

# PALEOCENE PRIMATES OF THE FORT UNION, WITH DISCUSSION OF RELATIONSHIPS OF EOCENE PRIMATES.

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## INTRODUCTION.

The first important contribution to the knowledge of Fort Union mammalian life was furnished by Dr. Earl Douglass and was based on a small lot of fragmentary material collected by him in the autumn of 1901 from a locality in Sweet Grass County, Montana, about 25 miles northeast of Bigtimber.<sup>1</sup> The fauna described by Douglass indicated a horizon about equivalent in age to the Torrejon of New Mexico, but the presence of unfamiliar forms, suggesting a different faunal phase, was recognized.

A few years later (1908 to 1911) this region was much more fully explored for fossil remains by parties of the United States Geological Survey and the United States National Museum. Working under the direction of Dr. T. W. Stanton, Mr. Albert C. Silberling, an energetic and successful collector, procured the first specimens in the winter and spring of 1908, continuing operations intermittently through the following years until the early spring of 1911. The present writer visited the field in 1908 and again in 1909, securing a considerable amount of good material. The net result of this combined field work is the splendid collection now in the National Museum, consisting of about 1,000 specimens, for the most part upper and lower jaw portions carrying teeth in varying numbers, but including also several characteristic foot and limb bones.

Although nearly 10 years have passed since the last of this collection was received, it was not until late in the summer of 1920 that the preparation of the material for study was completed. This task was especially tedious and difficult owing to the small size and exceedingly fragile condition of most of the specimens, it being necessary

<sup>1</sup> Douglass, Proc. Amer. Philos. Soc., vol. 41, No. 176, 1902, pp. 216-224, pl. 29; Annals Carnegie Mus., vol. 5, No. 2, 1908, pp. 11-26, pls. 1, 2.

to use a binocular microscope for much of the preparatory work as well as for detailed study of the smaller forms. The collection, representing as it does such a varied fauna, is proving to be most interesting and important, not only in increasing our none too adequate knowledge of earlier Tertiary mammalian life, but in its promise of aid in solving some of the puzzling correlation problems of Paleocene horizons in various localities of the Rocky Mountain region. At least 40 species, most of them new to science, distributed among not less than 15 families, and 6 or possibly 7 orders, are represented. A few of the new species have been described by the present writer in short papers,<sup>2</sup> but now that the whole collection is available for detailed comparison, it is proposed to continue the study by orders, or great groups, the whole eventually to be combined in a single monograph. The Primates form the basis for the present communication.

#### DESCRIPTION OF SPECIES.

### Order PRIMATES.

Up to the present time true Primates of unquestioned standing have not been reported in America from beds older than Lower Eocene, the Puerco and Torrejon having yielded nothing that could be referred with certainty to this order. However, it has been recognized that some, at least, of the Eocene Primates show such marked degrees of advance in development as to suggest a beginning much earlier than the age of the beds (Wasatch and Bridger) in which they have heretofore been found. It is not surprising, therefore, although of the greatest interest, that remains of true Primates are actually found to occur among the abundant faunas of the Fort Union Paleocene. Some of these seem to show undoubted relationship to the already known Primates of the Eocene, while others may represent hitherto unknown groups. All, however, are in general more primitive in type than their supposed relatives of later date, although their stage of development is sufficiently advanced to indicate beyond question that the greater groups, or families, to which they belong were almost as definitely marked out at this earlier period as in the Eocene, and lends abundant support to the suggestion that we must look to formations very much older than the beginning of the Tertiary for evidence, if ever found, of the much-sought root group, or beginning, of the Primates as a distinct order.

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<sup>2</sup> Notes on the fossil mammalian genus *Ptilodus*, with descriptions of new species. Proc. U. S. Nat. Mus., vol. 36, 1909, pp. 611-626.

An extinct marsupial from the Fort Union with notes on the Myrmecobidae and other families of this group. Proc. U. S. Nat. Mus., vol. 48, 1915, pp. 395-402, pl. 23.

Notice of a new Paleocene mammal, a possible relative of the Titanotheres. Proc. U. S. Nat. Mus., vol. 52, 1917, pp. 431-435, pl. 36.

New species of Claeodonts from the Fort Union (Basal Eocene) of Montana. Bull. Amer. Mus. Nat. His., vol. 41, 1919, pp. 541-555.

## Family TARSIIDAE

This family, as defined by Matthew,<sup>3</sup> seems to be represented in the Fort Union by six new species representing four genera, three of which are new. These suggest more or less close relationships to the known Eocene members of the group, but do not fall within the definition of any of the described genera of these later beds.

## PAROMOMYS, new genus.

*Genotype*.—*Paromomys maturus*, new species.

*Diagnosis*.—Dental formula:  $I \frac{?}{1 \text{ or } 2}, c \frac{1}{1}, p \frac{3}{3}, m \frac{3}{3}$ : Species of small size with anterior tooth modifications in general as in the Omomids; that is, with unreduced canine and enlarged median incisor; but with molar developments suggesting *Notharctus* or *Pelycodus* in that they have a lengthened and broadened heel in  $m_3$ , and the trigonid is composed principally of the subequal protoconid and metaconid which tend to unite at the summits to form cross lophs; trigonids relatively high and distinctly directed forward.

Other principal features are total absence of internal cingula on the upper molars, the complete continuation of the hypocone ridge to the summit of the protocone, and the relatively greater height of the trigonids of the lower molars. These last two characters seem to be directly associated with and to precede the stage in which a true hypocone is developed. In all forms of this group the development of a true hypocone is accompanied by a corresponding depression of the trigonid.

## PAROMOMYS MATURUS, new species.

Figure 1, and Plate 1, figure 3; also Figure 2, and Plate 2, figures 2 and 3.

*Type*.—Portion of a right lower jaw carrying four teeth,  $p_4$  to  $m_3$  and alveoli for the anterior teeth. (Cat. No. 9473, U.S.N.M. Coll.)

*Locality*.—"Gidley Quarry,"<sup>4</sup> sec. 23, R. 15 E., T. 5 N., Sweetgrass County, Montana.

*Horizon*.—Near top of Fort Union "No. 2," of Silberling (Paleocene Tertiary as published by Calvert and Stone). This level or stratum is about 1,300 feet above the base of the beds, which here lie apparently conformably on the Lance formation, and is more than 4,000 feet below the top of the Fort Union in this section.

The species is represented in the collection by portions of upper and lower jaws and teeth of more than 40 individuals, all from the "Gidley Quarry."

<sup>3</sup>Bull. Amer. Mus. Nat. Hist., vol. 34, 1915, p. 445.

<sup>4</sup>This name was given by Mr. Silberling in his field notes to designate this locality, and is here used for convenience.

*Specific characters.*— $M_1$  to  $m_3 = 9.4$  mm.;  $c$  (posterior border of alveolus) to  $m_3 = 17.2$  mm. Single enlarged and slightly compressed

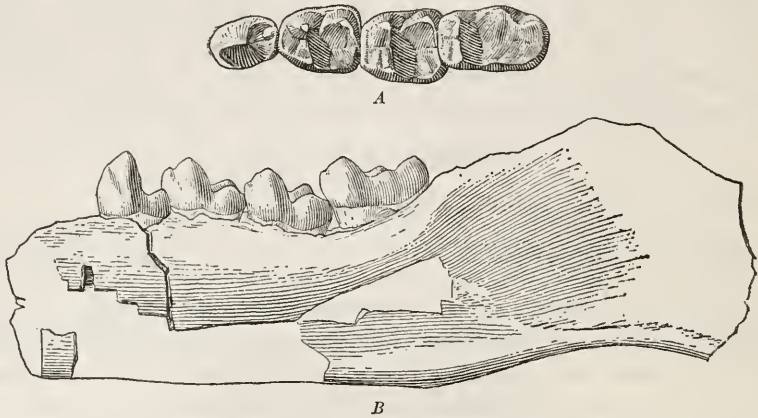


FIG. 1.—*PAROMOMYS MATUSUS*. PORTION OF A RIGHT LOWER JAW CARRYING POSTERIOR FOUR CHEEK TEETH. *A*, CROWN VIEW OF TEETH; *B*, INNER SIDE VIEW OF JAW AND TEETH.  $\times 4/1$ . CAT. NO. 9473.

incisor as in *Tetonius*, but with canines enlarged also as in *Omomys*;  $p_2$  and  $p_3$  much smaller than  $p_4$ ; paraconids internally placed and in  $m_2$  and  $m_3$  nearly connate with the metaconid, their summits often disappearing with slight wear;  $m_3$  narrowest but longest of molar series, with wide bicuspid heel as in *Notharctus nunienus* (Cope).

**PAROMOMYS DEPRESSIDENS, new species.**

Figure 3, and Plate 3, Figure 7.

*Type.*—Portion of a right maxillary carrying four teeth,  $p^4$  to  $m^3$ . (Cat. No. 9546, U.S. N.M. Coll.) Represented in the collection by several other specimens including both upper and lower jaw portions.

*Locality and horizon.*—Same as *P. matusus*.

*Specific characters.*—About one-fourth smaller than *P. matusus*.  $P^4$  to  $m^3 = 7.3$  mm.,  $m^1$  to  $m^3 = 5.5$  mm. Cusps and lophes depressed

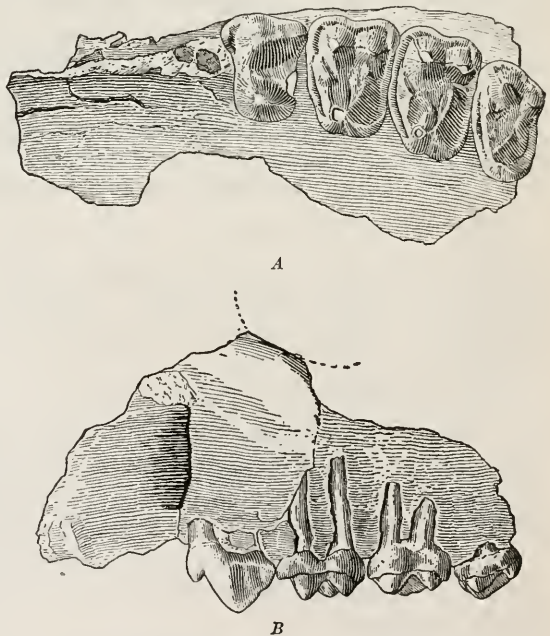


FIG. 2.—*PAROMOMYS MATUSUS*. PORTION OF LEFT MAXILLARY WITH POSTERIOR FOUR CHEEK TEETH. *A*, PALATE VIEW. *B*, OUTER SIDE VIEW.  $\times 4/1$ . CAT. NO. 9540.

and basins shallow; protoconules present but less well defined than *P. maturus*; metaconules absent.

This species further differs from *P. maturus* in the slightly less marked grooving of the inner wall of the protocone-hypocone shelf and the relatively narrower proportions of  $p^4$ . Differences correlated with those just pointed out for the upper teeth are effected in the lower teeth of the specimens here associated with this species, though in somewhat less degree. The paraconids are weakly developed, being almost vestigial on  $m_2$  and  $m_3$ , and are closely connate with the metaconids, while the trigonids are more depressed although having the same degree of forward slope as those of *P. maturus*.

Several upper-jaw portions carrying teeth which conform very exactly in size and general modifications with those of the lower series seem to leave little question that they represent the same species. One of these, a portion of a left maxillary carrying four teeth,  $p_4$  to  $m^3$  (fig. 2, Cat. No. 9540), shows the following characters: Molars wider than long with three main cusps and two intermediary cusps, but, while there is no true hypocone, the base of the crown is subquadrangular owing to a backward expansion of the base of the protocone. This expanded area is distinctly marked off from the protocone on the lingual side by a shallow, vertically directed depression, giving the impression of the birth of a hypocone. A low but well-defined ridge, continuing from the posterior cingulum, slopes abruptly upward to the summit of the protocone, thus forming a second shallow posteriorly placed basin of almost equal size and form with the one lying between the median conules. Thus the ridge and cingulum function almost as a hypocone and as already implied



FIG. 3.—*PAROMOMYS DEPRESSIDENS*. PORTION OF A LEFT LOWER JAW CARRYING THE THREE MOLARS. CROWN VIEW.  $\times 4/1$ . CAT. NO. 9485.

there is the suggestion of an early budding off of a mass from the posterior flank of the protocone to form such a cusp. The modification just described is more pronounced in  $m^1$  and  $m^2$ , but is also clearly indicated in  $m^3$ , and  $p^4$  has a well-developed posterior cingulum and ridge forming with the inner cusp (protocone) a similar basin on this tooth.  $P^4$  also has an incipient metacone placed well down near the posterior extremity of the external cingulum.  $P^3$  and  $p^2$ , as indicated by their alveoli, are much smaller than  $p^4$  and are primitively two-rooted; that is, the roots are antero-posteriorly placed. The posterior border of the alveolus for the canine indicates a tooth of moderate size; upper incisors not known. Length of upper cheek-tooth series from posterior border of canine alveolus to posterior border of  $m^3 = 15.5$  mm.;  $p^4$  to  $m^3 = 10.3$  mm. Length of molar series = 7.8 mm. The infraorbital foramen and a short sector of the orbital rim are preserved in this specimen, the latter indicating that the or-

bit was large but relatively not so forward in position as in *Tetonius*. The infraorbital foramen is large, narrow oval in outline, and placed directly above the junction of  $p^3$  and  $p^4$ .

**PALAECHTHON, new genus.**

*Genotype*.—*Palaechthon alticuspis*, new species.

*Diagnosis*.—Dental formula:  $I \frac{?}{1 \text{ or } 2}, c \frac{?}{1}, p \frac{?}{2 \text{ or } 3}, m \frac{3}{3}$ : Lower incisors reduced to a single enlarged pair, as in *Paromomys*. Canines unreduced, premolars three to two; molars differing from those of *Paromomys* in having relatively shorter basins, and the heel of  $m_3$  is less widened posteriorly; there is no connecting ridge between the subequal proto and meta conids, and the much-reduced but distinct paraconids of  $m_2$  and  $m_3$  are not connate with the metaconids, but are placed well down on the anterior borders of these cusps. The upper dentition is only known from the molar series. These teeth much resemble the corresponding ones of *Paromomys* but may be distinguished by their less expanded inner bases and in consequence more nearly trigonate form. The tendency to division of the lingual wall of the protocone, so characteristic of *Paromomys*, slightly indicated in  $m^2$ , but is not present in the other molars.

**PALAECHTHON ALTICUSPIS, new species.**

Plate 1, Figure 1.

*Type*.—Portion of a right lower jaw carrying five teeth,  $p_2$  to  $m_2$ . Collected by A. C. Silberling. (Cat. No. 9532, U. S. N. M. Coll.) Represented in the collection by other specimens including upper jaws.

*Locality and horizon*.—Same as *Paromomys maturus*.

*Specific characters*.—Slightly smaller than *Paromomys depressidens*.  $P_2$  to  $m_2 = 9$  mm., posterior border of canine to  $m_3$  (estimated) = 11.5 mm. Premolars three, the anterior two reduced and simple; trigonids of molars relatively higher and less forwardly directed than in the *Paromomys* species; cusps of the trigonids very distinct, with deep notches between the subequal protoconid and metaconid, and with small paraconids on all of the molars depressed well below the summit of the metaconid. The heel of  $m_3$  is relatively narrower and is not distinctly bicusped, and the talonid basins of all the molars are distinctly deeper than in the other species. These basins, however, are almost entirely open on the lingual side, there being but a low and deeply notched ridge connecting the entoconid with the metaconid. In *Paromomys* this ridge is nearly as high as the outer border of the basin.  $P_4$  of *P. alticuspis* is more progressive than in the species of *Paromomys*, it having a well-developed though short heel and a rudimentary but distinct metaconid.

The upper molars referred to this species show the following characters: Cusps in general moderately high, median cuspsules conspicuous; protocones relatively high and pointed. They differ also from those of the species of *Paromomys* in having the inner posterior portion of the base relatively less expanded and the posterior face of the protocone more steeply sloping. The area bounded by the meta-loph, the angulated ridge formed by the posterior basal cingulum, and the continuing ridge from the apex of the protocone, is less distinctly basined. Measurements of upper molars— $m^1$  to  $m^3 = 5$  mm.

**PALAECHTHON MINOR, new species.**

Plate 4, Figure 1.

*Type*.—Greater portion of a right lower jaw carrying four teeth,  $p_4$  to  $m_3$ , and the alveoli for  $p_3$  and apparently for a canine and an incisor. (Cat. No. 9639, U.S.N.M. Coll.) Collected by A. C. Silberling. The species is also represented in the collection by a few other specimens, including two upper jaw portions.

*Locality and horizon*.—Same as for *Paromomys maturus*.

*Specific characters*.— $P_4$  to  $m_3 = 5.3$  mm.;  $m_1$  to  $m_3 = 4.3$  mm. About one-third smaller than *P. alticuspis*, with apparently a reduction of premolars to two instead of three, but with canine of moderate size and an enlarged incisor as in the species described above.

This is by far the smallest species of the *Paromomys-Palaechthon* group, and while conforming in general characters with the others, it differs in so many details that its reference here is only provisional. Unfortunately all the jaws in the collection representing this species either have the anterior portion wanting or are broken in that region in such a way as to obscure the modifications that have taken place in the anterior teeth. It is certain, however, that the enlarged incisor was laterally compressed and was decidedly more procumbent than in other species of the group, and that  $p_2$ , as well as  $p_1$ , is wanting.  $P_3$  is reduced about as in the other species, but  $p_4$  is a high cusped, very much shortened tooth which, except for its shorter heel, more nearly resembles the corresponding tooth in species of *Nothodectes*. The lower molars closely resemble those of *P. alticuspis*, both in the relative height of the trigonids and the distinctness and position of the paraconids.  $M_3$ , however, differs from that of *P. alticuspis* in having a narrow, single-cusped heel.

A series of three upper molars of the left side (Cat. No. 9590) and a fragment of a left maxillary carrying  $m^1$ ,  $m^2$  (broken), and the alveoli of  $m^3$  (Cat. No. 9595), seems to be properly referable to this species. These teeth, more than the lower ones described, present the general characteristics of the genus, differing from those of



FIG. 4.—PALAECHTHON MINOR. A SERIES OF THREE UPPER MOLARS OF THE LEFT SIDE.  $\times 4/1$ . CAT. No. 9590.

*P. alticuspis* only in being proportionately wider, and in having the summit of the somewhat higher protocone relatively more nearly approached to the paracone.

Most of the differences noted above suggest for the species just described a slightly different line, or direction, of development than is indicated in *P. alticuspis*. It is possible, therefore, that more complete materials may prove that these two species do not form a natural generic group. However, for the present they may be treated as such.

#### RELATIONSHIPS OF THE GENERA *PAROMOMYS* AND *PALAECHTHON*.

In the species of genera just described, the molar teeth seem in certain respects to suggest relationship to the Notharctidae. This is especially true of the modifications of  $m_3$  and the position and mode of progressive disappearance of the paraconid in all the molars of the *Paromomys* group. Also there is a significant resemblance in the form and manner of development on the trigonids of the lower molars of an anterior ridge or shelf which takes over the function of the paraconid. This adaptive feature is directly associated with the development in the upper molars of a posterior basal expansion of the protocone, and the forming of a posterior basin, as already described (p. 5). This is similar to the condition observed in the species of *Pelycodus* which have not yet arrived at the stage where the true hypocone appears. It is also a feature of *Phenacolemur* of the Apatemyidae. In fact, this peculiar development of the upper and lower cheek teeth, apparently constitutes a distinctively primate characteristic, which, while not found in all families of the order, seems to have been repeated over and over again, with slight variations, in several related or unrelated groups, and, so far as I am aware, is not found in any other order of mammals. (This is, of course, assuming that the Plesiadapidae are true Primates.) It therefore follows that the apparent likeness of *Paromomys* to the Notharctidae, suggested by similarities of the molar teeth, may or may not denote relationship to this group and seems to be more than outweighed by the important differences observed in the modifications of the anterior teeth. Thus the reduction in *Paromomys* and *Palaechthon* of the premolar series to three or two, and the more advanced specialization and enlargement of a single pair of incisors in the lower jaws are far more important features than the molar resemblance, and seem to preclude the possibility of a near or at least ancestral affinity of the group to the Notharctinae. Also in this group the orbit apparently is of the enlarged type as in the Tarsiidae.

The molars of this group, in some respects also resemble those of the Nothodectids. However, the very marked difference of modifica-



tions observed in the last upper premolar, especially, and the different line of specialization indicated in the anterior teeth of the lower jaw (namely the presence in *paromomys* of a well-developed canine, which tooth is entirely wanting in *Nothodectes*) suggest that the relationship of these two groups is not particularly close, although possibly as close as that existing between the Omomids and Notharctids.

Comparing the *Paromomys-Palaechthon* species with the *Omomys-Hemiacodon* species, there is a striking similarity in the general modifications of the anterior teeth of the lower jaws, and it is this feature which has suggested the reference of the Paleocene genera to the Tarsiidae, as that family has been defined by Matthew. These two groups possess in common an unreduced canine and an enlarged incisor, with reduction or loss of the other incisors—an unusual modification. *Paromomys* and *Palaechthon*, although from the older horizon, had, however, reached a somewhat more advanced stage of development in respect to the incisors in that the inner one is relatively more enlarged and the lateral ones are either wanting or are reduced to a functionless remnant. Though usually small, the lateral incisor is always quite prominent in *Omomys* and *Hemiacodon*. In none of the specimens of the Fort Union species is this tooth clearly indicated, but its presence as a mere vestige is suggested in two of them by what appears to be a segment of a very small alveolar border. Hence this tooth, if present, is vestigial.

These differences would be considered slight were the geologic time of occurrence of the two forms reversed. Since, however, the more advanced stage belongs to the older form, it here becomes important and precludes the possibility of a direct genetic relationship, even if the marked differences in character of the molars were not considered. But the molars also, and especially those of the upper series, indicate, as already intimated, a distinctly different line of development than is suggested by those of the Omomid group.

From these comparisons it will be observed that the combined characters, especially of *Paromomys*, while presenting in the molars certain Notharctid features, indicate a nearer relationship to the Eocene Tarsiids, although they seem to represent a distinctly different line of development than any of the known later members of the group. The exact place of *Paromomys* and *Palaechthon* in the scheme of classification perhaps can not be assigned with certainty without a much wider knowledge of all of these early Primates than now exists, but I am inclined at present to consider the group represented by these genera as a sixth major division of Matthew's key to the genera of Tarsiidae<sup>5</sup> to be defined as follows:

<sup>5</sup>Bull. Amer. Mus. Nat. Hist., vol 34, 1915, pp. 447, 448

VI. Paraconids internal, more or less connate with metaconids, metaconids nearly opposite protoconids, no metastylids;  $m_3$  unreduced. One enlarged incisor, the second, if present, vestigial. Canine of moderate size. Jaw moderately slender, front teeth semierect. Premolars two-rooted, anterior ones decidedly smaller than  $p_4$ .

1.  $M_3$  with enlarged heel, paraconids vestigial except on  $m_1$ . Premolars reduced to three,  $p_4$  with triangular base, well developed heel, but no metaconid.

*Paromomys*.

2.  $M_3$  with slightly reduced heel; paraconids distinct. Premolars reduced to two;  $p_4$  with short, basined heel, and with small though distinct metaconid and incipient paraconid.....

*Palaechthon*.

#### ELPHIDOTARSIUS, new genus.

*Genotype*.—*Elphidotarsius florencae*, new species.

*Diagnosis*.—Lower molars of *Tetonius* type.  $M_3$  unreduced,  $m_1$  and  $m_2$  short and wide; the outer cusps, especially of the trigonids, set well in from the margin; paraconids distinct and internal on all the molars; subconnate on  $m_2$  and  $m_3$ ; metaconids more posterior than protoconids, especially on  $m_1$ ;  $p_4$  enlarged, wedge shaped, with quadrate base. (Anterior teeth and upper dentition not known.)

#### ELPHIDOTARSIUS FLORENCAE, new species.

Plate 4, Figure 2.

*Type*.—Portion of a left lower jaw carrying four teeth,  $p_4$  to  $m_3$ . (Cat. No. 9411, U.S.N.M. Coll.) Collected by J. W. Gidley.

*Locality and horizon*.—Fort Union "No. 2," "Gidley Quarry," Sweet Grass County, Montana.

*Specific characters*.—Size about one-third smaller than *Tetonius homunculus*.  $M_1$  to  $m_3 = 4.5$  mm.,  $p_4$  to  $m_3 = 6.2$  mm., length of  $m_3 = 2$  mm., paraconids internally placed about as in *T. homunculus*, but somewhat more distinct, decidedly more distinct than in *Absarokius abbotti*; metaconids distinctly more posterior in position than protoconids.

The modification of  $p_4$  is peculiar in that its summit is made up of three cusps of subequal size and height, arranged almost in line, giving it a bladelike appearance similar to the  $p_4$  of *Uintanius* as described and figured by Matthew. In addition to the cusps of the trigonid of  $p_4$  there is on its anterior border a small cuspule situated slightly below its summit, and there is a strong but relatively very short heel cusp.

The lower molars of *E. florencae* resemble those of *Absarokius* in having the outer cusps set far in from the margin, and those of *Tetonius* in the relative width of their crowns, which in  $m_1$  and  $m_2$  slightly exceeds their length. They also resemble those of the Eocene genera in that the height of the crowns progressively increases from back to

front in the series. In the general evolutionary stage of the lower cheek teeth of *Elphidotarsius* they differ from those of the Eocene members of the group in having the last molar unreduced, while the fourth premolar is well advanced in specialization.

This genus and species are known only from the type specimen, hence its present reference is provisional on what the anterior lower teeth and upper cheek teeth may show when discovered. From the characters presented in the type, the genus would seem to fit best into Division "V" of Matthew's key to the Tarsiidae, under a new subdivision as follows:

3.  $M_3$  unreduced, paraconids quite distinct; metaconids posterior to protoconids;  $p_4$  with rather high, laterally compressed summit composed of three cusps, the protoconid, paraconid, and metaconid, all of subequal size and height.

*Elphidotarsius.*

**TETONIUS REX, new species.**

Plate 3, Figure 4.

*Type.*—A second left lower molar. (Cat. No. 9828, U.S.N.M. Coll.) Collected by A. C. Silberling.

*Locality and horizon.*—"No. 12," sec. 22, R. 14, E. T. 5 N, Sweet Grass County, Montana. Fort Union "No. 3." In upper part of geologic section.

*Specific characters.*—Antero-posterior diameter 3.8 mm.; transverse diameter of heel portion 3.5 mm. Lower molars of the broad, low-crowned *Absarokius-Tetonius* type but larger than any described species of these genera.

This species is represented in the collection by the single tooth constituting the type. It merits this distinction only because of the scarcity of material coming from this particular horizon which is nearly 4,000 feet higher in the beds than in the "Gidley Quarry" and "Silberling Quarry" levels, and is therefore here recorded.

**Family PLESIADAPIDAE.**

As Matthew has defined this family,<sup>6</sup> it includes the "Apatemyidae" on the ground of the apparently close relationship of the American genus *Nothodectes* to the European genus *Plesiadapis*. The *Nothodectes* section of the American group is represented in the Fort Union material by several well-preserved lower jaw portions, a portion of an upper jaw carrying a series of four cheek teeth, and a few characteristic upper incisors. These indicate a new genus closely related to *Nothodectes* of the Tiffany beds.

<sup>6</sup>Bull. Amer. Mus. Nat. Hist., vol. 37, 1917, p. 833.

## PRONOTHODECTES, new genus.

*Genotype*.—*Pronothodectes matthewi*, new species.

*Generic characters*.—General characteristics similar to *Nothodectes*, but less advanced in development. Dentition: I  $\frac{2?}{1}$ , c  $\frac{1? \text{ or } 0}{1 \text{ or } 0}$ , pms  $\frac{4?}{4}$ , ms  $\frac{3}{3}$ . Cusps and cuspules of upper cheek teeth low and rounded; no mesostyles; no definite hypocene or posterior internal ridge, although the protocone is lengthened and slightly angulate in this region. Trigonids of lower molars relatively high with paraconids distinct, but closely connate with the metaconids, and with the nearly equal summits of the metaconids and protoconids relatively more nearly approached than in *Nothodectes*. P<sub>1</sub> and p<sub>2</sub> small and single rooted p<sub>4</sub> with simple high and very short protoconid and short single cusped heel. Upper p<sup>4</sup> submolariform with metaconid equal in height to paraconid and but little separated from it by a very shallow notch.

PRONOTHODECTES MATTHEWI, new species.<sup>1</sup>

Plate 3, Figure 2.

*Type*.—Three upper cheek-teeth (p<sup>4</sup> to m<sup>2</sup>) of the right side in a fragment of the maxillary. (Cat. No. 9547, U.S.N.M. Coll.)

*Paratypes*.—Greater portion of a left lower jaw carrying the enlarged incisor (broken), pms<sub>1, 2, 4</sub>, and ms<sub>1, 2, 3</sub> (Cat. No. 9332, U.S.N.M. Coll., see pl. 4, fig. 3; and two upper incisors. (Cat. Nos. 10005 and 10044, U.S.N.M. Coll.)

*Locality and horizon*.—All from "Gidley Quarry," near top of Fort Union "No. 2," Sweet Grass County, Montana.

*Specific characters*.—Size about one-fourth smaller than *Nothodectes gidleyi*. P<sup>4</sup> to m<sup>2</sup> = 5.9 mm.; m<sub>1</sub> to m<sub>3</sub> = 7.3 mm.; p<sup>4</sup> relatively narrower and all molars, both upper and lower, relatively wider than in species of *Nothodectes*. P<sup>4</sup> with paracone and metacone subequal but closely twinned; hypocone ridge only incipiently developed; no diastema in lower jaw; a very much reduced canine indicated; p<sub>1</sub> slightly smaller than P<sub>2</sub>; both these teeth simple and single rooted. Trigonid of m<sub>1</sub> with the three cusps about equal in size, their unworn summits forming a nearly equilateral triangle.

*Pronothodectes* belongs unquestionably to the Plesiadapidae, as defined by Matthew, and seemingly is so closely related to *Nothodectes* that the generic characters based on the material in hand can not be sharply defined.

<sup>1</sup> I take pleasure in naming this species in honor of my good friend Dr. W. D. Matthew, who has done such splendid work, especially in connection with problems pertaining to the study of the early primates.

It seems to hold about the same position in relation to *Nothodectes* as does *Pelycodus* to *Notharctus*. That is, *Pronothodectes* has not reached a stage so advanced as *Nothodectes*, and stands directly, or nearly directly ancestral to the latter. It is clearly distinguished from *Plesiadapis*, if reliance may be placed upon the figures and descriptions of Lemoine,<sup>8</sup> by the somewhat more advanced modification of the incisors combined with the less progressive condition of the premolars. Also, *Plesiadapis* differs from the related American Nothodectids in that the last upper molar, instead of the second, is the largest of the series.

Two upper incisors (Nos. 10005 and 10044 see pl. 3. figs. 11 and 12) of characteristic pattern, which are of appropriate size, are so very closely like those of *N. gidleyi* as, by analogy, to leave little doubt that they belong to the species here described. If this reference is correct, then the upper incisors of *N. gidleyi* and *P. matthewi* are almost exactly alike in general structure, both differing very distinctly from those of the species of *Plesiadapis* figured by Lemoine. The American species have a more elongate crown and the terminal cuspules are more massive and less sharply pointed, giving them a finger-like appearance.

The fourth upper premolar in *Pronothodectes* seems to be in about the same stage of development as  $p^3$  of *Nothodectes*, and closely resembles it in detail.

The mode of complication tending toward the molariform pattern in the hinder upper premolars of both the American genera (see pl. 3, fig. 3) is identical, and being peculiar, merits description. In general, they are transversely expanded, three-rooted teeth, with large protocone; well-developed protoconule situated in an unusual position between and directly in line with the protocone and paracone; paracone external with metacone budding off from the summit of its posterior flank but becoming progressively distinct. There is also a posterior cingulum running inward and continuing upward to the summit of the protocone, producing a more or less well defined hypocone ridge and basin as in the molars. The upper premolars of the other American members of this group are not known. But according to Lemoine's figures the upper premolars of *Plesiadapis* are of this peculiar type, suggesting that it is characteristic of the Plesiadapidae group and confirms Matthew's observation of the close relationship between *Plesiadapis* and *Nothodectes*.

#### OTHER PECULIAR INCISORS OF UNCERTAIN REFERENCE.

Plate 3, Figures 8, 9, 10, 13, 14, and 15.

In addition to the two incisors just described, there are in the Fort Union collection several isolated ones which show sufficient

<sup>8</sup>Bull. Soc. Geol. de France, ser. 3, vol. 19, 1891, pp. 278-280, pl. 10.

peculiarities to make them of interest, and they merit description, although the lack of any clue to their association with other teeth at present renders their reference too conjectural to be attempted.

Among these there are three types, differing in detail but of similar general form to those just discussed. The development of lateral cuspulus suggests affinity to the Nothodectids, although accurately associated material, when found, may show they belong rather with some one of the other Primates having a single pair of enlarged incisors, or possibly they are not Primate at all. This seems to be true especially of the smallest of these three types. This tooth (see pl. 3, fig. 10) is very minute and is of appropriate size to go with the diminutive species *Palaechthon minor* to which I am inclined to refer it for this reason. But, of course, correspondence in size alone is no proof of relationship. It must be borne in mind, however, that the material here under discussion came from a single small area of but a few feet in extent, and was confined to a stratum of an average thickness of not more than 4 inches. In such intimate association, size often becomes the key to the solution of proper specific association and sometimes even of individual identity of scattered anatomical parts.

The little incisor, which I take to be an upper one (No. 10090, see pl. 3, fig. 8) is relatively shorter crowned than the corresponding Nothodectid tooth, but gives similar evidence of being one of a single enlarged pair. The tooth is broken off near the base of the crown, obliterating the evidence of whether or not it possessed a heel cusp, but the normal presence of such a cusp is indicated by a sudden increase in convexity of the posterior face of the crown base at the point where it is broken. The crown consists of an elongated and slightly curved principal cusp with its anterior face strongly convex, and with a small concavity near the summit on the external posterior face. As in the Nothodectids, the incisors has two accessory cuspules of unequal size but differently arranged, one being placed above the other on the outer flank of the main cusp.

Based on proportionate size there are two other suggestions of species affiliation for this tooth. The first is that it possibly belongs to one of the small species of a multituberculate, remains of which are abundant in the "Gidley Quarry" material; the second is that it may appertain to a certain species of Insectivore, likewise well represented, which agrees very nearly in size with the little primate *Palaechthon minor*, the species to which I am more inclined to assign it. Against the probability of the Insectivore association is the fact that in none of the families of that group is there any species, known to me, possessing enlarged upper incisors in which the crown has developed lateral cuspules. The Sorecidae, as noted by Matthew, have reduced the number to a single enlarged pair, with elongated,

recurved crown on which is developed a posterior basal heel comparable to that observed in the *Nothodectids*. But this general resemblance seems to me to be only structural parallelism. In favor of the hypothetical reference of this tooth to one of the small *Multituberculata*, is the fact that, although not corresponding very closely with any known incisors of this group, it approaches the modification observed in certain *Multituberculates* in just the feature in which it differs the most from the *Nothodectid* type, namely, in that the accessory cusps are all on one side of the main cusp of the tooth crown, instead of the more symmetrical arrangement seen in *Nothodectes*.

The other two incisors referred to above more nearly conform to the *Nothodectid* type. One of these (No. 9928), in which there are five instead of three cuspules, has a strongly developed, blunt-heel cusp, a relatively short, posteriorly concave crown composed of a main slightly elongate cusp, with two closely placed cuspules on its inner flank, and two, more widely spaced ones on its outer side. The other tooth (No. 10010) is shorter crowned than the one just described, and the heel cusp is very incipiently developed. It has a single cuspule on either flank of the main cusp as in the *Nothodectid* incisor, but the flanking cuspules, instead of being rounded in cross section, are greatly expanded to more completely inclose the posterior basin of the crown. The inner cuspule, moreover, is situated much nearer the summit of the crown than is the outer one. In *Nothodectes* the flanking cuspules are of nearly equal height. It is possible that one or both of the last two teeth just described may be upper incisors of some species of the Tarsiid group described above.

The occurrence in this collection of so many incisors presenting variations of the general modification typified in *Nothodectes* and *Pronothodectes* is significant, and suggests that this development is a primate peculiarity which was especially emphasized in the *Plesiadapidae* with their precociously developed incisors. That the Primates were susceptible to this general type of modification has recently been pointed out to me by my colleague in anatomical research, Dr. Aleš Hrdlička, who has recently made some extended studies and interesting discoveries in connection with certain phases of development of the human teeth. He has found that, not only in man, but in many of the lower anthropoids, the incisor teeth, both upper and lower, frequently have the crown definitely divided into three or more cusps or lobes, a main median and two lateral ones, in varying proportions as to size, associated with two other flanking ridges, and a basal heel cusp. On examining embryos he frequently finds this heel cusp calcifying from a separate center from the remainder of the crown, with which it often very imperfectly fuses. This would seem to indicate that the acquirement of a heel cusp, at

least, on the incisors of Primates is a relatively ancient modification, reaching back to an early primitive stage.

*Affinities of the Nothodectids.*—As already mentioned, the fact is well known that in the study of the early Tertiary mammals one frequently meets with the closest similarity in general molar construction in totally unrelated species. For this reason it is sometimes impossible to assign a species even to its proper order on molar characters alone, and frequently the knowledge of other anatomical features is necessary to confirm actual relationships indicated by dental characters. Matthew, in his discussion of the affinities of Nothodectes, recognizing this fact, has stated that "as to the original reference of the Plesiadapidae I am, as previously, disposed to reserve final decision until the skull and skeleton characters are more fully known,"<sup>9</sup> and while admitting the "strong evidence" of the marked resemblance of the cheek teeth to those of the Eocene Primates, the characters upon which Stehlin based his conclusion that *Plesiadapis* is a true primate, did not consider the similarity of molar structure as a strong argument on the ground that "various other Eocene mammals which are certainly or probably not Primates equally resemble them in molar construction." Nevertheless, I am inclined to think that in his characteristically cautious manner, and with a very commendable desire not to go beyond what substantiated facts clearly warrant, Matthew has somewhat exaggerated the difficulty in distinguishing the teeth of early Primates from those of unrelated forms. Especially does this seem true of certain forms where combined characters of upper and lower dentitions may be considered. For example, in my own experience I know of no species, certainly not primate, in which is found the peculiar combination of modifications described above (p. 8) as characteristic of *Paramomys*, and which is observed also in the Notharctidae and in some at least of the Eocene Tarsiidae. These modifications include for the lower molars a broad basined heel and narrower, more or less forwardly sloping trigonid in which the paraconid is progressively diminishing, or absent, its function being taken over by the anterior cingulum ridge continuing with the anterior flank of the protoconid to form a trigonid basin similar to but smaller and more elevated in position than the talonid depression; while the correlated modifications of the upper molars are a shallow anterior basin external to the protocone, which basin and cone function with the talonid portion of the corresponding lower molar, and a posterior basin, somewhat higher in position, formed by the posterior cingulum ridge continuing with the backwardly expanded border of the protocone to the summit of that cusp. The latter basin and ridge function with the trigonid of the lower molar next behind. This peculiar structure of the upper molars at least, while apparently

<sup>9</sup> Bull. Amer. Mus. Nat. Hist., vol. 37, 1917, p. 837.



distinctively primate, is, however, not observed in all groups of the order. But the stage just described, which in the Notharctidae is followed by the budding off of a hypocone from the posterior flank of the protocone, seems to have been an important basis of modification in all the anthropoids, including man, and in some but not all groups of Lemurs. The molar pattern of modern anthropoids seems to have been built on this model.

The general molar structure just described is most clearly distinguished in some of the South American monkeys, but is somewhat obscured in most of the Old World forms through the greater development of the hypocene and the general evening up of the four principal cusps in all the molars to form a subequally quadricusped tooth. Even in these, however, the double basin, or valley structure still persists although greatly modified by the lowering and enlargement of the four main cusps of the molar crown, and the consequent shifting of the anterior and posterior basins to the same level.

It would thus seem that the similarity of the molars of *Nothodectes* to those of the Notharctidae after all has more significance than was conceded by Matthew, and, taken together with the character of the premolars and of the incisors as above interpreted, leaves little doubt regarding the primate affinities of the Plesiadapidae.

Since writing the above, Doctor Matthew has informed me in conversation that the American Museum now has additional material of *Nothodectes* which includes associated foot bones. These, according to Matthew, are "tupaoid-insectivore in type." For this reason he now concludes that the Plesiadapidae are not Primates but should be considered true insectivores. I can not, however, entirely concur with Matthew in this opinion, for, granting the tupaoid character of the foot bones of *Nothodectes*, this would mean nothing beyond indicating a primitive condition which might be expected in almost any of the earlier groups of Primates, especially in view of the fact that the living Tupaiids are primatelike in many important features.

In interpreting the meaning of a tupaialike foot structure in these early forms, the fact must be considered that the *Tupaia* foot more nearly resembles that of the little-specialized South American Primates than it does other living families of insectivores. Comparison of the hind foot of *Hapale* with that of *Tupaia* shows such striking resemblances that were the bones of these two types of feet found fossil in the same beds they would be difficultly separable, and would surely be considered not more than generically distinct. It would seem, therefore, that the tupaoid-insectivore, or Menotyphla, type of foot may have given rise to the primate types. If, therefore, a living primate has retained a foot structure which, if not typically tupaoid, is directly derivable from such a type, might it not natu-

rally be expected that many of the early Eocene and Paleocene representatives of the Primates would have just such a type of foot?

OBSERVATIONS ON THE EVOLUTIONARY STAGE AND SYSTEMATIC POSITION OF THE EARLY TERTIARY PRIMATES.

While great progress has been made in recent years in our understanding of tooth structure, giving more confidence in its use, it is fully appreciated as already acknowledged, that there are many difficulties and hazards to be encountered in attempting, on dental characters alone, criticisms of or deviations from widely accepted opinions. However, this brief restudy undertaken from the angle of an earlier phase has deeply impressed the present writer with the suggestion that certain widely accepted views regarding the Eocene Primates should be very considerably modified to come in agreement with our increasing knowledge of facts, acquired though it be for the greater part through the study of dental characters; for notwithstanding the greatly augmented collections of the past 20 years, it is on the study of those characters, for the most part, that we must still rely for our information regarding the greater number of species of the early Tertiary.

Owing to this treacherous resemblance of tooth structure in entirely unrelated forms (a fact long recognized) there existed, up to the time of the discovery of skull and skeleton portions which gave some knowledge of other anatomical characters, the widest differences of opinion regarding the proper ordinal position of the earlier described Eocene Primates. For example, when *Notharctus*, which was founded on a lower jaw, was described by Leidy in 1870, it was not definitely referred to any existing order of mammals, Leidy considering that it carried resemblances in tooth structure to both the Carnivora and to certain Eocene "pachyderms." The next year (1871) Marsh likewise described a similar lower jaw fragment, noting resemblances to a contemporaneous genus *Hyopsodus*, a supposed suilline. Cope, for some time misled by a false association of creodont unguis phalanges with teeth belonging to a species of the *Notharctus* group, failed to recognize the full primate affinities of the Notharctids and placed them with a rather heterogeneous group of genera under a new suborder, Mesodonta, which he considered as holding about the same relationship to the Primates as the Creodonta to the Carnivora. Later, each of these authorities recognized true Primate characteristics in this group as well as the contemporaneous "Anatomorphous" group, but got little further than that in their classification.

This illustrates well the rather chaotic condition of our knowledge of the early North American Primates up to the time of their first revision by Osborn in 1902,<sup>10</sup> and also emphasizes the difficulties en-

<sup>10</sup>Bull. Amer. Mus. Nat. Hist., vol. 16, art. 17 1902,, pp. 169-241.

countered in attempting to work out their relationships. Osborn cleared up much of this confusion, and laid the foundation for all systematic work on the *Notharctus* group which followed. Since the time of Osborn's revision, aided by the fine collections of better material, including skull and skeletal portions obtained by various expeditions of the American Museum of Natural History, the systematic development of the group has been wonderfully extended. The later researches, especially of Osborn, Wortman, Matthew, Gregory, and Granger in America, and Filhol, Schlosser, and Stehlin in Europe, have given a very comprehensive knowledge of the known groups of Eocene Primates, although there is still wide disagreement among students of the problem regarding their exact systematic position and the relationships they hold to the modern members of the order.

It is not within the scope of the present communication to enter into a detailed examination of all the wider aspects of these controversies. However, the foregoing studies of this newly discovered older Primate fauna, besides contributing to our knowledge of the Eocene groups to which they are related, seem also to throw added light on the more interesting problem of the origin of the Primates, and it is their bearing on this particular phase of the subject which seems important to discuss here.

Wortman went deeply into the study of these early forms, the results of his research, which was based in part on material of the Marsh collection at Yale University, being published in a series of articles under the subheading "Part II, Primates," in the *American Journal of Science* (vols. 15 to 17, 1903-1904). He there set forth and ably upheld the view that most at least of the known Eocene Primates are not Lemurs but true Anthropoids, and in defending this ground, proposed a new classification and arrangement of the greater groups of the order,<sup>11</sup> defining them to include the known extinct forms with the living species. In this rearrangement the Eocene genera *Adapis*, *Notharctus*, and *Limnotherium* (Adapidae), and the *Hemiacodon-Washakius* group (Tarsiidae of Matthew in part) are included with the "Cebidae, Cercopithecidae, Simiidae, and Hominiidae" under the "Neopithecini," a major group of the Anthropoidea, while the *Anaptomorphus* (= *Tetonius*) group was included with the living genus *Tarsius* under the "Paleopithecini" of this suborder.

A few years later, Gregory<sup>12</sup> likewise published a comprehensive restudy of the early Primates, based on extensive researches of both living and extinct forms of the order. In these treatises Gregory vigorously opposed Wortman's ideas of classification and phylogenies, taking the more generally accepted view that all the known Eocene

<sup>11</sup> *Amer. Journ. Sci.*, ser. 4, vol. 15, 1903, pp. 411-414.

<sup>12</sup> *Bull. Geol. Soc. Amer.*, vol. 26, 1915, pp. 419-442; *Bull. Amer. Mus. Nat. Hist.*, vol. 35, art. 19, 1916, pp. 239-355; *Mem. Amer. Mus. Nat. Hist.*, new ser., vol. 3, pt. 2, 1920, pp. 49-241.

Primates are primitive Lemurs, and classing them under "series Lemuriformes" of the suborder Lemuroidea which he defined to include them.<sup>13</sup> He here considered the Adapidae of both America and Europe "typically lemuriform," and not only concluded that this group "should be assigned to the suborder Lemuroidea" but "that the older North American representatives of the family are the most primitive known lemuroids." However, in criticising Wortman's treatment of the Adapidae, in which he placed this group together with the living Hapalidae of South America in the suborder Anthro-poidea, Gregory conceded the possibility that subsequent discovery might prove "that the earliest members of the Notharctine or North American division of this family gave rise to the Platyrrhinae, or monkeys of the New World."

Both these able authorities have brought forward many and vigorous arguments to sustain their opposing views, some of which will have to await further discovery and wider anatomical knowledge of many of the forms discussed to prove or disprove their validity. Others will lose or gain in weight in the mind of the future investigator, perhaps, according to his personal viewpoint or interpretation of the facts. The last statement is especially true respecting the conclusions which may be reached regarding the evolutionary stage which had been reached by the earlier Primates, especially as the list of known forms is now increased by the several additional species of Palaeocene age. In fact, different interpretation of characters seems to have been the real source of the disagreements encountered in the discussions defended by Wortman and Gregory. The latter seemed to hold the, I believe, usually accepted view that the Eocene Primates, while having fully attained the characters of the order, are exceedingly primitive creatures, none of them having passed beyond the early lemuroid stage, and between which and present-day forms exists an evolutionary gap sufficiently wide to admit the derivation of most if not all of the modern families of both Lemurs and Anthro-poids. Wortman, while apparently influenced by this general idea of antiquity, seemed to consider it possible, in some cases at least, to bridge this gap, and has gone more boldly into the problem of working out a phyletic classification based on actual anatomical similarities, which may characterize the several lines of descent as indicated by their supposed evolutionary history. It was on this basis that he reclassified the Primates, referring all the known Eocene forms to primary divisions of the Anthro-poidea. Besides the two major divisions already mentioned, Wortman, in this reclassification, recognized still another, the "Aretopithecini," adapted from Huxley's classification, and which includes the living marmosets. The Paleo-

<sup>13</sup>Bull. Amer. Mus. Nat. Hist., vol. 35, 1916, pp. 266,267.

pithecini, as already stated, includes the living *Tarsius* and part of the Eocene genera which later were referred to the Tarsiidae by Matthew; while in the Neopithecini, Wortman included *Omomys* and *Washakius*, (also referred by Matthew to the Tarsiidae) and the Adapidae, together with all the Old World families of living Anthropoidea and those of the New World except the Hapalidae.

The foregoing, in brief, seems to be about the present status of that part of the controversy which concerns the subject here under consideration. Gregory's views, based on later studies and somewhat fuller data, have received the wider acceptance. But the present restudy of the Eocene Primates, supplemented by the new material from the Fort Union beds described above, has brought to light certain features which lead me to views differing widely from those held by Gregory regarding both the extreme primitive character of these early forms and their relationships to the modern groups. Wortman's views in part seem to agree more nearly with my own interpretation of the facts, although his conclusions, especially regarding classification, apparently will require modifications in several very important particulars.

In this connection should be noted more fully Matthew's comprehensive revision of the Eocene Primates to which reference has already been made.<sup>14</sup> In this revision Matthew has most admirably worked out, so far as can be done on present known material, the interrelationships of the Eocene Primates, some of the genera and families being for the first time adequately defined. Two groups of undoubted primate affinities (the Adapidae and the Tarsiidae) were here recognized, and it was suggested that "some or all of the genera of the families Apatemyidae and Mixodectidae, here placed as Insectivora, may when better known have to be transferred to the Primates." Matthew included under the first family the American forms *Notharcus* Leidy and *Pelycodus* Cope as genera representing two successive stages of a single phylum. Under the Tarsiid group he recognized provisionally nine American Eocene genera as being more or less closely related forms of Tarsiid type, and because of the lack of knowledge of many of them by which they might be placed in families or subfamilies and adequately defined, he arranged them, with the living genus *Tarsius*, under a very convenient classificatory key of five major divisions.

The material from the Fort Union seems entirely to confirm Matthew's general conception of the early Primates in their relation to each other as expressed in this revision, but lends no support, as already intimated, to the prevailing ideas of their relationship to the modern groups of the order, except as regards *Tarsius*.

<sup>14</sup> Bull. Amer. Mus. Nat. Hist., vol. 34, 1915, pp. 429-483.

## RE-STUDY OF EOCENE AND PALEOCENE TARSIIDS.

In order to arrive at any definite or satisfactory conclusions regarding the approximate stages of evolution which may have been reached by any group of animals at a given geologic period, it is first necessary to determine as nearly as possible what characters presented are basic or primitive, and what features may be regarded as marking definite lines or trends in development. Where ancestral forms and immediate descendants are known, the problem is comparatively simple and there is little chance of disagreement; but where these are not known, the task is more difficult and the chances for agreement are, in the very nature of the case, much diminished since most of the conclusions are arrived at through inferences drawn from comparisons with similar but often wholly unrelated forms. The difficulty seems to be increased when dealing with an order such as the Primates, where many features in all groups even of its living representatives are still in a stage relatively not far removed from the generalized base-structure of primitive mammals.

Keeping these facts in mind, and also remembering that various specializations in certain groups have progressed much more rapidly than in others, and that as we approach the common origin of the groups the less conspicuous become the differences in these modifications, let us reexamine the evidence presented by the early Tertiary representatives of the order.

The Lower and Middle Eocene Tarsiids include nine genera referred by Matthew, as already stated, to four key groups, as indicated by lower jaw characters.<sup>15</sup> Among them are represented a rather wide variety of forms, yet all show a definite trend in the same general direction.

The Fort Union Tarsiids, represented by *Paromomys*, *Palaechthon*, and *Elphidotarsius*, as defined, add one or possibly two more groups of similar rank, making in all at least five major groups of the Tarsiidae represented in the early Tertiary deposits of America. The exact taxonomic rank of these groups is not known. As Matthew has quite justly concluded, our present knowledge is insufficient to properly define them as families or even subfamilies, either of which they may prove to be. The important fact in this connection is that as at present known they all exhibit certain features, some more than others, which suggest *Tarsius* affinities, and on present evidence seem properly to belong in the same family as the living Tarsiers, although none of the Eocene genera exhibit a combination of characters which would warrant considering them directly ancestral to the latter, and much less to any other modern group of Primates. In fact, there is little ground for assuming, as seems to have been done

<sup>15</sup> A fifth group (numbered "I" in Matthew's key) is represented by the living Tarsiers. For complete definitions of these groups see Matthew, Bull. Amer. Mus. Nat. Hist., vol. 34, 1915, pp. 429-483.

by certain authorities, that some members of the Eocene Tarsiids could have given rise to any part of either the Anthropeida or the modern Lemurs, exclusive of *Tarsius* and *Daubentonia* with the single possible exception of the South American squirrel-monkey group, which may have been derived from some member of this group more nearly related to the Notharctinae as suggested by Wortman. The special trend in development, as indicated by modifications of the anterior teeth, in many of these forms would alone seem not to be consistent with such a conclusion. Moreover, the skull and limb characters, so far as known, likewise indicate *Tarsius* affinities; hence it would seem that, as regards the relationship of this group of early Primates to the modern members of the order, it may be assumed that the most which can be claimed on present evidence is, that among the living Primates, the Tarsiers, only, are probable descendants of some as yet unknown genus of the group. Possibly, also but I think not probably, some genus now considered a member of the early Tarsiids may have given origin to the group represented by the modern Aye Aye (*Daubentonia*).

These conclusions regarding the phylogenetic position of the early Tarsiids are, in my opinion, greatly strengthened, and, to a degree, verified by the additional knowledge gained from the Fort Union members of the family. Although indicating a somewhat less specialized development, these older genera are apparently little or no nearer the condition required of a root group than are their relatives of the Wasatch and Bridger, their evolutionary trend being as clearly indicated as in the latter. Thus the evidence seems rather clear that the Tarsiidae represent a very ancient major group of the order having a pre-Tertiary origin, possibly in common with the Anthropeida, but developing, at least from the beginning of the Tertiary on, independently of either the anthropoids or true lemurs. This would seem to support Wortman's view in so far as he regarded *Tarsius* and its nearer Eocene relatives as having Anthropeida affinities; but it lends no support to his seemingly unnatural association in which he placed a part of the Tarsiidae with the Hapalidae under a major group of this suborder. The little marmosets, as rightly contended by Gregory, give every evidence of having had a common origin with the other families of the so-called Platyrrhinae and should not be separated from that group despite the unique features among modern Primates of the claw-like terminal phalanges and the nonopposability of the pollex. I do not, however, agree with Gregory's expressed belief that these are either retrogressive or specialized characters, but believe rather, as I have formerly held,<sup>10</sup> that both characters pertain to a primitive condition retained in this particular group because of their very diminutive size and slight weight, which did

<sup>10</sup> Washington Acad. Sci. Proc., vol. 9, 1919, p. 277.

not require opposability of the first digits to adapt them to a perfect arboreal life; the spreading, clawed foot being sufficient in these little creatures to give a firm and secure grasp of a tree trunk or limb under all conditions, just as they do for the tree-living squirrels, insectivores, etc. Thus in all these forms, opposability, if it may be so termed, is developed between two feet clasping opposite sides of a branch, instead of between the first digit and the others of each foot. The possible origin of the South American monkeys is discussed more fully under the next heading.

#### RESTDY OF THE AMERICAN NOTHARCTIDS.

Although no representative of the Notharctid group of Primates appears in the Fort Union collection, the fact that certain species found in these beds belong to well-developed major groups of the Tarsiids, which are almost as clearly defined as their Eocene relatives, makes it exceedingly probable that the Notharctids also existed at that time as a distinct group, and this fact furnishes good ground for a restudy of these Primates<sup>17</sup> from the viewpoint of their being a much less primitive and less basic group than has been assumed by Doctor Gregory. In his recent admirable and exhaustive monographic memoir on the subject,<sup>18</sup> Gregory has studied in detail the tooth, skull, and skeletal characters, comparing them at great length with the modern Primates, and especially the Madagascar lemurs. From this and earlier studies he has concluded that the members of the Notharctid group are "true lemurs;" sufficiently primitive to be considered as standing near the base of the order and "represent in many respects the earliest ancestors of the higher Primates" (see p. 22). In this connection he writes also that "they also tend to connect the Primates with some group of arboreal insectivores, probably of the Mesozoic ancestors of the Menotyphia."

I can not agree with Doctor Gregory in these conclusions, either as to his assumed ancestral relationship of the Notharctinae to the modern Primates or the extreme primitive stage to which he assigned this group. This for two reasons, first, because of the facts stated above regarding the relatively advanced condition of the major groups of the Tarsiidae including those discovered in the Fort Union (Paleocene), and second, because of different interpretations and values which may be given to many of the morphological characters exhibited in the known materials representing the Notharctid group.

<sup>17</sup> Since the present writer has not had for comparison at first hand any of the European Adapinae material, this group has for the most part been left out of the discussion. However, it may be stated that Gregory's disposition of the group, in which he follows Stehler, regarding its relationship to the Notharctinae is for the present accepted. Hence, the broader conclusions here reached regarding the Notharctinae may apply equally well to the Adapinae.

<sup>18</sup> *Memoirs Amer. Mus. Nat. Hist.*, new ser., vol. 3, pt. 2, September, 1920



It is not within the scope of the present discussion to review in its entirety this admirable memoir, much of which is devoted to the accurate working out and discussion in masterful detail of many important morphological features of both extinct and modern Primates. It suffices for the present purpose merely to reexamine critically some of the seemingly more important anatomical features discussed by Gregory which characterize the Notharctinae and relate especially to the question of the affinities of the group. In this regard Gregory has described in great detail the structural modifications of the skeletal elements of *Notharctus* based on the splendid material in the American Museum's collection, and in so doing has established beyond question the fact that the Eocene Notharctids were true Primates, and that they were still in a relatively primitive or generalized stage of development. But, in my opinion, he seemed too greatly impressed with the primitive features of the Notharctids and with the many resemblances he found between this group of early Primates and the Madagascar lemurs, and did not consider sufficiently, or has failed to interpret properly, the special trends in development indicated in the general skeletal structure of the Notharctids. This opinion is based on a detailed restudy of the problem in which the evidence presented by Gregory has been carefully considered, while the fine osteological collections of modern Primates in the United States National Museum, the casts of most of the skeletal elements of *Notharctus* kindly furnished by the American Museum, and a small amount of actual *Notharctus* material in the National Museum have been used for comparison and study. The following comparisons and criticisms are taken up in the order discussed by Gregory.

A portion of the lower end of a scapula of *Notharctus osborni* was described by Gregory (p. 63). Of this fragment he said: "By far the nearest resemblances of the part preserved are with the lemurs of Madagascar," and stated that the glenoid fossa, as seen from below, is like a "slender pear," and that "a very similar form is seen in a certain specimen of *Lemur mongoz*." He then pointed out differences between it and *Cebus*, *Alouatta*, and even *Hapale*, but did not note the striking resemblance of the *Notharctus* scapula fragment to the corresponding portion of that of *Hapale* and *Aotus*, in which forms this element is still in almost as primitive a stage as in *Notharctus*, and to which Gregory's description would apply almost equally well. Moreover, Gregory's figure of the *Notharctus* fragment (fig. 1, p. 63) shows a notch just above the coracoid. This is drawn apparently as though broken, but if, as seems possible, it should prove to be a true notch, it would have an important significance since it is in the exact position of the *suprascapular notch* of human anatomy. This characteristic notch is found in all the South American monkeys, sometimes becoming a more or less completely closed foramen as in

*Alouatta* and *Cebus*; and, so far as I have observed, does not occur in any modern lemurs or in the Old World anthropoids.

The *clavicle* of *Notharctus*, represented by the "medial half," is described as similar to that of *Lemur mongoz*, but, according to Gregory, it has a "stouter, less compressed shaft and a less expanded facet for the sternum." Gregory also stated that this portion of the clavicle is nearly straight. These features are true also of this portion of the clavicle in *Alouatta*. In this genus the medial portion is almost straight and is as round in cross section as in *Notharctus*.

In discussing the *humerus* of *Notharctus*, Gregory has said (p. 76) that "the nearest structural resemblances are to be found among the Lemuriformes, especially among the Adapidae and Lemuridae. Hence the humerus of *Notharctus*, as well as the great majority of all other elements of the skeleton, is plainly lemuriform, or better, in a prelemuriform stage of evolution." This statement, applied to a comparison of *Notharctus* with the Old World anthropoids and man, is in general quite true, as was clearly demonstrated by Gregory, but when the South American monkeys and the African continental and Asiatic lemurs are considered, the "lemur" characteristics seem not so well founded, and his conclusion of a "prelemuriform stage" does not seem to follow, unless we are to consider the modern Madagascar lemurs to be still in the prelemuriform stage. In fact, modifications noted in the humerus of the living South American group seem to have a definitely closer connection with the *Notharctid* type than do those of the modern true lemurs. For example, although the shaft is greatly lengthened (an obviously modern specialization), the sigmoid, or S-shaped contour of the humerus of *Alouatta*, viewed from the side, is almost as marked as in *Notharctus*, and as fully or even more marked than that of *Lemur catus*, while the deltoid ridge and supinator crest are almost as strongly prominent as in those of *Lemur*. In *Hapale* the deltoid ridge is more strongly produced than in *Lemur catus*. In *Cebus* and *Aotus* this element is more reduced. As noted by Gregory, in several of the South American monkeys the entepicondylar foramen is as prominently present as in *Notharctus*. Comparing further, the heads of the humeri in the various Platyrrhine are also but little modified beyond the stage observed in *Notharctus*, those of *Cebus* and *Hapale* being closely similar. That of *Alouatta* is slightly more compressed and less "globular" in form, while in all the inclination and direction of the head is directly toward the back of the shaft, as in *Notharctus*, and the bicipital groove is relatively wider and shallow. An apparently important character, not noted by Gregory, in which the *Notharctus* humerus differs from all lemurs and resembles the Anthropoidea, is the angle which the base plane of the ball portion of the head makes with the long axis of the upper shaft. In *Notharctus* this angle is about the same as in the South

American monkeys and the Anthroipoidea in general, namely, about 40°. In the Madagascar lemurs, even in such divergent forms as *Microcebus* and *Daubentonia*, this angle is diminished by nearly one-half, bringing the head closer to the shaft in the lemurs than in *Notharctus* and the Anthroipoidea. This feature denotes a similarity between *Notharctus* and the anthropoids in the angulation of the scapula with the humerus, which is not shared by the lemurs.

One other important feature of the humerus remains to be considered, namely the modifications of the distal end. In his table of comparisons between the humerus of *Notharctus* and those of the anthropoid apes and man, Gregory has noted that the capitellum is "ball-like in center, produced externally toward very inconspicuous external epicondyle" and that the trochlea is not grooved. The first of these distinctions is not quite clear, since the figures given by Gregory as well as the cast in hand indicate a very conspicuous external epicondyle. But the important observation in this connection would seem to be that the capitellum is but slightly more globular or "ball-like" than that of the South American monkeys, is decidedly more rounded externally than in many of the lemurs; and, with the diminishing of the supinator ridge, which would bring the epicondyle closer in, the modification to the condition found in the Platyrrhine monkeys would readily be accomplished. From the *Notharctus* stage to such a modification as that observed in the African lemur *Perodicticus potto*, in which there is a well-developed additional external groove and ridge not found among the Anthropoidae, the transition would be far more difficult. This feature in *Perodicticus* is indicated in the less progressive humerus of *Lepidolemur*, and is the more significant since between the humeri of the two lemurs just mentioned, there is about the same degree of progressive development as between those of *Notharctus* and *Alouatta* or *Hapale*, the Madagascar lemurs being nearer the stage of *Notharctus* with its broadly expanded supinator ridge and well-developed entepicondylar foramen, the continental lemur approximating the Platyrrhines just named in having no entepicondylar foramen, and having a greatly diminished supinator ridge.

Regarding the absence in *Notharctus* of the trochlear groove, this also is conspicuously absent in *Alouatta*, and absent or but slightly indicated in the other South American monkeys.

Still another anthropoid and nonlemurine feature of the *Notharctus* humerus is observed in the very pronounced upward sloping of the trochlear toward the base of the capitellum. This feature is also very marked in *Alouatta*.

Continuing with the *radius* and *ulna*, again Gregory has emphasized the special likeness of these elements to those of the lemurs, but many of the differences pointed out by him in comparing them with

*Lepilemur* and *Lemur* are just the differences observed in comparing the Platyrrhini with these lemurs, and again, the characters of these elements in *Notharctus* are either like or definitely tending toward the South American monkeys rather than the lemurs. For example, the greater width of the shaft at the lower end, the better development of the eminences for the attachment of the pronator radii teres on the mid-anterior border of the radial shaft, the less sharply marked interosseus ridge, the thinner anterior border of the radial shaft, characters noted by Gregory, are all Platyrrhine modifications. To these may be added the greater width of the proximal end of the shaft of the ulna; less curved distal portion of the ulnar shaft; the definitely greater relative distance of the biceps tuberosity below the head of the radius; and the modifications of the distal end of the radius which are definitely tending toward the Platyrrhine type, especially as exemplified in *Hapale*. In this respect the radius of *Hapale* seems to stand structurally almost intermediate between that of *Notharctus* and *Alouatta*.

The *manus* of *Notharctus* is unquestionably primitive in structure; and, as brought out but not so stated by Gregory, differs as widely from the lemur as from the Platyrrhine manus. For this reason, therefore, the evidence derived from it is largely negative in character and need not here be discussed in detail.

In describing the pelvis of *Notharctus*, Gregory stated (p. 83) "it is essentially of lemurine type," and that "it differed in many particulars from the pelvis of New World monkeys, Old World monkeys, apes, and man; it is in each case more primitive—that is, very close to the tupaoid or Menotyphla type." Continuing in more detail he stated that "as viewed from below, the opposite halves of the pelvis of *Notharctus* form a sort of lyre, the blades of the ilia diverging antero-externally beyond the first sacral vertebra," and that "in all lemurs this feature is still more pronounced," while in the New World monkeys "in the ventral view the opposite ilia are more parallel to each other and do not diverge anteriorly." He noted also the presence in the pelvis of *Notharctus* of a well-defined anteacetabular spine and other features which he considered lemurine and not anthropoid.

This presentation seems rather convincing as stated and as illustrated by the specimens of recent forms selected and figured by Gregory, but I do not find his contentions substantiated by the material I have had in hand for comparison. First of all Gregory's comparisons on the lemur side were evidently made with Madagascar species only, as his statements do not apply in any degree to the Continental or Asiatic lemurs. If such a form as *Perodicticus potto* is considered, the "lemurlike" characters of the pelvis of *Notharctus*, noted by Gregory, almost totally disappear. In this Continental lemur (see pl. 5, fig. 6) the ilia are almost straight and rodlike, and

the anterior ends, which extend but slightly beyond the sacrum attachment, are but little expanded vertically. There is no gluteal fossa and no vestige or suggestion of the antacetabular process noted by Gregory as being prominent "in *Notharctus* and in the lemurs." Moreover, the ilia in *Perodicticus* are strongly attached to two sacral vertebrae and the anterior part of a third, instead of one as noted by Gregory for the Madagascar lemurs. On the whole, the pelvis of *Perodicticus* much more nearly resembles that of the insectivore *Solenodon* (see pl. 5, fig. 4), and it is difficult to conceive of its derivation from any such form as that of *Notharctus*.

On the anthropoidian side, Gregory seems to have been unfortunate in choosing for his principal comparisons a pelvis of *Cebus* in which the basic characters are obscured by greatly expanded (modern) ilia. In fact, with all deference to Doctor Gregory's opinion to the contrary, my own investigations, which include a critical comparison of the pelvic structure in all the available forms of lemurs and of South American monkeys, lead me to conclude that after all there is between *Notharctus* and the South American monkeys a striking similarity in the fundamental structure of the pelvis, and that each modern form is directly derivable, with relatively slight modifications, from the *Notharctid* type. Comparing the pelvis of *Alouatta* (see pl. 5, fig. 2), the lyrate form is seen to be quite similar to that observed in *Notharctus*, and would be more strikingly apparent were it not for the slight expansion in *Alouatta* of the external iliac borders. This lyrate form may be seen also in the pelvis of *Cebus* and *Hapale* (see pl. 5, fig. 3) and may be traced, although it is much obscured by the still greater expanded ilia, in all anthropoid apes and even in man. Yet Gregory has mentioned this as being one of the main features in *Notharctus* which characterize it as being "essentially lemurine." Also, the antacetabular spine, which is conspicuous in *Notharctus* and the Madagascar lemurs, was considered a lemurine character; but this element is entirely wanting in the continental lemurs, while it is still a rather prominent feature in some species of *Alouatta*, *Cebus*, and *Hapale*. In fact, the transition from the *Notharctine* type of pelvis to that of any of the *Platyrrhini* is so slight as to present no difficulties, especially if obviously modern specializations in the latter are considered. These changes are in each case about what one might expect between an Eocene form and its present day descendants. In contrast with this in the modern lemurs, regardless of what group is considered, the pelvis has not advanced in development beyond, and is still in some respects even more primitive than that of their alleged Eocene ancestors. In view of these facts I can not concede that the *Notharctus* type of pelvis is "essentially lemurine," but believe rather that it stands morphologically between the lemurine and *Platyrrhine* types with a rather definite trend in development toward the latter.

Thus Gregory had discussed and compared the principal remaining skeletal elements of *Notharctus*, with no better success in establishing his hypothetical case of lemurine affinities of the group represented by this genus than is indicated in the foregoing pages.

In addition to, and perhaps of even more importance than, the evidence just reviewed, there are certain modifications in the skull and dentition of *Notharctus*, also discussed by Gregory and set aside as of but little importance, which seem to me to preclude the possibility of a derivation of any of the modern lemurs from the *Notharctine* group. I refer here especially to the fusion of the lower jaw symphysis; the modifications of the anterior teeth, which include the normal development and function of the incisors and canines above and below; and the form and position of the lachrymal which lies within the orbital rim. These are all strictly anthropoid and nonlemurine characters, as has been asserted by Wortman and others, and which, moreover, can not be explained away, as Gregory has attempted to do, without ignoring all known facts regarding progressive evolution, and relying on purely hypothetical conjecture. An ununited, or closely sutured lower jaw symphysis is the primitive condition in mammals, and a fused symphysis, in whatever group found, is always considered a specialized condition. To assume therefore that the lemurs, none of whose living representatives have a lower jaw with fused symphysis, could have been derived from an Eocene group in which the symphysis at that early date is either fused or shows an obviously strong tendency to fusion, as in the *Adapidae*, would be to assume a most improbable reversion of development for which there is not the slightest proof. The reduced lachrymal found in the *Adapidae* is another feature which can not be considered a primitive character for the Primates, as assumed by Gregory, without again resorting to a supposition of reversion in evolution of characters for which there is not the slightest evidence which might be taken as proof.

As regards the peculiar modifications of the anterior teeth observed in the true lemurs, in which the lower canines have become incisiform, taking a procumbent position with the incisors, and in which one of the premolars has become caniniform, it will again require a vast amount of explaining based on pure conjecture to derive this modification from such a condition as is found in *Notharctus* and *Adapis*. In these genera the lower canine is moderately large and functions normally as a canine, and there is a tendency to reduction rather than enlargement of the anterior premolars.

There still remains to be discussed the two principal skull characters upon which Gregory has seemed to rely in defending his theory for a lemuriform stage of development for *Notharctus*. These are the presence of the postorbital bar and the modifications of the audi-

tory region, both of which are found in *Notharctus* in practically the same stage of development as in the Madagascar lemures. The first of these seems to have little or no weight as a proof of affinity between an ancient Eocene group and living forms, when it is considered that all Primates which finally attain the condition of having the orbit separated from the temporal fossa by a bony partition, as in the living Anthropoidae, must have passed through just this stage at some time during its development. If, therefore, this feature has any significance, it is to the effect that it seems too advanced a stage for any true lemur at so early a geological age, and is about what would be expected in an Eocene anthropoid.

As to the modifications of the auditory region, here again the similarities of *Notharctus* to the Madagascar lemurs, pointed out by Gregory, seem to represent similar stages reached in development, rather than especial relationship. These similarities, consist principally in the presence of a bulla which covers over the petrous portion of the mastoid below and inclosing the tympanic ring; the course and disposition of the internal carotid artery and its principal (stapedial) branch; and the form of the cochlea. First of all, these characters would not apply, as already conceded by Gregory, when comparisons are made with the non-Malagasy lemurs. Therefore it would seem that the most which can be claimed for the possession in common of these characters by *Notharctus* and the Madagascar lemurs is that they are primitive primate characters to be expected in the former, because of the early geologic period, and which have been retained in the latter along with other primitive features. Therefore they can mean little or nothing as determining phyletic relationship.

The presence in *Notharctus* of a bony canal through which the internal carotid artery passes over the ventral surface of the petrosal to enter the brain case, and its relative size compared with the stapedial branch, is, however, an important feature in considering the possible affinity of the Notharctid group with any branch of the Anthropoidea. It would seem to be the primitive condition in the Primates that this artery was relatively small and of less importance in supplying the cerebral hemispheres with blood, and became more important for this function in proportion as the brain increased in size. Thus the relative size of the internal carotid canal is observed to increase and the stapedial branch to decrease, as noted by Wortman<sup>19</sup>, from the small-brained to the large-brained forms.

It is, therefore, at least significant, that in the relatively small-brained *Notharctus* of the Eocene, which has the stapedial branch relatively large, the two main branches of the internal carotid are in just the position and condition to be expected in a primitive anthro-

<sup>19</sup> Amer. Journ. Sci., vol. 15, 1903, p. 153.

poïd leading from the generalized insectivore type of internal carotid circulation to that of the Platyrrhins and all the modern Anthropoids while among the modern lemurs, only those of the Madagascar group may be considered as being particularly close to the Notharctid stage.

It is this condition of the internal carotid circulation in the otic region, and the development of the auditory bulla in connection with its relation to the tympanic ring, which Gregory especially emphasized as indicating peculiarly lemurine affinities of *Notharctus*. Yet his deductions are based almost exclusively on comparison of the Eocene Notharctids with the lemurs of Madagascar, in both of which the tympanic ring is entirely free and covered by the auditory bulla and in which the internal carotid artery in its course to the brain enters and passes through the auditory bulla, the especial "lemurine" feature being that the stapedial branch is larger than the arteria promintorii portion, while in the Anthropeïdea, the arteria promintorii is large and the stapedial portion wanting or much diminished.

If only the Malagasy, or Madagascar, lemurs were to be considered, Gregory's presentation would be rather convincing, for there can be no denying the fact that there is a striking similarity between *Notharctus* and this particular group of lemurs in the principal features of the auditory development so far as they can be made out from the bony structure. However, when the continental and other living lemurs of the Old World, including *Tarsius*, on the one hand, and the Platyrrhine monkeys of the New World on the other, are included, this similarity loses much of its significance and, as already intimated, this seems to admit of a different interpretation of relationship than the one advanced by Gregory.

As to the internal carotid arrangement observed in *Notharctus*, therefore, Gregory and I seem to agree as to its being a primitive primate condition, but we disagree regarding its significance.

Another important feature of Gregory's presentation is the similarity in the relation of the annulus to the tympanic bulla observed in *Notharctus* and the lemurs. But here again his comparison is made with the Malagasy group only, and thus loses much of its significance when the other living lemurs are included. In the Madagascar lemurs, as is well known, the annulus is entirely free and is completely hidden from beneath by the expanded bulla which extends well to the outside where it is completely fused with the squamosal, without forming a tubular external auditory meatus. However, in all other lemurs, including *Tarsius*, a tubular external auditory meatus is formed apparently from the outward extension of the annulus, which in turn is fused with the bulla, a condition observed in the Old World monkeys and in man. In the Platyrrhina the annulus is fused with the bulla but the external bony tube is usually not developed. According to



Gregory, the annulus in *Notharctus*, while free, is not so completely covered by the bulla as in the Madagascar lemurs. Thus it would seem that while structurally nearer this group the Notharctid stage of development, after all, takes an intermediate place tending toward the condition observed in the Platyrrhini and away from the true lemur type.

The development of the otic bulla in connection with its relation to the tympanic ring will be more fully discussed in another article now in preparation.

#### SUMMARY AND CONCLUSIONS.

As a result of the foregoing studies, several important conclusions are suggested, which, though for the most part still lacking positive demonstration, seem at least worthy of serious consideration. For it is only by such methods of comparison and discussion that one may hope ever to attain, or even approximate, the ultimate truth regarding the evolutionary history of animal life of the past as recorded by fossil remains. Especially is this evident when it is considered how very incomplete at best is the story of development in attempting to trace those ancient phyletic series which are based, as they necessarily must be, on the present relatively scanty and broken records. For at best, in our fossil records there exist many wide gaps, which in many cases probably will never actually be filled, although future discoveries in the fossil fields may greatly aid in this matter.

Some of the following conclusions have been advocated and defended in part or in whole by other authors, but in greater part they have been suggested by my own lines of investigation. These conclusions may be thus briefly summarized:

1. The evidence of the Fort Union mammals, as at present known, seems to show conclusively that the major groups at least of the Tarsiidae, as defined by Matthew, had their origin much earlier than the beginning of the Eocene, being almost as well marked in the Paleocene as in the Wasatch and Bridger.

2. The early Tarsiids, as at present understood, seem not to represent a natural group. That is, certain forms, now referred to this group on definition of tooth characters alone, when better known, may lose their present taxonomic arrangement of closely affiliated species.

3. It would seem, however, that within this group are to be found the ancestral stock which gave rise to the living Tarsiids, they being derivable from some such forms as *Omomyx* or *Anaptomorphus*; and possibly the origin of the aberrant lemur, *Daubentonia* of Madagascar also may be traced to some other form of this group with the dental modifications of *Phenacolemur*, or *Tetonius*.

4. Probably, also, as indicated by certain modifications noted in the Fort Union *Paromomys* and *Palaechthon*, some of the Eocene Tarsiid, at least, were rather closely related to the Nothartids, as was suggested by Wortman; in which case Wortman's other suggestion of a possible derivation of the marmoset branch of the Platyrrhini from some form of Eocene Tarsiid, as *Omomys*, is not entirely impossible. These conjectures regarding relationships, however, can only be tested by a knowledge of skull and foot structure, which, in most of the early Tarsiids, is at present almost entirely wanting.

5. Neither the Paleocene Primates nor a restudy of the Nothartid group itself seems to lend any support to the views held by Gregory, Stehlen, and others regarding the primitive ancestral-lemurine affinities of the Adapidae. That they have lemurine affinities can not be denied, but these Eocene Primates which were still in a primitive-primate or relatively generalized stage of development, appear to have been progressively advancing along lines leading definitely toward the modern Anthropeida, especially in the direction of the Platyrrhine group; and that their relationship to the lemurs, though apparently close to one living group, is to be traced backward from the Nothartids to a more remote common ancestor and not forward in geologic time. Or in other words, it may be assumed that the Adapidae represent a group of Primates which, while having been derived from an earlier group also giving rise to the modern lemurs, were as early as the Eocene already definitely progressing away from the lemurine and toward the anthropoid type of development.

6. It logically follows from the foregoing views that none of the now known early Primates fulfill the conditions required of an ancestral type from which the modern lemurs (excepting only the Tarsiidae and possibly the Daubentoniidae) were derived, and this hypothetical group still remains to be discovered. The same may possibly be said of the monkeys and apes of the Old World, at least so far as the Tertiary beds of North America are concerned. But the ancestral stock of these anthropoids, if found in beds of Eocene age, may be expected to show very close affinities with the Nothartinae.

7. The combined evidence of the known Eocene and Paleocene Primates indicate rather clearly that, although still relatively primitive and generalized in anatomical structure, the evolution of the Primates, even at this early time, was well under way, and we must look much further backward in time than to the beginning of the Tertiary for the origin of the principal major groups of this great order.

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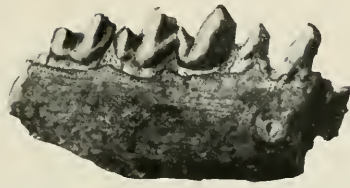
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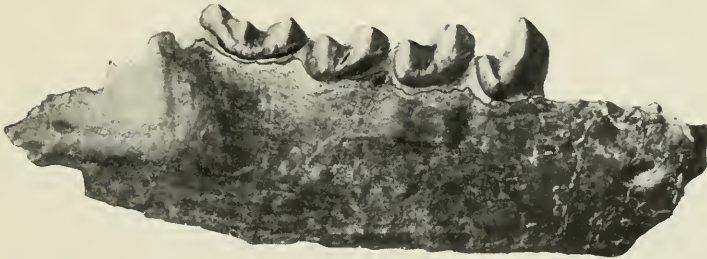
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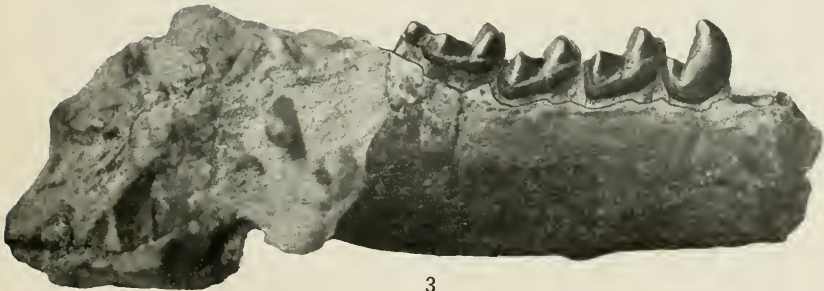
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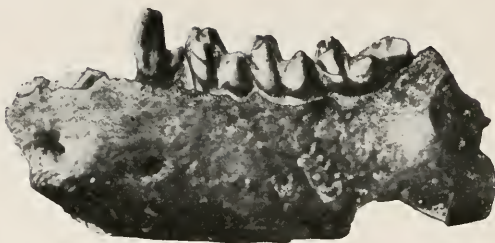
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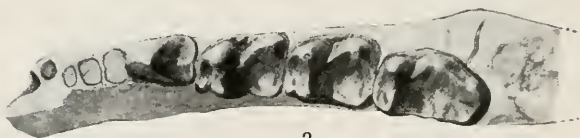
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LOWER JAWS OF EARLY PRIMATES

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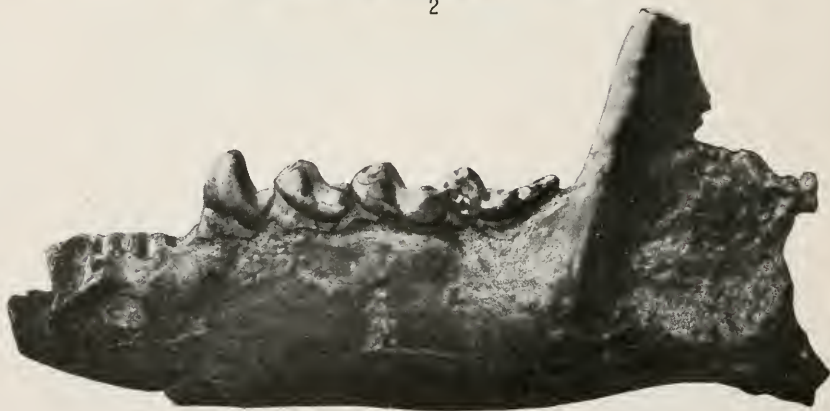
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TEETH OF EARLY PRIMATES.

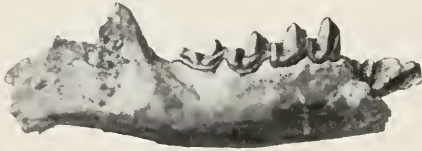
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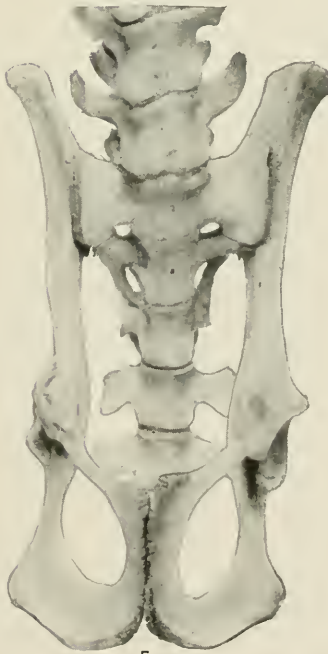
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