A STUDY OF THE PULP CAVITIES AND ROOTS OF THE LOWER PREMOLARS AND MOLARS OF PROSIMII, CEBOIDEA AND CERCOPITHECOIDEA[1]

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In a study published in 1939, I had stated: "*From the fact that the Eocene primates and the living Cercopithecidae appear to be cynodont it is inferred that the South American monkeys have acquired taurodontism independently of the higher Anthropoids and fossil Hominids.*"[2] During a second visit to the United States in 1946–1947, I had X-rayed a number of additional fossil[3] and recent specimens. In view of this additional material I have decided to reconsider the problem of taurodontism in Prosimii, Ceboidea and Cercopithecoidea and the light it throws on the origin of taurodontism in the South American monkeys.

THE MATERIAL

The number of the individuals X-rayed is listed in Table 1. Altogether I have so far had X-rayed the permanent teeth of 55 specimens belonging to Prosimii, Ceboidea and Cercopithecoidea. The

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[1] The classificatory terms Prosimii, Ceboidea and Cercopithecoidea are after Simpson, 1950, pp. 61-66.

[2] Şenyürek, 1939, p. 122.

[3] In 1939 a specimen of Pelycodus frugivorus, one Adapis parisiensis and one Microchoerus (Necrolemur) edwardsi had been X-rayed at Harvard University. During 1946 - 1947 I have had X-rayed the following fossil primates at the American Museum of Natural History of New York :

1 *Pelycodus trigonodus*
1 *Notharctus osborni*
1 *Notharctus crassus*
1 *Adapis magnus*
1 *Amphipithecus mogaungensis*
1 *Apidium phiomensis*

skiagrams of all the fossil genera X-rayed and most of the modern genera are shown in the plates appended to this study.[4] The material X-rayed was obtained from the Peabody Museum and the Museum of Comparative Zoology of Harvard University, the American Museum of Natural History of New York and the United States National Museum in Washington, D.C.[5]

DEFINITION OF TAURODONTISM

In the first decade of this century it was observed that the teeth of Neanderthal Man, though variable, had rather large pulp cavities.[6] Sir Arthur Keith, the eminent British palaeoanthropologist, in a paper published in 1913, designated the condition of the molars where the pulp cavities were enlarged at the expense of the roots

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[4] For comparison with the primates studied in this paper the skiagrams of one cynodont and one taurodont *Hylobates* and of two taurodont *Symphalangus* are appended to the plates (figs. 53-56).

[5] On this occasion I wish to extend my thanks to the Ministry of Education of Turkey and to the University of Ankara for sending me to the United States in 1946-1947 to continue my studies on the primates and to the Wenner-Gren Foundation for Anthropological Research (The Viking Fund, Inc.) of New York, for generously extending me an additional grant to further my researches.

At the same time I wish to express my gratitude to Prof. Dr. A. S. Romer of the Museum of Comparative Zoology of Harvard University for allowing me to X-ray the fossil material in his Department and to Professor Dr. E. A. Hooton of the Peabody Museum of Harvard for permitting me to X-ray the Hylobates and human material preserved in his Department. I am grateful to Prof. Dr. W. K. Gregory and Dr. E. H. Colbert of the American Museum of Natural History of New York for allowing me to X-ray the fossil and recent primates in this museum. I am thankful to Mrs. R. H. Nichols of the same museum for helping me to locate the material. I am grateful to Dr. R. Kellog of the United States National Museum of Washinton, D.C., for permitting me to study and X-ray the primates preserved in the Department of Mammals.

I am also grateful to Dr. H. Margolis of Harvard Dental School, Dr. D. F. Lynch of the Dental Hospital of Washington, D. C. (1149 16th Street, N. W.), and Mr. M. Patrick of the Diagnostic Laboratory of New York (115 Central Park West) for taking the X-rays with care and untiring patience.

Last but not least,I wish to take advantage of this opportunity for remembering the memory of the late Professor G. Allen of the Mammals Department of Harvard University for placing all the primate collections of his Department at my disposal.

[6] See Adloff, 1907-1908.

and were deeply embedded in the dental alveoli taurodontism.[7] In the same paper, Sir Arthur Keith used the term cynodontism for the condition of the molars in which the pulp cavities were small.[8]

Shaw, the famous South African odontologist, in his study of the taurodont teeth in ancient and recent natives of South Africa, has divided the taurodont teeth into three categories which are, in decreasing magnitude, termed by him hyper-taurodont, meso-taurodont and hypo-taurodont.[9] According to this South African author, the examples of hyper-taurodont, meso-taurodont and hypo-taurodont teeth are respectively the molars of some Krapina Neanderthals with very large pulp cavities, those of Heidelberg Man and the teeth of some living South African natives.[10] However, as far as I could judge from the pictures published by Shaw,[11] in at least some cases it is difficult to distinguish between the meso-taurodont and hypo-taurodont pulp cavities.[12] For this reason in this study no distinction is made between the hypo-taurodont and meso-taurodont categories, and teeth with pulp cavities of comparable size are collectively called moderately taurodont.

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[7] Keith, 1913, p. 104.

[8] Ibid., p. 104. In this connection it may be mentioned that Adloff (1907-1908) and Keith (1913, 1929 and 1931) supposed that taurodontism was a specialized feature and that the fossil hominids possessing this feature could not stand on the line of descent of Homo sapiens (see Şenyürek, 1949, p. 223). Subsequently, however, Black (1927), Shaw (1928) and Weidenreich (1937) considered taurodontism as a primitive hominid feature and admitted the fossil hominids displaying this feature into the line of evolution of *Homo sapiens* (see Şenyürek, 1949, p. 223). The researches made since 1937 have clearly shown that a moderate degree of taurodontism is a characteristic feature of the primitive hominids and that *Homo sapiens* has evolved from a moderately taurodont ancestor (see Şenyürek, 1939, p. 128 and Şenyürek, 1949, pp. 223 and 226). In this connection see also Pedersen, 1949.

[9] Shaw, 1928, pp. 479-481; Shaw, 1931, pp. 124-125.

[10] Shaw, 1928, pp. 479-581; Shaw, 1931, pp. 124-125.

[11] Shaw, 1928, fig. 3; Shaw, 1931, fig. 54.

[12] It must be noted that Shaw, in his study, has relied mainly on the external examination of the teeth. However, in the figures cited here (Shaw, 1928, fig. 3 and Shaw, 1931, fig. 54) he shows the skiagrams of a hypo-taurodont South African native in addition to those of Heidelberg Man and a strongly taurodont Krapina Neanderthal and a modern cynodont White.

Indices of the pulp cavities of some related genera and species [13] with cynodont and taurodont lower molars, based on measurements taken on the skiagrams,[14] are listed in Tables 2-4. From the figures listed in these tables it will be seen that Indices I and II, in related groups, increase from the cynodont to moderately taurodont teeth, and from the moderately taurodont to hyper-taurodont molars. That is to say, in related genera and species, in passing from the cynodont to moderately taurodont teeth and from the moderately taurodont molars to the hyper-taurodont ones the height of the pulp cavity constantly increases relative to the length of this cavity and relative to the length of the crown. On the contrary, a scrutiny of these tables (Tables 2-4) shows that in passing from the cynodont to moderately taurodont and from the moderately taurodont to hyper-taurodont lower molars, in related genera and species, Indices III and IV show a diminution. That is, in related forms, the taurodont teeth may even a have shorter length relative to the length of the crown and body. [15]

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[13] It is self-evident that of the forms listed in Tables 2-4, *Cercopithecus talapoin* (see Hooton, 1942, p. 223), being a member of the genus *Cercopithecus*, is closely related to other species of *Cercopithecus*. The indices of *Ateles* are compared with those of *Alouatta*, which according to Gregory (Gregory, 1951, p. 469) may be related to *Ateles*, and with those of the primitive genus *Callicebus* which may be distantly related to the former two genera (Gregory, 1951, p. 469).

[14] The measurements taken on the skiagrams are shown in Fig. 1. The measurements AB (height of the pulp cavity) and CD (length or mesio-distal diameter of the pulp cavity) are taken at the middle of the pulp cavity and at right angles to each other. Measurements EF and GH are respectively the lengths of the crown and body, the latter being taken at the same level as the length of the pulp chamber. The pulp cavity indices calculated from these measurements are as follows :

$$\text{Index I} = \frac{AB \times 100}{CD} \qquad \text{Index III} = \frac{CD \times 100}{EF}$$

$$\text{Index II} = \frac{AB \times 100}{EF} \qquad \text{Index IV} = \frac{CD \times 100}{GH}$$

[15] Shaw (1928, p. 483) describes "body" as follows: "*In this investigation it was essential to divide the taurodont molar tooth into three regions and to measure these regions separately(fig.4).I have adopted as more suitable the term introduced without definition by Keith, to distinguish the middle portion of the tooth, namely, the body. I have further taken the liberty to define the body for the purposes of this report as that portion of the tooth which intervenes between the lower edge of the enamel and the upper end of the groove which usually*

It has already been stated that in the taurodont teeth the size of the pulp cavity is larger than in the cynodont teeth. However, from the explanation given above it is clear that the main difference between the taurodont and cynodont teeth exists in the height of the pulp cavity. That is, in the enlargement of the pulp cavities, it is mainly the height of the pulp chamber that increases, while its length may, in at least some cases, even be reduced.

As has been pointed out by Keith,[16] in passing from the cynodont toward the taurodont teeth, as the pulp cavity enlarges, it usually encroaches more and more upon the roots (see figs. 18, 19, 20, 21, 22, 25, 26, 30, 31, 32, 40, 41, 42, 52, 53 and 54). In the hyper-taurodont teeth, this process of expansion may culminate in the extension of the pulp cavity down to the tip of the roots, and, as can be seen from figs. 21, 30 and 31, in such extreme cases of taurodontism there may not be any division of the roots at all.[17] Again as has been pointed out by Keith,[18] during this process of expansion, the pulp cavity extends more and more in the alveolar socket. A comparison of the cynodont, moderately taurodont and hyper-taurodont teeth (compare figs. 2, 5, 6, 9, 10, 12, 13, 16, 17, 21, 22, 29, 30, 37, 52 and 55) shows that the degree of extension or implantation of the pulp cavity in the alveolar socket is still relatively slight in the moderately taurodont teeth, although it is more extensive than in the cynodont teeth, in which this cavity is supra-alveolar, and that the maximum degree of extension of the pulp chamber in the alveolar socket is found in hyper-taurodont teeth.

AGE DIFFERENCES

It is a well-known fact that in the development of the molars the size of the pulp cavity diminishes gradually from the young and incompletely formed teeth to the completely formed mature teeth.[19]

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marks the division or partial division of the roots and which seems to correspond with the uppermost extent of the cementum."

[16] Keith, 1913, p. 104; Keith, 1929, p. 686.

[17] Keith, 1913, p. 104.

[18] Ibid., p. 104; Keith, 1929, p. 686.

[19] See Lyne, 1916, p. 35 and fig. 2; Shaw, 1928, pp. 484-485 and 495-496; Şenyürek, 1939, p. 120; Şenyürek, 1949, pp. 217-218 and 224-225; Tomes, 1923, p. 524; Weidenreich, 1937, p. 106.

The comparison of the immature first lower molar of a *Colobus polycomus* (Fig. 46) with the mature first lower molars of this species (Figs. 47, 48 and 49), and the comparison of the immature first lower molar of a *Cercopithecus mona* (Fig. 39) with the corresponding mature tooth of the same species (fig. 40) shows that in Cercopithecidae, also, the size of the pulp cavity diminishes from the immature toward the mature teeth.[20] Thus it is clear that this developmental process, well-known in man, is also common to the other primates.[21]

The indices of the pulp cavities of immature and mature first lower molars of *Colobus* and *Cercopithecus* are listed in Table 5. From this table it is observed that in *Colobus polycomus* and *Cercopithecus mona*, in passing from the immature toward the mature teeth Indices I, II, III and IV are reduced. However, diminution appears to be relatively more in Indices I and II than in III and IV.[22] That is, while, during the development of a molar, both the height and length of the pulp cavity diminish, the former appears to be more reduced than the latter.[23]

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[20] In a recent study Bennejeant (1953) has published the skiagrams of the teeth of some young individuals of primates. But Bennejeant has published these skiagrams only to show the sequence of eruption of the deciduous teeth and unfortunately has not discussed the size of the pulp chambers. However, a comparison of the skiagrams of the still immature permanent lower molars of a *Galago senegalensis* and a *Propithecus verreauxi*, still retaining the milk teeth, published by Bennejeant (see Bennejeant, 1953, figs. 15 and 16), with the skiagrams of the mature permanent lower molars of a *Galago crassicaudatus* and *Propithecus verreauxi* published in figs. 15 and 10 in the present paper, will show that in *Galago* and *Propithecus* also the size of the pulp cavity is diminished during the development of the teeth, as in other primates.

[21] See also Lyne, 1916, pp. 40-41; Campbell, 1925, p. 19; Shaw, 1928, p. 495.

[22] In Table 5 are listed also the indices of the pulp cavity of the immature first lower molar of a *Cercopithecus nictitans*.and those of the mature first lower molar of a *Cercopithecus mitis*. It will be observed that in the mature tooth Indices I and II are much lower than in the immature tooth, while Index IV is only minutely less in the mature specimen. On the other hand, in the mature tooth Index III is larger than in the immature tooth. However, as teeth of two different species are compared here, it is possible, but by no means certain, that this discrepancy may be due to specific differences.

[23] Courtney Lyne (1916, p. 35) attributes this process of reduction in the pulp cavity to age, while Campbell, in his excellent study on the teeth of Australian aborigines, attributes it to the progreess of attrition (Campbell, 1925, pp.

In his study of the teeth of South African natives Shaw states: "*It has been stated that in modern races the pulp cavity is relatively larger in teeth of young persons than in the teeth of adults and that this relatively large pulp character as an infantile condition is the persistence of a character that is primitive for the Hominidae.*

So far as the size of the pulp cavity is concerned, there is little doubt that teeth at an early age, not only in man but also in primates generally, do exhibit the condition of taurodontism to a more marked degree than do the teeth of adults.

It appears possible therefore that this infantile character does signify the persistence of a primitive feature." [24] Further on Shaw adds: "*From the occurrence of taurodontism, and the association of very primitive characters with taurodontism, in apes from early Pleistocene times, in primitive human fossil races from the earliest chapters of our history, in the developing teeth of primates generally and in the teeth of adults of many modern races, it appears that there is considerable support for the view that taurodontism is a primitive character.*"[25] However, as previously stated by me, the resemblance between an immature tooth that will at the end be cynodont (see figs. 39, 40, 41, 42 and 46) and a fully developed taurodont tooth (see figs. 22, 26, 30, 52, 54, and 55) is only a superficial one, and the similarity is merely confined to the fact that both have large pulp cavities.[26] A careful study of the figures cited will show that the immature tooth that will eventually be cynodont has a large pulp cavity because the roof, floor and the anterior and posterior walls of this cavity are still incompletely developed.[27] As the dentine is deposited on the roof, floor and side-walls of this chamber, during the development, the size of the pulp cavity is gradually diminished. In other words, the large pulp cavity of an immature tooth that

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18-19). The question of the reduction in size of the pulp cavity during the life of a tooth will be further discussed in detail in a coming paper on the pulp cavities of molars of ancient Anatolians.

[24] Shaw, 1928, pp. 495-496.

[25] Ibid., p. 496. It may be pointed out here that at that time Shaw was inclined to consider the Taubach tooth as that of an anthropoid, although we now know that this tooth belongs to Neanderthal Man (see Keith, 1929, p. 191 and Boule-Vallois, 1952, p. 170).

[26] Şenyürek, 1939, p. 120.

[27] Ibid., p. 120.

will eventually be cynodont is only a formative stage in the development of the tooth and is not strictly comparable to the large pulp chamber of a mature taurodont tooth.

As I have stated before, a tooth that will eventually develop into a taurodont one, starts development with a more extensive pulp chamber than a tooth that will at the end become cynodont. [28] A comparison of the immature first lower molar of *Colobus* (fig.46) and the first and second lower molars of *Cercopithecus* (Figs. 39-42) with the immature second lower molar of a *Hylobates hoolock* (fig. 54) will clearly show this. It will be seen that in the immature first lower molars of *Colobus polycomus*, *Cercopithecus mona* and *Cercopithecus nictitans* and in the second lower molar of *Cercopithecus mitis* the floor of the pulp cavity has already been formed, although it is still relatively undeveloped and thin. On the other hand, in the immature second lower molar of *Hylobates hoolock* (fig. 54) the pulp cavity is much more extensive than in these cercopithecoid teeth, almost extending down to the tips of the roots, but there is as yet no indication of the floor of the pulp chamber. If the floor of the pulp chamber had eventually been formed, it would be developed near the tip of the roots and thus this *Hylobates* tooth would be hyper-taurodont. The still immature second lower molar of this *Hylobates hoolock* shows that the taurodont teeth are formed by delaying the formation of the floor of the pulp chamber during the development of the tooth, as was described and shown by Keith [29].

Shaw considers the large size of the pulp chambers in the immature teeth as one of the indications of the taurodont ancestry of *Homo sapiens.* [30] Regarding this, in an earlier study, I made the following statement: "*Since the large pulp cavity of a young tooth represents only a formative stage its presence in young human teeth is not necessarily indicative of the taurodont ancestry of Homo sapiens, as has been suggested by Shaw (28)*" [31]. As I stated in my previous studies, there is ample evidence showing that *Homo sapiens* is derived from a moderately taurodont ancestor [32], but still the large pulp cavities of the immature teeth

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[28] Ibid., pp. 120-121 and Şenyürek, 1949, pp. 218 and 225.

[29] Keith, 1929, p. 212-213.

[30] Shaw, 1928, pp. 495-496.

[31] Şenyürek, 1939, p. 121.

[32] Ibid., p. 128 and Şenyürek, 1949, pp. 219 and 226.

cannot be used as an evidence for this. Similarly, as explained in the present paper, the large size of the pulp cavities of the immature teeth of Cercopithecidae cannot be taken as an indication that this family passed through a taurodont stage. Indeed, as will be discussed further on, there is no evidence to show that Cercopithecidae ever passed through a taurodont stage in its evolution.

It may also be mentioned here that this process of reduction in the size of the pulp cavities during the development of the teeth makes it imperative that in comparing the size of pulp cavities in various primates only the teeth which are in the same developmental stage should be compared with each other[33].

SERIAL ARRANGEMENT OF THE PULP CAVITIES

It has been known for some time that in the hominids, fossil as well as recent, and in the anthropoid apes the size of the pulp cavity increases from the first to the third lower molar[34]. For this Shaw states: "*This general transition as we proceed from the front to the back of a molar series, and which I have never seen recorded, nor have ever witnessed personally, as progressing in the reverse direction, is due, as previously discussed, to factors of age, attrition and perhaps still further undiscovered causes.*" [35] For this observation Weidenreich makes the following remarks: "*It is furthermore easy to demonstrate in almost every denture that the roominess of the pulp cavity decreases passing from the third to the first molar which, of course, corresponds to the differences in age, the third molar always erupting later than the first one. This holds good not only for recent man but also for the fossil hominids including Sinanthropus and the apes.*" [36]

The lower molars of the suborder Prosimii appear to be somewhat variable in this respect. In quite a number of the genera of Prosimii the size of the pulp cavity increases from the first to the third lower molar (figs. 6, 12, 13, and 17), in some there is not much difference between the sizes of the pulp cavities of the second and

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[33] See Weidenreich, 1937, p. 106; Şenyürek, 1939, p. 121.

[34] Keith, 1913, p. 104; Shaw, 1928, p. 486; Weidenreich, 1937, p. 106; Şenyürek, 1939, p. 121; Şenyürek, 1949, pp. 218 and 225.

[35] Shaw, 1928, p. 486.

[36] Weidenreich, 1937, p. 106.

third lower molars (figs. 10 and 11), while in one specimen of *Perodicticus potto* the first lower molar has a deeper pulp cavity than the second and third lower molars (fig. 14). On the other hand, in all genera and species of the suborder Anthropoidea, X-rayed, the size of the pulp cavity usually increases from the first to the third lower molar, as in the anthropoid apes and Man.

The increase in size of the pulp cavity from the first to the third lower molar seen in some genera of Prosimii, Ceboidea and Cercopithecoidea such as for example the ones shown in figs. 6, 32, 47, 48, 49, 50, 51, 52, 53 and 55, is probably due to age, as the third molar is the last of the permanent molars to erupt [37]. In one specimen of *Nycticebus bengalensis* (*Nycticebus coucang bengalensis*) [38] (fig. 13) and some members of Ceboidea, such as for example the ones shown in figs. 22, 23, 24, 25, 33 and 34, there is a conspicuous difference between the sizes of the pulp cavities of the second and third lower molars. The same conspicuous difference is also seen between the first and second lower molars of *Leontocebus* (figs. 19-21). It is evident that such conspicuous differences between the lower molars of the same individuals cannot be explained by age alone.

In short, the increase in size of the pulp cavities from the first to the third lower molar, seen in a large number of primates, is in the main probably due to age, while in some primates, in addition to the age factor, there is an inherent tendency to increase the size

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[37] For *Adapis* and *Notharctus* see Gregory, 1920, pp. 152-154; for Ceboidea, Cercopithecidae and the anthropoid apes see Schultz, 1935.

[38] Elliot (Elliot, 1912, pp. 23-24) recognizes ten species of *Nycticebus*: *N. borneanus*, *N. bancanus*, *N. tenasserimensis*, *N. coucang*, *N. javanicus*, *N. natunae*, *N. malaianus*, *N. hilleri*, *N. menagensis* and *N. pygmaeus*. Hill in his recent book (Hill, 1953, p. 157) makes the following statement on the subdivisions of the genus *Nycticebus*: "*As is not unexpected in a genus so widely distributed, a large number of forms have been described, many of them as distinct species. Material more recently collected from intermediate localities suggests, however, the desirability of uniting all of them under a single specific heading, Nycticebus coucang, with the possible exception of the Indo-Chinese pygmy form (N. pygmaeus) which is sufficiently distinct and appears to exist alongside a race of average dimensions.*" Hill (1953, pp. 159-163) recognizes the following subspecies: *N.c. bengalensis*, *N.c. tenasserimensis*, *N.c. coucang*, *N.c. insularis*, *N.c. hilleri*, *N.c. natunae*, *N.c. javanicus*, *N.c. borneanus*, *N.c. bancanus*, *N.c. pygmaeus*. Since whether we are going to call these distinct forms species or subspecies is mostly a matter of definition, in this paper I have used both the specific names and Hill's equivalents, the latter being placed in parenthesis.

of the pulp cavity from before backwards in the lower molars. It seems that some forms of Prosimii have developed a tendency, which must be considered as a secondary condition, to reduce the difference between the sizes of the pulp cavities of the second and third lower molars.

As in a large number of the primates, the size of the pulp cavity increases from before backwards in the lower molar series, in comparing the teeth of different genera and species, it is advisable to compare only the teeth having the same number in the lower molar series with each other, as for example, a third lower molar with another third lower molar. [39]

PULP CAVITIES AND ROOTS OF THE LOWER CHEEK TEETH OF PROSIMII INFRAORDER LEMURIFORMES [40]

In *Pelycodus trigonodus* (fig. 2) the last two lower premolars and the three lower molars are cynodont and possess two separate roots. From this skiagram it is also seen that P_2, of which the crown is missing, had two separate roots. The distal root of the third lower molar is elongated antero-posteriorly and exhibits a dilated root canal. The skiagram of one *Pelycodus frugivorus* (fig. 3) is not at all clear. But in the preserved teeth, as well as in the skiagram, the place where the roots bifurcate is seen and the body is very shallow. This indicates that in this species P_4, M_1, M_2 and M_3 were cynodont. The last lower premolar and the three lower molars have two separate roots.

In the skiagram of *Notharctus osborni* (fig. 4) the lower premolars are not clearly seen, but the three lower molars are cynodont and have two separate roots. In *Notharctus crassus* (fig. 5) the two last lower premolars and the three lower molars are cynodont and possess two separate roots. [41] In the skiagram, between C_1 and P_3, are seen the outlines of two alveoli belonging to P_1 and P_2. The configuration of the alveoli indicates that these teeth had single

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[39] Şenyürek, 1939, p. 121.

[40] After Simpson, 1950, p. 61.

[41] In 1939 (Şenyürek, 1939, p. 121) I had stated: "*Externally, the molars of Notharctus and Pelycodus too appear to be cynodont.*" Thus this statement has been confirmed by X-ray examination.

roots. [42] In this species also the distal root of the third lower molar is elongated antero-posteriorly as in *Pelycodus trigonodus*. [43]

In one *Adapis parisiensis* from the Eocene of Europe (fig. 6) the three lower molars are cynodont.[44] In this specimen the three lower premolars have larger pulp cavities than the molars. But it is evident that the premolars, which erupt later than the molars in this genus,[45] had just erupted as the side walls of the root canals and the floors of the pulp cavities are still thin and incompletely developed. So the larger size of the pulp cavities of the premolars may be at least partly due to the younger age of these teeth. In this species P_2, P_3, P_4, M_1, M_2, and M_3 had two separate roots. The distal root of the third lower molar is elongated antero-posteriorly as in some species of *Pelycodus* and *Notharctus*, from the Eocene of North America. The skiagram of *Adapis magnus* (fig. 7) is not too clear, but it is still seen that P_3, P_4, M_1, M_2 and M_3 are cynodont and possess two separate roots. Bennejeant in a recent study has published the skiagram of the mandible of an *Adapis parisiensis*.[46] Bennejeant's specimen is younger than the specimen studied by me, as in his the premolars had not yet erupted. But from his picture it is seen that in this *Adapis parisiensis* specimen also first and second lower molars are cynodont with two separate roots.

Thus the evidence of fossil Notharctinae (genera *Pelycodus* and *Notharctus*) and Adapinae (genus *Adapis*) clearly shows that in the

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[42] According to Gregory (Gregory, 1920, p. 131) P_2 of this species, as well as those of some other species, shows: "*a tendency toward the fusion of the roots.*" Regarding the first premolars of Notharctinae Gregory (Gregory, 1920, p. 127) says: "*The premolars of Notharctus may be divided into three categories: first the very small and simple $P^1/_1$, which are never replaced, erupt with the deciduous teeth, and may be homologous with them; in the upper jaw P^1 has only a single root; in the lower jaw P_1 has either a single root, e.g., Pelycodus trigonodus, N. osborni, tyrannus, pugnax, crassus, or there is a faint external groove, showing an incipient tendency to divide the root into anterior and posterior moieties (N. venticolus).*"

[43] From the photograph of the mandible of *Notharctus matthewi* published by Gregory (Gregory, 1920, pl. XL, figs. 5-6) it can be seen that the distal root of the third lower molar is elongtatd antero-posteriorly with a longitudinal groove on its buccal surface, dividing it into an anterior and a posterior portion.

[44] See Şenyürek, 1939, p. 121.

[45] For this see Gregory, 1920, p. 152.

[46] Bennejeant, 1953, fig. 7.

ancestral Lemuriformes the last two premolars (P_3-P_4) and the three lower molars were cynodont and possessed two separate roots. P_2 also very probably had two separate roots,[47] while P_1 must have been single-rooted.[48]

In the two specimens of the modern genus *Lemur* (family Lemuridae) X-rayed, the lower premolars and molars are cynodont (figs. 8 and 9). In *Lemur rubriventer* (fig. 8), only P_4-M_3 are X-rayed and they all possess two separate roots. In *Lemur variegatus* P_4-M_3 all have two separate roots, while P_2 is single-rooted (fig. 9).[49] Bennejeant has published the skiagram of the skull and mandible of a young *Microcebus myoxinus* (family Lemuridae) and from this skiagram,[50] it is seen that the lower molars are cynodont with two separate roots.

In one specimen of *Propithecus verreauxi* (fig. 10), of the family of Indriidae, the lower premolars and molars are definitely cynodont. The two lower premolars (P_3-P_4) have only one root, while the three lower molars possess two separate roots. Bennejeant has

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[47] It has already been noted that in *Pelycodus trigonodus* P_2 had two separate roots. In *Notharctus nunienus* and *Notharctus venticolus*, which are the earlier species of the genus *Notharctus*, the P_2, according to Hill (Hill, 1953, p. 501), is two-rooted. Thus it is clear that in primitive Notharctinae this tooth had two separate roots. On the other hand, in at least some species of the later forms of *Notharctus*, like the *Notharctus crassus* X-rayed, the number of roots of P_2 is reduced from two to one. For these later species of *Notharctus* Gregory (Gregory, 1920, p. 131) makes the following statement: "*P_2 exhibits considerable variation in form in the Notharctinae; in the more progressive larger species N. rostratus, N. pugnax, N. crassus it is quite different from P_3, being much smaller and simpler, with a tendency toward the fusion of the roots. This character is marked also in N. osborni and N. matthewi.*" Hill also records that in *Notharctus matthewi* P_2 has only one root (Hill, 1953, p. 502).

[48] Regarding P_1 of Notharctinae Gregory (Gregory, 1920, p. 130) states: "*The evidence, then, by no means indicates that there was a stage in the remote ancestry of Notharctus in which P_1 had two distinct roots and a more premolariform crown.*"

[49] It may be pointed out here that the original four premolars of the primitive Eutherian mammals and of some primitive Prosimii of the basal Tertiary have been reduced to three in modern Lemuridae, Lorisiformes and Ceboidea and to two in modern Indriidae (Pleistocene genera had 2 or 3 premolars), Cercopithecidae, anthropoid apes and man (see Gregory, 1920-1921, Le Gros Clark, 1934 and Hill, 1953), while in the highly specialized modern Daubentoniidae, there remains only one premolar, which is in the upper jaw, and none in the mandible (see Friant, 1948, p. 154, and Hill, 1953, p. 677).

[50] Bennejeant, 1953, ig. 14.

published a skiagram of the lower jaw of a young specimen of *Archaeolemur majori*,[51] which is a species of an aberrant and extinct genus of the family Indriidae from the Pleistocene of Madagascar.[52] From Bennejeant's skiagram it is seen that in the erupted, or nearly erupted, but still incompletely developed, lower molars of this extinct species the pulp cavities are slightly enlarged. This is probably due to the fact that the floors of the pulp cavities of these molars are still thin and undeveloped. If the floor had thickened, the size of the pulp cavities would be further reduced and would probably fall within the limits of cynodontism. But still it is possible that in this extinct species the size of the pulp cavities in adult stage may have been slightly larger than those of modern *Propithecus verreauxi*, which appears to be extremely cynodont.

To summarize the evidence of modern Lemuriformes, it can be stated that both *Lemur* and *Propithecus* have retained the cynodontism of the ancestral Lemuriformes. During the course of evolution of genus *Lemur*, P_2 has acquired a single root, while P_3, P_4 and the three lower molars have retained two roots which is the primitive condition. On the other hand, in *Propithecus* both P_3 and P_4 have been further modified and have come to possess only a single root, while the three lower molars have retained the primitive two roots.

INFRAORDER LORISIFORMES [53]

Subfamily Lorisinae of the modern Lorisiformes is represented in my series by four specimens, belonging to three genera, two Asiatic (*Loris* and *Nycticebus*) and one African (*Perodicticus*). In one *Loris tardigradus* (fig. 11), the lower premolars and molars are cynodont. P_2 has a single root, while P_3, P_4 and the three lower molars possess two separate roots. In the third lower molar of this specimen the distal root is elongated antero-posteriorly. In one specimen of *Nycticebus borneanus* (*Nycticebus coucang borneanus*) the three lower molars are clearly cynodont, with two separate roots (fig. 12) [54]. On the other

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[51] Ibid., fig. 13.

[52] See Piveteau, 1948, and Hill, 1953, pp. 630-642.

[53] After Simpson, 1950, p. 62.

[54] The skiagram includes the distal half of P_4 and from this it is clear that this tooth also had two separate roots.

hand, a specimen of *Nycticebus bengalensis* (*Nycticebus coucang bengalensis*) differs from the previous species, or subspecies, in its third lower molar. In this specimen (fig. 13), also, the lower premolars and the first and second lower molars are cynodont, while the third lower molar is clearly hyper-taurodont, the enlarged pulp cavity extending to the tip of the single, fused root. In this specimen P_2 and M_3 have a single root, while P_3, P_4, M_1 and M_2 possess two separate roots. In one *Perodicticus potto* (fig. 14) again the lower premolars and molars are cynodont. P_2 possesses a single root, while P_3, P_4 and the three lower molars exhibit two separate fangs.

Subfamily Galaginae of the Lorisiformes is represented by only one specimen in my series, of which P_4 and the three lower molars were X-rayed. In this specimen of *Galago crassicaudatus* (fig. 15) these teeth are cynodont and possess two separate roots. In the third lower molar the distal root is elongated antero-posteriorly and displays a dilated root canal.

In recent years several species of Prosimii have been described from the lower Miocene deposits of East Africa, all attributed to one genus (*Progalago dorae* MacInnes, *Progalago robustus* Le Gros Clark and Thomas, *Progalago minor* Le Gros Clark and Thomas and *Progalago sp.* Le Gros Clark and Thomas),[55] which, from the description of Le Gros Clark and Thomas,[56] may belong to Galaginae. It is unfortunate that these authors do not give the skiagrams of the teeth of Progalago and do not describe the condition of the roots, with the exception of P_2, to be referred to below.

As far as can be judged from the pictures published by Le Gros Clark and Thomas,[57] M_1 of *Progalago minor*,[58] M_1-M_2[59] and M_3[60] of *Progalago robustus*, M_2 of *Progalago dorae*[61] seem to have two

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[55] MacInnes, 1943, pp. 145-148; Le Gros Clark and Thomas, 1952.

[56] Le Gros Clark and Thomas, 1952, p. 19.

[57] Le Gros Clark and Thomas (1952, pls. 2 and 3) publish the pictures of several mandibles, but here mention is made of only the teeth where the condition of roots and bodies could be seen.

[58] Le Gros Clark and Thomas, 1952, pl. 3, fig. 17.

[59] Ibid., pl. 3, fig. 15.

[60] Ibid., pl. 3. fig. 12.

[61] Ibid., pl. 3, fig. 7. From pl. 2, figs. 4-5 of Le Gros Clark and Thomas (1952) it is seen that in *Progalago dorae* MacInnes M_1 - M_3, and probably also P_4, had two separate roots.

separate roots and very shallow bodies. The condition of the body suggests that all these teeth mentioned were probably cynodont.

Le Gros Clark and Thomas state that P_2 of *Progalago dorae* "*had only one root.*"[62] From a picture published by Le Gros Clark and Thomas it can be clearly seen that in *Progalago robustus* the distal root of the third lower molar is elongated antero-posteriorly and is divided into an anterior and a posterior portion by a vertical groove on the buccal surface.[63] The same feature seems to be also present in the distal root of the third lower molar of a modern *Galago senegalensis* published by the same authors.[64] This feature of the third lower molar of *Progalago robustus* and modern *Galago senegalensis* recalls the same condition seen in the third lower molar of *Notharctus matthewi*.

In summary, it can be stated that the Early Miocene genus *Progalago* seems to have retained the cynodontism of the primitive Eocene Lemuriformes. The same is also true for the specimens of modern *Loris*, *Nycticebus borneanus* (*Nycticebus coucang borneanus*), *Perodicticus* and *Gagalgo* studied. On the other hand, while in one specimen of *Nycticebus bengalensis* (*Nycticebus coucang bengalensis*) cynodontism has been retained in the lower premolars and the first and second lower molars, the third lower molar has acquired a strong degree of taurodontism. But since the Eocene Lemuriformes are cynodont and since the early Miocene *Progalago*, although perhaps on the Galaginae line, appears to be cynodont, the hypertaurodontism observed in the third lower molar of this *Nycticebus bengalensis* (*N. c. bengalensis*) must be regarded as a relatively recent acquisition.

As compared with the early Tertiary Lemuriformes, in the modern Lorisiformes, in at least the specimens studied, P_2 has been modified and has come to possess a single root. The presence of one root in P_2 of *Progalago robustus* shows that this specialization had been acquired at least as early as the lower Miocene times. However, the primitive two roots are retained in P_3, P_4 and the three lower molars of modern Lorisiformes, with the exception of the

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[62] Le Gros Clark, 1952, p. 5.

[63] Ibid., pl. 3, ig. 12.

[64] Ibid., pl. 3, fig. 13.

third lower molar of one specimen of *Nycticebus bengalensis* (*N.c. bengalensis*) in which this tooth possesses a single, fused root, which, as stated above, must be regarded as a relatively recent specialization.

INFRAORDER TARSIIFORMES [65]

In the specimen of *Microchoerus edwardsi* (*Necrolemur edwardsi*) [66] from the Eocene of Europe (fig. 16) the P_3, P_4 and the three lower molars are cynodont. [67] Thus as I have stated before, the evidence of Eocene Lemuriformes and the Eocene *Microchoerus edwardsi* (*Necrolemur edwardsi*) indicate that cynodontism is the primitive condition for all the primates.[68]

In this specimen of *Microchoerus edwardsi* (*N. edwardsi*) P_3 has one root, while P_4 and the three lower molars exhibit two separate roots. The description of Forster-Cooper shows that the same conditions exist in P_3 and P_4 of *Microchoerus erinaceus.* [69] Again, according to this author P_2 of *Microchoerus erinaceus* had a single root. [70] Teilhard de Chardin states that in *Pseudoloris parvulus* (Filhol), which is earlier than the genus *Microchoerus*, P_1 and P_2 had one root, while P_3 possessed two roots.[71] As can be seen from a drawing published by Teilhard de Chardin, P_4 of this species had two separate roots.[72] Thus *Microchoerus* is seen to be more specialized than earlier and more primitive *Pseudoloris parvulus* in having a single root in P_3. It is evident that already in Eocene times, in addition to P_2, also

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[65] After Simpson, 1950, p. 63.

[66] This specimen is labelled as *Necrolemur edwardsi* in the Museum of Comparative Zoology of Harvard University and was so recorded in my earlier paper (Şenyürek, 1939, p. 121). But Stehlin (1916, pp. 1374-1375) and Teilhard de Chardin (1916—1921, pp. 16-18) attribute this species to the genus *Microchoerus.*

[67] From the pictures published by Gregory (Gregory, 1920-1921, No. 3, Figs. 112, 114, 115, 119, 124, and 125) it can be seen that in the American species *Omomys sp., Hemiacodon gracilis, Washakius insignis, Tetonius homunculus, Anaptomorphus aemulus* and *Uintanius turricolorum* the lower molars had two separate roots and very shallow bodies, suggesting that these New World Tarsiiformes were also cynodont.

[68] Şenyürek, 1939, p. 121.

[69] Cooper, 1910.

[70] Ibid.

[71] Teilhard de Chardin, 1916 - 1921, p. 6.

[72] Ibid., fig. 1.

P_3 of some fossil Tarsiiformes had acquired a single root, which is a specialized condition in contrast to the two-rooted P_3 of Adapidae.

From the description of Forster-Cooper it would appear that the distal root of the third lower molar of *Microchoerus erinaceus* was bilobate.[73] Indeed, from Forster-Cooper's plate III, republished by Gregory, [74] it can be discerned that the distal root of the third lower molar of *Microchoerus erinaceus* was elongated antero-posteriorly and was divided by a vertical groove on the buccal surface into an anterior and a posterior portion.[75]

In my series the modern family Tarsiidae is represented by two specimens, one *Tarsius spectrum* (*T. philippensis*) from Mindanao in the Philippine Islands and one *Tarsius spectrum* (*T. fuscus*) from Celebes (Toli Toli). As can be seen from fig. 17 in both specimens of *Tarsius spectrum* the lower premolars and molars are cynodont. In both specimens P_2 has a single root, but the tooth of the Celebes specimen is smaller than that from Mindanao. In the specimen from Celebes P_3 has still two separate roots, while that from Mindanao possesses a single root, which is a specialized feature. It is thus clear that the number of roots of P_3 of *Tarsius spectrum* is variable. In both specimens P_4 and the three lower molars have two roots as in the Eocene Lemuriformes and Tarsiiformes. Again in both specimens the distal root of the third lower molar is somewhat elongated antero-posteriorly although the root canal is not unduly expanded.

It can be stated that modern *Tarsius spectrum* appears to retain the cynodontism of Eocene Tarsiiformes. The P_2 of *Tarsius spectrum* has one root, a specialization going back to the Eocene Tarsiiformes. On the other hand, P_3 of *Tarsius spectrum* is, in root number, intermediate between *Microchoerus* of Upper Eocene, P_3 of which has

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[73] Cooper, 1910.

[74] Gregory, 1920-1921, No. 3, p. 401, fig. 144 (3). Unfortunately at the moment I do not have the original copy of Cooper's article, save my notes taken from his article, but his plate III is republished by Gregory (1920-1921) which serves the same purpose.

[75] As far as can be judged from a drawing published by Gregory (Gregory, 1920-1921, No. 3, fig. 115), in *Washakius insignis*, from the Eocene of North America, the antero-posteriorly elongated distal root of the third lower molar also is divided into an anterior and a posterior portion by a vertical groove on the buccal surface, as in *Microchoerus*.

a single root, and more primitive Eocene Tarsiiformes with two roots. In having two roots, P_4 and the three lower molars of modern *Tarsius spectrum* seem to have retained the primitive condition.

As P_3 of *Tarsius spectrum* has one or two roots, it is evident that the upper Eocene genus *Microchoerus*, in which this tooth had acquired a single root, cannot be a direct ancestor of the modern *Tarsius*. In my study on the "Trigonid-Talonid Height Relation Indices of the Permanent Lower Molars of Primates" I stated: "*Similarly, Necrolemur may not be considered a direct ancestor of modern Tarsius...*"[76] On *Necrolemur*, because of the disappearance of lower incisors, Gregory has stated: "*This specialization, with others, removes Necrolemur from the line of ascent either to Tarsius or to any of the higher primates.*"[77] Thus, in addition to the reasons advanced by Gregory,[78] there are other specializations in Necrolemurinae[79] (*Necrolemur* and *Microchoerus*) which eliminate them from being the direct ancestors of modern *Tarsius spectrum*. On the other hand, it looks more probable that the modern *Tarsius spectrum* is derived from the primitive *Pseudoloris*, or from a close relative of this form[80].

PULP CAVITIES AND ROOTS OF THE LOWER CHEEK TEETH OF ANTHROPOIDEA

SUPERFAMILY CEBOIDEA[81]

In my series the superfamily Ceboidea is represented by 19 specimens, of which five belong to the family Callithricidae and fourteen to Cebidae. In one specimen of *Callithrix* (*Hapale*) *santaremensis* of Callithricidae, the first lower molar is almost cynodont, while the second lower molar is moderately taurodont (fig. 18). In P_4 the root canal is single. In this specimen P_4 has one root, while first and second lower molars possess two separate roots.

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[76] Şenyürek, 1951, p. 466. This statement is based on a specimen of *Necrolemur antiquus* (M.C.Z. No. 8880) preserved in the Museum of Comparative Zoology of Harvard University.

[77] Gregory, 1920-1921, No. 3, p. 396.

[78] Ibid., pp. 396.

[79] Subfamily after Simpson, 1950, p. 63.

[80] Regarding *Pseudoloris parvulus*, Teilhard de Chardin (1916-1921, p. 12) states: "*Tant d'harmonies dans les ressemblances et les différences portent à croire que Pseudoloris (son nom devrait être Protarsius, ou Tarsiculus) appartient réellement au groupe dont sont issus les Tarsiers.*" See also Le Gros Clark, 1934, p. 269 and Gregory, 1951, p. 466.

[81] After Simpson, 1950, p. 64.

In four specimens of *Leontocebus*,[82] belonging to Callithricidae, in the first lower molar the size of the pulp cavity is variable, being nearly cynodont in two and moderately taurodont in two specimens, whereas in all of them the second lower molar is hyper-taurodont (figs. 19-21). In P_2-P_4 the root canal is single. The available P_2, P_3 and P_4 of *Leontocebus* are single-rooted. M_1 of *Leontocebus* has two separate roots, while in M_2 there is a single fused root. In one of the specimens, however, M_2 displays a notch at the apex (fig. 19).

In 14 specimens, belonging to the family Cebidae, the majority are taurodont. In one specimen of *Alouatta palliata* (fig. 32) all three lower molars are cynodont. In two specimens of *Cebus* (*Cebus macrocephalus* and *Cebus fatuellus*) the first lower molar is cynodont, the second lower molar is moderately taurodont, while the third lower molar is hyper-taurodont (figs. 33-34). The irst lower molar of one specimen of *Ateles fusciceps* (fig. 25) is nearly cynodont, while the second and third lower molars are moderately taurodont.

Aside from these, the first, second and third lower molars of the specimens of the genera X-rayed (*Aotus*, *Callicebus*, *Cacajao*, *Ateles and Saimiri*) are taurodont, taurodontism ranging from moderate to extreme. In the specimens of *Aotus*, *Callicebus* and *Cacajao* (figs. 22, 23 and 24), the first and second lower molars are moderately taurodont and the third lower molars are hyper-taurodont.

One of the first lower molars of Ateles, as stated above, is nearly cynodont, five are moderately taurodont and one is hyper-taurodont (figs. 25-31). Three of the second lower molars are moderately taurodont and four are hyper-taurodont. Of the three third lower molars, one is moderately taurodont, approaching hyper-taurodontism, and two are hyper-taurodont. An external examination has shown the lower molars of four other *Ateles*, not X-rayed, to have large bodies, indicating that these, too, are probably taurodont.[83] Thus, as I stated before, it is evident that taurodontism is a generic characteristic of *Ateles*.[84] In one specimen of *Saimiri*, X-rayed, the

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[82] These four specimens were labelled as *Mystax graellsi*, *Mystax rufimanus*, *Oedipomidas geoffroyi* and *Leontocebus midas*, but in accordance with the classification adopted by Simpson (Simpson, 1950, p. 65) they have all been included in the genus *Leontocebus*.

[83] Şenyürek, 1939, p. 122.

[84] Ibid., p. 122.

first lower molar is moderately taurodont, whereas the second and third lower molars are hyper-taurodont (fig. 35). The third lower molars of two specimens of *Saimiri*, examined externally, also were seen to have a single root, indicating that these teeth were probably hyper-taurodont. In all the specimens of Cebidae X-rayed, the lower premolars have only a single root canal. [85]

From an examination of the plates it is seen that in the taurodont lower molars of Ceboidea there is a marked constriction at the cemento-enamel junction above which the crown, in lateral view, bulges conspicuously. In this feature the taurodont lower molars of Ceboidea differ from the moderately taurodont first lower molar on an ancient Egyptian shown in fig. 1 and from the taurodont lower molars of the hominids in which this constriction usually tends to be erased, [86] although, as has been shown by Weidenreich, this feature is somewhat variable in Sinanthropus. [87]

The presence of taurodontism in both Callithricidae and Cebidae, indicates that the common ancestors of these two families were either taurodont, [88] or had, at least, a potential tendency in the direction of taurodontism.

As for the roots of the lower cheek teeth of Cebidae, in the specimens X-rayed, P_2 and P_3 have a single root. The same is also true for P_4. [89] However, in one specimen of *Alouatta palliata* (fig. 32) the fused root of P_4 clearly bifurcates at the tip, showing that the fusion of the roots is not yet complete. Thirteen of the first lower molars X-rayed have two roots, while one, belonging to an *Ateles paniscus* (fig. 31), has a single fused root, with a notch at the apex. Ten of the

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[85] Bluntschli (Bluntschli, 1929, fig. 133) has published the skiagram of the face of a *Lagothrix*. As far as can be judged from this skiagram, in the first and second lower molars the pulp cavity is slightly enlarged, while the third lower molar appears to be hyper-taurodont. The three lower premolars of this *Lagothrix* have one root, first and second lower molars two roots and the third lower molar, one fused root, which seems to display a notch at the bottom. I examined externally the third lower molars of two specimens of *Lagothrix*, in both of which this tooth had one fused root, suggesting that they were hyper-taurodont.

[86] Shaw, 1928, p. 484 and 1931, p. 122; Keith, 1929, p. 687.

[87] Weideneich, 1937, p. 105.

[88] Şenyürek, 1939, p. 122.

[89] Tomes (1923, p. 505) records that in *Ateles* the three lower premolars possess one root each.

fourteen second lower molars have two roots, but in most of these the free portion of the roots is usually shorter than that of the first lower molar. In four second lower molars the roots are fused. However, fusion is complete only in one specimen, while one presents a notch at the tip and in two the two roots bifurcate near the apex. The third lower molar of one *Alouatta palliata* possesses two separate roots, while ten third lower molars belonging to other genera have only a single fused root. From the account given it is clear that in Cebidae, as in Man, the fusion of the roots increases from the first toward the third lower molar.

It is clear that moderate to extreme degrees of taurodontism occur very frequently in the lower molars of Ceboidea. [90] The extreme cases of taurodontism observed in some genera and species may equal and even surpass some of the Krapina Neanderthals, in nearly half of which,[91] the pulp cavity extends almost to the tip of the roots, the separate parts of which being in consequence very stumpy, [92] as in the second lower molar of a *Hylobates hoolock* [93] shown in fig. 54. As is well known, taurodontism occurs in some anthropoid apes, [94] primitive fossil hominids [95] and even some of the recent races.[96] It is evident that in this respect Ceboidea resembles the higher primates and especially some hominids. In the tendency of the lower molars to have fused roots, which is not however due to the fusion of the two separate roots but to the downward extension of the pulp cavity, Ceboidea again recalls the *Hylobates* mentioned and some hominids. Again in tending to have a single root in P_3 and P_4, Ceboidea resembles *Homo sapiens* in which, in the vast majority of cases,

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[90] See also Şenyürek, 1939, pp. 121-122.

[91] Tomes, 1923, p. 521.

[92] See Gorjanovic- Kramberger, 1907, fig. 5, and Keith, 1913, p. 104 and fig. 1.

[93] It may be mentioned here that in the third lower molar of a Gibbon (*Hylobates sp.*) published in my earlier study (Şenyürek, 1939, fig. 4) the pulp cavity extends to the tip of the fused root.

[94] See Miller (1918), Weidenreich (1937), Şenyürek (1939) and Hooton (1946).

[95] See Gorjanovic- Kramberger (1907), Keith (1913, 1929 and 1931), Black (1927), Shaw (1928), Weidenreich (1937) and Şenyürek (1939).

[96] See Miller (1918), Shaw (1928-1931), Weidenreich (1937), Şenyürek (1939, 1949 and 1952), Pedersen (1949) and Tratman (1950).

these two teeth have a single root.[97] However, all these resemblances in taurodontism, in the tendency to have fused roots in the lower molars [98] and a single root in P_3 and P_4, [99] between Ceboidea and some of the higher primates are of independent origin and are due to parallelism, evidences of which, as has been discussed by Le Gros Clark, are not at all infrequent in the primates. [100]

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[97] See Tomes (1923), Shaw (1931), Nelson (1938), Pedersen (1949) and Şenyürek (1952).

[98] It may be mentioned here that while in reference to the teeth discussed in this paper the term "fused roots" is used, this does not mean that these roots were originally separate and then fused, but that the pulp cavity has extended down (see also Şenyürek, 1939, p. 122).

[99] In this connection it may be mentioned that in *Paranthropus crassidens* P_3 possesses two partially fused roots and P_4 two distinct roots (Broom and Robinson, 1952, pp. 59 and 63). As for *Plesianthropus*, Broom and Robinson (1952, pp. 60-61) describe the root of P_3 as follows: "...*this is a short stout single root, with a groove down the buccal side. This groove represents remnants of a division, but there are no other grooves or longitudinal depressions on the remainder of the root.*" On the other hand, P_4 of *Plesianthropus* displays two distinct roots (Broom and Robinson, 1952, p. 64). In *Paranthropus robustus* also P_4 appears to possess two roots (Broom and Schepers, 1946, p. 104 and Broom and Robinson, 1952, p. 64). Broom and Robinson (Broom and Robinson, 1952, p. 113) describe the root of P_3 of *Telanthropus capensis* as follows: "*The root tapers evenly downward to a blunt, single apex-thus differing considerably from the more complex root of P. crassidens. There is the remnant of a division between a mesial and a distal root but this is situated on the lingual side of the root, whereas in P. crassidens it is usually shifted on to the mesial face and is well developed.*" From this description of Broom and Robinson it appears that the root of P_3 of *Telanthropus capensis* is considerably more advanced than that of *Paranthropus crassidens*. In *Sinanthropus pekinensis* P_3 consists frequently of two fused roots (see Weidenreich, 1937, p. 44 and figs. 82 and 86). One P_4 of *Sinanthropus* described by Weidenreich is also clearly made up of two fused roots (see Weidenreich, 1937, pp. 48-49, 166, and fig. 98). Weidenreich describes the root of P_4 of *Sinanthropus* (Weidenreich, 1937, p. 166) as follows: "*The root is very robust and shows the same tendency as observed in the first premolar, namely to divide into two or three branches.*" From the condition of the roots of the lower premolars of these fossil forms, which are to various degrees intermediate between the two-rooted lower premolars of the anthropoids and the single-rooted P_3 and P_4 of recent man, it is quite evident that the single-rooted lower premolars, which are characteristic of the majority of *Homo sapiens*, are, relatively speaking, a recent development. Thus, there can be no doubt that the similarity in the root number of P_3 and P_4 between Ceboidea and *Homo sapiens* is due to parallelism.

[100] Le Gros Clark, 1936. In this connection it is worthwhile also to recall the statements of Straus regarding some of the similarities between Ceboidea and

To summarize the account on Ceboidea, it can be stated that they differ from the Eocene Lemuriformes and Tarsiiformes in exhibiting a strong tendency to have taurodont teeth. It is clear that taurodontism prevalent in Ceboidea was developed later in post-Eocene times, as this feature is lacking in the Eocene Prosimii. The single-rooted P_2 of Ceboidea may have been derived from the single-rooted P_2 of some Eocene Tarsiiformes. It is probable that P_3 of Ceboidea also developed a tendency to have a single root after the progenitors of Ceboidea were distinctly differentiated from the Eocene Tarsiiformes.

It may perhaps be asked whether P_3 of Ceboidea could not have been derived from the single-rooted P_3 of *Microchoerus* of the subfamily Necrolemurinae, which is known to exhibit a number of pithecoid tendencies. Regarding Necrolemurinae Gregory states: "*The differences separating Necrolemur and Microchoerus from any of the New World or Old World monkeys are numerous and important, and there is no evidence for deriving any of the higher types directly from this source. Nevertheless these genera exhibit certain important advances in the direction of the Old World primates, among which may be noted the development of quadrate upper molars with subequal anterior and posterior moieties, the development of hypoconulids in the lower molars* (fig. 143), *the final loss of the paraconids in the lower molars and the tendency for the reduction of the trigonid basins, the tendency for P^4 and P^3, and the corresponding lower teeth, to become bicuspid, the incipient development of a bony postorbital partition, the lateral expansion of the base of the braincase, the development of a tubular external auditory meatus, and the tendency for the angle of the mandible to be expanded and for its posterior border to become very large and rounded. Thus Necrolemur and Microchoerus have advanced far from the primitive tarsioid type and indicate some of the structural stages through which the actual ances-*

Catarrhinae. Straus (Straus, 1953, p. 87) states: "*The matter of a possible tarsioid origin for the catarrhines has already been discussed. Granting its probability, it remains a question whether any or all of the Anthropoidea of the Old World arose as such directly from prosimian ancestors or whether they first passed through a 'platyrrhine' stage more or less resembling the more generalized of the living New World monkeys. Each of these suppositions has its advocates. The many remarkable morphological resemblances between the more advanced platyrrhines and some of the catarrhines bear upon this question. It remains to be determined whether these are merely evolutionery parallelisms or are evidences of an even closer relationship. At the moment, the former interpretation appears to be the more reasonable one.*"

tors of the Old World series probably passed."[101] In view of the fact that the known forms of Necrolemurinae are too specialized to be the direct ancestors of Suborder Anthropoidea,[102] and also taking into consideration the condition of the roots in P_3 of Eocene Lemuriformes and that of Eocene Tarsiiformes with three or four premolars I consider it more probable that in the forerunners of Ceboidea P_3 had two separate roots and that the tendency to have one root developed in post-Eocene times.

On the other hand, from the evidence of Eocene Lemuriformes and Eocene Tarsiiformes, it is evident that in the Tarsiiforme ancestors of Ceboidea P_4 and the three lower molars had two separate roots and that the tendency of present Ceboidea to have a single root in P_4 and fused roots in lower molars developed in post-Eocene times.

SUPERFAMILY CERCOPITHECOIDEA[103]

The skiagram of the mandibular fragment o *Amphipithecus mogaungensis* Colbert (fig. 36) from the upper Eocene of Burma, first described by Colbert,[104] is not at all clear.[105] In the skiagram of *Amphipithecus* which, although considered to be of pongid affinities by Colbert[106] and Gregory,[107] is still of uncertain taxonomic position,[108] the pulp cavities of P_3, P_4 and M_1 cannot be discerned.

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[101] Gregory, 1920-1921, No. 3, pp. 400-402.

[102] Ibid., p. 396 and 400.

[103] After Simpson, 1950, p. 66.

[104] Colbert, 1937 and 1938, pp. 290-298.

[105] *Amphipithecus* is included here not because it is a cercopithecoid, but because its affinities seem to be closer with the Catarrhinae than with Platyrrhinae or Prosimii, as well as for the reason that it is an early primate that throws light on the evolution of pulp cavities and roots of the lower cheek teeth of Catarrhinae.

[106] Colbert, 1937, p. 15 and 1938, p. 297.

[107] Gregory, 1951, p. 475.

[108] Simpson (1950, p. 68) describes *Amphipithecus* under the heading of "*Possible pongids of uncertain affinities.*" Referring to the time of the separation of the cercopithecoid and anthropoid ape-Man line Le Gros Clark (1950, p. 231) states: "*The meagre evidence of these Oligocene fossils, taken in conjunction with other further evidence now available that the cercopithecoid type of dentition had already become well differentiated and established by Miocene times, and taking into consideration also the morphological contrasts in molar structure, certainly appears to lead to the provisional inference that the cercopithecoid and hominoid sequences had separated in their evolutionary history at least as far back as*

But from the skiagram as well as the drawing published by Colbert,[109] it can clearly be seen that the first lower molar of this form had two separate roots and a very shallow body, the place of separation of the two roots being very near the enamel margin. The presence of a shallow body indicates that this tooth is very probably cynodont. The same may be true also of P_3 and P_4 of this form. As can clearly be seen from the skiagram and the drawings of Colbert,[110] P_3, P_4 and M_1 of this form had two separate roots.[111] In this form, with three premolars of which the first one, corresponding to P_2 of Ceboidea and Prosimii, represented in the mandibular fragment by its root, is, as pointed out by Colbert,[112] clearly reduced, indicating that this Burmese fossil genus was evolving in the direction of Catarrhinae. In the skiagram the root of P_2 can be discerned before the mesial root of P_3 and it is seen that this tooth (P_2) had a single root, which may have been derived from the single-rooted P_2 of Eocene Tarsiiformes.

In contrast to the skiagram of *Amphipithecus*, that of *Apidium phiomensis* Osborn, which is a primitive cercopithecoid monkey from the Oligocene of Fayum in Egypt,[113] first described by Osborn,[114] is very clear indeed (fig. 37). From the skiagram of *Apidium phiomensis* which represents a young individual, it can be seen that P_4, M_1 and M_2 had erupted but had not yet completed their development as the tips of their roots are still open. Although they have not yet completed their development, first and second lower molars are strongly cynodont. In the third lower molar, which is still in its socket, the floor of the pulp cavity had just started to be formed together with a part of the two roots. The pulp cavity of this immature

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Oligocene times. It seems probable, indeed, that the dichotomy may even have occurred at a stage of evolution represented by Amphipithecus, as suggested in the diagram in Pl. XI, fig. 1." The taxonomic position of *Amphipithecus* which I had examined in New York, through the kind permission of Dr. Colbert, will be discussed in a coming study.

[109] Colbert, 1937, figs. 1-2.

[110] Ibid.

[111] Colbert describes P_4 and P_3 of this form as having respectively 4 and 3 roots and P_2 as possessing two roots (Colbert, 1937, pp. 2-5).

[112] Colbert, 1937, p. 8 and 1938, p. 295.

[113] Gregory, 1920-1921, No. 4, pp. 616-618; Le Gros Clark, 1950, pp. 230-231; Şenyürek, 1951, p. 462.

[114] Osborn, 1908, pp. 271-272.

third lower molar is, because of its younger age, larger than that of the second lower molar and is, relatively speaking, as deep as that of the immature first lower molar of a *Colobus polycomus* shown in fig. 46. There can be no doubt that when this M_3 had matured, it would be strongly cynodont. In this third lower molar the root canal of the distal root, which is elongated antero-posteriorly, is very extensive, the significance of which will be discussed later.

From the skiagram it is seen that the top of the crown of P_4 is still at a somewhat lower level than that of M_1. Also, in P_4 the root canals of the roots are larger, the walls of the roots and the floor of the pulp cavity are thinner than those of the second lower molar. Thus it is evident that in this Oligocene genus P_4 erupted after M_2. This would explain the slightly deeper pulp cavity of P_4 than that of M_2. However, it is clear that when this tooth had finally fully matured, the size of the pulp cavity would be further reduced and would probably be only as large as those of the cynodont P_4 of a *Cercocebus*, a *Colobus* and a *Pygathrix* shown respectively in figs. 43, 47 and 51.

It is evident that in *Apidium* P_4 erupted somewhat later than M_2 and long before M_3, which is still in its socket, as is also the case in the majority of Ceboidea, Cercopithecidae and the anthropoids,[115] and unlike the Eocene Lemuriformes *Adapis* and *Notharctus* in which the premolars erupted after M_3.[116] From the evidence of *Apidium* it is clear that the sequence of eruption of the premanent teeth characteristic of a large portion of Catarrhinae (anthropoid

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[115] See Schultz, 1935, fig. 2. According to Schultz, in the series of Anthropoidea studied by him, only in the mandibles of a few *Saimiri* and in both the upper and lower jaws of a large series of the genus *Pygathrix* do the premolars erupt after the eruption of third molars (Schultz, 1935, pp. 512 and 519). However, it can be seen from the skiagram of a *Pygathrix aurata* (labelled in the Museum of Comparative Zoology as *Pithecus aurata*) shown in fig. 51 that in this specimen P_4 had fully formed and erupted, while M_3 was still immature. This finding supports the sequence of eruption in *Pygathrix aurata* observed by Bolk (cited by Schultz, 1935, p. 519), according to which, as cited by Schultz, in this species the premolars erupt after the second and before the third molars. Thus, from the findings of Schultz and Bolk and the specimen examined by me, it appears that the sequence of eruption in genus *Pygathrix* is variable and that the species *Pygathrix aurata* seems to deviate in this respect from the other species studied by Schultz (1935).

[116] See Gregory, 1920, pp. 152-154.

apes, Cercopithecinae and the majority of Colobinae), in which the premolars usually erupt after M_2 and before M_3,[117] goes back, at least, to the Oligocene times.[118]

From the skiagram of *Apidium* it is seen that P_4, M_1, M_2 and M_3 of this form have two completely separate roots. In the skiagram, in front of the mesial root of P_4, is seen a long vertical socket which represents the distal root of P_3 and from the configuration of this socket it seems probable that this tooth of *Apidium* also had two separate roots. In the first and second lower molars of *Apidium* the two roots are nearly vertical, while in P_4 the tips of the two roots approach each other. The configuration of the roots in P_4, M_1 and M_2 of *Apidium* probably represents the primitive condition for the roots of the corresponding teeth of modern Cercopithecidae.

To summarize the account on *Amphipithecus*, whatever its affinities may be, and the cercopithecoid *Apidium*, it can be stated that these early primates had preserved the cynodontism of their Eocene Tarsiiforme ancestors. P_2 of *Amphipithecus*, which was lost in later Catarrhinae, may have derived its single root from the single-rooted P_2 of some Eocene Tarsiiformes. On the other hand, *Amphipithecus*, in its preserved P_3, P_4 and M_1, and *Apidium*, in P_4, M_1, M_2 and M_3 and probably also in P_3, had retained the primitive two separate roots of their Eocene Tarsiiforme ancestors. The presence of two separate roots in P_3 of *Amphipithecus* and probably also in P_3 of *Apidium* indicates that these early primates and also the later Catarrhines could not have been derived from *Microchoerus* of Necrolemurinae in which this tooth had only a single root. It is evident that the ancestors of Catarrhinae must be sought among the Eocene Tarsiiformes, at a more primitive level of evolution than Necro-

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[117] See Schultz, 1935, fig. 2.

[118] The seqence of eruption observed in the Eocene Lemuriforme genera *Adapis* and *Notharctus* (see Gregory, 1920, pp. 152-154) and the Oligocene cercopithecoid genus *Apidium* and the mode of eruption prevailing in the majority of modern Anthropoidea, support the conclusion of Schultz that the condition prevailing in *Homo sapiens*, in which the premolars erupt before the second molars, is a highly modified mode of eruption (see Schultz, 1945, pp. 542 and 576). For this Schultz (1935, p. 542) states : “ *In other words, it is unquestionably a new and exclusive acquisition of man that his M2 erupt comparatively late and his Premolars and, particularly, Canines relatively early.*”

lemurinae and with two roots in P_3. Furthermore, the evidence of *Amphipithecus* and *Apidium* clearly shows that the taurodontism and the tendency to have a single root in P_3 and P_4 and fused roots in some lower molars observed in modern Ceboidea, in which these South American monkeys resemble some forms of higher primates, are definitely of independent origin.

In my series the modern Cercopithecidae is represented by 17 specimens of which eleven belong to Cercopithecinae and six to Colobinae. As can be seen from an examination of the skiagrams, some of the teeth had not yet completed their development, while some were mature. But still in 15 of the specimens the available P_4 and the lower molars are cynodont and indeed in some cases strongly so (figs. 38-51). The only exceptions to this rule are found in two specimens of *Cercopithecus talapoin* from French Congo, shown in fig. 52 (*a* and *b*), which are the only two specimens of this species X-rayed. In one of these P_3 and P_4 are moderately taurodont, M_1 is cynodont, while M_2 and M_3 are moderately taurodont (fig. 52 *a*). In the other specimen of *Cercopithecus talapoin* P_4 is hyper-taurodont, while M_1, M_2 and M_3 are moderately taurodont (fig. 52 *b*).

Lyne has published the skiagram of the mandible of a *Papio* ("*Cynocephalus babouin*"). [119] From an examination of Lyne's skiagram it can be seen that in his specimen also P_3, P_4, M_1, M_2 and M_3 are strongly cynodont, as the first and second lower molars of the specimens of *Papio* X-rayed by me (figs. 44 and 45). Thus it appears that the norm for modern Cercopithecidae is cynodontism, [120] and that the cases of taurodontism seem to be rare.

P_3 of one specimen (a *Cercopithecus talapoin*) and P_4 of three specimens(a *Cercocebus albigena*, a *Colobus polycomus* and one *Pygathrix aurata*) have two separate roots (figs. 52*a*, 43, 47 and 51), which is also true for the P_3 and P_4 of the *Papio* published by Lyne .[121] However, P_4 of the *Cercopithecus talapoin* cited (fig. 52*a*), differs from those of *Cercocebus*, *Colobus* and *Pygathrix* in having a larger body, a moderate degree of taurodontism and relatively shorter roots, of

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[119] Lyne, 1916, fig. 4.

[120] See Şenyürek, 1939, p. 121 and p. 127.

[121] Lyne, 1916, fig. 4.

which slightly more than half are free. The same is also true for P_3 of this specimen (fig. 52*a*). In P_4 of the second specimen of *Cercopithecus talapoin* (fig. 52 *b*), the tendency seen in P_4 of the individual shown in fig. 52*a* has been carried further. In P_4 of this individual nearly three-quarters of the roots are fused with a large pulp cavity, only about a quarter of the two roots being free in the tip portion. [122] In having largely fused roots, P_4 of this *Cercopithecus talapoin* differs conspicuously not only from the corresponding teeth of other modern cercopithecoids but also from *Apidium* and *Amphipithecus* which had in this tooth two separate roots.

In all the specimens of modern Cercopithecidae X-rayed, including the two individuals of *Cercopithecus talapoin*, the available M_1, M_2 and M_3 have two separate roots, the same also being true for the three lower molars of the *Papio* published by Lyne. [123] However, it may be mentioned here that the lower molars and especially M_2 and M_3 of *Cercopithecus talapoin* differ from those of other modern cercopithecoid genera and species in having relatively larger bodies and relatively shorter roots.

An examination of the skiagrams will show that the distal root of M_3 in *Colobus* (figs. 48-49) and *Pygathrix* (figs. 50-51) is double. When these teeth are examined externally, it is seen that the distal root of M_3 is, on the buccal side, divided by a vertical groove into an anterior and a posterior portion, the latter supporting the large hypoconulid. This same double distal root is also seen in the M_3 of *Papio* published by Lyne. [124] In the third lower molars of some specimens of *Papio* and *Nasalis*, examined externally, I found that M_3 in both genera had a double distal root and a large hypoconulid, with sometimes even a 6th cusp. In contrast to the above, in the specimen of *Cercocebus albigena*, with a relatively small hypoconulid, shown in fig. 43, the distal root of M_3 is single. But in the third lower molars of two other *Cercocebus* I examined externally, I observed that the distal root was double and there was a large hypoconulid. On the other hand, in both specimens of *Cercopithecus talapoin* X-rayed

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[122] It may be mentioned here that in this tooth also the fusion is due to the extension of the pulp cavity.

[123] Lyne, 1916, fig. 4.

[124] Ibid.

(fig. 52, *a* and *b*) the distal root of the third lower molar is single and the hypoconulid has been lost, as is true also of the other species of *Cercopithecus.* From the account given it is clear that double distal roots occur in the third lower molars of some genera of both Cercopithecinae and Colobinae.

In the specimen of *Pygathrix aurata* shown in fig. 51 and in the *Papio* published by Lyne, [125] the distal root of the third lower molar, which is still immature, has a large antero-posteriorly elongated root canal which is divided by a thin vertical partition, which seems to have just started forming, into an anterior and a posterior canal. In the still immature third lower molar of a *Cercocebus*, examined externally in the United States National Museum, I observed that the root canals of anterior and posterior parts of the double distal root were completely confluent. In the not yet completely developed third lower molar of a *Colobus polycomus* shown in fig. 47, which is older than that of *Pygathrix aurata* shown in fig. 51, the dilated root canal of the distal root is single without any partition. On the other hand, in the fully mature third lower molars of a *Pygathrix potenziani* (fig. 50), and of two *Colobus polycomus* (figs. 48-49), the root canal of the anterior portion of the distal root is separated by a thick partition from the posterior portion of this root.

As was stated before, in *Apidium* the distal root of the immature third lower molar, which is younger than that of *Pygathrix aurata* shown in fig. 51 and that of *Papio* published by Lyne, [126] has an antero-posteriorly elongated distal root with a very large root canal in which there is no sign of partition. Although the third lower molar of *Apidium* is still in its socket and could not be examined externally, from the account given above it is apparent that in *Apidium* we are dealing with a double distal root which is characteristic of some modern cercopithecoids. We have already noted that a double distal root is present in the third lower molars of some Prosimii, fossil as well as recent, viz., *Washakius insignis*, *Microchoerus erinaceus*, *Notharctus matthewi*, *Progalago robustus* and *Galago senegalensis.* Thus it is probable that the double distal root in the third lower molar of some

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[125] Ibid.

[126] Ibid.

modern cercopithecoids and *Apidium* was derived from that of some Eocene Tarsiiformes.

To summarize the account on modern cercopithecoids it can be stated that most of them have retained the cynodontism seen in *Apidium*, *Amphipithecus* and the Eocene Prosimii. From the fossil record it is evident that the taurodontism seen in *Cercopithecus talapoin* is a relatively new feature, that was acquired in post-Oligocene times. Indeed, as the teeth of other species of the genus Cercopithecus X-rayed are cynodont (see figs. 39-42), it is very probable that the taurodontism manifested in the modern *Cercopithecus talapoin* is, relatively speaking, a fairly recent development. In the lower premolars and molars of most of the modern cercopithecoids the primitive two separate roots have been retained. From the fossil record it is evident that the largely fused roots of P_4 in one specimen of *Cercopithecus talapoin* X-rayed is a fairly recent development.[127] The same can be said to be true for the larger bodies and relatively shorter roots in the lower premolars and molars, especially the second and third lower molars, of *Cercopithecus talapoin*. It is probable that the double distal root of the third lower molar of *Apidium* and some modern cercopithecoid genera was derived from that of some Eocene Tarsiiformes and that of this double root, the posterior portion, which originally supported a large hypoconulid in the third lower molar, was lost with the reduction or disappearance of hypoconulid in the course of evolution of some modern cercopithecoids.

CONCLUSION

1. As is true for man, in infrahuman primates also the size of the pulp cavity diminishes gradually during the development, from the immature toward the mature teeth.

2. The increase in size of the pulp cavities from the first to the third lower molar, observed in many primates, is in the main probably due to age, but in some primates, in addition to age, there

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[127] The form of the root of P_4 of this *Cercopithecus talapoin* recalls that of the corresponding tooth of Siamang shown in fig. 56. But from the fossil record it is apparent that this similarity in root form of P_4, as well as the resemblance in taurodontism seen between *Cercopithecus talapoin* and some of the higher primates are of independent origin.

is also an inherent tendency to increase the size of the pulp cavity from before backwards in the lower molars. It also seems that some forms of Prosimii have acquired a tendency to reduce the size difference between the pulp cavities of the second and third lower molars.

3. The Eocene Lemuriformes and Tarsiiformes are cynodont. The fossil record clearly shows that cynodontism is the basal primitive condition for all the later forms of primates.

4. The primitive cynodontism of Eocene Prosimii has been retained by the modern Lemuriformes, most of the Lorisiformes and in *Tarsius spectrum*. The hyper-taurodontism observed in the third lower molar of one specimen of *Nycticebus bengalensis* (*Nycticebus coucang bengalensis*) is probably a recent acquisition.

5. Modern Ceboidea exhibit a strong tendency to have taurodont teeth, which is a post-Eocene development, as this feature is not present in Eocene Prosimii.

6. Most of the modern cercopithecoids have retained the cynodontism seen in *Apidium*, *Amphipithecus* and the Eocene Prosimii. The taurodontism seen in modern *Cercopithecus talapoin* is probably a fairly recent development.

7. The taurodontism found in modern Ceboidea, in one *Nycticebus bengalensis* (*Nycticebus coucang bengalensis*) and in *Cercopithecus talapoin* are clearly of independent origin.

8. In the primitive ancestors of primates P_2, P_3, P_4, M_1, M_2 and M_3 probably had two separate roots and P_1, which is lost in all modern forms, probably had one root. But by the end of the Eocene period P_2 of some species of *Notharctus* and of some Tarsiiformes had already acquired a single root.

9. In modern Lemuridae, P_3, P_4, M_1, M_2 and M_3 have retained the two separate roots of the primitive Prosimii, while their P_2 has acquired a single root. On the other hand, in *Propithecus* of Indriidae in which P_2 has been lost, P_3 and P_4 have acquired a single root, which is probably a post-Eocene development, while the lower molars retain the primitive two roots.

10. Modern Lorisiformes have retained the primitive two roots in P_3, P_4, M_1, M_2 and, in most cases, in M_3. On the other hand, P_2 of Lorisiformes has acquired a single root, which can be traced

back to the early Miocene period.[128] The fused single root seen in the third lower molar of one individual of *Nycticebus bengalensis* (*Nycticebus coucang bengalensis*) is evidently a recent development.

11. P_4, M_1, M_2 and M_3 of modern *Tarsius spectrum* has retained the two separate roots of primitive Eocene Tarsiiformes. P_3 of *Tarsius spectrum* may have one or two roots, which shows that the modern genus could not have been derived from *Microchoerus* of upper Eocene in which P_3 had already acquired a single root. As *Pseudoloris parvulus* had two roots in P_3, it is probable that the tendency to have a single root in P_3 of some individuals of *Tarsius spectrum* developed in post-Eocene times. On the other hand, the single-rooted P_2 of *Tarsius spectrum* is probably directly derived from the one-rooted P_2 of the primitive *Pseudoloris*. The single-rooted P_2 of Tarsiiformes and those of modern Lemuriformes-Lorisiformes apparently are of independent origin.

12. Modern Ceboidea shows a strong tendency to have a single root in the three lower premolars and a tendency to fuse the roots of some lower molars. It is probable that the single-rooted P_2 of Ceboidea is derived from the single-rooted P_2 of Eocene Tarsiiformes. On the other hand, the tendency of modern Ceboidea to have a single root in P_3 and P_4 and fused roots in some of the lower molars must have developed in post-Eocene times. It was stated before that P_2 of modern Lemuriformes-Lorisiformes, P_3-P_4 of *Propithecus* and M_3 of one *Nycticebus* also had one root. It is evident that the similarities in the roots of these teeth of Ceboidea to those of the other forms mentioned are clearly of independent origin. Similarly, the single-rooted P_3 of some individuals of *Tarsius spectrum*, in which this tooth may have one or two roots, and the single-rooted P_3 of Ceboidea are due to parallelism.

13. P_2 of *Amphipithecus mogaungensis*, which tooth is lost in later Catarrhinae, may have derived its single root from the one-rooted P_2 of Eocene Tarsiiformes. Most of the modern cercopithecoids have

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[128] Although some later forms of *Notharctus* had acquired a single root in P_2, as the genus *Notharctus* is too specialized and is not on the line of ascent to the modern Lemuriformes (see Le Gros Clark, 1934, pp. 82-83, 259 and fig. 87), it is probable that the single-rooted P_2 of modern Lemuriformes and Lorisiformes developed independently of that of the later species of *Notharctus*.

A STUDY OF THE PULP CAVITIES AND ROOTS

ERRATA

During the course of printing of the pictures some figures have been further enlarged and some reduced, necessitating a correction in the scales of the enlargements which had already been published with the text. The correct sizes of the figures are as follows:

Fig. 1. Enlarged about 2.2 times.
Fig. 2. Enlarged about 1.6 times.
Fig. 8. Enlarged about 3.3 times.
Fig. 13. Enlarged about 2.1 times.
Fig. 20. Enlarged about 2.3 times.
Fig. 21. Enlarged about 3.3 times.
Fig. 23. Enlarged about 4.4 times.
Figs. 25-29. About natural size.
Fig. 30. Enlarged about 2.9 times.
Figs. 31-33. About natural size.
Fig. 34. Slightly larger than natural size.
Figs. 39-48. Slightly larger than natural size.
Fig. 52. Enlarged about 3.4 times.
Fig. 53. Slightly larger than natural size.
Fig 56. Slightly larger than natural size.

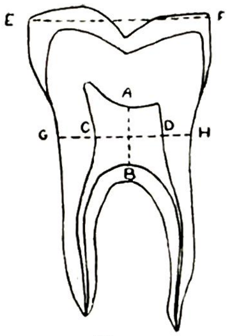


Fig. 1

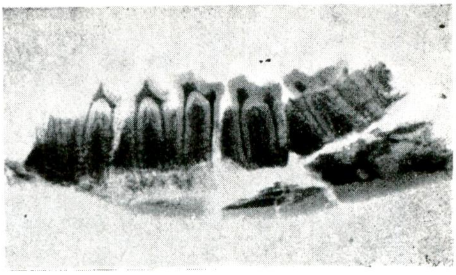
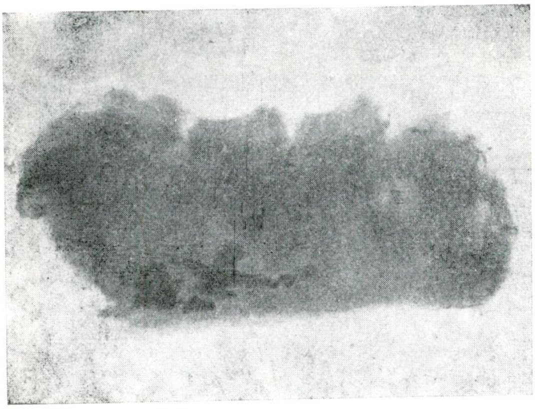


Fig. 2



← Fig. 3

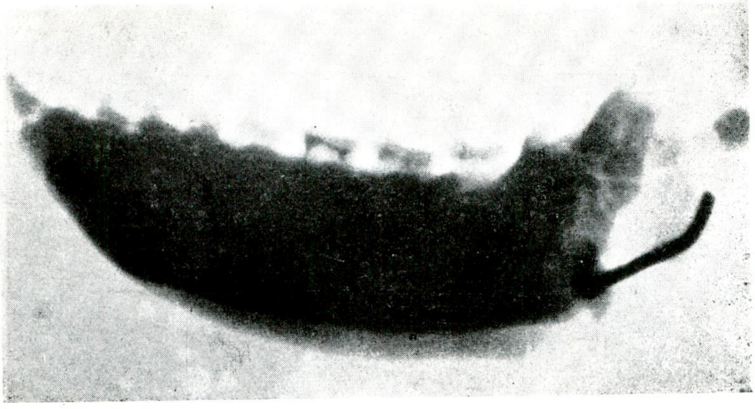


Fig. 4

Fig. 5

Fig. 6

Fig. 7

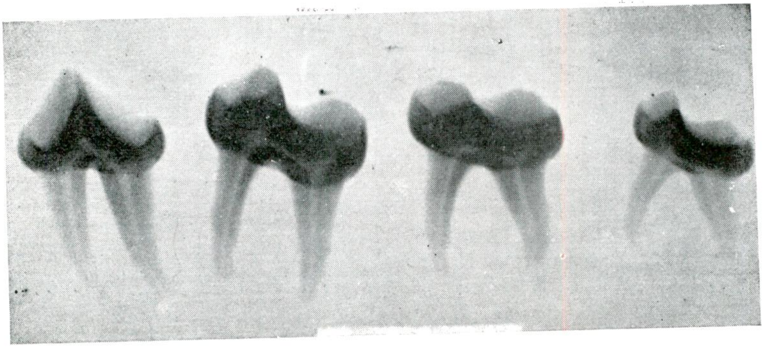


Fig. 8

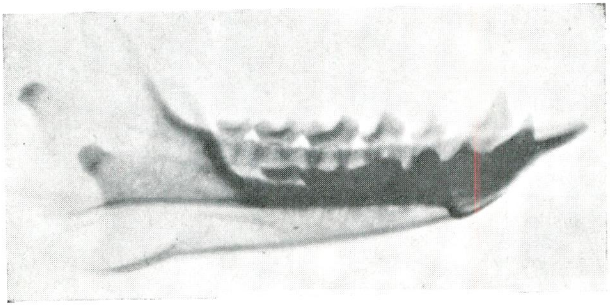


Fig. 9

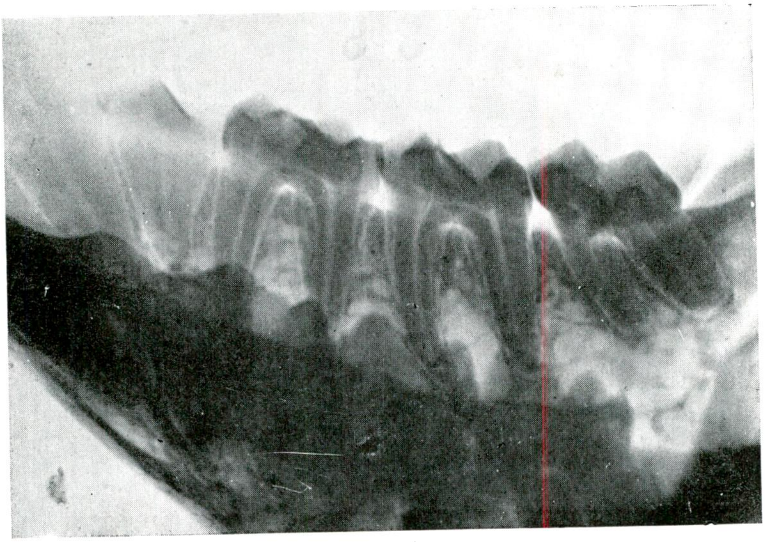
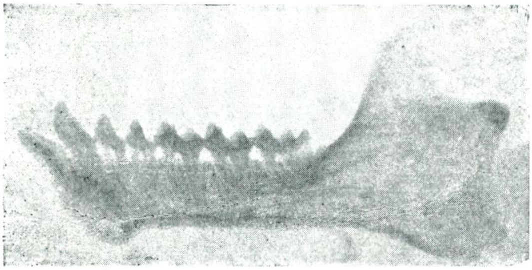
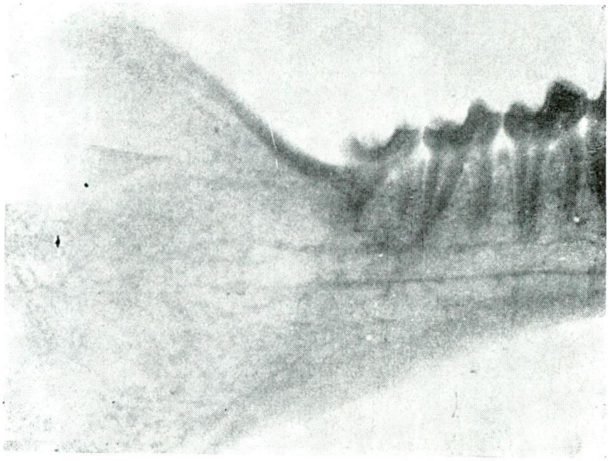


Fig. 10



← Fig. 11

Fig. 12 →



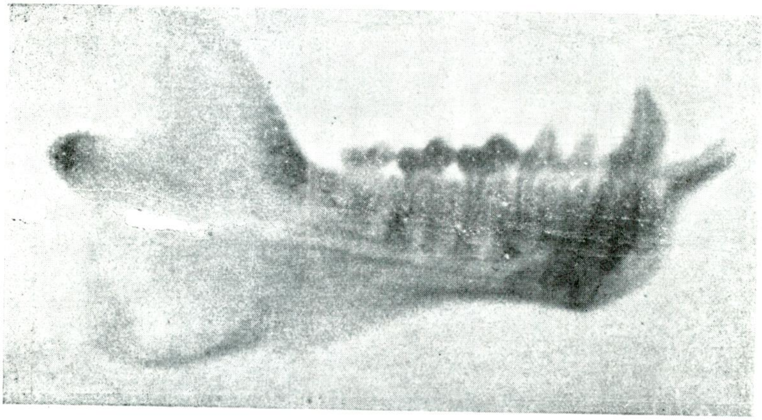


Fig. 13

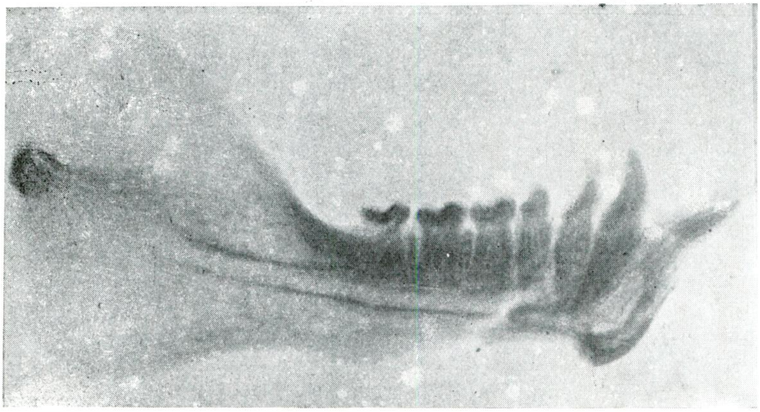


Fig. 14

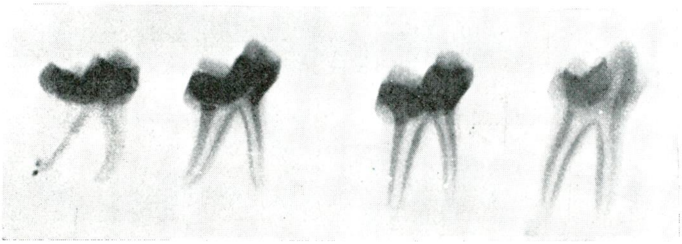


Fig. 15

Fig. 16

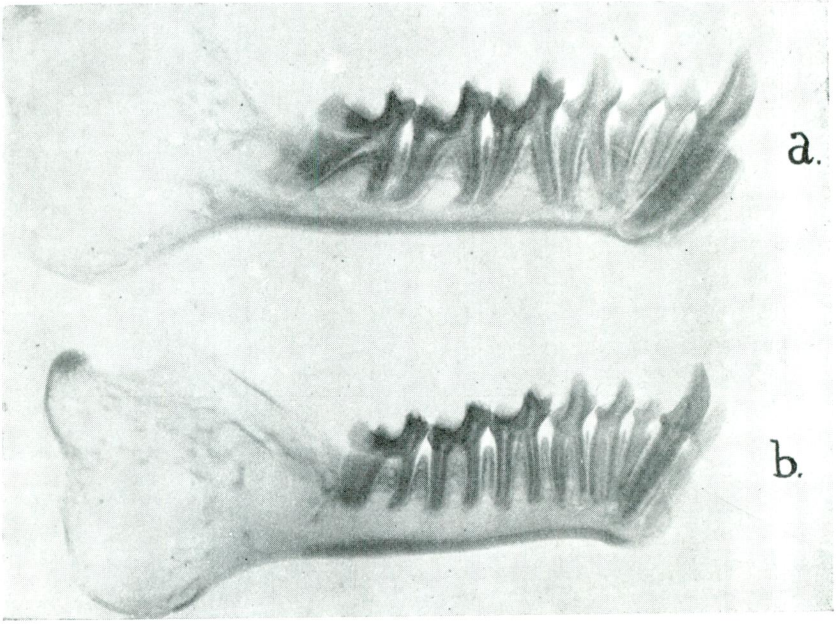


Fig. 17

Fig. 18

Fig. 19

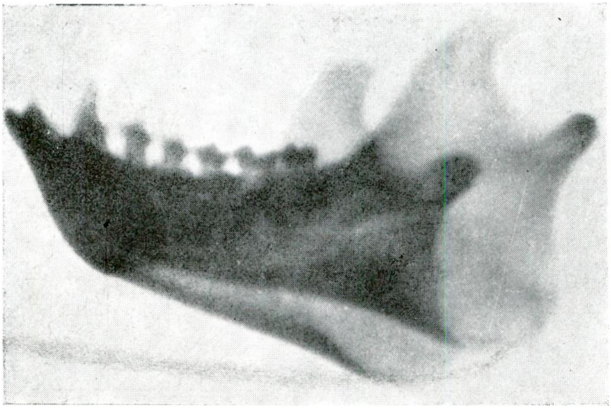


Fig. 20

Fig. 21

Fig. 22

Fig. 23

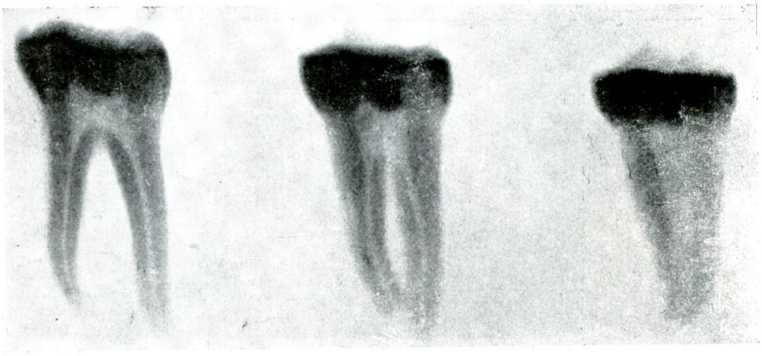


Fig. 24

Fig. 25

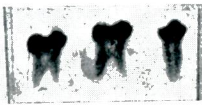
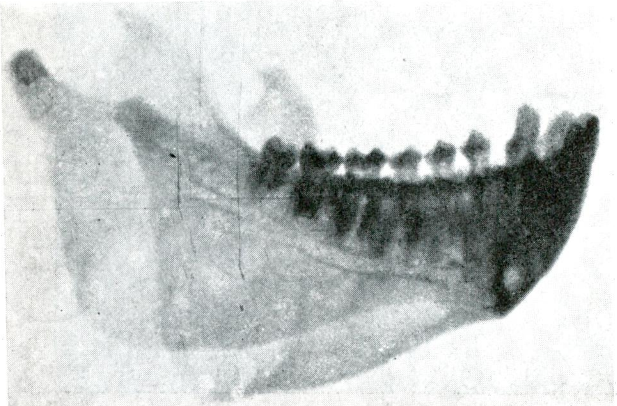


Fig. 26

Fig. 27

Fig. 28



← Fig. 29

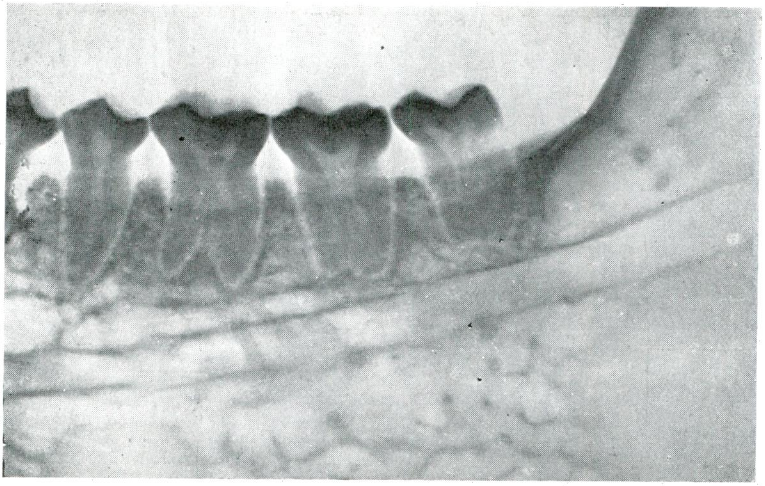


Fig. 30

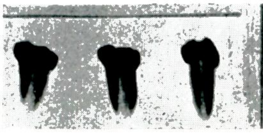


Fig. 31

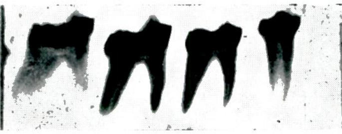


Fig. 32

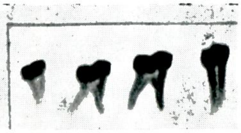


Fig. 33

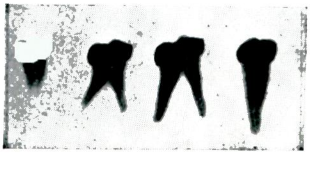


Fig. 34

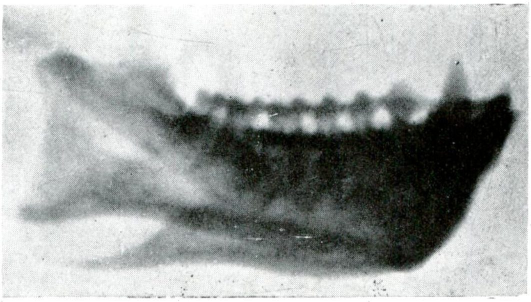


Fig. 35

Fig. 36

Fig. 37

Fig. 38

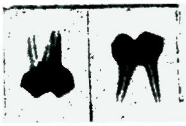


Fig. 39

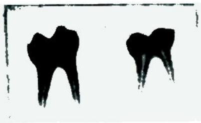


Fig. 40

Fig. 41

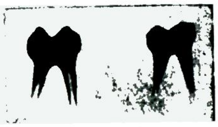


Fig. 42

Fig. 43

Fig. 44

Fig. 45

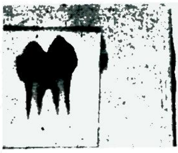


Fig. 46

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Fig. 50

Fig. 51

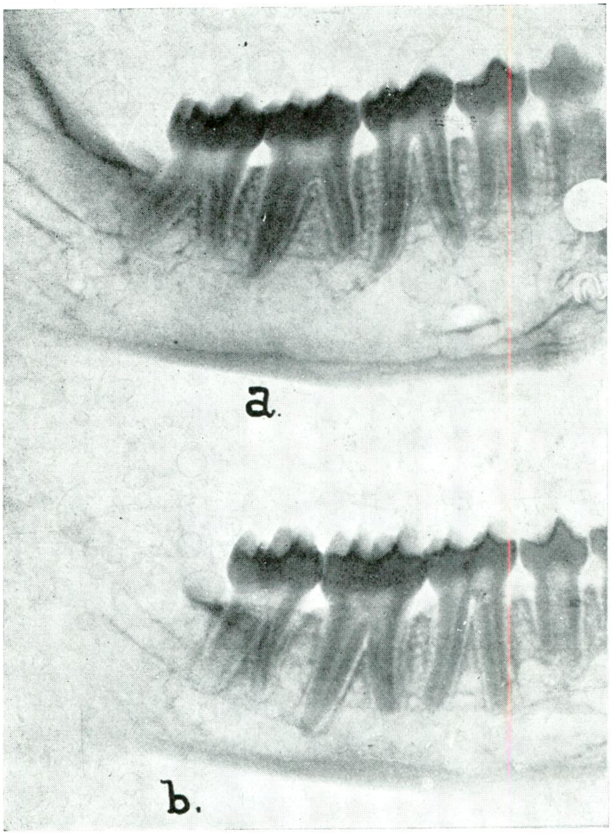

Fig. 52

Fig. 53

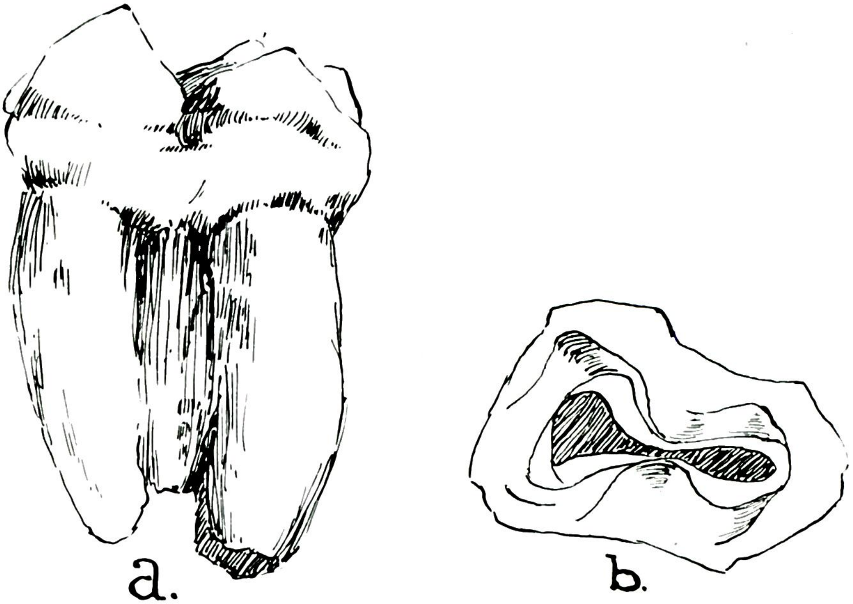

Fig. 54

← Fig. 55

Fig. 56 →

retained the primitive two roots in P_3, P_4, M_1, M_2 and M_3. The largely fused roots of P_4 of one specimen of *Cercopithecus talapoin* and the relatively shorter roots of the lower premolars and molars of this species are very probably fairly recent acquisitions.

14. The double distal root of the third lower molars of some modern cercopithecoids is probably due to the retention of a primitive feature, that goes back to *Apidium* and Eocene Tarsiiformes and during the evolution of cercopithecoids the posterior portion of this double distal root has been lost in the third lower molars of some modern genera.

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[129] In the text reference to this publication is made as Gregory, 1920-1921, to distinguish it from the other monograph of this author also published in 1920.

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EXPLANATION OF THE FIGURES

Fig. 1. Ancient Egyptian. Peabody Museum, no. 59243. M_1. Enlarged about 3 times (Drawn from Şenyürek, 1939, fig. 6).

Fig. 2. Pelycodus trigonodus. American Museum of Natural History, No. 15017. P_3, P_4, M_1, M_2 and M_3. Enlarged about 2 times.

Fig. 3. Pelycodus frugivorus. Museum of Comparative Zoology, No. 3523. P_3, M_1, M_2 and M_3. Enlarged about 2.5 times.

Fig. 4. Notharctus osborni. American Museum of Natural History, No. 11466. Mandible and permanent lower teeth. Enlarged about 2 times.

Fig. 5. Notharctus crassus. American Museum of Natural History, No. 11982. Mandible and permanent lower teeth. Natural size.

Fig. 6. Adapis parisiensis. Museum of Comparative Zoology, No. 8893. P_2, P_3, P_4, M_1, M_2 and M_3. Enlarged about 3 times.

Fig. 7. Adapis magnus. American Museum of Natural History, No. 10511. P_3, P_4, M_1, M_2 and M_3. Natural size.

Fig. 8. Lemur rubriventer. Museum of Comparative Zoology, No. 8045. P_4, M_1, M_2 and M_3. Enlarged about 3.5 times.

Fig. 9. Lemur variegatus. American Museum of Natural History, No. 77792. Mandible and permanent lower teeth. About natural size.

Fig. 10. Propithecus verreauxi. Museum of Comparative Zoology, No. 16397. P_3, P_4, M_1, M_2 and M_3. Enlarged about 3 times.

Fig. 11. Loris tardigradus. American Museum of Natural History, No. 34257. Mandible and permanent lower teeth. Enlarged about 2.5 times.

Fig. 12. Nycticebus borneanus (N.c. borneanus). United States National Museum, No. 142238. P_4, M_1, M_2 and M_3. Enlarged about 3.5 times.

Fig. 13. Nycticebus bengalensis (N.c. bengalensis). American Museum of Natural History, No. 87279. Mandible and permanent lower teeth. Enlarged about 2.2 times.

Fig. 14. Perodicticus potto. American Museum of Natural History, No. 52692. Mandible and permanent lower teeth. Enlarged about 2 times.

Fig. 15. Galago crassicaudatus. Museum of Comparative Zoology, No. 26877. P_4, M_1, M_2 and M_3. Enlarged about 3 times.

Fig. 16. Microchoerus edwardsi (Necrolemur edwardsi). Museum of Comparative Zoology, No. 8881. P_3, P_4, M_1, M_2 and M_3. Enlarged about 3 times.

Fig. 17. Tarsius spectrum. Enlarged about 3.7 times.

a: Tarsius spectrum (T. philippensis). United States National Museum, No. 144643. Mandible and permanent lower teeth.

b: Tarsius spectrum (T. fuscus). United States National Museum, No. 220282. Mandible and permanent lower teeth.

Fig. 18. Callithrix (Hapale) santaremensis. Museum of Comparative Zoology, No. 30586. P_4, M_1 and M_2. Enlarged about 5.6 times.

Fig. 19. Leontocebus (Mystax graellsi). Museum of Comparative Zoology, No. 27331. P_4, M_1 and M_2. Enlarged about 3.5 times.

Fig. 20. Leontocebus midas. American Museum of Natural History, No. 37463. Mandible and permanent lower teeth. Enlarged about 2.5 times.

Fig. 21. Leontocebus (Oedipomidas geoffroyi). United States National Museum, No. 240423. P_3, P_4, M_1 and M_2. Enlarged about 3.5 times.

Fig. 22. Aotus lanis. United States National Museum, No. 241414. P_3, P_4, M_1, M_2 and M_3. Enlarged about 3.4 times.

Fig. 23. Callicebus remulus. Museum of Comparative Zoology, No. 30564. P_4, M_1, M_2 and M_3. Enlarged about 4.7 times.

Fig. 24. Cacajao rubicundus. Museum of Comparative Zoology, No. 1957. M_1, M_2 and M_3. Enlarged about 4.7 times.

Fig. 25. Ateles fusciceps. Museum of Comparative Zoology, No. 27327. M_1, M_2 and M_3. Natural size.

Fig. 26. Ateles geoffroyi. Museum of Comparative Zoology, No. 29628. P_4, M_1 and M_2. Natural size (After Şenyürek, 1939).

Fig. 27. Ateles geoffroyi. Museum of Comparative Zoology, No. 29642. M_1 and M_2. Natural size.

Fig. 28. Ateles geoffroyi. Museum of Comparative Zoology, No. 37322. P_4, M_1, M_2 and M_3. Natural size.

Fig. 29. Ateles paniscus. American Museum of Natural History, No. 94134. Mandible and permanent lower teeth. Natural size.

Fig. 30. Ateles paniscus. United States National Museum, No. 194337. P_3, P_4, M_1, M_2 and M_3. Enlarged about 3.2 times.

Fig. 31. Ateles paniscus. Museum of Comparative Zoology, No. 31775. P_4, M_1 and M_2. Natural size (After Şenyürek, 1939).

Fig. 32. Alouatta palliata. Museum of Comparative Zoology, No. 27325. P_4, M_1, M_2 and M_3. Natural size.

Fig. 33. Cebus macrocephalus. Museum of Comparative Zoology, No. 15325. P_4, M_1, M_2 and M_3. Natural size.

Fig. 34. Cebus fatuellus. Museum of Comparative Zoology, No. 32173. P_4, M_1, M_2 and M_3. Natural size.

Fig. 35. Saimiri sp. American Museum of Natural History, No. 76371. Mandible and permanent lower teeth. Enlarged about 2 times.

Fig. 36. Amphipithecus mogaungensis. American Museum of Natural History, No. 32520. P_3, P_4 and M_1. Natural size.

Fig. 37. Apidium phiomensis. American Museum of Natural History, No. 13370. P_4, M_1, M_2 and M_3. Enlarged about 2.7 times.

Fig. 38. Cercopithecus mona. Museum of Comparative Zoology, No. 8112. dm^2 and dm_2. Natural size.

Fig. 39. Cercopithecus mona. Museum of Comparative Zoology, No. 8112. Permanent M^1 and M_1. Natural size.

Fig. 40. Cercopithecus mona. Museum of Comparative Zoology, No. 24784. M_1 and M_2. Natural size.

Fig. 41. Cercopithecus nictitans. Museum of Comparative Zoology, No. 24332. M_1. Natural size.

Fig. 42. Cercopithecus mitis. Museum of Comparative Zoology, No. 22742. M_1 and M_2. Natural size.

Fig. 43. Cercocebus albigena. Museum of Comparative Zoology, No. 22736. P_4, M_1, M_2 and M_3. Natural size.

Fig. 44. Papio doguera. Museum of Compartive Zoology, No. 23091. M_1 and M_2. Natural size.

Fig. 45. Papio doguera. Museum of Comparative Zoology, No. 29786. M_2. Natural size.

Fig. 46. Colobus polycomus. Museum of Comparative Zoology, No. 32005. M_1. Natural size.

Fig. 47. Colobus polycomus. Museum of Comparative Zoology, No. 22629. P_4, M_1, M_2 and M_3 (the distal side of M_3 is facing the other teeth). Natural size.

Fig. 48. Colobus polycomus. Museum of Comparative Zoology, No. 21151. M_1, M_2 and M_3. Natural size.

Fig. 49. Colobus polycomus. Museum of Comparative Zoology, No. 23191. M_1, M_2 and M_3. Natural size.

Fig. 50. Pygathrix potenziani. Museum of Comparative Zoology, No. 16722. M_2, M_1 and M_3 (distal surface of M_3 is facing M_1). Natural size.

Fig. 51. Pygathrix aurata (labelled as Pithecus aurata). Museum of Comparative Zoology, No. 12734. P_4, M_1, M_2 and M_3. Natural size.

Fig. 52. Cercopithecus talapoin. Enlarged about 3.5 times.
a: Cercopithecus talapoin. United States National Museum, No. 220338. P_3, P_4, M_1, M_2 and M_3.
b: Cercopithecus talapoin. United States National Museum, No. 220330. P_3, P_4, M_1, M_2 and M_3.

Fig. 53. Hylobates lar. Peabody Museum, no. N/3052. P_4, M_1, M_2 and M_3. Natural size.

Fig. 54. Hylobates hoolock. Museum of Comparative Zoology, No. 43067. M_2. Enlarged.
a: Lateral view.
b: Apical view.

Fig. 55. Symphalangus syndactylus. United States National Museum, No. 271048. P_4, M_1, M_2 and M_3. Enlarged about 3.4 times.

Fig. 56. Symphalangus syndactylus. Museum of Comparative Zoology, No. 27831. P_4, M_1, M_2 and M_3. Natural size.

TABLE 1

The Material X-Rayed[1]

Family	Subfamily	Number of Individuals
Adapidae	Adapinae	2
	Northarctinae	4
Lemuridae	Lemurinae	2
Indriidae		1
Lorisidae	Lorisinae	4
	Calaginae	1
Anaptomorphidae	Necrolemurinae	1
Tarsiidae		2
Cebidae	Aotinae	2
	Pitheciinae	1
	Alouattinae	1
	Atelinae	7
	Cebinae	3
Callithricidae		5
Cercopithecidae	Cercopithecinae	11
	Colobinae	6
	Apidium (subfamily not yet known)[2]	1
Amphipithecus (of uncertain position)[3]		1
TOTAL		55

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1. The names of the families and subfamilies are taken from Simpson, 1950, pp. 61-67.
2. Simpson, 1950, p. 67.
3. Ibid., p. 68.

TABLE 2

Average Indices of Some Cynodont and Taurodont First Lower Molars

	INDEX I $\frac{AB \times 100}{CD}$	INDEX II $\frac{AB \times 100}{EF}$	INDEX III $\frac{CD \times 100}{EF}$	INDEX IV $\frac{CD \times 100}{GH}$
2 Cercopithecus[1] (cynodont)	12.78	6.63	52.15	65.92
1 Cercopithecus talapoin (cynodont)	17.85	7.63	42.74	53.33
1 Cercopithecus talapoin (moderately taurodont)	33.33	13.17	39.53	49.03
1 Alouatta palliata (cynodont)	17.14	9.42	55.26	64.02
1 Callicebus remulus (moderately taurodont)	33.33	15.86	47.58	60.00
1 Ateles fusciceps (nearly cynodont)	27.27	10.71	39.28	48.88
4 Ateles[2] (moderately taurodont)	112.23	38.87	25.66	35.39
1 Ateles paniscus (hyper-taurodont)	414.28	105.45	25.45	38.88

1. 1 Cercopithecus mona and 1 Cercopithecus mitis. In these tables figures in front of specific names refer to the number of individuals measured.

2. 3 Ateles geoffroyi and 1 Ateles paniscus. The specimen of Ateles paniscus shown in fig. 29 has not been measured.

TABLE 3

Average Indices of Some Cynodont and Taurodont Second Lower Molars

	INDEX I $\frac{AB \times 100}{CD}$	INDEX II $\frac{AB \times 100}{EF}$	INDEX III $\frac{CD \times 100}{EF}$	INDEX IV $\frac{CD \times 100}{GH}$
2 Cercopithecus[1] (cynodont)[2]	18.54	9.42	51.16	62.25
2 Cercopithecus talapoin (both moderately taurodont)	55.00	20.42	37.31	47.12
1 Alouattta palliata (cynodont)	17.18	9.73	56.63	65.30
1 Callicebus remulus (moderately taurodont)	49.18	20.54	41.78	56.48
3 Ateles[3] (moderately taurodont)	127.52	35.59	28.09	38.52
3 Ateles[4] (hyper-taurodont)	410.65	84.77	21.07	13.17

1. 1 Cercopithecus mona and 1 Cercopithecus mitis.
2. These teeth have not yet completed their development.
3. 1 Ateles fusciceps and 2 Ateles geoffroyi.
4. 1 Ateles geoffroyi and 2 Ateles paniscus.

TABLE 4

Average Indices of Some Cynodont and Taurodont Third Lower Molars

	INDEX I $\frac{AB \times 100}{CD}$	INDEX II $\frac{AB \times 100}{EF}$	INDEX III $\frac{CD \times 100}{EF}$	INDEX IV $\frac{CD \times 100}{GH}$
2 Cercopithecus talapoin (both moderately taurodont)	65.20	21.48	32.96	43.87
1 Alouatta palliata (cynodont)	18.30	11.11	60.44	65.38
1 Callicebus remulus (hyper-taurodont)	250.87	100.00	39.86	62.41
1 Ateles fusciceps (moderately taurodont?)	175.00?	36.84?	23.07	30.00
2 Ateles[1] (both hyper-taurodont)	447.26	75.98	17.20	24.66

[1] 1 Ateles geoffroyi and 1 Ateles paniscus.

TABLE 5

Differences in the Indices of Pulp Cavities of Immature and Mature First Lower Molars

	INDEX I $\frac{AB \times 100}{CD}$	INDEX II $\frac{AB \times 100}{EF}$	INDEX III $\frac{CD \times 100}{EF}$	INDEX IV $\frac{CD \times 100}{GH}$
1 Colobus polycomus Immature	44.18	26.76	60.56	79.62
3 Colobus polycomus Mature (average)	11.17	5.89	52.88	64.25
1 Cercopithecus mona Immature	17.72	9.45	53.37	71.81
1 Cercopithecus mona Mature	13.88	6.84	49.31	63.71
1 Cercopithecus nictitans Immature	24.00	11.25	46.87	68.80
1 Cercopithecus mitis Mature	11.68	6.42	55.00	68.14