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NOTES ON THE CLARK FORK, UPPER PALEOCENE, FAUNA

By George Gaylord Simpson

The first and, as yet, the largest Clark Fork collection was made by American Museum parties under Dr. Walter Granger principally in the years 1911-1912. The mammals then found, and a few from later years, were included in their Lower Eocene revision by Matthew and Granger (see references at end of paper) and most of the Clark Fork species have been named, described and figured by them. Of the few groups not included in their work, the tillodonts are described in this paper, the uintathere was described by me (Simpson, 1929) and the coryphodont does not merit full description but is mentioned below.

A few additions to the fauna were made by Jepsen (1930A), and as Princeton parties under him are continuing work in that region further additions may be expected.

The high quality of the work already done makes thorough revision unnecessary, and the continuance of field work makes a general review premature, but these same circumstances do make it advisable to fill the few gaps in publication of our collection and to make its data as complete and accessible as possible.

The tillodonts are here discussed for the first time and two other forms which Matthew did not, but which I do, consider as new are named and diagnosed. Aside from these additions to the faunal list, this paper is devoted to a more exact characterization of such Clark Fork animals as are well enough represented to make this possible, and to an analysis of their precise relationships to their Sand Coulee[1] and Gray Bull relatives.

[1] Jepsen (1930B) notes that *Homogalax* occurs in the Sand Coulee and therefore suppresses the name and includes the corresponding strata in the Gray Bull. That it is very close to the typical Gray Bull both faunally and stratigraphically is clear, and Jepsen's attitude seems justified on his more recent data. At the same time the Sand Coulee fauna was not wholly defined by Granger on the absence of *Homogalax* but also by the generally slightly less advanced character of its mammals. This is confirmed by our collections. Several instances of the distinction between Sand Coulee and Gray Bull mammals of the same species or genus are incidentally mentioned in the comparisons in this paper, and others exist. Such distinctions are slight but they are increasingly important as this part of the sequence is studied in greater detail, and they can only be made if some exact records of horizon, such as those proposed by Granger, are maintained in field records and in publications, as far as possible. Whether in this case this be done by using the name Sand Coulee, or some other, such as Lower Gray Bull, is immaterial. Since, however, previous publication has used Lower Gray Bull in another sense while most of the animals of the base of the Lower Eocene have already been published as the Sand Coulee fauna, it appears somewhat confusing to change these usages at present. It is evident from Jepsen's work that Sand Coulee does not apply to a major unit nor have the scope of a formation in common usage, but it is distinguishable by careful methods, and an unambiguous, preferable, alternative notation for these minor horizons is not available at present. I therefore shall continue to use Sand Coulee until or unless such a notation is proposed.

In practically all older paleontological work and far the greater part of that recently done, comparisons are made on the basis of individual specimens only. Even when groups of specimens are available and are compared, the comparison is in fact of the several individuals of the group and not of the group itself as a unit. Where it is possible, in this paper the method used is to compare the groups as such, to use the individual specimens only as representatives of a group rather than thinking of the group as secondary and the individuals as the essential units. Although the distinction may seem unduly subtle, it is in fact fundamental. This approach obviously is not of universal applicability, but where it can be used to advantage it seems absolutely essential for the placing of paleontology on a more exact, more objective and less intuitive basis. It is in many cases the only way in which the minor distinctions essential for progress in the present stage of study can be determined and evaluated on sound principles. Among other important points, it is doubtful whether such differences as that between the Sand Coulee and Gray Bull faunas can be clearly recognized in any other way. Distinctions of this sort involve, for instance, the characterization of units of about the value of subspecies in Holocene taxonomy. Subspecies can rarely or never really be recognized in vertebrate paleontology, whether they be successive or geographic, except by statistical methods, since these furnish the only means other than intuition (thoroughly unreliable in this respect) for distinguishing real group differences from individual variation.[1]

CLARK FORK MAMMALIAN FAUNAL LIST

MULTITUBERCULATA
- Ptilodontidae
  - *Parectypodus* sp. (auct. Jepsen, 1930)

?INSECTIVORA
- Apheliscidae
  - *Apheliscus nitidus*, new species
- Nyctitheriidae
  - Gen. et sp. indet.

PRIMATES
- Plesiadapidae
  - *Plesiadapis dubius* (Matthew, 1915)
  - *Plesiadapis cookei* Jepsen, 1930
- Carpolestidae
  - *Carpolestes dubius* Jepsen, 1930

[1] The constants and methods here employed are in wide use in other fields, although few paleontologists have hitherto used them. All are given in the following manual:
Fisher, R. A., 1925, 'Statistical methods for research workers.' Biological Monographs and Manuals, V.
They are also explained and their peculiar adaptability to paleontological work discussed in a paper on the use of numerical data soon to go to press.

TILLODONTIA
- Esthonychidae
  - *Esthonyx ? bisulcatus* Cope, 1874
  - *Esthonyx grangeri*, new species
  - *Esthonyx latidens*, new species

PALAEANODONTA
- Metacheiromyidae
  - *Palaeanodon parvulus* Matthew, 1918

CREODONTA
- Arctocyonidae
  - *Thryptacodon antiquus* Matthew, 1915
- Mesonychidae
  - *Dissacus praenuntius* Matthew, 1915
- Oxyaenidae
  - *Oxyaena aequidens* Matthew, 1915
  - *Dipsalidictis platypus* Matthew, 1915
  - *Dipsalodon matthewi* Jepsen, 1930
- Miacidae
  - *Didymictis protenus proteus*, new subspecies

CONDYLARTHRA
- Phenacodontidae
  - *Phenacodus primaevus* cf. *primaevus* Cope, 1873
  - *Phenacodus primaevus* cf. *intermedius* (Granger, 1915)
  - *Ectocion osbornianus ralstonensis* (Granger, 1915)
  - *Ectocion parvus* (Granger, 1915)
- Hyopsodontidae
  - *Haplomylus speirianus* (Cope, 1880)

PANTODONTA
- Coryphodontidae
  - *Coryphodon* sp.

DINOCERATA
- Uintatheriidae
  - *Probathyopsis praecursor* Simpson, 1929
  - *Probathyopsis* sp. (auct. Jepsen, 1930)

Parectypodus and *Carpolestes* are not present in the American Museum collection but are recorded by Jepsen (1930A). *Plesiadapis cookei* is represented in our collection only by an incomplete upper incisor, the affinities of which were unrecognizable when Matthew wrote, and this species is likewise based on Jepsen's material. *Dipsalodon* is doubtfully represented in our collection by a few uncharacteristic fragments. Jepsen (1930A, p. 493; 1930B, p. 129) notes the occurrence of a second, more primitive species of *Probathyopsis*, but he has not named or further characterized it.

Most of the Clark Fork animals belong to typically Paleocene groups and have ancestors or close relatives in the Torrejon and its equivalents. Some of the characteristic Middle Paleocene forms had, however, died out, or at least are not represented in the fairly large Clark Fork collections (e.g., the previously very abundant periptychids). Although the fauna is thus essentially Paleocene in origin and affinities, almost all its genera and larger groups survived into the true Eocene. The Sand Coulee-Gray Bull fauna is essentially that of the Clark Fork greatly enriched by additions probably due in greatest part to immigration. At least one order (Perissodactyla), several families (e.g., Adapidae) and numerous genera (e.g., *Hyopsodus*) are common in the Gray Bull (plus Sand Coulee) but are as yet unknown in the immediately antecedent Clark Fork or earlier levels. It is this marked migrational movement that is taken to mark the most convenient position for the Paleocene-Eocene boundary, a line necessarily somewhat conventional and even arbitrary in a series that is essentially continuous.

?INSECTIVORA

Apheliscidae

Apheliscus nitidus, new species

TYPE.—Amer. Mus. No. 15849, maxillary fragment with left P^4–M^1.

HORIZON AND LOCALITY.—Clark Fork, head of Big Sand Coulee, Wyoming.

DIAGNOSIS.—P^4 with external and posterior cingula, basal contour of whole tooth more triangular than in *A. insidiosus*, M^1 with sharp anterior, external and posterior cingula, hypocone small but sharply differentiated. P^4 length 2.6 mm., width 3.0. M^1 length 2.6, width 2.8.

Matthew (1918, p. 596) mentioned this specimen with the comment that it might represent a primitive mutant of *A. insidiosus*. As it is very readily distinguishable from the Gray Bull form, referred to the New Mexican "Wasatch" species, it seems best to give it a distinctive name and standing in the faunal lists. The type was figured by Matthew.

?Nyctitheriidae

For the purposes of future comparison, it may be recorded that Amer. Mus. No. 15850 is suggestive of *Nyctitherium* but certainly belongs to no described species and is probably of a new genus. It is inadequate as a type and is therefore not named or described.

TILLODONTIA

The section on tillodonts in the Matthew-Granger "Wasatch and Wind River" revision has not been completed or published and the Clark Fork (but not the Lower Eocene) tillodonts are therefore named and described now. Dr. Granger has had this subject in hand for some time. He identified the specimens and directed the preparation of the illustrations of tillodonts here published (drawn by the late L. M. Sterling). Since, however, his administrative duties and the work of the Central Asiatic Expeditions have made it impossible for him to complete this study he has asked me to include it here. Dr. Granger insists that he be excluded from co-authorship of this paper or of this section of it and the results are in some details different from those of his preliminary study, but the fact that he did much of the work involved is gratefully acknowledged.

Esthonychidae

Esthonyx bisulcatus Cope, 1874

The nomenclature and taxonomy of *Esthonyx* are in a somewhat confused condition and cannot be entirely cleared up in this paper. The following species have been named:

E. bisulcatus Cope, 1874 (designated as genotype).
E. burmeisterii Cope, 1874.
E. acer Cope, 1874.
E. spatularius Cope, 1880.
E. acutidens Cope, 1881.

The first three types were from the "Wasatch" (Largo and Almagre) of New Mexico and the last from the Wind River Basin. In the original description *E. spatularius* was recorded as from the Wind River Basin, but in 1884 the same specimen, now Amer. Mus. No. 4809, was said to be from the Bighorn Basin. Cope's label gives the locality as "Bighorn B." On the other hand, Matthew concluded that Wind River Basin was correct or at least more probable, as shown by his labels and catalogue cards. In fact, it is possible to match the specimen almost exactly by others from the Gray Bull of the Bighorn Basin, and not so well with Wind River material. Together with the evidence that Cope's later statement was a correction, this seems to me to establish a strong probability that this is a Gray Bull species. The point is important because, if this conclusion is correct, this is the only species of *Esthonyx* based on a Gray Bull specimen and because some of the Clark Fork material is particularly close to this type.

E. burmeisterii and *E. acer* are probably synonyms of *E. bisulcatus*, or at least, the types do not seem to me to warrant specific distinction at present. *E. spatularius* is very doubtfully distinct, as will be shown. *E. acutidens* appears to be a good species characterizing later horizons.

Esthonyx is abundant in the Gray Bull. At least fifty individuals are represented by lower jaws and teeth in our collections.[1] As is so often true in large collections, it would be easy to pick out two or three strongly distinctive types and define them as species, yet it is practically impossible to separate the whole collection into two or more clearly defined groups. The essential homogeneity is seen in data for the length of P_4, which are corroborated by those for the other dimensions of P_4–M_3, also calculated but not published here:

Number	Observed Range	Mean	Standard Deviation	Coefficient of Variation
20	7.1–8.7	7.90 ± 0.08	0.35 ± 0.06	4.5 ± 0.7

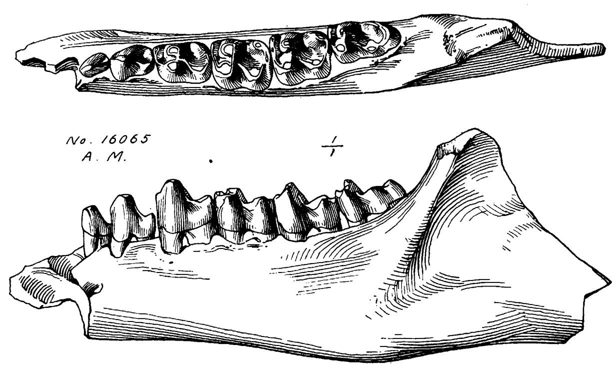

Fig. 1. *Esthonyx ? bisulcatus* Cope, 1874. Referred specimen from the Clark Fork. Amer. Mus. No. 16065, left lower jaw with P_2–M_3. Crown and external views. Natural size.

The distribution, grouped, is as follows:

7.1–7.3	1
7.4–7.6	4
7.7–7.9	7
8.0–8.2	5
8.3–8.5	2
8.6–8.8	1

The highest coefficient of variation is for length of M_3 and is 7.0 ± 1.0.

There is certainly nothing in this to show or even to hint that more than one species is present. P_4 also shows the greatest morphological variation and here again the extremes are decidedly unlike but every intergradation occurs and there is no evident natural grouping.

At present there is little choice but to call all these varied Gray Bull

[1] Most of these are recorded only as Bighorn "Wasatch," but from locality records, faunal associations, etc., it is evident that nearly or quite all of them are from the Gray Bull.

specimens *Esthonyx bisulcatus,* since they are not themselves separable and include as variations all the characters of the New Mexican form. Typical *bisulcatus* is not at the mean for the Gray Bull material and perhaps a racial difference will later be established, but I cannot do this on present data.

The best tillodont in the Clark Fork collection is Amer. Mus. No. 16065, a left lower jaw with P_2–M_3. This differs markedly from the majority of the Gray Bull specimens. It is below their average size in all dimensions. P_2 is relatively small, P_3 relatively high and simple, and on P_4 the trigonid is more compressed anteroposteriorly and its two crests are more transverse than is usual in the Gray Bull. The same difference in the trigonids but in less degree is perceptible on M_{1-3} and their metastylids are rather small. In all these respects, however, the whole Gray Bull series could include this specimen as a variant. Of course, no Gray Bull specimen is exactly like this, but various of the Lower Eocene forms bracket all the deviations of the Upper Paleocene specimen.

If it could be established that the Clark Fork specimen is near the mean for that horizon or that it is a variant toward the Gray Bull type, then a distinctive Clark Fork species or subspecies would be recognizable. There is some probability that this will prove to be true, but at present only this one Clark Fork specimen is available and a separation cannot be statistically and logically maintained.

The type of *E. spatularius,* consisting essentially of a single M_3 (also anterior teeth but the association is uncertain and adequate comparative material lacking), likewise falls within the range of variation for the Gray Bull *E. bisulcatus* group but near its lower limit. It follows that this type is particularly similar to the Clark Fork specimen and even if the latter were provisionally separated from *E. bisulcatus,* it would be quite impossible to distinguish it from *E. spatularius.* In view of the nature of the evidence, however, it is not established either that *E. spatularius* is a valid species or that the Clark Fork specimen is conspecific with its type. M_3 of *E. spatularius* measures 8.9 by 5.1 mm. The dimensions of Amer. Mus. No. 16065 are as follows:

P_2		P_3		P_4		M_1		M_2		M_3	
L	W	L	W	L	W	L	W	L	W	L	W
4.2	3.0	6.1	4.3	7.6	5.2	7.9	6.5	7.8	6.4	9.3	5.0

These are all within the known ranges of the Gray Bull material, except for the width of M_3, which is 5.1 mm. in the smallest Gray Bull example.

The deviation from the Gray Bull mean is −.68, which is −2.2 times the standard deviation, not surely significant.

It may be noted that the Sand Coulee beds have yielded certainly three and possibly four species of *Esthonyx*. One is *E. grangeri* (see below) and one is indistinguishable from the Gray Bull *E. bisulcatus* group. There is also a very small form surely distinct from the Gray Bull group. Its length P_4, for instance, deviates by −1.3 mm. from the Gray Bull

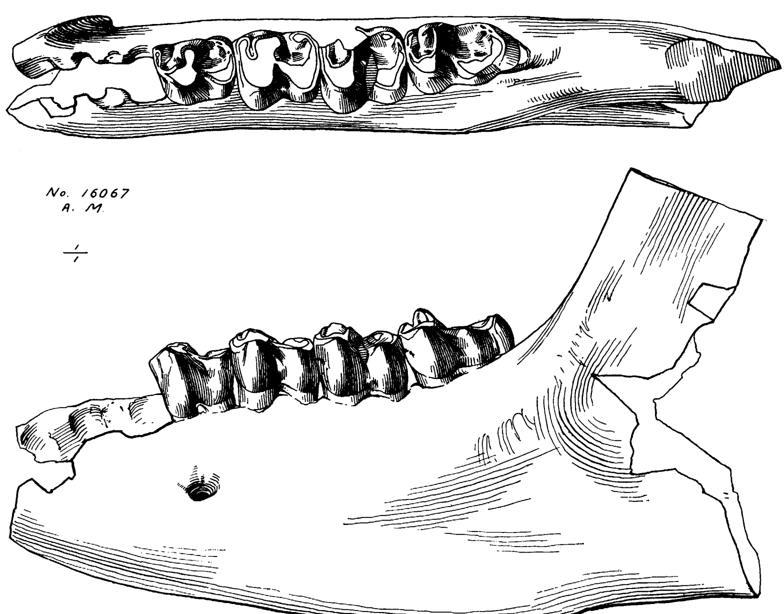

Fig. 2. *Esthonyx grangeri*, new species. Type, Amer. Mus. No. 16067, left lower jaw with P_4–M_3. Crown and external views. Natural size.

mean, which is −3.7 times the standard deviation of the latter and is surely significant, as are some other dimensions. It is entirely possible that the Clark Fork specimen here discussed is really a large variant of this Sand Coulee species, which may be *E. spatularius* or may (with more probability) be an unnamed species. This to some degree increases the probability that the Clark Fork specimen does not really belong to *E. bisulcatus* in spite of now being inseparable from the latter. It is further possible that *E. latidens* occurs in the Sand Coulee (see below).

Esthonyx grangeri,[1] new species

TYPE.—Amer. Mus. No. 16067, left lower jaw with P_4–M_3.

HORIZON AND LOCALITY.—Type either from top of Clark Fork or base of Sand Coulee beds, at head of Big Sand Coulee, Clark's Fork Basin, Wyoming. Referred specimens from undoubted Clark Fork and Sand Coulee horizons.

DIAGNOSIS.—Significantly larger than any other species of *Esthonyx* (measurements given below). Teeth and jaw in general within the structural range of Gray Bull referred *E. bisulcatus*, but very heavily built. P_4 comparable to Gray Bull variants with more advanced molarization.

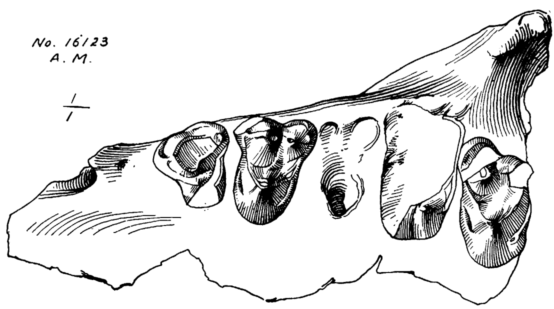

Fig. 3. *Esthonyx grangeri*, new species. Referred specimen, Amer. Mus. No. 16123, left upper jaw with P^{3-4}, M^3, and alveoli or roots. Crown view. Natural size.

The size of this large species is decisively distinctive from any other referred to the genus. For instance, comparing with the Gray Bull series the difference of this type from their mean divided by the corresponding standard deviation is +8.9 for length P_4, +6.0 for length M_3, and correspondingly great for all other dimensions. There seem to be no positive morphological distinctions from large and progressive Gray Bull variants aside from the generally heavier structure, both relatively and absolutely.

A referred specimen, Amer. Mus. No. 16123, from the type horizon and locality shows part of the upper dentition. P^4 has a large metacone, as in the more progressive Gray Bull specimens, but a very small hypocone. In the Gray Bull large metacone and large hypocone seem to be associated, so that this may prove to be a specific character.

The type and four referred specimens are from a horizon not positively

[1] Dr. Walter Granger. He had already given this species a different catalogue name, but as he has assigned its publication to me I take the opportunity of thus commemorating his collection of most of the known material and his first recognition of the species.

identified as it is near the indefinite Clark Fork- Sand Coulee boundary. There are, however, various specimens referable to this species with little or no doubt and known to be of both Clark Fork and Sand Coulee age, so that the species occurs in both those faunas. Its complete absence from the much larger Gray Bull collections may be one of the faunal differences between Sand Coulee and Gray Bull.

The dimensions of the type teeth are as follows:

P_4		M_1		M_2		M_3	
L	W	L	W	L	W	L	W
11.0	8.3	11.2	10.1	11.3	ca. 11	14.6	9.4

Esthonyx latidens,[1] new species

TYPE.—Amer. Mus. No. 16066, associated parts of juvenile dentition including left dm^3–M^1, right dm^4, left dm_3–M_1, and several anterior teeth.

HORIZON AND LOCALITY.—Type from Clark Fork beds, 3 miles east of mouth of Pat O'Hara Creek, Clark's Fork Basin, Wyo. Specimens referred (without certainty) from transitional Clark Fork-Sand Coulee.

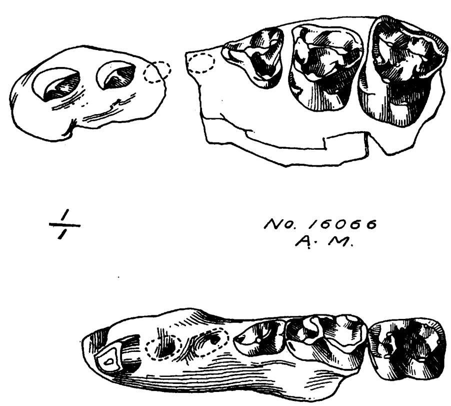

Fig. 4. *Esthonyx latidens*, new species. Type, Amer. Mus. No. 16066, left upper jaw with I^{2-3}, dm^{3-4}, and M^1, and left lower jaw with I_2 (broken), dm_{3-4}, and M_1. Crown views. Natural size.

DIAGNOSIS.—Intermediate in size between *E. grangeri* and Gray Bull referred *E. bisulcatus* and outside the known or probable range of either. Ratio of width to length in M^1 of type 1.22, smaller than in other species as far as known.

This form is definitely too large to belong with the Gray Bull *E. bisulcatus* group. It might conceivably be a small variant of *E. grangeri*, but the probability against this is strong enough to warrant definition of the present species. In four specimens of *E. grangeri* the length of M_1 is

[1] Name from labels (not manuscript) by Granger.

11–12, mean 11.4, while in the present type this is 10.3; moreover this type is unworn, hence has maximum length, while all the specimens of *E. grangeri* have the length reduced by wear. The true whole range for unworn teeth in the latter will in all likelihood be found to begin above 10.5, at least, and probably higher. M_1 is unknown in *E. grangeri*, but in Amer. Mus. No. 16123 the alveoli and adjacent teeth are preserved, evidently with no distortion. They indicate a transverse and *bisulcatus*-like tooth, probably, indeed, even more transverse than the Gray Bull average. The width: length ratio cannot have been much less than 1.45, and perhaps was greater. In seven specimens from the Gray Bull the range is 1.35 – 1.45, mean 1.39. *E. latidens*, with this ratio 1.22, is significantly different.

CREODONTA

Arctocyonidae

Thryptacodon antiquus Matthew, 1915

In the Sand Coulee and Gray Bull there are perhaps two subspecies of *Thryptacodon antiquus*, as the eleven measurable specimens of our collection fall into two groups, one smaller in size with four individuals and one larger with seven individuals. Two of the smaller individuals are labeled as from the Sand Coulee, the other two only as Wasatch. The type, belonging to the larger group, is from the Gray Bull, the other six larger specimens labeled only "Wasatch" but apparently from Gray Bull localities. It is thus possible, but the data cannot prove, that a smaller subspecies occurs in the Sand Coulee and a larger in the Gray Bull.

The range of the length of M_2 of the six larger specimens is 6.7 – 7.1 and the mean 6.9 (type 6.8). The range of the four smaller specimens is 5.9 – 6.3 and the mean 6.1. The two Clark Fork specimens, all that are available, measure 7.0 and 7.2 in this dimension. They are thus comparable with the larger specimens of the larger "Wasatch" group. On the basis of these small samples the difference is not shown to be significant (would be exceeded by mere chance in collecting one or two times out of ten).

The length-width M_2 ratio of the larger "Wasatch" specimens has the range 1.15 – 1.35 and mean 1.24. That of the smaller specimens has range 1.20 – 1.27, mean 1.23. The two Clark Fork specimens have the ratios 1.17 and 1.22. While they are thus slightly below the average for the later specimens, they are within the range of the latter and are so near that mean that the chances of such a difference being due to mere chance of sampling are better than even.

The "protostyle on M_2" of which Matthew speaks is a small basal cuspule between the protoconid and hypoconid. It is present on one Clark Fork specimen, absent on the other. It is present, but weak, on two of the seven larger "Wasatch" specimens. No valid difference between Clark Fork and later specimens is demonstrated by these data. This cusp, incidentally, is extremely variable both in arctocyonids and in phenacodonts. On two specimens almost certainly of exactly the same race one may have it very large and prominent and the other lack it entirely.

Matthew's conclusion (1915A, p. 8) that the Clark Fork specimens probably represent a new species or subspecies characterized by broader teeth (smaller length–width ratio of M_2) and distinct protostyle on M_2 is thus not supported by the available material. Larger samples might demonstrate mean differences of subspecific value, but the specimens in hand do not do so.

It is interesting to note the possibility, not proven in this case but very suggestive of the condition in *Didymictis* and in *Haplomylus* (see below) that the Clark Fork representatives of this species are as large and generally advanced as the most progressive Gray Bull specimens and more so than those of the intervening Sand Coulee, a condition to be interpreted only as indicative of migrational and facies changes.

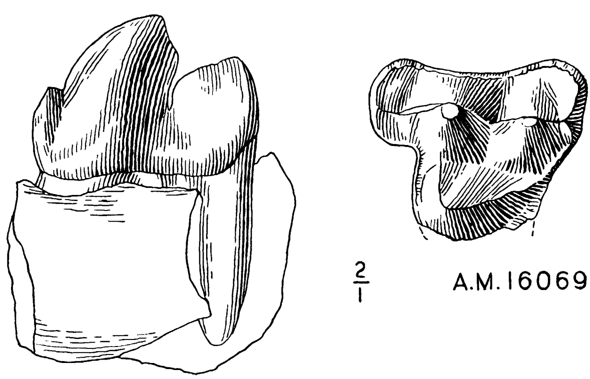

Fig. 5. *Dissacus praenuntius* Matthew, 1915. Type, Amer. Mus. No. 16069, left P_4, external view, and left M^1. Crown view. Twice natural size.

Mesonychidae

Dissacus praenuntius Matthew, 1915

This species was adequately characterized, but not figured, by Matthew. It is here figured.

Oxyaenidae

All three known Clark Fork oxyaenid species are confined to that horizon, although *Oxyaena aequidens* and *Dipsalidictis platypus* have successors in the Lower Eocene. Matthew (1915A, p. 47) mentioned and briefly described a Clark Fork specimen which he considered as representing a new species possibly of *Oxyaena*. Comparable parts are too limited for decision, but it seems possible that this is the form later named *Dipsalodon matthewi* by Jepsen. Matthew's specimen is, in any event, scarcely determinable in itself. There are also some other oxyaenid scraps evidently not *O. aequidens*, but too imperfect for determination.

Ambloctonus priscus does not belong in the Clark Fork fauna. Matthew (1915A, p. 60) states that the paratypes Amer. Mus. Nos. 16116 and 16117 are from this horizon, but this was apparently a *lapsus calami*. The field records give "Intermediate Beds" as the horizon, a field designation for the Sand Coulee, before the latter name was given, and the labels, in Matthew's hand, give "Sand Coulee." The locality is given as "2 miles S.-E. of m'th of Pat O'Hara Cr'k." There are many Sand Coulee specimens, including *Hyracotherium*, with these locality data, but no Clark Fork specimens, although several of the latter are labeled as from east, or three miles east (but not southeast) of the mouth of Pat O'Hara Creek. There can be no doubt that the specimens are from the Sand Coulee, not the Clark Fork.

Miacidae

Didymictis protenus proteus, new subspecies

TYPE.—Amer. Mus. No. 16071, parts of lower jaw with right P_4 (broken), left M_1 (broken), and right M_2.

HORIZON AND LOCALITY.—Clark Fork Beds, head of Big Sand Coulee, Clark's Fork Basin, Wyoming.

DIAGNOSIS.—Characteristic *D. protenus*, dimensions intergrading with those of Gray Bull and Almagre specimens, but differentiated by the dimensions of M_2, mean length 8.2, mean width 4.6, mean length–width ratio 1.8. See data below.

Matthew (1915A) considered the more common *Didymictis* of the Clark Fork and Lower Eocene as showing a series of progressive mutants distributed as follows:

Didymictis protenus leptomylus (Cope, 1880)—Clark Fork to Lower Gray Bull.
Didymictis protenus protenus (Cope, 1874)—Middle and Upper Gray Bull.
Didymictis protenus lysitensis (Matthew, 1915)—Upper Gray Bull and Lysite.
Didymictis altidens (Cope, 1880)—Lost Cabin.

These were supposed to be progressive, in the order given, in size and, less explicitly, some other characters.

An adequate revision is beyond the scope of these notes (and is hardly possible), but the series has been carefully examined for its bearing on the Clark Fork specimens and the use of other methods of study suggests that Matthew's conclusions may be in part ill founded and in part erroneous.

The Wyoming "Wasatch" forms, for the most part Gray Bull and possibly including some from the Sand Coulee although none is explicitly so recorded, show considerable variation in dimensions even among those referred with high probability to *D. protenus*. The four coefficients of variation given below, 5.0, 5.2, 7.1, and 8.4, are, in conjunction, high

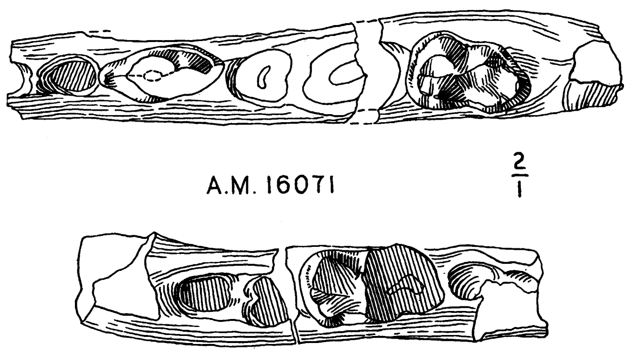

Fig. 6. *Didymictis protenus proteus*, new subspecies. Type, Amer. Mus. No. 16071, right lower jaw with P_4 and M_2, and associated left lower jaw with broken M_1. Crown views. Twice natural size.

enough to include more than one pure local race, but not so much so as to warrant, without other data, the assumption that more than one race is in fact present. As a considerable span of time is represented, it is reasonable to suppose that progressive changes did take place and that the range of variation is due in part to such changes, and not purely to contemporaneous fluctuation. No basis for separation exists in the characters of M_2, the commonest and in many respects most characteristic tooth in the collections. M_1, however, could separate the Gray Bull *D. protenus* into three groups, but there is no statistical probability that such separation is valid, it cannot be shown to be associated with differences in age, and it does not even approximately correspond with Matthew's three-fold separation into *leptomylus*, *protenus*, and *lysitensis*. It is probable that a two- or three-fold subspecific division of Gray Bull (and Sand Coulee) *Didymictis protenus* would be warranted with more accurate data, but this is necessarily deferred.

D. protenus lysitensis is about intermediate between the general Gray Bull groups and *D. altidens*, but in several respects it falls rather within the *D. altidens* group, as a variant, than within that of the Gray Bull specimens. Thus its length M_1 in the type is almost exactly at the mean for the general *altidens* group but distant nearly four times the standard deviation from the mean for the Gray Bull specimens. If it is not a synonym of *D. altidens*, it seems a much better representation of its character to make this a subspecies of *altidens*, as *Didymictis altidens lysitensis* (Matthew), rather than of *protenus*. No specimen probably referable to the *altidens* group is known from the Gray Bull, or labeled "Wasatch" in the old collections, nor does any occur in the Clark Fork.

D. leptomylus Cope was described as from the "Wind River," but certainly is very distinct from the *altidens-lysitensis* group and may be from the Gray Bull. Matthew believed it to be applicable to a small subspecies of Clark Fork and Gray Bull *D. protenus*. On the revaluated data, the type of *D. leptomylus* seems on the contrary to be either a highly abnormal individual or the sole representative of a distinct species (of unknown exact horizon). It has far the smallest M_1 of any specimen in the collection (deviation from the mean for the Gray Bull group about three times the standard deviation). Its M_2 is almost at the mean for the Gray Bull, or *protenus*, group in length, but is narrow (deviation 2.3 times standard deviation), giving it a high length–width ratio (deviation 3.3 times standard deviation in comparison with *protenus* group). It is extremely improbable that any of the Gray Bull specimens referred by Cope or Matthew to *leptomylus* belong there, and for any practical purpose it is certain that Matthew's referred Clark Fork specimens do not.

The type of *protenus* is from the New Mexican "Wasatch." In all its dimensions it falls within the range of variation of the Gray Bull specimens, but it is decidedly marginal in several respects, short M_1, long M_2, high length-width ratio of M_2. The combination is peculiar, and it is improbable that the Gray Bull forms are in fact, identical with *D. protenus*, but distinction is not positively demonstrable. They should probably be referred to one or more distinct subspecies, which might acquire specific rank with increased knowledge of topotypic *protenus*, for which (or for the larger subdivision of which) the name *curtidens* is available, *D. curtidens* Cope being based on a fairly typical, but poorly preserved, Gray Bull specimen. If there are two subspecies (or other groups) in the Gray Bull, *curtidens* applies to the larger animals.

The Clark Fork specimens are within the range of those from the Gray Bull in every dimension, but they nevertheless are significantly different as a group, and they do not, as Matthew thought, compare with the smaller Gray Bull forms. M_1 (a single specimen) does not differ significantly from the Gray Bull mean, its deviation being only 0.5 times the standard deviation. M_2, however, is significantly longer than the mean of the Gray Bull specimens. Here five individuals are available, and Fisher's[1] more exact test for the significance of the deviation of the means of two small samples can be applied. By this method, for length M_2 P (see Fisher) is less than 0.01, for width M_2 it is greater than 0.1 and for the length-width ratio it is between 0.05 and 0.02. In other words it is extremely likely (for all practical purposes certain) that the greater length of M_1 in the Clark Fork specimens is due to a real difference in the animals of that time and not merely due to the chance that larger specimens happen to have been found in that level, the slightly greater width of M_2 may very well be due to chance, and the greater length-width ratio is probably not, but might be, due to chance (chances less than one in twenty). The group is thus different and this may be signalized by making it a subspecies of the general *protenus* group.

It may be noted that the Clark Fork to Lost Cabin specimens do not form a single linear sequence. Several lines are present, and some migration or change of facies, possibly of a local nature, is indicated between the Clark Fork and Gray Bull, the differences not being explicable with any probability as due to evolution *in situ*.

Some of the available data are given below. The Lysite and Lost Cabin specimens have also been measured and their constants calculated, but they are not pertinent to the present discussion.

Clark Fork *Didymictis, D. protenus proteus:*

Variate	Number	Observed Range	Mean	Standard Deviation	Coefficient of Variation
Length M_2	5	8.0–8.3	8.2 ± 0.1	0.12 ± 0.04	1.4 ± 0.5
Width M_2	5	4.4–5.0	4.6 ± 0.1	0.21 ± 0.07	4.6 ± 1.5
$\frac{\text{Length}}{\text{Width}}$ M_2	5	1.7–1.9	1.8 ± 0.0	0.08 ± 0.02	4.4 ± 1.4

Sand Coulee and Gray Bull *Didymictis, D. protenus curtidens* and possibly another closely related subspecies:

Variate	Number	Observed Range	Mean	Standard Deviation	Coefficient of Variation
Length M_2	26	6.7–8.3	7.5 ± 0.1	0.39 ± 0.05	5.2 ± 0.7
Width M_2	26	3.7–5.1	4.4 ± 0.1	0.31 ± 0.04	7.1 ± 1.0
$\frac{\text{Length}}{\text{Width}}$ M_2	26	1.5–1.9	1.7 ± 0.0	0.09 ± 0.01	5.0 ± 0.7
Length M_1	16	10.0–13.0	11.1 ± 0.2	0.93 ± 0.17	.48 ± 1.5

[1] The t test, given in Fisher's manual cited in a previous footnote.

CONDYLARTHRA

Phenacodontidae

Phenacodus primaevus

Granger (1915) made a four-fold division of the larger Gray Bull *Phenacodus*, as follows:

Phenacodus primaevus robustus
Phenacodus primaevus primaevus
Phenacodus primaevus hemiconus
Phenacodus intermedius

It is probable that this division is valid, at least in a general way. Upon consideration of the whole series, however, the demarcation proves to be difficult or impossible in some cases. *P. p. robustus* is represented by a small number of specimens rather closely clustered about their mean. They are not far removed from the next smaller specimens, large variants of *P. p. primaevus*, but in our material, at least, there is a discontinuity, the two groups can be distinguished almost at a glance, and there is no specimen of doubtful position between them. It may be taken that *robustus* is surely valid and it is so much more distinct than are the other three groups that I believe that it should be raised to full specific rank, as *Phenacodus robustus* (Granger, 1915).

Omitting this large species, the other specimens of this group form an essentially continuous distribution. In individual measurements, the distribution tends, indeed, to have two or three modes. The length of M_3, for instance, suggests modes at or near 10.7, 12.3 or 12.4, and 14.0, which may correspond with *P. intermedius*, *P. p. hemiconus*, and *P. p. primaevus*, respectively. But even in cases of single dimensions this polymodality is not sufficiently pronounced to be statistically significant, and when the whole character of each specimen is considered it disappears altogether. That is, the segregation vaguely suggested by a single character is not positively correlated with groupings suggested by other characters and the whole series takes on the appearance of an indivisible but highly variable and very flat (in statistical terms platykurtic) distribution.

It is highly unlikely that such a distribution belongs to a single pure race. It could, and probably does, represent sampling from several, perhaps three, closely related races or subspecies, but the only hope of making a separation of any really probable validity would be to obtain several fairly large samples of completely unified origin, each from a single horizon and locality. Such samples are not now at hand and the present situation is that the subspecies cannot be distinguished in any natural way.

It does not follow that they are synonymous, for the fact that they cannot be fully distinguished does not prove that they are the same thing. They may also be convenient conventional designations for the smaller, medium, and larger specimens, respectively, which are felt probably to represent different races even though this cannot be proved. *P. intermedius* is, however, so intimately connected with the others that its status as a separate species can hardly be maintained and if distinguished, it should be referred to as *P. primaevus intermedius.* (Note that it is the smallest, not medium-sized, group in this species.)

A first approach toward an adequate sample is afforded by the Clark Fork phenacodonts. Their origin is not fully unified but their distribution, both geographically and stratigraphically, is much more limited than for the Gray Bull specimens. There are twenty-five specimens in our collection. One of these may be omitted as it consists of scraps of doubtful association some of which are highly aberrant or abnormal. Another specimen is so distinct from the rest (which are rather unified among themselves) that the probability is very great that it is a stray of a different race. Some of the statistical constants for the remaining twenty-three specimens are as follows:

Variate	Number	Observed Range	Mean	Standard Deviation	Coefficient of Variation
L M_1	8	12.2–13.6	12.9 ± 0.2	0.46 ± 0.12	3.6 ± 0.9
W M_1	7	9.8–11.8	10.8 ± 0.3	0.69 ± 0.18	6.4 ± 1.7
L M_2	11	12.2–14.4	13.3 ± 0.2	0.60 ± 0.13	4.5 ± 1.0
W M_2	10	10.4–12.2	11.4 ± 0.2	0.58 ± 0.13	5.1 ± 1.1
L M_3	14	12.2–15.0	13.1 ± 0.2	0.77 ± 0.15	5.9 ± 1.1
W M_3	13	9.2–10.6	9.8 ± 0.1	0.47 ± 0.09	4.8 ± 0.9

For comparison, the constants of one dimension, length of M_2, for the Gray Bull *intermedius – hemiconus – primaevus* group are given.

L M_2	61	10.6–13.8	12.1 ± 0.2	0.96 ± 0.09	7.9 ± 0.7

And the same for *P. robustus:*

L M_2	6	14.4–14.8	14.6 ± 0.1	0.14 ± 0.04	0.9 ± 0.3

This is, on our specimens, the least variable dimension of *P. robustus* but none of its dimension distributions overlaps those of the *primaevus* group and none shows a significantly closer approach to the Clark Fork group.

The difference between the Clark Fork *Phenacodus* and Gray Bull *P. robustus* is certainly significant. The difference between the Clark Fork group and the whole Gray Bull *P. primaevus* group is also certainly significant, that is to say, it would be impossible (for all practical purposes) to take a random sample of eleven specimens of M_2 from the Gray Bull *P. primaevus* and have the mean of their length as large as that for the Clark Fork (and the same is true of the other dimensions). However, it has already been concluded that the Gray Bull specimens probably include several subspecies, and if this is true the largest of these may not be significantly different from the Clark Fork specimens.

The biological conclusion is that the Clark Fork specimens are a nearly or quite homogeneous sample of one subspecies and that this subspecies may occur also in the Gray Bull (in which case it is probably *P. primaevus primaevus*) or may be distinct. These alternatives cannot at present be adequately checked. It seems somewhat more probable that the subspecies is distinct. In any event reference to the species *P. primaevus* is justified.

The aberrant Clark Fork specimen which probably is not of the common subspecies mentioned above is Amer. Mus. No. 16053 and has these dimensions:

M_1		M_2		M_3	
L	W	L	W	L	W
11.0	...	10.8	9.8	11.2	8.7

All these dimensions are distant between two and three times the standard deviation from the mean of the other specimens. This could belong to the smallest Gray Bull subspecies (*P. p. intermedius*), if that is distinct, might (but very improbably) be a variant of the common Clark Fork form, or might be separable from either. It may be listed as *Phenacodus primaevus*, small var. cf. *intermedius*.

Ectocion osbornianus ralstonensis (Granger, 1915)

Granger (1915) recognized four species of *Ectocion*, as follows in order of size:

E. parvus
E. ralstonensis
E. osbornianus
E. superstes

E. parvus is based on a single specimen from the Clark Fork. The next two species were reported from Clark Fork, Sand Coulee, and Gray Bull, with the note that the smaller form is more abundant in the older beds. *E. superstes* is from the Lost Cabin, with two specimens doubtfully referred from the Gray Bull.

Detailed statistical study of the whole collection fully confirms the general sequence as pointed out by Granger, but suggests a slightly different formalization and interpretation.

E. parvus is rather distinctive. It is either a highly aberrant individual or a straggler of another species, and, while it is naturally dubious as long as only one specimen is known, it may be retained as a species, and disregarded so far as study of the more common and typical animals is concerned.

The following grouped distribution is typical of that for all the available variates of *Ectocion* not referable to *E. parvus:*

Length of M_1	Clark Fork	Sand Coulee	Gray Bull	All
5.7–6.0	1	0	0	1
6.1–6.4	6	3	1	10
6.5–6.8	4	4	7	15
6.9–7.2	1	3	2	6
7.3–7.6	0	0	2	2

The number of specimens being rather small, some of the other variates are not so evenly distributed, but none shows deflections that are significant. Neither in any single formation nor in all taken together is there any probable indication that the population is not homogeneous. It is highly probable that only one species is represented and that the specimens called *E. ralstonensis* are simply the smaller and those called *E. osbornianus* the larger specimens of the same species. There is, however, an interesting difference between the samples from successive horizons.

All the data give about the same result. As an example the constants for the length of M_1 are given:

Horizon	Number of Specimens	Observed Range	Mean	Standard Deviation	Coefficient of Variation
Clark Fork	12	5.9–7.1	6.5 ± 0.1	0.32 ± 0.06	4.9 ± 1.0
Sand Coulee	10	6.2–7.2	6.7 ± 0.1	0.33 ± 0.07	5.0 ± 1.1
Gray Bull	12	6.4–7.4	6.8 ± 0.1	0.39 ± 0.08	5.7 ± 1.2

The ranges overlap extensively, but with the passage of time there is a slow increase in the value of the mean. Between successive horizons, Clark Fork and Sand Coulee or Sand Coulee and Gray Bull, the change is not statistically significant[1]—the possibility of its arising from random sampling of a homogeneous population is too great to rely on the difference in itself as real. But between the earliest and the latest populations it is probably significant.

Since the sample from the intermediate horizon is also intermediate in all the means of its variates this association makes it practically certain that the difference here is likewise significant.

Granger clearly brought out this difference when he mentioned the greater abundance of smaller animals in the older beds. It appears extremely probable, however, that instead of there being two species that run through three horizons, the larger slowly increasing and the smaller decreasing in numbers, there is a single species, variable in all horizons but slowly increasing in size with the passage of time. The Lost Cabin *E. superstes*, which is still larger and considerably later, is perhaps the continuation, and end, of the same sequence.

The expression of this relationship in Linnaean taxonomy is necessarily conventional and a matter of personal preference. It is, perhaps, most satisfactory to use the name *E. osbornianus* for the whole phylum and to apply the name *ralstonensis*, as a subspecies, not to the smaller individuals of all horizons, surely an unnatural arrangement, but to the whole ancestral and on the average smaller (and also slightly more primitive in some morphological respects) group from the Clark Fork. This is conventional, as any system that draws boundaries in a continuous series must be, but it is logical and is natural in the sense of grouping together all the various animals that constituted the species at a given time.

This concrete example which seems open to little doubt, suggests that many of the supposed cases of the parallel development, or orthogenetic evolution, of closely allied phyla through several geological horizons may be misinterpretations of conditions similar to these: that in fact only one variable phylum is present and that the several supposed phyla are constructed by selecting variants in the same direction from each horizon and supposing them to form separate series (see Simpson, 1937).

The principal statistical constants of *E. osbornianus ralstonensis* that can be calculated from our material are as follows:

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[1] Tested by Fisher's formula for comparing means of small samples, cited above. Between Clark Fork and Sand Coulee the value of P is between 0.1 and 0.05, for the variate given above. Between Clark Fork and Gray Bull it is less than 0.05.

Variate	Number of Specimens	Observed Range	Mean	Standard Deviation	Coefficient of Variation
L P_4	13	6.3–7.2	6.7 ± 0.1	0.23 ± 0.04	3.4 ± 0.7
W P_4	13	4.2–5.8	4.9 ± 0.1	0.36 ± 0.07	7.3 ± 1.4
L M_1	12	5.9–7.1	6.5 ± 0.1	0.32 ± 0.06	4.9 ± 1.0
W M_1	12	4.9–5.7	5.4 ± 0.1	0.24 ± 0.05	4.5 ± 0.9
L M_2	12	6.1–7.2	6.7 ± 0.1	0.38 ± 0.08	5.3 ± 1.1
W M_2	12	5.1–6.1	5.6 ± 0.1	0.31 ± 0.06	5.5 ± 1.1
L M_3	11	7.1–8.2	7.6 ± 0.1	0.39 ± 0.08	5.2 ± 1.1
W M_3	11	4.6–5.5	5.1 ± 0.1	0.27 ± 0.06	5.3 ± 1.1

Hyopsodontidae

Haplomylus speirianus (Cope, 1880)

This species is abundant in the Gray Bull, uncommon in the Sand Coulee, and rare in the Clark Fork, from which only three specimens are known. I have measured all the sufficiently well-preserved lower jaws in the American Museum collections (forty in all) and have calculated the statistical constants of the most abundant group, those from the Gray Bull. An interesting relationship appears. The Sand Coulee specimens, although their range overlaps (but is not entirely included in) that of the Gray Bull specimens, average smaller, and the difference in size is decisively significant (the chances that such a difference would be due to random sampling of the same race are considerably less than one in a hundred). The three Clark Fork specimens, however, more closely resemble those from the Gray Bull, and not those from the Sand Coulee as one would expect from their ages. They are relatively large, even for the Gray Bull series, but could be three random specimens drawn from the same subspecies or race as that occurring in the Gray Bull. They cannot be exactly the same race as that in the Sand Coulee.

As they bear only indirectly on the characters of the Clark Fork forms, the full data for the Sand Coulee and Gray Bull are not here published, but one variate is given, and the measurements of the Clark Fork specimens:

Length of M_2 in Gray Bull *Haplomylus speirianus:*

Number	Observed Range	Mean	Standard Deviation	Coefficient of Variation
23	2.5–3.1	2.79 ± 0.04	0.19 ± 0.03	6.7 ± 1.0

Clark Fork specimens:

	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
16074	3.4	1.8	2.9	2.4	...	...	...	...
16072	...	...	...	...	3.0	2.6	2.9	1.9
.....	...	...	3.1	2.7	3.0	2.8	...	...

These measurements are all large in comparison with the Gray Bull specimens, lying at or near the observed upper limit for the latter. In the small sample available, they fall just short of statistical significance.[1] If several more Clark Fork specimens were found and these were also large, the probability of a real difference would be sufficiently great to warrant separating these early individuals as a large race or subspecies, but of course this possible or probable future discovery cannot be anticipated.

PANTODONTA

Coryphodontidae

Coryphodon sp.

The principal evidence of *Coryphodon* in the fauna is a single specimen, No. 16078, which includes $P_3 - M_3$, P^{2-4}, and an upper molar. The teeth are very badly preserved and no specific determination is possible.[2] They do, however, demonstrate that the genus is *Coryphodon* and not *Titanoides* or *Barylambda.*

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[1] By Fisher's t test the dimensions of M_{1-2} give P in the neighborhood of 0.1 or (length M_1) less, but all greater than 0.05. Individual deviations from Gray Bull means are up to 1.9 times (for the length of P_4) the standard deviation of the latter. Taken together, and with their association with age, the differences on these data are possibly significant, but with probability not quite great enough to be accepted as reliable.

[2] The genus is furthermore in need of revision and the true characters of its species are not understood.

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