UNIVERSITY OF KANSAS PALEONTOLOGICAL CONTRIBUTIONS
VERTEBRATA, ARTICLE 5, PAGES 1-15, PLATES 1, 2, FIGURES 1-11

SKULL AND SKELETON OF A MUSTELID, *BRACHYPSALIS*, FROM THE MIOCENE OF NORTHEASTERN COLORADO

By EDWIN C. GALBREATH [1]

CONTENTS

ILLUSTRATIONS

ABSTRACT

Skull, jaw and parts of the postcranial skeleton of *Brachypsalis modicus* MATTHEW from ?upper Miocene deposits in northeastern Colorado show this mustelid to be structurally less advanced than the small mustelids and different from the large, heavy-skulled, heavy-limbed, contemporary mustelids of the middle part of the Tertiary. A close relationship, but not direct descent, seems to exist with *Oligobunis* and *Paroligobunis*. The skull is intermediate between those of the early canoids and the Recent mustelids, being somewhat procyonid-like. The known parts of the postcranial skeleton resemble those of large Recent mustelids (especially *Gulo*) and show that the genus was subplantigrade in gait and light-limbed.

INTRODUCTION

In the summer of 1949 I collected a skull, right jaw, and fragments of the postcranial skeleton of *Brachypsalis modicus* MATTHEW from silts judged to be early Barstovian in age. Although slightly crushed and distorted, the skull is practically complete except for the loss of part of the occipital bone which was exposed. The right lower jaw was articulated with the skull. Two deciduous teeth and the left M^2 were loose in the matrix. The postcranial skeletal parts consist of limb and foot bones. Because of the friable nature of the bone, the compactness of the silt, and the occurrence of the find high on the face of a vertical cliff, several bones suffered damage during removal. Despite the damage and the immaturity of the individual, this specimen represents the best material yet assigned to any of the species of this genus.

I am indebted to Drs. E. RAYMOND HALL and ROBERT W. WILSON of the Museum of Natural History at the University of Kansas for facilities that made the study of this specimen possible. In appreciation of these many kindnesses I have presented the material to that institution.

In this paper the references to carnivores by their generic names alone are to the following named species: *Canis latrans* SAY (for example, adult, no. 156-361); *Procyon lotor* (LINNAEUS) (young and adult specimens); *Gulo luscus* (LINNAEUS) (skull of adult; skeleton otherwise of young to subadult and adult); *Lutra canadensis* (SCHREBER) (subadult); and *Taxidea taxus* (SCHREBER) (adult from NE Colorado). I am indebted to Dr. HALL for determining the ontogenetic age of these specimens.

1. Department of Anatomy, University of Kansas.

DESCRIPTION

ORDER CARNIVORA BOWDICH, 1821

FAMILY MUSTELIDAE SWAINSON, 1835

GENUS BRACHYPSALIS COPE, 1890

Brachypsalis modicus MATTHEW

Brachypsalis modicus MATTHEW, Bull. Am. Mus. Nat. Hist., vol. 38, art. 7, p. 195, fig. 4,5, April 18, 1918.

Referred material.—Skull, right jaw, fragment of ilium, three caudal vertebrae, humerus, ulna, radius, femur, patellae, tibia, fibula, tarsal bones, metatarsal bones and phalanges; all a part of one individual from SW ¼ Sec. 26, T. 12 N., R. 55 W., Logan County, Colorado (University of Kansas, Museum of Natural History, no. 9,903).

Geological age.—The geological age is Miocene, probably early Barstovian but possibly late Barstovian. Less likely, but not ruled out, is a Hemingfordian age. This specimen was found in bed No. 2 of measured section II of GALBREATH (1953, p. 22). In the same paper, on page 27, fig. 8, under the column headed Sand Canyon, the Miocene deposits marked by a question mark are the beds from which this specimen was collected.

General characters.—The species called *Brachypsalis modicus* is a large mustelid, approximately the size of *Gulo* and probably much like it in general appearance, but more primitive and different in structure (Pls. 1, 2; Figs. 1-11). The snout is slightly shorter than in most canids and the cranial region is expanded but less so than in *Gulo* or *Taxidea*. In lateral aspect the skull seems "high-browed," almost certainly because of its immaturity. The fore- and hind-limbs are probably lighter than those of *Gulo* but damage and immaturity limit any description or discussion of these elements. The incomplete nature of the limb bones has been summarized in Table 1. Because certain dimensions (mostly measurements not involving the ephyseal endings) are close to those of *Gulo*, I have figured the limb bones of our specimen in association with the corresponding bones in *Gulo* (Pl. 2). In this way the proportions and size of the parts that are preserved may be appreciated. The following detailed descriptions of the individual bones are strictly attempts to depict the appearance of the various parts by using well-known common carnivores for comparison and without regard to phyletic relationship.

Nasal.—Both nasal bones are present, although damaged at the anterior and posterior ends. The shape is close to that of *Canis*, except for relatively greater width of the fossil bones. Despite damage to the anterior end, the anterior border probably was not emarginate medially. The shape of the frontal and maxillary at their junction with the nasal bone suggests that the posterior end of the nasal did not differ from that in *Canis*. More certainly, the posterior end was not wide and relatively blunt, as in *Procyon*, nor narrow and sharply pointed, as in *Taxidea*.

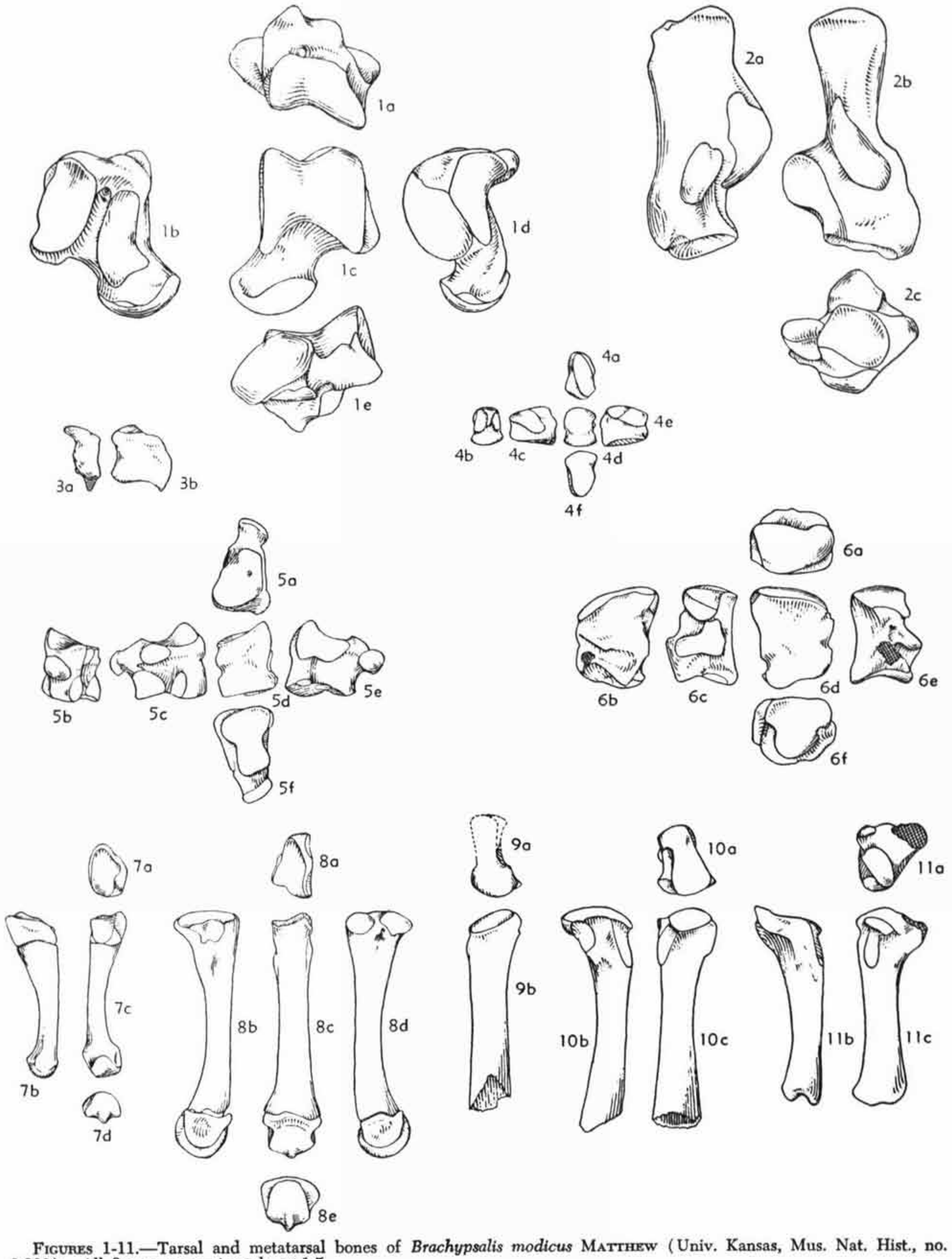
Premaxillary.—The alveolar part of this bone is foreshortened, as in *Procyon*. The ascending ramus, which has about the same massiveness as that in *Procyon*, arises almost vertically from the base of the bone. Dorsally, the ascending ramus turns back, tapering rapidly to form a spine that terminates above the canine, thus being shorter than the spine seen in *Canis* or *Procyon*. The suture between the premaxillary and maxillary on the palatal surface is between the canines. The incisive foramina are small and elongate (Table 2) and are completely enclosed by the premaxillary.

Maxillary.—The maxillary bone is intermediate in appearance between that of *Procyon* and *Canis*. The major feature of the external surface is the relatively long low-placed infraorbital canal. In this feature the maxillary is more nearly like that of *Gulo* or *Canis* and unlike that of *Procyon, Taxidea,*

TABLE 1. *Summary of the preservation of the post-cranial skeleton of Brachypsalis modicus Matthew (Univ. Kansas Mus. Nat. Hist. no. 9,903).*

Right ilium, fragment showing sacral attachment scar.
Vertebrae, centra preserved (possibly of first three caudals).
Right humerus, proximal end not preserved; distal end damaged and fragment of articular surface preserved but not in contact with shaft.
Right ulna, distal end and olecranon missing.
Right radius, complete.
Left fifth metacarpal, distal epiphysis preserved.
Right femur, shaft damaged; fragment of greater trocanter preserved.
Right tibia, posteromedial fragment of proximal epiphysis detached and damaged; shaft damaged.
Left tibia, distal epiphysis preserved.
Left fibula, distal epiphysis and fragment of shaft preserved.
Right and left patellae, complete.
Left calcaneum, lacks epiphysis.
Left astragalus, complete.
Left cuboid, complete.
Left ectocuneiform, complete.
Left mesocuneiform, complete.
Left entocuneiform, complete.
Left navicular, damaged.
Left metatarsal I, complete.
Left metatarsal II, complete.
Left metatarsal III, distal end missing.
Left metatarsal IV, distal end missing.
Left metatarsal V, distal epiphysis missing.
Left proximal pedal phalanges [a] no. 3 complete, nos. 1, 2, 4, and 5 without proximal epiphyses.
Left medial pedal phalanges [a] no. 2 complete, nos. 3, 4, and 5 without proximal epiphyses.
Left distal pedal phalanges [a] nos. 3, 4, and 5 present but damaged.

[a] The left pedal phalanges were found in association with the other bones of the hind foot but not in articulation. The identification of these elements was made on the basis of similarity to the bones in the foot of the badger.



FIGURES 1-11.—Tarsal and metatarsal bones of *Brachypsalis modicus* MATTHEW (Univ. Kansas, Mus. Nat. Hist., no. 9,903). All figures approximately × 1.5.

1, Left astragalus. *a*, Posterior view; ***b*, plantar view**; *c*, dorsal view; *d*, lateral view; ***e*, anterior view.**

2, Left calcaneum. *a*, Medial view; *b*, dorsal view; *c*, anterior view.

3, Left entocuneiform. *a*, Plantar view; *b*, medial view.

4, Left mesocuneiform. *a*, Proximal view; *b*, plantar view; *c*, medial view; *d*, dorsal view; *e*, lateral view; *f*, distal view.

5, Left ectocuneiform. *a*, Proximal view; *b*, plantar view; *c*, medial view; *d*, dorsal view; *e*, lateral view; *f*, distal view.

6, Left cuboid. *a*, Proximal view; *b*, plantar view; *c*, medial view; *d*, dorsal view; *e*, lateral view; *f*, distal view.

7, Left metatarsal I. *a*, Proximal view; *b*, medial view; *c*, dorsal view; *d*, distal view.

8, Left metatarsal II. *a*, Proximal view; *b*, medial view; *c*, dorsal view; *d*, lateral view; *e*, distal view.

9, Left metatarsal III. *a*, Proximal view; *b*, dorsal view.

10, Left metatarsal IV. *a*, Proximal view; *b*, medial view; *c*, dorsal view.

11, Left metatarsal V. *a*, Proximal view; *b*, medial view; *c*, dorsal view.

or *Lutra*. The anterior end of the canal is completely enclosed by the maxillary bone. The orbital opening of the canal is a pit and groove, like that in *Gulo* but not so deep or so pronounced. The maxillary makes up part of the anterior border of the orbit; the place of the maxillary in the orbital rim is further commented on in discussion of the lacrimal.

In the present crushed condition of the fossil, it is difficult to judge accurately the width of the palate. Although the palate is not so wide as long, probably it was relatively wider than the palates of *Procyon, Taxidea*, or *Canis*. The palato-maxillary suture seems to be bowed and extended forward to the anterior end of the P_4, like that of *Canis*.

Lacrimal.—Insofar as can be ascertained, the lacrimal forms a small part of the interorbital wall, no more than the posterior wall of the lacrimal foramen, and little, if any, of the anterior border of the orbit. This condition is closest to that in *Taxidea*, the greatest difference between the two being the more circular shape of the lacrimal in *Brachypsalis*.

The relationship of the lacrimal, maxillary, and jugal bones in the orbital rim is probably best understood by visualizing a change in primitive to more advanced carnivores wherein the lacrimal is becoming smaller in the orbital rim, the maxillary is making up more of the rim and, in turn, is being encroached upon by the jugal and frontal bones. *Brachypsalis* occupies an intermediate position in this transition where there is less encroachment by the jugal, the maxillary having a place in the orbital rim, as in *Gulo*.

Jugal.—The jugal is relatively as heavy as in *Gulo* and as in *Gulo*, the anterior arm (maxillary process) forms no more than the ventral border of the orbit. The postorbital process is distinctive in that it is extraordinarily long and well developed, exceeding in size those of *Canis, Procyon, Taxidea*, and *Gulo*. The posterior arm (squamosal process) extends back almost to the glenoid fossa but does not arch upward, thus resembling the arm in *Gulo*.

Palatine.—The palatine bones are cracked and distorted, making it impossible to determine location of the bordering sutures definitely. As already mentioned, the suture between the palatal process of the palatine and the maxillary is bowed forward. Posteriorly, the ventral palatal processes extend the roof of the palate back to a point midway between the last molars and the auditory bullae—a feature seen in procyonids, mustelids, and viverrids, but not in canids. Seemingly, the size and extent of the orbital process is close to that in *Taxidea* or *Gulo*.

Pterygoid.—Both pterygoid bones are damaged, but there is no evidence that they differ to any extent from those of *Taxidea* or *Gulo*.

Presphenoid.—The presphenoid is crushed. Nothing can be determined about this bone, other than that probably it was similar to the presphenoid in *Taxidea*.

Alisphenoid and *orbitosphenoid*.—The alisphenoid is basically as in *Taxidea*. The swollen braincase gives an inflated appearance to the ascending wing of this bone and causes the orbitosphenoid and areas adjacent to the alisphenoid to appear recessed, as in *Procyon* or *Gulo*. However, each side of the skull is badly damaged in this area; therefore, a more exact description must await the discovery of better material.

Basisphenoid.—The basisphenoid resembles that of *Procyon* in all respects except for the presence of a heavy median ridge on the ventral surface, as in *Gulo*. The part that the basisphenoid plays in roofing over the eustachian tube and the median lacerate foramen is discussed in the section on the auditory bulla.

Frontal.—The frontals are damaged in the interorbital areas and along the margins. The brow has a bulged-out or expanded appearance like that to some extent seen in *Procyon*, although some of this expansion is probably due to immaturity of the specimen. The postorbital process is developed as in *Gulo* and more than in *Taxidea* or *Procyon*. The anterior end of the frontal is damaged, but it seems to have nearly the same shape as the frontal of *Procyon*. The part of the frontal extending into the orbital area seems to be about the same as in *Taxidea*. The posterior border of the frontal resembles that in *Taxidea* or *Procyon*.

Parietal.—The parietals are damaged and somewhat distorted. With exception of a greater development of the parieto-occipital crest, where the posterior border is turned outward to form a definite ridge like that seen in *Procyon*, the parietal resembles that of *Taxidea* in practically all respects, being short anteroposteriorly, expanded posterolaterally, similar in pattern of union with neighboring bones, and having a parieto-squamosal nutrient foramen.

Occiput.—The occiput is severely damaged. The part of the occipital condyle present shows a greater resemblance to the condyle of *Gulo* and *Procyon* than to that of *Canis* or *Taxidea*. The rear of the occiput seems to be relatively smooth. The basioccipital has a weak ridge like that of *Gulo* or *Procyon*. There is some evidence that the bone was perforated between the ridge and the condyles. The anterior condylar foramen opens as a large pit, as in *Taxidea*, and is not directed anteriorly, as in *Procyon* and *Canis*.

Fortunately, the paraoccipital process is preserved on both sides. It is canid-like, only heavier and more expanded at the free posterior border. The tip is not hooked, as in adult *Taxidea* or *Procyon*. The part of the process abutting against the bulla is spread out, as in *Canis*, and viewed ventrally, it has a dumbbell outline, the ridge being constricted between the tip and the part adjacent to the bulla. The mastoid extends backward so as to jut against the lateral border of the paraoccipital, from the bulla nearly to the posterior tip.

Squamosal.—The squamosal is like that of *Taxidea* except for outward extension of the lateral border which turns up to form a lip above the glenoid fossa, external auditory meatus, and mastoid process, thus making a trough between the lip and cranial wall of the squamosal. This trough has its closest counterpart in the Recent bears and, to a less extent, in *Hemicyon* and *Tomarctus*. The posterolateral part of the "lip" (*i. e.* that part of the squamosal that rests on the mastoid process) is more horizontal than in *Taxidea*. Although now missing, an elongate flat bone was wedged between the tips of the mastoid process and the border of the squamosal. This accessory center of ossification is common to the Ursidae, Procyonidae, and Mustelidae.

The glenoid fossa is relatively larger than in *Procyon*, *Taxidea*, or *Canis*. There is only the faintest suggestion of an anterior lip and certainly nothing similar to that of *Gulo* or *Taxidea*. On the other hand, the posterior lip is strong and wide, with greatest development at the median end. Unlike that of most carnivores used here for comparison, it is not sharply reduced at the midpoint of the fossa but, instead, slopes gently upward to the outer border of the fossa.

Mastoid.—The mastoid is flat and uninflated. It projects laterally below the squamosal, as discussed above. Posteriorly, the mastoid extends upward between the occiput and parietal, being truncated at the top, as in *Taxidea*, rather than pointed, as in *Gulo*, *Procyon*, or *Canis*. The relationship of the mastoid to the tympanic is discussed in the section on the auditory bulla.

Auditory bulla.—The auditory bulla is deep and broad. Its size in relation to that of the skull is intermediate between *Taxidea* and *Procyon*. The longitudinal axis of the bulbous part is directed anteromedially and posterolaterally. In general shape the bulla is like that of *Taxidea* and *Procyon* but with the external auditory meatus placed farther forward. The specimen has undergone some distortion, making uncertain how far the bulla overlapped medially onto the basioccipital and basiphenoid bones. On the other hand, the bulla was not recessed, as in *Gulo*.

Anteriorly, the bulla is in contact with the posterior lip of the glenoid fossa and seems to crowd at one point onto the process. The postglenoid foramen lies in a recessed notch anterior to the opening of the external auditory meatus. The large median lacerate foramen (or canal) and anterior opening of the eustachian tube lie in the dorsal anteromedial angle of the bulla.

Medially, the median lacerate foramen is bordered by a long process that projects anteromedially onto the basisphenoid. A reduced styliform process and a ridge on the sphenoid (probably the alisphenoid) separate the foramen and eustachian tube dorsally but the ventral part of this barrier is retracted so that separation is not carried completely out to the margin of the bulla.

Anterolaterally, a well-developed process borders the eustachian tube and (although I cannot be sure) the Glaserian fissure seems to open next to this process. The sphenoid (probably the alisphenoid) provides the roof for the anterior end of the eustachian tube and the part of the canal anterior to the anterior carotid foramen. More posteriorly, the carotid canal is roofed over by the bulla, but there is no evidence that any part of the eustachian tube is similarly covered.

The posterior carotid foramen lies anterior to the posterior lacerate foramen and is approximately 4 mm behind the transverse midline of the bulla. The posterior lacerate foramen has an elongate tear-shaped outline, with the tapering anterior part extending forward toward the posterior carotid foramen; it occupies a topographic position at the rear of the skull similar to that seen in *Procyon*.

The extreme rear part of the bulla abuts firmly against the paroccipital process. Posterolaterally, that is to say behind the external auditory meatus, the bulla is completely fused with the squamosal bone. Medially, but lateral to the paroccipital process, the boundary between the bulla and the mastoid process is marked by a groove, the walls of which are formed by the bulla anteriorly and the mastoid posteriorly. This groove extends posteromedially across the mastoid process behind and above the expanded rear of the bulla and leads into the area, mentioned in the preceding sentence, where the mastoid and bulla are unfused. The stylomastoid foramen lies at the medial end of this groove and, seemingly, is formed on three sides by the mastoid and by the tympanic anteriorly. Internally, the foramen opens above the posteriorly facing cochlear fenestra.

As regards the stylomastoid foramen and the manner in which the facial nerve leaves the tympanic cavity, I cannot see any difference between this specimen, *Procyon*, and *Taxidea*, except that the amount of tympanic bone involved and its compression against the pterotic and mastoid is greater in *Taxidea*. Because the tympanic is not compressed tightly against the pterotic and mastoid in *Brachypsalis*, this area seems to be more like that in *Procyon*.

The tubular meatus is long, oval in cross section, and directed posteromedially at an angle of 45 degrees. The anterior wall of the meatus is formed by the bulla which terminates at the summit of the meatus. The posterior wall has the bulla and the squamosal fused but I judge that at least one half of the meatus is formed by the bulla. No evidence of a suprameatal fossa, like that in *Procyon*, is seen in the part of the squamosal bone making up the posterodorsal surface of the meatal tube. The small epitympanic recess has an opening in the dorsal aperture of the bulla and lies above the upper wall of the auditory meatus. There is no sign of a mastoid sinus. The crista tympanica extends approximately half way into the bulla and is supported by small radiating septa that rest on the floor of the bulla. These septa are like those in the bulla of *Gulo*, but not so widespread and well-developed. Some of the radiating septa on the posterior side of the crista tympanica seemingly have cross walls that enclose air spaces. As a whole this internal structure appears as an elongate saucer supported by buttresses and cross walls. Except for the septa on the floor, the bulla is simple and without any other partitions.

The bulla is expanded posteriorly and medially. The walls are reflected back over the pterotic so that little of the promontorium is exposed, the anterior wall turning back to reach the fossa for the M. tensor tympani and the posterior wall turning forward to reach the cochlear fenestra. These reflected margins give a purselike appearance to the bulla. In this way the bulla forms most of its own roof, leaving the pterotic to supply a small part of the roofing in the center. The path of the canal carrying the internal carotid artery is plainly visible on the internal surface of the bulla. The canal runs anterolaterally at about a 45-degree angle across the roof of the bulla to a point bordering the medial side of the exposed promontorium and approximately 14 mm from the anterior end of the bulla. Here the canal turns abruptly forward and runs 7 mm, where it turns anteromedially and opens into the middle lacerate foramen and the anterior carotid foramen. Between the posterior carotid foramen and the middle lacerate foramen the canal is entirely closed by the tympanic bone. The path of the facial nerve across the pterotic could not be examined to best advantage without damaging the specimen, but it seems not to differ in any important way from that of the mustelids and procyonids.

In the auditory region of *Brachypsalis* and *Procyon* the interior of the bulla, promontorium, and tubular meatus are similar. Although the radiating septa that support the crista tympanica in *Brachypsalis* are not strictly duplicated by similar septa in specimens of *Procyon*, a few weak ridges surrounding the crista tympanica show that the septa are incipiently developed in the latter.

Malleus.—The malleus was found in the left auditory bulla. The lamina and manubrium were damaged in preparation before I realized that I had encountered this small bone. The contour of the head of this bone is a flattened oval with nearly parallel sides, a feature which SEGALL (1943, p. 58) considers to be typical of most mustelids. SEGALL's illustration (fig. 12) of *Mustela vison* most closely approximates the appearance of the head of this specimen. On the lateral side, a deep fossa comprises a continuation of the lateral surface of the lamina under the border of the neck. This fossa is on the malleus of *Procyon lotor* and unlike that in *Mustela vison*. SEGALL does not comment on this fossa. To judge from the broken surface of the lamina, it was rather broad, more as in *Procyon* than in *Mustela*. The manubrium seemingly was directed rather sharply anteromedially. There is no evidence of a muscular process, but a damaged area suggests that one was present.

Incus.—The incus is globular. The smaller process is conical and heavy at the base. The longer process has a well-developed groove on one side. The articular facet is not well defined.

Lower jaw.—The lower jaw is well preserved except for the tip of the coronoid process. In most features the jaw bears close similarity to the jaw of *Brachypsalis modicus* figured by MATTHEW (1924, fig. 30). The condyle lies below the level of the teeth, like that of *Plesiogulo*, *Gulo*, and *Taxidea*. The neck of the condyle is so short—in fact almost non-existent—that the articular surface is almost in contact with the ascending ramus, as in *Gulo*. The tip of the coronoid process turns back, as in *Gulo* and *Procyon*. The angular process is slightly weathered, but is large knoblike and seemingly not "hooked" or recurved, thus being more like that of *Taxidea*, than of *Procyon*, *Gulo*, or *Canis*. The symphyseal scar extends back to P_2. The muscle attachment scars are not prominent.

Dentition.—The dental formula is

$$\frac{\text{I1-I3, C, P1-P4, M1-M2}}{\text{I1-I3, C, P1-P4, M1-M2}}$$

There is little space between the third incisor and canine or canine and first premolar. The remainder of the premolars seem crowded. Inasmuch as this interpretation of spacing between the teeth is made on partly erupted teeth and damaged alveoli, it should be accepted with caution.

The upper incisors are canid-like but the first and second are slightly narrower and the third slightly heavier than in *Canis*. The medial arms of the cingula of the first and second incisors are reduced and fail to provide the distinct medial cusps seen on canid incisors. The cingulum on the third incisor is reduced.

The canine is heavy. Enough of the alveolus is missing from the right side of the skull to show that the tooth is expanded anteroposteriorly at the base.

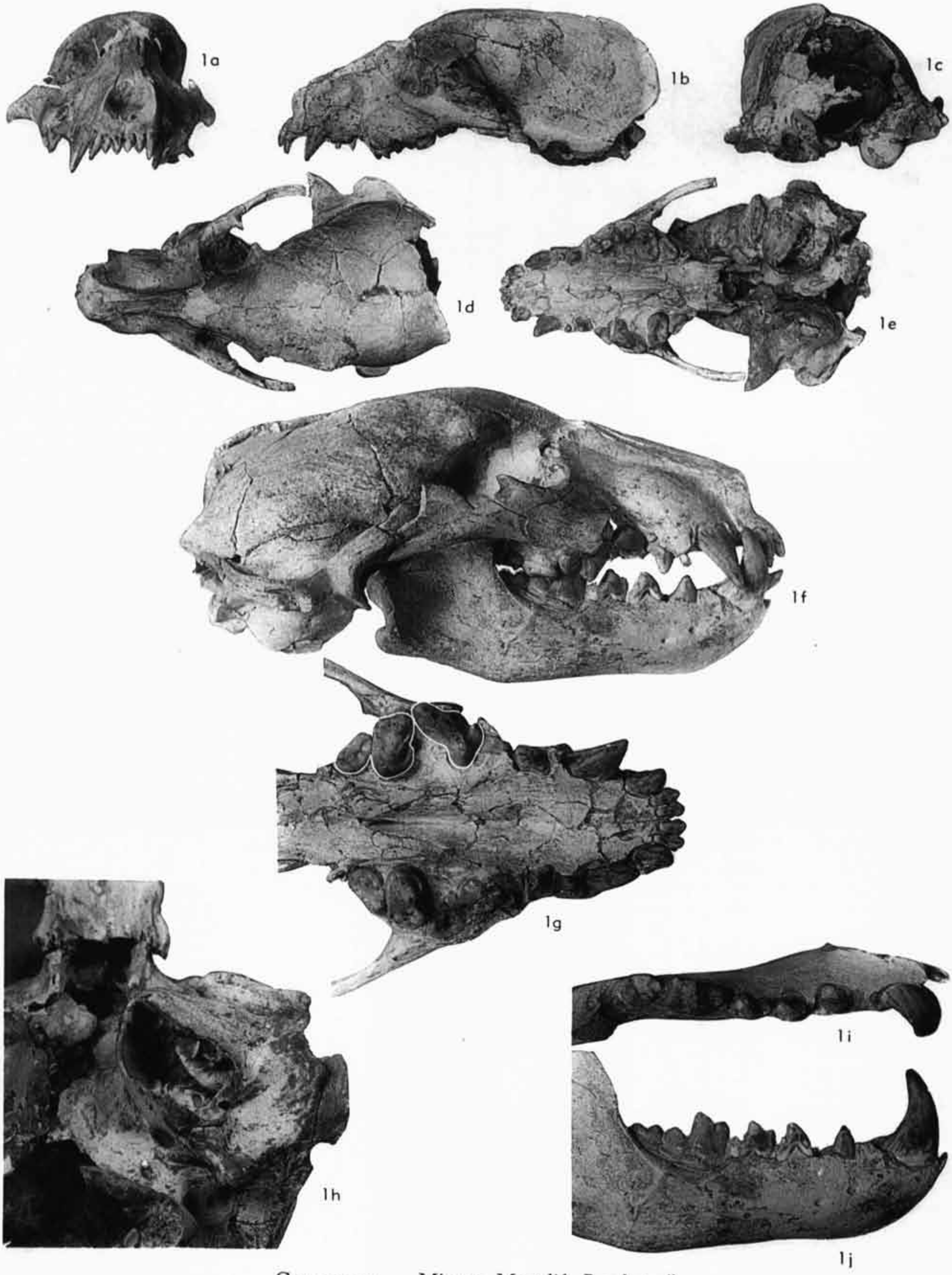
P^1 is a minute, peglike tooth having a weak anteroposterior ridge forming the single cusp.

P^2 is large heavy carinate and slightly expanded at the posterointernal quarter of the base. A faint trace of a cingulum encircles most of the tooth and forms minute cuspules at the anterior and posterior ends. The heel is long. This tooth closely resembles P^3 of *Taxidea*.

EXPLANATION OF PLATE 1

FIGURE 1. Skull and jaw of *Brachypsalis modicus* MATTHEW (Univ. Kansas Mus. Nat. Hist. no. 9,903).

- *1a*, Anterior view of skull, × 0.5.
- *1b*, Left lateral view of skull, × 0.5.
- *1c*, Posterior view of skull, × 0.5.
- *1d*, Dorsal view of skull, × 0.5.
- *1e*, Ventral view of skull, × 0.5.
- *1f*, Right lateral view of skull and jaw, × 1.1.
- *1g*, Ventral view of palate with right molars outlined in white, × 0.9.
- *1h*, Left auditory area viewed from the rear at an angle of 45 degrees from the anteroposterior axis, × 1.5.
- *1i*, Occlusal view of right jaw, × 0.9.
- *1j*, Lateral view of right jaw, × 0.9.



GALBREATH — Miocene Mustelid, *Brachypsalis*

Galbreath — Miocene Mustelid, *Brachypsalis*

The one exposed P^3 is turned on its side, thus hiding the heel, but certain features of the heel were examined by carefully removing pieces of bone which were subsequently replaced. The tooth is larger and heavier than P^2. An anteroposterior keel like that of P^2 is present but, because of the plumpness of the principal cusp, this keel is not so prominent. The widest part of P^3 is nearer the transverse midline of the tooth, rather than farther back, as in the P^2. The wide base combined with the more trenchant top one-half of the principal cusp and absence of an internal cusp of any kind gives an appearance to this tooth which I have not seen in any other carnivore examined by me.

P^4 is slightly smaller than in the specimen figured by MATTHEW (1924, fig. 31). The ratio of greatest length to greatest breadth, however, is practically the same in the two specimens. I have not examined the specimen figured by MATTHEW, but judging from a cast of the specimen, it seems that the base of the paracone and metacone of our P^4 tended to bulge slightly (being 1 mm wider at the paracone) on the lingual side. Like the P^4 described by HENSHAW (1942, p. 117), our specimen has a low cingulum along the posterointernal base of the metacone.

M^1 is smaller and relatively thicker than the M^1 of the American Museum specimen, but the relatively greater thickness is so little that it hardly merits mention. Although M^1 of the specimen in the American Museum is worn, and ours is unworn, I judge that the paracone and metacone are smaller, the protocone and hypocone (posterointernal crest?) equal in size, and the parastyle larger in our specimen. However, these differences between the two specimens are slight. The hypocone, being larger and heavier, dominates all the structures on this tooth. The cingular arms of the hypocone embrace the protocone anteriorly and posteriorly. The anterior cingular arm is swollen and projects forward beyond the anterior border of the outer part of the tooth. The posterior cingular arm is more nearly confined to the posterior border of the tooth and unites with a minute cuspule which probably is an extremely reduced metaconule. The protocone is large and distinct. There is no evidence of a protoconule. The paracone is smaller than the protocone and the metacone is still smaller. The parastyle is distinct but overshadowed by the swollen remnant of the external cingulum.

M^2 is oval; its cusps, excepting the hypocone, appear as small, sharp-pointed, distinct cones. The hypocone is almost indistinguishable from the bordering cingulum. Although the cusps are vestigial bumps, it is possible to recognize the parastyle, paracone, metacone, and protocone. Surprisingly enough there is a small bump anterolateral to the protocone —seemingly a protoconule.

The first and third lower incisors seem to have laterally compressed roots, and certainly the root of the second incisor is compressed.

The lower canine is large, heavy, and swollen at the base. Except for being smaller, more curved posteriorly, and relatively a little thinner transversely, it is like that of AMNH No. 17,209, the type of *Brachypsalis modicus*.

The alveolus of P_1 occupies the same position near P_2 in our specimen as is seen in No. 17,209. However, there is more space between P_1 and the canine in our specimen, but this difference may be due to the immaturity of our specimen.

P_2 is sharp-pointed, keeled, and has practically the same maximum dimensions as the P_2 of No. 17,209. The only dissimilarity between the two teeth is that the maximum transverse diameter is in the trigonid of our specimen whereas it is in the heel of No. 17,209.

P_3 and P_4 are unerupted. X-ray examination does not show any major difference from the P_3 and P_4 of the type specimen. The presence of the posterior cuspule on P_4 was verified by uncovering that part of the tooth.

Except for its size and relatively greater width, M_1 does not differ in any respect from the cast of the M_1 of No. 17,209. Notches between the paraconid and protoconid and the metaconid and protoconid are present but closed. The hypoconulid is composed of three small cuspules, the one on the entoconid side being the largest and the cuspule on the hypoconid side being the smallest. The hypoconid is closer to the metaconid in our specimen. The three principal cusps of the heel are separated from each other and from the trigonid by V-shaped notches. No cingulum is present.

M_2 is oval in outline and has the trigonid reduced almost to the height of the talonid. The principal

EXPLANATION OF PLATE 2

Parts of postcranial skeleton of *Gulo luscus* (LINNAEUS) (male from upper Hunt Fork River, Brooks Range, Alaska; Univ. Kansas Mus. Nat. Hist. no. 45,179) and *Brachypsalis modicus* MATTHEW (Univ. Kansas Mus. Nat. Hist. no. 9,903). All figures approximately $\times$ 0.7.

FIGURE
- *1, 2*—Right humerus of *G. luscus* and *B. modicus*.
- *3, 4*—Right ilium of *G. luscus* and *B. modicus*.
- *5, 6*—Right femur of *G. luscus* and *B. modicus*.
- *7*—Right patella of *B. modicus*.
- *8, 9*—Right ulna of *G. luscus* and *B. modicus*.
- *10, 11*—Right radius of *G. luscus* and *B. modicus*.
- *12*—Dorsal view of articulated left tarsals, metatarsals, and phalanges of *B. modicus*. (feet of *Gulo*, *Taxidea*, and *Lutra* used as guides in arranging the bones as shown here)

FIGURE
- *13*—Right tibia of *G. luscus*.
- *14*—Tibia of *B. modicus*; *a*, posteromedial fragment of proximal articular surface of right tibia; *b*, shaft of right tibia; *c*, distal articular surface of left tibia.
- *15*—Left fibula of *G. luscus*.
- *16*—Left fibula of *B. modicus*; *a*, proximal fragment of shaft; *b*, distal end.

cusps are arranged around the periphery of the tooth, thus virtually forming a large basin. The protoconid and metaconid are of the same size and are opposite each other transversely on the inner and outer borders of the tooth; the paraconid is slightly lower and is placed transversely on the tooth, being separated equally from the protoconid and metaconid; the entoconid is equal to the protoconid and metaconid in size and is separated from the protoconid by a broad notch; the hypoconulid is reduced in height and is separated from the entoconid by a small shallow notch and from the hypoconid by a wide shallow notch. The hypoconid is reduced and almost lost in the inner rim of the tooth. Only a faint trace of a notch occurs between the hypoconid and metaconid. The crowns of the cusps are compressed slightly but the bases are rounded and extend into the basin as rounded ridges. No cingulum is present.

Compared to the permanent carnassial of *Brachypsalis*, the dP^3 is thin-bladed and has the well-developed protocone opposite the tip of the paracone. This tooth differs from the dP^3 of *Taxidea* in having a shallower notch between the paracone and metacone.

The postcarnassial tooth, dP^4, may best be described as like that of a dog but compressed anteroposteriorly. The paracone and metacone are about equally developed and are slightly smaller than the protocone. The parastyle and metasyle are small.

The dP_3 is the size of that of a large dog [2] and shows the same general pattern. However, the anterior and posterior cuspules are weaker on the tooth of *Brachypsalis* and the heel is more expanded on the lingual side.

The dP_4 is the size of that of *Taxidea* but otherwise resembles the dP_4 of the dog. The principal difference between the two teeth is in the heel which is basin-shaped in *Brachypsalis* and open in the dog. The entoconid is relatively small and the metaconid seems to be no more than part of the rim of the basin-like heel. Relatively the heel is slightly smaller.

Ilium.—The part of the ilium between the acetabulum and the sacral scar is heavier and thicker than the corresponding part in *Gulo* but at the attachment scar the wing is noticeably less deep and relatively much thicker. How much these proportions would have changed with further growth is unknown. The sacral scar covers most of the ilium, dorsoventrally, and shows some evidence of being excavated, as in *Gulo*.

Vertebrae.—Three vertebrae found with this specimen are badly damaged, but their size and shape best match the first three caudal vertebrae of *Gulo*.

Humerus.—The preserved part of the humerus does not differ greatly from that of *Gulo*.

Ulna.—The preserved part of the ulna differs from that of *Gulo* in several respects. The shaft, below the semilunar notch, is thin and compressed but broadens considerably near the distal end. The distal part of the humeral facet seems to be narrow. The radial facet is relatively flat and long dorsoventrally.

Radius.—The radius is the only "complete" limb bone present. It is a slender, straight bone almost as long as the radius of *Gulo*, and equal to that bone in dimensions of the proximal and distal epiphyses. The head is irregularly oval, being more like that of *Taxidea* than *Gulo*. The humeral facet is concave and has the border opposite the notch extending proximally in such a way that a lip is formed at the rear and side of the facet. The anterior notch is deep. The bicipital tubercle, crest, and pit on the posteriormedial side of the neck are almost as well developed as those on *Gulo*. Unlike *Gulo*, there is a large oval depression bordering the crest on the opposite side from the tuberosity. The distal end differs from that of *Gulo* in several ways. The carpal facet is actually larger and more oblique because of the distal extension of the dorsal lip and the larger size of the styloid process. The distal ulnar facet is small flat circular and not developed into a process. The distal tendinal sulci are well developed and occupy approximately the same position in *Brachypsalis* as in *Taxidea*.

Femur.—The preserved part of the femur shows that the greater trochanter was probably about as well developed as in *Gulo* but that the trochanteric fossa was shallower. The lesser trochanter is an elongate ridge, as in *Taxidea*, not a rounded knob-like tubercle, as in *Gulo* or *Lutra*.

Patella.—The patella is thick, broad, heavy, and oblong, and therein unlike the patella in other mustelids that I have examined or in *Canis*. The patella of *Gulo* is oblong but thin; the patella of the coyote is thick but coffin-shaped.

Tibia.—The complete medial condyle is present on the preserved fragment of the proximal epiphysis of the right tibia. The facet is even more flattened than that of *Taxidea* in both anteroposterior and transverse directions. This facet is excavated in *Gulo*. The spine accompanying the medial condyle is low but distinct. The popliteal notch is shallow. The shaft, in cross-section throughout its length, resembles that of *Gulo*, thus being less angular than that of *Taxidea*. The distal epiphysis is intermediate in shape between that of *Gulo and Taxidea*. The grooved medial part of the trochlear facet is shallower than in *Taxidea* but, as in *Taxidea*, is blocked posteriorly by the distally projecting border. The lateral part of the facet is expanded anteroposteriorly, more so than in *Taxidea* but less than in *Gulo*. The distal fibular facet is elongate anteroposteriorly and narrow. The posteromedial tuberosity that borders the tendinal groove above and behind the internal maleolus is well developed and seemingly extends almost to the distal border of the maleolus.

Fibula.—The preserved part of the shaft of the fibula is thin and smooth. The distal end of the fibula is generally like that of *Gulo*. Certain differences between the distal parts of the fibulae of *Brachypsalis* and *Gulo* are: greater transverse

2. The dog used here for comparing the deciduous teeth is the large wolflike dog of the Plains Indians in South Dakota.

width, larger astragalar facet, much deeper excavation on the medial surface posterior to the astragalar facet, and wider posterior tendinal groove in *Brachypsalis*. The distal tibial facet is elongate, narrow, and confluent with the upper border of the astragalar facet. I have discussed, on the astragalus, an out-turned spur at the distal end of the fibular facet. On the fibula, the anterodistal border of the astragalar facet is turned outward and fits the articular surface on the astragalar spur. When the tibial and fibular fragments are fitted onto the astragalus, a perfect articulation is made between all the bones.

Calcaneum.—The calcaneum has the same general proportions and shape as that of *Lutra* or *Gulo* —*i. e.*, tuber short and narrow, but deep, and sustentacular process sharply set off from the distal end. However, the process on the lateral side, as on the calcaneum of *Gulo* and *Lutra*, is not well developed on the calcaneum of *Brachypsalis*. The dorsoplantar dimension of the calcaneum is increased by the lateral astragalar facet which is well developed and almost vertical to the transverse axis of the bone. A vestigial remnant of the fibular facet is confluent with the lateral astragalar facet at its distal end. The medial (sustentacular) facet is bilobed. It covers all of the sustentacular process, narrows as it passes onto the body, and expands on the mediodorsal surface where it is confluent with the cuboid facet. The cuboid facet is roughly circular, moderately concave, slightly oblique and its outer edge projects distally beyond the rest of the margin.

Astragalus.—The basic plan of the astragalus, in general, resembles that in carnivores whose feet are not modified for a cursorial, plantigrade (in the sense of the heavy-footed bear), or scansorial mode of locomotion. To me, this general resemblance indicates that the astragalus has not undergone an appreciable amount of modification away from that in the subplantigrade type of foot that probably was common to the miacoids at the time of the development of the modern families. A primitive feature, also common to several mustelids [3], is the astragalar foramen, which passes from a point posterior to the tibial (trochlear) facet through the body and opens into the astragalar groove on the plantar surface. This groove is formed by the fairly straight and more or less parallel borders of the two calcaneal facets. Another feature that may be primitive is the transverse sulcus that lies at the rear of the tibial facet and in front of the groove for the flexor muscles (the astragalar foramen opens into this transverse sulcus) [4]. The body is not expanded on the medial side behind the medial maleolar facet and the neck is constricted. The head is large, divergent, and depressed in relation to the body. The neck is short. The tibial facet occupies all the dorsal surface of the body and extends onto the neck on the inner crest. Posteriorly the facet is limited by the shallow transverse sulcus mentioned above. The outer (or fibular) crest is higher than the inner (or tibial) crest. Both crests are sharp. The trochlear groove is not deep and the surfaces are flat; the bottom of the groove forms an angle rather than a curve. The fibular facet is broad and bordered distally by a laterally projecting spur. The medial maleolar facet is narrow and extends onto the neck. The lateral (external) calcaneal facet is broad and made up of one concave plane. The medial (sustentacular or internal) calcaneal facet forms an S-curved plane extending from the neck to the plantar(?) process at the rear of the bone. Both of the calcaneal facets are longer than broad and irregular in shape. The navicular facet is wide, convex, thickest at its lateral end and has its long axis turned 35 degrees from the transverse plane. The cuboid facet lies on the lateral side of the head but is not so plain as is indicated in Figure 1d.

Navicular.—The navicular is damaged, but enough of the dorsal part is preserved to show that the astragalar facet (proximal surface) was deeply concave. Judging from the shape and mode of articulation of the astragalus and navicular, I think that the astragalar facet was more or less oval in shape, possibly with the long axis directed dorsoposteriorly. From the evidence shown by the facets on the cuboid, there seems to be little doubt that the navicular had a cuboid facet on the posterolateral border. Likewise, an articular facet on the entocuneiform shows that an entocuneiform facet must have been present on the medial side of the distal surface below the mesocuneiform facet. The mesocuneiform facet is oval and elongate dorsoposteriorly. The ectocuneiform facet is oval (Fig. 5a) and transversely convex. Together, the mesocuneiform and entocuneiform facets on the inner side and ectocuneiform facet on the outer side form a flat wedge of the distal end of the navicular which fits into the "basin" or "trough" made by the proximal surfaces of the ectocuneiform, mesocuneiform, and entocuneiform bones.

Cuboid.—The cuboid is large and heavy. It can not be compared satisfactorily with the cuboids of the Recent carnivores that I have used heretofore. The closest approximation to the proportions of this bone is seen in the cuboid of *Gulo*, but there are differences, the most important of which are the positions of the groove for the peroneus longus tendon, the articular facets for the astragalus and navicular, and the tarsal canal. The groove for the peroneus longus tendon extends obliquely from the lateral side to the rear of the bone. The tuberosity that overhangs the lateral end of the groove is not so enlarged and prominent as to be visible when the cuboid is examined from the dorsal aspect. The

3. MATTHEW (1909, p. 551) regarded the astragalar foramen as generally absent in the Mustelidae but noted its presence in *Meles*, *Megalictis*, ?*Mellivora*, and *Taxidea*. I find this structure also in *Lutra*, *Mephitis*, *Gulo*, *Enhydra*, *Martes*, and in PETERSON's figure (1909, p. 274, fig. 68) of *Paroligobunis simplicidens*. This foramen is infrequently found as a vestigial structure in *Procyon* and *Ursus* and is present in specimens of *Potos* and *Ailuropoda* that I have examined.

4. A transverse sulcus, in various stages of preservation, is seen in *Taxidea*, *Lutra*, *Enhydra*, and *Gulo*. PETERSON (1909, p. 275) noted this sulcus in *Paroligobunis simplicidens*. Although the sulcus is best developed in the nonmusteline mustelids, I can not think that the sulcus developed after the mustelids branched from the parent stock. Spcimens of *Hoplophoneus* and *Procyon* that I have examined show vestigial remnants of the sulcus and it is well developed in the giant *Panda*.

area below the calcaneal facet and above the groove on the plantar surface is excavated. The articular facets for the astragalus and navicular are on the medial surface of the proximal end. The facets are confluent, and the line that divides them is directed obliquely across the medial surface. The ectocuneiform facet is in the center of the medial surface. Below the ectocuneiform facet is the tarsal groove which passes across the medial surface from the dorsomedial border around the facet for articulation with the 4th metatarsal and to the distomedial border where it forms an indentation in the distal surface. A corresponding tarsal groove is on the lateral surface of the ectocuneiform, and together these grooves form the tarsal (or vascular) canal for passage of the perforating tarsal artery.

Ectocuneiform.—The ectocuneiform is relatively large and has the general proportions of the ectocuneiform of *Gulo* or *Procyon*, but less of a diamond-shaped dorsal surface. The internal (or tibial) surface has three facets—a proximal one for the mesocuneiform, and two distally placed facets for the second metatarsal. The area between the three facets is deeply excavated. The distal surface is more or less parallel to the transverse axis of the bone, whereas the proximal surface is strongly concave and oblique, having the anteroexternal edge projecting up between the navicular and the cuboid. The cuboid facet covers the fibular face of this upward projecting spur. A small facet for the dorsal part of the inner edge of the fourth metatarsal lies on the dorsal part of the distolateral angle and is confluent with the dorsal part of the facet covering the distal surface. However, I can not find any sign of a facet on the posterior part of the outer distal edge that would articulate with the posterior part of the fourth metatarsal, nor does the metatarsal show any corresponding articular surface. The tarsal groove, already mentioned in the description of the cuboid, is present on the external surface. The plantar process is transversely compressed.

Mesocuneiform.—The dorsal surface of the mesocuneiform is roughly rectangular in outline, being slightly higher than wide. From the proximal and ventral aspects the bone is wedge-shaped. The navicular facet is roughly convex and covers most of the proximal surface. The entocuneiform and ectocuneiform facets are confluent with the navicular facet at the proximoposterior angles of the bone. The lower border of the ectocuneiform facet is developed into a slight lip, which gives this face a concave appearance. The entocuneiform facet is flat. The facet for the 2nd metatarsal is flat and covers all of the distal surface.

Entocuneiform. — The entocuneiform is compressed—more so dorsally than posteriorly—thus being opposite from the condition seen in the mesocuneiform. To some extent the bone is also compressed proximally, thus making the distal end appear rather broad. However, the proximal compression is obscured by the projection of the proximoposterior angle of the bone into a spur which supports the navicular facet (which is the only flat proximal surface on this bone). The mesocuneiform facet lies near the proximal edge of the inner surface of the bone anterior to the spur described above. The facet for the 1st metatarsal is deeply concave anteroposteriorly and covers most of the distal surface.

Metatarsal I.—In the individual structural details of the metatarsals the similarity of each feature lies with *Gulo* or *Taxidea*. In the following description of each bone, the features not mentioned may be understood to resemble those of *Gulo*.

As has been pointed out, metatarsal I is reduced, especially in robustness. Compared to that of *Gulo*, the shaft is slender, short, and arched dorsally. The proximal articulating surface is fundamentally like that of *Taxidea*. The entocuneiform facet is transversely concave. Posteriorly (*i. e.*, on the plantar side), this facet is bordered by a large tubercle (relatively larger than those in either *Gulo* or *Taxidea*). On the posterolateral angle (*i. e.*, next to metatarsal II) a second tubercle of smaller size is present. The two tubercles are separated by a notch, as in *Gulo*, rather than being united, as in *Taxidea*. It is this second tubercle that is so enlarged in *Gulo*. The articular surface on metatarsal I, where this bone contacts metatarsal II, is a concave roughened pit, completely unlike the movable joint on *Gulo*. This suggests, but does not necessarily prove, less freedom of action in the foot. The proximal end yet retains some of its dorsoplantar depth but the transverse width is noticeably less. This narrower transverse width probably is a heritage from the early carnivores.

The distal facet is essentially like that of *Gulo*, although the keel on the plantar side is less sharp.

Metatarsal II.—The second metatarsal has the mesocuneiform facet transversely oblique to the axis of the shaft as in *Taxidea* and *Daphoenus*. The dorsal end of the facet is concave where it extends onto the tubercles that bear the entocuneiform facet. The ectocuneiform facets are oval, concave in the dorsoplantar direction and flattened proximodistally. The entocuneiform facet is roughly triangular in shape and depressed. Below the entocuneiform facet a weak ridge articulates with metatarsal I.

The distal epiphysis is present on this bone simply because it fits there. There is no reason why it could not as well belong to the third or fourth metatarsal. There is little difference between the articulatory surface of this epiphysis and those of the 2nd, 3rd, and 4th metatarsals of *Gulo*, except that the dorsal surface is slightly less depressed.

Metatarsal III.—Metatarsal III has the plantar half of the proximal end damaged. However, it can be seen that the ectocuneiform facet is more convex anteroposteriorly, and that the lateral margin is more indented than in *Gulo*. The articulation for metatarsal II is a roughened concave area. The dorsal articular facet for metatarsal IV is relatively larger than that in *Gulo*. The posterior articular facet for metatarsal IV is considered in the discussion on metatarsal IV. Otherwise this bone is similar to that in *Gulo*.

Metatarsal IV.—Like metatarsal III, only the proximal part of metatarsal IV is present. This bone differs from that of *Gulo* in the following respects: the proximal end does not project so far above metatarsal III and V; the cuboid surface is more convex anteroposteriorly; the lateral margin of the cuboid facet is concave and the medial margin is more indented; the facet on the plantar surface is not so deep but, instead, is wider and more convex; and the facets that articulate with metatarsal III and V differ.

The two facets for articulation with the third metatarsal differ from those in *Gulo* in being smaller, farther apart, of different shape, and different orientation on the shaft. The anterior facet is slightly convex and is separated from the cuboid facet by a distinct groove. The posterior facet projects medially at its upper end because of the broad plantar process—hence is concave. The anterior facet faces almost anteriorly (or dorsally) and the posterior facet faces medially. In this way the surfaces of the two facets bear the same relationship to each other as do the facets on *Gulo*, which in turn suggests that the damaged posterior facet on metatarsal III had the same relationship to its accompanying anterior facet.

On the lateral side, the facet for articulation with metatarsal V is a large cuplike surface bordered on the front and top by a single smooth confluent facet. There is no articulating area that corresponds to the posterior facet on *Gulo*.

Metatarsal V.—Metatarsal V has the head expanded laterally by a large fibular process which makes the head actually larger than in *Gulo*. Posteriorly the plantar process is likewise enlarged and bears a wide, but not deep, facet on the plantar surface that is directed more distally than in *Gulo*. The cuboid facet is oblong, less convex than in *Gulo*, and does not extend so far back toward the plantar process. There is no posterior facet for metatarsal IV corresponding to the one in *Gulo*. The distal epiphysis is missing.

Pedal phalanges.—The pedal phalanges differ from those of *Gulo* in that the proximals are arched dorsally; the medials are concave on the dorsal surface; and the distals are relatively smaller and shorter. As a whole, the phalanges are somewhat catlike, and the depressed areas on the medials suggest that the claws were at least subretractile.

DISCUSSION

SIZE

The probable size of a fully adult *Brachypsalis modicus* can be predicted from the parts that are preserved. The skull and tarsal bones have the size of corresponding parts in *Gulo*. The long bones of our specimen are shorter than those of *Gulo*, while the few distal and proximal ends preserved are as large. Inasmuch as the ends of a long bone attain maximum size earlier than does the shaft, the limb bones of our young specimen probably had not reached their full length. Furthermore, a rough correlation between length of the limb bones and size of the ends that holds for adult individuals of *Gulo*, *Taxidea*, and *Lutra*, probably holds equally well for *Brachypsalis*. For these two reasons, I think that the limb bones of *Brachypsalis* could be as long as those of *Gulo*. The bones of the hallux are short and slender. The proportionate difference in size between the hallux and the remaining toes is near the difference seen in *Didymictis* and *Daphoenus* — to cite two fossil carnivores — and greater than in *Gulo* or *Taxidea*, thus making the hallux much too reduced to be of use in determining the size of *Brachypsalis*. The remaining metatarsals and phalanges of the hind foot are shorter but otherwise (size of shaft, depth and width of proximal and distal ends) are nearly as large as in *Gulo*. As with the limb bones, the shortness of the metatarsals and phalanges may be because of the immaturity of our specimen. The size of the skeleton of *Brachypsalis* probably was near that of *Gulo*, but, if a noticeable difference did exist, the fore- and hindlimbs, especially the forelimbs, probably were smaller rather than longer and thicker.

Measurements of skeletal parts of *Brachypsalis modicus* are recorded in Table 2.

APPEARANCE

The skull of *Brachypsalis modicus* suggests that of a "long-faced" wolverine or a composite skull formed from the facial region of a long-snouted raccoon, the cranial region of a badger, and the large postorbital process and long, low infraorbital canal of a coyote. The immaturity of this specimen, however, no doubt masks its mature appearance. In the adult skull, the snout was probably larger and more like that of a canid.

The left hindfoot is relatively complete and allows a reconstruction of the foot to be made that shows its probable stance (Pl. 2, fig. 12). The tarsal and proximal ends of the metatarsals are moderately close fitting and form a transverse arch similar to that in *Gulo*, whereas, distally, the metatarsals are spread out. The articular surfaces show that the foot was somewhat flexible and adaptable for leaping, walking, or running. This freedom of movement, the pattern of articulation, and the construction of the individual tarsal bones suggest that the foot was subplantigrade or subdigitigrade, rather than digitigrade or plantigrade. The depressed dorsal surfaces of the metatarsals brings up a problem in interpreting the locomotion of *Brachypsalis*. In *Gulo*, the distal ends of the metatarsals are extremely convex and the dorsal surfaces above the distal

Table 2. *Measurements of Brachypsalis modicus Matthew, in millimeters.*

Skull	KUMNH[a]	AMNH[b]
Length, incisor to occipital condyle	136.5	....
Greatest width of skull (regardless of distortion)	78.2	....
Estimated possible maximum width of skull at zygomatic arch	90.0	....
Estimated possible minimum width of skull at zygomatic arch	80.0	....
Width of skull through center of auditory bullae	74.7	....
Length of incisive foramen	4.5	....
Width of incisive foramen	2.0	....
Length of left auditory bulla	25.0	....
Width of left auditory bulla	23.5	....
Projection of auditory bulla below basioccipital	14.0	....
Teeth		
P^2, anteroposterior length	7.70	....
P^2, transverse width	4.72	....
P^3, anteroposterior length	10.05	....
P^3, transverse width	7.00	....
P^4, anteroposterior length	14.05	15.5
P^4, transverse width	10.64	11.0
M^1, anteroposterior length[c]	7.90	8.4
M^1, transverse width[c]	12.90	14.0
C(lower), anteroposterior length[d]	9.85	11.0
C(lower), transverse width[d]	6.70	8.0
P_2, anteroposterior length	7.36	7.23
P_2, transverse width	4.70	4.64
M_1, anteroposterior length	13.41	15.50
M_1, transverse width	7.05	7.81
M_2, anteroposterior length	8.34	....
M_2, transverse width	6.61	....
dP^3, anteroposterior length	8.73	....
dP^3, transverse width	6.29	....
dP^4, anteroposterior length	5.29	....
dP^4, transverse width	7.22	....
dP_3, anteroposterior length	7.52	....
dP_3, transverse width	3.74	....
dP_4, anteroposterior length	9.17	....
dP_4, transverse width	4.28	....
Ilium		
Depth of ilium behind sacral attachment scar	15.7	....
Transverse width of ilium behind sacral attachment scar	11.9	....
Humerus		
Anteroposterior diameter of shaft at midpoint	15.5	....
Transverse diameter of shaft at midpoint	10.0	....
Ulna		
Anteroposterior diameter at coronoid process	18.8	....
Transverse width at coronoid process	8.9	....
Radius		
Length	98.3	....
Anteroposterior diameter of shaft at midpoint	6.0	....
Transverse diameter of shaft at midpoint	6.8	....
Transverse width of proximal end	16.4	....
Transverse width of distal end	22.5	....
Femur		
Anteroposterior diameter of shaft at midpoint	9.0	....
Transverse diameter of shaft at midpoint	11.0	....

Patella	KUMNH[a]	AMNH[b]
Length	18.0	....
Width	14.9	....
Depth	9.5	....
Tibia		
Anteroposterior diameter of shaft at midpoint	11.5	....
Transverse diameter of shaft at midpoint	8.3	....
Transverse diameter at distal end	23.3	....
Fibula		
Anteroposterior diameter of shaft near midpoint	3.3	....
Transverse diameter of shaft near midpoint	4.2	....
Anteroposterior diameter of distal end (est.)	14.0	....
Calcaneum		
Proximodistal length	37.6	....
Mediolateral width	20.5	....
Dorsoplantar depth	18.3	....
Astragalus		
Proximodistal length	25.5	....
Mediolateral width	23.4	....
Dorsoplantar depth	17.6	....
Width of body	17.9	....
Width of tibular facet	15.3	....
Greatest width of head	14.2	....
Cuboid		
Proximodistal length	15.2	....
Mediolateral width	12.4	....
Dorsoplantar depth	10.5	....
Ectocuneiform		
Proximodistal length	11.8	....
Mediolateral width	9.0	....
Dorsoplantar depth	14.4	....
Mesocuneiform		
Proximodistal length	6.1	....
Mediolateral width	4.6	....
Dorsoplantar depth	7.1	....
Entocuneiform		
Proximodistal length	10.1	....
Mediolateral width	5.5	....
Dorsoplantar depth	9.0	....
Metatarsal I		
Length	25.0	....
Depth of proximal end	7.3	....
Width of proximal end	5.6	....
Width of distal end	5.3	....
Metatarsal II		
Length	36.4	....
Depth of proximal end	9.9	....
Width of proximal end	6.0	....
Width of distal end	9.1	....
Metatarsal III		
Depth of proximal end (est.)	12.7	....
Width of proximal end (est.)	7.8	....
Metatarsal IV		
Depth of proximal end	11.0	....
Width of proximal end	9.1	....

	KUMNH[a]	AMNH[b]
METATARSAL V		
Depth of proximal end	10.5	....
Width of proximal end (est.)	11.0	....
PROXIMAL PEDAL PHALANX I		
Width of distal end	3.7	....
PROXIMAL PEDAL PHALANX II		
Width of distal end	6.3	....
PROXIMAL PEDAL PHALANX III		
Length	20.3	....
Width of proximal end	8.2	....
Width of distal end	6.4	....
PROXIMAL PEDAL PHALANX IV		
Width of distal end	5.8	....
PROXIMAL PEDAL PHALANX V		
Width of distal end	5.8	....
MEDIAL PEDAL PHALANX II		
Width of distal end	5.4	....

	KUMNH[a]	AMNH[b]
MEDIAL PEDAL PHALANX III		
Length	12.5	....
Width of proximal end	6.5	....
Width of distal end	5.8	....
MEDIAL PEDAL PHALANX IV		
Width of distal end	5.6	....
DISTAL PEDAL PHALANX II		
Width of proximal end	4.7	....
DISTAL PEDAL PHALANX III		
Width of proximal end	5.4	....
DISTAL PEDAL PHALANX IV		
Width of proximal end	5.0	....

a Kansas Univ. Mus. Nat. Hist. no. 9,903.
b Am. Mus. Nat. Hist. nos. 17,209, 17,210, casts of the type and a referred specimen of *B. modicus.*
c Greatest anteroposterior length and greatest width are measured on axes perpendicular to and parallel to a line through the tips of the paracone and protocone.
d Measurements made at the alveolus on our specimen and the cast.

facets are depressed. Such features imply a digitigrade foot, although the foot of *Gulo* is subplantigrade. Nevertheless, I am informed that *Gulo,* whether moving slowly or fast and for short or long distances, often "bounds" or "leaps"; otherwise it walks awkwardly. The heels of the fore- and hindfeet are padded. The padded heels and "bounding" habit could explain the structure of the distal ends of the wolverine metatarsals. Could *Brachypsalis* have walked or "bounded" in the same manner?

Without the bones of the trunk, nothing definite can be said about the bodily proportions of this animal. In the light of what is known of the hindfoot and limbs, the simplest deduction is that the body was like that of the wolverine, rather than long and slender.

COMPARISON WITH FOSSIL AND RECENT MUSTELIDS

MATTHEW, at one time or another in the Snake Creek papers (MATTHEW & COOK, 1909; MATTHEW, 1918 and 1924), compared *B. modicus* with all of the *Brachypsalis* material known to him. Subsequently, HALL (1930) described and named *B. angustidens* but pointed out that his reference of this species to the genus *Brachypsalis* was questionable. This species is much smaller and has narrower teeth than *B. modicus.* HENSHAW (1942) reported additional specimens which he assigned to *B. pachycephalus.* Inasmuch as our specimen closely matches *B. modicus* there is little that I can add in the way of comparisons that was not considered by MATTHEW or HENSHAW. The fragments of maxillaries of *B. pachycephalus* reported by COPE & MATTHEW (1915, pl. 119a) and HENSHAW are, in general, like the maxillary of our specimen.

Study of casts of *Oligobunis* and *Paroligobunis* and the descriptions, figures, and discussions by MATTHEW (1907) and PETERSON (1909) indicate that *Brachypsalis* had a shallower skull, relatively longer muzzle, and lighter lower jaws than the two genera just named.

I repeatedly used *Gulo* as a basis of comparison in describing this specimen of *Brachypsalis* but do not want to leave the impression that the two genera closely resemble each other. Most of the comparisons involving *Gulo* could have been made equally well by using other carnivores but without the advantage of near equivalence in size. Furthermore, *Gulo,* like *Brachypsalis,* is not an especially highly modified or advanced mustelid; consequently, some features (such as the infra-orbital canals, lacrimals, jugals, and septa of the bullae) are close in resemblance. On the other hand, the basi-cranial region (especially including the squamosal, mastoid, and auditory bulla) is decidedly dissimilar in the two genera. Although both have thick, heavy teeth, the cingula, semi-shearing heel on M_1, reduced M_2, and expanded M^1 of *Gulo* are in direct contrast to the condition in *Brachypsalis.* Insofar as I can determine, *Plesiogulo* differs from *Brachypsalis* in the same ways that *Gulo* does.

Seemingly, the mustelids have retained a more or less primitive skeleton which has been slightly specialized in conjunction with their habits. This is especially true of the foot. Though this specimen is immature, it has the foot well enough developed to show its relative size and to indicate similarities and dissimilarities in comparison with the feet of other carnivores. In a comparison of the minute details of the individual tarsal bones, close similarities to those of several Recent genera are shown, especially *Gulo, Taxidea, Lutra,* and, to a lesser extent, *Procyon.* The shape, extent, and arrangement of the facets and processes of the calcaneum, for example, are in some ways more nearly like those of *Procyon* than *Taxidea* or *Lutra,* whereas the massiveness and depth of the bone are nearer conditions in *Lutra* and *Gulo.* In a like manner, the other tarsal bones show a mixture of similarities and dissimilarities in the features of each bone when compared to those of the various genera. This suggests to me that the differences, if not trivial and of little phyletic value, should be treated with caution in any case. In Miocene time, there probably was even less departure than now from the basic pattern of the foot to show phyletic trends. Imposed on this pattern, of course, are the modifications of habitat. So far, I have been unable to separate small differences into two categories, "phyletic trend" and "habitat modification." Therefore, I hesitate to attribute any differences in the postcranial skeleton to phyletic lines at this stage in our study of the mustelid phylogeny.

STAGE IN MUSTELID EVOLUTION OF BRACHYPSALIS

Brachypsalis has not lost all signs of its evolutionary passage from a primitive carnivore to a mustelid. The skull still retains a length of snout more nearly like that of the early carnivores. The jugal-lacrimal-maxillary relationship is intermediate between that of early carnivores and Recent mustelids. The auditory bulla shows its intermediate position in having the medial part of the floor of the bony meatus large but it does not yet have septa or "rafters" enlarged to the extent observed in some mustelids. The stage of evolution shown by the auditory region might be described as procyonid-like. This implies that the auditory region, in its evolution from that of the primitive type, passed through a structural stage much like that shown by the procyonids today. HOUGH's (1944, 1948) work on some Tertiary canoids suggests that this may have happened in more than one line of the mustelids, each line independently following the same path at one time or another.

The skeleton, in common with those of most Recent mustelids, remains relatively primitive, that is to say, it is not modified for a highly cursorial or arboreal life. Nor is it modified for support of a heavy body, as in ursids.

RELATIONSHIPS

This specimen contributes little toward answering questions about the relationship to one another of the several species in the genus but does offer some help in clarifying the relationship of the genus (actually some species of the genus) to some of the large middle Tertiary mustelids of North America.

In his evaluation of the species of *Brachypsalis*, MATTHEW (1924, p. 134) stated that "*B. pristinus* and *modicus* are intermediate stages [between ?*B. matutinus* and *B. pachycephalus*] but the latter is clearly off the direct line of descent, if the series be considered as such, having a longer jaw, accessory cusp on p_4, entoconid on heel of m_1 and metastyle on m^1 to distinguish it. Better knowledge of the dentition of the four species would probably show that they represent at least two, probably three distinct phyla." I have nothing to add now to these comments except to recall that both MATTHEW (1924, p. 134) and HALL (1930, p. 26) have remarked on the possibly composite nature of this genus.

Brachypsalis has been placed in the subfamily Mustelinae and I know of no evidence suggesting closer relationship to any other mustelid subfamily. Within the subfamily, the relationship seems to be clearly with the oligobunines. I use this term as a name for the mustelids, particularly *Oligobunis crassivultus*, *Paroligobunis*, and *Brachypsalis*, that MATTHEW (1924, p. 129) thought to be a natural group (Group I of his key). MATTHEW (1924, p. 131) was of the opinion that: "This genus is still imperfectly known but it appears probable that it represents an extinct phylum, derived from *Oligobunis* through the lower Miocene *Paroligobunis*, characterized by progressively more robust teeth, shortened jaws, enlargement of the tubercular and reduction of the sectorial dentition." I agree with MATTHEW to the extent of thinking that *Brachypsalis* is allied with these two oligobunines but, as both have, for one thing, deeper and more massive skulls than *Brachypsalis*, I doubt that the lineage was direct. Of greater concern is the direction of change shown by the teeth. In my opinion, the oligobunines, like the gulonines, are characterized by progressively more robust teeth, shortened jaws, and a tendency to reduce the entoconid of M_1. However, the oligobunines never reached the stage of having a markedly reduced metaconid on M_1, and flattened semishearing type of heel nor did they have the accompanying changes in the upper molars as among the gulonines. Probably the ancestral oligobunines had a tooth-pattern in many respects like that of *Parictis*.

Granting that *Brachypsalis* is an oligobunine, the relationship of the group is yet to be determined. The features common to the oligobunines and gulonines are certainly suggestive of a common ancestor. But, from the viewpoint of ancestry, neither the oligobunines nor gulonines seem to be closely related to the small mustelines, such as *Paleogale*, *Plesictis*, or *Promartes*, which were already too specialized in having shortened snouts and modified molars. It might be possible, although I think unlikely, that the oligobunines were independently derived from a Miocene immigrant of some Old World stock. More certainly, I do not think that *Brachypsalis*, alone, had such an origin.

CONCLUSIONS

Brachypsalis is a mustelid, structurally less advanced than the small mustelids and different from the large, heavy-skulled, heavy-limbed, contemporary mustelids of the Middle Tertiary. *Brachypsalis* is closely related to, but seems not to have descended from, *Oligobunis* and *Paroligobunis*. The skull is intermediate between those of the early canoids and the Recent mustelids, being somewhat procyonid-like. The known parts of the postcranial skeleton are like those of large Recent mustelids and show that the genus was subplantigrade in gait and slender-limbed.

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