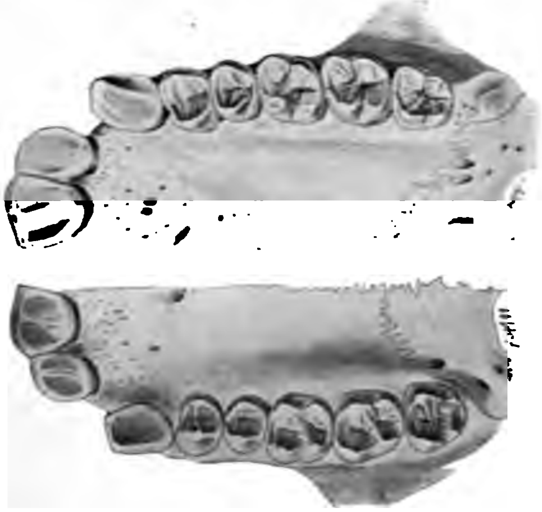


FIG. 275. CHIMPANZEE

Fig. 276. Gorilla

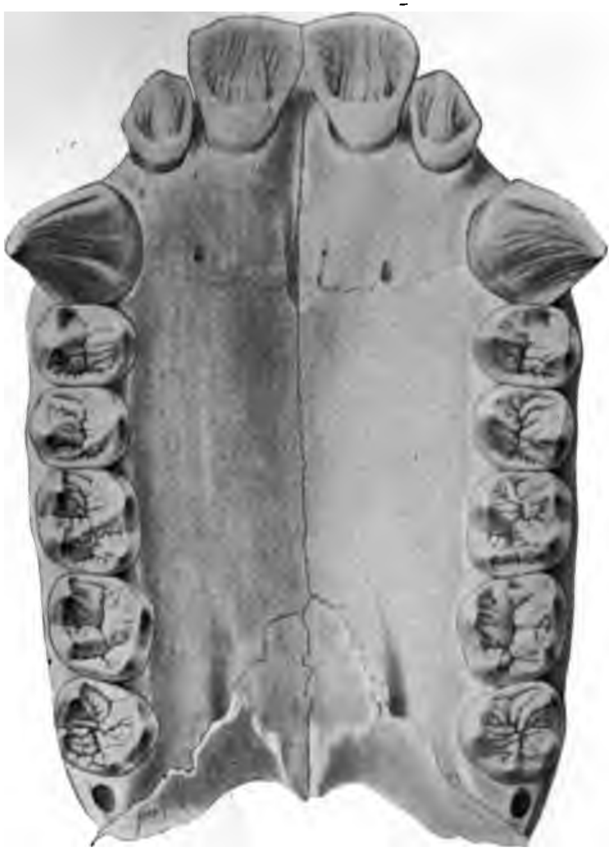


Fig. 274. Orang

Figs. 273 to 277, Inclusive. Comparative Series: Upper Dental Arches of Anthropoids and Man. Rearranged from Salensky, After Röse

FIG. 278. GIBBON

FIG. 282. MAN

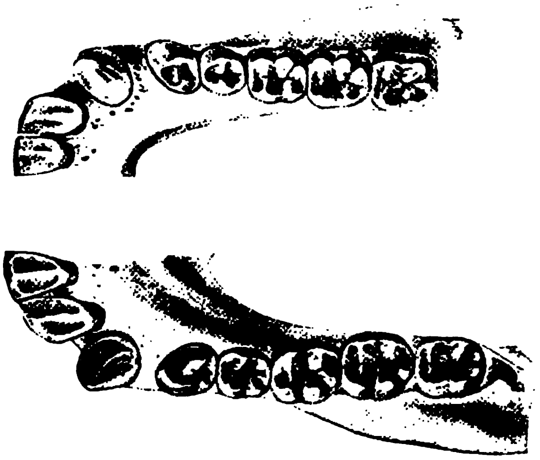
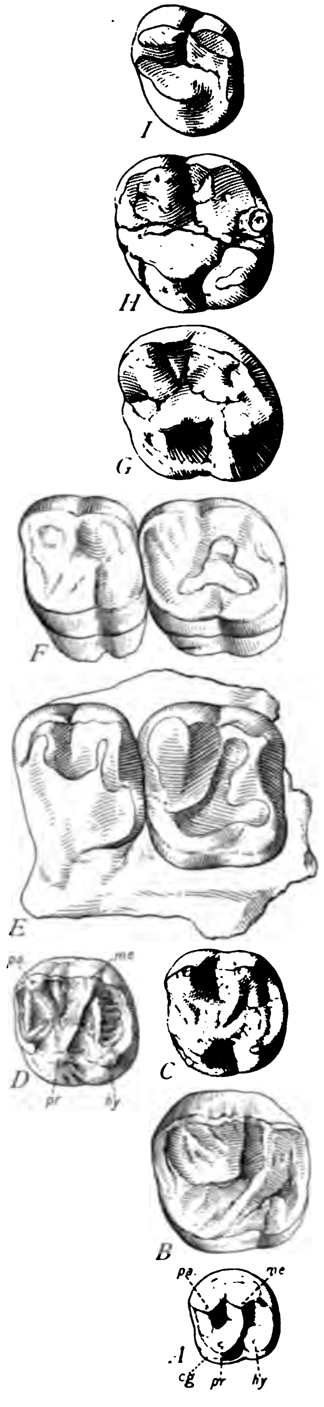


FIG. 280. CHIMPANZEE

FIG. 281. GORILLA

FIG. 279. ORANG

FIGS. 278 TO 282, INCLUSIVE. COMPARATIVE SERIES: LOWER DENTAL ARCHES OF ANTHROPOIDS AND MAN. REARRANGED FROM SALENSKY, AFTER RÖSE



I.—*Homo sapiens*, m$^2$. Brachycephalic Caucasian.

H.—*Homo sapiens*, m$^2$. Kaffir from South Africa

G.—*Homo neanderthalensis*, m$^2$. From the Pleistocene of Krapina. After Gorjanovic-Kramberger.

F.—*Palæopithecus sivalensis*, m$^1$, m$^2$, much worn. From the Pliocene of Jobi, India. After Dubois.

E.—*Sivapithecus indicus*. Referred m$^1$, m$^2$, much worn. From the Upper Miocene of Haritalyangar, India. After Pilgrim.

D.—*Dryopithecus rhenanus*. Lower Pliocene Bohnerz of the Swabian Alps. From a cast. (m$^1$.)
C.—*Pan* (*Anthropopithecus*) sp. Recent chimpanzee. (m$^1$.)

B.—*Dryopithecus punjabicus*, m$^2$. Upper Miocene of Haritalyangar, India. After Pilgrim.

A.—*Pliopithecus antiquus*, m$^2$. Upper (?) Miocene of Göriach, Austria. After Hoffman.

FIG. 283. COMPARATIVE SERIES SHOWING CHIEFLY THE SECOND LEFT UPPER MOLAR IN HOMINIDÆ AND TERTIARY ANTHROPOIDS. × 3

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 (1), 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.

while possessing some of the sectorial oblique face, is also becoming distinctly bicuspid and its parts may be closely homologized with those in primitive human stages.

(5) Posterior lower premolars ($p_4$) originally (*Parapithecus*) much like $p_3$, with high apex, but with low metaconid and low talonid cingulum; in some orangs acquires a submolariform crown with high trigonid and low talonid. In *Sivapithecus* this tooth becomes strongly bicuspid and subhuman in type, but it retains two external roots.

(6) Both upper premolars more or less bicuspid; in *Dryopithecus punjabicus* (*fig. 251*), gorilla and chimpanzee approaching the human type and closely comparable with it in all their parts.

Palæontological experience warrants us in assigning a relatively great phylogenetic value to such resemblances in the premolar patterns of different genera.

(7) First and second upper molars with four cusps and rhomboid contour, the three primary cusps preserving their triangular arrangement and situated at the extreme corners of the tooth. Hardly a trace of the "primary trigon" of Mesozoic mammals is retained, the external cingulum being vestigial or absent and the para- and metacones widely separated, in correlation with the great expansion of the talonid of the lower molars. Paracone usually larger and more protuberant than metacone, the external border of the crown often sloping obliquely inward toward the metacone. Hypocone often on a lower level than the protocone and projecting obliquely backward from the crest connecting the proto- and metacones. Carabelli's cusp (protostyle) not developed but potentially represented[4] by the antero-internal cingulum. No external styles or intermediate conules. Four cusps of varying height and sharpness, highest and sharpest in the gorilla, lowest in the orang. Surface of enamel more (orang) or less (gorilla) furrowed and wrinkled. All the above-named characters of the first and second upper molars are retained in primitive human dentitions.

(8) Third upper molar of varying size and form, the posterior moiety reduced, the hypocone rarely large or protuberant.

(9) First and second lower molars with five cusps (the proto-, meta-, hypo-, an entoconid and the hypoconulid) separated by

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[4] Except, rarely, in the gibbons

furrows, the whole constituting the "*Dryopithecus* pattern," which is exhibited with minor modifications by all mid-Tertiary and later anthropoids. An allied and, as I maintain, a derived pattern, is present in primitive Hominidæ (see below). A sixth cusp, on the medial slope of the hypoconulid, between the hypoconulid and the entoconid, present in orangs, in several members of the *Dryopithecus* group and in certain primitive human dentitions. "Fovea anterior" (the reduced basin of the trigonid) and "fovea posterior" (the vestigial depression in front of the posterior cingulum) often present, especially on the third molar. Fovea anterior often, and fovea posterior occasionally, present in primitive human teeth. An external cingulum present in the primitive *Dryopithecus fontani* (*fig. 248*), but lost in most later types. First lower molar more conservative in pattern than second and still more than third. Hypoconid varying in relative size, sometimes [e.g., $m_1$ of *Dryopithecus chinjiensis* (*fig. 283*), $m_2$ of *Sivapithecus* (*fig. 247*), many primitive human molars] projecting buccally beyond protoconid, making posterior wider than anterior

FIG. 284. ANTHROPOID HERITAGE IN THE LOWER MOLAR PATTERN OF MAN

B.—A primitive lower first molar of man, compared with those of two Miocene anthropoids: (A) *Sivapithecus indicus* (drawn from a cast of the type specimen) and (C) *Dryopithecus chinjiensis*. After Pilgrim. All figures × 3/2.

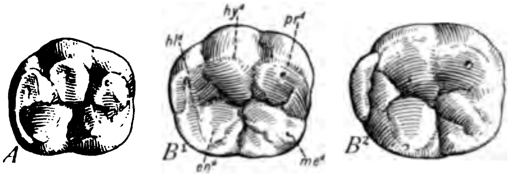

FIG. 285. ANTHROPOID HERITAGE IN THE LOWER MOLAR PATTERN OF MAN (CONTINUED)

Comparison of B¹, B², the fossil human molar (left $m_1$), discovered by the Selenka expedition near Trinil, Java (A), with the corresponding molar of *Dryopithecus chinjiensis*. B¹, after Deek; B², after Walkhoff; A, after Pilgrim. All figures × 3/2.

moiety of tooth. Hypoconid crowded toward protoconid and entoconid further removed posteriorly from metaconid, as hypoconulid enlarges and shifts from medial to lateral position. In man (*figs. 284, 265*) a secondary enlargement of the entoconid finally brings the furrow between the entoconid and the metaconid into transverse alignment with the furrow between the protoconid and the hypoconid. This process, accompanied by an equalization in size of the four main cusps and by a reduction of the hypoconulid, finally results in a +-shaped pattern of the furrows and a subquadrate contour of the whole tooth (*fig. 265*); but many stages in the evolution of the new pattern from the "*Dryopithecus* pattern" may be traced.

(10) Third lower molar of varying size and form, sometimes (*Neopithecus, fig. 256*) long and narrow, sometimes (*Dryopithecus*

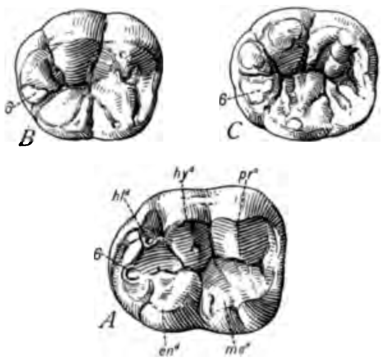

FIG. 286. ANTHROPOID HERITAGE IN THE LOWER MOLAR PATTERN OF MAN (CONTINUED)
ALL FIGURES × 3/2

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 in a +-shaped, or cruciform pattern.

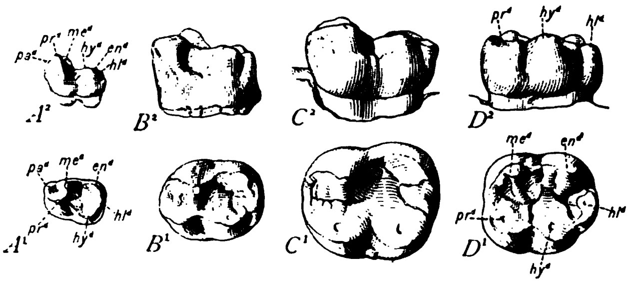

Fig. 287. Lower Posterior Deciduous Premolar of (D) *Homo sapiens*, (C) Chimpanzee, (B) *Dryopithecus rhenanus* (from a Cast); Compared with (A) a Permanent Molar of an Eocene Tarsioid (Omomys)

$A^1$, $A^2$ × 3/1; remaining figures, × 3/2.

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

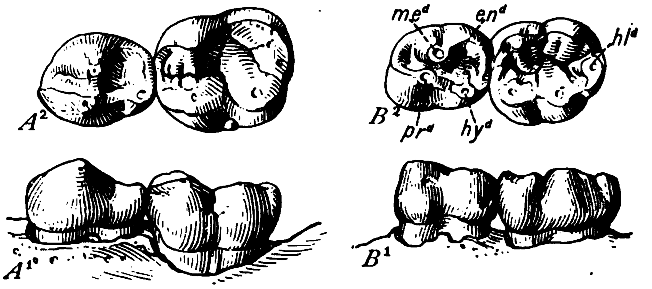

Fig. 288. Inferior Deciduous Premolars of ($A^1$, $A^2$) Chimpanzee and of ($B^1$, $B^2$) *Homo sapiens*, Showing Agreement in Fundamental Pattern

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. × 3/2.

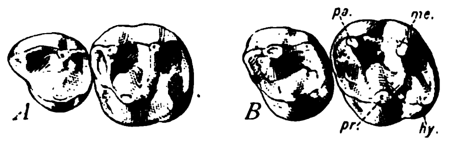

Fig. 289. Superior Deciduous Molars of (A) Chimpanzee and of (B) *Homo sapiens*, Showing Agreement in Fundamental Pattern

The last deciduous premolar, as in all other mammals, is molariform. × 3/2.

*darwini, fig. 253)* short, wide and rounded, approaching human types. Sixth cusp and foveæ as described above. Hypoconulid usually more lateral in position than it is in $m_1$, $m_2$. Breadth of $m_3$ across posterior moiety varying with the size and prominence of hypoconid and metaconid, sometimes (*Sivapithecus*, *Dryopithecus chinjiensis*) becoming wider than anterior moiety, as it is often in man.

(11) Deciduous dentition almost unknown in extinct anthropoids, except posterior deciduous molar ($dp_4$) of *Dryopithecus rhenanus* (*fig. 287*), which is more primitive than that of a modern chimpanzee in retaining more than distinct traces of the primitive tuberculo-sectorial pattern: the trigonid being smaller and higher than the talonid, the hypoconid less protuberant laterally. "*Dryopithecus* pattern" in slightly modified form. Homologous tooth of an Indian child (*fig. 288*) exhibiting similar, but further modified, form of "Dryopithecus pattern," the +-shaped pattern of the permanent molars not being developed; trigonid on same general plane with talonid, hypoconulid large and well defined, metaconid shifted to lingual border of crown, and size of four main cusps subequal.

(12) Posterior upper deciduous premolar molariform (as in most other mammals), with sharply ridged secondary trigon and prominent hypocone. The homologous tooth of man closely similar in general type but with expanded protocone and central fossa.

(13) Anterior lower deciduous molar ($dp_3$) in recent anthropoids of subsectorial type with more or less flattened antero-external shearing face and low talonid, correlated with more or less compressed and shearing deciduous canines. Corresponding tooth in man of plainly derived pattern but considerably modified: anterior moiety non-sectorial, in correlation with small size of deciduous canines, posterior moiety (talonid) more expanded in correlation with expansion of occluding protocone of posterior upper deciduous molar.

(14) Upper and lower deciduous canines of anthropoids very much smaller, shorter, and less tusk-like than the permanent canines. Deciduous canines of human races normally of same generic type as permanent canines, but plainly representing shortened modifications of the homologous teeth of primitive anthropoids; lower deciduous canines of man set more erectly in mandible than those of anthropoids, their tips not normally exposed laterally in occlusion, but covered

FIG. 291. ORANG

FIG. 290. GIBBON

FIG. 294. MAN

FIG. 292. CHIMPANZEE

FIG. 293. GORILLA

FIGS. 290 TO 294, INCLUSIVE. COMPARATIVE SERIES: DECIDUOUS UPPER TEETH OF ANTHROPOIDS AND MAN. REARRANGED FROM SALENSKY, AFTER RÖSE

FIG. 295. GIBBON

FIG. 296. ORANG

FIG. 299. MAN

FIG. 298. GORILLA

FIG. 297. CHIMPANZEE

FIGS. 295 TO 299, INCLUSIVE. COMPARATIVE SERIES: DECIDUOUS LOWER TEETH. REARRANGED FROM SALENSKY, AFTER RÖSE by adjacent parts of lateral upper incisor and upper canine; the last two not separated by diastema as they are in anthropoids.

(15) Deciduous incisors of anthropoids and men representing smaller and narrower variants of the homologous permanent incisors of the same genus. Human upper and lower deciduous incisors set more erectly in jaws.

(16) With regard to the chronological order of eruption of the deciduous teeth, in orang, chimpanzee, and gorilla, according to Selenka (1898, pp. 131–141), the deciduous canine is the last to erupt, whereas in man, according to Tomes, the deciduous canines are usually the next to the last.

As to the eruption of the permanent teeth, in anthropoids the permanent canines erupt after the premolars, as in man. In man the second and still more the third molars are delayed in eruption. Otherwise the general order of eruption of both sets is similar in anthropoids and man.

(17) Form of dental arches highly variable in anthropoids (Hellman, 1918, 1919), the upper more than the lower. Lower and probably upper arch pointed in front in the primitive genus *Parapithecus;* opposite rows of upper cheek teeth often strongly divergent in front in highly specialized modern anthropoids with greatly enlarged and tusk-like upper canines. Diastemata behind upper incisors becoming large in forms with tusk-like canines. Opposite rows of lower cheek teeth often more or less parallel.

Upper incisor arches varying more or less with the form and inclination of the incisors and with the varying relations of the centrals and laterals; often pointed in individuals with narrow centrals, wide and flat in those with wide centrals and much protruded laterals. These diverse specializations probably less pronounced in *Dryopithecus rhenanus* than in modern anthropoids.

In man curve of upper dental arch normally more or less elliptical, parabolic or hyperbolic (Leavitt, 1919), but opposite tooth rows more nearly parallel in some extremely dolichocephalic Australians. In general the human dental arch (*figs. 303, 304, 277*) is relatively shorter and wider, and its sides more convergent in front, than those of anthropoids, this condition being associated especially with the increased width of the intercondylar diameter, with the reduction of the canines and with the more vertical position of the incisors. The human teeth are normally placed in a closed series, the loss of the diastemata being associated with the conditions described above. From very early times there is a marked tendency for the incisors to become crowded so as to overlap at the edges. The lower canines tend to be aligned with the incisor arch, the upper canines with the cheek teeth, the upper canine showing a tendency to become premolariform. The wide differences between modern men and anthropoids in the form of the dental arches (*fig. 277*) is perhaps even greater than the differences between them in the form of the canine teeth. If the Piltdown jaw be associated with the Piltdown skull it affords an example of an anthropoid type of lower dental arch in a human or subhuman race; but the association is denied by some authorities on apparently valid grounds. Again if Smith's restoration (1918) of the upper dental arch of the Talgai man is correct, we have an almost anthropoid form of upper arch in a human skull. But the correctness of this restoration is denied by Hellman, who, after examining the cast of the original, holds that if the canine be put in its right place and the distortion of the tooth rows be corrected, the upper arch will be not very dissimilar to that of the Neanderthaloids. For the present, then, it is conservative to affirm that, with regard to the differences between anthropoids and men in the form of the dental arches, there is as yet no generally accepted palæontological evidence of transitional stages. Nevertheless the comparative anatomical evidence (*e.g.*, *figs. 218*, *258*, *302*) shows that forwardly diverging tooth-rows are associated with tusk-like canines, long jaws, and other conditions noticed above, while converging tooth-rows are associated with reduced canines, short jaws, and widened intercondylar diameters. In man the great widening of the tongue may also have contributed to the end result.

### EVIDENCE OF THE DENTITION AS TO THE PHYLOGENETIC RELATIONSHIPS OF THE SIMIIDÆ WITH THE HOMINIDÆ

In spite of the differences between men and anthropoids in the size of the canines and incisors, and in the form of the dental arches, it is quite obvious from the foregoing review that the resemblances are far more numerous, detailed and fundamental than the differences, both in the permanent and in the deciduous dentures. Of all known primates the anthropoids stand by far the nearest to man in the totality of their dental characters; the Platyrrhinæ are much further off, while the position of *Tarsius* is extremely remote. The natural assumption that these degrees of resemblance correspond roughly to degrees of kinship would doubtless be denied by Wood Jones, who holds that many of the resemblances of man to the anthropoids have been independently acquired and that man's nearest existing relative is *Tarsius*. But his arguments have been discussed by several eminent authorities and shown to have little weight.[5]

Although some palæontologists, anatomists, and anthropologists may be inclined to discount the phylogenetic value of the numerous resemblances in the dentition between anthropoids and men and to ascribe them largely to "convergence," the resemblances in question are so intimate and fundamental that the case seems rather to fall under a general principle enunciated by Osborn (1908) and familiar to all close students of mammalian phylogeny, namely, that identical characters are often developed by divergent descendants of a common stock. Another applicable principle is that, in general, the more numerous and detailed are the special resemblances between divergent offshoots of a common stock the nearer is the relationship between them; a third is that while *general* resemblances between single parts of the dentition are often produced by convergent evolution in widely different stocks in adaptation to similar habits, *coincident* resemblances in the dental formulæ of both dentures, and in the fundamental plan and even minor details of each tooth, are not found to exist between members of widely unrelated families. In other words a similar "habitus" in parts of the dentition is sometimes assumed by members of different stocks, but on close examination their "heritage" is seen to be different. For example, among the "pseudo-horses," or horse-like litoptern ungulates of the Miocene of Patagonia, the upper molar teeth bear a superficial resemblance to those of *Mesohippus* and other three-toed horses, but the dental formula and the incisor teeth are different, and upon close examination even the patterns of the molars

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[5] See a recent discussion of the zoölogical position and relationships of *Tarsius*. *Proceedings of the Zoological Society of London*, 1920 (Feb.), p. 465.

and premolars, although superficially similar, are seen to differ in certain important diagnostic characters that separate the "pseudo-horses" and their allies from the true horses. When, on the contrary, we compare the dentition as a whole of anthropoids and men we find that they resemble each other in their heritage of ancient common characters but differ widely in their habitus of lately acquired specializations, such as those of the incisor and canine teeth and dental arches.

Most authorities are willing to admit that the anthropoids are the nearest existing relatives of man, although many regard the Hominidæ as an exceedingly ancient stock which may have diverged from the group that gave rise to the Simiidæ in Eocene or even earlier times. *But the conclusion indicated by the foregoing review of the dentition and to which all the rest of my investigations have also led, is that the Hominidæ have been derived from the Dryopithecus group of the Simiidæ in the late Tertiary.* This conclusion is supported by the concurrent testimony of comparative anatomy, which as will presently be shown, points to a very near relationship of the Hominidæ to the gorilla-chimpanzee division of the Simiidæ.

In the preceding pages (Part IV) our attention has been focussed first upon the dentition of recent and fossil anthropoids, secondly upon the resemblances and contrasts between the dentition of anthropoids and that of men, and thirdly upon the phylogenetic relationships of the two families, Simiidæ and Hominidæ, in so far as it may be inferred from the foregoing evidence. In Part V we may consider in more detail the dental characters of extinct and recent races of man, dealing again with their resemblances with and differences from the anthropoids, and considering such objections to the foregoing conclusions as are based on the deficiency of palæontological evidence.

# PART V

## Later Stages in the Evolution of the Human Dentition; with a Final Summary and a Bibliography

# I. ORIGIN AND RISE OF MAN (SERIES CATARRHINÆ, FAMILY HOMINIDÆ)

## INTRODUCTION: PRESENT DIVERSITY AND CONFUSION OF OPINION REGARDING THE ANCESTRY OF MAN

Darwin, in his immortal work on "The Descent of Man," says (p. 200): "It would be beyond my limits and quite beyond my knowledge, even to name the innumerable points of structure in which man agrees with the other Primates. Our great anatomist and philosopher, Professor Huxley, has fully discussed this subject,[2] and concludes that man in all parts of his organization differs less from the higher apes than these do from the lower members of the same group. Consequently 'there is no justification for placing man in a distinct order.'" In another passage Darwin says: "Now man unquestionably belongs in his dentition, in the structure of his nostrils, and some other respects, to the Catarrhine or Old World division; nor does he resemble the Platyrrhines more closely than the Catarrhines in any characters, excepting in a few of not much importance and apparently of an adaptive nature. It is therefore against all probability that some New World species should have formerly varied and produced a man-like creature, with all the distinctive characters proper to the Old World division; losing at the same time all its own distinctive characters. There can, consequently, hardly be a doubt that man is an offshoot from the Old World Simian stem; and that, under a genealogical point of view he must be placed with the Catarrhine division" (pp. 205, 206).

Again (pp. 206–207): "If the anthropomorphous apes be admitted to form a natural sub-group, then as man agrees with them not only in all those characters which he possesses in common with the whole Catarrhine group, but in other peculiar characters, such as the absence of a tail and of callosities, and in general appearance, we *may infer that some ancient member of the anthropomorphous sub-group gave birth to man* [italics mine]. . . . . It is not probable that, through

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[2] Evidences as to Man's Place in Nature, 1863, p. 70, *et passim.*

the law of analogous variation, a member of one of the other lower sub-groups should have given rise to a man-like creature, resembling the higher anthropomorphous apes in so many respects. *No doubt man, in comparison with most of his allies, has undergone an extraordinary amount of modification, chiefly in consequence of the great development of his brain and his erect position* [italics mine]; nevertheless, we should bear in mind that he 'is but one of several exceptional forms of Primates.'"[3]

During the fifty years which have elapsed since these words were first published the evidence for their exact truth has become so vast in extent that no single investigator fully understands more than a part of it. Darwin's passages quoted above seem indeed to have been lost sight of under the accumulation of details. Nevertheless all those who have succeeded in retaining a view of the field as a whole and who have not allowed themselves to be misled by minor difficulties, have always clearly perceived the truth and manifold implications of the following propositions:

1. That man is a member of the order Primates.
2. That man is an offshoot not of the platyrrhine but of the catarrhine or Old World division of the apes and monkeys.
3. That man is descended from some ancient member of the anthropomorphous sub-group of the catarrhine division.

Of course a great number of zoölogists besides Darwin, such as Linnæus, Blumenbach, Cuvier, Owen, Huxley, Haeckel, had provided the material for these generalizations, but Darwin displayed his usual skill and sagacity in synthesising the results of comparative anatomy with those of taxonomy and in deriving therefrom the most important genealogical deductions.

Now it is the universal experience of mankind that it is not enough to discover and proclaim the truth once for all. For no sooner has the truth been discovered and proclaimed than schismatics and heretics begin their destructive but inevitable analyses. If it is to survive, the truth must be defended and renewed generation after generation by those who perceive the truth. And so it is, with regard to the truths of man's taxonomic relationships and genealogical origin, as perceived by Darwin, Huxley, Haeckel, Gaudry and many

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[3] St. George Mivart: *Transactions of the Philosophical Society*, 1867, p. 410.

others. These truths are in danger of being crowded out of sight by many "heresies."

If any of these opposing views of man's origin is true, much of the present review of the evolution of the human dentition is worthless. But as space is lacking for a detailed examination of each one, I shall attempt only to list a few of the more important and to indicate the general nature of my objections to each.

*(1) The "Tarsius theory" of Wood Jones (1918), called the "new heresy of man's descent" by Pocock (1920), but really dating in essentials to Cope (1882) and Hubrecht (1897).* This hypothesis, which considers *Tarsius* as the nearest living relative of man, was discussed at length by a number of eminent anatomists and zoölogists, in a special "Symposium on *Tarsius*" in the *Proceedings of the Zoölogical Society of London*, for 1919. The consensus of their opinion was that the hypothesis is based on incorrect interpretation of relatively unimportant points of agreement between *Tarsius* and man. The hypothesis has also been considered and rejected by Gerrit S. Miller (1920) and by R. I. Pocock (1920), and it has been referred to from time to time in other parts of this review. In my opinion it rests upon a wholly incorrect analysis of the taxonomic, palæontological and anatomical evidence bearing on the evolutionary histories both of man and of *Tarsius*. In discussing the anatomical characters of man, Wood Jones shows that he does not know how to distinguish the "habitus" of more recently acquired characters, by which man is adapted to his peculiar life habits, from his "heritage," which he shares in common with the anthropoid apes. He also fails to appreciate the fact that the catarrhine or Old World series is a natural group and that man belongs with the anthropomorphous subdivision of that group. Thus he ridicules the "Linnæan system" without knowing how to make effective use of it.

*(2) Misapplication of the "law of polyphyletic evolution."* Adloff (1908), totally ignoring the facts of taxonomy and palæontology, gives a fanciful diagram of the supposed genealogical relationships of man and other primates, in which each group is made to run back on parallel lines which are just as far apart in earlier geological epochs as they are at present. Such parallelogenic concepts, as they may be called, must imply that the very numerous special resemblances between man and the anthropoids are wholly due to "parallelism"

and "convergence," neglecting the well established principle that the closer the parallelism the closer the relationship. Other forms of the "polyphyletic" view, while less extreme than that of Adloff, rest on the erroneous inference that because some other phyla of mammals have been shown to run far back into the Lower Tertiary, therefore the human line does also. This bald "fallacy of the undistributed middle" is quite popular at the present time, especially among palæontologists, who, in their otherwise praiseworthy caution, are very apt to ignore the cumulative evidence for the relatively close relationship of man with the anthropoids.

An extreme and peculiar form of the "multiple-origin" idea has lately been produced by Sera (1917). According to his phylogenetic diagram, the group of Primates comprises many parallel offshoots from the theromorph reptiles coming down through the later ages and giving rise to different races of men, apes and monkeys, some of the phyla, however, recombining in relatively recent times! Such a concept may be acceptable to some of those who reject the whole Linnæan system of classification as a totally artificial device, but it can never be viewed seriously by those who are convinced from experience that the families of the Primates are natural groups, i.e., the diversified descendants of remote common stocks.

(3) *Misapplication of the "law of the irreversibility of evolution."* Because (a) evolution *is* irreversible in one sense, and because (b) in many wellknown cases remote ancestral forms foreshadow their highly specialized descendants, and because (c) man is evidently now widely different from the anthropoids, it is erroneously assumed that the early Tertiary ancestors of man must have been man-like. *Ergo* they must have had large foreheads, small canines, an erect posture and human feet! This view ignores the important principle of "change of function" by which human have been derived from unhuman characters. The matter is touched upon below and will be more fully dealt with in other papers.

(4) *"Uniformity in the rate of evolution."* It is often implied that the second half of the Tertiary Period (amounting perhaps to a couple of million years) is too short a time for man to have evolved from a primitive anthropoid, because during the last few thousands of years the change has been slight or negligible, and because evolution is somehow assumed to have proceeded at a uniform rate. But this

view ignores the overwhelming evidence that *rates of evolution are as variable and as specific as anatomical characters themselves.*

(5) *Misapplication of the "law of non-correlative evolution."* Balzac's famous version of Cuvier's principle of correlation is admittedly erroneous. Hoofs are not invariably associated with herbivorous dentitions. But from such facts the generalization has been drawn that there is no correlation of parts. The real fact is, however, that there are all degrees of correlation of parts from zero to 100. If we find the highly characteristic lower molars of an extinct species of anthropoid ape closely allied to the chimpanzee, there is little risk in assuming that the upper molars and even the rest of the dentition will also be more or less like the corresponding parts of a chimpanzee. And if we find that the several species of Miocene anthropoids all have less specialized teeth than those of their modern relatives, it seems conservative to assume that even the limbs were nearer to a primitive anthropoid type, always making allowances for peculiar and unexpected characters. But this is precisely the kind of inference that we are warned against by those who point to the "principle of non-correlative evolution" and who insist on waiting for "more fossils and many more fossils" before making full use of those that we have.

The present diversity and confusion of opinion regarding the problem of man's ancestry has partly resulted from the regrettable isolation and lack of coördination of research on the part of the following classes of workers:

(A) Such anatomists as have become lost in the vast field of descriptive and unphylogenetic anatomy, who do not realize that it is futile to make comparisons of the conditions represented in a few widely separated twigs on the great phylogenetic tree of the vertebrates, who do not feel the need of proceeding systematically to examine a given structure in closely related forms before passing to comparisons on a wider scale, who in a word *ignore the taxonomic positions* of the forms they have dissected; who too often ignore also the available palæontological and comparative evidence concerning the history of the forms examined.

(B) Such anthropologists as lack a practical and effective knowledge of mammalian evolution.

(C) Such palæontologists as realize too keenly the insufficiency of the palæontological evidence, but who do not realize that in many cases the evidence of taxonomy and comparative anatomy may often surely supply that which the palæontological record lacks. It is literally true that in many cases the evidence of morphology and taxonomy is complete and convincing, while the evidence of palæontology is defective. In the case of man, for instance, the taxonomic and morphologic evidence for Darwin's conclusions is overwhelming, while the palæontologic evidence is extremely imperfect. And yet palæontologists have so long asserted that the final decision must always rest with palæontology that morphologists have weakly and quite unnecessarily concurred.

(D) Such writers of semi-popular, semi-scientific articles as desire either to record something new and startling, or, with praiseworthy caution, suggest that the whole subject of man's ancestry is a "mystery" and that the most that can be safely admitted is that man is derived from some as yet wholly unknown form of Primate.

(E) Such scientists and others as are ashamed of their poor relations and are looking for more genteel ancestors than the brutal and disgusting apes.[4]

## COMPARATIVE ANATOMICAL AND OTHER EVIDENCE SHOWING THE RELATIVELY CLOSE KINSHIP OF MAN WITH THE ANTHROPOID APES

For thirty years past Professor Arthur Keith, of the Royal College of Surgeons in London, has been collecting the data resulting from his own and from other investigators' observations on the comparative anatomy of anthropoid apes and man. From time to time he has assorted these observations and presented the results in numerical form (1911, 1916). Of 1065 human characters he gives 312, or about one-third, as peculiar to man, and a total of 623 shared by man with one or another of the anthropoids or with all of them together; the remaining 120 human characters are held in common either with Old World monkeys (53), with New World monkeys (60) or with lemurs (17).

These figures, especially the high number of human characters shared by man with one or more anthropoids, and the large number of peculiar human characters, are in harmony with Darwin's conclusions, "that some ancient member of the anthropomorphous subgroup

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[4] On this head compare Wood-Jones's remarks (1918) on the degrading effect of Darwin's theory on mankind.

gave birth to man," and that "man, in comparison with most of his allies, has undergone an extraordinary amount of modification, chiefly in consequence of the great development of his brain and his erect position." But that a mere summation of characters is not always sufficient, is fully recognized by Professor Keith and is further indicated by the fact that in the list as drawn up man has a slightly greater number of characters in common with the New World monkeys (60) than those in common with the Old World monkeys (53), to which he is undoubtedly more nearly related.

As stated above and also in Part II of this review, it is important to realize that the cænotelic or relatively recent characters of the habitus or present complex of adaptive characters, tend to conceal the more remote relationships of any given animal, while its heritage, or residuum of characters acquired in earlier stages of evolution, tends to reveal them.

In the following pages we may review briefly some of the more striking points of resemblance between man and one or more of the anthropoid apes. Of course, such a review will not be convincing to those who regard the Linnæan system of classification as wholly artificial and who believe in the almost infinite ability of "parallelism" to produce close resemblances between organisms belonging to widely different stocks. In the end all I can do is to assert again that such a concept is not compatible with a practical knowledge of mammalian evolution and to submit references to other papers[5] in which the matter is more fully discussed. Meanwhile *the anthropoid heritage of man* is revealed in the facts set forth below.

The wellknown tests of blood relationships, by means of "anti-human" and "anti-primate" sera, have been described by Nutall in his work on "Blood Immunity and Blood Relationship." In discussing the tests with anti-primate sera, Nutall says (p. 214): ". . . . The degrees of reaction obtained indicate a close relationship between the Hominidæ and Simiidæ, a more distant relationship with the Cercopithecidæ, the bloods of Cebidæ and Hapalidæ giving still smaller reactions than the last, when we consider the results obtained with the first three antisera. The tests with antiserum for *Cercopithecus* give the largest reactions with bloods of Cercopithecidæ, next with those of Hominidæ and Simiidæ but slight reactions with those of Cebidæ and Hapalidæ. All four antisera failed to produce reactions

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[5] Gregory: 1910, pp. 258, 463; 1920, pp. 192–193.

with the two bloods of Lemuridæ tested, except when sufficiently powerful also to produce reactions with other mammalian bloods. From this we may conclude that the Lemurs properly belong to an Order separate from the other Primates."

That the main physiological reactions of the great apes, especially the chimpanzee and the gorilla, closely resemble those of man is indicated not only by the blood tests above noted but also by Keith's (1899) description of menstruation in the chimpanzee; by Huntington's (1913) description of the salivary gland complex; and by Duckworth's (1915, pp. 204, 209) description of the alimentary canal of the gorilla. Convincingly human is the appearance of the pregnant female chimpanzee, and the same is true of the genitalia of both sexes of the chimpanzee and of the gorilla. The pendent breasts of old female chimpanzees and gorillas are also equally suggestive of human relationship. Retzius, quoted by Duckworth (1915, p. 210), found that with regard to the spermatozoa, the gorilla is of all the primates the form most similar to man.

All modern observers testify to the elaborate and fundamental resemblances of the brains of chimpanzees and gorillas to the human type, not only in general form and position of the principal fissures and convolutions, etc. (Duckworth: 1915, pp. 188–196), but also in the arrangement of the various centers, detailed architecture of the brain-stem, etc. Professor Frederick E. Tilney, who is now engaged in a comparative study of many hundreds of serial sections of a gorilla brain-stem, has informed me that the detailed construction of the brain-stem of the gorilla is extremely close to the human type.

Of course the marked differences in habits and mental capacity between men and apes are reflected in the vastly superior development of certain parts of the human brain, but modern anatomists are agreed that the difference is one of degree rather than of kind. The search for large-brained human ancestors in early Tertiary times is based first on the too prevalent fallacy that remote ancestral stages must already foreshadow all the characters of their distant descendants, and secondly, upon naïve faith in the biogenetic law, in so far as it is inferred that the swollen brains of young stages are reminiscent of adult brain-form of ancestral stages.

As the braincase in general is only a sort of bony wrapping around the brain and its membranes, modified by crests for the jaw muscles

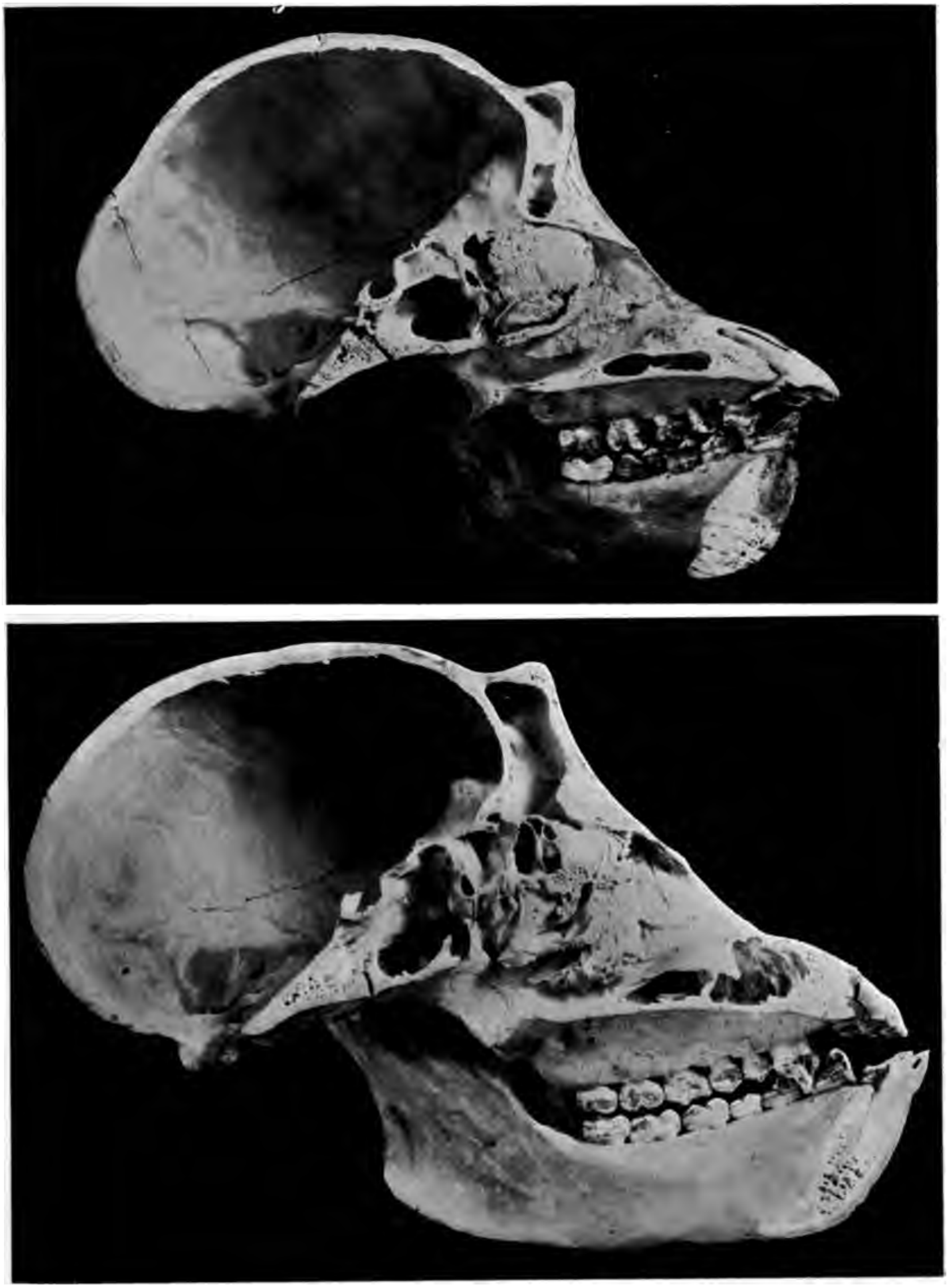

Fig. 300. Sagittal Sections of the Skulls of a Young and of an Adult Female Chimpanzee, Showing Strong Similarity to the Human Type

Note the inferior, middle, and superior nasal meatus, the frontal and the sphenoid sinus, the ethmoid cells, the position of the sphenopalatine foramen, etc. The prepituitary plane of the braincase is not as much deflected as it is in man. The fossa subarcuata, lying behind and above the internal auditory meatus is much reduced, especially in the adult.

The occlusal relations of the cheek teeth are the same as in man, but the lower canine is more in front of the upper, and the incisors are strongly procumbent.

and by specializations of the parts covering the sense organs, it is not surprising that the interior of the braincase, especially of the female chimpanzees and the gorillas, should strongly resemble the human type. This is seen not only in the general architecture of the braincase, but in such minor details as the development of sphenoid and frontal sinuses, the form of the sella turcica, and the arrangement of the foramina for the cranial nerves, arteries and veins. Even certain wellknown differences between typical human and typical anthropoid skulls, such as the squamoso-frontal contact shutting out the usual frontosphenoid contact, are occasionally bridged by low

FIG. 301. YOUNG FEMALE GORILLA

Courtesy of the New York Zoological Society. Photographed by Elwin R. Sanborn
Showing the sub-human appearance of the nose, the use of the hand in feeding, the habit of crouching or sitting nearly upright, etc.

human skulls; the skulls of the extinct Neanderthal race contained several simian characters that are ordinarily lost in the higher human races, such as the small size of the mastoid process, the flatness of the glenoid eminence, the retreating chin, wide ascending ramus of the mandible, very low forehead, projecting tori orbitales, very wide nasal opening, lack of canine fossa in the superior maxilla, etc.

FIG. 302. A TASMANIAN WOMAN, SHOWING A VERY LOW TYPE OF FACE, WITH AN EXCESSIVELY WIDE FLAT NOSE

Courtesy of Sir Harry Johnston. Photograph by J. W. Beattie, Hobart, Tasmania

Especially strong evidence for the close relationship of the gorilla and chimpanzee with man is afforded by the construction of the nasal chamber (*fig. 300*). The turbinate bones, the lower, middle and upper nasal meatus, and the frontal, ethmoid and sphenoid sinuses, have substantially identical interrelations, differing chiefly in the degrees of development of certain parts, in correlation to some extent with the condition that in the ape the prepituitary portion of the braincase is not sharply bent downward as it is in man. Keith (1916) has noted that in the possession of a frontal sinus which is lacking in the orang,

FIG. 303. PHOTOGRAPH OF A CHIMPANZEE FOCUSSING THE EYES ON A NEARBY OBJECT
Courtesy of Professor W. T. Shepard

the chimpanzee and the gorilla agree with man. All such remarkable agreements reinforce the conclusion that the relationship of the chimpanzee-gorilla stock is relatively close to man, and that "the closer the parallelism the closer the relationship."

The anatomy of the nose testifies in the same direction. According to Professor J. Howard McGregor the gorilla nose, although repulsive in human eyes, has in it all the "makings" of a human nose, and acquires chiefly a forward and downward growth of its tip to be transformed into a subhuman type. The lowest existing types of human nose (*fig. 302*) indeed retain much of the gorilloid heritage.

The eyes of the great apes could hardly be more human than they are. The fundus of the eye of a chimpanzee, as figured by Johnson (1901), exhibits the most detailed resemblance to that of a negro. Every close observer of the living animals must have been impressed with their power to focus both eyes at once on a nearby object although, like other simians, they are unable to sustain convergence, except for a brief time.

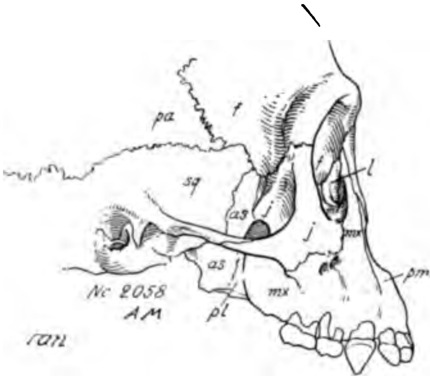

FIG. 304. FRONT PART OF THE SKULL OF A YOUNG CHIMPANZEE, TO SHOW THE SUB-HUMAN CONSTRUCTION OF THE ORBITAL REGION

The lacrymal bone of the anthropoids, as described by Le Double (1900) is similar to that of man and even exhibits similar variants.

Since Darwin's classic studies on the expression of the emotions in man and apes, it is well known that in the general arrangement and functions of the mimetic muscles the great apes are very man-like, except in the degree of development of certain muscles which have become more or less degenerate in man. In the gorilla, according to Duckworth (1915, p. 180), "differentiation of the muscles of expression has reached a stage not far removed from that obtaining in man."

The ear of the gorilla is essentially of human type. Keith (1906) has made extended statistical records of the frequency of "orang," "chimpanzee" and "gorilla" types of ear in modern Europeans.

The auditory ossicles of the chimpanzee, according to Doran (1875, p. 379) "are, taken as a whole, most like those of *Homo*. *T. gorilla* closely resembles *Homo* in its incus and stapes, but less in its malleus; *Simia* more resembles *Homo* in the head and articular surface of the malleus. . . . . Though the incus of some species of *Hylobates* exhibits a tendency to low type in the malleus, and particularly in the stapes, this genus is quite anthropoid. In their ossicula, but most markedly in the stapes, these apes are much more allies to *Homo* than to the lower monkeys."

The whole morphology of the tympanic cavity and surrounding parts, as set forth by van Kampen (1905) and verified by the writer, shows (a) that man is a member of the catarrhine or Old World series, (b) that his nearest relatives are the great apes, especially the gorilla and chimpanzee, and (b) that he has advanced beyond them, especially in the specialization of the tympanic bone into a tympanic plate.

The course of the internal carotid artery and its branches in the auditory region adds further evidence in the same direction (Gregory, 1920).

The fossa subarcuata on the medial encephalic surface of the periotic bone is present and of large size in all the lower primates from the Eocene lemuroids up to and including the gibbon, but it is vestigial in the adult chimpanzee (*fig. 300*) and gorilla, and is variously reduced or vestigial in adult human skulls. It is well developed in infant and fœtal human skulls, and in the fœtal gorilla skull figured by Deniker (*1885, Pl. xxv, fig. 3*), but is vestigial in an infant gorilla. The delay in its closure in man may be secondary, but it is significant that only in man and the great apes among the primates do we find the marked reduction or virtual loss of this fossa.

In a review of the evolution of the dentition it seems hardly appropriate to digress from the main subject even so far as I have, but the reader will understand that unless the anthropoid apes are the nearest living relatives of man, it is quite useless to attempt to trace the evolution of human dentition along the paths followed in this review. One is tempted to go on and show that the same or similar degrees of resemblance between the great apes and man obtain in many other parts of the organism, particularly in the locomotor skeleton, but I must be content with the assertion, based chiefly on my own observations, that the resemblance holds good in the vertebral column as a whole; in the scapula, coracoid, clavicle, humerus, radius and ulna; in the bones of the manus; in the pelvis, femur, tibia and fibula; and (with certain conspicuous exceptions noted below) in the bones of the foot. As to the locomotor musculature, it is well known that certain variants in man may be regarded as ataval reversions to the conditions preserved in anthropoid apes (Huntington, 1918). With regard to the muscular system of the gorilla, Duckworth (1915, p. 179) says: "The muscles correspond severally with very close accuracy to those of man, and in fact the number of distinctive human muscles,

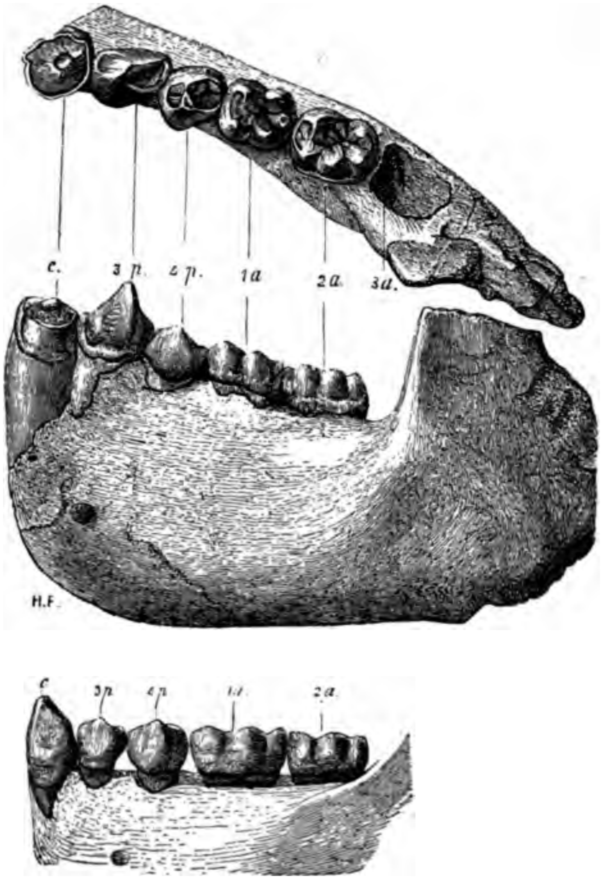

Fig. 305. Lower Jaw of *Dryopithecus fontani* and Lower Teeth of a Tasmanian Youth, with the Lower Canine Projecting above the Level of the Cheek Teeth. After Gaudry

at one time thought to be thirteen, is now reduced to three (M. plantaris, peroneus tertius and serratus posticus inferior). The acromio-trachelian and dorsi-epitrochlear muscles distinguish the gorilla, not being normal in man."

Many of the resemblances referred to in the foregoing pages may have been developed by parallelism or "analogous variation" after the human and chimpanzee-gorilla stems began to diverge from each other, but taken as a whole the testimony of comparative anatomy affords cumulative evidence for Darwin's inference "that some ancient member of the anthropomorphous subgroup gave birth to man." *The detailed studies of the dentition in Part IV of this review leads me to the conclusion that that "ancient member of the anthropomorphous subgroup" was closely allied to or even identical with either Sivapithecus or Dryopithecus (fig. 305) of the Miocene Simiinæ.*

## EVOLUTION OF THE DENTITION IN CORRELATION OR COADAPTATION WITH THE EVOLUTION OF THE LOCOMOTOR APPARATUS

In the later stages of human ascent the characters of the human dentition have doubtless been influenced by the upright posture assumed by man and his immediate ancestors; even in the earlier stages changes in the locomotor apparatus, connected with a shift from one sort of environment to another, doubtless affected indirectly the jaws and dentition. It may then be advantageous at this point to review the coincident evolution of the locomotor apparatus and of the dentition.

With regard to the earlier stages of the limbs and the posture of the body in the line of human ascent, Klaatsch and Wood-Jones (1918, p. 18) have vigorously insisted that "man and his ancestors were never quadrupeds as the dog or the elephant or the horse." But has any competent authority ever maintained that they were? There never has been any necessity for assuming that the more remote primate ancestors of man were highly specialized for quadrupedal locomotion on the ground. The comparative anatomical and, as is now known, the palæontological evidence (Gregory, 1920) decisively indicates that in Lower Eocene and probably even earlier times the Primates were not like ordinary terrestrial quadrupeds, with extremities adapted for swift running on the ground, but were arboricolous animals, with extremities adapted for leaping and climbing in the trees. As this subject is more fully considered elsewhere (1920, pp. 233–241), the main stages in the evolution of the locomotor apparatus and their general relations with the skull and dentition, from the primitive reptilian to the human stage, may here be reviewed very briefly as follows:

*Stage 1.* Primitive reptilian stage, represented by lizard-like reptiles of the Carboniferous, Permian and later Ages. Body elongate, dragged or propelled near the ground, limbs held out at elbows and knees, extremities pentadactylate, with spreading digits. Neck short, skull large, more or less like that of a lizard, slightly bent upon vertebral column; face elongate; teeth numerous, simple. Food habits carnivorous or insectivorous. (See Part I, pp. 13 and 14.)

*Stage 2.* Advanced mammal-like reptiles (small cynodonts) of the Triassic. Body raised well off the ground in walking, but elbows and knees still everted. Skull opossum-like, with carnivorous-insectivorous dentition. (See Part I, pp. 14–23.)

*Stage 3.* Primitive *Amphitherium*-like mammals of the Jurassic. Skeleton unknown, but very probably of primitive placental type with pentadactylate extremities, including a more or less divergent first digit in manus and pes. Dentition of primitive insectivorous type. (See Part I, pp. 35–39.)

*Stage 4.* Primitive lemuroid primates of the lower Eocene. Habits arboricolous, skeleton adapted for leaping, climbing and perching in the trees; extremities quadrumanous, with strongly divergent hallux in pes; skull like that of *Notharctus;* dentition adapted for mixed diet of insects, fruits, eggs, small birds, etc. Dental formula $I\frac{2}{2}C\frac{1}{1}P\frac{4}{4}M\frac{3}{3}$. (See Part II, pp. 123–136.)

*Stage 5.* Ancestral catarrhine primates of the Lower Oligocene (e.g., *Parapithecus*). Fossil remains of locomotor skeleton not yet discovered, but all their modern descendants have the important power of sitting more or less upright on the ischial tuberosities (*fig. 214*). This habit encourages the use of the hands to assist the lips, tongue and teeth in the manipulation of the food. Cranium carried at moderate angles to vertebral column. Optic and auditory parts of skull probably well developed but not excessively enlarged. Muzzle short; dentition much as in *Parapithecus* with dental formula of $I\frac{2}{2}C\frac{1}{1}P\frac{2}{2}M\frac{3}{3}$. Incisors simple, with cingulum; canines small, not enlarged for offense or defense; premolars more or less bicuspid; molars with low, round cusps; upper molars quadri-, lower quinquetubercular. Diet probably mixed: insects, fruits, eggs, etc. (See Part IV.)

*Stage 6.* Primitive anthropoid apes of the Miocene of India, Egypt and Europe. Again the locomotor skeleton remains to be discovered, the chief parts known being jaws and isolated teeth, but there is strong indirect evidence afforded by the existing anthropoids and by the humerus of *Dryopithecus* that their more primitive Miocene ancestors were already acquiring the enormously important

FIG. 306. YOUNG FEMALE GORILLA

Courtesy of the New York Zoological Society. Photograph by Elwin R. Sanborn. Shows the sub-human form of the foot, which, however, retains the grasping form of the great toe, as in all other known primates but man.

ability to "brachiate," or swing from branch to branch with the body suspended from the upraised arms. Pes probably with grasping hallux.[6] Sitting upright, and erect progression on the ground, both more or less highly developed. Skull sharply deflected on vertebral column. Upper jaw deepened obliquely forward and downward beneath overgrowing frontal portion of skull. Diet mixed: including large fruits with tough rinds, insects, small animals. Central incisors not much enlarged in primitive forms, but becoming very wide in orangs and chimpanzees. Both upper premolars bicuspid; anterior lower premolar with more or less sloping, enlarged antero-external face and compressed tip which shear behind enlarged upper canines. First and second upper molars quadrate with low cusps, becoming wrinkled in orang and to a less extent in chimpanzees. Lower molars with "*Dryopithecus* pattern" of five cusps. (See Part IV, pp. 328–339.)

In the modern anthropoids (*fig. 306*) the head is supported on top of the more or less erect vertebral column, especially in the sitting or squatting posture. Locomotion, even on the ground, is no longer quadrupedal in the primitive way, the gibbon often walking erect and the chimpanzee and gorilla frequently balancing the body from the hips and touching the ground with more or less folded hands. Thus the anthropoids, in acquiring the mode of locomotion called "brachiation," diverged from the primitive catarrhine mode of progression on all fours, and made possible the adoption of fully bipedal habits.

*Stage 7.* Human stage. ?Pliocene, Pleistocene, Recent. Wood Jones frequently speaks of the "basal mammalian primitiveness" of the human skeleton, without offering any substantial evidence in support of such assertions. He does not recognize the fact that for true "basal mammalian primitiveness" or rather basal placental primitiveness, we must have recourse to studies of the skeleton of the primitive Paleocene and Eocene mammals and of the less specialized

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[6] There is weighty palæontological and comparative anatomical evidence for the view that a strongly divergent, grasping type of hallux was a primitive primate character which has been transmitted, with minor modifications, to all later lemuroids, tarsioids, Platyrhinæ and Catarrhinæ *except man*, who has very probably lost this primitive prima'e character in adaptation to his upright, bipedal posture and gait. For opposing views on this subject see Gregory (1920, pp. 239–241) and Miller (1920, pp. 229–245).

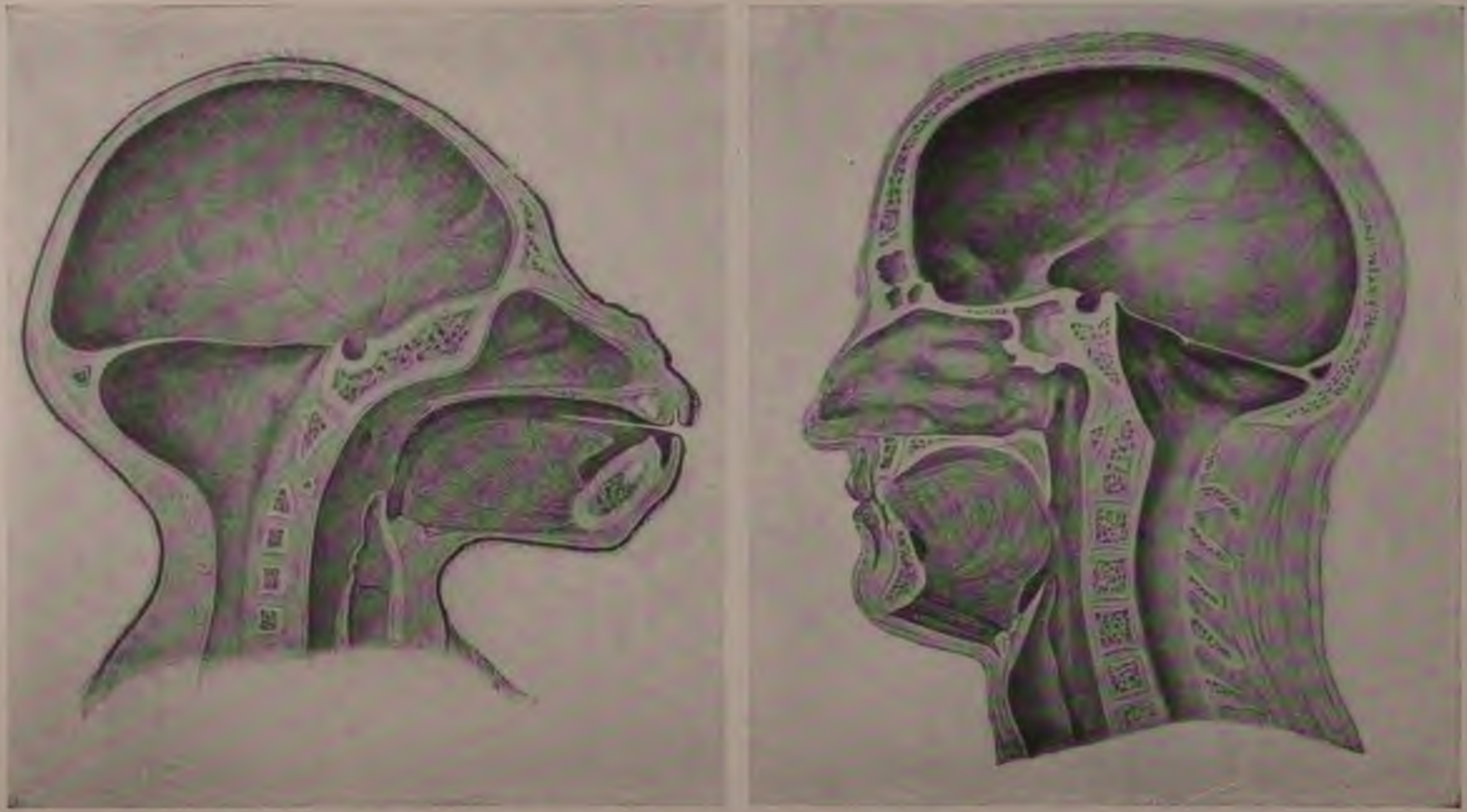

FIG. 307. SAGITTAL SECTION OF HEADS OF YOUNG GORILLA AND OF MAN. AFTER KLAATSCH

unguiculate mammals of the present time. He has also failed to appreciate the fact that the humerus and whole forearm of man are closely related in construction, not to the arm and hand of any of the truly primitive mammals mentioned above, but to the highly specialized "brachiating" type of the chimpanzee and gorilla. Hence it is not necessary, and is indeed directly against the evidence, to push the divergence of man from the other primates back to a point long antecedent to the differentiation of the anthropoid stock; nor is it necessary to ascribe the upright posture of man to direct inheritance from an upright-standing tarsioid, such as *Tarsius; because the cumulative evidence of comparative anatomy shows that man is a specialized offshoot from the anthropoid stem, probably arising after the assumption of upright-sitting, of brachiation, and of more or less erect progression on the ground.*

*The erect or semi-erect posture, together with the increasing use of the hands as such and the correlated swelling of the brain, has conditioned or is associated with (a) the forward growth of the cranium and the deflection of the prepituitary plane (Keith), (b) the forward growth of the upper part of the face, and (c) the reduction in size and retraction of the jaws and dentition beneath the overhanging nose and forehead, which is so characteristic of the higher races of man.*

## THE TRANSFORMATION OF GROUND APES INTO MEN, WITH SPECIAL REFERENCE TO THE DENTITION

The lack of extinct races of men in known fossiliferous formations of the later Tertiary has been most frequently ascribed to "the incompleteness of the geological and palæontological record." The "mystery of man's origin" is widely accepted as a palæontological fact and some hope to discover early representatives of the human phylum far back in Lower Oligocene or Eocene deposits of Asia or even of North America. Such was the concept of Cope, who regarded his Lower Eocene "*Anaptomorphus*"[7] as a direct ancestor of man, while Hubrecht, Wood Jones, and Boule[8] have adopted similar views.

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[7] Cope: *Tetonius (Anaptomorphus) homunculus*, Part II.

[8] In his latest work (1920), Boule favors the more conservative view that man is probably an offshoot of the "Old World" stock, which also gave rise to the anthropoids and to the cynomorphous monkeys.

Those who hold such opinions concerning the origin of man must explain all the profound anatomical, physiological and psychological resemblances between existing Simiidæ and Hominidæ as owing to convergence and to homoplastic (parallel) evolution. To the same modes of evolution they must ascribe all the minute and fundamental resemblances between Simiidæ and Hominidæ in respect of the dental characters set forth in Parts IV and V of this review. Finally, they must postulate the existence of a long series of genera and species representing an unknown and very distinct family of primates, ranging from the Lower Eocene onward, but of which (unless "*Anaptomorphus*" be accepted as a direct ancestor of man) no trace has ever been found in any age.

Such assumptions seem reasonable to me only when considered in the abstract and without due realization of the force of the contrary evidence. I, on the contrary, must and do accept the palæontological record much as it stands; I must hold that *as the evidence from taxonomy, palæontology, comparative anatomy, physiology and psychology for a very near relationship of the Simiidæ and Hominidæ is cumulative and decisive, there is no necessity for postulating the existence of Eocene Hominidæ as a family distinct from the Simiidæ. A fair series of structural gradations lies already at hand, leading from the oldest lemuroid primates, through the stem of the tarsioids, to Parapithecus of the Lower Oligocene, and thence through Propliopithecus, Dryopithecus,*[9] *Sivapithecus, Pithecanthropus, or through genera nearly allied to these, to the emergence of the Hominidæ as a distinct family in Pliocene and early Pleistocene times.* Such a series may be deemed too strongly monophyletic at a time when the fact of polyphyletic branching of mammalian groups is sometimes mistakenly assumed to mean that the known phyla run back on parallel lines to infinitely remote "premammalian" stocks. This much I am willing to concede to the "imperfection of the palæontological record:" that possibly one or more of the above-named genera may eventually be shown not to lie in the *direct* line of human ascent, but to be set a little way off to one side by the possession of some distinctive and peculiar special-

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[9] The recently discovered species (?) *Dryopithecus mogharensis* (Fourtau, 1920), from the Lower Miocene of Egypt, adds an important item, tending to bridge the gap between the older genus *Propliopithecus* and the later and more advanced genus *Dryopithecus*.

ization. But so far as I am able to judge, the known remains, regrettably imperfect as they are, afford at least a fair structural series illustrating the evolution of the dentition and lower jaw, from *Parapithecus* to the anthropoids and to the Hominidæ.

From this wide contrast in view-point it will follow that, *if I am right, then those who hold the opposing views would fail to recognize a direct ancestor of man of Miocene age even if it were represented by a complete skeleton*, since they would expect to find it abounding in the diagnostic characters of recent Hominidæ and to be widely different from the contemporary Simiidæ. *Again, if my conclusions are correct, the precursors of man should be found in rocks of Miocene age and should be large ground apes closely allied to or identical with Pithecanthropus; while if the others are right, the "real Eoanthropus" should be sought in the Lower Eocene and should be a large-brained primate of small size, perhaps more or less transitional between the Eocene tarsiods and the Hominidæ.*

In fairness to those who hold different views from mine of the origin of the Hominidæ, I must emphasize the fully human character of the Heidelberg dentition (see p. 427 below) and the lack of transitional stages of Pliocene age.

No matter what view we take as to the origin of man from other primates: where were the Pliocene Hominidæ and what were they like? Extensive mammalian faunas of Pliocene age have been described from various places in Asia, Europe and North America, but the Hominidæ are so far conspicuously absent from the records. Although such negative palæontological evidence is by no means decisive, it would seem likely that if the Hominidæ had been both widely distributed and plains-living mammals during the Miocene and Pliocene, some hint of their remains would have been found in some part of the globe along with those of the numerous known plains-faunas of late Tertiary age. *Such as it is, the negative palæontological evidence seems in harmony with the hypothesis that, during the late Tertiary, the Hominidæ had not yet extensively invaded the plains, and that in some restricted and more or less isolated Palæarctic region they were in course of differentiation from ground-living apes inhabiting the border regions between forests and plains.*

*If the femur of Pithecanthropus be associated with the skull, as held by nearly all authorities, then we have definite proof that early Hominidæ or progressive Simiidæ of late Pliocene or early Pleistocene age already walked erect upon the ground.* There is some evidence for the view of Pocock (1920) that even the earlier anthropoids were already adapted for erect progression on the ground, and that the modern orang and gibbon have become secondarily specialized for arboreal life

The thoroughly terrestrial rather than semi-arboreal characters of the skeleton of the Pleistocene neanderthaloids and of all later races of men, show that the erect gait was assumed at a relatively early date. It is, as noted above, extremely probable that many of the diagnostic characters of the human dentition were more or less connected with the complex series of readjustments that took place when the skull became balanced on top of an erect backbone, and when the hands, set free entirely from the locomotive functions, became increasingly skillful in assisting the teeth in the killing, preparation and manipulation of food.

Such a radical transformation of the jaw and dentition from a *Dryopithecus*-like type was correlated, apparently, with a pronounced change in food habits, from a prevailingly frugivorous to an omnivorous-carnivorous stage, and was even more intimately dependent upon a still greater transformation in the brain and braincase, from a primitive anthropoid to a human condition, which brought with it revolutionary disturbances and readjustments of the digestive apparatus and of the ductless-gland complex that controls the growth and proportions of skeletal parts.

It may well be that this transformation was more complete and far reaching in the Hominidæ than any which had taken place in other mammals during the same period. But in this connection we must bear in mind in the first place the vast extent of a single geological epoch, all recent work indicating that the older estimates were far too low, so that the time from the Middle Miocene to the Lower Pleistocene, during which, according to my view, the transformation in question took place, may represent more than a million years—long enough perhaps for the brain to expand from an anthropoid to a low human stage and for the accomplishment of all the correlated changes, including those in the dentition. And in the second place

FIG. 308. SERIES OF SKULLS OF OLD WORLD PRIMATES. AFTER HAECKEL

Seen from below, showing the relation between the length of the head and the form of the mandible. The forms figured are: (1) gibbon, (2) young chimpanzee, (3) baboon, (4) dolichocephalic Australian (*Homo sapiens australianus*) and (5) brachycephalic German (*Homo sapiens alpinus*).

there are other groups of mammals for which we have evidence of very extensive and revolutionary changes in structure during the second half of the Tertiary period. During this time the tree-sloths evolved out of ground-sloths (Matthew), the whalebone whales lost their teeth and substituted baleen plates (Abel), and the ancestors of the sperm whale acquired very extraordinary specializations of the whole skull (Abel).

FIG. 309. WELL PRESERVED HUMAN DENTURE, SHOWING NORMAL OCCLUSION
Courtesy of Dr. Bernhard W. Weinberger

In contrast to such radical and profound changes in function, and in the direction of evolution, are the many well-known cases involving rather an intensification of given functions and further progress in the same direction as in earlier stages. Such has often been the case in animals that have remained in the same environmental zone, as have the plains-living ungulates, and have simply improved their

FIG. 310. SKULLS OF AUSTRALIAN NATIVE (FEMALE) AND OF YOUNG GORILLA

Oblique view of under side, showing marked divergence in habitus (enlarged teeth of gorilla, enlarged braincase and reduced teeth of man) associated with fundamental unity of heritage.

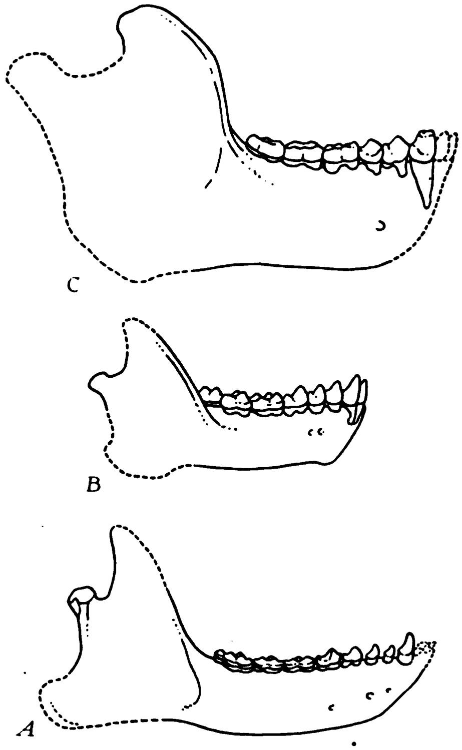


FIG. 311–312, INCLUSIVE. EVOLUTION OF THE HUMAN MANDIBLE. SIDE VIEW

Fig. 311. First stage: Eocene lemuroid, represented by *Notharctus osborni*, Middle Eocene, Wyoming. Dental formula: $\mathrm{I}_{\overline{2}}\ \mathrm{C}_{\overline{1}}\ \mathrm{P}_{\overline{4}}\ \mathrm{M}_{\overline{3}}$. Jaw elongate, with primitive form of angle (A).

Second stage: represented by *Parapithecus fraasi*, Lower Oligocene, Fayûm, Egypt. Dental formula: $\mathrm{I}_{\overline{2}}\ \mathrm{C}_{\overline{1}}\ \mathrm{P}_{\overline{2}}\ \mathrm{M}_{\overline{3}}$. Jaw shortened, angle beginning to expand (B).

Third stage: represented by *Propliopithecus haeckeli*, Lower Oligocene, Fayûm, Egypt. Dental formula: $\mathrm{I}_{\overline{2}}\ \mathrm{C}_{\overline{1}}\ \mathrm{P}_{\overline{2}}\ \mathrm{M}_{\overline{3}}$. Jaw much shortened and deepened, angle expanded (C).

Fig. 312. Fourth stage: represented by *Dryopithecus* (A) and *Sivapithecus* (B), Miocene of Europe and India, respectively. Dental formula: $\mathrm{I}_{\overline{2}}\ \mathrm{C}_{\overline{1}}\ \mathrm{P}_{\overline{2}}\ \mathrm{M}_{\overline{3}}$. Jaw much deepened, incisors slightly procumbent.

Fifth stage: lowest human type, represented by jaw of *Homo heidelbergensis*, Pleistocene, Germany. Dental formula as before. Jaw very massive, without protruding chin. Incisors erect, canine reduced to level of other teeth (C).

Sixth stage: low human type, represented by the jaw of an Australian native (*Homo sapiens australianus*). A bony chin developed, ascending ramus narrower (D).

Seventh stage: modern man. Bony chin protruding, ascending ramus weak (E).

mode of locomotion and dental apparatus without radically altering the plan of them. These cases being numerous and well-known are apt to be taken as the standard examples of the way that evolution normally proceeds, and from thence may arise the unconscious impression that nature is limited to that kind of "orthogenetic" evolution. *But all the great evolutionary advances, as when tetrapods evolved from fishes, or when mammals evolved from reptiles, have been revolutionary in character, since they involved profound changes and readaptations in the methods of locomotion and of feeding.*

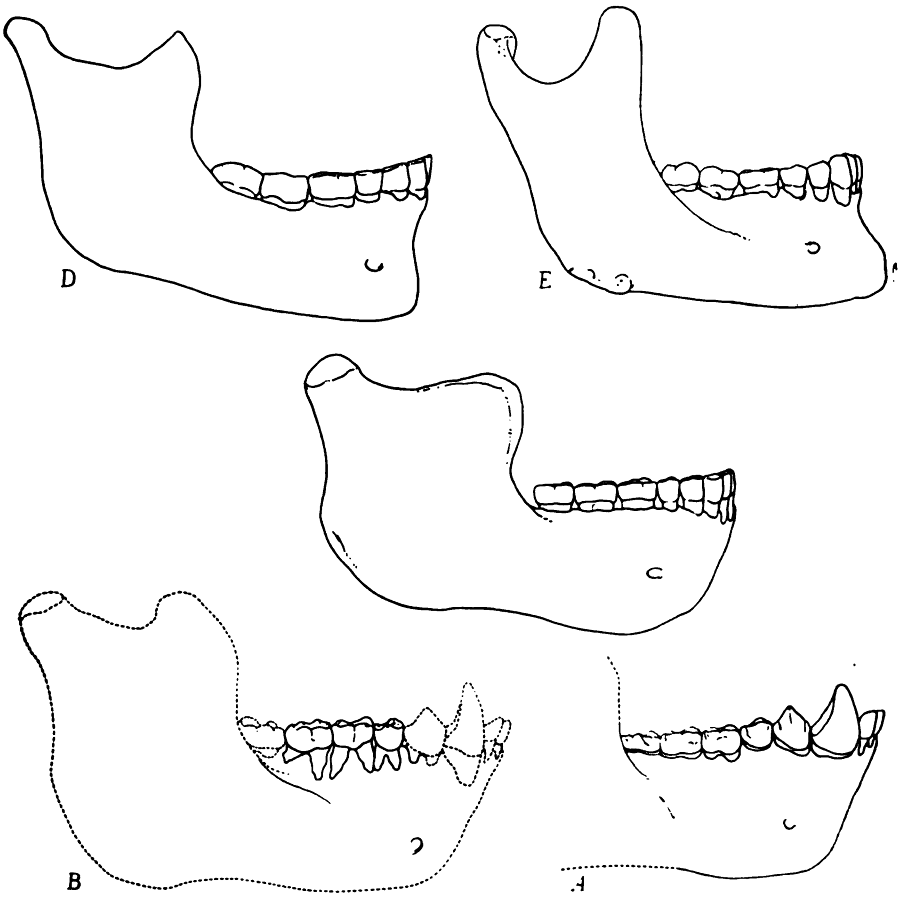


FIG. 312. EVOLUTION OF THE HUMAN MANDIBLE (CONTINUED)

The supposed transformation in skull and dental characters by which the human stage was finally attained, is thus described in my "Studies on the Evolution of the Primates" (1916, pp. 277–280):

> "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.

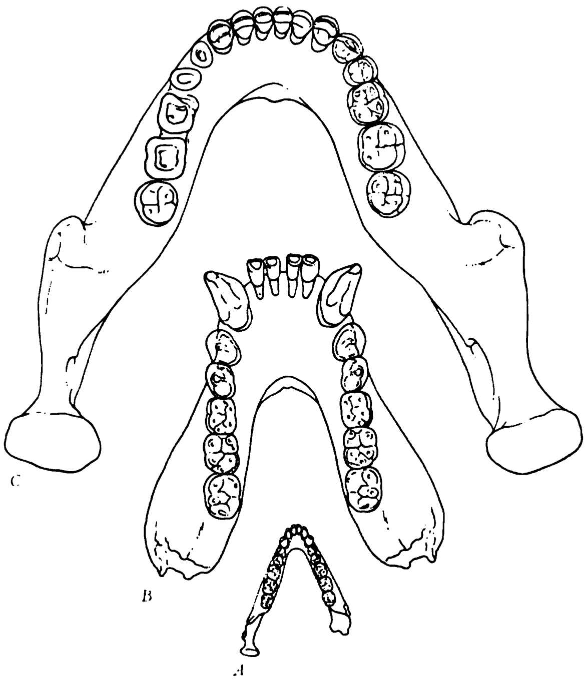


Fig. 313. Evolution of the Human Mandible and Lower Dental Arch. Viewed from Above

First or super-tarsioid stage: represented by *Parapithecus.* Opposite halves of mandible converging (A).

Second or *Dryopithecus* stage: *Dryopithecus fontani,* composite restoration, based mostly on the figure given by Smith Woodward (1914); front teeth supplied from Gaudry. Intercondylar diameter increased, dental arch Π-shaped, tooth rows parallel, canine enlarged (B).

Third or primitive human stage: *Homo heidelbergensis.* Intercondylar diameter excessively increased, dental arch Ω-shaped, canine reduced (C).

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.

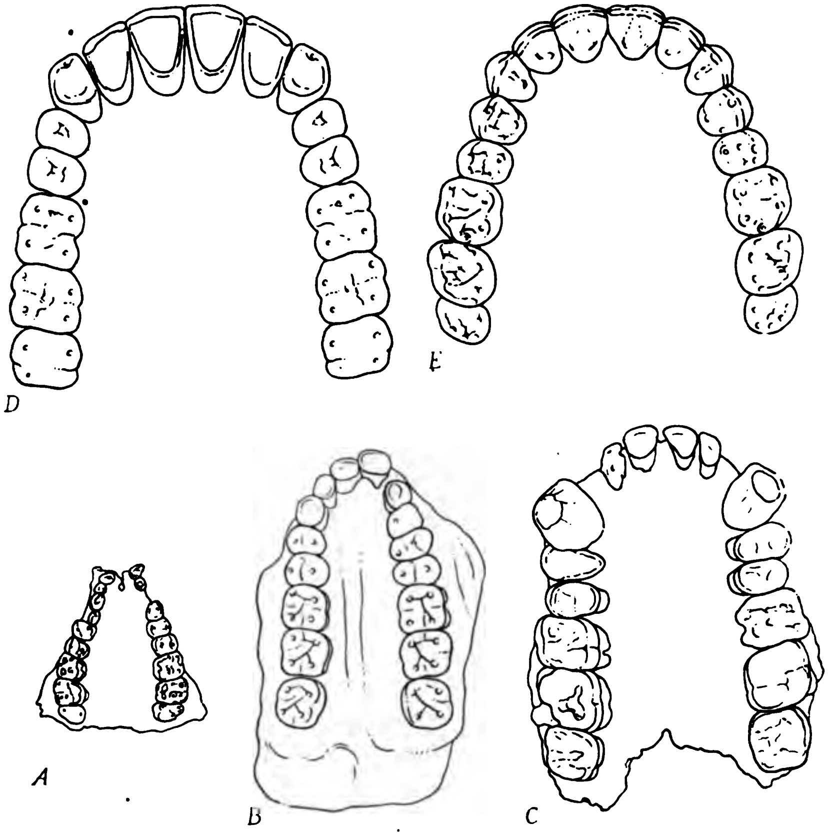


Fig. 314. Structural Series Showing Evolution of Human Palatal Arch

First stage: represented by *Necrolemur*, with convergent or Λ-shaped palatal arch (A).

Second stage: represented by *Oreopithecus*. After Schwalbe. (Palate crushed laterally) (B).

Third stage: represented by *Palæopithecus*, with enlarged canines and straight tooth rows (C).

Fourth stage: represented by "Mousterian youth," with small canines and rounded palatal arch (E).

Fifth stage: represented by Tasmanian (after Keith), with ∩-shaped arch (D).

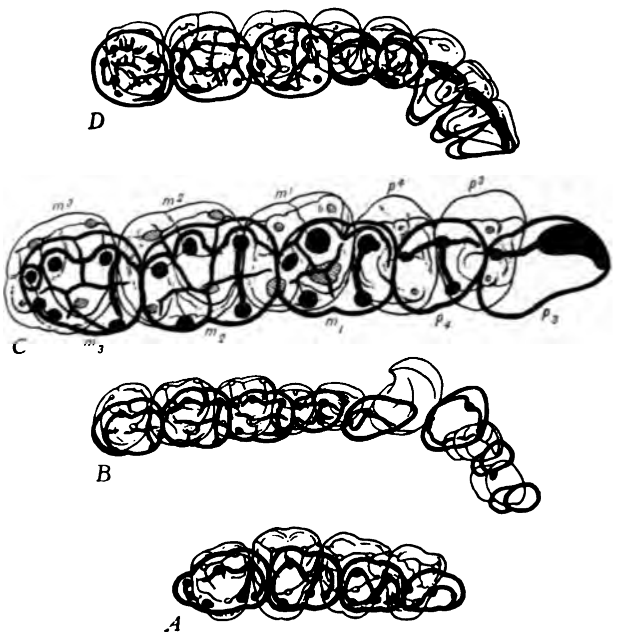


FIG. 315. EVOLUTION OF OCCLUSION. EOCENE LEMUROIDS TO MAN

A.—Eocene lemuroid *Pelycodus*. B.—Modern gibbon *Hylobates*. C.—Modern gorilla. D.—Modern man.

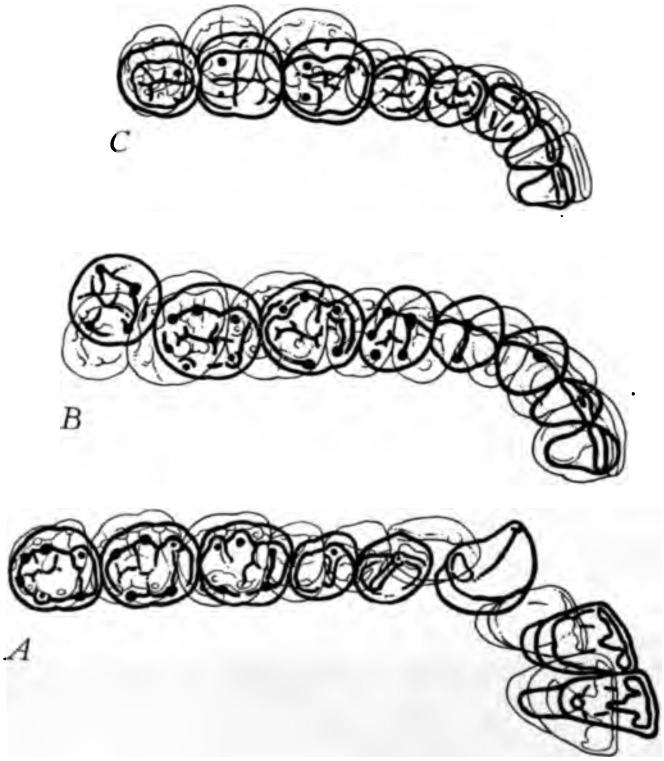


FIG. 315 *bis*. EVOLUTION OF OCCLUSION (CONTINUED)

A.—Chimpanzee. B.—Mousterian youth. C.—Modern man

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.

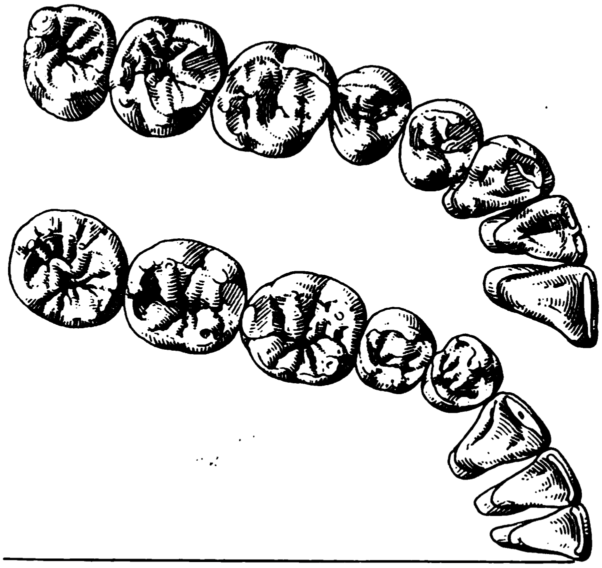


FIG. 316. RIGHT UPPER AND LEFT LOWER HUMAN TEETH

Specimen loaned by Dr. Bernhard W. Weinberger. (Cf. *fig.* 315)

FIG. 317. EXHIBIT ILLUSTRATING THE ANCESTRY AND RELATIONSHIPS OF MAN, IN THE AMERICAN MUSEUM OF NATURAL HISTORY

1.—Gibbon (*Hylobates*); 2.—Orang; 3.—Gorilla, female; 4.—Gorilla, male; 5.—Gorilla, young; 6.—Reconstruction of *Pithecanthropus* skull, and bust of same, by Prof. J. H. McGregor; 6.—Cast of skull top of *Pithecanthropus*; 7.—Reconstruction of *Pithecanthropus* skull, by J. H. McGregor; 8.—Cast of skull of the "old man of La Chapelle aux Saints" (Neanderthal race); 9.—Cast of Talgai skull (primitive Australian race); 10.—Cast of skull of old Crô-Magnon man; 11.—Skull of modern man (?Mediterranean race).

The black lines indicate genealogical relations, so far as inferred by the writer. The small objects represent casts of teeth and jaw fragments of extinct anthropoids and men, as described in Parts IV. V. The one at the bottom of the phylogenetic tree represents *Propliopithecus*.

"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:

(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 bicuspid character.

(5) Increasing convergence of the opposite tooth rows and widening of the intercondylar diameter of the mandible (*figs. 300, 308*).

(6) Rounding of the molar crowns (*fig. 283*), progressive obliteration of the *Dryopithecus* pattern of the molars (*fig. 286*) 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 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, comes to articulate [on the outer side] chiefly with only one upper molar.[10]

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

---

[10] Although this "end-to-end" articulation of upper and lower molars is regarded by orthodontists as abnormal, yet it represents a structural stage beyond the normal and further away from the primitive anthropoid condition; and as it occurs in a considerable percentage of well-preserved modern dentures, it may become more frequent in the future.

enormous expansion and deepening of the braincase; extreme shortening of the face;

retraction of the front part of the lower dental arch;

reduction in size of the dentition;

upper and lower tooth rows forming a more or less rounded arch; canines not protruding much above the level of the other teeth; anterior lower premolars transversely widened and fully bicuspid;

fusion of the premaxillaries with the maxillaries;

lower jaw with progressively protruding chin, early losing the inferior symphyseal ledge;

reduction of the supraorbital crest (tori supraorbitales);

extreme retraction of jaws beneath braincase;

articular eminence for the lower jaw small and strongly convex . . .;

glenoid fossa becoming 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. . . . . (*fig. 310*)."

## II. THE DENTITION OF EXTINCT AND OF RECENT HOMINIDÆ

In the succeeding pages I shall review further evidence tending to show that the jaws and dentition of the extinct Hominidæ, especially those of the Heidelberg man and of the Mousterian youth, retained numerous characters reminiscent of the *Dryopithecus* group of the Simiidæ; that many of their diagnostic human characters may fairly be interpreted as quantitative, or allometric, changes from the *Dryopithecus* type, while others, such as the substitution of the +-shaped for the "*Drypopithecus*" pattern of the lower molars, arise through a mingling of "allometric" and "rectigradational," or qualitatively new, changes; also that distinct traces of the evolution of the older or simian condition into the newer or human stage are observable.

### PITHECANTHROPUS ERECTUS

In Part IV it was noted that the exact geological age of *Pithecanthropus erectus* has been long disputed, its discoverer, Dubois, assigning it to the Pliocene, but later investigators regarding it as of early or mid-Pleistocene age. It was associated with a varied fauna of mammals closely related to those of the Indian Siwaliks, of Pliocene age (Osborn, 1915, p. 76) and it thus affords another item of evidence in favor of the widely accepted opinion that man originated in central Asia. The precise zoölogical status of *Pithecanthropus* is also still unsettled; and at present it is largely a matter of definitions and of individual viewpoint whether we regard it as a very progressive but aberrant ape, a very primitive man, or a true "missing link." In any event its value is not lessened, as indicating the close relationship of the Simiidæ and the Hominidæ.

If the Hominidæ, as I believe probable, have been derived, in Miocene times, from that section of the *Dryopithecus-Sivapithecus* stock which gave rise to the gorilla-chimpanzee group, then the Pliocene Hominidæ or "precursors" must have had canine teeth and dental arches which were in a transitional stage between that of the Miocene *Dryopithecus* and the definitive human stage attained in Pleistocene and later men. Such transitional conditions have been assigned to *Pithecanthropus*, in the reconstructions of its skull and dentition by Dubois, McGregor and others, and would seem to be warranted by the more ape-like form of its calvarium and temporal muscle-area and by the extremely large size and low characters of its upper molar teeth. But the palæontological proof is not yet at hand.

The two upper molar teeth assigned to this genus have been described in Part IV, fig. 269. The pattern of $m^3$, it was observed, may perhaps have been derived from that of the corresponding tooth of *Dryopithecus punjabicus*. The internal and external roots are large and very widely divergent. The second upper molar, if correctly identified as such, has the posterior external cusp reduced perhaps even to a greater degree than it is in later races.

### HOMO HEIDELBERGENSIS

This famous lower jaw (*fig. 318*), which was described by Schoetensack in 1908, was found embedded in undisturbed sand, in a quarry at Mauer, near Heidelberg, Germany, at a depth of more than 76 feet below the surface. Schoetensack took every precaution to secure and record the most irrefutable evidence of the genuineness and geological antiquity of the specimen, which was found in a stratum containing the fossil bones of several extinct Pleistocene mammals, including the ancient elephant (*Elephas antiquus*), the lion and the Mosbach horse. These animals, together with the Heidelberg jaw, are regarded by Osborn (1915, pp. 95, 96), as belonging to the Second Interglacial Stage of the mid-Pleistocene, but Schoetensack, Geikie and other authors assign them to the First Interglacial Stage of the Lower Pleistocene. If of Lower Pleistocene age, the Heidelberg jaw shows that the most important diagnostic characters of the dentition of the Hominidæ had already been acquired at the beginning of the Pleistocene epoch and indicates that prehuman transitional conditions must be sought in earlier geological ages. If, on the other hand, the Heidelberg jaw dates only from the Middle Pleistocene, then transitional conditions may be looked for as late as the Lower Pleistocene or Upper Pliocene. In any event, if, as I deem probable, the Hominidæ began to diverge rapidly from the *Dryopithecus*-group in the Middle or Upper Miocene, then transitional stages may be sought from the Upper Miocene through the Upper and Lower Pliocene into the Lower Pleistocene.

As to the detailed characters of the Heidelberg jaw and dentition, it is evident that, as compared with those of all known earlier primates, it has assumed a new and distinctly human habitus. The lower dental arch is short, wide, and evenly round in front, the teeth disposed in continuous series without diastemata, the crowns of all the incisors and canines forming an even series; the canines small and not protruding above the level of the other teeth, the lower canines somewhat suggesting incisors in form; the incisors with nearly vertical rather than procumbent crowns; premolars small, the anterior premolars without the "sectorial" form of the antero-external face; the lower molars wide and rounded, with five main cusps and flat-topped crowns, the pattern being of primitive human type; the whole tooth row apparently adapted for a rotary, grinding motion of the jaw; molar taurodontism, or vertical deepening of the pulp cavity at the expense of the roots, much more pronounced than in modern jaws, but much less so than in Krapina neanderthaloids.

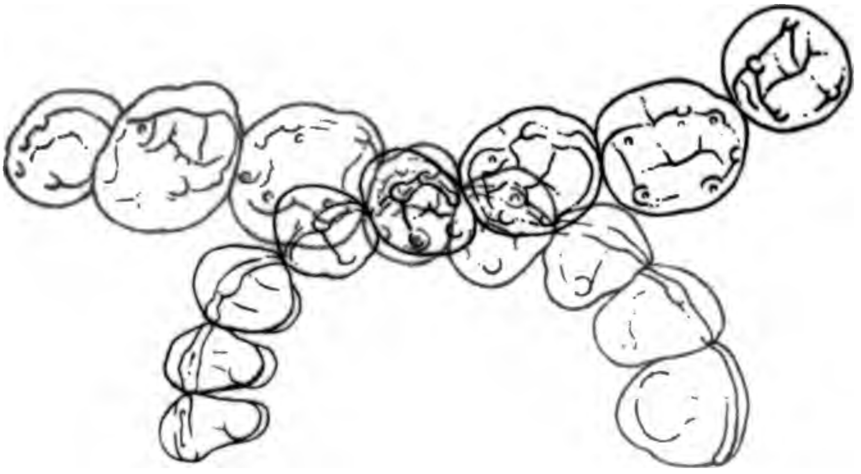
The jaw itself recalls the anthropoid type in the strongly receding chin, in the extreme stoutness of the corpus mandibulæ, in the great width of the ascending ramus, and of the diameter across the condyles, in the shallowness of the sigmoid notch, and in the restricted space in front for the tongue; but it is essentially human in the shortness of the bony shelf below the "genial tubercles," in the placing of the bony attachment points of the digastric, geniohyoid and geniohyoglossus muscles (A. S. Woodward, 1900) and in the marked divergence of the opposite rami. All of these and other characters collectively indicate that the Heidelberg race was more primitive than and probably ancestral to, the Neanderthal race; and Professor McGregor, after extremely thorough consideration of the subject, has reconstructed the palate and skull along pre-Neanderthaloid lines, giving the skull a quite low forehead, prominent supraorbital tori, an elongate form and rounded upper dental arch.

Beneath the primitive human habitus of the dentition some remains of an older simian heritage are still preserved. Thus, as shown in *fig. 265*, the premolars have the patterns fundamentally identical with those of *Sivapithecus*, the most conspicuous difference being the more symmetrical form of the anterior premolar, the anterior external face of which is non-sectorial, in correlation with the reduced size of the upper canines. But the resemblance is much closer to *Sivapithecus* than to the much older *Propliopithecus* in the premolars and in the molars, and this is one reason (although not the principal one) why the relationship seems nearer to the later than to the earlier anthropoid. The *Dryopithecus* pattern is still fairly well preserved in the first molar, which is always the most conservative of the series, but in the second molar the enlargement and widening of the two main cusps of the posterior moiety, namely, the hypo- and entoconids, and the reduction of the hypoconulid, has brought the furrow that separates the meta- and the entoconid, into transverse alignment with the one between the proto- and the hypoconid, while the median longitudinal furrow is becoming straighter, less meandering in its course, so that the human +-shaped pattern is nearly complete. In the third molar the crown is becoming short and rounded, as in man, but although the evidence is not entirely clear it seems probable that a reduced sixth cusp, homologous with that of the *Dryopithecus punjabicus* group, was in process of fusing with the hypoconulid.

Fig. 318. Mandible of *Homo heidelbergensis*. After Schoetensack. One-half Natural Size

## PLATES 14–15

(GREGORY: EVOLUTION OF THE HUMAN DENTITION)



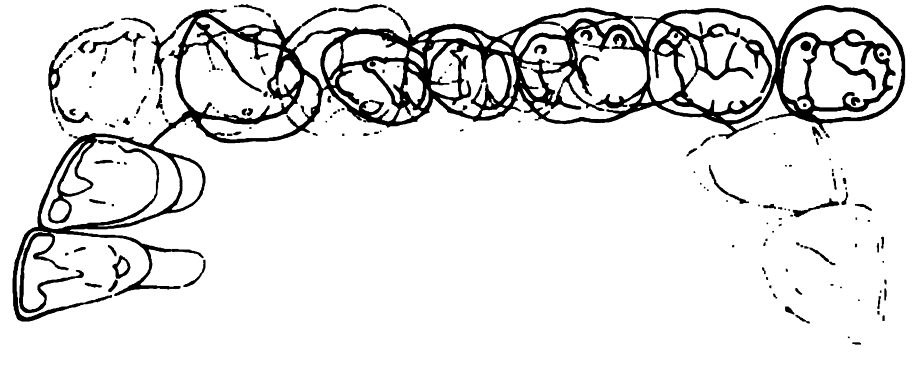
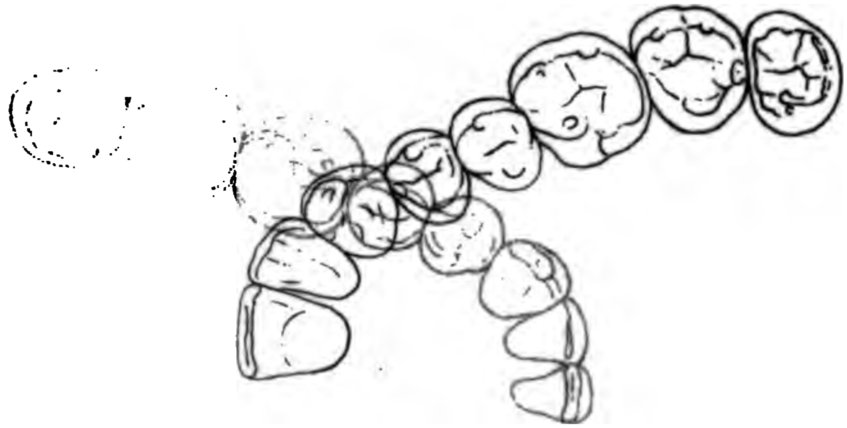
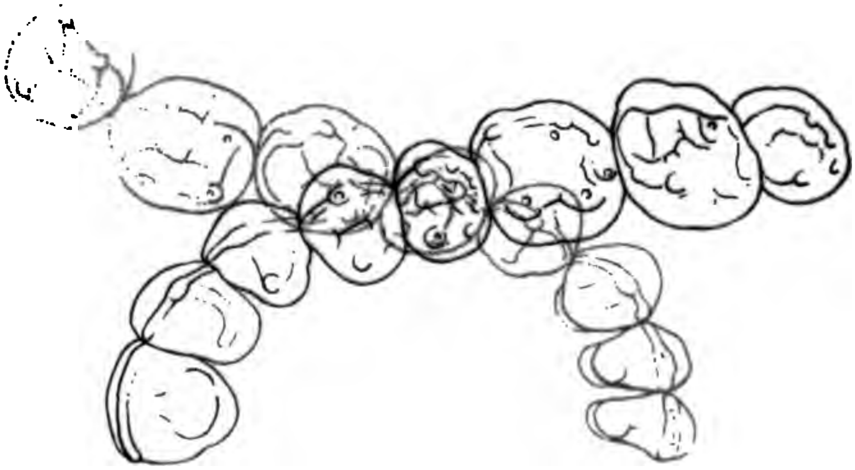
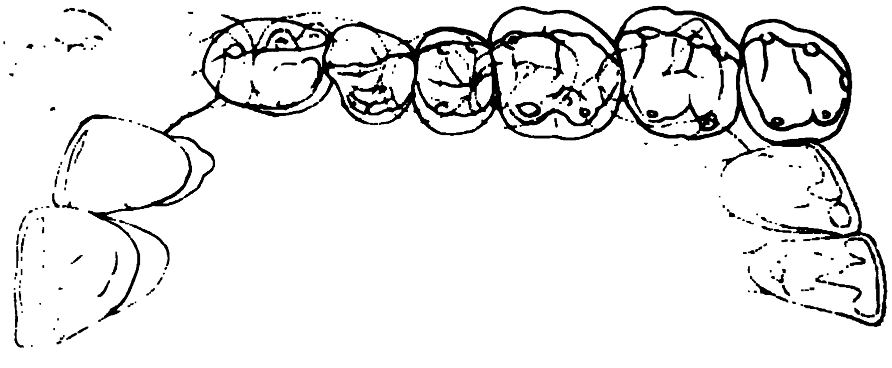


Fig. 318. Mandible of *Homo heidelbergensis*. After Schoetensack. One-half Natural Size

PLATE 1.







The phyletic relationship of *Homo heidelbergensis* is discussed in my "Studies on the Evolution of the Primates" (1916, pp. 322–323) as follows:

> ". . . . 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.
>
> "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 abandonedthe 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. . . . . 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 NEANDERTHALENSIS

Toward the end of the Third Interglacial Period of the Pleistocene or, as some hold, during the Second Interglacial Period, remains of the Neanderthal race were left in various cave deposits in central

Europe. A long line of investigators have contributed to our knowledge of the skeletal anatomy of these extraordinary beings, perhaps the most complete memoir being Boule's description of the old man of Chapelle-aux-Saints.

Although the Neanderthaloids had reached the human grade of organization in most parts of the skeleton, they retained some important characters reminiscent of an early semi-erect heritage. The massive head, instead of being fully balanced on top of the column, was supported by a short, heavy, forwardly-sloping neck, the bones of which recall those of a chimpanzee in having elongate neural spines. In association with the posture of the head and the relatively feeble development of the fore-part of the brain, the prepituitary plane of the skull was much less bent downward than it is in modern human skulls.

As shown by Keith (1914), the combination of a lesser deflection of the forepart of the brain-floor with a forwardly-sloping neck affords room for the massive, deep lower jaw; which could not be accommodated beneath an erectly placed head with sharply deflected prepituitary plane. The depth of the lower jaw, the strength of the ascending ramus, the depth of the alveolar process, and the great development of the supraorbital tori, are possibly all more or less closely correlated with a peculiar specialization of the teeth known as taurodontism and with the powerful grinding action of the lower jaw, which in old individuals causes all the lower teeth to be worn down nearly to the same plane. The lower molars (and probably the upper molars) show a progressive deepening of the pulp cavity and concomitant shortening of the roots, as we pass backward from $m_1$ to $m_3$, so that in extreme cases the molar becomes almost as hypsodont as it is in some ruminants (whence the name "taurodont").

The taurodont condition of the cheek teeth has been cited by Adloff (1908) and accepted by Keith (1913) as a specialization (possibly for triturating tough vegetable food [Keith]) which definitely excludes the Neanderthaloids from direct ancestry to any of the later human races. Keith at first supposed that the taurodont characters had been lost in later races, but afterwards he fully accepted Adloff's conclusion. To those who, like the writer, believe that degeneration or loss of characters, has played a large part in human evolution, the loss or reduction of taurodontism is easily conceivable. But as the molars of the Galley Hill jaw (a specimen which may be older than any of the Neanderthaloids) show only a slight degree of taurodontism, it is possible that Adloff and Keith may be right, and that the extreme Pleistocene Neanderthaloid specialization may bear somewhat the same relation to the modern specialization as the excessive increase in number and fineness of plates in the molars of the Pleistocene mammoth bear to the more primitive condition which has been retained by the modern Indian elephant.

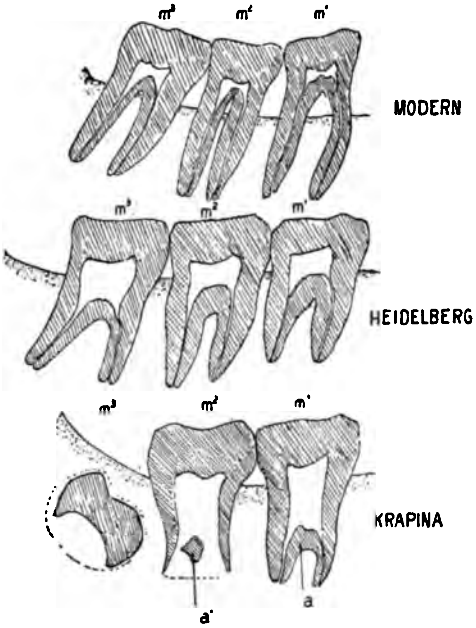


Fig. 330. Drawings from Skiagrams of Right Lower Molars. After Keith

(1) Modern European, (2) Heidelberg mandible, (3) a Krapina mandible; a, $a^1$, inner root septum. (1) and (2) after Schoetensack; (3) after Kramberger. Natural size.

Perhaps in correlation with the rotary action of the mandible and with the edge-to-edge bite of the incisors, the articular eminence of fully adult Neanderthaloid skulls is much less pronounced than it is in most modern races, and the glenoid fossa much shallower. The form and relations of these parts and of the tympanic plate and mastoid process are indeed to some extent reminiscent of conditions in the anthropoids (Boule, Keith).

### *Dentition of the "Mousterian youth"*

The skull and dentition of the "Mousterian youth" are represented by an excellent cast, showing many of the finer details of the dentition, in the J. Leon Williams Collection of the American Museum of Natural History. I also had for comparison some photographs of the original skull and dentition kindly supplied by Dr. J. A. Harris. This is the famous type of "*Homo mousteriensis Hauseri*" that was excavated at Le Moustier in the Vézère Valley, France, in 1908 and described by Klaatsch (1910). It was associated with flint implements of earliest Mousterian age (Osborn, 1915, p. 222). The individual was a young male, judged to be about sixteen years old, with the third upper and lower molars of both sides nearing the period of eruption. The left permanent canine was impacted, and is preserved in the jaw, the deciduous canine being still in place The dentition of this remarkable specimen was briefly noticed by Klaatsch (1910) and more carefully described by Adloff (1910) but neither of these authors mention the fact that the little worn crowns, especially of the cheek teeth, retain many highly important primitive or simian characters.

The dentition as a whole (*fig. 324*) is distinctly macrodont, though not nearly as large as that of the Talgai youth. The large, wide *central upper incisors* have a sharp, flat cutting edge, the right central apparently showing a faint trace of the denticulation so often seen in anthropoid incisors. The cutting edge of the left central incisor has a slightly indicated apex, a remnant of the original apex in more primitive forms. As seen in side view, the long roots of the two central incisors are markedly inclined backward, in accordance with the very strong prognathism of the upper jaw. The labial face of the centrals is gently convex in the middle, flattened below and strongly convex at the sides. As seen in front view the sides of the central incisors converge rapidly toward the neck and there is a marked excess in the transverse diameter of the lower end of the tooth. But the central incisors are not as wide as they are in many chimpanzees and there is less excess of the transverse diameter of the lower end. The lingual surface shows a slight folding around at the sides in continuation with the cutting edge, so that if the tooth were much worn it would approximate the shovel-shaped section seen in the Krapina men and in various modern races, but there is little if any fossa or concavity on the lingual face. The basal tubercle (tuberculum dentale) seen in many anthropoids is represented by a wide eminence, the broadly convex surface of which is interrupted by one or more vertical grooves, and on the left central by a feeble trace of the median ridge of anthropoids and of primitive human incisors. Thus the central upper incisors are of quite low human type, clearly allied in form especially to those of chimpanzees and gorillas, but differing in the smaller size of their roots and in their decidedly less protruding or prognathous form and position.

The *lateral upper incisors* differ from those of chimpanzees and gorillas in their alignment, since their labial surface faces obliquely outward rather than forward. This is correlated with the loss of the diastema between the lateral incisor and the canine, and with the reduction in size of the lower canine, the tip of which is no longer thrust between the lateral upper incisor and the upper canine. The roots of the lateral upper incisors are much smaller than those of the centrals. The whole tooth, crown and root together, is curved well backward, lying behind the central incisor and in front of the canine. The lower part of the labial surface differs from that of most apes in being nearly vertical instead of being inclined forward; the upper part, on the other hand, slopes upward and backward toward the recumbent root. As seen from in front, the labial surface has its sides less sharply divergent than in the centrals. On the left side the labial surface is higher, narrower and less divergent toward the lower end than on the right.

The loss of a diastema between the lateral incisor and the canine has been one of the conditions that has permitted the lateral incisor to become an intermediate in form between the central and the canine. At least in most of the great apes, on the other hand, the lateral incisor is widely different in form from the canine—as a rule much more primitive, more like the lateral incisor of the gibbons, of *Propliopithecus* and the lower primates. Hence the lateral upper incisor of the Mousterian youth of Upper Pleistocene age is in a far more advanced stage of evolution than that of typical modern anthropoids. This is especially conspicuous on the lingual view of the tooth; on the right side this is provided with a deep central fossa, a prominent cusp-like tuberculum dentale which is connected with the greatly thickened cingulum, which, in turn, runs respectively to the "mesial" and "distal" borders, the whole arrangement being a notable advance toward the deeply fossed lateral incisors of certain existing Hominidæ. That this relatively high specialization should be attained as early as Upper Pleistocene times is in no way surprising, in view of the fact that some other Pleistocene mammals are actually in a more advanced stage of evolution than that which is preserved in their more conservative modern relatives. The fact of this specialization by no means excludes the Hominidæ from relatively close relationship with the existing anthropoids, which have usually retained a more primitive condition of this tooth, while at the same time they have specialized in other ways, such as the extreme width of the central incisors.

There are numerous examples of convergence in form between adjacent teeth, as when the lower canines have been taken over into the incisor series (e.g., lemurs, ruminants) or when an upper canine has become premolariform (e.g., *Saghatherium*). Adloff and other writers, neglecting such well-founded palæontological facts and noticing in the Mousterian youth and other dentures the structural transition from the central upper incisors to the laterals, to the canines and thence to the premolars, assume that it proves that all the teeth have acquired their existing form through the transformation of one ground plan (Adloff); only we have a marked divergence of opinion as to what that ground plan was, from the double triconodont plan of Bolk to the "biscuspid" plan of many authors. *But to search among modern and extinct Hominidæ rather than among the theromorph reptiles for traces of the "original ground plan" of the human dentition, is to commit an anachronism, the enormity of which is measured by the time interval between the Permian and the Pleistocene!*

The *upper canines* of the Mousterian youth are approaching the bicuspid pattern in the form of their crowns, but their roots retain much of the anthropoid heritage, since they are large and long and project upward above those of the premolars; they are also inclined backward, but to a less degree than those of the incisors. The crowns are unlike those of female chimpanzees, but could be derived from them by a marked vertical shortening, so as to reduce the tip nearly to the level of that of the anterior premolar. Allowing for differences in wear, the crown of the canine is more abbreviate vertically than that of the Piltdown canine (which may be an upper). On the whole the crown of the upper canine is decidedly more like those of Verneau's Grimaldi dentition (1916, *fig. 23*), of Adloff's native of New Britain (1908, Taf. III), and of certain Chinese and Indian dentures in the American Museum of Natural History. *Here then is the greatest difference between the anthropoid type of dentition and that of the Mousterian youth. In the view of many, this difference will doubtless far outweigh the innumerable characters which link the existing anthropoids and man as divergent descendants of the "ancient anthropomorphous stock."*

The lingual surface of the upper canine is distinguished by the unusually strong development of the basal tubercle, which has been derived (as shown by comparison with more primitive Primates) through the upgrowth of the middle portion of the basal cingulum, as has so often happened in the premolar teeth of many phyla of mammals. The cingulum, as in the incisors and premolars, is continued downward and merges with the "mesial" and "distal" (anterior and posterior) edges of the crown—a direct advance upon conditions observable in the canines of female chimpanzees. A prominent medial ridge runs downward on the lingual surface of the canine from the basal tubercle to the conical tip. The homologue of this ridge may readily be identified in the upper canines of various anthropoids of both sexes. As may be seen by articulating the cast of the lower jaw with that of the upper, the internal spur (tuberculum dentale) of the upper canine would assist in holding the food against the upward thrust of the lower canine and anterior lower premolar; it comes nearly opposite the line of contact of these two teeth It is plainly analogous with the internal spurs (deuterocones, inner cusps) of the true premolars, which cusps press the food against the talonid fossæ of the lower premolars.

The lower incisors and canines of the Mousterian youth are as well preserved as the upper and fully as important from an evolutionary viewpoint. The *lower dental arch* is essentially similar to that of the Heidelberg man and very unlike those of anthropoids, probably as a result (a) of the reduction of the canines, (b) of the more vertical position of the incisors, and (c) of the widening of the intercondylar diameter. Although the crowns of the *lower incisors* are nearly vertical, and meet their opponents of the upper jaw in an edge-to-edge bite, the roots are inclined gently forward, producing a moderate alveolar prognathism, the effect of which is heightened by the lack of a forwardly projecting bony chin.

The *central lower incisors* are distinctly smaller than those of typical modern anthropoids and have the wearing edges much narrower transversely. On the other hand, they are much larger than those of most modern Hominidæ. The cast shows no trace of the median ridge on the lingual face of the central lower incisor, which is frequently prominent in the homologous teeth of anthropoids; nor is this ridge shown in the Krapina specimens (Kramberger, Taf. VII, fig. 2a), nor do I find it in various modern human specimens examined. (Its presence in the lateral lower incisor is noted below.)

The *lateral lower incisors* of the Mousterian youth are considerably larger and wider than the centrals. They differ from those of modern chimpanzees, gorillas, orangs and gibbons in that their edges lie on a plane which is little if any above the general plane of the molar crowns, while in anthropoids the plane of the incisors lies much above that of the molars. This relation in the Hominidæ is partly associated with the reduction in size of the canines. In connection with the lack of a diastema and the relatively small size of the canines, the wearing surfaces of the lateral incisors are expanded laterally and sharply truncate all across the crown, whereas in modern anthropoids the lateral edge of the lateral incisor slopes downward. Very little is known of the form of the crown of the lateral lower incisors in fossil anthropoids, but there can be no doubt that in recent anthropoids the general form of the crown of this tooth is on the whole more primitive, more like the conditions in recent and fossil lower primates (e.g., *Oreopithecus*, *Dolichopithecus*). Hence the truncate form of the wearing edge of the lateral incisor of the Mousterian youth and of all other Hominidæ is without doubt a distinctively human trait, but deriyed from the more primitive conditions in the anthropoids.

The lingual surface of the lateral lower incisor bears a distinct median keel, confluent below with the median tubercle, which, as in the upper incisors, is continued laterally and medially into a marginal rim running up toward the wearing surface of the crown The median keel and bordering rim are less sharply defined than in many anthropoids examined. In the Mousterian youth the keel seems to fade out before it reaches the wearing edge, whereas in many anthropoids and even in some modern Hominidæ it runs up to the wearing edge and is continuous with the middle cusp or tip of the crown. The outer or labial surface of the incisor crown shows little if any tendency to develop a corresponding median keel, as it does in many anthropoids.

The *lower canine*, as shown on the right side of the jaw of the Mousterian youth, tends to be aligned with the incisors rather than with the premolars, as it is in anthropoids; its large, forwardly-curved root and backwardly-curved crown as seen in side view, enhance its resemblance to the incisors. It resembles the incisors also in the vertical depth of its labial surface and, when the lower jaw is articulated with the upper, one see clearly that the lower canine aligns itself with the incisors in function as well as in position. On the other hand, the obtusely-pointed form of its tip suggests the anterior premolar. The lingual surface shows a prominent basal tubercle and a wide median ridge running up to the apex. The basal cingulum is continued upward into the "mesial" and "distal" borders of the crown. That this raised rim as well as the basal tubercle have arisen from the cingulum, and become confluent with the median and lateral borders of the crown, is proven first by comparing these structures in the Mousterian youth and other Hominidæ with the plainly homologous elements in the Simiidæ, and secondly by following these structures down through the lower primates (e.g., *Oreopithecus*, *Mesopithecus*, *Parapithecus*) to the highly primitive conditions in Eocene lemuroids.

*From the mixture of "incisor" and "premolar" characters of the lower canine in the Mousterian youth and other Hominidæ, we should assuredly not draw any such inference as that in the ancestors of the Hominidæ all the teeth were once much alike in form or that they were much like the bicuspids.* To do so would be to neglect the important and well established principle that adjacent teeth often tend to become alike.

The crown of the lower canine of the Mousterian youth, as of all Hominidæ, doubtless represents a shortened derivative of a crown much like that of the lower canine of *Dryopithecus*, which has a pointed tip and faces laterally rather than antero-laterally. If the remote ancestors of the Mousterian youth did not have a canine of more normal simian form, how are we to account for the innumerable ties of structural and genetic affinity of man with the primitive giant-ape stock? That the Hominidæ have not been derived from a *Parapithecus*-like stock before the enlargement of the canines, is indicated by the relatively close resemblances of the premolars and molars of the Mousterian youth to those of such advanced anthropoids as *Dryopithecus* and the chimpanzee.

On the left side the permanent canine is impacted and the small *deciduous canine* is still in place. Its tip, although worn, was never high, and its basal tubercle is relatively quite large. This fact may lend further color to the rather widespread view that the canine of the ancestral Hominidæ was a sort of middle term between the incisors and premolars. But those who assume that the deciduous dentition is more primitive (the contrary can be shown in some cases!) do not reflect, first, that a suckling mammal will rarely if ever have the muscular power to fight as vigorously as an adult and hence it would have no need of enlarged canines; and secondly, that for various reasons (cf. page 470 below) the deciduous dentition, instead of repeating adult ancestral history, in each case follows its own line of evolution, which it is true often parallels that of the permanent dentition in many but not all respects. Hence the proper object of comparison for the deciduous canine of the Mousterian youth is not the adult but the deciduous canine of various anthropoids. And in fact we find that it bears some resemblance to the deciduous canines of anthropoids but differs in the lowness of the crown and in the pronounced development of the basal tubercle, both progressive characters of the Pleistocene Hoimnidæ.

The *upper premolars* are distinguished by the more pithecoid characters of their crowns, as may be seen in comparison with those of *Dryopithecus punjabicus* (*fig. 251*), or even with those of modern chimpanzees (*fig. 275*) and gorillas (*fig. 276*).

Along with these resemblances there are certain notable and important differences due to the more advanced stage of evolution of the Mousterian youth as compared with most known anthropoids. In *Dryopithecus punjabicus* (*fig. 251*) each upper premolar, as figured by Pilgrim (1915, pl. 3), bears on the surface of the crowns three distinct fossæ which may be named, respectively, the anterior, the middle and the posterior fossa. The middle fossa is well separated from its neighbors by two sharp transverse ridges, lying respectively in front of and behind the middle of the tooth, and connected on the buccal side with the main external cusp and on the lingual side with the internal cusp. These three fossæ are more or less distinctly developed in all modern anthropoids examined by me, but sometimes, as in a certain orang (Amer. Mus., no. 19,548) the transverse ridges are low and not very conspicuous, the central fossa is small and is represented by a pit or fissure which on the right anterior premolar is extended antero-posteriorly, dividing the crown into lingual and buccal moieties and tending strongly to obscure the more primitive arrangement.

In the upper premolar of the Mousterian youth one may easily identify the anterior and the posterior fossæ, but in the cast only a trace of one of the transverse crests is indicated, while the middle transverse fossa is no longer clearly identifiable, the anterior and posterior fossæ being connected by a narrow isthmus, so that there is now a division of the crown into buccal and lingual moieties; although the resulting antero-posterior isthmus is not as fissure-like as it is in more modernized dentures. In the second upper premolar the anterior and the posterior transverse fossæ are still strongly marked, but the two transverse crests have apparently united into one, and they are interrupted in the middle of the tooth, so that here again there is a beginning of the division of the crown into buccal and lingual moieties.

That the foregoing is the correct interpretation of the morphology of the upper premolar crowns of the Mousterian youth is indicated in several other primitive human dentures, as well as in the anthropoids. In a palate of the Krapina race, figured by Adloff (Taf. VIII, *fig. 33*), the posterior upper premolar shows clearly the anterior and the posterior fossæ, together with a vestige of the buccal half of the middle fossa and of the paired transverse crests; the antero-posterior isthmus-fissure is in an early stage of development. In the anterior upper premolar of a Melanesian (New Britain) child, figured by Adloff (Taf. V, fig. 19a), the anterior fossa is very sharply defined anteriorly by a bowing out of the border of the crown (as in anthropoids) and posteriorly by a sharp transverse crest which appears to represent the anterior one of the transverse pair of anthropoids. What is apparently homologous with the middle fossa of anthropoids is in this tooth greatly enlarged, the posterior transverse crest being crowded back toward the rear end. The posterior fossa is also well developed, lying beind the last-named crest. Again, in the very large palate of a male native of New Britain, figured in Adloff's Taf. IV, fig. 18a, the premolars show clearly the anterior and the posterior fossæ; but while both premolars of the left side bear remnants of the pair of transverse crests, the anterior premolar of the left side has so deep an anteroposterior isthmus that no trace of the crest shows, at least in the figure. *The "Mousterian youth" and these other relatively primitive dentures therefore reveal to us some of the steps by which the modernized bicuspid crown pattern has very probably been attained; namely, by the loss of the paired transverse crests and middle fossa and by the substitution of an antero-posterior fissure or isthmus connecting the anterior and the posterior fossæ.*

The buccal roots of both premolars, so far as exposed, are single and therefore probably represent a complete fusion of the two outer roots of Miocene anthropoid premolars. Even in modern human races the premolars occasionally have two outer roots (Wortman, 1886, p. 443).

The *lower premolars* are very reminiscent of anthropoid conditions. Each one bears on its lingual side prominent anterior and posterior fossæ separated by transverse ridges. The anterior fossa of the first bicuspid as seen from above is triangular in outline with the apex directed forward. The posterior fossa of the second bicuspid is much larger than the anterior fossa and is plainly homologous with the corresponding fossa of anthropoids.

The more important differences from anthropoids are the following: (1) In correlation with the smaller size of the upper canine, the tip of the first bicuspid of the Mousterian youth is lower than that of anthropoids and the antero-external face is but slightly flattened. (2) In the second bicuspid, the apex and the trigonid (anterior) fossa are reduced nearly to the level of the posterior moiety or incipient talonid. (3) Both bicuspids are much wider in proportion to their antero-posterior length than are the homologous teeth of anthropoids. (4) The first bicuspid is turned somewhat mesially toward the incisor-canine arch, whereas in anthropoids, which have a longer, less widened and shortened jaw, the first bicuspid is antero-posterior in position. (5) The roots of the bicuspids are crowded and reduced in number, whereas in anthropoids they are unreduced. *In all these, as in many other particulars, the anthropoids, especially Dryopithecus, are plainly more primitive, less different from still older and lower primates, while the Mousterian youth represents a highly progressive family (Hominidæ) in which the jaws have been greatly shortened, the intercondylar diameter excessively widened, the molars and premolars widened transversely and shortened antero-posteriorly.*

*Upper molars.* The first upper molar is perhaps the most primitive and conservative of all the upper teeth. The general contour as seen from above is somewhat rhomboid, with the hypocone projecting well backward. The primitive crest connecting the protocone with the metacone is well developed and the transverse fissure separating the adjacent bases of the para- and metacones is almost as sharply defined as it is in the homologous tooth of *Dryopithecus punjabicus*. The cleft separating the hypocone from the protocone is likewise deep and sharp. Thus, as in the last-named anthropoid, the surface of the first upper molar presents four transverse fossæ separated by oblique crests: the first, lying immediately behind the anterior border, presses the food against the protoconid of the lower molar, while the oblique ridge behind it fits between the proto- and the hypoconid; the second or central fossa of the upper molar receives the hypoconid of the lower molar, while the ridge behind it fits between the hypoconid and the hypoconulid of the lower molar; the third fossa lies on the lingual side of the crown between the proto- and the hypocone, and receives the transverse crest on the entoconid; the fourth fossa lies buccad to the hypocone and receives the hypoconulid of the lower molar.

These and other fundamental agreements with the primitive anthropoid type of upper molar are naturally accompanied by numerous important differences, perhaps acquired by the human ancestors of the Mousterian youth in the immense interval between the Upper Pleistocene and the Miocene.

(1) In the first place the first upper molar bears a distinct but not large Carabelli cusp on its antero-internal corner, but neither in this skull nor in the Krapina specimens figured by Adloff and by Gorganovic-Kramberger does this cusp attain sufficient size to reach the general wearing level of the crown. Indeed the cusp itself in the Upper Pleistocene Hominidæ is plainly a derivative of the basal cingulum, which in many anthropoids has a pronounced development on the antero-internal corners of the crown.

Many authors (including Cope, Adloff, Osborn, Schwalbe and Jeanselme) have recognized that the Carabelli cusp (tuberculum anomalum) has been derived from the cingulum. But, from the absence or great rarity of this cusp in anthropoids (Adloff has figured it in a single gibbon), from its prevalence in the adult first molar of the Krapina men and of many lower existing races, and from the high frequency of the cusp in the second milk-molar of modern races, Adloff (pp. 125–129) concludes that the possession of a Carabelli cusp is a primitive human character which sharply separates man from the anthropoids.

From this and certain other considerations Adloff concludes that man and the anthropoids are independent derivatives of different and wholly unknown pre-Eocene mammals. I, on the other hand, while recognizing that the Carabelli cusp (although in an imperfectly developed stage) was already attained by some Pleistocene Hominidæ, conclude that *the presence of the external cingulum at the antero-internal corner of the first and second upper molars in primitive anthropoids, and its occasional development into a Carabelli cusp in the gibbon, provide us with the starting point for the human line of specialization, and that a comparison of the incipient Carabelli cusp in the Mousterian youth with the vigorous development of the antero-internal cingulum in a certain chimpanzee (Amer. Mus., no. 10,276) only serves to emphasize the relatively close structural and phyletic relationship between these two genera.*

Other important differences of the upper molars of the Mousterian youth from those of modern chimpanzees and gorillas in the same stage of wear are the following: (2) The crowns as a whole are more hyposodont (taurodont). (3) The principal cusps are lower, more obtuse. (4) The small accessory cusp, which in many chimpanzees lies behind the metacone, is absent (it is present in *Dryopithecus rhenanus* but apparently not in *D. punjabicus;* on the other hand, it is present in $m^1$, $m^2$, of a certain Indian from Peru). (5) The postero-external borders of $m^1$, $m^2$ slope backward obliquely, while in the *Dryopithecus* they are more transverse. (6) The hypocones of $m^1$, $m^2$ are relatively larger and project further inward than they do in some modern chimpanzees and gorillas. (7) The hypocone of $m^2$ in the Mousterian youth does not project downward to the level of the protocone, whereas in modern chimpanzees and gorillas the homologous cusp of $m^2$ reaches or even goes beyond the level of the protocone (in $m^2$ of *Dryopithecus punjabicus*, however, the hypocone is lower than the protocone). (8) The surfaces of the crown of $m^1$, $m^2$ are less delicately furrowed than is the case in many modern chimpanzees, and apparently less than in *Dryopithecus rhenanus*. In the Krapina specimens (Gorjanović-Kramberger, Taf. XIII), however, the upper molars have a few delicate furrows in addition to the main ones. In view of the wide range of variation in the degree of furrowing in Hominidæ and Simiidæ, no great phylogenetic importance may be ascribed to this character. (9) In $m^1$, $m^2$ a distinct cuspule at the junction of the oblique protocone crest with the anterior cingulum is present in *D. rhenanus*, *D. punjabicus* (Pilgrim, Pl. 2, *fig. 14*) and in some gorillas and chimpanzees. In the Mousterian youth a similarly placed cuspule is indicated in the cast of the second right upper molar, but is hardly distinguishable from the protocone crest in the cast of $m^1$, of both sides. In one of the Krapina dentures figured by Gorjanović-Kramberger (1906, Taf. IV, *fig. 2*), the oblique protocone crest is angulate but apparently bears no distinct cusp. In $m^2$ of another Krapina specimen, figured by Adloff (Taf. VIII, *fig. 3*), the angle of the oblique protocone crest is more or less cusp-like. Cusps in this position, namely, buccad to the locus of the Carabelli cusp and on or near the anterior rim of the tooth, are shown on $m^1$, $m^2$, and $m^3$ in Adloff's figure of a palate of a native of

New Britain (Taf. VI, *fig. 28*) and in $m^1$ of a certain Swabian skull (Amer. Mus., $\frac{99}{4556}$). (10) The two outer roots of $m^2$ of the Mousterian youth are straighter and less divergent than are those of *Dryopithecus punjabicus* and many modern anthropoids. (11) The third upper molar of the Mousterian youth has the hypocone smaller but projecting further inward than in *Dryopithecus punjabicus* (Pilgrim, pl. 2, *fig. 5*). In these characters it agrees with one of the Krapina specimens (Gorj.-Kramberger, Taf. XIII, *fig. 3*). (12) The third upper molar of the Mousterian youth, as in all Hominidæ, was delayed in its eruption until long after the other upper teeth, especially canines, were in place; whereas, as in all modern Simiidæ and probably also in *Dryopithecus fontani*, the third molars came into place quite early. But, as I have shown elsewhere, a very early eruption of the third molar is surely a primitive character for primates as a whole, and the progressively delayed reduction in the Hominidæ is surely a specialization which is not to be expected in their simian ancestors.

The *lower molars* (especially $m_1$, $m_2$), as already stated, retain much of the primitive *Dryopithecus* pattern; and as we pass from $m_1$ to $m_3$ we observe the progressive obliteration of this pattern, although the cruciform or +-shaped pattern is not fully attained. The first molar, as in all other Hominidæ, is the most conservative. The molars differ from the primitive anthropoid type in the following characters:

(1) They are all much widened transversely, the width across the posterior moiety being relatively far greater than in typical anthropoids. (2) As we pass from $m_1$ to $m_3$ the "taurodont" condition (see above, p. 442) increases. (3) The hypoconids are larger and the hypoconulids smaller than in typical anthropoids. (4) All the main cusps are lower and blunter, so that the general wearing surface of the crown would have been nearly flat when much worn. (5) The antero-posterior length of $m_1$, as compared with the combined length of the two bicuspids, is much greater in the Mousterian youth and in other Hominidæ than in *Dryopithecus rhenanus*, as shown in the following comparative table:

*Length of* $m_1 \div$ *length of* $p_3 + p_4$

| | |
|---|---|
| *Dryopithecus rhenanus* ♂ | 0.57 |
| Mousterian youth ♂ | 0.75 |
| Illinois Indian ♂ | 0.88 |
| "Hindoo" (South India) ♂ | 0.84 |
| "Bedouin" ♀ | 0.75 |

This means that in the primitive anthropoid, *Dryopithecus rhenanus*, the premolars are relatively long, the jaw itself being elongate. In the Mousterian youth the space for the premolars has been decidedly shortened, while the first molar is relatively and absolutely larger. This tendency is still more pronounced in the male Indian jaw, which has a very large first molar. But when we come to the small-jawed female Bedouin, the first molar has lost some of its superiority in size over the small premolars and the ratio falls to 0.75.

(6) In *Dryopithecus rhenanus* the second lower molar is decidedly larger than the first, but in the Mousterian youth, and still more in modernized human dentitions, the second lower molar decreases in relative size as shown below:

*Ant.-post. length of* $m_2 \div$ *ditto of* $m_1$

| | |
|---|---|
| *Dryopithecus rhenanus* ♂ | 1.95 |
| Mousterian youth ♂ | 1.00 |
| Illinois Indian ♂ | 0.90 |
| "Hindoo," So. India ♂ | 0.86 |
| Bedouin ♀ | 0.99 |

### *Dentition of the Krapina sub-race*

The dentition of the Krapina sub-race of *Homo neanderthalensis* has been described and figured by Gorjanović-Kramberger (1906, pp. 181–207). The central upper incisors are of great interest because they afford what is apparently a stage in the evolution of the shovel-shaped or mongoloid condition, the cutting edge being folded around at the sides and being confluent with prominent rims which lead upward to the large basal tubercle. The latter is subdivided by clefts into two ridges. Both in the central and lateral incisors the cutting edge of certain unworn specimens is more or less notched near the middle; and from this fact, as well as from the division of the basal tubercle and from the occasional grooving of the anterior root, Gorjanović-Kramberger infers (p. 206) that each human incisor has arisen from the fusion of two incisors. Similar considerations lead him (p. 207) to conceive an upper premolar as arising from the fusion of two canine-like teeth, while the molars are regarded as arising from clusters of 4½ or more cusps. This application of the well-known "concrescence theory" will be considered below. Meanwhile it may be noted that according to Gorjanović-Kramberger's view the remote ancestors of the Krapina race must have had not less than 155 teeth in the adult dentition! On the whole the dentition of the Krapina subrace agrees in essentials with that of the Mousterian youth, except that the crowns of the lower molars are much wrinkled and furrowed and the main cusps of all the molars are lower and less distinct. The "fovea anterior" of the lower molars is plainly the last remnant of the trigonid fossa of anthropoids.

### *Conclusion as to the origin and relationships of the Neanderthal group*

To sum up as to the origin and relationships of the Neanderthal group: It has been suggested (Smith Woodward, 1900) that even the lowness of the forehead and excessive development of the supra-orbital tori of the neanderthaloids may be a secondary gorilloid sort of specialization along with the taurodont condition of the molars; and from the palæontological-archæological evidence it has indeed been shown that the Crô-Magnons of western Europe, which were of *Homo sapiens* type, did not evolve out of the neanderthaloids but invaded their territory and overwhelmed and partly absorbed them. Nevertheless I think there is still something to be said in favor of those (e.g., Hrdlička) who regard the neanderthaloids, or some of them, as structural ancestors—primitive or perhaps archaic types surviving into a later epoch—of the higher races. For even the extreme condition of taurodontism is found in company with a large series of characters which most authorities would regard as very low (e.g., small development of the front part of the brain, slight downward bending of the prepituitary plane, enormous size and width of the nose, flat articular eminence, gorilla-like cervicals, primitive form of astragalus, etc., etc.).

If we assume that high foreheads, small jaws and other "high" characters are really primitive for the Hominidæ, then of course the neanderthaloids are highly specialized. But there are several items of evidence to which perhaps sufficient importance has not been attached. First, the Heidelberg jaw is admittedly very ancient and nobody has yet claimed that its lack of a chin or the great width of its ascending ramus are specializations that rule it out from structural ancestry to the higher types. And yet it will be widely admitted that the Heidelberg skull was probably of a pre-neanderthaloid and more *Pithecanthropus*-like type. But the crown patterns of the lower molars of the Heidelberg jaw are also generally recognized as of primitive human type, although the molars were also at least subtaurodont in the depth of their pulp cavities and shortness of their roots. Secondly, the dentition of the "Mousterian youth," as shown above, retained a number of extremely primitive or simian characters in the patterns of the cheek teeth. Here again we find *very primitive features in the crown pattern associated with at least a moderate degree of taurodontism.*

If the Piltdown lower jaw be associated with the skull, as maintained by many authorities, it will provide another example of the coexistence of primitive features in the jaw and dentition, with a deeper pulp cavity than is common among recent jaws. In a jaw of a modern European figured by Adloff (1910, plate 2, jaw H) the pulp cavity is much deeper and larger than in ordinary teeth. From all this I therefore conclude that *at least a moderate degree of taurodontism may be a primitive character for the Hominidæ.*

Adloff concludes (1910, p. 144) that the newest discoveries of Palæolithic races have brought no conclusions which could be of significance for our knowledge of the development (evolution) of the human dentition and that they only furnish proof that the human dentition has undergone no significant change during the time in which the jaw itself has passed through important modifications. In view of the facts set forth here, I, on the contrary, conclude that *the dentition of the "Mousterian youth" and of the Krapina people afford important additional evidence for the conclusion that the human dentition has been evolved from a primitive anthropoid type and has undergone highly significant changes (especially in the crown patterns of the premolars and molars) during the time in which the jaw itself has been evolving toward the "modern" or high type.*

## HOMO SAPIENS

Neither the writer's knowledge nor the available space are sufficient for an adequate treatment of the morphology of human jaws and teeth, or for a detailed account of racial characters of the dentition. Nevertheless a few notes on these subjects may now be submitted, together with a conspectus of the species, races and subraces of the Hominidæ, for the purpose of completing the main outlines of this review of the evolution of the human dentition.

### *Fusion of premaxilla and maxilla*

With regard to the premaxillary bone, Wood Jones (1918, p. 36) has emphasized its very early fusion with the maxilla in man and states that: "In all the monkeys and apes, as in all other mammals, this premaxillary element is mapped out on the face by suture lines marking its junction with the maxillary bones. In man alone has an alteration of the method of growth of this region led to a loss of the individuality of the premaxillary element. This is a human specific character. From all orthodox teaching we should therefore expect it to be very late in its appearance in the human embryo; we should hardly look for it earlier than the fifth month. As a matter of fact this character is established as soon as ever the future bones of the human face are first represented as cartilaginous nuclei.

"It has become a character of the human embryo at a stage when the development has proceeded so little way that the future being is no longer than ten times the diameter of an ordinary pin's head. Such a finding, in the development of any animal, forces the conclusion that a distinctive feature, so early acquired in embryology, was early acquired in history, and that the species must be very old indeed. It therefore seems possible that not only is man an excessively primitive animal, which originated right at the base of the Primate stem, but he probably also acquired his specific characters in an extremely remote past."

When writing that "in all the monkeys and apes, as in all other mammals, this premaxillary element is mapped out on the face by suture lines marking its junction with the maxillary bones," Wood Jones could hardly have had before him many specimens of anthropoid skulls. In a young female chimpanzee skull (Amer. Mus., no. 51,211), a wild specimen with the deciduous canines and molars in place, I find only the faintest indication of the premaxillary-maxillary suture on the face, although remnants of the suture are visible on the palate; and in various adult anthropoids of all genera the fusion of the premaxilla with the maxilla seems complete, so that the anthropoids have attained in this character a condition that in the light of other evidence may reasonably be regarded as prehuman. Although the premaxilla of man does begin to fuse with the maxilla as early as the seventh week (Ferber, 1919), this is only in keeping with great acceleration of other characters (e.g., of the foot) in human development.

The concept of the biogenetic law invoked by Wood Jones to disprove the relationship of man with the anthropoids happily belongs to a past century. *It is nowadays realized by many embryologists that at least in many cases the order of appearance of structures in ontogeny by no means corresponds to their order of evolution.* It would be interesting to know whether the fusion of the premaxilla with the maxilla is as early in individuals with large prognathous incisors as it is in those with small incisors and orthognathous face.

### *The concrescence theory and the origin of human incisors*

The ontogeny of the teeth has afforded innumerable pitfalls for those who have not realized that *in modern mammals developmental processes are adjusted primarily to relatively modern requirements and conditions.* Various parts of the teeth, such as cusps, cingula, etc., appear as more or less separate elements and afterward fuse into an undivided whole. But as the presence of many ossific centers in the developing humerus by no means indicates that phylogenetically the humerus is a composite of as many separate bones, so also a similar reasoning applies to the teeth; because the palæontological, comparative and taxonomic evidence is cumulative that the normal crowns of mammalian teeth have evolved by differentiation, not by concrescence.

By this time the theory of concrescence in all its varied forms should be as dead as the Copernican theory, but, strange to say, it is still cherished by many European writers. A few of the many fundamental objections to the theory are as follows:

(1) It neglects the well established principle cited above, namely that dental development in modern mammals is largely directed toward the production of highly specialized dental forms with but little "recapitulation" of remote ancestral history. For example, the laminæ of elephant molars appear to form separately and later to coalesce, but the palæontological evidence shows clearly that these many-plated molars have arisen phylogenetically, not through concrescence but by differentiation of less complex molars.

(2) The theory makes the wholly unwarranted assumption that because individual teeth often become wholly or in part divided, therefore the divided parts represent the original components of an ancient concrescence. This assumption is often contrary to evidence. For example, in the special case of the Krapina teeth cited above, the grooving of one of the roots, the notching of the crown of the incisor, etc., are supposed by Gorjanovic-Kramberger to indicate that these teeth have arisen from the fusion of originally separate elements. From what he assumes as to the number of originally separate teeth entering into the composition of the incisors, canines, premolars and molars, it follows directly that the dental formula of the remote ancestors of the Krapina race must have been as follows: $I^{2(\times 2)}_{2)\times 2)}\ C^{1(\times 2)}_{1(\times 2)}\ P^{2(\times 2\times 2)}_{2(\times 2\times 2)}\ M^{3(\times 4.5+)}_{3(\times 4.5+)}$, or a minimum number of 155 teeth in all! But the palæontological, taxonomic and morphological evidence is cumulative that the Krapina race belongs to an order of mammals which, from a very remote antiquity (Lower Eocene), had a dental formula never exceeding $I^2_2\ C^1_1\ P^4_4\ M^3_3$, or 40 teeth in all. The Old World or catarrhine division, to which the Hominidæ belong, by the elimination of the first two premolars in both jaws, early reduced the formula to $I^2_2\ C^1_1\ P^2_2\ M^3_3$, or 32 teeth in all, the reduction occurring not by concrescence but by reduction and final elimination of the first and second premolars.

(3) The concrescence theory assumes, as atavistic, variations which are often plainly teratological. For example, a recent author (Pohle, 1900) records an actual case of concrescence of adjacent teeth in two modern musteline carnivores as evidence for the origin of teeth by concrescence. But from palæontological, taxonomic and comparative evidence it is highly probable that the variation above described is teratological, not atavistic.

The special form of the concrescence theory advocated by Bolk (1913, 1914) is based, like other forms of the theory, chiefly upon an erroneous phylogenetic interpretation of certain ontogenetic facts. Bolk's excellent contributions to our knowledge of the facts of development are overlaid by his peculiar hypothesis that every tooth, from the incisors to the last molars, represents a "dental family" of two (or more?) successional tooth germs, and consists of two parts: an outer, labial or buccal part, called the protomere; and an inner or lingual part, the deutomere. From various indications among modern mammalian teeth, proto- and deutomere are each inferred to be potentially equivalent to a triconodont crown, so that every tooth potentially or actually carries six primary cusps!

But it has already been shown in previous parts of this work that, *in the long series of forms that stand in or near the line of human ascent, from the rhipidistian fishes up through the primitive amphibians and reptiles to the mammal-like reptiles, thence through the Mesozoic trituberculates to the Eocene primates there is not one whose incisor, or any other teeth, conform to Bolk's ideal pattern.*

More in detail, not one of the incisors or canines of these Lower Eocene lemuroids, or of any other Paleocene or Eocene placental mammals of any order, approach even remotely the six-cusped stage which Bolk assumes as the starting-point for all the teeth of primitive mammals. This six-cusped stage is a pure inference from his primary assumption that every placental mammalian tooth consists at least of two parts, a protomere and a deutomere, each equivalent to a triconodont tooth. The evidence in the first place is against the derivation of tritubercular teeth from a triconodont type; secondly, the double or even single triconodont form is never apparent in the incisor and canine teeth of any of the mammal-like reptiles, the protodonts or the triconodonts themselves.

The more or less tricuspidate, cingulate incisor and premolar crowns of the galagos, Hapalidæ and Cebidæ, which Bolk refers to, afford no real support to his view. The incisor teeth in most families of mammals are highly adaptive organs, which assume such useful forms and functions as their positions, with reference to the food, to the jaw muscles and to adjacent and opposing teeth, will permit. It is proven from much palæontological and comparative evidence that in primitive primates the incisors, like those of other mammals, were provided with a cingulum on the lingual side, which was possibly associated with the alveolar borders of the crown and with the zone of fusion of the crown with the root. The basal cingulum often or usually thickened into a more or less well-marked swelling or tuberculum dentale, and on the sides of the tooth it was continued upward into the cutting edges of the crown. The lingual side of the tooth was often buttressed by a more or less well-defined vertical ridge running up to the tip of the crown. In the very primitive Eocene lemuroids of the family Notharctidæ, the above described condition may be observed not only in all the incisors but also in the canines and anterior premolars; and as we pass backward the premolars become more complex, through the growth of the tuberculum dentale, inward in the upper, backward in the lower jaw, and through the modelling of the median ridge, development of accessory cusps, etc. But in this connection it is important to remember that *the four classes of teeth, incisors, canines, premolars and molars, were more or less differentiated from each other, not only in the earliest Lower Eocene primates but in the vastly older Mesozoic trituberculates and even in the higher mammal-like reptiles.*

From the primitive conditions of the incisors in the Notharctidæ we may securely trace their progressive evolution, starting with *Parapithecus*, the most primitive known member of the Old World series and, passing upward through the conditions preserved in the existing gibbons, to the relatively long-crowned incisors of all the giant anthropoids and of man. In the anthropoids the crowns, especially of the central incisors, often become excessively long, perhaps in correlation with frugivorous-omnivorous habits, and the wearing edges of the centrals become excessively wide. Correlated with the width of the cutting edge and with the development of the strengthening median and accessory ridges, the edges of the central incisors become either denticulate or trifid. In the latter case the middle cusplet is continuous with the median ridge. But this denticulate or cuspidate condition of the edge of the incisors of the chimpanzee has nothing whatever to do with the primitive form of the incisor crown of pre-Tertiary mammals, except in so far as it represents an end stage of specialization. *In man the trifid or trident-*

*like condition of the incisors, both in the deciduous and permanent dentures, is clearly related to the conditions observed in the anthropoids and has just as little to do with the original ground-plan of the mammalian teeth.*

Now it is a peculiarity of ridges, separate cusps, etc., that as soon as they have established themselves their development tends to be accelerated; and in the case of the notches and cuspules on the surface of the incisor crown, it sometimes happens that one of the clefts becomes rapidly enlarged in ontogeny, extending downward to the base of the crown and giving a twinned or double appearance to the tooth. As we have seen above, such a notch in the wearing edge of one of the Krapina incisors was cited by Gorjanović-Kramberger as evidence of the origin of the teeth by concresence.

A further development of the cingulum and tuberculum dentale, together with a folding around of the wearing edges of the incisor crown, leads to the shovel-shaped or "rim-and-fossa" condition which has been so thoroughly investigated by Hrdlička (1921) and which is prevalent in many primitive races of Hominidæ from the Pleistocene Krapina race onwards.

### *Origin of human canine teeth*

Both the direct palæontological evidence afforded by the Heidelberg and Neanderthal dentitions and the comparative evidence of the dentures of existing races indicate that, if the tips either of the upper or of the lower canines ever projected beyond the level of the cheek teeth, the reduction in size took place at some time anterior to the Middle Pleistocene. The Piltdown race forms a possible exception to this statement; but as the association of the ape-like canine and jaw with the man-like skull still seems doubtful, this evidence may be set aside for the present. Very rarely, in low human races (e.g., *fig. 305*) the tip of the lower canine projects above the level of the premolars, but these cases are so rare, and there is always such danger of confusing abnormal neomorphs with reversions, that they too may be left out of consideration. Add to this the fact that the oldest known members of the Old World series, *Propliopithecus* and *Parapithecus*, both had low-crowned lower canines, and the case for the human races ever having had enlarged canines may seem pretty weak.

Nevertheless there is considerable indirect evidence for this view. In certain mammals (e.g., *Homalodotherium*) the loss of diastemata and the closure of the tooth-row has gone hand in hand with the reduction of the canines to the level of the other teeth. There is little doubt that in the primitive man-anthropoid stock the lower incisors were slightly procumbent and that the vertical or recurved incisors of man are specialized. The increased verticality of the incisors, perhaps correlated in part with a change from frugivorous to omnivorous diet and the rotary action of the mandible, are perhaps unfavorable to the retention of large caniniform canines. The anatomical evidence for a relatively near relationship of man with the gorilla is so overwhelming that it is difficult to conceive the common stem-form as having a man-like lower dentition, especially in view of the fact that in the patterns of the premolars and molars the gorilla is plainly more primitive. Again the form of the lower dental arch in man appears to be derived from the more primitive conditions in *Dryopithecus*, which had pointed lower canines of primitive anthropoid type (*fig. 312*). We have seen that in the case of a certain species of monkey (*fig. 218*) a convergent or closed incisor arch and pronounced diastemata are associated with the small canines of the female, while a wide incisor arch and pronounced diastemata are associated with the large canines of the male, and that in female orangs with small canines the upper dental arch makes some approach to the human form. The anomalous position of the lower canine in higher races, with its tip lying on the lingual side and overhung by the upper lateral incisor and upper canine, is largely due to the loss of the diastema and probably also to the erect position and reduction of the canines. In brief, the larger canines of *Dryopithecus* and female anthropoids are associated with a more primitive form and arrangement of the incisors, of the symphyseal region, of the dental arches and of the muscles of the lips. Conversely, small canines of human form are associated with a complex of conditions which few (except Wood Jones), could regard as primitive. Hence it seems probable, though not demonstrated, that the small canines of man are no more primitive than his other distinctive characters of the dentition.

### *Supernumerary dental elements and the confusion of neomorphs with reversions*

A prolific source of confusion in odontology is the occurrence of supernumerary teeth in man and other mammals, which, being mistaken for reversional phenomena, lead to erroneous inferences regarding the dental formula of the human precursors. The most notable case is the occasional occurrence in man and anthropoids of a fourth molar. But it has already been shown in Part III (p. 233) that the fourth, and even the fifth molar when present, are in all probability neomorphs both in man and in anthropoids, and that the various phyla of the man-anthropoid group are independently acquiring a new growth-power at the posterior end of the dental lamina, as has happened in other groups of mammals (e.g., *Myrmecobius* among marsupials, sirenians, toothed whales, armadillos, *Otocyon*, etc., among placental mammals).

Adloff (1908) infers that in the precursors of man the dental formula was $I_3^3\ C_1^1\ P_2^2\ M_3^3$, and that the dental formula of $I_2^2\ C\frac{1}{1}$ $P\frac{2}{2}\ M\frac{3}{3}$ has been acquired by man and by anthropoids in different ways and by convergence. But this assumption, which is supported by very little evidence, is contradicted by the enormous number of characters which prove that man and the existing anthropoids are divergent descendants of a common stock having the dental formula of the whole Old World series.

One line of evidence upon which Bolk relies for the support of his theory is the occasional occurrence in man of "paramolars," or small teeth on the buccal side of the upper molars which are sometimes fused with them. The occurrence of these elements is interpreted as a "reversion." But by what right have such variations to be regarded as reversional in spite of the cumulative palæontological, comparative and taxonomic evidence that no such assumed stage ever stood in the line of human ascent? In order to account for the supposed homologies of the "paramolars" and true molars, Bolk assumes that the conditions in the marmosets (which have already lost the third molars) have given rise to the conditions observed in man. But, as already shown in Part III of this work, this assumption is contradicted by weighty taxonomic considerations, since the Hapalidæ are highly specialized members of the New World series and have only the most distant indirect relationship with the Hominidæ. The latter, as we have seen, are highly specialized members of the Old World series, and there is no substantial evidence that the dental formula of this group since its first differentiation, from some super-tarsioids allied to *Parapithecus*, has ever been different from $I^2_2$ $C^1_1$ $P^2_2$ $M^3_3$.

The constant mistaking of abnormal or new variations for atavistic reversions, together with a total disregard of taxonomic and palæontological evidence, has been one of the worst sources of erroneous conclusions in comparative anatomy, including odontology, and has contributed greatly to the present confusion in opinion as to the evolution of the human dentition and to the low regard in which morphology is held by many modern biologists. This unfortunate mistake has been well exposed by Raymond C. Osburn (1912) in a paper which seems to have been overlooked or little appreciated by many odontologists. In this paper Osburn reviews the evidence showing that many dental variations cannot possibly be considered as atavistic, because the known earlier stages of dental evolution are wholly unlike the assumed stages.

Those who mistake cænogenetic developmental conditions, secondary simplifications, and abnormal variations for atavistic reversions seldom hesitate to assume the existence of wholly unknown orders and families (having the peculiar characters required by their hypotheses) rather than adjust their hypotheses to the known facts of palæontologic history. For example: Chiavaro (1920), after noting certain cases in which the tuberculum dentale of human incisors was exceptionally developed, and after comparing this with the duplicidentate arrangement of the upper incisors of the rabbit, reaches the startling conclusion that it would not be surprising if in an earlier stage of his evolution man might have once been a "Duplicidentatus;" while Sera (1920), in order to accommodate his theory that all the teeth have been derived from molariform, many-cusped teeth, ignores the cynodont reptiles, which actually stand in or near the line of human evolution, and invents a queer hypothetical animal with a skull like *Oudenodon* but with a row of multicuspid molariform teeth all around the margin of the upper jaw! Small wonder it is that the veteran anthropologist Sergi, perhaps disgusted with the multitude of mutually contradictory and fictitious human ancestors, and evidently misreading the facts of mammalian evolution, throws over (in his work "L'Origine e l'Evoluzione della Vita") the whole idea; and in a letter to the writer claims "that there is not a transformation in evolution, as now is the general theory, but that the types of animals and plants have independent origin and there are no progenitors whatever."

### *Parallel, convergent and divergent evolution of the deciduous and permanent dentures; interaction of the two sets*

It is becoming increasingly obvious that many characters of form and of position in both sets of teeth are predetermined by the topographic relations, relative size, degree of crowding, etc., of the germs of the teeth during development and replacement, as when the lateral upper incisor is overlapped by the central, or when one of the lower incisors is crowded out of the incisor arch. Such relations of the incisors to developmental conditions are now being investigated by Dr. Milo Hellman with illuminating results which will be reported elsewhere.

The growth energy available for the jaws and teeth, especially in the higher races of man, has been restricted more or less as the relative size and dominance of the brain has increased. Not only have the dental germs decreased in size, but the two sets are so crowded together that some of the permanent teeth, notably the third molars, are greatly delayed in their eruption.

At least after the period of infancy and lactation the digestive tracts and foods of most young placental mammals are very similar to those of the adult. Hence, perhaps through natural selection, the deciduous teeth often resemble the adult teeth of the same animal in many important characters.

It is often assumed, through an unwarranted application of the "biogenetic law," that the deciduous are more primitive than the adult teeth. Sometimes it does happen that the deciduous teeth have not evolved as fast as have the corresponding teeth in the adult sets, perhaps because the deciduous set are relatively shortlived and do not have to provide for so long a period of attrition as do the permanent teeth. Moreover the young animal being small and its strength less, the deciduous teeth will in general receive less severe impacts and stresses. On the other hand, the available space for the deciduous teeth being less, while the food is often just as resistant as in the adult, some of the deciduous teeth, especially the deciduous molars, must be of relatively large size and have a highly efficient crown pattern. Hence it happens that the crown pattern of the *last deciduous molars often converges in its evolution toward that of the last permanent molars.* Here we can see clearly that we are dealing with a convergence between differently numbered representatives of the two sets; and in many groups, including the whole catarrhine series, the posterior deciduous molars are fully molariform and very unlike the posterior true premolars which replace them. But an uncritical application of the biogenetic law would lead to the erroneous inference that the posterior premolars had been derived by degeneration from earlier adult teeth which resembled the posterior deciduous molars.

While the two sets of teeth parallel or converge toward each other in many respects, there are also many conditions that tend to bring about the characteristic differences between them, especially the following well-known factors:

(1) The development of the first set must be started in the intrauterine period, when available space is at a high premium. Hence the first ones to erupt must be as small as practicable.

(2) The deciduous teeth must draw their own nourishment in the jaws of the animal, which at first is of small size, requiring less food, but increases rapidly in bulk and in food requirements according to a variously accelerated rate. The developing teeth, in other words, must conform as far as possible to conditions arising from the excessive growth of the brain and from the ripening of the various endocrine or hormone-producing glands at different periods.

(3) Before eruption the tooth germs are drawing upon borrowed capital, but when they come into use each one is expected, so to speak to contribute more or less to the income by its service in cutting off and subdividing the food.

(4) But as the extent of their services at any given moment is limited by their cutting area, while the requirements are constantly increasing in some relation to the cube of the animal's height, there

would come a time when the deciduous set as a whole would not be large enough for the needs of the animal.

(5) It is not practicable to replace them all at once, hence the process is distributed over a long period.

(6) The process of replacement must not interfere with, but must even assist in maintaining, effective occlusal relations at all periods.

(7) Owing to the relatively small size and strength of the very young and to the undeveloped condition of the sex glands, the pugnacity of very young animals is notably less than that of adults and where the young are shielded from harm, as in man, there is less need for tusk-like canines.

(8) On the other hand, the food of the young being often as tough and resistant as that of the adult, it has proved advantageous in man to have the first permanent incisors and first molars come into use at an early period.

Although the interaction of these and of many similar factors (which will occur to every observer) is too complex to be considered here at any length, it is obvious that these factors and their interaction are responsible for many of the following classes of facts:

(1) Differences between the deciduous teeth and the teeth that replace them (e.g., divergence of roots of deciduous teeth to accommodate replacing teeth, resorption of roots of deciduous teeth as the period of replacement approaches).

(2) Elaborately adjusted relations of size and of time of replacement between deciduous teeth and their successors and neighbors; resulting malocclusions when such normal size and time relations are disturbed.

(3) Delayed eruption (as compared with prehuman stages) of permanent canines, anterior premolars and third molars.

(4) Ontogenetic changes in form of the palatal arch as a whole and in its several parts, resulting from successive replacement of deciduous teeth.

(5) Ontogenetic changes in the chin, made possible by the replacement of the deciduous incisors and canines and by the moving up of the permanent incisors out of their place of origin immediately behind the chin.

### *The superior and inferior dental arches*

Osborn (1902) showed that in many phyla of mammals there is a relatively high degree of correlation between the breadth of the braincase and that of the palatal arch, and Angle (1905) and R. C. Osburn (1910) have shown that, at least in many cases, a wide, short skull will bear a wide palatal arch and *vice versa*. But Sullivan (1918) showed that "the principle of dolichocephaly and brachycephaly, in itself, is not sufficient to explain the form of the alveolar arch;" and that in many human races and individuals, and in various species of other primates, there are striking exceptions in which a wide palate is associated with a narrow braincase and *vice versa*. Thus in man the Eskimo have a very wide palate and a very long braincase, while among other primates "*Hapale* shows the longest braincase and the shortest alveolar arch . . . . *Macacus*, *Gorilla* and *Orang* show a relatively short, wide braincase and a very elongated palate."

These and similar exceptions to the "principle of dolichocephaly and brachycephaly" are obviously due to the fact that the palate and the braincase are subject to a complex of similar and different forces both in ontogeny and in phylogeny.

Chief among the conditions that tend toward the association of width of palate with width of braincase is this: That an increase in width in the lower part of the brain will often tend to cause an increase in width of the intercondylar diameter of the skull, since the temporal bones and the glenoid will be displaced laterally. This will tend to widen the distance between the condyles of the mandible. This in turn will leave room for a transverse expansion of the tongue. It is indeed probable that in man both the palatal arch and the lower jaw are, so to speak, moulded around the greatly enlarged tongue which appears very early in development as the "tuberculum impar;" and it is evident that the tongue of man as compared with that of anthropoids, tends to be short, thick and wide. Again a reduction in size of the incisors, canines and premolars will tend to shorten the palate at the front end, while the reverse will lengthen it. Increasing verticality of the incisors will again tend to shorten it. These contrasts are well brought out in comparing prognathous, macrodont and dolichocephalic skulls with orthognathous, microdont, brachycephalic types.

On the other hand, a wide palate may become associated with a narrow cranium in opposite ways, as follows:

(1) By a secondary narrowing of the braincase, as probably in the Eskimo, which may have been derived from mongoloids with a wide palate and short skull.

(2) By a direct shortening of the palate, due to the loss of one or more molars, as in *Hapale*. Here the extreme antero-posterior diameter of the braincase has little if any relation to the form of the palate.

Conversely a long palate may be found with a short, wide cranium in the following ways:

(1) Through a marked increase in antero-posterior diameter of the molars, as in the gorilla.

(2) Through marked increase in length of the whole muzzle, as in baboons.

(3) Through an increase in size and procumbency of the incisors as in many orangs.

Sullivan (1918, p. 9) also showed that in the races of man there is a more constant relation between width of face and width of palate. In other words, where the cheek bones project laterally, as in mongolians, the palate is usually wide.

Hellman (1918, 1919) has shown that in the anthropoid apes the upper and lower dental arches of the same animal may differ widely from each other and that this is also true, perhaps even in greater degree, in man.

It has been noted above (p. 472) that the form of the front part of the palatal arch is naturally influenced by the form, size and position of the various teeth, and that when we find wide or procumbent centrals coincident with small vertical canines and bicuspids, the upper incisor arch may be more or less convergent or Λ-shaped. (*fig. 340*). In the Mousterian youth, as noted above (p. 450), the small left lower deciduous canine is in place and consequently the left half of the arch is more convergent than is the right, in which the large permanent canine is in place.

Hellman observes that an edge-to-edge bite often conditions a regularly arranged lower incisor arch, while the overbite relation favors a crowding and overlapping of the lower incisors.

## *Individual differences in the details of normal occlusion*

I have often observed that in mammals having an orthodont or vertical jaw movement the blades of the upper and lower teeth are closely adjusted to each other, and that this permits but little variability except in non-articulating parts of the teeth. On the other hand, in mammals having varied lateral and rotary movements of the jaw, as in certain Eocene lemuroids, as long as certain main adjustments are conserved (such as the fitting of the hypoconids of the lower into the centra fossæ of the upper molars) there is opportunity for many individual differences in detail, as to degree of development of certain parts (such as the mesostyle) and in the paths of the mandible at different times. The low-crowned teeth of man, with rotary and oblique movements of the mandible, afford opportunity for considerable individual differences. Hellman (1919) has shown that the classic concept of normal occlusion is far too rigid and restricted, since it has left out of account the wide range of variability in the details of occlusion.

The occlusal relations of the upper and lower cheek teeth are illustrated in *figs. 315, 316* and *319–323.*

## *Origin of the chin*

Various authors have advanced different views of the mode of origin of the bony chin. Perhaps the most probable explanation is that upheld by Hrdlička (1911) in the following passage:

> "As to the chin, the inferior part of the lower jaw is quite passive, and man, especially the white man, has a pronounced chin to his jaw today not because of a growth of chin but mainly because of reduction of the dental arch, which was not attended to an equal degree by reduction of the parts underneath. The inferior or chin portion of the lower jaw has not degenerated, or degenerated but little; it is functional as a supporting part and remained in length, more than the alveolar arch, as it was in older times. The alveolar arch, diminishing gradually further and further, left the lower anterior part of the horizontal rami, formerly more posterior than the foremost part of the arch, protruding, and this protrusion became shaped into a chin. Somewhat similar results are observable today in persons of different ages. In the old, where the alveolar arch has been still

more reduced through loss of teeth and absorption, there is as a direct result more prominence to the chin. The so-called lantern jaw of the aged is well known to all of you."

The shrinking of the dental arch in front and the increasing verticality of the incisors and canines are no doubt important factors in the production of a protruding bony chin. One reason for the fullness of the jaw in the chin region is the presence there, in the young, of the relatively large but as yet unerupted permanent incisors and canines. The long roots of these teeth when erupted also necessitate a deep chin. Robinson (1913) emphasizes the importance of the muscles of the tongue as a factor in the evolution of the chin, since these muscles require a firm base of attachment furnished by the lingual side of the jaw bone behind the chin.

### *The premolars and molars*

The range in size of the premolars in *Homo sapiens* shows considerable variation from the very large premolars of the Talgai youth to the small premolars prevalent in the higher races. The pattern of the premolar crowns varies from the relatively primitive condition shown in certain natives of New Britain (cf. Adloff, 1908) to the reduced or simplified premolar bicuspid patterns of higher races (see pp. 451–452 and *figs. 324–329*).

The molars of modern men show a conspicuous variation in the number of cusps, which has been studied by many authors. In 1888 Cope published an extended and well-illustrated account of his observations on the molar-cusp formula of many races, which varies from $\frac{4-4-4}{5-5-5}$ in primitive types to $\frac{4-3-3}{4-4-4}$. Zuckerkandl (quoted by Adloff), Adloff (1908, p. 58), Sullivan (1920) and others have also contributed to the subject, Adloff recording also the number of cusps in the neanderthaloids.

More or less in association with the reduction in number of cusps, the upper molars, especially the second, gradually lose their quadrate form and become secondarily "tritubercular." Meanwhile the lower molars, with the loss of the hypoconulid, lose nearly all traces of the *Dryopithecus* pattern, which is completely replaced by the +-shaped pattern. These degenerative changes in the pattern of the crowns are also accompanied by reduction in size, and Keith (1913) distinguishes "supra-plenal," "plenal" and "sub-plenal" stages.

As the third upper and lower molars are also greatly delayed in eruption, especially among higher races, they are evidently decadent teeth which may eventually be entirely lost. The first upper and lower molars are usually more conservative, both in the crown patterns and in size, than the second and still more than the third molars.

Another character of the molars which has been studied by many authors is the Carabelli cusp, or tuberculum anomalum. Cope (1888), Schwalbe, Adloff (1908) and others have recognized that this cusp has been derived from the basal cingulum. Jeanselme (1917) has refuted the suggestion that the cusp is associated with hereditary syphilis. He frequently found it among negroid and Asiatic races, among the Malagasy, or natives of Madagascar, among the Indians of the New World and among the inhabitants of the islands of the Pacific Ocean (Micronesians, Indonesians, Polynesians). Its occurrence among the Neanderthal race is discussed above (p. 454).

### *Racial characters of the dentition*

Apart from a few striking cases, presently to be noted, racial characters in the teeth are at most not very conspicuous. The matter has been ably summarized by Hrdlička (1911) in the following passages:

> "I want now to say a few words about the *differences of the denture and dentition in various races*. And it may be stated right from the start that should we eliminate the white race from comparison such differences would be small. With the exception of the size of the teeth, which is greater in some of the primitive peoples than in the civilized whites, and which also differs from one group to another among these races themselves according to their habits, there is but little variation. The type of human denture can be said to be today, with a few exceptions, radically everywhere the same. About the greatest of these exceptions concerns the form of the upper permanent incisors, which in one respect are radically different in the Indians from what they are in the whites, negroes, and at least some other races. The upper and particularly median upper permanent incisors of the Indian are, as you will observe in the specimens brought here for your examination, peculiarly and pronouncedly concave on the buccal surface. I call these teeth shovel-shaped. The condition is seen with

special clearness before the teeth have suffered any wear. I have called attention to this feature in a number of my publications. It is due to an extraordinary development of the lateral borders of the ventral surface of the crown. Sometimes these borders are so developed that they appear as if folded over the sides of the buccal surface of the tooth. They converge upwards, and at the points of convergence there is often seen a more or less rudimentary cusp. At the same time the dorsal surface of the crown is frequently more convex from above downwards than in the whites. This form of an incisor is found only seldom in the white, and, on the other hand, is but very seldom wanting in the Indian. Generally all the four upper incisors will be thus marked, but occasionally the condition is limited to the median incisors.

"Other racial differences in the teeth concern the cusps, roots, etc. They have in part been already mentioned in other connections. The white man shows more often a reduction in number of the cusps on the second and third molar than the negro and some other of the primitive races, and more frequently congenital absences of teeth, especially of the third molar. The root and crown of the third molar, and also the roots of the other teeth, are often more reduced in the whites. Finally, irregularities in position and the occurrence of decay are also most common in the white man.

"As to racial differences in dentition, i.e., the eruption of the teeth, our knowledge is as yet very defective. However, the white and the Indian have been investigated in this respect. I shall read a few lines based on my own studies of a large series of pure Indian children free from mixture, and you will see how insignificant, with perhaps one exception, the differences in the process of the eruption of the teeth are between the Whites and the Indians, two branches of humanity that are so far separated, or seem to be.

"The conditions found as a result of the investigation of 960 Apache and Pima children were as follows: All the teeth of the *first dentition* appear in the same order in the Indian children as in the white. As to time, the temporary incisors erupt on the average at about the same age in the two races; the appearance of the first temporary molars and the canines seems to be somewhat belated in the Indian; the eruption of the posterior temporary molars and the completion of the first dentition are accomplished earlier in the Indian than in the Caucasian.

"As to the permanent teeth, the incisors and bicuspids appear at nearly the same period of growth, as indicated by the height of the body in both races; the canines erupt possibly a little earlier in the Indians; the second molars appear decidedly earlier in the Indians than in whites; and the appearance of the last molars is also probably on the average somewhat earlier than in whites. The earlier eruption of the second and also the third permanent molars, with probably that of the permanent canine, are, in the speaker's opinion, signs of a somewhat less advanced evolution, as explained before, of the teeth in the Indian than of those in the white people.

"Exactly what the conditions regarding dentition may be in other primitive races we do not know, but there are signs that they are in the main as in the Indian. The lack of pronounced racial differences in teeth or dentition indicates strongly a unity of origin of mankind."

Concerning the "shovel-shaped" incisors, Hrdlička (1920) has recently published the results of his intensive and widely extended observations. He found these characters to be frequently present in members of the yellow-brown races, less frequently among negroes and very rarely among whites.

The racial characters of the labial surface of the incisors have been investigated by Azoulay and Regnault (1893) and by Leon Williams (1914). The first two authors measured the difference between the length of the lower border of the central upper incisor and the length of a wire placed parallel to its upper border. They give the following table:

| RACES | NUMBER OF SPECIMENS | DIFFERENCE |
|---|---|---|
| Apes (chimpanzees and gorillas, male and female) | 5 | 3.04 |
| Various negroes | 41 | 2.39 |
| New Caledonians, and New Hebrides | 13 | 2.19 |
| Australians | 10 | 2.00 |
| Polynesians | 14 | 2.01 |
| Annamese and Chinese | 13 | 1.78 |
| Europeans | 18 | 1.61 |
| Hindoos, Bengalis | 7 | 1.27 |

From this they conclude that the inferior races (negroes, Papuans) have incisors which approach those of apes (in being wide at the bottom and narrow at the top.) The "yellows," the Europeans and the Hindus, on the contrary, have teeth with parallel borders.

Leon Williams (1914), on the contrary, although expecting to find racial differences in the form of the incisors, found his three types A, B, C, in all the races of men and of anthropoid apes. However it seems possible that if the subject could be studied statistically one or the other type would be found more prevalent in the lower types of dentures.

One of the most conspicuous of dental racial characters is seen in the second upper molar of the Eskimo. Cope (1888) and Wortman observed that in these people the second upper molar loses its hypocone, and the remaining lingual cusp (protocone) becomes narrower, so that the tooth assumes a pseudo-tritubercular appearance.

As an aid to the study of racial differences in the dentition I have complied the appended conspectus of the species and chief races of the Hominidæ, after a critical study of the best modern authorities, especially Deniker (1915) and Haddon. But on account of the almost unlimited migration, mixture and local differentiation of races, it is extremely difficult in many cases to recognize the component elements of races, to distinguish convergent and independent resemblances from genuine marks of kinship, and finally to express the relationships in a linear system of classification. In spite of these difficulties the study of racial characters of the dentition and dental arches may yet assist in the solution of such questions as the following:

(1) Is the Caucasian race a natural group, or have the Mediterraneans, the Nordics, Alpines, etc., independently acquired pale skins? So far as the dentition indicates they seem to be closely related, all having "high" types of incisors, premolars and molars.

(2) Are the Mongolians and Alpines divergent derivatives of a single stock or do they merely parallel each other in certain characters?

(3) Were the neanderthaloids an entirely distinct race, or did some neanderthaloids somewhere give rise to *Homo sapiens?*

An understanding of the relationships of races and a correct evaluation of the racial characters of the dentition may be facilitated if we distinguish carefully between low or primitive and high or specialized characters. In general "low" characters include the following: The skin is dark, often very dark; it is uncertain whether the curly or the woolly form of hair is most primitive; the forehead is low, retreating, supraciliary ridges prominent, extending across the eyes, nose deeply notched at base, low and very wide below; face short, lower lip probably thick, but not excessively everted, upper lip thin; eyes small, deeply sunk, orbits with angulate corners; cheek bones moderately high; skull dolichocephalic, with prominent parietal eminences; an edge-to-edge bite, crowns of incisors nearly vertical but roots of incisors directed backward; incisors often with rim-and-hollow; prognathous; palate Ω-shaped; chin not prominent; jaw massive, with wide ascending ramus; dentition macrodont, molar cusp formula $\frac{4-4-4}{5-5-5}$; $m^3$ and $m_3$ erupting relatively early and of large size; Carabelli's cusp frequently present on $m^1$, $m^2$; upper molars ($m^1$, $m^2$) of rhomboid form; *Dryopithecus* molar patterns more or less retained in lower molars; traces of *Dryopithecus* premolar patterns in the bicuspids.

"High" characters, on the contrary, include the following: The skin is light; hair straight or wavy; forehead steep, broad, no supraciliary ridges; face "long," nose long, delicate, narrow; lips not much everted; eyes large, orbits with rounded corners; cheek bones not high, skull brachycephalic or secondarily (?) dolichocephalic. Overbite of upper incisors; rim-and-hollow form of incisors rare; orthognathous; palate paraboloid to hyperboloid; chin prominent; jaw delicate; dentition microdont, molar cusp formula $\frac{4-3-3}{4-4-4}$; $m^3$ and $m_3$ erupting very late, often suppressed; Carabelli cusp not common; second upper molars with rounded three-cusped crown; lower molars with +-shaped pattern; bicuspid patterns of conventional type.

## III. CONSPECTUS OF THE SPECIES AND CHIEF RACES OF THE HOMINIDAE

### Pithecanthropus

*Pithecanthropus erectus.* ? Lower Pleistocene, Java. Skull-top almost gibbon-like; referred $m^2$, $m^3$ very large, with divergent roots. Femur man-like, indicating erect gait. (See Part IV, p. 358.) Probably standing near the base of the human stem. (See p. 517, below.)

### Palæanthropus

*Homo* (*Palæanthropus*) *heidelbergensis.* Middle Pleistocene, Germany. Mandible of great size, with no bony chin; ascending ramus very wide. Dentition distinctly human, allied to Neanderthal type. (See pp. 427–441.)

Extremely ancient and primitive. Probably ancestral to the Neanderthal race and at least near to the ancestors of the higher races.

*Homo (Palæanthropus) neanderthalensis.* Uppermost Pleistocene (Mousterian) of Europe. Skull very large, with very low retreating forehead and great supraorbital tori; skull wide posteriorly. Jaw stout, with retreating chin, dentition "taurodont." Palatal arch horse-shoe-shaped, wide. Stature short. (See pp. 442–458.)

The extreme taurodont condition of certain Neandethaloids is regarded as a specialization which carries this species off the line leading to higher races; but the condition was much less pronounced in certain specimens and the crowns of all the teeth in the Mousterian youth (see p. 444) are extremely primitive, retaining many simian features that are lost in later races.

### Eoanthropus (?Homo)

*Homo (Eoanthropus) dawsoni.* Pleistocene, or possibly Upper Pliocene, Piltdown, England. Skull very large, with forehead steep and very little if any projection of infraorbital tori. Cranial walls extremely thick. Temporal region and other parts resembling Aurignacian skull (Ramström). If lower jaw be correctly associated, it and the dentition were extraordinarily chimpanzee-like. (See Part IV, p. 350.)

Relationship of skull with *Homo* turns largely on the moot question of association of the mandible with the skull.

### Homo sapiens

#### A. CRÔ-MAGNONS AND OTHER DOLICHOCEPHALIC UPPER PALÆOLITHIC RACES

(1) *Homo sapiens Galley Hill.* England. Skull very dolicho. Jaw with well-formed chin. Lower molars very slightly taurodont. Lower molar cusp-formula: 5, 5, 5; transverse diameter of $m_2$ slightly less than antero-posterior diameter, a primitive character (Keith, 1913).

(2) *Homo sapiens Brünn-Prĕdmost.* Upper Palæolithic (Post-Glacial), Moravia. Skull dolicho., forehead retreating, supraorbital tori prominent. Chin prominent. Orbits broad, low. First lower molar with five cusps and *Dryopithecus*-pattern. Second lower molar with reduced hypoconulid and incipient +-pattern (cf. Adloff, 1908, plate IX, *figs. 53, 54*).

A primitive race which may be allied with the Galley Hill type. (See Osborn, 1915, p. 336.)

(3) *Homo sapiens Crô-Magnonensis (aurignacensis).* Late Palæolithic (Aurignacian), Italy, France. Skull of high type, with reduced supraorbital tori. Dolicho., but with very broad, short, face and projecting cheek bones. Space between the eyes small, orbits wide, nose narrow,

aquiline. Jaw with complete chin. Palate narrow. Dental arches and dentition of relatively high type (Combe-Capelle skull). Stature very tall (Crô-Magnon) or very short (Obercassel).

The Crô-Magnon race is generally supposed to have become extinct or to have left but few traces in the modern populations of Europe, which for the most part are descended from the Neolithic and later invaders from Asia. The extinct race from Obercassel, in Bonn, differed from the Crô-Magnons chiefly in their very short stature.

### B. NEGROIDS

(4) *Homo sapiens Grimaldiensis.* Upper Palæolithic, France. Skulls negroid, dolicho., but regarded by Keith as allied with Crô-Magnon. Dentition macrodont, of very low type. Upper dental arch narrow; prognathism marked. (*Figs. 331, 334.*) Probably an intrusive element in Europe (M. Grant).

(5) *Homo sapiens Boskop* (*H. capensis Broom*). Age and relationships uncertain. Boskop, South Africa. Compared with Crô-Magnon and Bantu skulls by Haughton.

(6) *Homo sapiens Bushman.* Bushmen, Hoi-koi, Hottentots (in part). Hair woolly ("peppercorn"). Skin yellowish. Skull dolicho., forehead steep. Nose very broad, cheek bones high. Orthognathous. Dentition (*fig. 265G*) occasionally with primitive features; lower molar crowns with wrinkled surface (cf. Adloff, 1908, plate V, *fig. 25*). Stature very short; steatopygous.

An ancient but specialized offshoot of the negroid stock; possibly represented in the Upper Palæolithic of France by ivory figurines of steatopygous women. The pictorial art of the Bushmen presents many curious points of resemblance to that of the Crô-Magnons (cf. Sollas, "Ancient Hunters").

(7) *Homo sapiens niger.* Sub-races: (a) Negrito, (b) Negro, (c) Melanesian. Hair woolly. Skin brownish or reddish-black to black. Skull usually dolicho., sometimes brachycephalic (Andamanese). Forehead often "bombed" in negroes. Nose broad. Prognathous. Lips often everted. Dentition macrodont (*figs. 283H, 265F*), especially in Melanesians, to microdont; primitive to specialized. Palatal arch Ω-shaped (many Melanesians) to Λ-shaped. Stature: short (Negrito), tall (some negroes), medium (Melanesians). Melanesians probably more primitive than negroes.

(8) *Homo sapiens tasmanianus.* Tasmanians (extinct). Hairy frizzy or woolly, skin chocolate-brown, skull subdolicho.; face broad, nose very broad and flat; prognathous; palatal arch sometimes Ω-shaped (*fig. 314*).

Differ from Australians and resemble Melanesians chiefly in their frizzy hair (*fig. 302*).

(9) *Homo sapiens australianus.* (a) Talgai (*figs. 337–338*), Queensland (?Pleistocene); (b) recent Australians (*figs. 308, 339*). (a) Skull of extremely low type, with very large palate and teeth, and marked prognathism. (b) Hair wavy or curly, beard abundant, skin chocolate-brown, skull dolicho., with prominent supraorbital tori; nose broad; prognathous. Dentition often macrodont and of low type. Palatal arch variable, often Ω-shaped. Molar-cusp formula often of "low" type $\left(\frac{4\text{–}4\text{–}3\frac{1}{2}}{5\text{–}5\text{–}5}\right)$. Stature moderate. Limbs slender.

The Australians are regarded by Deniker and Haddon as a "Pre-Dravidian" race, driven southward from southeastern India.

### C. MELANOIDS OR MEDITERRANOIDS

(10) *Homo sapiens veddalis.* Veddas of Ceylon. Hair long, black, coarse, wavy or curly. Skin dark brown. Skull very dolicho. Face broad, orthognathous. Nose broad, depressed at root.

A very primitive race, possibly allied with the Dravidians.

(11) *Homo sapiens dravidicus.* Short, dark peoples of the Deccan. "Melano-Indians." Hair curly or wavy. Skin brownish black. Skull dolicho. Stature short. Deniker divides this group into two sub-races, as follows:

Sub-race a, platyrrhine: Nose broad, flat, face rounded.

Sub-race b, leptorrhine: Nose narrow, prominent, face elongate.

The Melano-Indians[11] are on the whole a primitive group. The platyrrhine, flat-faced, division affords a structural intermediate between the Australians below and the Indonesians above. The leptorrhine, long-faced, division, especially in the case of the Todas, show structural affinities on the one hand with the Ainus and on the other with the Indo-Afghans.

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[11] There are a dozen or more "Hindoo" skulls (*fig. 340*) from southern India, in the American Museum of Natural History, which probably represent the dental characters of the Melano-Indians, possibly more or less mixed with other strains. The skull is dolicho- or mesocephalic. The palatal arch is more or less Λ-shaped or convergent in front; palate vaulted; the central incisors, often long-crowned, have the lingual face either flat or with one or more low vertical ridges, a few of them have the rim-and-hollow formation, but not in extreme form. The upper canines in males are rather large, with conical crowns. The molar-cusp formula varies from $\frac{4\text{–}4\text{–}4}{5\text{–}5\text{–}5}$ to $\frac{4\text{–}3\text{–}4}{4\text{–}4\text{–}4}$. Here then we have a mingling of "low" and "high" characters, in harmony with the supposed position of the Melano-Indians near the point of divergence of the Mediterranean and Indo-Afghan groups.

Fig. 333

Fig. 332

Fig. 331

Figs. 331-333, inclusive. Palatal Arch and Upper Teeth of Grimaldi, New Britain and Modern French Skulls. Modified from Verneau; After Gaudry

**FIG. 336**

**FIG. 335**

**FIG. 334**

FIGS. 334–336, INCLUSIVE. LOWER DENTAL ARCH AND TEETH OF SAME SERIES AS IN FIGS. 330–333. MODIFIED FROM VERNEAU; AFTER GAUDRY

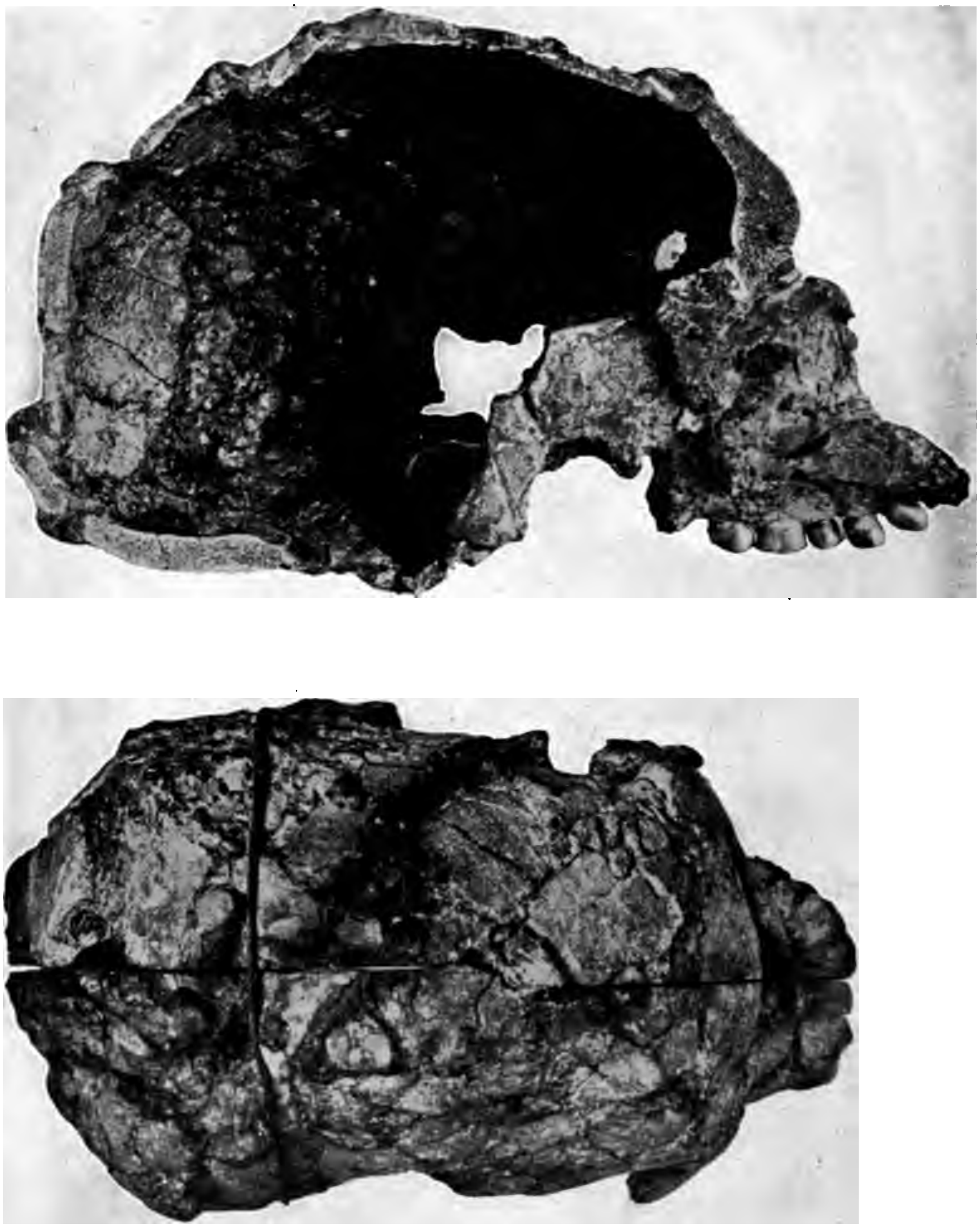


FIG. 337. FOSSIL SKULL FROM TALGAI, QUEENSLAND, AUSTRALIA
Courtesy of S. A. Smith. Normal verticalis, and sagittal section of crushed skull

(12) *Homo sapiens indo-afghanus.* According to Deniker this race predominates in the northwest of India and includes Siks, Rajputs, some Hindus, Punjabi, Todas (in part); also among the Afghans. Hair wavy or straight, complexion light brown or tanned. Skull dolicho.; nose thin, prominent; stature high.

The Indo-Afghan race may have derived some of its "high" characters (tall stature, narrow nose, light color) by mixture with "Aryan" invaders, related to the Nordics. (Cf. Haddon, pp. 58, 59, 49; M. Grant, 1921.)

FIG. 338. PALATE OF TALGAI SKULL. × 1. AFTER S. A. SMITH

Deniker (1915, p. 289), in his "grouping of the human races according to their affinities," places the Indo-Afghan race next to the Arab-Berber group, which they resemble in many characters.

(13) *Homo sapiens ethiopicus.* Ethiopians (Kushito-Hamites) of northeast Africa, including ancient and modern Egyptians (in part), Beja, Galla, Somali, etc. Hair curly or frizzy. Skin reddish brown to chocolate-colored. Skull dolicho. Nose prominent, often long and narrow; face elongate, oval, not prognathous. Stature moderate to high. (Deniker, p. 438.)

The Ethiopians, although often having frizzy hair and very dark skins, differ from the negroid group in their "high" characters.

(14) *Homo sapiens mediterraneus.* "Mediterranean" group in part. Hair wavy, black; skin tawny-white (melanochroic), eyes dark. Skull usually dolicho.; nose narrow. Deniker divides this group as follows:

FIG. 339. SKULL OF AUSTRALIAN FEMALE

American Museum of Natural History, no. 3,280

Sub-race: *mediterraneus berber.* Berbers (Hamites) of northern Africa. Although there is a very great variety of types in this sub-race, Denike. (p. 432) gives the following as a "quite general characterization:" Nose straight or concave rather than aquiline; a transverse depression on the forehead above the glabella; face almost quadrangular. Skull, generally speaking, not so long as that of the Arab; occiput not so prominent; stature scarcely above the average. Often more or less "Arabised" in language and usages.

FIG. 340. SKULL AND MANDIBLE OF "HINDOO" FROM SOUTHERN INDIA
American Museum of Natural History, no. $\frac{99}{7772}$

FIG. 341. SKULL AND MANDIBLE OF "BEDOUIN, FEMALE" FROM SYRIA
American Museum of Natural History, no. $\frac{99}{7725}$

Sub-race b: *mediterraneus arabicus.* Arabs or Semites of Arabia, Mesopotamia, North Africa, etc. Nose aquiline, face elongate, oval. Skull typically dolicho., with prominent occiput. Stature tall, slim.

The true Bedouins of Arabia are more or less mixed with Assyroids, Turcoids, etc. (Deniker, p. 423). The skull shown in *fig. 341,* labelled "Bedouin, Syria," may not be a pure Arab type. It shows a thoroughly modernized dentition.

Sub-race c: *mediterraneus littoralis.* "Littoral or Atlanto-Mediterranean," Deniker. Mediterranean shore of northern Italy, southern France, Spain. Nose straight, fine; face oval, skull mesocephalic. Stature above the average (1 m. 66). Eyes and hair very dark. Status somewhat doubtful. May be a result of averaging dark, broad heads of the "Old Black Breed" type, with true Mediterraneans (Fleure and James, quoted by Madison Grant, 1921).

Sub-race d: *mediterraneus Ibero-insularis* (Deniker). Most Portuguese, Spanish, South Italians, Sicilians, Corsicans, "and the dolicho. . . . . neolithic inhabitants of Western Europe and the British Islands" (Haddon). Nose straight or turned up. Skull dolicho. Stature short. This sub-race differs widely from the other sub-races of this group, possibly as a result of crossing with Nordics and Alpines. It may be of Asiatic rather than North African origin.

The Mediterranean group may also be represented by some of the Upper Palæolithic skulls of Ofnet, on the Danube, northwest of Munich. Skull very dolicho., with narrow forehead and broad interparietal region. Face narrow. (Osborn, 1915, p. 480.)

### D. AINU

(15) *Homo sapiens ainu.* Ainu of northern Japan. Hair wavy, very abundant as beard and on body. Skin light brown. Skull dolicho- or mesocephalic; supraorbital ridges prominent; face broad, orthognathus, with high cheek bones; os japonicum often present. Eyes large, horizontal; Mongolian fold usually absent. Nose concave, broad; stature short, thickset.

A race of uncertain relationships, resembling the Todas in their excessive hairiness, but certainly with a Mongoloid strain. Possibly related to the Proto-Nordics (M. Grant).

### E. XANTHOIDS

(16) *Homo sapiens nordicus.* (*H. sapiens europæus* Linnæus.) The Nordic race, now centering in Sweden. Hair wavy, yellow, brown or red-

dish; eyes blue or grey; complexion reddish white; skull dolicho. Face elongate, nose prominent, straight. Orgnathous. Dentition "modern." Stature tall.

Sergi derived the Nordics from the "Eurafrican' or Mediterranean group of longheads, but Madison Grant (1915, pp. 170, 213) concludes that the Nordics "developed in eastern Germany, Poland and Russia, together with the grasslands which stretched from the Ukraine eastward into the steppes south of the Ural." Von Luschan (1911) also regards some of the Kurds and other longheaded peoples of western Asia, which have narrow nose and light eyes, as the descendants of primitive Nordics. In early times Nordics (Sacæ, etc.) penetrated far to the east, entering India and possible even reaching China (cf. M. Grant, 1915). Some of the Galtchas of East Turkestan described by Ujfalvy (1887) present a remarkable mixture of apparent Nordic, Alpine and perhaps Indo-Afghan characters. They speak very primitive Aryan languages. Their "Nordic" characters (e.g., occasional blondness and blue eyes) may be due to ancient crossing with eastern offshoots of the Nordics. On the other hand, "the Galtcha skull measured by Topinard was said to present not only simple resemblances, but even an identity almost complete with the best characterized skulls of Savoyards (Alpine type)." (Topinard, quoted by Keane.) According to Keane (1900, pp. 553-556) the Galtchic-speaking tribes of the Hindu Kush, Kafirstan, Upper Indus, etc., include one group of brachycephalic Alpine type and another of the long-headed, blond Aryan type.

The more remote origin of the Nordics and their phyletic relationships with the Mediterraneans and the Alpines remain to be demonstrated.

The problem of the origin of the Nordics is bound up with the following questions, the solution of which may perhaps be approached not only through studies on the modern dentitions and skulls, but especially through a study of past migrations and racial contacts:

(a) In general is the "Caucasian race" a natural group, or have Nordics, Alpines, and Mediterraneans been derived from quite different stocks by convergence toward a "Caucasian" type?

(b) More in detail, are the Nordics more nearly allied with the Alpines, and is their dolichocephaly thus due to a secondary elongation of a hypsi-brachycephalic skull?

(c) Or are the Nordics derived from some relatively primitive dolichocephalic type such as von Luschan's Kurds, proto-Ainus, Tajiks, Galchas?

(d) Are the Mediterraneans of Europe derived from North Africa or from Asia?

(e) Are the Alpines, and with them the Armenians, derived from a primitive Central Asiatic Turco-Tartar-like group, and

(f) Are the latter related to the Ugrians and other Mongolians?

(g) Or are the Alpines derived from some ancient Galtcha-like race near to the stem of Nordics and Mediterraneans?

### F. ALPINOIDS

(17) *Homo sapiens assyroideus.* Represented on the Assyrian monuments. Now much mixed with other races, but its traits seen among Hadjemi-Persians, Ayssores, some Armenians and some Jews. Hair wavy, or curly, skin tawny-white, skull brachycephalic. Nose in the form of a figure 6, thick at top, eyebrows united, lower lip thick. Possibly related to Indo-Afghan type (Deniker). Arabized Hittites (M. Grant).

(18) *Homo sapiens armenianus.* Hittites. Represented on the Hittite monuments. Now much mixed with other races, especially Armenians, Arabs, Turks, Greeks (von Luschan, 1911). Skull excessively high (hypicephalic), with flattened occiput (planoccipital); nose typically of great size, long, narrow and protruding far in front of chin. Skin tawny-white. Believed by von Luschan to have once been widely distributed in Western Asia and to be somehow connected with the origin of the "Alpine" races of Europe.

(19) *Homo sapiens adriaticus* (Dinaric). Coast of Northern Adriatic; especially in Bosnia, Dalmatia, Croatia, Tyrol, central France, etc. Skin dull white; hair brown. Skull very brachycephalic; face elongate. Stature tall. Deniker. (Probably related to no. 18 above.)

(20) *Homo sapiens alpinus* (Cevenole). "Western European." Abundant in southern Germany, Russia, the Balkans, central and northern Italy, central France. Skin dull white, hair dark brown, eyes hazel gray. Skull very brachycephalic, face round, nose often sharp. Stature short; palate often wide; dentition of "modern" type, not differing greatly from Nordic type.

Much mixed with Nordics in Germany, France, Belgium, Russia; with the Mediterraneans, in southern Italy and elsewhere. The "Eastern European" of Deniker has the round head of the Alpines combined with the fair skin, light yellow hair and blue or gray eyes of the Nordics and is often regarded as a cross between these two. In northern Russia and elsewhere the Eastern European is again crossed with Ugrians, Lapps, Turco-Tartars and other races of more recent Asiatic origin. Possibly the Furfooz-Grenelle race of the Late Palæolithic of Belgium and France may represent an early immigration of Alpines from Asia (Osborn). The Beaker-maker type of tall round heads, found in some of the Neolithic "round barrows" of England, and the Borreby type of Denmark, which have strong supraciliary ridges, may be allied to the Dinaric or Adriatic type (Madison Grant).

## [illegible]

I. Homo sapiens [illegible]. Turkish race. Eastern Europe and central Asia. Best preserved in the "Turks of the Central group" (Deniker, p. 377), comprising among others the Kirghiz-Kazak of the plains between the [illegible] and the [illegible], the Kara-Kirghiz of the Tianchan mountains, the Uzbegs and Sartes of Russian Turkestan, and the Tatars of the Volga and the Astrakhan Turks.

Hair straight [illegible], moderately developed. Skin yellowish-white; skull extremely brachycephalic; face elongated, oval; eyes not Mongoloid oblique, but [illegible] with the [illegible] [illegible]. Cheek bones broad, lips thick. Nose straight, somewhat prominent; eyes not Mongolian. Stature above the average. A tendency to obesity.

In the eastern group profoundly modified by intermixtures with the Mongolian, Tungus, and Ugrian races, in the central group by crossing with Assyroid, Armenoid, Indo-Afghan, Arab and certain European races, chiefly Adriatic (Deniker). The Osmanli Turks of Asia Minor and Turkey are mixed with Armenoids and other races (von Luschan). The characters of the existing Turkish race are widely different from those of the typical Mongoloids, and suggest relationship with the Armenoid race, as well as with the Ugrian group of Mongoloids.

II. *Homo sapiens mongolianus.* Hair straight, skin pale yellowish, body smooth. Skull mostly brachycephalic. Face broad, typically orthognathous, with projecting cheek bones. Eyes usually oblique, with Mongoloid fold. Nose usually short, often concave. Upper incisors usually shovel-shaped. Palate wide. Stature mostly low. The following subdivision into sub-races is modified from Haddon and Deniker:

Sub-race a: *mongolianus ugrianus.* Ugro-Finns, Yeniseans, Eastern Finns (in part). Peoples of western Siberia, especially Ostyaks, Tubas, Voguls, Samoyads; Votyaks and Cheremiss of Russia. Extensively mixed with other races and represented in the Finns, Esthonians, Livonians, Bulgars, Magyars, etc. Hair straight, skin yellowish white. Skull "meso- or dolichocephalic" (Deniker), "brachycephalic" (Haddon). Nose straight or concave, cheek bones projecting. Stature short.

Sub-race b: *mongolianus lapponicus.* Lapps of northern Scandinavia. Skin yellowish-white; hair straight, dark brown. Skull extremely brachycephalic. Face very broad, cheek bones prominent, orthognathous. Stature very short. Closely allied with the Ugrian race.

Sub-race c: *mongolianus palaeasiaticus.* East Siberians: Yukaghirs, Chukchis, Gilyaks (in part), etc. Hair long and lank, beard sparse. Color yellowish brown. Eyes oblique. Skull often meso-cephalic. Stature low.

Sub-race d: *mongoloideus Tungus-Manchu.* Skull meso- or slightly dolichocephalic, face rather elongated. Stature taller.

Sub-race e: *mongoloideus Koreanus.* Eyes with Mongoloid fold; beard long, thin. Skull brachycephalic; face long, narrow, often prognathous; nose narrow, aquiline. A modification of the Tungus type (Haddon, p. 17).

Sub-race f: *mongoloideus mongol.* Mongols proper.

(a) Western Mongols: Kalmuks of Astrakhan and the Caucasus.

(b) Eastern Mongols: Of Mongolia (Khalkhas; Buriat, in part).

Hair straight, black; skin pale yellowish or brownish; hair scant on body and face. Skull sub-brachycephalic. Cheek bones prominent; nose thin, straight; eyes Mongoloid.

Sub-race g: *mongoloideus australis.* Southern Mongols. "Most of the peoples of this group are considerably mixed with other races; they comprise the Tibetans, Himalayans, Chinese proper, and the bulk of the populations of further India and Indo-China. Those members who spread into the East Indian Archipelago are often called Oceanic Mongols, but a little better term is Proto-Malays; and it is from these the true Malay is derived." (Haddon, p. 18.)

Hair black and lank, with little hair on the face; skin color varies from yellowish on the north to olive and coppery brown on the south. Skull brachycephalic, often prognathous; nose short and broad; eyes often very oblique, with Mongolian fold. Stature generally short, often thick-set (Haddon).

(23) *Homo sapiens eskimo.* Labrador Eskimo, Greenland Eskimo, Aleuts (in part). Hair straight, skin brownish-yellow. Skull dolicho.; skull-top "scaphoid," with a compressed vault. Face round and flat, with projecting cheek bones. Eyes straight and black. Palate typically wide. Second upper molars relatively small, with only three cusps, the hypocone being lost. Lower jaw large. Stature short.

The Eskimo are often thought to be allied with the American Indians, but the connection is not clear; and they are regarded by Hrdlička (1911, p. 7) as a branch of the yellow or "Mongolic" race. They exhibit some characteristics of the Ugrian sub-race (short stature, dolichocephaly, shape of the eyes, etc.). (Deniker, p. 521.)

### H. AMERINDS

(24) *Homo sapiens amerind.* American Indians. Hair typically straight, skin yellowish, brownish-yellow or brown. Skull often brachycephalic, but sometimes dolicho. Face has typically high, projecting cheek bones.

FIG. 342. SKULL AND MANDIBLE OF ESKIMO, FEMALE
American Museum of Natural History, no. $\frac{99}{166}$

FIG. 343. SKULL OF INDIAN FROM ILLINOIS
American Museum of Natural History, no. $\frac{99}{3651}$

Nose usually straight or aquiline. Eyes black. Palate often broad. Upper incisors shovel-shaped. Molars, often large, $m_1$ often with *Dryopithecus*-pattern (see Part IV, p. 378). Stature short, intermediate, sometimes tall.

Haddon, largely following Deniker, gives the following classification:

Sub-race a: *Palæo-Amerinds.* Botocudos and other South American tribes. Hair wavy or curly. Body smooth. Skull dolicho- or mesocephalic. Nose prominent, straight or concave. Stature short.

Sub-race b: *Patagonians.* Hair straight; nose straight. Skull brachycephalic; face square. Stature very tall.

Sub-race c: *Southern Amerinds.* Hair straight, skin yellow, body smooth, nose straight or concave, stature short. Skull meso- or brachycephalic.

Sub-race d: *Central Amerinds.* Central American tribes. Hair straight; skin brownish-yellow or brown. Skull brachycephalic; nose straight or aquiline. Stature short.

Sub-race e: *Northwestern Amerinds* of the Pacific slope. Hair straight, skin warm yellow. Skull brachycephalic; face usually rounded. Stature intermediate.

Sub-race f: *Northern Amerinds* of the Atlantic slope. Hair straight; skin warm yellow. Skull mesocephalic; face oval; nose straight or aquiline. Stature tall.

It is usually supposed that the Indians reached North America from the north; but some hold that the small yellow-skinned tribes of South America are connected wtih the Indonesians. The western spreading of the Indonesians and Polynesians, however, may be comparatively recent, while the Indian race has inhabited both North and South America for a very long period, probably since late glacial times. The extremely primitive character of many Indian molars and premolars suggests that the race has been derived from some very low group preceding the Crô-Magnons and allied to the stem of the Mongoloids.

### I. OCEANIANS

(25) *Homo sapiens indonesianus.* Certain Indonesian tribes of Borneo, of the East Indian Archipelago and of the Philippines. Hair wavy, black; skin tawny, often light; body smooth; nose flat, sometimes concave; cheek bones often projecting. Skull dolicho. to brachycephalic.

More or less mixed with Proto-Malays, Hindus, Papuans, Melanesians, Polynesians, etc. Possibly derived from Dravidians, some of which approach the Indonesians in certain characters.

(26) *Homo sapiens polynesianus.* Hawaii to New Zealand. Hair wavy, long; skin yellowish; body smooth; skull brachy- or mesocephalic; nose prominent; face long, "elliptical." Stature tall.

"The Polynesians are a mixed people. Their original home was perhaps somewhere in Eastern India, whence shortly before our era, they migrated to the East Indian Archipelago, where we may speak of them as Indonesians. The Proto-Malays were about this time pressing down south from the mainland of Asia, and eventually a mixed population seems to have gone further east. . . . . ." (Haddon, p. 21.) The latter spread into the islands of the Pacific.

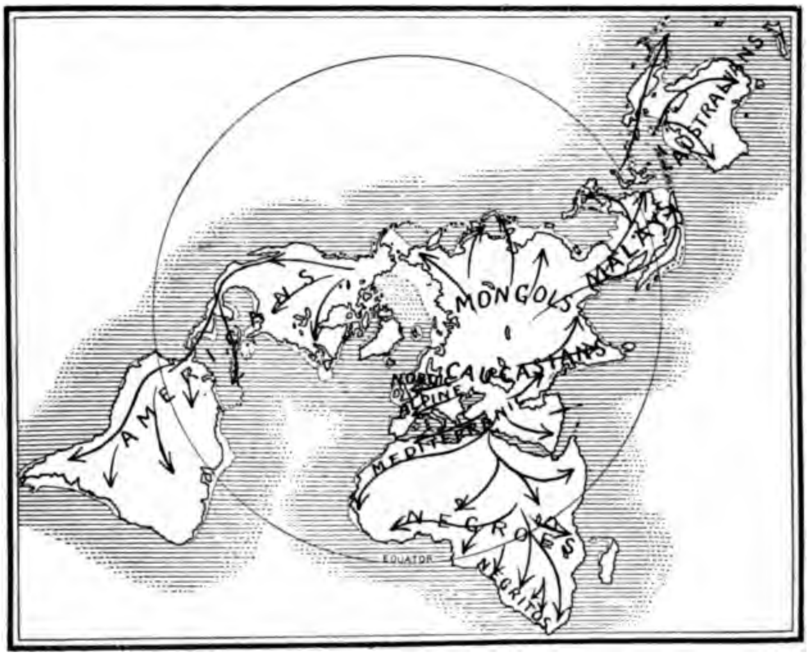


FIG. 344. DISPERSAL OF THE RACES OF MAN. AFTER MATTHEW

## IV. SUMMARY AND CONCLUSIONS FOR PART V

Darwin's conclusion was that "some ancient member of the anthropomorphous sub-group (of the Old World, or catarrhine series) gave birth to man." If this is incorrect then much of Parts IV and V of the present review is practically worthless, since all resemblances of the dentition between anthropoid apes would be based not on genetic kinship but on convergence, and the course of the supposed evolution of the dentition, as traced in this review, would be illusory rather than real.

It is illusory and unreal if Wood Jones instead of Darwin is right. Wood Jones (1918) holds that the existing *Tarsius* is the only living survivor, now highly specialized in certain features, of the very remote primate stock that gave rise to man; he approves Klaatsch's view that the monkeys and apes are best regarded as degenerate branches of the pro-human stock; he considers the apes more specialized than man, and suggests that many of the resemblances of apes to man are due to parallelism or convergence; he proclaims the "basal mammalian primitiveness" of the human skull and skeleton as well as many other human characters; finally he insists that palæontologists should acquaint themselves with the profound differences between human and anthropoid anatomy because these differences in his opinion far outweigh the resemblances in the bones and in the teeth; and he intimates that the skeletal parts are the only ones to which palæontologists have given due consideration.

The corner stone of Wood Jones' entire theory is the "basal mammalian primitiveness" of the human skull and skeleton. But as I have shown elsewhere (1920, *Pl. XXVII*), this assumption is flatly contradicted by the evidence of palæontology, taxonomy and comparative anatomy.

If we lay out on a long table a series of humeri, placing at the left those of various Paleocene and Eocene mammals, next the humeri of Eocene primates and at the right those of existing lemurs, platyrrhines, catarrhines, anthropoids, *Dryopithecus* and man in the order named, we shall see that the most primitive primate humeri, that is those most like the humeri of other Paleocene and Eocene mammals (which are known and universally admitted to be primitive), are not the humeri of man and of the anthropoids but the humeri of Eocene primates. We shall also see that there is a gradual change in form from the humeri of Eocene primates, which are most like those of quadrupedal Eocene mammals, to the humeri of the chimpanzee and of man, the latter two belonging to upright sitting animals that have real hands.

The "basal mammalian simplicity of the human skull" is equally an erroneous concept. For real "basal mammalian simplicity," or rather basal primate simplicity (which is a very different thing, although Wood Jones confuses the two), we must look not to man but to the Eocene primates, such as *Notharctus* (Part II), the skull of which approaches that of other Eocene placental mammals in very many characters not found in man.

As to the "wide differences" between human and anthropoid anatomy the answer is: first, that however numerous and great these differences may be, they have doubtless been acquired during the vast time since the human branch separated from the gorilla-chimpanzee stock; and secondly, that these differences are far outweighed in importance by the still more numerous and profound resemblances.

The latter has been widely recognized as a fact by all those who have made or are still making the most solid contributions to our knowledge of the comparative anatomy of the anthropoids: such as Deniker in his classic memoir (1886) on the anatomy of a fœtal gorilla; Keith, who for the past thirty years has continued his comprehensive and illuminating studies of the subject; Retzius, who described the remarkably human characters of the spermatozoa of the gorilla; Tilney, who testifies to the fundamentally human construction of the gorilla brain-stem; and many others.

It is an easy answer to almost any question concerning human evolution that "we must await palæontological evidence" rather than admit that the main outline of human evolution is already plain to all who can read the available record. In the case of man the palæontological part of the record is admittedly incomplete, and taken by itself would prove little. But when, from comparative anatomical evidence, we recognize the closeness of the relationship between man and the gorilla-chimpanzee group, the palæontological record is seen to be entirely in harmony with my conclusion that man is a late Tertiary offshoot of the *Dryopithecus-Sivapithecus* group, or at least of apes that closely resembled these genera in the construction of the jaw and dentition.

Two principal objections to this conclusion will doubtless be made by many palæontologists. The first is that the human grade of organization was already attained as far back as the Middle or Lower Pleistocene and may at any time be expected to be found in the Pliocene, and that there is therefore not sufficient time to effect such a great transformation between the Pliocene and the Miocene. My answer to this is that it is a "fallacy of the undistributed middle," since it assumes that the rate of evolution for man is the same as that for horses and proboscideans, whereas the facts prove that *rates of evolution differ enormously in different phyla and at different times; that rates of evolution are as individual and specific as are the corresponding anatomical characters; that in the case of man all the evidence suggests that during late Tertiary times the rates of transformation were greatly accelerated, especially in the structure of the brain and of the feet.*

The second objection that will be raised against the conclusion cited above is that, with possibly two exceptions, all authors, from Darwin and Gaudry to Wood Jones, have recognized that *Dryopithecus* was already an ape and *therefore* that it cannot be in the human line. Smith Woodward (1914) on the other hand showed that, as regards the construction of the mandibular symphysis and the arrangement of the attachments for the tongue muscles, *Dryopithecus* appears to afford a starting point not only for the anthropoid but also for the human lines of specialization; while I, in earlier papers as well as in the present review, have shown that *Dryopithecus* as well as *Sivapithecus* give us an excellent starting point for the diverging specializations of the dentition of anthropoids and men. This can hardly be denied in so far as it applies to the upper and lower molars and premolars; but it will be objected that it is the presence of ape-like canines and ape-like lower premolars in *Dryopithecus* and *Sivapithecus* that rules them out of the line of human ascent. I on the other hand hold that the *conditions in which the tips of all the lower teeth are reduced to the same general level and the diastemata are closed up, is just as secondary in man as it is in Homalodotherium; that it is connected with the general reduction of the facial part of the skull and correlated with obvious changes in habits of feeding and of fighting; that there is no more "basal mammalian primitiveness" to be found in the human dentition than there is in the mandible or maxilla.*

The structural resemblances and differences between man and *Dryopithecus* with reference to characters of the jaws and dentition are summarised in *table 1*.

In respect of every one of these characters *Dryopithecus* is more primitive, more like other primates, than is typical man. And it should not be forgotten that the "Mousterian youth" and many Indian, Australian, Melanesean and other primitive dentitions retain intermediate or transitional features, which add their quota of evidence for the conclusion that the *Dryopithecus* group is structurally ancestral to man.

The wide differences between high human characters on the one hand and low, *Dryopithecus* characters on the other, are an expression of the difference in life habits between primitive apes and typical men. As Darwin and most anatomists have recognized, the direction of evolution rapidly changed and the old ape-like "heritage" was largely replaced by the new human "habitus." But many have forgotten the principle of "change of function;" they have in mind only the kind of predetermined and straightforward evolution that is illustrated in the palæontological history of the horses; they cite Dollo's "law of irreversibility of evolution" as a reason for doubting radical changes in the direction of human evolution, forgetting that great changes in function and in the direction of evolution were the very phenomena that Dollo used so brilliantly in formulating his law. Rightly perceiving that most groups are polyphyletic, many authors conceive those phyla as continuing backward indefinitely on parallel lines, so that the anthropologist Sergi has finally concluded that there never was any transformation, but that the various "types" of animals and plants were produced independently! Other authors, impressed by the great antiquity of many mammalian groups and by the extreme slowness of evolution in general, assume that the rate of evolution of man has been equally slow, so that they expect to find the human phylum already set off from other primates at a very early time, perhaps even in the Eocene.

Lartet, Gaudry, Dubois, Schlosser, Pilgrim, by their discoveries of fossil anthropoids, have prepared the way for the recognition of the truth of Darwin's conclusion that man was derived from "some ancient member of the anthropomorphous subgroup;" Schlosser (quoted

TABLE 1

*Contrasts between Dryopithecus and man in the lower jaw and teeth.*

| FEATURE | DRYOPITHECUS | MAN (TYPICAL) |
|---|---|---|
| Dental formula | $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{2}{2}\ M\frac{3}{3}$ | $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{2}{2}\ M\frac{3-2}{3-3}$ |
| Lower incisors | Slightly procumbent, not crowded | More erect, crowded, often more or less displaced |
| Diastema between lateral lower incisor and canine | Present | Closed |
| Diastema between lower canine and anterior premolar | Present | Closed |
| Crown of lateral lower incisors | Less expanded transversely, with remains of primitive tip | Expanded transversely and truncate at top |
| Lower canine | With pointed tip projecting considerably above level of premolars | With obtuse tip projecting but little above level of premolars |
| Axis of lower canine crown | Slightly inclined forward | Vertical |
| First lower bicuspid | Asymmetrical, with high tip and two roots | Symmetrical, with low tip and single root |
| Second lower bicuspid | Asymmetrical, with high tip, high trigonid and low talonid | Symmetrical, with low tip and reduced trigonid and talonid basins |
| First lower molar | Smaller than second lower molar, with five cusps and "*Dryopithecus*-pattern" | Longer than second molar, with five cusps and remnants of *Dryopithecus*-pattern |
| Second lower molar | With five cusps and *Dryopithecus*-pattern | With four cusps and + -shaped pattern |
| Third lower molar | The longest of the series, with five cusps and *Dryopithecus*-pattern | The shortest of the series, often with four cusps and modified *Dryopithecus*-pattern |
| Proportions of lower molars | Long and narrow | Short and broad |

TABLE 1—*Continued*

| FEATURE | DRYOPITHECUS | MAN (TYPICAL) |
|---|---|---|
| Intercondylar diameter | Relatively narrow | Very wide |
| Lower dental arch | With parallel sides | With converging sides |
| Space for tongue | Contracted, narrow | Expanded, wide |
| Symphysis | Relatively long and sloping | Very short and vertical |
| Bony chin | Retreating | Protruding |
| Ascending ramus | Very wide | Narrow |

by Branco, 1898, p. 126) even regarded man as a derivative of those Upper Miocene anthropoids which gave rise to the gorilla, *Dryopithecus*, chimpanzee and orang, a view that very nearly anticipates my own.

Those who do not realize the cumulative and convincing character of the anatomical evidence for the close relationship of man with the gorilla-chimpanzee stock, and who look for ancestral Hominidæ in the early Tertiary, would probably fail to recognize a real human precursor as such, if it were found in the late Tertiary. We already have—to go back no further—*Parapithecus*, *Propliopithecus*, *Dryopithecus*, *Sivapithecus*, *Pithecanthropus*, *Homo* (*Palæanthropus*) *heidelbergensis*, *H. neanderthalensis* and many grades of *H. sapiens*. But many do not perceive that this forms an admirable structural sequence; they insist, with Boule, on "more fossils and many more fossils." Adloff and others reject Darwin's conclusion that man is an offshoot from "some ancient member of the anthropomorphous subgroup," but they have no difficulty in believing in the impossible[13] "concrescence theory" as applied to the origin of the human dentition.

The remaining conclusions for Part V will be found in the italicized sentences and headings on pages 411–480 above. They are also expressed graphically in *figs. 311–317*, and *319–329*.

[13] My reasons for calling the concrescence theory "impossible" are given above, on pages 461–465.

T

*Twenty-six structural stages in the a*

| GEOLOGICAL AGE | STAGE NUMBER | STAGE | EXAMPLE, OR RELATED |
|---|---|---|---|
| Recent | 26 | "High" human type (microdont) | *Homo sapiens* |
| Upper Pleistocene | 25 | "Low" human type | (*Homo "mousteriens* |
| Middle Pleistocene | 24 | Heidelberg race | *Homo heidelbergensis* |
| Lower Pleistocene | | ? | |
| Pliocene | 23 | Human precursor | *Pithecanthropus* |
| Miocene | 22 | Advanced pre-human anthropoid | *Sivapithecus*<br>*Dryopithecus* |
| Oligocene | 21 | Primitive anthropoid | *Propliopithecus* |
| " | 20 | Supertarsioid | *Parapithecus* |
| Upper Eocene | 19 | Progressive tarsioid | (*Necrolemur*)[1] |
| Middle Eocene | 18 | Primitive pro-tarsioid | (*Omomys*)[1] |
| Lower Eocene | 17 | Primitive lemuroid | (*Pelycodus*)[1] |
| Paleocene | 16 | Insectivorous preprimate | (*Indrodon*)[1] |
| Cretaceous | 15 | Insectivorous preplacental | ? |
| Jurassic | 14 | Pre-trituberculate mammal | *Amphitherium* |
| Triassic | 13 | Protodont mammal | *Dromotherium* |
| " | 12 | Advanced mammal-like reptile | *Ictidopsis* |
| Upper Permian | 11 | Intermediate mammal-like reptile | (*Cynosuchus*)[1] |
| Middle Permian | 10 | Early mammal-like reptile | (*Moschops*)[1] |
| Lower Permian | 9 | Primitive pelycosaurian reptile | (*Mycterosaurus*)[1] |
| " | 8 | Progressive cotylosaurian reptile | (*Captorhinus*)[1] |
| Upper Carboniferous | 7 | Primitive cotylosaurian reptile | ? *Eosauravus* |
| Lower Carboniferous | 6 | Primitive amphibian | (*Loxomma*)[1] |
| Uppermost Devonian | 5 | Pro-tetrapod | *Thinopus* |
| Upper Devonian | 4 | Progressive crossopterygian fish | *Eusthenopteron* |
| Middle Devonian | 3 | Primitive crossopterygian fish | *Osteolepis* |
| ? | 2 | Primitive fish with[2] gill-arch jaws | ? |
| Upper Silurian | 1 | Primitive jawless fish | *Birkenia*[1] |

[1] Not in direct line but more or less related thereto.

[2] *Cladoselache* of the Upper Devonian is a late survivor of this grade (*fig. 2*).

*d in the evolution of the human dentition*

| E<br>AL | TAXONOMIC POSITION OF EXAMPLE | | | |
|---|---|---|---|---|
| | Class | Order | Suborder or section | Family |
| 9 | Mammalia | Primates | Catarrhinæ | Hominidæ |
| 8 | " | " | " | " |
| 13 | " | " | " | " |
| | " | " | " | " |
| | " | " | " | Simiidæ |
| 55 | " | " | " | Simiidæ |
| | " | " | " | Parapithecidæ |
| | " | " | Tarsioidea | Necrolemuridæ |
| | " | " | Tarsioidea | Tarsiidæ |
| | " | " | Lemuroidea | Notharctidæ |
| | " | Menotyphla | | Mixodectidæ |
| | " | "Bunotheria" | | |
| | " | Trituberculata | | Amphitheriidæ |
| | " | Protodonta | | Dromotheriidæ |
| | Reptilia | Therapsida | Cynodontia | Cynognathidæ |
| | " | " | Gorgonopsia | Cynosuchidæ |
| | " | " | Dinocephalia | |
| | " | Theromorpha | Poliosauria | |
| | " | Cotylosauria | Captorhinomorpha | Captorhinidæ |
| | " | " | | Sauravidæ |
| | Amphibia | Labyrinthodontia | Embolomeri | Loxommatidæ |
| | " | Protetrapoda | | |
| | Crossopterygii | Rhipidistia | | Rhizodontidæ |
| | " | " | | Osteolepidæ |
| | Ostracodermi | Anaspida | | Birkeniidæ |

# V. FINAL SUMMARY: TWENTY-SIX STRUCTURAL STAGES IN THE ASCENT OF MAN AND IN THE EVOLUTION OF THE HUMAN DENTITION.

## DESCRIPTION OF STAGES 1–26

(1) *Primitive jawless fish.* Known relatives: Silurian anaspid ostracoderms (*Birkenia*, etc.).

Life zone: Freshwater streams, etc. Locomotor habitus: fish-like, but without pectoral and pelvic fins.

Food habits: probably sucking in minute organisms and organic matter.

Mouth and jaws suctorial.

Cartilaginous gill-arches not developed or not calcified.

Teeth, none.

Skin covered with denticles or flattened scutes.

(2) *Primitive gnathostome or jaw-bearing fish.* Known relatives: primitive Devonian sharks (*Climatius*, *Cladoselache*).

Life zone: freshwater streams, etc. Locomotor habitus: fish-like, with pectoral and pelvic fins of fin-lappet origin.

Jaws cartilaginous, calcified, derived from modified gill-arches and operated by modified gill-arch muscles.

Jaws, temporal region and whole body covered with skin bearing shagreen denticles.

Teeth derived from enlarged shagreen denticles, formed in many successive sets on skin covering the jaws.

(3) *Primitive crossopterygian.* Example: Devonian rhipidistian fish, *Osteolepis*.

Life zone: streams and swamps. Locomotor habitus: fish-like; pectoral and pelvic fins feather-shaped, with fleshy axis supported by cartilage rods.

Food habits predatory.

Gill-arch or primary jaws covered with ossified skin.

Jaws hyostylic, that is, supported by large hyomandibular.

Temporal region with continuous imperforate osseous dermal covering, including intertemporal, supratemporal, squamosal, quadrato-jugal and jugal.

Teeth sharply differentiated in form from scales, covering margins and inner sides of jaws and roof of mouth.

Marginal teeth pointed, with complexly infolded bases (labyrinthodont).

A series of derm bones covering opercular region and underside of throat.

(4) *Progressive crossopterygian.* Example: Upper Devonian rhipidistian fish, *Eusthenopteron.*

Life zone: streams and swamps.

Locomotor habitus: fish-like; pectoral fins fan-shaped, with abbreviate, thick, fleshy axis, supported by skeleton of pro-cheiropterygial type; pelvic fins of similar construction but narrower.

Food habits, jaws and skull, differing only in details from stage 3.

(5) *Protetrapod.* (Transitional from rhipidistian fish to primitive tetrapod.) Known only from a foot-print (*Thinopus antiquus* Marsh) from the Upper Devonian of Mauch Chunk, Pennsylvania.

(6) *Primitive amphibian.* Example: Lower Carboniferous stegocephalian, *Loxomma.*

Life zone: swamps. Locomotor habitus: primitive tetrapod type, with short, pentadactylate extremities.

Food habits predatory.

Jaws autostylic; upper jaw attached to base of cranium by basipterygoid processes; maxilla and dentary of moderate size.

Temporal region imperforate.

Opercular and gular elements lost; skull otherwise much as in stage 4.

Teeth much as in stage 4.

Palate in primitive forms much as in stage 4, in later Amphibia becoming widely open.

(7) *Primitive cotylosaurian reptile.* Example: Upper Carboniferous cotylosaur, *Eosauravus.*

Life zone: swamps. Locomotor habitus: primitive reptilian type.

Skull of *Eosauravus* not known, but skull of Lower Permian *Seymouria* will serve to represent this stage.

Otic notch (between tabular and squamosal bones well developed).

Temporal region imperforate, with separate intertemporal and supratemporal bones.

Jaws and teeth much as in stage 8.

(8) *Progressive cotylosaurian reptile.* Example: captorhinid cotylosaurs of the Permian.

Life zone: mostly dry land. Locomotor habitus: primitive reptilian type.

Food habits ?insectivorous, or perhaps feeding on crustaceans.

Jaws autostylic; maxilla and dentary much as in stage 7.

One of the coronoid and one of the splenial series lost.

Temporal region with imperforate bony covering; inter- and supratemporal bones lost. Otic notch lost.

Palate with Λ-shaped brace formed by pterygoids and quadrates.

Ectopterygoids forming downwardly projecting guards to prevent lateral displacement of the mandible.

Teeth losing the labyrinthodont structure, generally small and peglike, becoming protothecodont.

(9) *Primitive pelycosaur (theromorph)*; Permian. Example: *Mycterosaurus.*

Life zone: dry land. Locomotor habitus: primitive lizard-like type.

Food habits insectivorous to carnivorous.

Skull more compressed, vertically deeper.

Jaws autostylic; maxilla and dentary becoming larger, dentary with a coronoid process.

Temporal region perforate, a temporal opening (the lateral temporal fenestra) lying below the postorbital-squamosal arch and above the jugal-squamosal arch.

Orbit bounded posteriorly by the postorbital-jugal bar; zygomatic arch (jugal-squamosal arch) homologous with that of mammals.

Palate braced as in stage 8.

Teeth conical, compressed, thecodont, often differentiated into incisors, canines and a postcanine series.

(10) *Early mammal-like reptile.* Example: *Moschops* (a specialized side branch).

Life zone: dry land. Locomotor habitus: somewhat as in pelycosaurs, but body well raised off the ground in walking.

Skull deep vertically.

Jaws autostylic.

Coronoid process of dentary meeting large surangular.

Temporal region much as in stage 9.

Teeth in two successional series, an outer and an inner one.

Front teeth specialized (in Dinocephalia), with high tip and very large basal swelling.

(11) *Intermediate mammal-like reptile.* Examples: primitive gorgonopsians of the Permian of South Africa.

Food habits predatory.

Ascending coronoid process of dentary becoming more prominent.

Teeth compressed recurved.

Pterygoids relatively weaker, quadrate reduced in size.

Temporal opening lying below postorbital-squamosal arch and above jugal-squamosal arch.

(12) *Advanced therapsid or theriodont.* Example: cynodont reptiles of the Triassic of South Africa.

Life zone: dry land. Locomotor apparatus: approaching monotreme mammalian type.

Food habits predatory.

Dentition differentiated into incisors, canines, premolars and molars.

Deciduous and permanent series as in mammals.

Cheek teeth compressed, incipiently triconodont, *or* with widely oval ridged upper molars articulating with subcircular lower molar crowns.

Each tooth supported by a single root.

Dentary the predominant element of the lower jaw; post-dentary elements (angular, surangular, articular and prearticular) becoming much reduced in size.

Quadrate small, its dorsal process received into a deep pocket in the squamosal.

Ascending ramus or coronoid process of dentary of very large size, the whole dentary bone approaching in form the mammalian mandible, but the mandibular condyle not yet developed.

Temporal region essentially mammal-like, with mammalian temporal fossæ; zygomatic arch formed by squamosal and jugal and postorbital.

Postglenoid and post-tympanic processes of squamosal developed.

Maxilla vertically deepened, in broad contact above with nasals.

A secondary palate, of submammalian type.

Pterygoids weakened posteriorly and barely reaching the quadrates.

(13) *Primitive mammalian stage.* Examples: *Dromotherium*, *Microconodon;* Upper Triassic, North America.

Food habits insectivorous.

Skull unknown, but probably retaining many characters from stage 12.

Lower jaw with small condylar process, implying the establishment of a secondary articulation between the squamosal and the dentary; otherwise ascending ramus of dentary much as in stage 12. Post-dentary elements probably reduced.

(In earlier stages the quadrate and articular bones were probably connected more or less directly with the tympanic membrane, as they are in recent reptiles. This condition persists in mammals where the quadrate has given rise to the incus and the articular to the malleus.)

Teeth differentiated into incisors, canines, premolars and molars.

Molar crowns compressed, protodont, with high central cusp and small anterior and posterior cusps.

Division of roots into anterior and posterior moieties more or less completely effected.

(14) *Pre-tritubercular stage.* Example: *Amphitherium*, of the order Trituberculata, Lower Jurassic, England.

Food habits insectivorous.

Skull not known, but probably without postorbital bone: with an elongate facial portion slightly deflected upon the low braincase.

Mandible with well defined pedunculate condyle and distinct angular process, the latter not inflected; inclination of coronoid process to body of dentary steeper; coronoid process wide, recurved above; condyle slightly above level of cheek teeth; mandible deeply grooved on inner side for reduced Meckelian cartilage and inferior dental nerve and vessels.

Dental formula: $I\frac{4}{4}\ C\frac{1}{1}\ P\frac{5}{5}\ M\frac{6}{6}$.

Cheek teeth supported by anterior and posterior roots; premolars with simple, compressed, conical crowns and incipient talonids; molars with well defined trigonid and small talonids on inner surface of crown; protoconids asymmetrical, the metaconids directly medial to the protoconids.

Upper molars of *Amphitherium* not known, but, from evidence afforded by later trituberculates, they must have been triangular in form, separated by triangular interdental spaces; apex of each molar homologous with that of the premolars, as shown in *Peralestes* and *Dryolestes* of the Upper Jurassic; the primary apex, together with the outer border of the crown, forming the primary trigon.

(15) *Hypothetical stage.* Undiscovered ancestral insectivorous placentals ("Bunotheria") of the Cretaceous period.

Food habits insectivorous.

Dental formula: $I\frac{3}{3}\ C\frac{1}{1}\ P\frac{4}{4}\ M\frac{3}{3}$.

Premolars retaining the primary trigon, but posterior upper premolars with small internal spur, the serial homologue of the future protocones.

Upper molars triangular, the apex of the primary trigon beginning to divide into two cusps, the para- and metacones. Lower internal spurs from the basal cingulum foreshadowing the future protocones.

Lower molars with high trigonids fitting into interdental spaces, and small talonids, narrow transversely, and bearing entoconid only.

The zalambdodont insectivore *Palæoryctes* of the Paleocene represents a structural survivor of this hypothetical ancestral group, which, in turn, may have been derived from the lower Jurassic trituberculates, especially *Amphitherium*, by the reduction in number of the molars from six to three.

(16) *Insectivorous pre-primate.* Possibly represented by *Indrodon* of the Paleocene. *Nothodectes* is a side branch of this group, with specialized front teeth.

This pre-primate stock is represented in the existing fauna by the tree-shrews (family Tupaiidæ), which are extremely primitive in many characters.

Life zone: arboreal. Locomotor apparatus: adapted for active arboreal life.

Food habits insectivorous-frugivorous.

Dental formula $I\frac{2}{2}$ $C\frac{1}{1}$ $P\frac{4}{4}$ $M\,\frac{3}{3}$.

Incisors, canines and first two premolars all simple, with single roots, conical tips, and internal cingulum. In $p^3$, $p^4$ the internal cingulum gives rise to the internal spurs ("deuterocones," homologous with "protocones" of molars). In $p_3$, $p_4$ the posterior cingulum gives rise to the talonids; $p^4$ and $p_4$ of sub-molariform type.

In this stage the primary trigon of the upper molar has lost its triangular appearance through the division of its apex into para- and metacones and the reduction of the outer side of the crowns, including the external cingulum cusps. The secondary trigon has arisen through the development of the internal spurs, or protocones, and the division of the para- and metacones. These changes are correlated with the transverse widening of the talonids, the development of a hypoconid and its interjection between the para- and metacones in occlusion, and with the further expansion of the protocones; the talonid basins into which the protocones fit have also widened and are wider than the trigonids.

Interdental spaces between the upper molars becoming crowded by the spreading of the protocones, in correlation with which the paraconids of the lower molars become reduced.

(17) *Primitive lemuroid stage*, represented in many respects by *Pelycodus* and *Notharctus*. Eocene, North America.

Life zone: arboreal. Locomotor apparatus adapted for perching and leaping in the trees. Pes with grasping hallux.

Food habits insectivorous-frugivorous.

Dental formula: $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{4}{4}\ M\frac{3}{3}$

Incisors and canines not aberrantly specialized. First and second premolars with simple conical cusps; third and fourth upper premolars retaining the primitive trigonal apex; upper molars tri- to quadritubercular.

In the Notharctidæ the postero-internal cusps arise by fissure from the antero-internal cusps, but in the related Adapidæ they arise in the normal manner from the internal cingulum.

Lower molars tuberculo-sectorial, with small trigonids and wide talonids.

Skull with primitive elongate face, not sharply inclined to the basis cranii.

Orbit bounded posteriorly by postorbital processes of frontal and malar.

The American Notharctidæ are possibly ancestral to the South American monkeys, but not to the Old World series, including man. Nevertheless they illustrate the transition from the primitive menotyphlan insectivorous to the primitive primate stage.

(18) *Primitive pro-tarsioid.* Represented in certain characters by *Omomys* and *Hemiacodon.* Middle Eocene, North America.

Life zone: arboreal. Locomotor apparatus adapted for leaping in the trees, but limbs not excessively elongate. Pes with grasping hallux.

Food habits insectivorous-frugivorous.

Dental formula: $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{3}{3}\ M\frac{3}{3}$

Skull with orbits, braincase and and auditory parts moderately but not extremely enlarged.

Lower incisors gently procumbent, not enlarged. *Omomys* and *Hemiacodon* somewhat too specialized in the enlargement of the lower central incisors and other details, but in the general form of the premolars and molars they afford relatively primitive conditions for two divergent lines of specialization leading on the one hand to the New World series (Platyrrhinæ) and on the other hand to *Parapithecus* and the Old World group.

First upper and lower premolars already eliminated and second becoming very small. Third and fourth upper molars showing tendency to become bicuspid.

Third and fourth lower premolar with posterior cingulum-talonid in an arrested stage of evolution, incipient trigonids asymmetrical, the metaconid of $p_4$ foreshadowing the lingual cusp of the homologous tooth in the higher primates.

Upper molars tritubercular, with conical para- and metacones, small proto- and metaconules, a cingulum-hypocone and an antero-internal cingulum.

Lower molars with small trigonids and enlarged hypoconids. An antero-external cingulum.

(19) *Progressive tarsioid.* Upper Eocene. Not in direct line but represented in certain characters by *Necrolemur.*

Life zone: arboreal. Locomotor apparatus adapted for leaping in the trees. Pes with grasping hallux, but without great elongation of tarsus of known tarsioids.

The differences separating *Necrolemur* and *Microchœrus* from any of the New World or Old World monkeys are numerous and important, and there is no evidence for deriving any of the higher types directly from this source. Nevertheless these genera exhibit certain important advances in the direction of the Old World primates, among which may be noted the development of quadrate upper molars with subequal anterior and posterior moieties; the development of hypoconulids in the lower molars; the final loss of the paraconids in the lower molars; and the tendency for the reduction of the trigonid basins, the tendency for $p^4$ and $p^3$ and the corresponding lower teeth to become bicuspid; the incipient development of a bony postorbital partition; the lateral expansion of the base of the braincase; the development of a tubular external auditory meatus; and the tendency for the angle of the mandible to be expanded and for its posterior border to become very large and rounded. Thus *Necrolemur* and *Microchœrus* have advanced far from the primitive tarsioid type and indicate some of the structural stages through which the actual ancestors of thd Old World series probably passed.

(20) *Pre-catarrhine, or super-tarsioid stage.* Represented by *Parapithecus* of the Lower Oligocene of Egypt.

Food habits insectivorous-frugivorous.

Dental formula: $I\frac{?}{2}\ C\frac{?}{1}\ P\frac{?}{2}\ M\frac{?}{3}$

Lower incisors partly procumbent, not specialized.

Lower canine small, slightly larger than incisors and anterior premolars.

$p^1$, $p^2$ and $p_1$, $p_2$, lost; $p^3$, $p^4$ and $p_3$, $p_4$, retained, the latter incipiently bicuspid. Posterior premolars becoming unlike molars, losing the incipiently molariform pattern of earlier mammals.

Lower molars with low, conical cusps, the talonid about as high as the trigonid. Paraconids lost, the four remaining cusps grouped into two pairs. Hypoconulids or mesoconids present.

The construction of the lower molars indicates that the upper molars were quadrate, with the anterior and posterior cusps arranged in two pairs.

Body of mandible and ascending ramus not so broad as in later members of the anthropoid-man series.

Skull unknown.

The direct derivation of *Parapithecus* and the Old World series not known. The tarsioids foreshadow them in certain respects, such as the loss of the anterior two premolars, but all known tarsioids are excluded from direct ancestry by specialization of the front teeth, of the orbits, and of the lacrymal region. Nevertheless it is probable that the unknown predecessors of *Parapithecus* might be included in a widened definition of the Tarsioidea.

(21) *Primitive anthropoid stage.* Represented by *Propliopithecus* of the Lower Oligocene of Egypt.

Food habits frugivorous-omnivorous.

Dental formula: $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{2}{2}\ M\frac{3}{3}$

Incisors not specialized; canines considerably larger than incisors, but crown of lower canine not very high.

Premolars bicuspid; molars with four main cusps arranged in two pairs; hypoconulids median.

The dentition of *Propliopithecus* is structurally ancestral to that of all the higher apes and man, as noted by its discoverer, Schlosser.

(22) *Advanced pre-human anthropoid.* Middle Tertiary. Represented by *Sivapithecus* and *Dryopithecus*. Miocene of India and Europe.

Food habits frugivorous-omnivorous.

Dental formula: $I\frac{2}{2}\ C\frac{1}{1}\ P\frac{2}{2}\ M\frac{3}{3}$

Lower incisors with crowns not widely expanded.

Lower canine with pointed, erect tip.

Lower anterior premolar with slightly flattened anteroexternal face, articulating with large upper canine. Posterior premolars bicuspid.

Lower molars with four main cusps arranged in two pairs; stout median hypoconulids.

Lower molars with "*Dryopithecus* pattern;" paraconids absent; trigonid basins reduced, talonid basins expanded. Upper molars $m^1$ and $m^2$ quadritubercular.

(23) *Human precursors.* Pliocene. *Pithecanthropus* of the Pliocene or Lower Pleistocene (?) of Java possibly a representative. Skull top of very low type, much like a greatly enlarged gibbon skull.

Forehead extremely low and retreating, supraorbital tori protruding far in front of narrow frontal region.

Two upper molars found in same stratum but further down stream and referred to individual represented by skulltop.

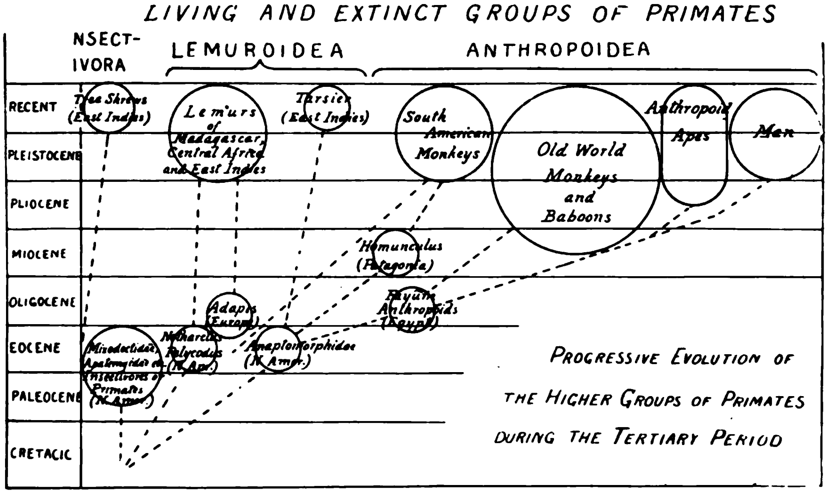


FIG. 345. PHYLOGENY AND GEOLOGICAL SUCCESSION OF THE PRIMATES. AFTER MATTHEW

Third upper molars very large, of advanced anthropoid or primitive human type.

Large femur found in same stratum supposed to indicate erect gait.

(24) *Heidelberg race.* Lower or Mid-Pleistocene, Europe.

Mandible of great size, with very massive body, very broad ascending ramus and backwardly-sloping chin. Dentition of primitive human type with tips of incisors and small canines on same level with premolars and molars.

Molar-cusp formula: $_5, _5, _5$

Molars moderately taurodont.

Skull probably of pre-Neanderthal type.

FIG. 346

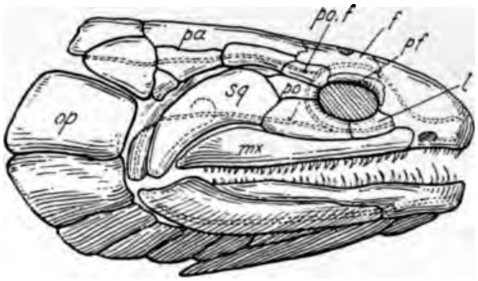


FIG. 347

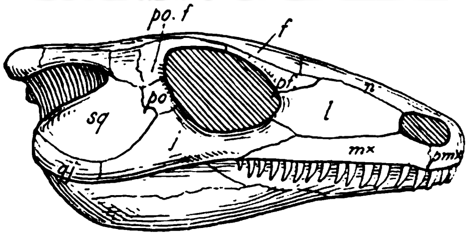


FIG. 348

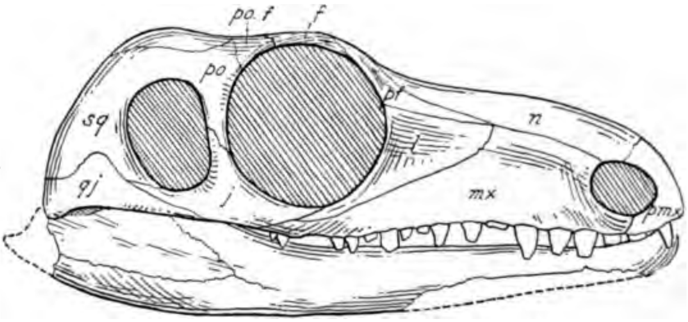


FIG. 349

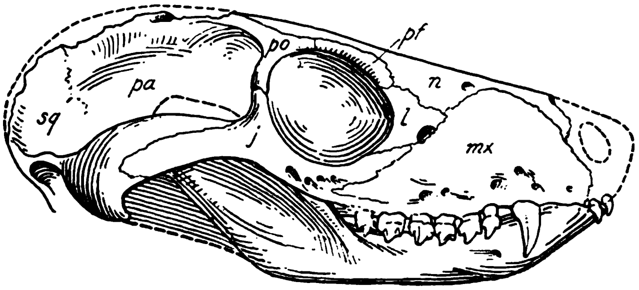
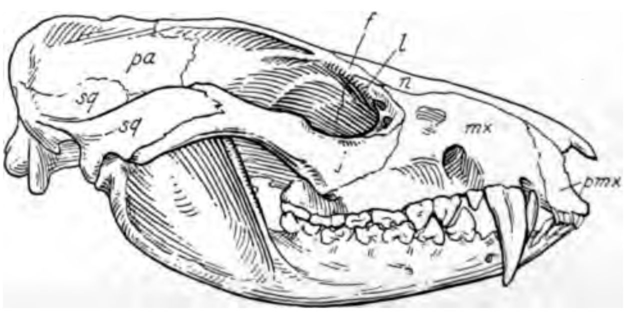


FIG. 350



FIGS. 346–353, INCLUSIVE. STAGES IN THE EVOLUTION OF THE HUMAN FACE AND DENTITION. COMPARE DESCRIPTION OF STAGES ON PAGES 508–520, ABOVE

346. Stage 3. Primitive Devonian crossopterygian fish, *Osteolepis*. After Goodrich.
347. Stage 7. Primitive Permian cotylosaurian reptile, *Seymouria*. After Williston.
348. Stage 9. Primitive Permian pelycosaurian reptile, *Mycterosaurus*. After Williston.
349. Stage 12. Advanced Triassic mammal-like reptile, *Ictidopsis*.
350. Stage 13 *bis*. Primitive metatherian (here represented by a modern opossum).

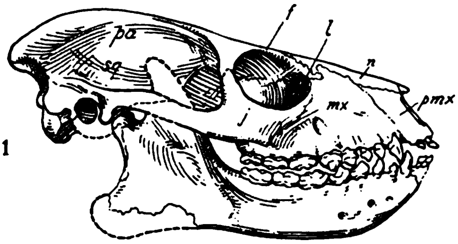


FIG. 351

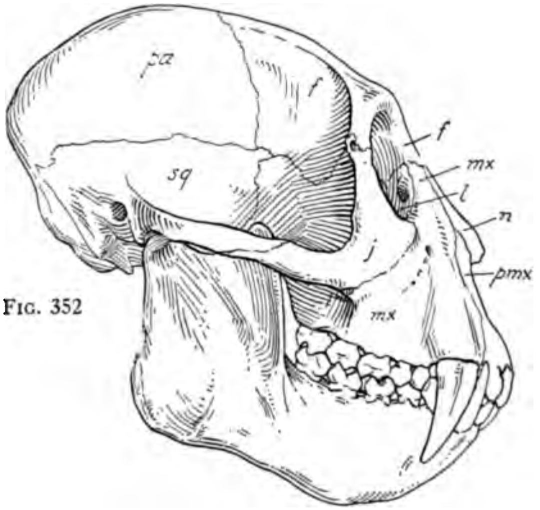


FIG. 352

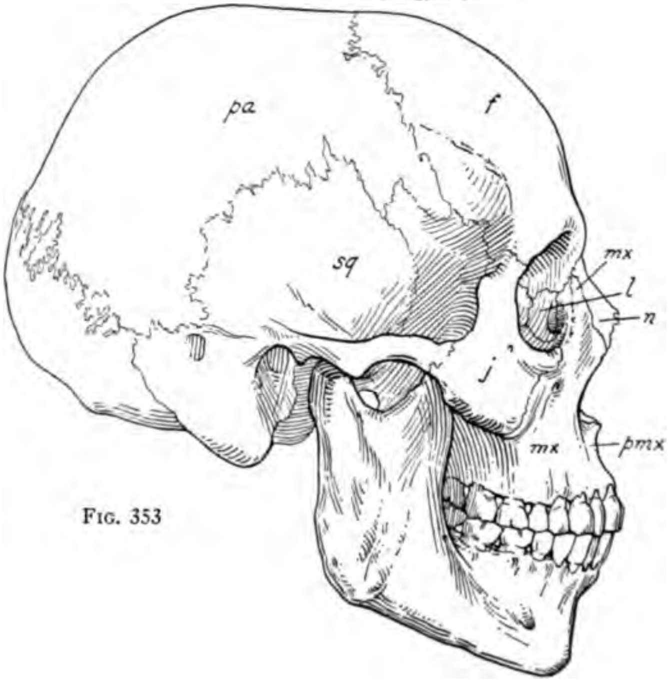


FIG. 353

**351.** **Stage 17.** Primitive Eocene lemuroid, ***Notharctus.***
**352.** **Stage 20.** Primitive catarrhine (here represented by a modern macaque).
**353.** **Stage 26.** Modern man, ***Homo sapiens*** (Chinese)

(25) *Low human type.* Example: the "Mousterian youth."

Skull large, with very low forehead, dolicho., with great supraorbital tori, and very large prognathous face, with enormous platyrrhine nose. Chin retreating. Skull narrow anteriorly and broad posteriorly.

Incisors with edge-to-edge bite.

Molar teeth moderately taurodont. Premolar- and molar-crown patterns retaining many simian or primitive details. Second lower molars with five cusps and *Dryopithecus*-pattern. Second upper molar with four cusps, projecting hypocone.

(26) *High human type.* Example: *Homo sapiens nordicus.*

Skull with steep forehead, secondarily (?) dolicho., with no supraorbital tori.

Face orthognathous, long, with delicate, straight, narrow nose. Chin prominent. Incisor overbite.

Molar teeth short-crowned. Second lower molar with four cusps and +-shaped pattern. Second upper molar with three cusps, i.e., hypocone greatly reduced or absent. Third upper and lower molars greatly delayed in eruption, often failing to erupt at all.

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