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Earlier Forms of Prehistoric Man

BY

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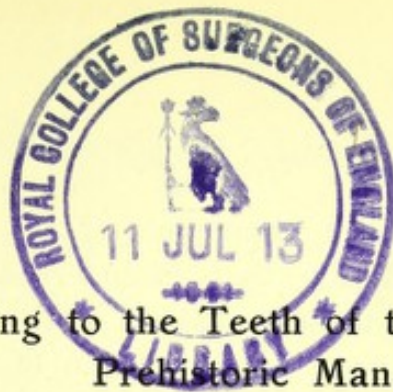
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Problems relating to the Teeth of the Earlier Forms of Prehistoric Man.

By ARTHUR KEITH, F.R.S.

THE chief problems which at present exercise the minds of anthropologists relate to the nature of the physical characters of Neanderthal man, especially to the characters of the teeth of that ancient and peculiar race. At the end of last century anthropologists had come to regard Neanderthal man as representative of mankind of the Pleistocene period; he was regarded as a stage leading on to the more modern type of man now diffused over the whole earth. At that time—some twenty years ago—the problem of man's evolution was regarded as a comparatively simple one. It was then expected that as we went backwards, in time we should find mankind becoming more and more primitive in structure, more and more simian in its affinities. Indeed, we expected to find, as we went backwards, in time, a linear series of human forms, which would link modern man with an ancient simian form, and that Neanderthal man would prove to be one of the later links in the chain which carries mankind into the far past. This simple conception was disturbed by Professor Schwalbe, of Strassburg, early in the present century;¹ from an examination of the physical characters of Neanderthal man, he came to the conclusion that this race formed a totally distinct species of humanity, that when found there could be no difficulty in recognizing its remains, so differently were they shaped and formed when contrasted with the remains of modern man. No intermediate forms between the two types are known, and Professor Schwalbe concluded that Neanderthal man was not an ancestor of modern man, but represented a collateral species which had become extinct in the Pleistocene period. Professor Keith admitted that he was at first unconvinced by the facts and reasoning advanced by Professor Schwalbe.

Dr. Paul Adloff's famous paper² on the teeth of the Neanderthal people, founded chiefly on those discovered by Dr. Gorjanović-Kramberger, at Krapina, Croatia, served to emphasize the truth of Schwalbe's

¹ Schwalbe, "Die Vorgeschichte des Menschen," Braunschweig, 1909.

² Adloff, "Das Gebiss des Menschen und der Anthropomorphen," Berlin, 1908.

opinion. From the peculiar characters of the Krapina teeth, Dr. Adloff came to the conclusion that Neanderthal man, at least the Krapina form, could not represent a stage in the evolution of modern man. The features on which this conclusion of Dr. Adloff's is based will be seen from fig. 1. The lower right molars of three dentitions are shown: (1) Modern Europeans; (2) the Heidelberg molars; (3) the molars of one of the Krapina series, that of a lad in which the premolars and last molar are not yet erupted. In the modern mandible the body of the tooth containing the pulp cavity is supra-alveolar, only the roots are embedded in the mandible. It will be observed that in passing from the first to the third molar the pulp cavity tends to enlarge at the expense of the roots, and that the body of the tooth tends to become embedded more and more within the alveolar process of the jaw. In the Heidelberg mandible, which represents by far the most ancient remains of the Neanderthal type yet discovered, the tendency seen in the last molar of modern man is much exaggerated. In all the molars the pulp cavity is large and the body of the tooth tends to be implanted in the alveolar border. As in modern man, the tendency increases from the first to the last molar. In the Krapina teeth the tendency is so marked that the pulp cavity extends deeply into the region of the roots, and the body of the tooth is enlarged at the expense of the roots. The tendency may culminate as in the figure shown of the Krapina teeth (fig. 1) by the inner root septa, or inner walls of the roots, forming a mere cap or lid at the lower or alveolar end of the prismatic body of the tooth (*see* fig. 1, a).

We are thus made aware of a curious process or condition of the molar teeth for which we ought to have a distinctive name, a tendency for the body of the tooth to enlarge at the expense of the roots. It is a tendency to assume the condition seen in the teeth of ungulate or cud-chewing mammals, the condition seen in the ox. For this condition or tendency Professor Keith proposed the name of "taurodontism." The opposite condition—that seen in the teeth of carnivora—where the body of the tooth is above the alveolar border, he proposed the name of "cynodontism." The names he regarded as capable of improvement and brought them forward provisionally. There can be no doubt as to the reality of the processes or conditions the names represent. It was the degree of taurodontism in the Neanderthal teeth, a specialized or retrograde, not a primitive feature, which led Adloff to the belief that Neanderthal teeth did not represent a stage in the evolution of modern teeth, which are more cynodont or primitive.

He was also aware that it was not very rare to find a marked degree of taurodontism in the last molars among modern Europeans.

Two years ago the nature of Neanderthal teeth was brought home to Professor Keith by a discovery made in a buried cave at St. Brelade's Bay, in the south coast of Jersey. Ancient hearths, with flints of the Mousterian period, and remains of Pleistocene animals were discovered and with them a number of human teeth. On being shown these teeth by Mr. R. R. Marett, he had no difficulty in recognizing from their characters that they were those of an individual belonging to the

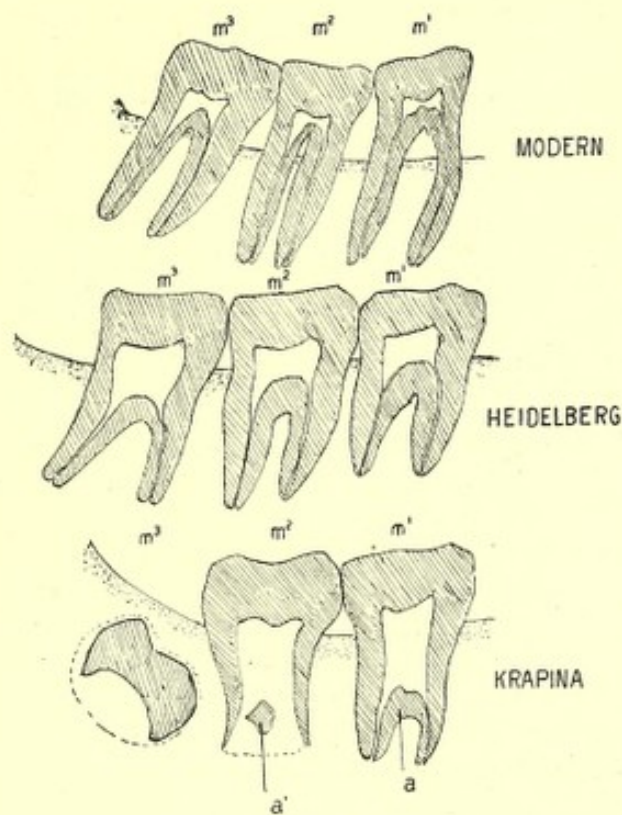


FIG. 1.

Drawings from skiagrams of the lower right molars of (1) modern European, (2) Heidelberg mandible, (3) a Krapina mandible; *a*, *a'*, inner root septum: (1) and (2) after Schoetensack; (3) after Kramberger. (Natural size.)

Neanderthal species of man. There was no need to give a description of these teeth, as Mr. Knowles and Professor Keith had published a full description of them in the *Journal of Anatomy and Physiology*, 1911, xlv, p. 12. The teeth found were members of a single dentition, and the molars showed a high degree of taurodontism. The other teeth, premolars and incisors, also showed a tendency to thickening and enlargement, not elongation of their roots. One illustration (fig. 2)

will suffice to show the characters of the Brelade dentition. The illustration shown in fig. 2 is that of the second left lower molar. The fusion of the roots is not due to an approximation of the roots, the result of a retrograde development, but it is due to an opposite process, the extension of the body of the tooth into the region of the roots, with a fusion of the roots owing to a hypertrophy of their substance. The condition supports Adloff's contention—viz., that it represents a specialization. The teeth of the Gibraltar skull show a similar condition, a marked degree of taurodontism. There is no doubt that the degree of taurodontism varied widely in the examples of Neanderthal man so far discovered. It was extreme in a number of the Krapina specimens; it was less marked in those found at Spy, but in every case the degree exceeded that found in any modern race. Gorjanović-

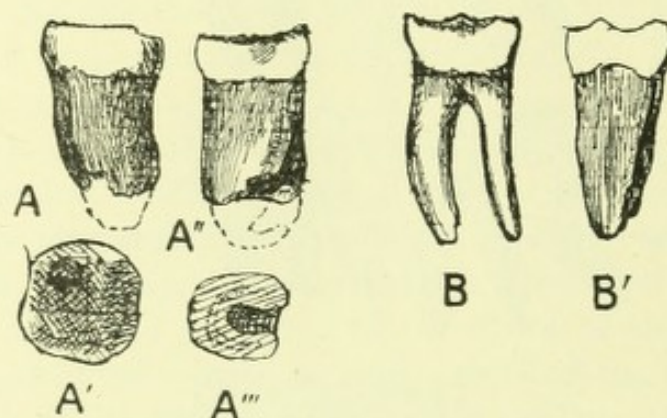


FIG. 2.

A labial aspect of second lower molar of Brelade dentition. A', its chewing surface; A'', distal aspect; A''', section of root; B, labial aspect of the same tooth of a modern English dentition; B', the distal aspect of the same. (Natural size.)

Kramberger had pointed out that the condition occurs in the Eskimo, but a slighter degree is represented than in any form of Neanderthal man. Taurodontism is a character of Neanderthal man's dentition. Lately Professor Keith had visited the Royal Museum at Brussels, where Dr. Rutot gave him an opportunity of examining his extensive collections of Pleistocene fossils and implements. Amongst those was the Naulette mandible: the tooth sockets are shown in the photograph (Dr. Rutot's) reproduced in fig. 3. With the photograph is reproduced a drawing giving the size of the dental crowns; they apparently increased in size from the first to the third, with outlines which show the fusion of the roots. From the condition of the tooth sockets there could be

no doubt that the Naulette mandible—probably that of a woman—manifested a high degree of taurodontism.

When Dr. Adloff's paper appeared in 1907, Professor Keith questioned the validity of the reasoning employed. It was some years later, when recent discoveries of Neanderthal man were made in France, and when it became apparent that Neanderthal man, so far as concerns the later part of the Pleistocene period, was sharply limited to one particular period—the Mousterian—that the conviction was forced upon him that Schwalbe, Adloff, and Dr. Rutot, of Brussels, were right in excluding

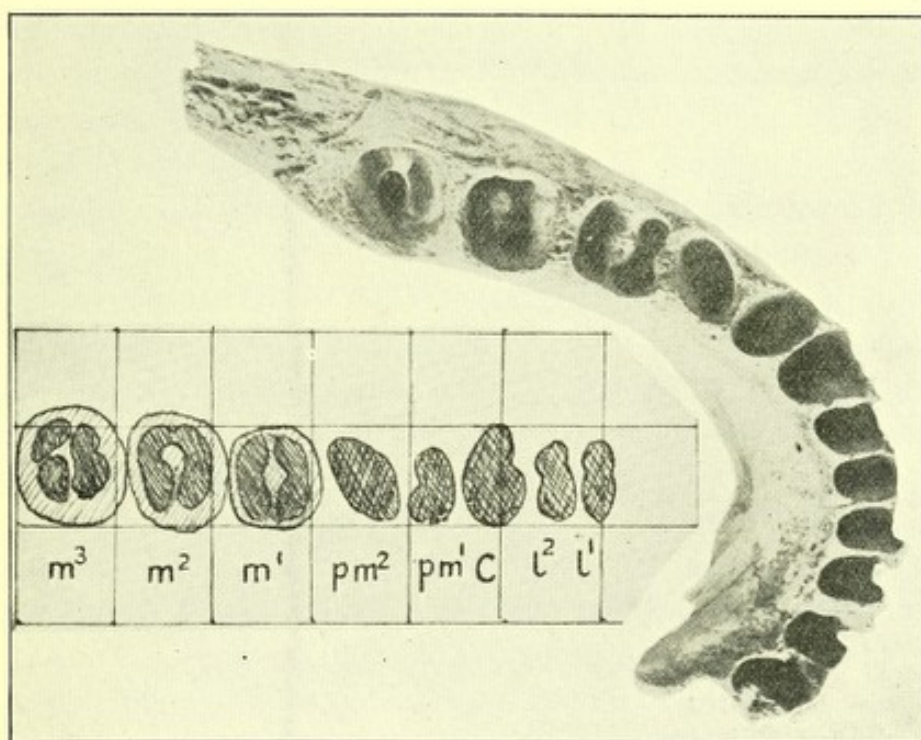


FIG. 3.

The tooth sockets of the Naulette mandible (Rutot). Inset is a sketch of the probable size of the molar crowns and dimensions of the roots.

this primitive race from our ancestry. No geological section yet exposed gave a better idea of the distribution of man in the Pleistocene period than the strata of the sand-pit at Mauer, near Heidelberg, where the famous mandible was discovered by Professor Schoetensack in 1907. The strata are reproduced diagrammatically in fig. 4. The mandible was discovered at a depth of a little over 76 ft., towards the bottom of a series of river-bed deposits known as the Mauer sands. The strata in which the mandible was found belong to an early part of the Pleistocene period. It is probable that the more recent of the Mauer sands belong

to that period of Pleistocene culture known as the Chellean. Then follows the deposit of ancient loess representing the Acheulean period. The Mousterian period—the one to which the various remains of Neanderthal man have been ascribed—is represented at the junction of the ancient and recent loess. Then follow the deposits of recent loess—the formation of which appears to cover the later phases of Pleistocene culture—the Aurignacian, Salutrean and Magdalenian. We know a considerable number of remains of men who have lived in these latter periods—the Magdalenian, Salutrean and Aurignacian. They are people like ourselves, their teeth and ours belong to the same type. When we pass into the older Mousterian period the type of man changes. No representative of modern man of that period has yet been discovered in Europe; all the men so far found in strata of the Mousterian culture are Neanderthal in type. It is impossible to believe that in the passage from the Mousterian to the Aurignacian periods the inhabitants of Europe were suddenly altered in type: the only possible explanation is that Europe was invaded by a type—the modern type—of man who replaced the Neanderthal man. The historical sequence in the Pleistocene period is in favour of the contention that Neanderthal man was not transformed into modern man, but became extinct when Europe was invaded by the modern type of man, who seems to have been evolved outside Europe.

The statements so far given merely serve as an introduction to another problem, the problem of the Galley Hill man. Four years ago, when Professor Keith was preparing a small book on “Ancient Types of Man,” he was still dominated by the idea that Neanderthal man was the only form of Pleistocene man and represented a stage in our evolution. He realized then that Galley Hill man was out of place, if the stages of man moved steadily forwards in progressive stages to the modern type. At that time there was still doubt as to the relationship of our river valley deposits to the various cultural cave strata of the Continent. Accordingly, he was prepared to think that a fuller knowledge of Pleistocene formations would show that in point of time Galley Hill man would come after Neanderthal man. The opposite has proved true; the Acheulean and the Chellean cultures belong to an infinitely older part of the Pleistocene period than the Mousterian, the culture of the Neanderthal period. The 100-ft. terrace in which the remains of Galley Hill man was found was laid down during the age when the Chellean culture prevailed in the Thames Valley—the Mousterian culture belongs to more recent deposits laid down when the valley had

nearly reached its present form and depth. One easy solution of the difficulty is to regard the Galley Hill as an interment of a more recent date than the deposition of the 100-ft. terrace. Those, however, who have examined the evidence relating to the discovery of the Galley Hill skeleton can find no loophole of escape; all the evidence points clearly

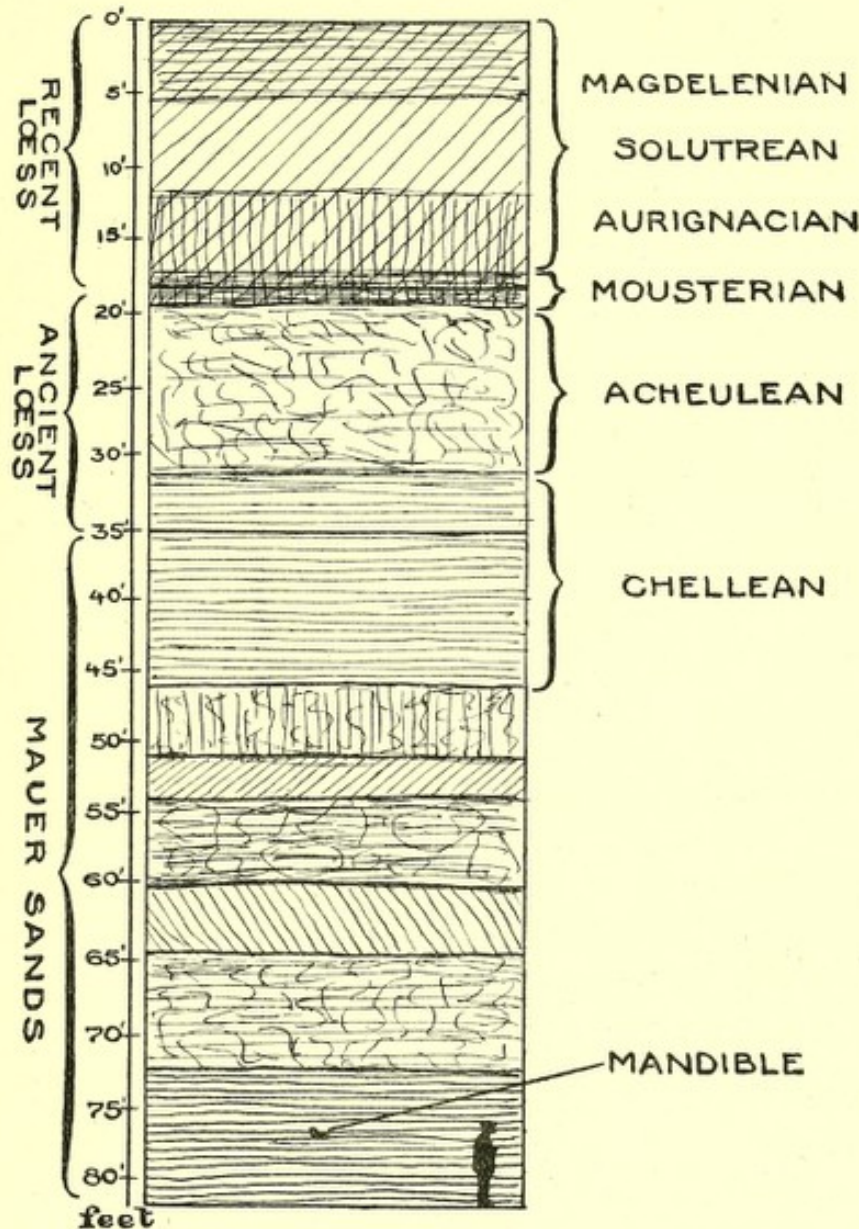


FIG. 4.

Section of the strata at the sand-pit of Mauer, showing approximately the periods of culture in existence when the various layers were deposited.

to its age being contemporaneous with the formation of the 100-ft. terrace. The real evidence against its authenticity is, that it is in type of skull, teeth, and limb-bone of the modern human form, and cannot, therefore, be older than the more simian form—Neanderthal man.

When, however, we look at the teeth of Galley Hill man we must admit that they are really more primitive or simian than even the teeth of Neanderthal man. In fig. 5 four molars are represented, amongst them, B, the second left lower molar of the Galley Hill mandible. The roots are short and not widely separated; the crown and body are above the alveolar border. On one side of the drawing (B) is placed the chimpanzee's second lower molar (C); on the other side the corresponding tooth from a modern English jaw. The second left molar from the Brelade dentition is also shown (D). It will be seen that the least simian—taking the chimpanzee's molar as our type—is the Brelade or Neanderthal tooth; the Brelade tooth is the most specialized or taurodont. The tooth of Galley Hill man in this respect is more positive or simian than that of Neanderthal man; there is nothing in its form which precludes us from attributing to it the antiquity suggested

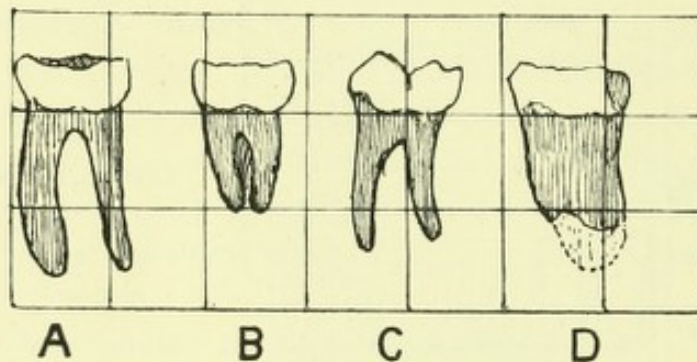


FIG. 5.

The second left lower molar of modern English jaw (A); Galley Hill (B); Chimpanzee (C); Neanderthal (D). (Natural size.)

by the site in which the Galley Hill skeleton was discovered. The teeth of many examples of Pleistocene man of the modern type have short roots.

As no minute description has been given of the Galley Hill teeth, the drawing represented to scale in fig. 6 may be welcome. Only one half of the mandible was found, with the premolar and molar teeth in situ. As in modern teeth there is a slight increase in taurodontism as one proceeds from the first to the last molar. There are five cusps on the crown of each of the lower molars. The length or medio-distal diameter of the crown of all three is approximately equal, 11 mm., the middle tooth being slightly the smaller, the labio-lingual diameter of the crown is slightly less than the medio-distal diameter, 10.5 mm.; whereas in Neanderthal man the width is usually greater than the

length of the molar crowns. In the proportion of the diameters of the molar crown the Galley Hill teeth are the more simian, the medio-distal diameter of pm^1 is 6.5 mm.; of pm^2 6.8 mm. Thus, although like modern teeth, the Galley Hill dentition is in reality more primitive or simian, and less specialized than the teeth of Neanderthal man; far from refusing the Galley Hill remains as authentic because of their characters, we ought to accept them if the evidence of their geological age is sound.

What principles are we to apply in determining the degree of primitiveness to any given dentition? The condition of taurodontism has been already mentioned. It does not occur amongst primates, at least amongst those who have a structural relationship to man. We

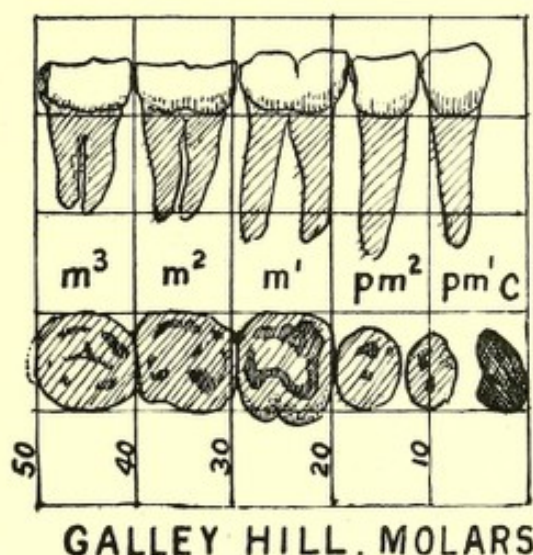


FIG. 6.

Drawings of the premolar and molar teeth of the Galley Hill skeleton.

must regard its presence in Neanderthal man as a specialization which takes that race away from the ancestral line of more modern man. It is probably a modification correlated with the nature of diet, a root or vegetable diet, requiring greater grinding power. The shape of the palate of Neanderthal man—but as yet we know very little of the shape of his palate—indicates a peculiar specialization. In fig. 7 is represented a drawing made to scale of the palate of the Gibraltar cranium, the earliest discovered of all the remains of Neanderthal man. Beside it is placed the palatal arcade of a native Tasmanian. Of the two the Tasmanian palate is the more simian; the molar sides of the arcade assume the parallel arrangement seen in anthropoid palates.

chimpanzee the last is usually the smallest of the series. In the upper molars, the third is distinctly the smallest of the series in the chimpanzee, but in the gorilla it is but a little less than the first. The crowns, cusps and roots of the gorilla's molars have a more robust development than in the chimpanzee. The molar length of the gorilla represented in fig. 8 is 52 mm.; in the chimpanzee 35 mm. We have every reason to suppose that the gorilla and chimpanzee dentitions are derived from a common form—the gorilla's representing a progressive, and the chimpanzee's a retrogressive development from that common form. The term wanted is one to indicate these opposite phases of a common process. If the orang dentition (*see* fig. 9) be taken as representing a mean or plenal degree of development, then the gorilla's dentition

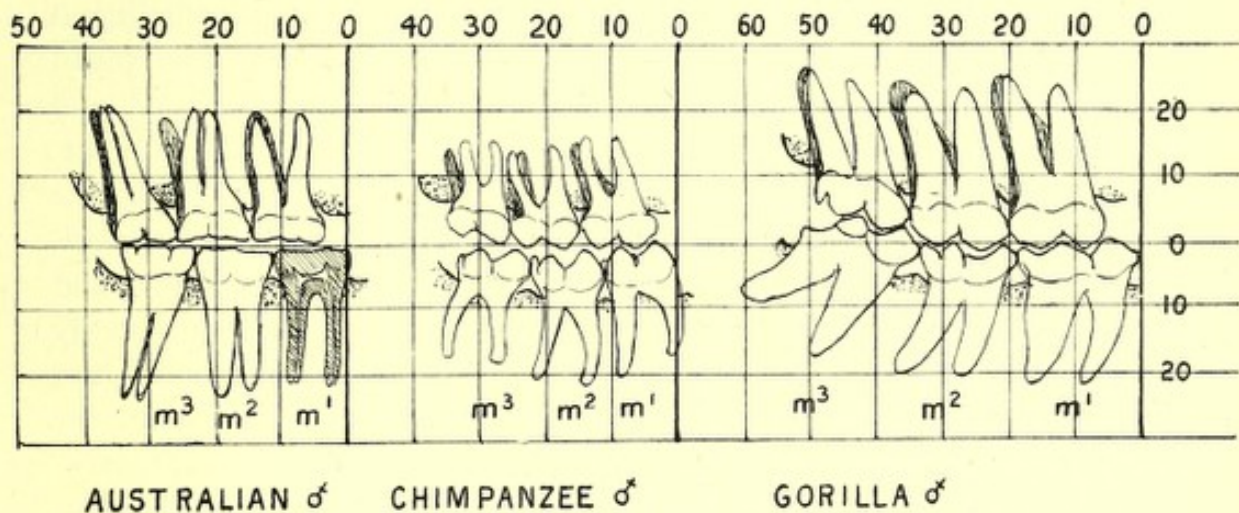


FIG. 8.

The molar dentition of a native Australian compared with those of a chimpanzee and a gorilla. The scale is represented in millimetres.

represents a supra-plenal phase, and the chimpanzee's the infra-plenal phase. When dealing with human teeth we have always supposed that an infra- or sub-plenal phase—one in which the third molars were, on the average, smaller than the second molars—represented a degenerate, and therefore a modern form. We find, however, that various forms of primates—both ancient and modern—may show a sub-plenal phase. The chimpanzee is as primitive as any human ancestor we are ever likely to find, yet we find its teeth in this sub-plenal phase. It is clear then that we cannot apply the law of plenal molar development as a sure criterion of either modernity or of antiquity of any given form. So far as the lower molars of the Galley Hill man is concerned the plenal form is represented. As a rule the Neanderthal

lower molars show the supra-plenal condition. From fig. 8 it will be seen, that although the crowns of the chimpanzee's dentition represent a retrogressive phase, the roots do not undergo a corresponding alteration. In even the most primitive of modern dentitions (*see* fig. 8), the roots of the distal molars do show a tendency to fusion. We must suppose that man comes of a stock in which the roots were widely and separately implanted in the alveolus, and we expect that the very early forms of man will show discrete and widely separated roots.

In fig. 9 is shown the degree of plenal development of molars in anthropoids and man. It will be most convenient to consider first the development in modern Englishmen. The diagram in fig. 9 represents the mean molar development in twenty-two English medical students—measured from impressions taken on plates made of paraffin wax. The upper molars decrease from the first to the third—the medio-distal diameter of the crowns being 10.3, 9.4, and 8.6 mm. The mean development of cusps is also given in the table—3.9, 3.6 mm., and 2.8 mm., showing the degree of retrogression in cusp development. In the lower molars there is also a decrease from first to last, the measurements being 10.2, 10.1, and 9.1 mm., and there is a corresponding retrogression of cusp development represented by 4.2, 4.7, and 3.7 mm. cusps. The condition of the molar development is markedly sub-plenal. This is also the case, but to a less degree, in the Tasmanian molar development (*see* fig. 9). In Neanderthal man the dentition, so far as relates to the size of the crowns, is supra-plenal—the table being compiled from all available measurements—the lower molars increase from the first to the third; in the upper molars the second and third are of nearly equal size. As regards cusp development the Neanderthal teeth show a degree of retrogression almost as great as in modern Europeans. The upper and lower third molars are irregular and anomalous as regards their cusp development. It is unnecessary to analyse in all their details the formulæ given in Table 9 for the molar development of the gorilla, orang and chimpanzee. As already said, in size of crown and in cusp development, the gorilla represents the supra-plenal, the orang the plenal, and the chimpanzee the sub-plenal degree of molar development.

The table is founded on measurements made of anthropoid dentitions in the various London collections, numbering in all about 150 individuals. It is also easy to see that retrogression and progression affects the molar teeth in a definite order. The third upper molar is the first to be affected, either in progression or retrogression; the postero-internal

cusp is the first to become reduced, to become irregular, or in the progressive form to become stronger. When the change, be it progressive or retrogressive, proceeds further, the second molar becomes affected, the postero-internal cusp being the first to manifest the change. The first molar is the most conservative, and the least liable to alter either in progressive or retrogressive changes. In the lower series the third molar is also the first to alter, its posterior cusps being the point which reflects the phase. Owing to the forward displacement of the lower as

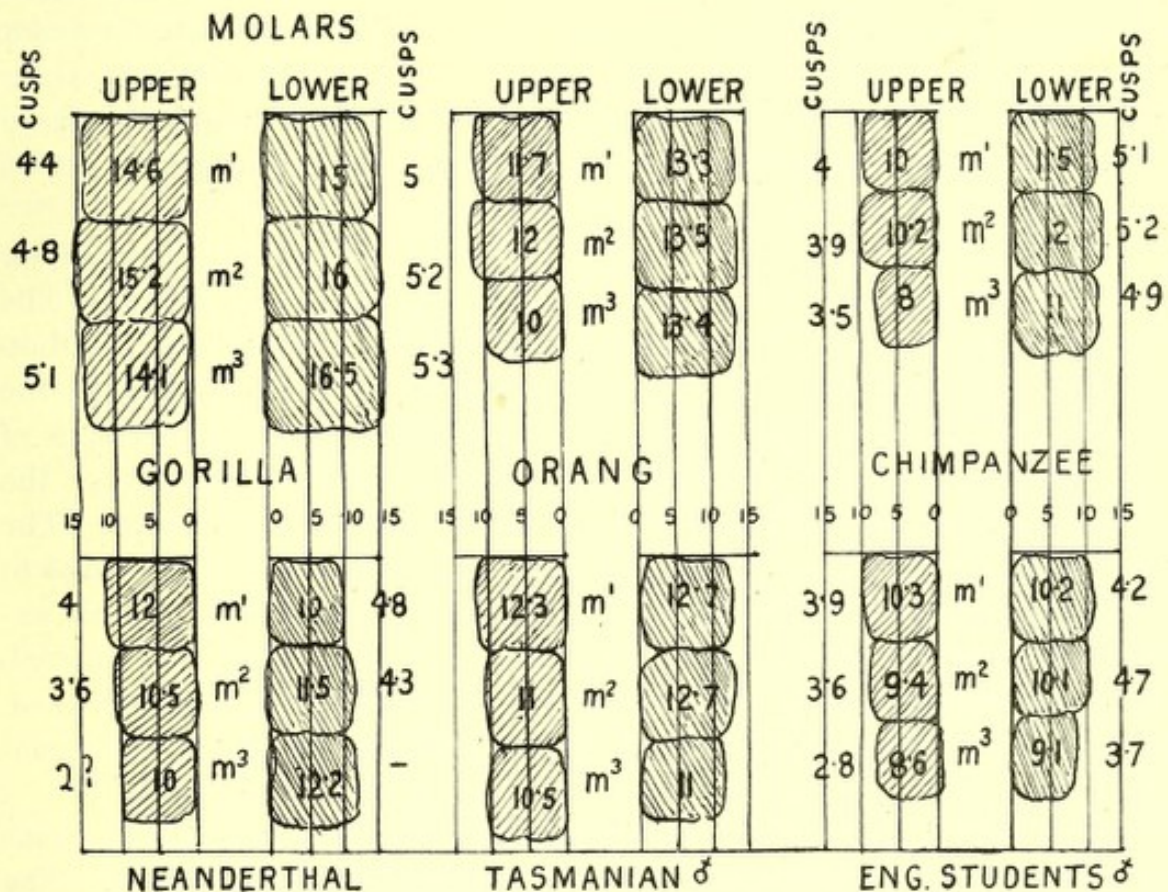


FIG. 9.

Diagram showing the development of molars in various forms of the higher Primates; the teeth are placed in the diagram so as to contrast their length or medio-distal diameters. The parallel lines which cross the length of the crowns are 5 mm. apart. The cusp development is also given in the diagram.

compared with the upper molars, the change in the third lower molar is later in appearing than in the corresponding upper molar. As in the upper series, the first is the most stable tooth—the least liable to be affected in either progressive or retrogressive changes. In supra-plenal dentitions it is the smallest of the lower series; in sub-plenal forms it becomes the largest. It will be thus seen that even in primate

dentitions, which are of an ancient or primitive type, as are those of the great anthropoids, various degrees of plenal molar development are found.

We are therefore justified in inferring that, in the various species or genera, into which the earlier forms of man must have branched, similar degrees of plenal development had occurred. If, therefore, we find forms of man with a sub-plenal development, that feature need not indicate that the form is of recent date. On the other hand, we must recognize that there is a marked tendency amongst all highly civilized modern races to a subplenal molar development, and unless the geological evidence is to the contrary, must presume that a marked degree of molar retrogression is a presumption in favour of any given dentition being of a modern date. Contracted palates, and crowded, irregularly placed teeth, have not been seen in human remains which belong to a period preceding the Bronze Age.

In fig. 10 is reproduced Dubois's drawing of the third upper molar of *Pithecanthropus*. The roots are short, stout, and widely spread. The two labial roots are fused, but there is no trace of the taurodont condition seen in all Neanderthal teeth. We have certainly in this tooth the representation of a primitive human form. The actual dimensions of the crown are great: the length or proximo-distal diameter of the crown is 11.3 mm., its width or labio-lingual diameter 15.3 mm. The fusion of the labial roots, the reduction of the two posterior cusps to form a crenulated distal margin for the crown, show that in this extremely primitive human form the dentition was reduced or sub-plenal. Unfortunately no figures of the two premolar teeth have been published. They should throw further light on the peculiar nature of *Pithecanthropus*.

The discovery of the Piltdown skull by Mr. Charles Dawson adds to a rapidly growing list a very primitive form of ancient man. The molar teeth show no degree of taurodontism; they show the opposite condition cynodontism. The three molars were probably of about equal size; there is a degree of fusion of the roots of the last molar. There are five cusps on each molar present. The molar development is plenal. Further details of the dentition will be found in Dr. Smith Woodward's paper, and in Professor Underwood's account of the teeth. The main interest of the Piltdown dentition relates to the region of the canine teeth. ~~The evidence is decidedly in favour of a simian development of the canine teeth in that individual—as the authorities who have investigated the remains have declared.~~ That a human form should be discovered with a large canine tooth was expected by all of those who recognized the

close structural relationship between man and the great anthropoids and the manner in which the canine tooth is developed and formed in modern man.

In fig. 11 is represented various degrees of the canine development met with in the higher primates. The teeth are drawn to scale with the palate placed in true profile. Four individuals are represented in fig. 11, a native Australian with a well-developed dentition, a female chimpanzee, a male chimpanzee, and a gorilla. These individuals represent various degrees in the plenal development of the canine region of the palate. The changes in this region—both progressive and retrogressive—proceed independently of the changes affecting the molar region. The molar series of the Piltdown mandible has a total length of about 36 mm.; the three molars were thus of moderate size, but the teeth of the canine region must have reached dimensions far

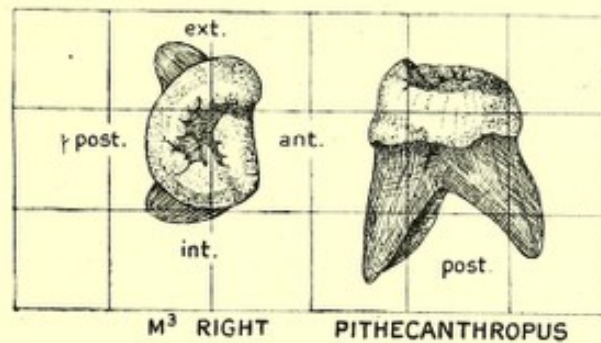


FIG. 10.

Two views of the third upper right molar of *Pithecanthropus* (after Dubois).
The squares represent centimetres.

beyond any human dentition yet known. Amongst higher living primates the teeth of the canine region of the jaw find their maximum development in the male gorilla. In the specimen shown in fig. 11 the teeth of the anterior or canine region extend in an antero-posterior or sagittal direction—from the crowns of the mesial incisors in front to a line joining the distal margins of the second premolars for a distance of 52 mm. (see fig. 11); in the male chimpanzee the extent is 45 mm.; in the female chimpanzee 57 mm.; in the Australian palate shown in fig. 11, 27 mm. Using the same terms as before, it may be said that in the male gorilla caninism reaches a supra-plenal degree; in the Australian, an infra-plenal development; while in the female chimpanzee a mean or plenal phase is represented. The effect of caninism is not confined to the canine teeth alone; the first premolar is affected in every phase of

development of the canine teeth. The first lower premolar is the fulcrum or blade against which the upper canine tooth works; its development and specialization depend on the size of the canine teeth. In turn the first lower premolar acts against the first upper premolar, hence the premolar teeth form an intrinsic part of the canine mechanism.

We are still in ignorance of the exact use of the canine teeth in anthropoids. They are certainly organs of defence or attack, but they are evidently used also for certain masticatory purposes. They are regulated in their degree of development by the same factors as regulate sexual characters by secretions arising in the genital glands. In all modern human races—in all races so far discovered, except that

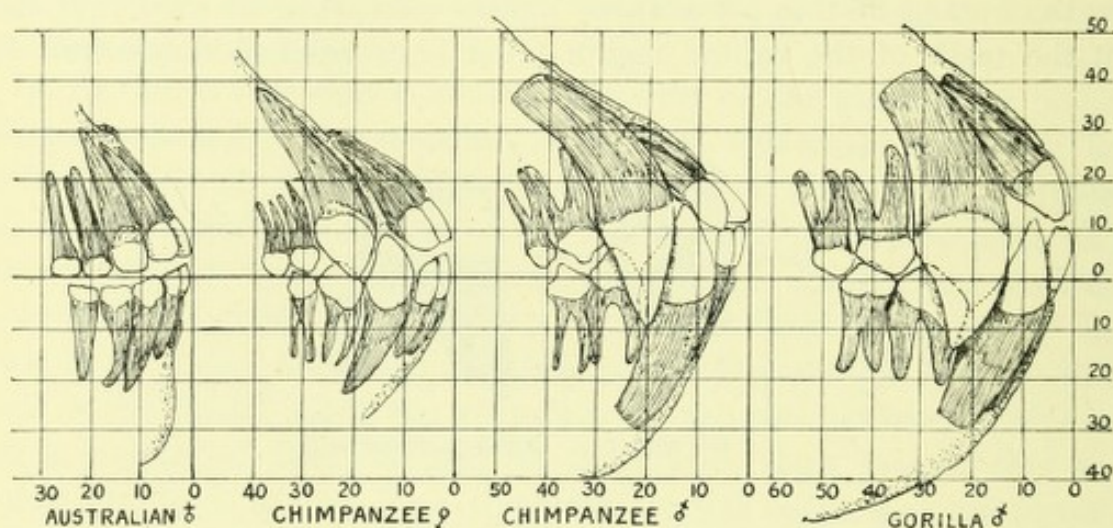


FIG. 11.

Various phases in the evolution of the teeth of higher Primates in the canine region.

to which the Piltdown individual belongs—an extreme retrogression of the canine series has been reached—a marked degree of infra-plenary caninism. Projecting canines have certain disadvantages: they prevent any free side-to-side movement of the jaws in chewing; the long canines imply a scissors-like action in biting and chewing. With the disappearance of the canines a side-to-side movement of the molar crowns becomes possible, and it is strange that the chewing surfaces of the Piltdown molars are worn as if there had been a side-to-side movement, and as if the canines had not been long enough to prevent this movement.

Professor Keith was not prepared to find a comparatively large brain—the Piltdown brain falls within the lower limit of human brains as

regards size—accompanied by a degree of caninism so great as is suggested by the Piltdown mandible. It has usually been inferred from the characters of the temporal ridges in the calvaria of *Pithecanthropus*, and from the characters of the last molar, that there was not any marked degree of caninism in that human form. In the Heidelberg jaw the canines have subsided to their modern dimensions, and yet the strata in which the mandible was found belongs to an early phase of the Pleistocene period. The date of the Piltdown man is an open question. Flints of the Chellean period were found with or near the remains; so were those of Pliocene mammals. Seeing that we know that in one species of man at least—the early Neanderthal type of Heidelberg—the canine teeth had receded to a human stage of development at the beginning of the Pleistocene period, it is clear that the Piltdown man should belong to a much earlier date than the Chellean period; it is most probable that it will ultimately prove to belong to a Pliocene in date. We may safely regard the features of the Piltdown teeth and mandible as representative of one genus of man of the Pliocene period.

SUMMARY.

In this paper an attempt is made to sketch the various features of a dentition which should guide us in estimating the degree of antiquity, and the degree of primitiveness in any discovery of ancient or fossil man; the teeth of Neanderthal man, although primitive or simian in some features, in others are highly specialized. They show the condition of taurodontism beyond any other known form of man or ape, surviving or extinct. The condition of molars and of canines described here as plenal, supra-plenal and infra-plenal have also to be taken into account. The various plenal phases apparently represent the result of physiological processes, and are usually, but not necessarily, indications of antiquity and primitiveness. As regards the teeth of the Galley Hill mandible, they are essentially more simian or primitive than those of Neanderthal man.

