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NOTES ON THE TYPE OF *HESPEROPITHECUS HAROLD- COOKII* OSBORN

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Through the courtesy of Professor Osborn, who has recently described¹ the type of *Hesperopithecus haroldcookii*, we have had the opportunity of making further studies upon this already famous specimen, the results of which are submitted below.

ANALYSIS OF CHARACTERS OF THE TYPE

A careful consideration of the characters afforded by the badly eroded and worn type, an upper molar, leads us to distribute them under the following categories.

I.—CHARACTERS DUE TO LONG EXPOSURE TO WEATHERING, EROSION AND STREAM OR WIND ACTION

- (a) Extreme rounding of all angles margins, ridges, and projections of crown and roots.
- (b) Breaking off of postero-external (disto-buccal) root and smoothing of site of root.
- (c) Loss of enamel on entire external and half of posterior surface.
- (d) Presence of numerous large and small cracks and fissures and rounding of the margins of the cracks, causing them to simulate the natural fissures between cusps.

II.—CHARACTERS DUE TO EXTREME NATURAL WEAR OF THE CROWN

- (a) Extreme shortness or apparent brachydonty of crown and loss of all main cusps.
- (b) Close apparent approximation of hypocone to protocone.
- (c) Evenly concave wearing surface.
- (d) Deposition of secondary dentine on roof of pulp cavity, beneath wearing surface.
- (e) Diminished size of root canals.

III.—CHIEF DIAGNOSTIC CHARACTERS OF *Hesperopithecus* TYPE

- (a) Upper molar crown conforming to the general type that is common to the anthropoids and man.
- (b) Evenly concave masticating surface, as in *Pithecanthropus*, certain chimpanzees¹ and Australian aborigines.

¹Osborn, Henry Fairfield, 1922, '*Hesperopithecus*, the First Anthropoid Primate Found in America.' American Museum Novitates, No. 37. 5 pp., 3 figs. (reprinted without figures in Science, LV, pp. 463-465, May 3, 1922).

²Fide G. S. Miller, *in litteris*.

- (c) Very large divergent roots, a primitive character retained in the gorilla, in *Pithecanthropus*, and in certain human teeth.
- (d) Transverse diameter of antero-external root smaller than in human molars.
- (e) Floor of pulp-cavity raised well above bifurcation of roots, as in man (Fig. 5).
- (f) Form of floor of pulp-cavity resembling that of anthropoids and man.

REMARKS ON FIGURES 1 TO 4

FIGURE 1

The crown of the *Hesperopithecus* molar was worn down by use nearly to the base, so that the cusps had entirely disappeared. After death the tooth was badly cracked, battered and waterworn. The cracks and rounded edges are due to these processes.

The upper row of figures shows that the occlusal surface of the *Hesperopithecus* molar is more or less intermediate in contour between m^3 and m^2 of the chimpanzee.

In the middle row the rounding of the antero-buccal edge of the crown is probably due to extreme wear and subsequent erosion; so also the bluntness of the root ends. The enamel on the lingual surface, unlike that of the chimpanzee here figured, is not reflected toward the root along the neck of the tooth. The lingual root (1) was extremely robust.

In the lower row we see the site of the postero-external (disto-buccal) root, which has been broken off, and the site subsequently smoothed down by erosion.

FIGURE 2

In *Hesperopithecus* the antero-external (mesio-buccal) root is very large. The site of the missing postero-external root is also shown, as well as the buccal aspect of the lingual root. The deep fissures and cracks are probably due to erosion.

In the middle and lower rows the great width of the lingual root in *Hesperopithecus* is well shown. The lower row shows the site of the missing postero-external root and the deep groove on the buccal side of the lingual root. The great antero-posterior width of the lingual root, as well as the extreme wear of the occlusal surface, indicates that the tooth is an m^2 or m^1 rather than an m^3 .

FIGURE 3

The evenly concave wearing surface of the *Hesperopithecus* molar is seen to resemble that of *Pithecanthropus*.¹ In the upper row we note the

¹Dr. Miller informs us that he finds nearly the same condition in certain chimpanzees, and we find it also in a gorilla and in Australian aborigines and American Indians.

far greater antero-posterior diameter in *Pithecanthropus*, which has a very large hypocone.

The righthand figures in the upper and middle rows represent the second upper molar of an American Indian, which has been artificially ground down to near the base of the crown. The appearance of this tooth indicates that the rounding of the edges in *Hesperopithecus* may be due to erosion, since similar erosional features have been produced experimentally in the modern tooth. Secondly, it shows the rapid lessening of the antero-posterior diameter of the inner or lingual side of the tooth near the base of the crown.

The middle row shows the doubling of the antero-external (mesio-buccal) root in *Pithecanthropus* and the extreme divergence of its inner and outer roots. In *Hesperopithecus* the lingual root is much wider transversely than that in the human molar and the antero-external root is narrower. The lack of a sharp reflection of the enamel toward the lingual side is seen also in the human molars here figured.

The lower row shows well the even concavity of the wearing surface in *Hesperopithecus* and *Pithecanthropus*. The divergence of the lingual and buccal roots is greater than that in the human molar figured.

FIGURE 4

In the upper row we see the doubling of the antero-external root in *Pithecanthropus*, this root being single in *Hesperopithecus* and in the human tooth here figured. The grooving of the lingual root in *Hesperopithecus* is well shown, also the markedly asymmetrical contour of the crown as seen from above. This view especially, together with Fig. 2, lower row, affords evidence that the type specimen of *Hesperopithecus* is an upper molar of a member of the anthropoid-man group.

In the middle row considerable resemblance to the second upper molar of *Pithecanthropus* and to the first upper molar of an American Indian is shown.

In the lower row the Indian molar (m^2), which had been artificially ground down to near the base of the crown, is compared with the unground but worn second molar of the opposite side. Compare Fig. 3, upper row, with remarks above.

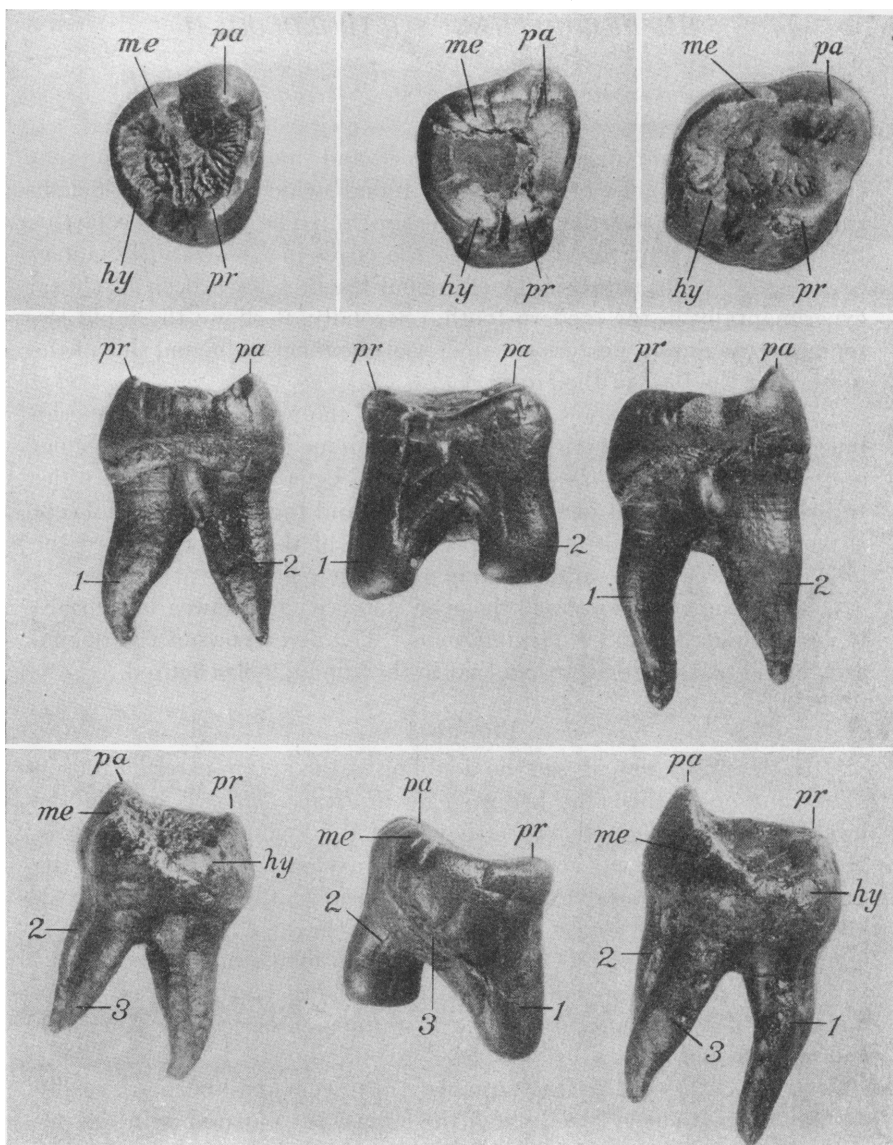


Fig. 1. Comparative figures of upper molars of *Hesperopithecus* and modern chimpanzee (*Pan schweinfurthii*), $\times 2$.

UPPER ROW: occlusal aspect, third upper molar of chimpanzee, second (?) upper molar, type of *Hesperopithecus*, second upper molar of chimpanzee.

MIDDLE ROW: anterior (mesial) aspect of same specimens.

LOWER ROW: posterior (distal) aspect.

Pr, protocone (mesio-lingual cusp); pa, paracone (mesio-buccal); me, metacone (disto-buccal); hy, hypocone (disto-lingual). 1, lingual root; 2, antero-external (mesio-buccal) root; 3, postero-external (disto-buccal) root or site of same.

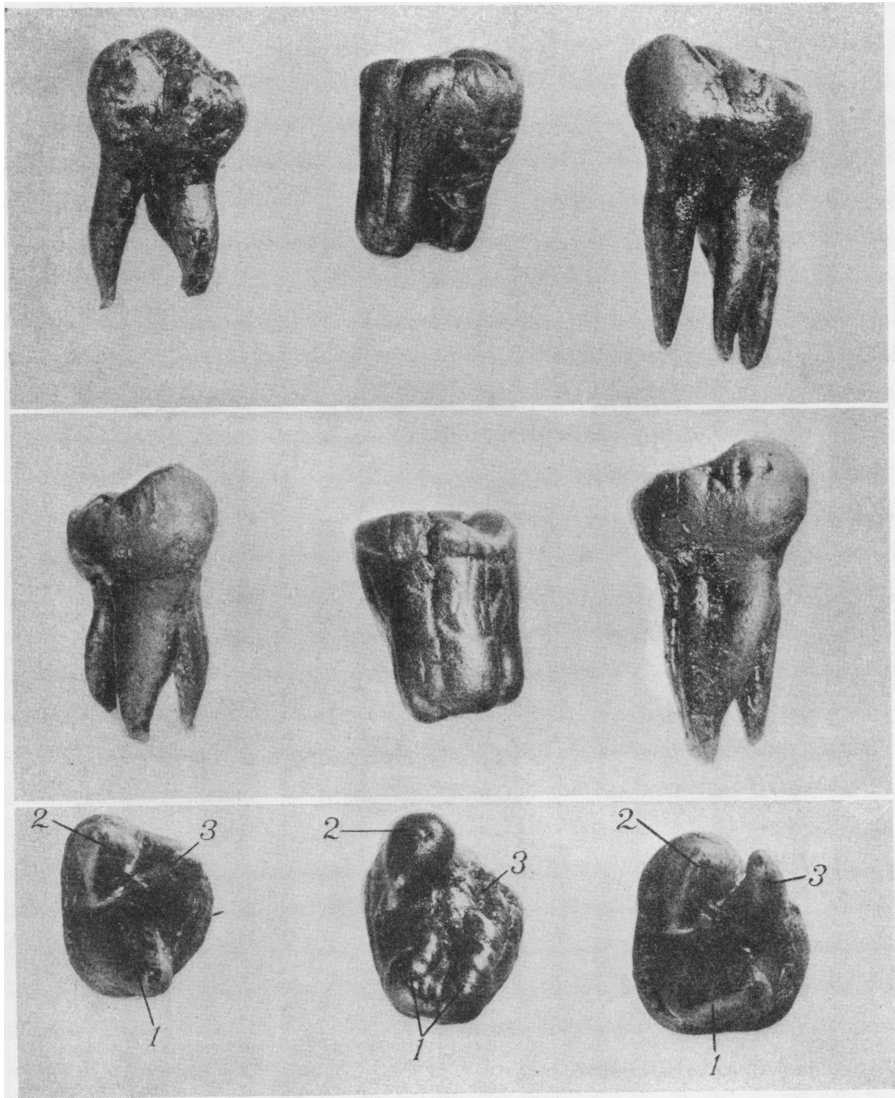


Fig. 2. Comparative figures of upper molars of *Hesperopithecus* and modern chimpanzee (continued), $\times 2$.

UPPER ROW: buccal aspect, m^2 chimpanzee, m^2 (?) *Hesperopithecus*, m^2 chimpanzee.

MIDDLE ROW: lingual aspect, same series.

LOWER ROW: view from above, showing roots.

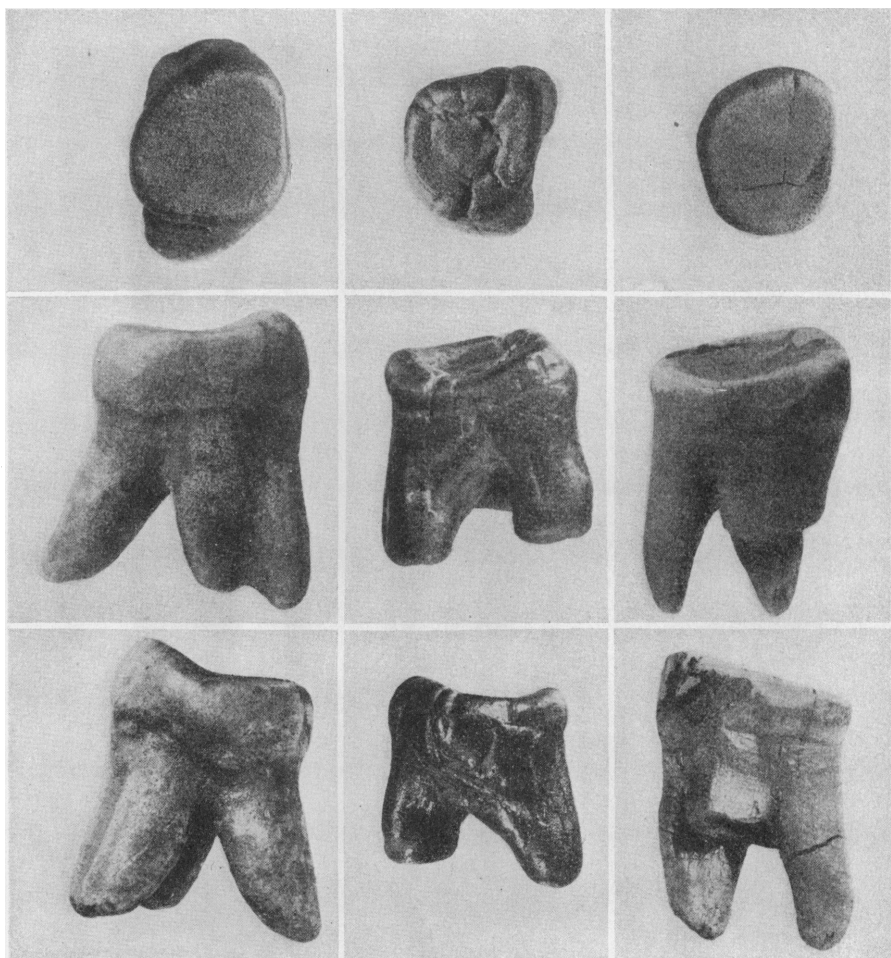


Fig. 3. Comparative figures of upper molars of *Pithecanthropus*, *Hesperopithecus* and modern American Indian, $\times 2$.

UPPER ROW: occlusal aspect, second upper molar (cast) referred to *Pithecanthropus*, type upper molar of *Hesperopithecus*, and second upper molar of modern American Indian (ground down to near base of crown).

MIDDLE ROW: anterior or mesial view of same series.

LOWER ROW: posterior or distal view of *Pithecanthropus*, *Hesperopithecus*, and m¹ American Indian.

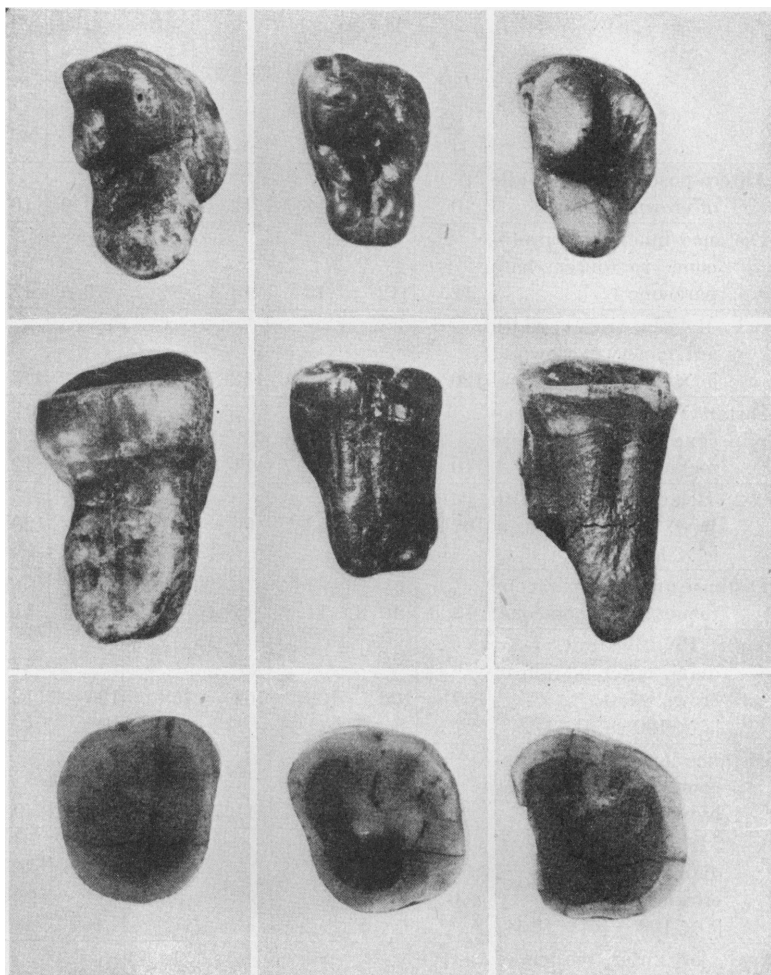


Fig. 4. Comparative figures of upper molars of *Pithecanthropus*, *Hesperopithecus* and modern American Indian (continued).

UPPER ROW: view from above, showing roots; second upper molar (cast) referred to *Pithecanthropus*, type upper molar of *Hesperopithecus*, first upper molar of American Indian (postero-external root broken off).

MIDDLE ROW: lingual aspect of same specimens.

LOWER ROW: occlusal aspect of molars of American Indians. Second upper molar ground down to near base of crown, second upper molar of opposite side natural wear, first upper molar much worn.

TABLE I.—COMPARATIVE MEASUREMENTS¹ AND INDICES OF *HESPEROPITHECUS* TYPE UPPER MOLAR

	<i>Hesperopithecus</i> Type m ¹ ?	Chimpanzee A. M. N. H. m ³ 51278	Chimpanzee A. M. N. H. m ² 51278	<i>Pithecanthropus</i> Cast m ²	American Indian A. M. N. H. m ² 2161 Crown ground down	American Indian A. M. N. H. m ² 2161 Natural wear	American Indian A. M. N. H. m ¹ 22166 Natural wear
a.—Antero-post. diam. middle of crown at base	10	10	11.5	12	10	10.2	10
b.—Distance inner base protocone to outer base paracone	12	12	13	13.4	12.2	12.5	12.3
Index 1: Relative transv. width ant. moiety of crown [b × 100 ÷ a]	120	120	113	112	122	123	123
c.—Distance inner base hypocone to outer base metacone	10.2	9	10.7	11.5	11.5	11.8	12
Index 2: Relative transv. width post. moiety of crown [c × 100 ÷ a]	102	90	93	96	115	116	120
d.—Distance ant. base paracone to post. base metacone	10.5	10.2	11.8	12.2	10.8	10.8	11.2
Index 3: Relative ant. post. diam. outer margin of crown [d × 100 ÷ a]	105	102	103	102	108	106	112
e.—Distance ant. base protocone to post. base hypocone	9.3	9.2	10.5	11.7	9.5	10	9.8
Index 4: Relative ant. post. diam. inner part of crown [e × 100 ÷ a]	93	92	91	97	95	100	98
f.—Angle of outer border of crown to ant. border	62°	68°	60°	60°	70°	70°	70°
g.—Ant. post. diam. lingual root	6.8	5	6.2	7.7	5.7	5.7	6.5
Index 5: Relative ant. post. diam. of lingual root [g × 100 ÷ a]	68	50	54	64	57	56	65
h.—Angle of axis of lingual root to that of antero-buccal root	21.5°	25°	22.5°	m ² 27° m ³ 35°	5°	5°	18°

¹Measurements are in millimeters.

TABLE II.—VARIABILITY OF ANGLE OF AXIS OF LINGUAL ROOT TO THAT OF ANTERO-BUCCAL ROOT IN HUMAN MOLARS

	Am. Ind.		Bedouin	White Man	Am. Ind.
	A. M. N. H. 2161	A. M. N. H. 22166	A. M. N. H. 7224		A. M. N. H. 22165
m ²	5°	13°	14°		
m ¹		18°	18°	28°	43°

REMARKS ON THE MEASUREMENTS AND INDICES

(Cf. Tables I, II and Figures 1-4)

The type upper molar of *Hesperopithecus* approaches the third upper molar of a certain chimpanzee in the general dimensions of the base of the crown, that is in four measurements, *a*, *b*, *d*, and *e*, and in two indices, 1, 4. This is the greatest number (six) of agreements recorded in the table. It differs from the same in the much greater relative width of the posterior moiety of the crown (index 2), in the much greater relative antero-posterior diameter of the lingual root (index 5) and in the lesser divergence, or forking, of the lingual and antero-buccal roots (*h*).

It approaches the second upper molar of the same chimpanzee in the transverse diameter of the posterior moiety of the crown (*c*), in the angle of the outer surface of the crown to the anterior surface (*f*), and in the degree of divergence of the axis of the lingual root to that of the antero-buccal root (*h*). All these are important points in favor of the view that the type is an m² rather than an m³.

The type upper molar of *Hesperopithecus* differs from the m² (cast) of *Pithecanthropus* in nearly all the absolute measurements, but approaches it in the great size of the lingual root (index 5), in the angle of the outer side of the crown to the anterior side (*f*), and especially in the evenly concave form of the grinding surface.

While approaching the second upper molars of certain American Indians in four absolute measurements, *a*, *b*, *d*, and *e*, and in two indices, 1 and 3, the type upper molar of *Hesperopithecus* differs widely in the more asymmetrical form of crown with narrower posterior moiety (index 2),¹ in the greater size of the lingual root and especially in the greater

¹The apparent asymmetry and relative narrowness of the posterior moiety of the crown in the type may be due in a considerable degree to the advanced condition of wear in the region of the hypocone. A difference of this character may be noticed in the comparison of a less worn and a more worn second upper human molar of the same dentition (Figure 3).

divergence of the lingual and antero-buccal roots,¹ and in the smaller transverse diameter of the antero-buccal root.

The marked asymmetry and small transverse diameter of the posterior moiety are pronounced in the second upper molar of the "Moustertian youth" of the Neanderthal race, as well as in certain Australian skulls

The type of *Hesperopithecus* approaches the first upper molar of a certain American Indian (Table I) in three important characters (*a*, *g*, and index 5).

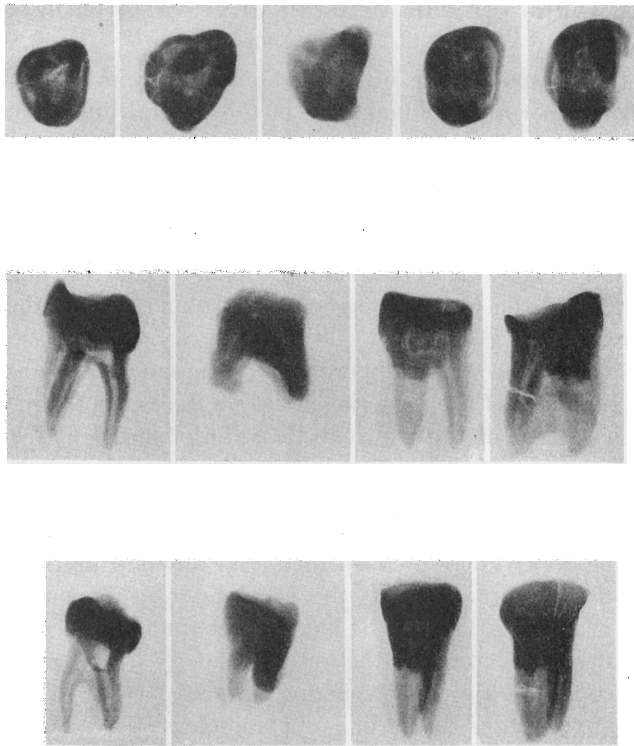


Fig. 5. Comparative radiographs of upper molars of chimpanzee, *Hesperopithecus* and American Indians.

UPPER row: vertical projection; chimpanzee m³, chimpanzee m², *Hesperopithecus*, American Indian m², American Indian m¹.

MIDDLE row: antero-posterior projection; chimpanzee m², *Hesperopithecus*, American Indian m², American Indian m¹.

LOWER row: transverse projection; chimpanzee m², *Hesperopithecus*, American Indian m², American Indian m¹.

¹There is, however, a wide range of variability (from 5 to 43°) in this character in man (see Table II).

RADIOGRAPHIC EXAMINATION OF TYPE SPECIMEN

Dr. George Palmer Ratner, D.D.S., has kindly submitted the following report, New York, August 25, 1922.

Under radiographic examination the specimen submitted has the appearance of a molar tooth, i.e., crown portion and two roots: mesial-buccal and lingual; distal buccal apparently missing. Occlusal aspect discloses pulp floor having three openings for three independent roots.

There is present the pulp chamber in crown portion of tooth, also outline of one pulp in mesial-buccal root, terminating in two foramina. Large root, or lingual, discloses two independent pulps present in this root.

Remarks¹

Radiographic examination of the type molar tooth of *Hesperopithecus* reveals a triangular outline of the floor of the pulp chamber. At the angles of this triangle corresponding to the position of the roots there are three openings corresponding with the root canals. The floor of the pulp-cavity is well raised above the bifurcation of the roots, as in man (cf. Fig. 5). The floor of the pulp-cavity resembles that of anthropoids and man.

GEOLOGICAL OCCURRENCE OF THE *HESPEROPITHECUS* TOOTH

In response to our request Dr. W. D. Matthew has kindly supplied the following statement.

This specimen was found by Harold J. Cook in the upper level of the Snake Creek quarries at a point which has been named Olcott Hill, on the ranch of Mr. Harry Ashbrook, twenty miles south of Agate, Nebraska. The Upper Snake Creek at this point consists of sand, pebbles and numerous fragments of bone, forming irregular lenses, or pockets, on the eroded surface of an older formation, the Sheep Creek beds. They appear to be channel-fill lenses and extend for a distance of about three miles to the westward, cropping out at the heads of a series of little 'draws,' or dry gullies on the southwest margin of the sand-hill area between the Niobrara and North Platte valleys. Associated with the channel-beds are finer, uniform, clean sands, partly of eolian deposition, partly water-deposited, and varying in thickness from twenty feet to zero, covered by the sodded surface of the plains.

Fossils are abundant and varied in the channel-beds but mostly very fragmentary and usually rolled or waterworn to a varying degree. Generally they are mineralized to the extent of partly filling the minute canals and pores of the bones, but the larger hollows are either filled with loose sand or empty. The color is usually blue-black from iron phosphate. Sometimes the bones are mottled light yellow, or completely dead white, and the degree of mineralization varies to a considerable extent.

The finer sands contain the same or a slightly later faunal phase but fossils are rare in them, although apt to be well preserved when found.

¹By Milo Hellman.

The fauna found in these upper Snake Creek beds has been extensively collected and carefully studied by the writer, Harold Cook and others. It appears to be a unit fauna and of Lower Pliocene age, save for occasional specimens of the Upper Miocene Lower Snake Creek fauna, presumably due to re-deposit. Except for a single specimen, a Bison jaw found on the surface in 1908 (we have no exact record or recollection of the exact circumstances), no fossils have been found at this locality which would indicate an admixture of Upper Pliocene, Pleistocene or recent faunas. Thousands of equid teeth have been found, all of the older Pliocene (or Upper Miocene) species, not one that would suggest Pleistocene age. In view of the great number of fossils it is safe to say that no Pleistocene admixture is present.

As regards the *Hesperopithecus* tooth, it was found by Mr. Cook in place in the Upper Snake Creek channel-beds, and as the finder is an experienced geologist and palæontologist, thoroughly familiar with this fossil locality and the fauna, his reports and conclusions are considered exceptionally valid proof of its occurrence. The preservation of the tooth is entirely normal and similar to the rest of the Upper Snake Creek fauna.

The following list of the associated fauna is not complete, but suffices to show its relations:

- Carnivora.—Ursidæ—*Hyænarcos* sp.
 Mustelidæ—*Brachypsalis* sp.
 Canidæ—*Aelurodon haydeni* var.
 " *sævus* var.
 Felidæ—*Machærodus* sp.
 Perissodactyla.—Equidæ—*Pliohippus leidyianus*
 " cf. *mirabilis*
 Protohippus cf. *perditus*
 " *placidus* var.
 Hipparion affinis
 " *gratum* var.
 Rhinocerotidæ—*Peraceras* sp.
 Aphelops sp. indesc.
 Teleoceras cf. *fossiger*
 Artiodactyla.—Dicotylidæ—*Prosthennops* cf. *serus*
 Camelidæ—*Alticamelus* cf. *procerus*
 Pliauchenia gigas
 ? *Procamelus* sp.
 Cervidæ—? *Cervavus* sp.
 Antilocapridæ—? *Merycodus* sp.
 Bovidæ—*Neotragoceras improvisus*
 Edentata.—Megalonychidæ—*Megalonyx* cf. *leptostomus*
 Glires.—Sciuridæ—*Sciurus* cf. *aberti*
 Mylagaulidæ—*Mylagaulus* sp.
 Geomyidæ—*Thomomys* sp.
 Proboscidea.—Mastodontidæ—*Miomastodon matthewi*
 Trilophodontidæ—? *Trilophodon* sp.
 Insectivora.—Talpidæ—*Scalops* sp.

The above fauna is comparable with that of the Republican River of Kansas, Nebraska and Colorado, with the Rattlesnake of the John Day basin in Oregon, the

Thousand Creek beds of Nevada and various early Pliocene formations in the western United States. These are regarded by Osborn, Merriam and the writer as a practical equivalent in a broad way of the *Hipparion* fauna of Europe and Asia, which is assigned by most authorities to the Lower Pliocene.

The above data are considered by the writer to furnish fairly conclusive proof of the Lower Pliocene age of the *Hesperopithecus* tooth. There is no reasonable doubt as to its age.

CONCLUSIONS

1.—The differences from the third lower molar of *Hyænarctos*, with which Dr. Smith Woodward¹ suggested that the type upper molar of *Hesperopithecus* should be compared, are so fundamental that it is difficult to find any significant points of agreement. The third lower molar of *Hyænarctos* and of the modern bears has been derived by degeneration of a normal tuberculo-sectorial molar, as may be seen readily by comparison with various amphicyonines and other canids, while the molar of *Hesperopithecus* very clearly conforms to the modified tri- to quadritubercular type that is characteristic of the upper molars of anthropoid apes and man. The illustrations in the plates surely establish this beyond reasonable dispute.

2.—The posterior upper molar of the procyonid carnivore *Cercoleptes* (*Potos*) shows a distant resemblance to the type of *Hesperopithecus* which does not stand close comparison.

3.—There is a certain superficial resemblance of the worn third upper molar crown of *Lagothrix*, a South American monkey, to the type of *Hesperopithecus*. But in the former the lingual root in old specimens is directed strongly upward and backward, while in the latter it is directed upward and forward, with reference to the general plane of the masticating surface. Moreover, the great differences in size and in the detailed characters of the teeth do not favor the possibility of a near relationship of the two genera.²

4.—Of the higher primates, the Old World monkeys are excluded from close relationship to *Hesperopithecus* by the oblong contour of the upper molar crown; the gibbons come nearer but have much smaller molars, which are more elongate antero-posteriorly; in the gorilla, the antero-posterior elongation attains an extreme, and this ape also surpasses *Hesperopithecus* in the antero-posterior width of the lingual root and in the degree of its divergence from the outer roots; the orang has

¹Woodward, A. Smith, F. R. S., 1922, 'A Supposed Ancestral Man in North America.' *Nature*, CIX, No. 2745, p. 151.

²Comparisons with all other known genera of South American monkeys show marked differences from the type of *Hesperopithecus* either in crown or roots.

quadrate molar crowns with extremely wide lingual roots¹; the chimpanzees, while varying considerably in molar characters, appear to come nearest to *Hesperopithecus*, but the specimens here figured differ from it in the weakness of the roots, in the lingual reflection of the enamel upon the neck, and in the greater relative antero-posterior diameter of the crown (assuming that the type of *Hesperopithecus* is either an m² or an m¹).²

5.—Our results thus afford additional evidence in favor of Professor Osborn's conclusion³ that the type of *Hesperopithecus haroldcookii* represents an hitherto unknown form of the higher primates. It combines characters seen in the molars of the chimpanzee, of *Pithecanthropus*, and of man, but, in view of the extremely worn and eroded state of the crown, it is hardly safe to affirm more than that *Hesperopithecus* was structurally related to all three.

6.—Whether *Hesperopithecus* itself is or is not ancestral to man can only be determined by subsequent discovery, but meanwhile the only part definitely known of it, namely, the much worn type upper molar, represents a stage of evolution which comparative morphological evidence indicates as preceding the following definitely human specializations: (a) the reduction of the lingual root; (b) the lessening of the divergence of the lingual and buccal roots; (c) the widening of the antero-external root; (d) the antero-posterior shortening and transverse widening of the crown; (e) the tendency toward rectifying the asymmetry due to the narrowness of the posterior moiety of the crown. The *Hesperopithecus* molar shows the opposites of all these characters and such an assemblage of primitive features has not hitherto, so far as we are aware, been found in any single human molar.

7.—The anatomical, palæontological, and other evidence⁴ already accumulated tends to show that man, *Pithecanthropus*, *Hesperopithecus*, and the various anthropoids form a natural superfamily group, which may now be named the **Hominioidea**, in contrast with the **Cercopithecoidea**, or Old World monkeys.

8.—The palæontological, anatomical, and taxonomic evidence considered together indicates that the stem forms of this group arose in the early Tertiary times from primates that were closely allied to or identical with the Lower Oligocene *Parapithecus*, which in turn, so far as

¹That is in m¹ m²; m³ varies greatly.

²Dr. Miller notes that in other specimens of chimpanzees the weakness of the roots seems to hold as a constant character; but that the reflection of the enamel upon the neck may be reduced by wear.

³*Op. cit.*

⁴See W. K. Gregory, 1921, 'The Origin and Evolution of the Human Dentition.'

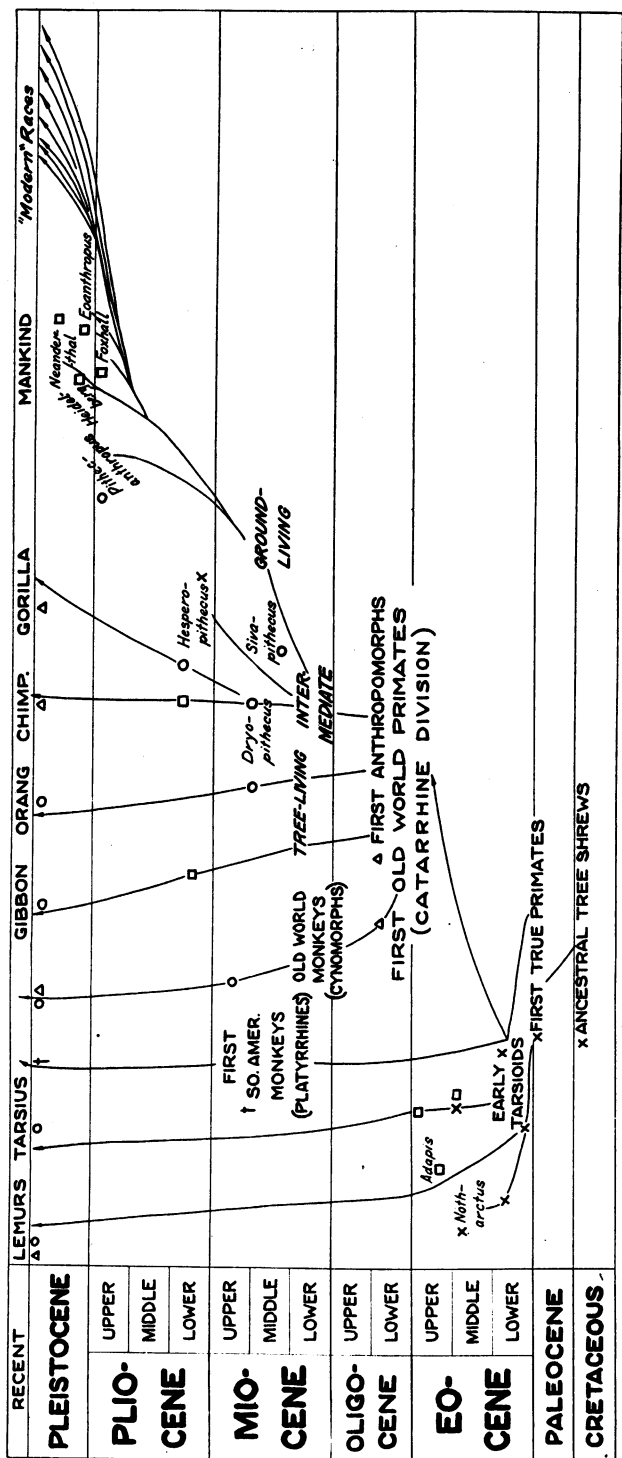


Fig. 6. Geological succession and relationships of the principal types of Primates, according to present evidence from palaeontology, comparative anatomy, anthropology, etc. W. K. Gregory, 1922.

known, shows a remarkable mingling of characters tending to connect the whole Old World series of primates with the stem of the Eocene tarsoids (Schlosser, Gregory).

9.—There was a wide adaptive radiation of this group in the Middle Tertiary, very diverse species having been found fossil in western and eastern Europe and India. *Hesperopithecus* was one of the Lower Pliocene survivors of this group, which had apparently spread northeastward along the route followed by various mastodons, antelopes, and other mammals described by Professor Osborn.¹

¹Osborn, Henry Fairfield, 1922, '*Hesperopithecus*, the Anthropoid Primate of Western Nebraska.' *Nature*, Aug. 26, 1922, p. 281. For a fuller discussion of the palaeontological evidence for the faunal connection of western North America with northeastern Asia in late Tertiary times, see Matthew, W. D., 1915, 'Climate and Evolution,' *Ann. N. Y. Acad. Sci.*, XXIV, pp. 234-255; also Matthew and Cook, 1909, 'A Pliocene Fauna from Western Nebraska,' *Bull. Amer. Mus. Nat. Hist.*, XXXVII, pp. 367-390, 413.