Some Biological Aspects of Prognathism and Occlusion of the Teeth

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The human body constitutes a functional entity, no part of which can be varied without entailing some changes in other parts. Similarly, the facial skeleton and the dentition are functional parts of the skull as a whole. It follows therefore, that variations in the bite will be largely related to the facial and cranial structure.

In order to gather some idea of the formations of the face and dentition, the following biological classification of the determining factors may be employed:

1. The evolutionary changes found in the ascending series of vertebrates.

2. The factors which determine the different cranial and bite formations in existing human races.

3. The factors which are responsible for variations in formation within a given racial group, *i. e.* the variations between individuals of the same racial stock.

4. The growth changes that take place in the individual, *i. e.* the alterations in the facial proportions during the growth period.

In addition to these are the factors which may be considered to influence and alter the formation of the facial skeleton and the dentition in existing human races.

5. The effect of "domestication", *i. e.* those changes to which primitives are subjected in the process of altering their mode of life to that of a civilized community, and finally

6. The effect of racial mixture on the facial skeleton and the dentition.

When studying the facial bone structure and the bite it has been found that in addition to methods of direct anthropological measurements, the use of X-ray greatly facilitates the measurement of variations in the facial skeleton which cannot readily be obtained on living specimens owing to the presence of the soft tissues. This applies particularly to the determination of one racial characteristic of the cranium, namely the prognathism.

The X-ray method also enables the facial bone formations of living subjects to be compared with that of cranial material, and also to compare the structural variations in human beings with those of other higher primates. X-ray photography also facilitates the taking of measurements which cannot be obtained in any other way.

Among the drawbacks of the method may be mentioned the magnification of the image which necessitates using a standardized procedure in order to ensure that the results shall be fully comparable. Broadbent (1931) has done much valuable work in laying down the general principles governing cephalometric X-ray procedure.

The cephalometer or head holder used by the present author, shown in fig. 1, has been specially designed with a view to carrying out field work and using it in museums and the like. It is of portable design, having a total

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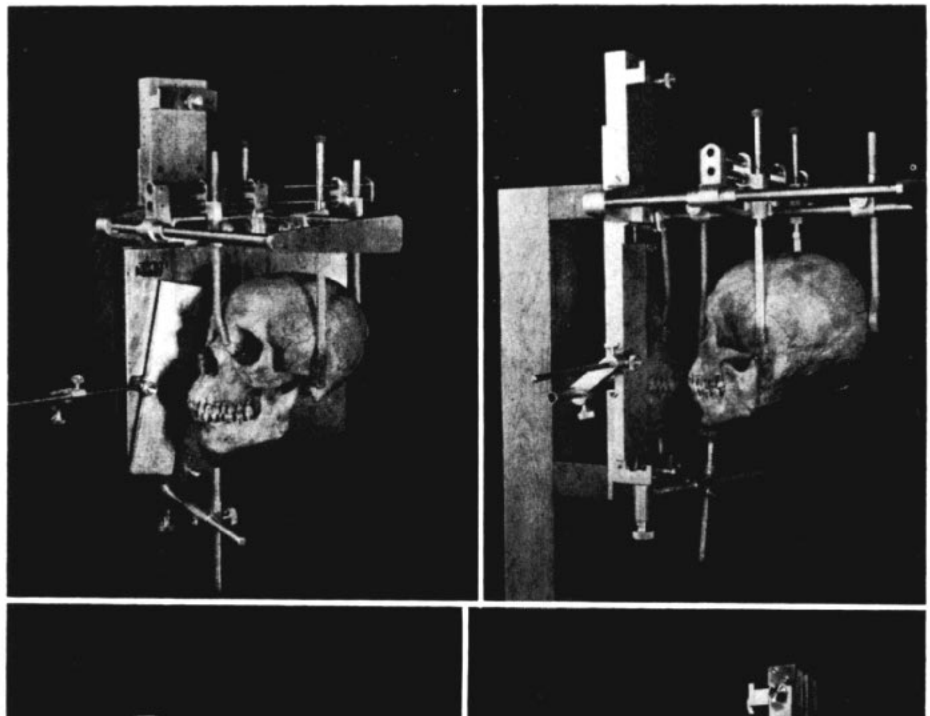


Fig. 1. Portable head holder for X-ray photography. The photographs illustrate how the head holder is used when taking lateral, frontal and basal exposures of the skull, as well as joint exposures.

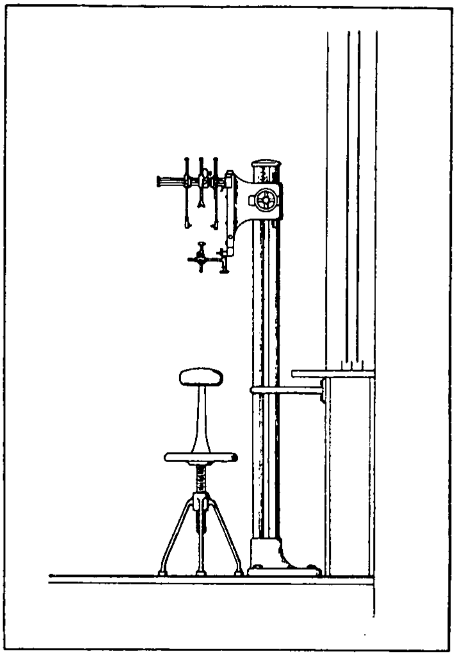


Fig. 2. The head holder with fixed mounting.

weight of 15 lbs., and can be mounted on a packing case, a wall, or even in an automobile. It may also be equipped with a fixed frame for stationary use, fig. 2. This type of instrument enables different projections to be obtained with the same X-ray equipment. The profile of the soft tissues may be brought out on the film by inserting a wedge-shaped aluminum filter between the subject and the film, as shown in fig. 1.

The head holder may be used for obtaining films of living subjects as well as crania up to the size of a gorilla skull. It is also provided with a device for photographing the jaw joint according to the method devised by Lindblom (1936). The joint can be photographed with the head located with the same degree of accuracy as that employed when photographing the skull.

Of the head exposures, the lateral one is found to be the most useful. By keeping the distance between the focal X-ray point and the median plane of the head constant and also maintaining a fixed distance between the median plane and the film, the magnification will always be identical, irrespective of the breadth of skull, as the majority of reference points are located in the median plane and the central ray is made to coincide with both ear holes. The distances used by the present author are 155 cm. and 9 cm. respectively. Consequently, the distance between the cassette and the median plane does not vary with the breadth of head (cf. Margolis, 1940).

With the other projections, norma frontalis and norma basilaris (figs. 1, 3 and 4), the different reference points will be located at varying distances from the film for different types of skulls and hence the measurements obtained from them will not be directly comparable. Nevertheless, the latter projections also provide a good general picture of the bone structure. The basal projection in particular is very useful when studying the asymmetry of the skull. What constitutes the most suitable datum plane for the purpose of locating the head in the head holder is a debatable point. The Frankfort plane (cf. fig. 4)

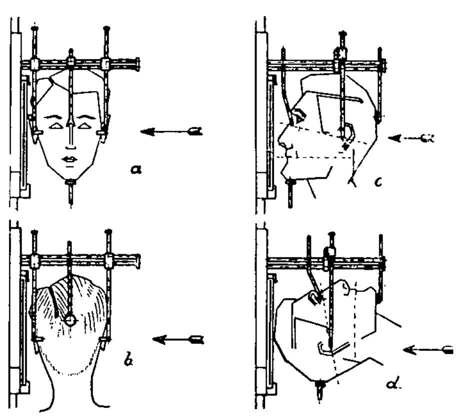


Fig. 3. Diagrammatic sketch of method of locating the skull when taking different X-ray projections, using the occlusion plane as a datum.

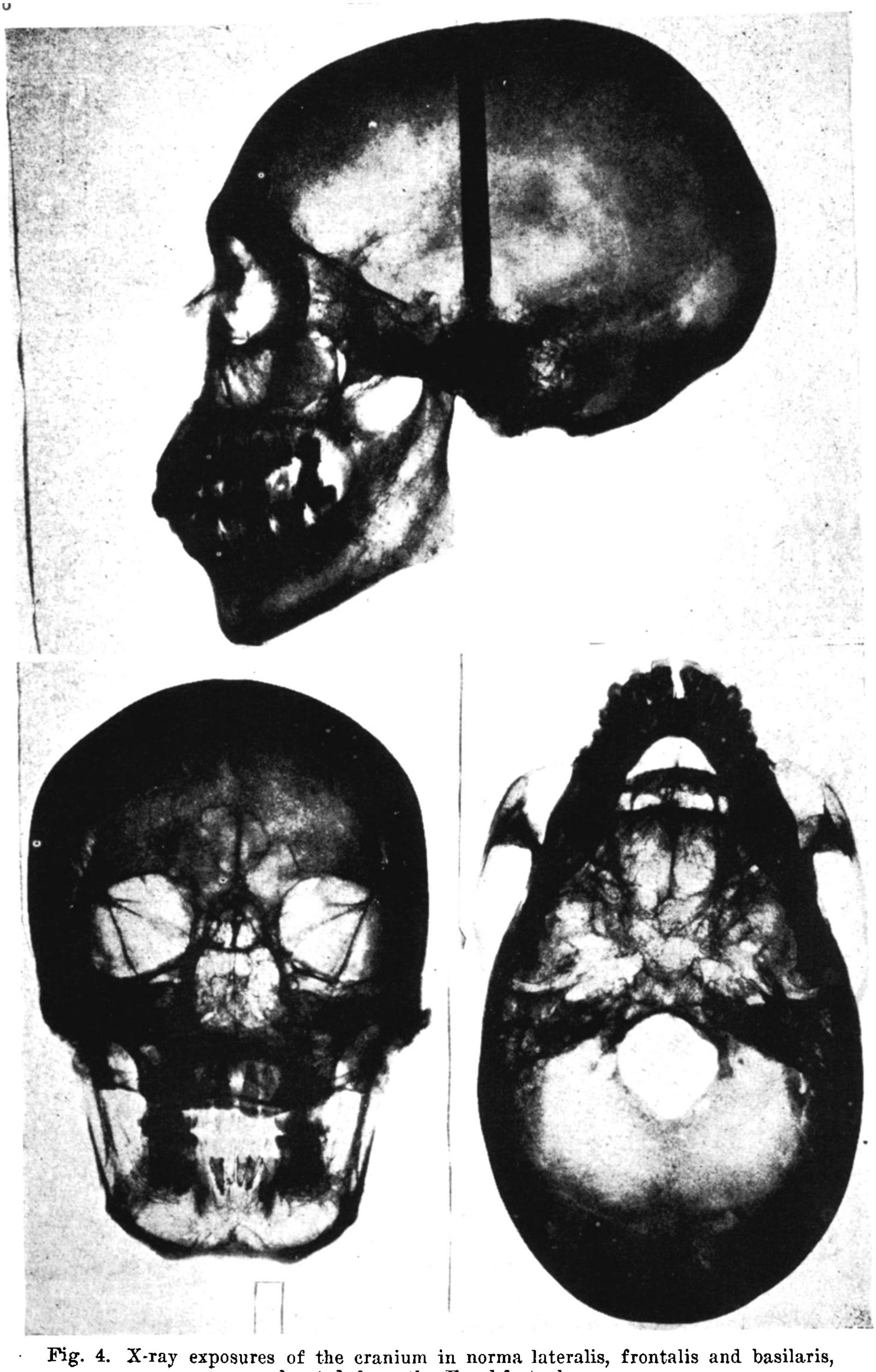


Fig. 4. X-ray exposures of the cranium in norma lateralis, frontalis and basilaris, located from the Frankfort plane.

may be used in the same manner as when locating the skull in cubus cranioforus. In this case it will be necessary to calculate the individual variations in the projection which arise with differing degrees of prognathism due to the considerable variation in the position of the bite in relation to the cranial base (cf. fig. 10, 11). The occlusal plane may also be used as a datum plane (see fig. 3) and is probably the preferable method when studying the bite in particular. In any case, the variation in the facial structure is a factor which must be taken into account when using films obtained with frontal or basal exposure.

It is quite evident that the roentgenogram can tell us no more than what we can derive from our knowledge of biology. The biological study of the variation in the facial structure is as yet only in the initial stage, and no generally applicable principles have so far been formulated for anthropological X-ray studies. The method of approach given in the following is based on a mode of investigation employed by the present author in his investigations into the nature of prognathism in humans and anthropoids.

Prognathism is the characteristic which determines the general shape of the facial profile. By differing degrees of prognathism is meant the prominence of the facial skeleton in relation to the brain case, according to Prichard's definition. Prognathism is therefore a biological conception which is not governed by any specific method of measurement. On roentgenograms the degree of prognathism may be determined by measuring the angle formed between the facial profile and the cranial base.

The cranial base is defined as the wall separating the brain case and the facial skeleton, fig. 5. One datum plane is drawn through the frontal part

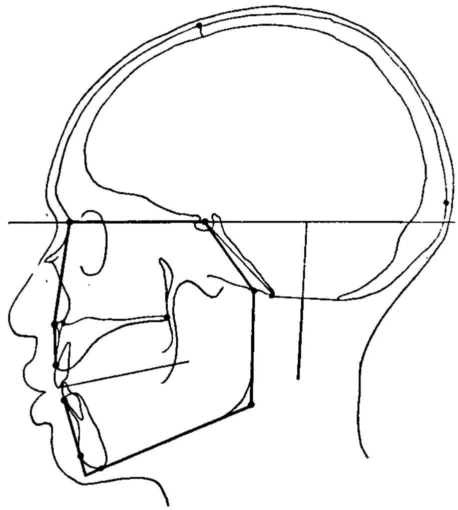


Fig. 5. Facial diagram for measuring variations in facial structure and the cranial base from a lateral X-ray exposure.

of the cranial base and passing through nasion and the center of sella turcica, as described by Brodie (1941). The errors of measurement which arise when using these reference points are quite insignificant according to statistical investigations carried out by the present author with a view to determining the relative accuracy of measurement of the different points obtained in lateral X-ray projection (1947). By selecting the center of sella turcica as a point of measurement instead of, say, some anatomical point, *e.g.* the apex of proc. alae parvae, it has been found possible to eliminate the difficulty which sometimes arises when photographing ancient crania from which these processes are often missing. It may also be mentioned that in the case of gorillas it is difficult to distinguish this anatomical point in the X-ray, in contrast with the chimpanzee and the orang-outan.

The degree of prognathism is thus determined by measuring the angle formed between the frontal part of the cranial base and various profile lines drawn from nasion to different profile points on the facial skeleton, see fig. 6.

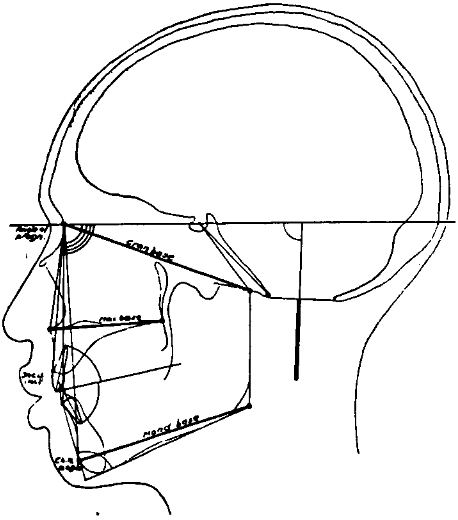


Fig. 6. Diagram indicating the method of measuring the angles of prognathism and the size of the jaws and the cranial base from a lateral X-ray exposure.

1. Maxillary b a s a l prognathism: The angle formed by the cranial base and a profile line through nasion and the nasal spine.

2. Maxillary alveolar prognathism: The angle formed by the cranial base and a profile line through nasion and prosthion.

3. Mandibular alveolar prognathism: The angle formed by the cranial base and a profile line through nasion and infradentale.

4. Mandibular basal prognathism: The angle formed by the cranial base and a profile line through nasion and pogonion.

As the roentgenogram provides a direct measurement of the shape and size of the cranial base, it is preferable to measure the prognathism from the cranial base rather than from the Frankfort plane; the latter passes through the face and is therefore subject to variations in the facial skeleton. This means that the variation in prognathism will be greater when measured from the cranial base, as shown previously by the author (1947). The standard deviation ($\bar{\sigma}$) of the angle denoting the degree of maxillary prognathism as determined on 281 adult Swedish males was found to be 3.6° when measured from the Frankfort plane in accordance with the definition given by Luthy, *i.e.* the usual method employed in craniometry, while the corresponding figure when measuring the angle from the cranial base was 4.1°. In the following it will be shown that the shape and relative size of the cranial base is highly significant as regards the degree of prognathism and that it is therefore natural to measure the prognathism from the cranial base. Using the Frankfort plane as a datum does not give the same pronounced relationship between the configuration of the cranial base and the prognathism — the above quoted figures for the standard deviation also bear this out.

The length of the cranial base has been defined in two different ways. First, it is desirable to measure that part of the cranial base which is directly connected with the jaw structure, *i. e.* the distance between nasion and the jaw joint (point of measurement: articulare). A n o t h e r measurement which we require is the overall length of the cranial base, from nasion to basion, *i.e.* to the frontal ridge of foramen magnum. The latter point of measurement is distinguished both on roentgenograms of living subjects and on crania, provided a suitable degree of hardness of the X-ray illumination is chosen.

The shape of the cranial base, *i. e.* its deflection, is given by the angle formed by the front and rear parts of the cranial base. This angle is measured partly between nasion—sella turcica—articulare and partly between nasion—sella turcica—basion. The location of the spinal column on the underside of the skull can be determined from the angle formed by the reference plane of the cranium, passing through nasion and sella turcica, and a line projected perpendicularly to the plane of foramen magnum.

The methods used for determining the shape and size of the cranial base are naturally, as all measurements of this type, influenced by individual variations in anatomical details. The prognathism of the maxillary base has been measured both to the apex of the nasal spine and to its base. The drawings in this paper refer to the first method, but for comparative studies the second method may be preferable as the nasal spine varies in size in different races, being short in Bantus in comparison with Swedes. In apes it is mostly absent. Further details regarding the method of measurement are to be found in an earlier work (Björk 1947).

Facial prognathism refers to the prominence of the facial skeleton as a whole, while alveolar prognathism indicates a protrusion of the alveolar arches beyond the jaw bases. Facial and alveolar prognathism are not always concurrent.

Regarding the nature of facial prognathism the author has concluded that it may arise in different ways:

1. Due to a shortening of the cranial base.

2. Due to angular bending of the cranial base.

3. Due to changes in the shape of the facial skeleton which cause the angle formed between the ramus and the cranial base to diminish.

4. Due to increased jaw length.

These different causes of prognathism may combine in various ways, and the effect of one or more causes which are active simultaneously may be compensated by one or more of the other factors having a counteracting effect, *i. e.* they tend to cancel each other out. The biological factors mentioned in the introduction will now be discussed briefly in the following, with special reference to normal variations in prognathism and occlusion.

Evolutionary Changes

It is a well-known fact that the facial structure and the dentition have passed through a great number of phases during the evolutionary history of mankind. The variety of the species which have arisen in the course of time, and of which only a few have developed into existing types, exhibit a very wide range of variation.

This development, which has materially influenced the facial structure and the dentition, has been described in innumerable works on anthropology (Bolk 1926, v. Eickstedt 1937—1943, Weidenreich 1946, 1947, Broom & Schepers 1946, Hooton 1946, Gates 1948, Keith 1949, Simpson 1949 and Straus 1949).

A diagram devised from X-ray films of baboon, gorilla, Plesianthropus transvaalensis (Broom), and Bantu (fig. 7) shows the phylogenetic differences in prognathism in the lower apes, the man-like apes, the fossile ape-man and recent homo. This difference may be summarized as follows:

1. Increasing brain volume is accompanied by a corresponding increase in the size of the brain case. The forehead also becomes more prominent.

2. The shape of skull suffers a gradual change, brought about by a deflection of the cranial base, which in the lower vertebrates consists of a more or less flat plate, such that the rear part of the cranial base is progressively swung forward in relation to the forward horizontal portion. This occurs in connection with the increasingly upright stance of the body with a progressive forward displacement of the spinal column on the underside of the skull. In the human skull the two parts of the cranial base form a fairly acute angle.

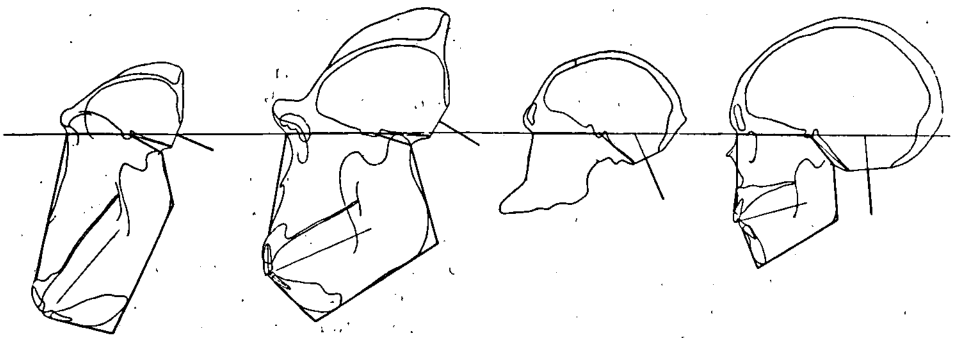


Fig. 7. Composite X-ray diagram, illustrating the phylogenetic difference in prognathism in (a) baboon (papio porcarius), (b) gorilla (gorilla gorilla, (c) fossile ape-man (plesianthropus) and (d) recent homo (Bantu).

3. The degree of prognathism diminishes, so that the snout is progressively retracted. The diminution is partly connected with the increasing breadth of the skull, and consequently of the jaws, and partly with the shortening jaw length.

These three factors, increase in brain size, deflection of the cranial base and shortening of the jaws, may theoretically develop independently. In the course of evolution these formative changes of the skull are more or less concurrent, and it is an intricate problem to determine which change came first. (Cf. Weidenreich 1943, Hooton 1946.)

As a result of the increasing skull breadth, the angle right condyle — chin point — left condyle, becomes more obtuse. The condyles move apart, the jaws become broader and therefore less prominent. The shortening of the jaws is also accompanied by a number of different changes. It affects the alveolar portions of the jaws more than the basal arches. This has the effect of straightening the facial profile from the root of the nose to the chin. The profile becomes progressively straighter, *i. e.* a condition referred to as orthognathism, which term was introduced by Retzius. Owing to the more rapid shortening of the alveolar portions as compared with the bases, the mid-facial profile and the chin appear more prominent. In this way man has developed a chin and the so-called simian shelf disappears. As the alveolar prognathism diminishes, the incisors of both jaws also become more vertical.

Owing to the reduction in the jaw length, the teeth become more closely spaced in the dental arches and it is even possible for crowding to appear as in Europeans, Eskimos (Pedersen 1947) and other racial groups.

This reduction in jaw length is also accompanied by a simultaneous rearrangement of the dentition which leads to the dental formations characteristic of different species and races (Gregory 1922, 1929, Pedersen 1949).

Summarized, the evolutionary changes may be expressed thus:

The prognathism diminishes because of a shortening of the jaws. Simultaneously with the reduction in prognathism there is also a deflection and shortening of the cranial base; the reduced prognathism does not arise from this concurrent process, but is due to the shortening of the jaws.

Prognathism in animals therefore depends upon the length of the jaws.

Racial Variations

The study of human racial characteristics is rendered more difficult by the fact that there are today no pure

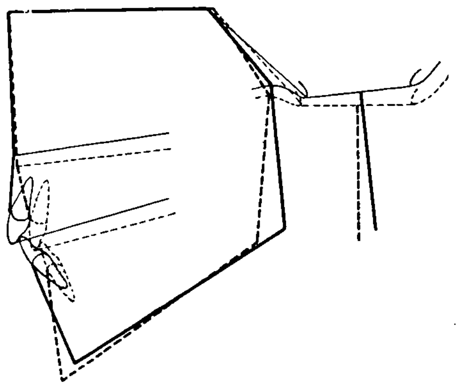


Fig. 8. Diagram showing the mean difference in facial build and prognathism between adult male Bantus (full lines) and adult male Swedes (broken lines.)

races in the true sense of the word, and therefore, if we are to find racially pure specimens, it is necessary to go back some considerable time in the history of mankind (Backman 1935, Dahlberg 1942, Lundman 1943).

Prognathism is one of the racial characteristics which has received least attention, chiefly because of the difficulty of carrying out the requisite measurements on living material. Data gathered from cranial material is more informative about the degree of prognathism than about its nature.

The question of racial variations will be illustrated here by comparing the nature of prognathism as it manifests itself in Swedes and Bantus. The differences in the facial structure seen in profile will be demonstrated by means of diagrams constructed from mean values representing these two racial groups and obtained from statistically calculated mean values of roentgenographic measurements of 281 Swedes and 238 Bantus, all adult males (see fig. 8). A more complete description of the Swedish material will be found elsewhere (Bjork 1947), while the latter material was obtained from an examination of 400 Bantus, mainly belonging to the Shona tribe, which was carried out by the author in Southern Rhodesia in 1948.

A comparison of the two diagrams will show that the alveolar prognathism is more pronounced in the Bantus, which has the effect of making the incisors more protrudent and the chin more recessive. Nevertheless, the difference in the degree of facial prognathism between the two groups is less marked than the difference in its nature.

In the Bantus the jaws are longer in relation to the cranial base than in the Swedes, at the same time as the cranial base is flatter and foramen magnum is located further back on the underside of the skull. The wide angle that the ramus makes with the cranial base, *i.e.* its backward slope, may possibly also be regarded as a primitive feature. The jaw angle is small.

In the Swedes the shortening of the jaws is accompanied by a forward deflection of the rear part of the cranial base. As already mentioned in connection with the evolutionary changes, the more pronounced bending of the cranial base, instead of retracting the jaw profile, has the very opposite effect. This, combined with the relatively shorter cranial base, causes the jaws to protrude, and explains why the angle of facial prognathism does not diminish in proportion to the shortening of the jaws. Another factor which also contributes to this effect is the greater forward inclination of ramus.

Regarding the dental arches in the Bantus it will suffice to mention here that they are spacious, the jaws as well as dental arches being well developed (cf. Shaw 1931). There is ample room for the wisdom teeth, which are seldom missing, and wide spacing of the teeth is very common, especially in the form of diastema mediale of the upper jaw, and frequently also in the lower jaw, cf. fig. 9.

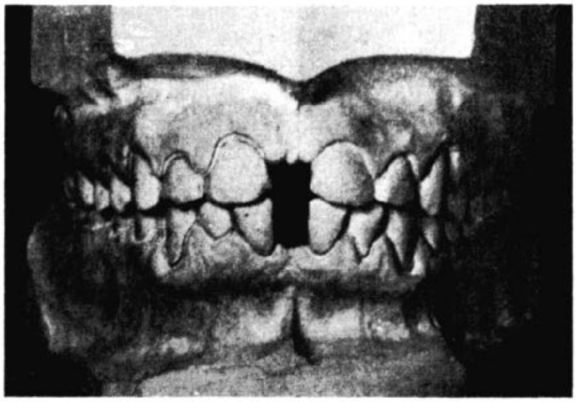


Fig. 9. Dental cast of a Shona tribesman (Bantu), showing the typical diastema mediale.

Extensive investigations covering many racial groups would naturally have to be carried out before pronouncing any more generally applicable conclusions regarding prognathism as a racial characteristic. One racial group that would be particularly worthwhile to investigate is the relatively pure West-African negroes, who have exceptionally prognathic features.

In conclusion, it may be said that the prognathism of the Bantus relative to that of the Swedes is due mainly to the size of the jaws.

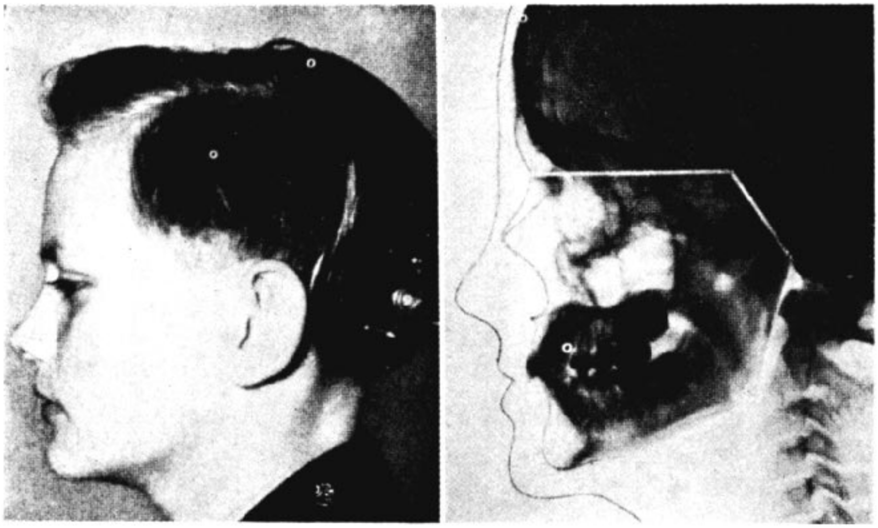
Individual Variations

Variations in prognathism also follow another line, namely the variations which characterize individuals within the same ethnic group and which are referred to as individual variations.

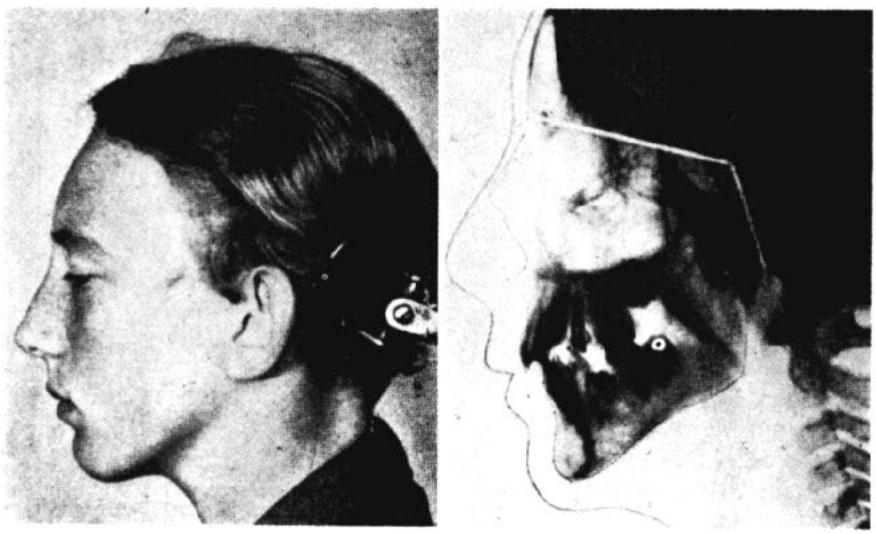
Even within the same racial group the prognathism is found to serve as a measure of the characteristic facial formation. The varying degrees of prognathism observed in a given racial group is not very intimately connected with the size of the jaws. The most significant factors are instead found to be the shape and size of the cranial base although this condition varies from individual to individual. The degree of individual prognathism is thus seen mainly to depend upon the degree of prominence of the facial skeleton as a whole due to a shortening or deflection of the cranial base. The individual variations in facial prognathism give rise to two different characteristic facial types in Swedes as may be seen from fig. 10. It shows the difference in the facial structures representing maximum and minimum degrees of facial prognathism as measured on 322 12-year-old Swedish boys.

The prognathic, prominent facial build (fig. 10a) gives the individual a characteristic appearance, which may be termed rectangular. The cranial base, measured from nasion to articulare or basion, is short compared with the length of the jaws. This is either due to a deflection of the cranial base or to a shortening of its anterior or posterior parts. The ramus is high and inclined forward, while the frontal height of the face is small, causing the jaws to be more or less parallel with the cranial base. The facial profile is fairly well in line with the forehead.

A lesser degree of prognathism (fig. 10b) results in a more triangular facial structure. The cranial base is flat, or long in relation to the size of the jaws. The ramus is short or inclined backward, the frontal facial height is great, and in this way the jaws are given a marked rearward inclination in relation to the cranial base. The facial profile forms a relatively acute angle with the forehead.



(a)



(b)

Fig. 10. Facial build representing (a) maximum and (b) minimum facial prognathism in Swedish boys.

A more detailed description of the individual prognathism will be found in an earlier work by the author (1947), containing references to statistically calculated measurements obtained from an examination of 603 Swedes.

A similar analysis has also been carried out on the data furnished by measurements taken on the previously mentioned Bantus as well as from roentgenograms of collections of crania, representing Bushmen, among other races. Statistically computed measurements indicate that the individual prognathism in Bantus follows the same lines as in Swedes, a condition which is illustrated by fig. 11, showing

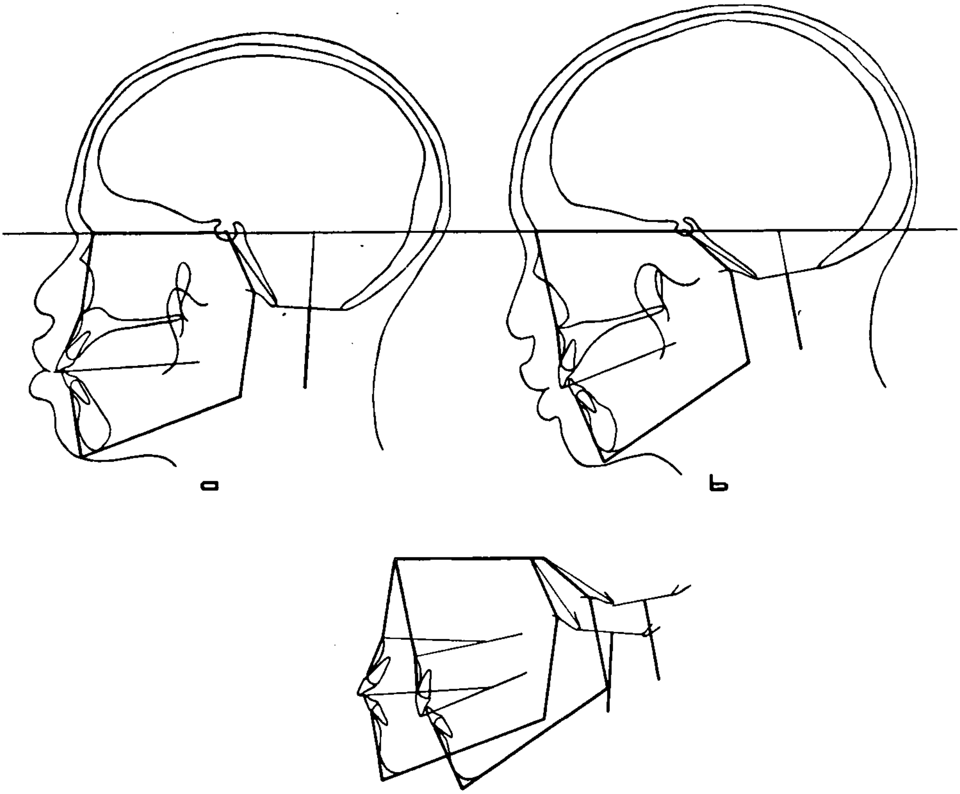


Fig. 11. X-ray diagram illustrating the difference in facial build in the case of (a) maximum and (b) minimum facial prognathism in adult male Bantus. A comparison of these diagrams is given in the lower figure.

a comparison between the facial structures representing maximum and minimum facial prognathism as measured on 238 adult male Bantus. Also in this material the individual difference in the facial prognathism is mainly dependent upon the formation of the cranial base. In the case of highly developed prognathism the entire facial skeleton protrudes owing to the cranial base being short or bent, and foramen magnum therefore being displaced forward on the underside of the skull. Again the difference in jaw size between individuals possessing greater or lesser degrees of prognathism is not very marked. According to the X-ray measurements taken on crania, the relationship is also very similar in the Bushmen.

The shortening of the cranial base and the forward displacement of the spinal column which occur in the course of evolution do not enhance the simultaneous reduction in prognathism, as already pointed out, but rather serve to counteract it. A shortening of the jaws has the effect of drawing in the snout, causing the highly prognathic facial profile to straighten out, *i.e.* it becomes more orthognathic.

In the human being the individual prognathism mainly depends upon a forward displacement of the entire facial skeleton, which is connected with the shortness and pronounced bending of the cranial base; this has also brought about a more forward location of foramen magnum and the spinal column on the underside of the skull, and has to some extent affected the shape of the brain case, see fig. 11. This implies that the balance of the head will differ with this form of prognathism.

In conclusion it may be said, that the individual facial prognathism mainly depends upon the formation of the cranial base.

Ontogenetic Changes

Considered from an ontogenetic viewpoint, one of the differences between humans and other mammals is the fact that the human cranium does not undergo the same growth changes as, for instance, the apes (Krogman 1931 a, b and c, Schultz 1940, 1941, 1944, Randall 1943-1944). Morphologically, humans and apes are therefore more closely akin at the infant stage than when adult. These growth changes in the facial prognathism and the occlusion are now briefly described in the present section.

In young apes the shape of the skull is very similar to that of the human skull. It is only at a later stage that it assumes the characteristic anthropoid features, with well developed supraorbital ridges and crests, at the same time as the facial prognathism become more pronounced. This accentuation of the prognathism, due to an elongation of the jaws, is also accompanied by a rearward displacement of foramen magnum on the underside of the skull and a flattening of the cranial base.

This elongation of the cranial base and the displacement of the spinal column has by Keil (1933) been denoted as the cause of the marked increase in prognathism during growth in the anthropoids, an explanation also accepted by Selmer-Olsen (1936). After studying some 130 roentgenograms of crania of the great apes in various stages of development, the present author has concluded that the elongation of the cranial base is to be regarded as a compensatory development, necessary in order to counteract the pronounced increase in jaw length. The rearward displacement of foramen magnum may, in other words, be said to counteract the forward protrusion of the facial structure.

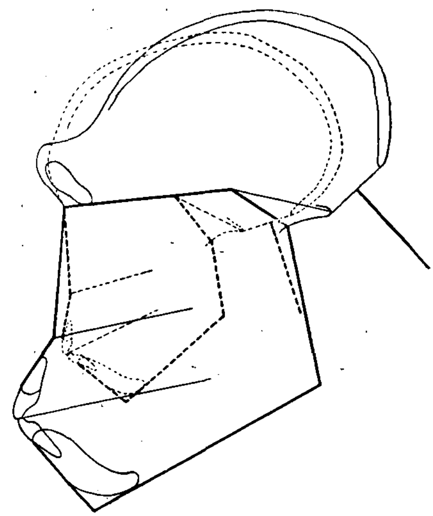


Fig. 12. X-ray diagram illustrating the differences in prognathism and configuration of the cranial base between a young (deciduous dentition) and a fully grown female chimpanzee.

It will also be seen from fig. 12 that the increase in prognathism as measured from the cranial base is quite moderate. The usual method of measuring it from the Frankfort plane gives an exaggerated estimate of the changes in the prognathism, owing to the change in the position of this plane itself during growth.

It is a well known fact that the growth changes in man are much smaller than in apes. According to Brodie (1941) the degree of maxillary prognathism in Americans remains practically unaltered during the first years of infancy of the human. However, the investigations carried out by the present author all go to show that the rate of increase in prognathism is greater during the later years of adolescence, which is in keeping with the fact that the development of the cranial base is

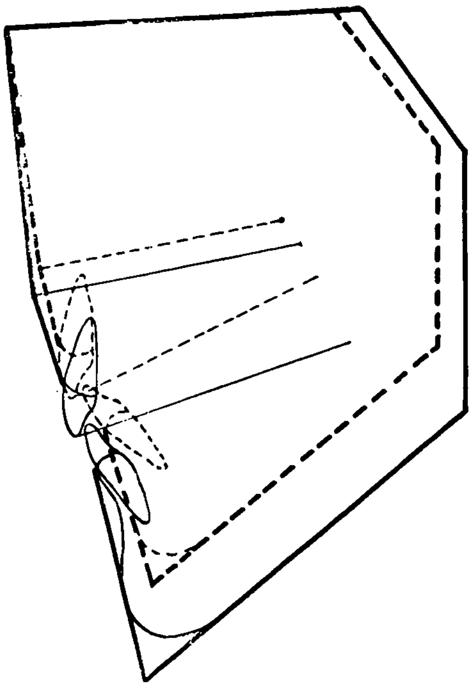


Fig. 13. Diagram illustrating the mean difference in pronathism between Swedish twelve-year-old boys and adult men.

(Since the preparation of this engraving, Dr. Bjork has submitted a new figure which adds lines of axial inclination to the incisors above. The upper incisor is labeled 3, the lower 6. The art work arrived too late for inclusion here. —Ed.)

concluded earlier than the growth of the jaws. A comparison of the facial prognathism of 322 twelve-year-old Swedish boys with that of 281 adult males indicated that the prognathism increases somewhat during growth, fig. 13. As no changes in the shape of the cranial base could be detected in the Swedish material, the altering relation between the cranial base and the jaw length will consequently entail an increase in prognathism. The increment in jaw length is almost proportional in both jaws. A slightly greater increase in the mandibular prognathism than in the upper jaw is explained by the whole mandible being displaced forward somewhat in relation to the upper jaw. This movement of corpus mandibulae is associated with the increasing height of the ramus, which during the same period grows at double the rate of increase of the frontal facial height.

The greater rate of mandibular as compared with maxillary prognathism serves to straighten the facial profile as the individual grows older. Another factor which contributes to this effect is the slower rate of increase in alveolar compared with basal prognathism, so that the incisors tend to become more upright and the chin more pointed. The forward displacement of the lower in relation to the upper jaw also changes the occlusion in such a manner that the dental arch of the lower jaw moves forward somewhat in relation to the maxillary dental arch.

Owing to the lagging increase in alveolar prognathism compared with the basal prognathism, and the consequent erection of the incisors, the crowns of the teeth are pressed closer together. This ontogenetic factor is the second reason mentioned here for the crowding observed in the Swedish material.

The present author has also carried out an investigation of the growth-changes in the Bantus, based on X-ray films of Shona tribesmen taken in S. Rhodesia in 1948. As the members of the primitive Shona tribe are not acquainted with the conception of time as reckoned in years, they were unable to state their ages, and it was instead necessary to divide them into groups according to dentition. Group I includes 24 boys and covers a range extending from milk dentition up to completed eruption of the first molars, group II, 47 boys and covers the period up to eruption of the second molars, while group III embraces 238 adult men. Also in the Bantus the changes in prognathism and occlusion follow the same lines as the author has indicated to be the case with the Swedes, *i.e.* the prognathism of both jaws increases with age, the increment

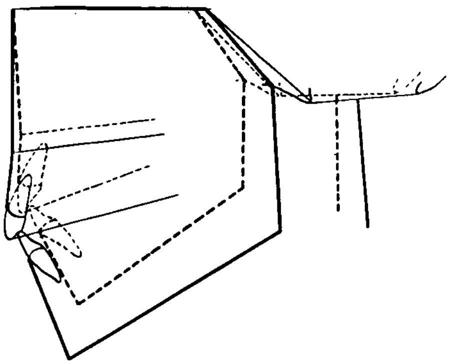


Fig. 14. Diagram illustrating the mean difference in prognathism between Bantu boys (mixed dentition) and adult male Bantus.

in mandibular prognathism being greatest, the incisors become more erect and the chin less recessive, etc., fig. 14.

The dentition of the Bantus will be dealt with in another paper describing about 200 dental casts taken by the author in the course of his Bantu investigation.

It has been found in the Swedish material that the lower jaw exhibits a proportionally greater growth increase in height than the upper part of the face. Such is also found to be the case with the Bantus. A comparison of the facial profile height in young Bantu boys with that of the adults reveals that the increment in the size of the lower jaw is 19 per cent against 12 per cent in the upper jaw and nasal part of the facial skeleton, fig. 14. The same relation also exists in other mammals, *e.g.* the horse, as demonstrated by Lundholm, and in the apes according to Schultz and others.

The present author has demonstrated that the growth changes are widely different for different parts of the facial skeleton, and that a significant change in the facial profile and shape of the jaws occurs during childhood and adolescence. These are significant factors in judging the normal development of the dentition. However, it should be noted that the proportional growth changes are not constant but appear to vary from individual to individual. Cf. the serial studies of facial growth (Brodie 1941) and dentitional development (Broadbent 1941, Sillman 1948). This fact naturally complicates the question of deciding the changes that have been brought about by orthodontic treatment.

The relative growth changes as between the cranial base and the jaws appear to be essential factors in the formation of the facial skeleton. An investigation into this question which was carried out on the Shona tribe has also furnished some interesting results.

The Shona people are dolichocephalic, the cranial index of the adults being 73.1. The shape of the brain case does change, in that the forehead becomes more recessive with increasing age. The cranial base also undergoes a change in shape, becoming flatter, and foramen magnum suffers a rearward displacement. The angle formed between nasion — sella turcica and basion consequently widens with age, see fig. 14. In other words, the balance of the head changes in the same manner as in the anthropoids. The question therefore arises, what is the reason for the greater retention of shape of the cranial base in Swedes? It might be thought that this is due to a racial difference, but there is also the possibility that it is the result of domestication.

The problem of the influence of domestication is dealt with in the following section.

Domestication

In the following section we shall consider the factors which may affect and alter the prognathism and dentition in existing racial groups. Cultural and racial changes within a given people are usually concurrent, and it is therefore not an easy matter to distinguish between the effects of these two influences on the facial structure and on the dentition. Regarding the cultural changes, we do not yet know what effects a change from a primitive to a civilized mode of life has on the human being. This question has been more thoroughly investigated in relation to animals, in which the species and racial groups are more distinct. By comparing the effect of captivity and domestication on different animals it may be possible to throw some light on the problem.

In the literature on biology in general, and zoology in particular, there are several extensive works which deal with the nature of captivity and domestication (Colyer 1936, Herre 1943, Lundholm 1947). By the effect of domestication is meant the changes which take place in successive generations of a species of animal when its mode of life becomes dependent upon the human being. Our domestic animals were originally wild, and have undergone the domestication process in the course of many generations. Even wild animals which are held in captivity in parks, zoological gardens, etc. are subject to marked changes in a morphological and psychological nature (Zuckerman 1932, Yerkes and Yerkes 1945). The changes entailed by captivity are supposed to be more or less identical with the effects of domestication, excluding pathological changes.

From a morphological viewpoint the effect of domestication is to widen the range of variation, *i.e.* to give rise to a greater variety of morphologic character. The changes brought about in this manner find different forms of expression in different animals, certain species apparently being more resistant in this respect than others.

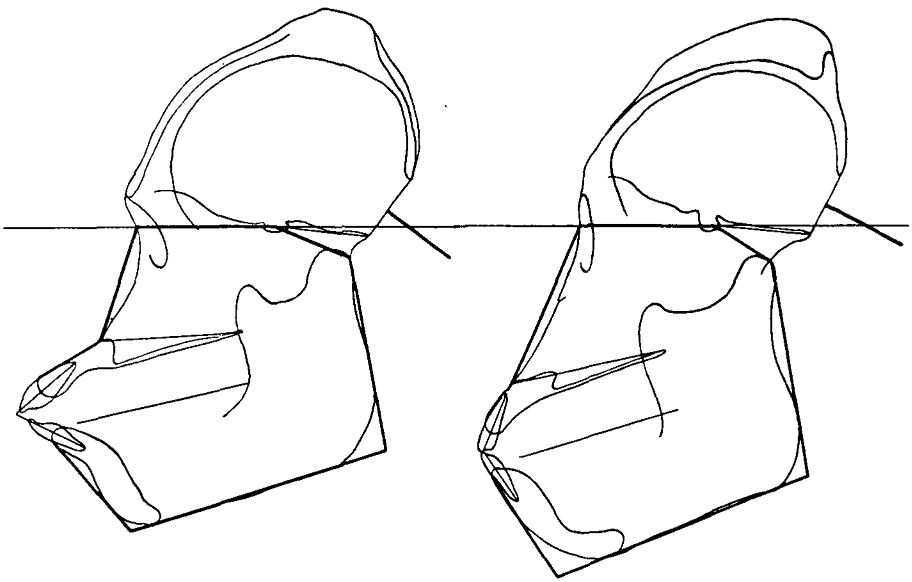
In his highly interesting thesis on the nature of domestication, Lundholm (1947) deals with the problem very thoroughly in relation to the horse. It appears from the literature on the subject that it is possible to distinguish between different features of domestication. One such feature is a general reduction in the size of the body. In some animals there is a reduction in the size of the head, and thus also in the brain volume. In the latter case there may be no proportional diminution in the size of the teeth, corresponding to that of the jaws and brain case, so that there is less space available for them in the jaws and crowding results, as in the domestic dog.

Yet another feature of domestication is an increase in the breadth of the head in relation to its length, as in pigs. The same feature is also observed in captive lions as demonstrated by Hollister (1917). The resultant effect is to make the skull proportionally broader.

Other distinct changes in the shape of the skull may also occur, and this is particularly noticeable in the pig. The skull of the wild pig is narrow and elongated, whereas in the domesticated pig the skull rises sharply at the back. Hilzheimer (1937) has also described a marked change in the shape of the skull of the gorilla Bobby, which was reared in the Berlin Zoo.

The present author has also detected cranial signs of captivity in the orang-outan Jacob, which was reared in the zoological gardens in Copenhagen. The cranium and skeleton are preserved in the University Zoological Museum in Copenhagen.

In fig. 15, a diagram from an X-ray exposure of Jacob is compared with that obtained from a wild specimen. Another comparison of the shape of Jacob's skull and face with that of a wild orang-outan is given in figs. 16 and 17. It will be seen that in the case of the captive ape the shape of the skull is different. The absence of the sagittal crest and the low points of fixture for the temporal muscles are naturally accounted for by the subnormal development of the jaw muscles due to captivity. (Cf. experimental study by Washburn 1947.)



(a) (b)

Fig. 15. X-ray diagrams of (a) the orang-outan Jacob, and (b) a wild orang-outan of the same age and sex, showing the reduced facial prognathism of Jacob who was reared in captivity.

As regards the facial structure, there is a marked reduction in the degree of prognathism; the reduction is greater in the basal than in the alveolar prognathism, which has the effect of giving the facial profile an outline hardly found among wild specimens, and resulting in a horizontal position of the incisors and in a bite which is open at the front. The same concavity of the upper facial structure is also a familiar feature of the domestic dog.

The biological nature of domestication cannot be regarded as fully investigated. In any case, it is a highly complicated process, involving a multitude of cooperating factors.

Transition from a natural life of freedom to one of captivity implies a radical change of living conditions, especially feeding habits. In many cases the food provided in capacity is both more nourishing and more abundant, but it may of course be deficient in vitamins and the like.

In captivity the freedom of movement is also very restricted, with the obvious result that the muscles are not exercised as in a natural existence.

According to Lundholm (1947) these two factors are not sufficient to explain the radical changes that occur in connection with domestication.

The most marked effect of domestication must be ascribed to other causes. One very evident difference between wild and tame animals is that the latter reach puberty at an earlier age, and consequently they have a longer life of sexual maturity, which implies a different hormone balance than in the wild animals during the growth period, resulting in a different development. Other important factors are the influence of the selection and isolation and other conditions of domestication.

Lundholm (1947) subscribes to the opinion that the effect of domestication may to some extent influence the hereditary characteristics. The well known distinction between modifications and hereditary changes is that the former are due to environmental fac-

Fig. 16. Changes in the skull structure due to captivity in the orang-outan Jacob. (Photographs provided by Dr. Phil. M. Degerbol, Univ. Zool. Mus., Copenhagen.)

tors, whereas the latter are caused by mutations. Changes in the balance of the hormones would therefore be assumed to have the effect of increasing the mutation frequency. The radical changes brought about by the domestication process cannot be accounted for by modification alone.

Since man can hardly be regarded as different from other primates the changes which the human being undergoes in adopting a civilized mode of life are likely to influence his development, morphologically as well as psychologically. In his book "Up from the Ape," Hooton says: "You are an animal, a vertebrate, a mammal, a primate, and a man because of your individual heredity — and for no other reason, whether you like it or not."

Fig. 17. Skull structure in a fully grown male orang-outan, the same as in fig. 15b. (Photographs provided by Dr. Phil. M. Degerbol, Univ. Zool. Mus., Copenhagen.)

In studying the changes in the dentition due to the process of civilization, it is necessary to take into account other factors than merely changes in diet. It is also essential to distinguish between cultural and racial changes when pursuing the studies — this distinction is not always observed (Price 1945). To what extent the civilized mode of life will increase the variety in occlusion and spacing of the teeth, and the mechanics of such changes, is not yet clear. It will be mentioned here that the analysis of the Swedish material (1947) will show that in cases of crowding of the teeth the facial prognathism is reduced due to shortening of the facial structure as a whole, not only of the alveolar arches. Crowding is thus, besides local variations in the dental arches, a symptom of reduced facial prognathism.

In summarizing the effect of domestication on prognathism in animals we may say that the degree of prognathism in both jaws may be reduced by a shortening of the jaws, which, provided that the same applies to the human being, will be the third cause of crowding mentioned above.

Racial Mixture

The factors discussed hitherto have affected both jaws about equally, and the bite has therefore also been regarded as an entity so far. However, there is not full correlation between maxillary and mandibular prognathism, and in the Swedes the coefficient of correlation is 0.62. It follows therefore that the degree of prognathism may in certain cases be different in the upper and lower jaw. This difference in prognathism is also the most dominant cause of the variation in the sagittal occlusion, which has been demonstrated statistically by the author (1947). In Swedish male adults the average maxillary overjet (horizontal overbite) was found to be 3 mm, as determined by X-ray measurements. The individual variation, however, was considerable, the biggest figures being 16 and 9 mm for maxillary and mandibular overjet respectively. It is evident that a range of variation which covers 25 mm cannot be altogether caused by local changes in the dental arches. (Cf. Seipel 1946, Downs 1948, Elsasser and Wylie 1948, Heath 1948, Lundström 1948.)

Considered from a morphological viewpoint, differences in prognathism in the upper and lower jaw may arise in two different ways. Firstly, there is the relative size of the jaws, which may be of significance in many cases. The most important factor influencing the sagittal occlusion is, however, the relative position of the jaws. The diagram in fig. 18 illustrates how such differences in the relative jaw position may arise. It shows how the mutual position of jaws of a given size may be varied by combining them with different lengths of cranial base. See also fig. 19. The previously used methods of measuring the degree of prognathism from the Frankfort plane have not been able to demonstrate the manner in which the configuration of the cranial base influences the prognathism and the occlusion.

It is evident that changes in jaw position may also to some extent be

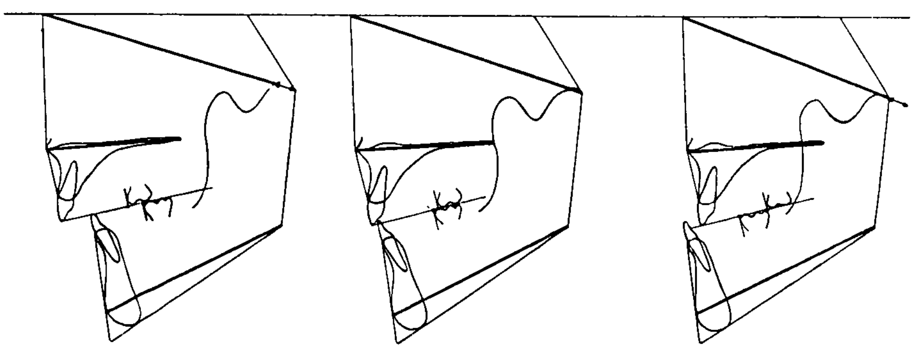


Fig. 18. Diagrammatic sketch showing the significance of the formation of the cranial base in relation to changes in occlusion. The jaws are the same size in all the diagrams. Diagram (b) depicts normal occlusion when the jaws and the cranial base are in proportion. If the cranial base is elongated (a), a corresponding increase is obtained in the maxillary overjet (horizontal overbite). If, on the other hand, it is shortened (c), the relative position of the jaws is altered to produce mandibular overjet.

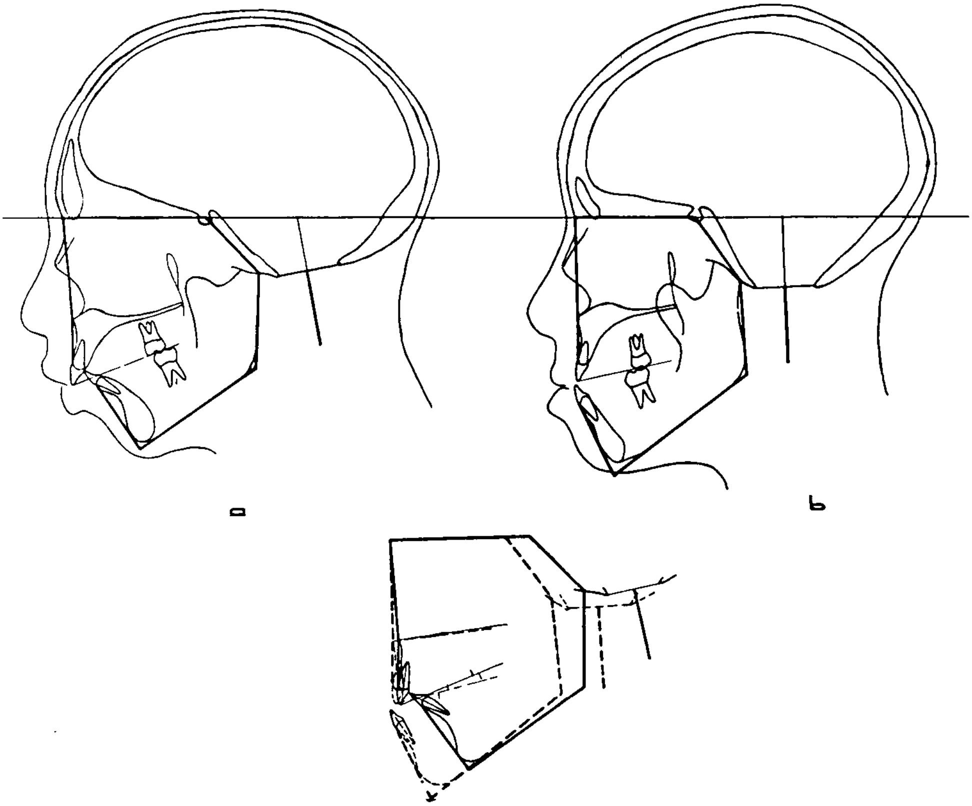


Fig. 19. Facial diagram exhibiting (a) pronounced maxillary overjet (horizontal overbite), and (b) pronounced mandibular overjet in primitive adult male Bantus. A comparison of these two diagrams is given in the lower figure.

affected by a displacement of the condyles in the fossa in different cases of forced bite, as demonstrated by Thompson (1946, 1949) with X-ray exposures, taken with the lower jaw in the rest position. It is also appropriate to mention here that in different individuals the different causes of variation in sagittal occlusion may combine in different ways.

One method of obtaining an estimate of the variation in the relative size of the jaws is to calculate the index expressing the length of the upper jaw as a percentage of that of the lower jaw, see fig. 6. Similarly, the influence of the cranial base on the relative position of the jaws may be expressed by another index denoting the length of the jaw base in relation to that of the cranial base. The result will be the same whether the total length of the cranial base, from nasion to basion, is measured, or only the distance to the jaw joint, provided that there is no major displacement in the jaw joint.

The important point is now to determine the biological factors which may account for the widely varying degree of prognathism in the upper and lower jaw in the human being. It appears obvious to assume that the highest degree of correlation between maxillary and mandibular prognathism will be found in unmixed races, and that the correlation will diminish with racial mixture. One consideration in support of this assumption is the fact that changes in molar occlusion are very rare in the other primates, the species and racial groups of which are more clearly defined. The investigations carried out by Pedersen in Greenland (1947) also established that such irregularities in sagittal occlusion are extremely rare among the racially pure East Greenlanders. It is a known fact that racial mixture increases the varieties, as borne out by Fischer's investigation of Boer-Hottentott hybrids (1913). Naturally it is also feasible that hybrids will exhibit a wide variation in respect of size of teeth and dental arches, and hence also in crowding, or in spacing as in the Bantus, fig. 9.

According to early Portuguese records the Shona tribe examined by the present author in Southern Rhodesia were already settled in the country by the sixteenth century. In the course of time the Shona tribe has intermingled to some extent with members of the surrounding Bantu tribes. Very little is known about the origin of the Shonas or any of the other Bantu peoples. According to Dart (1946 a) the Bantus of South Africa arose from the fusion of three other groups possessing greater racial stability, namely West African Negroes, Hamites and Bushmen. Whether this thesis is correct or not, the Bantus must in any case be regarded as being of mixed racial origin, and their component racial features are characterized by a varying degree of prognathism and a varying shape of the cranial base. Although the occlusion in the Shona people is usually perfect, and crowding is rare, the individual variation in occlusion is relatively wide. As they are a primitive people this variation can hardly be ascribed to the effects of "domestication," and therefore it appears more reasonable to seek the explanation in the mixed racial composition, evidence of which is also found in the very wide variation in the facial structure, indicated by the facial photographs of about one hundred individuals which are included in the material gathered by the author in S. Rhodesia.

The average maxillary overbite in the Shona is 3.3 mm and the range of variation 16 mm. The biggest maxillary overbite in adult males examined is 11.2 mm, and the biggest mandibular overbite 4.8 mm. Fig. 19 shows a comparison of these extreme cases, and incidentally also exhibits a noticeable difference in the length and shape of the cranial base.

As there are no comparable measurements of occlusion and prognathism available for representative groups of Negroes, Hamites or Bushmen, it is naturally not possible to reach any final conclusion regarding the influence of racial mixture on occlusion. Judging from the available literature (Drennan 1929, Abel 1932) and from the cranial X-ray plates gathered by the author during his visit to S. African museums, it appears that the prognathism and occlusion of the Bushmen is more constant.

Both domestication and racial mixture have the effect of increasing the variety. Zoological material indicates that domestication in some animals brings about a marked change in the skull structure and a reduction in the prognathism of both jaws. Apart from the variations in the position of the incisors, which is a condition observed in many primates living wild, changes in molar occlusion are very rare occurrences, even in domesticated species of animals. Neither does there appear to be any proof to show that changes in occlusion increase with domestication, but the possibility of a functional change in the muscular system of the head and neck must be considered in this connection (Dart 1946 b).

The significance of racial mixture in relation to irregularities in occlusion, such as discussed in the above, would be to bring about a greater variety, with a consequent reduction in the correlation between maxillary and mandibular prognathism.

This account of the various biological problems related to the facial formation is primarily intended as a brief survey. Extensive comparative investigations would naturally be needed in order to clarify these points which are of fundamental significance in understanding the cause of anomalies of the face and bite.

Much of the cranial material required for the purpose of this investigation was placed at my disposal by various institutions, and in particular I wish to express my gratitude to Professor H. Rendahl, Riksmuseum, and Professor G. Lindblom, the Ethnographical Museum, Stockholm, Associated Professor H. Berlin, the Zoological Institution, Lund, to Dr. Phil. M. Degerbol, the Zoological Museum, and K. Bröste, M.D., the Anthropological Laboratory, Copenhagen, to Dr. R. Broom, Transvaal Museum, Pretoria, to Professor M. R. Drennan, the Anatomical Institution, Dr. K. H. Barnard and Miss M. Shaw, South African Museum, Cape Town. I am also indebted to Professor P. O. Pedersen of the Dental School, Copenhagen, for permission to study the collection of dental casts from Greenland. Through the kind offices of the Swedish Church Mission I was able to carry out the Bantu investigations at the Mnene Hospital in S. Rhodesia, Head Dr. L. Hallström. I am also indebted for a research fellowship at the Northwestern University Dental School, Chicago, for the purpose of furthering my studies in the U.S.

Summary

The nature of prognathism has been studied on more than 1,000 individuals by the use of lateral X-ray exposures of the skull. These investigations have been carried out on living groups of people (Swedes and Bantus) as well as on cranial material (Bushmen, etc.).

The method employed in measuring the degree of prognathism and variations in the facial structure is illustrated in fig. 6. The result of these investigations may be summarized as follows:

1. A prognathic facial build may arise in different ways:
   a) Due to a shortening of the cranial base.
   b) Due to angular bending of the cranial base.
   c) Due to changes in the shape of the facial skeleton which cause the angle formed between the ramus and the cranial base to diminish.
   d) Due to increased jaw length.

These different causes of prognathism may combine in various ways, and the effect of one or more causes which are active simultaneously may be compensated by one or more of the other factors having a counteracting effect, *i.e.* they tend to cancel each other out.

2. Prognathism may express itself differently in different races. The question of racial variation will be illustrated by comparing the nature of prognathism as it manifests itself in Swedes and Bantus, fig. 8 (mean value diagrams of adult males). In Bantus the jaws are longer in relation to the cranial base than in the Swedes. At the same time the cranial base is flatter and foramen magnum is located further back on the underside of the skull, which has the effect of counteracting the forward protrusion of the facial structure, *i.e.* diminishes the degree of prognathism. A similar effect has the rearward inclination of ramus.

The alveolar prognathism is more pronounced in the Bantus, which has the effect of making the incisors more protrudent and the chin more recessive.

3. A varying degree of prognathism within a population is mainly due to variations in size and shape of the cranial base. Even within the same

ethnic group the prognathism is found to serve as a measure of the characteristic facial formation. The varying degrees of prognathism observed in a given racial group is not very intimately connected with the size of the jaws. The degree of individual prognathism is thus seen mainly to depend upon the degree of prominence of the facial skeleton as a whole due to a shortening or deflection of the cranial base, foramen magnum being displaced forwards on the underside of the skull. The individual variations thus give rise to different characteristic facial types, as will be seen from figs. 10 and 11. (Fig. 10 illustrates maximum and minimum degrees of facial prognathism in Swedish boys, and fig. 11 in adult male Bantus.) The individual variation in prognathism follows the same line also in Bushmen.

4. The degree of prognathism increases somewhat during the growth, owing to the greater rate of increase of the jaw length as compared with the length of the cranial base. The mandibular prognathism increases slightly more than the maxillary prognathism because of the proportionately large increase in the ramus height. This gives rise to a change in the occlusion, see fig. 13 (mean value diagram of Swedish boys and adult males).

5. On an average, prognathism affects both jaws equally — total prognathism. In certain cases the maxillary prognathism is greater than the mandibular prognathism, while in others it is the converse, accompanied by corresponding changes in the occlusion.

The difference between maxillary and mandibular prognathism is partly due to the varying size of the jaws, and partly to the variations in length of the cranial base which joins the two jaws. The influence of the cranial base on the occlusion is illustrated in fig. 19. (Extreme variations in occlusion exhibited by Bantus.)

6. The correlation between maxillary and mandibular prognathism appears to diminish as a result of racial mixture.

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