

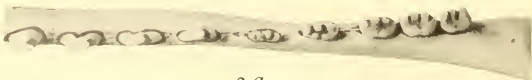
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JAWS OF MYRMECOBOIDES AND MYRMECOBIUS.

FOR EXPLANATION OF PLATE SEE PAGE 395.

AN EXTINCT MARSUPIAL FROM THE FORT UNION WITH
NOTES ON THE MYRMECOBIDAE AND OTHER FAMILIES
OF THIS GROUP.

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In a small lot of Fort Union mammals recently collected by Mr. A. C. Silberling in Sweet Grass County, Montana, there is a lower jaw which, though small in size, is of great importance, since it apparently represents an unexpectedly early appearance of a possible relative of the Myrmecobidae a family of marsupials hitherto known only from a single living genus, *Myrmecobius*. The description given below is followed by a brief discussion of the peculiar features of the species, its possible affinities, and some short notes on the probable derivation of the marsupials in general.

MYRMECOBOIDES, new genus.¹

This genus, represented by a single species of small size, may be distinguished as follows: Canine semipremolariform, being irregularly triangular in cross section and but slightly curved; canine and the three simple premolars evenly spaced with short intervening diastemata. There is also a short diastema between the canine and i_3 (the position of the other incisors is not known). Fourth tooth behind the canine (probably dp_4 retained) completely molariform; true molars tritubercular, with well-developed basin heel, but with inner cusps of trigonid (paraconid and metaconid) as high or higher than main outer cusp (protoconid).

Ordinal affinities of this genus marsupialian, and it is probably related to the *Myrmecobidae*.

MYRMECOBOIDES MONTANENSIS, new species.

PLATE 23.

Type-specimen.—(Cat. No. 8037, U.S.N.M.). A left lower jaw carrying a series of 8 teeth, c to m_3 . Collected by A. C. Silberling.

Type-locality and horizon.—Sweet Grass County, Montana, "Gidley Quarry," about the middle of the Fort Union deposits of that locality.

¹ This name is given to the ancient form on account of its likeness to *Myrmecobius* rather than as a positive assumption of real relationship.

Description.—Dental formula: $i_2^1, c_1^1, pm_3, dp_1, m_3$. Jaw relatively long and slender; length of tooth series, including canine and m_3 , 20 mm.; depth of jaw at c , 2.5 mm.; at m_2 , 3.7 mm. P_1 single rooted but compressed laterally and with small posterior heel; p_2 and p_3 with anterior cusp budding off from the main cusp and a posterior basal cusp (p_3 is somewhat larger and has slightly more prominent accessory cusp than p_2); dp_4 completely molariform with the metaconid and protoconid subequal in size, but otherwise differing from the true molars in the somewhat narrower and smaller heel and in the position and relatively larger size of the paraconid which is a well-developed, anteriorly directed cusp quite distinct from the metaconid. All the molars have low, basin-like heels with relatively high inner cusps and high trigonids in which the metaconids and paraconids are closely appressed, forming a column which exceeds the protoconid in height and equals it in bulk. The paraconid, though close to the metaconid, is quite distinct at the summit. The entoconid is an irregularly rounded and pointed cusp showing on the inner side a tendency to split into two cusps.

Possible affinities and comparison with Myrmecobius.—The little Fort Union mammal jaw described above presents some interesting features. While these can not be interpreted with absolute finality, or with more than a limited degree of certainty, because of the great time interval between the Paleocene and the present day, and the absence of known intermediate forms, the specimen nevertheless strongly suggests relationship to the Myrmecobidae, as now represented by the single living species *Myrmecobius fasciatus*. Making due allowance for its more primitive condition, this lower jaw, aside from its fewer teeth, resembles that of *Myrmecobius* in a marked degree. The special points of resemblance (see plate 23) are these: (1) The jaw is elongated anterior to the four molariform teeth and has a well-marked but short diastema between each of the premolars, the first premolar and the canine, and the canine and last incisor. The jaw is broken at the latter point and none of the incisors is preserved, but enough remains to show (2) that the jaw extended straight forward from the canine and probably carried spaced incisors as in *Myrmecobius*. (3) The canine is laterally compressed and semi-premolariform, and the manner in which it is set into the jaw also resembles a premolar. (4) Premolars 2 and 3 are narrow transversely and long at the base, with well-developed anterior cusps budding out from the main cusps, high above their bases, as in *Myrmecobius*; p_1 is small and single rooted, though laterally compressed like the others. (5) All the teeth are entirely without cingula. (6) The inner main cusps (metaconid and entoconid) of the molars are apparently developing toward conate forms, while they equal or exceed the two

main outer cusps (protoconid and hypoconid, respectively) in height. The relatively small size of the latter, and especially the protoconid, which is apparently diminishing, is a modification toward the condition reached in *Myrmecobius*, and away from the usual development of primitive tri-tuberculate teeth. In fact, all these characters denote progressive development away from the type characteristic of the primitive insectivores, carnivores, and creodonts, and toward *Myrmecobius*.

A point of difference is the very close approximation of the paraconid to the metaconid. Although quite distinct at the summit, the paraconid forms a part of the elevated metaconid column. In *Myrmecobius* this cusp is usually distinct and directed forward but as pointed out by Dr. B. Arthur Bensley¹ in his valuable contribution on The Evolution of the Australian Marsupialia, the dentition in the living genus is exceedingly variable in detail. One of the two specimens in the U. S. National Museum collection shows a much closer approximation to *Myrmecoboides* in this respect than does the other; hence it is possible that the more anterior position of the paraconid in *Myrmecobius* may have been secondarily acquired as a result of the extreme lengthening of the jaw. Another point of difference between the living and the extinct forms is the relatively greater elevation and better definition of the trigonid in the latter. This, however, is doubtless due to its more primitive condition.

The first molariform tooth in *Myrmecoboides montanensis*, which stands in the position of p_4 , is worthy of special notice. It differs in some important features from those behind it, but is so typically and completely molariform as to suggest a true molar or more probably a tooth of the deciduous series. However, it is not possible to say in the absence of proof whether it may not be after all a highly specialized molariform premolar. Its very complex structure in contrast with p_3 , which is a simple, unspecialized tooth, is against this supposition and strengthens the view that it is more probably a retained milk molar. Special features of the tooth itself favor this conclusion and seem to preclude the other alternative of considering it also a true molar. It has the same number of cusps as the molars, and these, with the exception of the paraconid, have the same general form, proportions, and arrangement. The crown is proportionally narrower, the talonid is relatively smaller, and the large paraconid is directed well forward, making up the whole anterior portion of the trigonid, and is quite distinct. In this respect this tooth differs markedly from the true molars.

It thus appears that in this specimen we have real evidence confirming the view held by Winge and supported by Lydekker, Bensley, and others that the first molariform tooth in all the marsupials is a

¹ Trans. Linn. Soc. London, ser. 2, Zool., vol. 9, pt. 3, 1903, p. 102.

fourth milk molar which is never replaced by a premolar as in the placentals. The development of a fourth molariform tooth and the loss of a premolar, however accomplished, must be considered one of the earliest specializations of the marsupials since this reverse tooth formula is characteristic of the entire group.

An apparent objection to considering the Fort Union species as in any way related to the ancestral line which gave rise to *Myrmecobius* is the fact that it possesses only the normal number of post-canine teeth, namely, seven, while *Myrmecobius* has eight or frequently nine in the lower jaw. The importance of this difference however, depends entirely on the source of the supernumerary teeth in *Myrmecobius*. If this characteristic is an ancient survival resulting from the derivation of *Myrmecobius* from some one of the Jurassic mammal-like forms having more than the normal number of post-canine teeth, as suggested by Owen, Thomas, Leche, and others, then such a form as *Myrmecoboides* could not be placed in the line of descent. But if, on the other hand, as seems more probable, the increase in number of teeth in *Myrmecobius* came about secondarily through the permanent retention of deciduous premolars, as suggested by Winge, there is nothing inconsistent in considering the Montana species an ancestral relative of the later genus. A significant point in this connection is the fact that in the *M. montanensis* jaw the longest diastema is between p_3 and dp_4 .

ADDITIONAL NOTES ON THE ORIGIN OF MYRMECOBIUS.

There is in our present knowledge nothing to support Owen's hypothesis regarding the derivation of *Myrmecobius*. On the other hand, as has been pointed out especially by Bensley,¹ there is considerable evidence for, and a reasonableness in assuming that this genus has, like the other marsupials, descended from an ancestral form with a normal primitive marsupial dentition. In consequence of its ant-eating habits, resulting in the modification of the entire series as well as the great lengthening of the jaws anteriorly, the condition was acquired whereby a second and finally a third additional tooth of the remaining milk series were retained permanently, in the manner suggested by Winge.

The dental characters of the genus *Myrmecobius* have been very fully described and discussed and the literature on the subject reviewed by Bensley. Hence it is not necessary to enter into much detail here. A few additional points suggest themselves, however, and some of those advanced by Bensley and others are seemingly somewhat altered by a restudy of the lower jaw of *Myrmecobius*, when comparing it with the Montana specimen. While not entirely disregarding the theory advanced by Winge, Bensley

¹ Trans. Linn. Soc. London, ser. 2, Zool., vol. 9, pt. 3, 1903, p. 102.

seems rather to favor the view that the excessive number of molars in *Myrmecobius* is due to "a simple reduplication of teeth from the posterior portion of the dental lamina," the minute size of the molars and the great lengthening of the jaws offering just the conditions favorable for an intercalation of new teeth. In defense of this he observes that "even assuming a retention of the deciduous teeth, we would still have to account for the occasional presence of an additional lower molar."¹ The application of this observation, however, is not clear, since, beginning with the normal marsupial dental series, viz., p_3, dp_1, m_3 , it requires but the addition of two more permanently retained deciduous molars to equal the greatest number of post-canine teeth found in this species, namely, 9, making the dental formula for the lower jaw as follows: $i_3, c_1, p_3, dp_3, m_{2 \text{ or } 3}$. This would still leave two teeth less than the normal combined number of the milk and permanent series of post-canine teeth found in both the marsupials and placentals, the missing ones being dp_1 of the first series, probably very early shed or never replaced, and p_4 of the permanent premolar series, either early absorbed or never developed. The variability in the molar series in *Myrmecobius* seems due to the presence or absence of the last molar, probably a disappearing tooth. In the upper jaw the last molar seems to be normally wanting, while the second is apparently in the process of disappearing, being sometimes present and sometimes wanting. There is also an occasional variation in the number of milk molars retained, the upper jaw of a specimen in the United States National Museum collection having two such teeth on one side and only one on the other.

However regarded, the teeth of *Myrmecobius*, as pointed out by Blesley, show every indication that the genus was derived from a primitive form with normal tritubercular teeth of the general insectivorous type. The present specialization is toward a pseudotricodont type, evidently acquired through the peculiar development of the inner and the atrophy of the outer cusps of the lower molars, with a similar but reverse modification of the upper molars, with the addition to the series of supernumerary teeth accomplished through the retention of milk molars. Conceding this to be the true history of the development of *Myrmecobius*, the little lower jaw from the Fort Union formation, whether considered ancestrally related or not, is morphologically intermediate in nearly every particular between such a jaw as that of *Myrmecobius* and those of the generalized primitive types of trituberculate mammals. It stands nearer to the tritubercular form, it is true, but is nevertheless intermediate in development,

¹ Trans. Linn. Soc. London, ser. 2, Zool., vol. 9, pt. 3, 1903, p. 100.

and if regarded as ancestral furnishes very good evidence against the earlier supposition that *Myrmecobius* is a direct and little-changed descendant of some one of the Jurassic mammal-like forms having more than the normal number of teeth. It is indeed very doubtful whether the latter gave rise to any of the higher mammals, and such forms as *Dryolestes*, *Dicrocynodon*, *Tinodon*, etc., of the Jurassic, with their many post-canine teeth, were probably not marsupials at all. A recent restudy of these ancient forms leads me to believe that there are good reasons for regarding them rather as monotremes, and in this group may possibly be found the early representatives of the living members of this strange order of mammals.

In considering the derivation of the marsupials and placentals it must not be overlooked that regardless of the origin of the fourth molariform tooth in the marsupials the normal number of post-canine teeth of primitive or generalized forms in both groups is invariably seven, any deviation from this number being due to a loss or addition through specialization. The obvious inference, then, is that the common ancestral forms from which these great groups were originally derived had a like normal dental formula. Such a genus, therefore, as *Triconodon*, or some other form having four premolariform and three molariform teeth behind the canine, would be a more logical Jurassic ancestral type for the higher mammals than would such forms as *Dryolestes*, *Dicrocynodon*, etc., which have many more than the normal number of both premolariform and molariform teeth. The ultimate origin of these great groups is, however, at best largely speculative with our present knowledge.

NOTES ON THE ORIGIN OF THE MARSUPIALS.

From expressing disbelief in Owen's hypothesis regarding the origin of *Myrmecobius*, Bensley seems to have gone to the other extreme in suggesting the derivation of all the living marsupials from an Oligocene form (*Peratherium*) of the Didelphidae. Osborn¹ seems to have adopted this view also, while Gregory² in his recent contribution on The Orders of Mammals, seemingly accepts Bensley's views in general but gives much greater antiquity to the ancestral stock of the marsupials. I can not regard Bensley's view as wholly tenable, even if the didelphid prototype were carried to a much more remote time than the Oligocene. If the Fort Union mammal here described, whether directly ancestral or not, is in any way related to the living *Myrmecobius*, we have evidence that the Myrmecobidae had at least reached a marked degree of specialization which separated this family distinctly from the other marsupials at a much earlier date than is assumed by Bensley for the differentiation of the whole order. Even

¹ Evolution of the mammalian molar teeth. Biol. Studies and Addresses, vol. 1, 1907, p. 109.

² Orders of Mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, 1910, p. 229.

at this early period (Paleocene) there is no evidence of a close similarity to a didelphid type of dentition, nor is there a suggestion of any particularly close affinity to the dasyurids, which are considered by Bensley to be direct derivatives of the early didelphids, as represented by *Peratherium*. It is obvious that if the Myrmecobidae had a beginning so very much earlier, as is indicated by the Fort Union specimen, so likewise must the Dasyuridae and probably all (certainly some) of the other living families of marsupials.

This conclusion also is not in accordance with the view expressed by Osborn¹ regarding the origin of marsupials of Australia, which he suggests were derived from the "introduction into Australia of some small arboreal opossum of *Didelphys*-like form as the source of the wonderful adaptive radiation of the marsupials of this continent." The fossil evidence at present available, as I interpret it, does not apparently support either Osborn's or Bensley's view concerning the origin of the modern families of marsupials, nor in reality does it give more than a small part of the life history of this great order of mammals. In fact, it seems reasonable to assume that at present nothing is definitely known regarding the ancestry of several of the living marsupial families, including probably all the diprotodonts,² because they are not represented in our collections from beds older than the Pleistocene, and that in the known fossils we have only an incomplete and indefinite history of the origin and development of a part only of the polyprotodonts. Thus it seems from the paleontological evidence we are at present not justified in assuming more than that the Didelphidae only are represented in such forms as *Peratherium* (Oligocene), *Proteodidelphus* (Paleocene?), and possibly *Didelphops* of the Lance formation. The Myrmecobidae are presumably represented by *Myrmecoboides* of the Fort Union (Paleocene), while *Dasyurus* and possibly the Peramelidae may have been derived with the Didelphidae from differing forms of the *Didelphops* (Lance) group. The Thylacinidae and Caenolestidae are apparently not known from fossils older than the Miocene where they had reached almost their present state of specialization.

Such a view, I am aware, assumes a vastly more ancient origin for all the living families of marsupials than has hitherto been held for them while it must be conceded that the greater part of their evolutionary development remains practically unknown.

In the early attempts of vertebrate paleontologists to read the life-history of the globe as recorded by the fossil animal remains, it appears to have been too often assumed that the known fossils of a few widely scattered localities told the greater part of the whole story of the

¹ The Age of Mammals, 1910, p. 78.

² The Caenolestidae have been placed in this great group apparently on the diprotodont-like development of the lower jaw. However, this may be an entirely independently acquired character. This family more probably belongs with the Polyprotodonts.

origin and development of the great groups of animals which have inhabited the earth, sufficient account not having been taken of the great number of chapters which are as yet unsupplied by the discoveries of collectors. Thus, in the genus *Phenacodus* from the Wasatch, Cope at one time believed he had discovered a generalized type from which had originated all the Perissodactyls. It is now known, however, that this great group probably had a very much earlier beginning, and it was not derived, at least, from any of the known condylarths. This is one of numerous instances in which too broad or sometimes obviously false generalizations have been made by investigators in their search among the incomplete fossil records for ancestral forms, and in their attempts at working out lines of descent. Even to-day a strong tendency toward this method of reasoning seems to prevail among paleontologists. It is usually assumed, in a general way, that the earliest-discovered recognizable representatives of a group indicate the actual first appearance of that group among the faunas of the earth, and the absence of fossil remains of a group in the known collections is usually treated as indicating its nonexistence. Such assumptions, while in great part excusable perhaps, have nevertheless resulted in the assigning of a much too recent date for the origin and differentiation of most, if not all, of the living orders and families of mammals, and doubtless have caused much of the confusion and disagreement that now exists among authorities in working out correlations and phyletic lines of descent. Many instances might be given in which recent discoveries have corrected errors of this kind, the tendency being to carry periods of origin further and further back in time. Thus, group after group when studied in the light of our increased knowledge is seen to have a much earlier beginning than was assigned it a few years ago. The archaic aspect of the Paleocene fauna is frequently spoken of, but such specimens as the one here described, and others of similar character from the Fort Union beds, make it seem probable that the very ancient appearance of the known faunas of the Paleocene may be attributed in a marked degree to the fact that our collections are representative of limited facies and do not happen to contain many forms, doubtless living elsewhere at the time, which if present would give a far more modern aspect to the fauna of this age. The known Paleocene faunas are from relatively small areas, and these of a comparatively uniform environment (probably in greater part forest and swamp); hence it may well be that the greater number of the then existing ancestors of living groups are yet unknown.