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OSTEOLOGY OF MYLAGAULUS LAEVIS, A FOSSORIAL RODENT FROM THE UPPER MIOCENE OF COLORADO

By SYLVIA ROBINSON FAGAN
(Contribution from the Museum of Natural History)



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**OSTEOLOGY OF MYLAGAULUS LAEVIS, A FOSSORIAL RODENT FROM
THE UPPER MIOCENE OF COLORADO¹**

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¹ A dissertation submitted in partial fulfillment of the requirements for the Degree of Master of Arts in Zoology at the University of Kansas in August, 1956. Modifications as of May, 1959.

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ABSTRACT

A skeleton of *Mylagaulus* (Mylagaulidae), a fossorial rodent from upper Miocene beds in Colorado is compared with *Aplodontia*, the only living member of the Aplodontidae. These comparisons suggest that certain common characters are due to phyletic relationship and others to a similar fossorial habit. *Mylagaulus* is more fossorial than *Aplodontia*. The fossorial trends seen in *Mylagaulus* foreshadow the fossorial structures seen in *Epigaulus*, last of the Mylagaulidae.

INTRODUCTION

The rodent family Mylagaulidae, ranging from early Miocene to middle Pliocene, is regarded as an offshoot of the family Aplodontidae. Both groups became fossorial, the Mylagaulidae notably more so than the Aplodontidae. The discovery of an excellent skeleton of *Mylagaulus*, from upper Miocene beds in northeast Colorado, affords an opportunity to compare a member of the Mylagaulidae (suborder Sciuro-morpha) with *Aplodontia*, the only living member of the Aplodontidae.

Comparisons aim to reveal: (1) which common characters are due to phyletic relationship and which are due to a similar habitat, (2) what differences are caused by a difference in degree of adaptation, (3) something of the life habits of *Mylagaulus*, and (4) structural relationship of *Mylagaulus* to *Epigaulus*, the last of the Mylagaulidae. Determination of the difference in degree of fossorial adaptation may help clarify the effect of fossorial adaptation on basic rodent morphology.

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After the main part of my study was completed, the pertinent material of the genus *Mylagaulus* in the collection of the American Museum of Natural History, in New York City, was examined. For the privilege of studying the last-mentioned material, I thank Dr. George Gaylord Simpson and Mrs. Rachel Nichols.

MATERIALS AND METHODS

The material used, in the University of Kansas Museum of Natural History unless otherwise noted, was as follows.

FOSSIL SPECIMENS

Specimens	Locality	Nature of material
KU9808	SW $\frac{1}{4}$ sec. 26, T. 12 N., R. 55 W., Logan County, Colorado	Damaged skull, lower jaws and postcranial skeleton
KU9807	W $\frac{1}{2}$ sec. 27, T. 12 N., R. 55 W., Logan County, Colorado	Anterior part of skull without cheek teeth
KU9969	E $\frac{1}{2}$ sec. 27, T. 12 N., R. 55 W., Logan County, Colorado	Complete humerus, fragments of cranial and postcranial skeleton, several cheek teeth
AMNH9043	Cedar Creek, Logan County, Colorado	Anterior part of skull with teeth, damaged right mandible with teeth, right and left ilia with attached sacrum
AMNH17576	Sinclair Draw, Sioux County, Nebraska	Well-preserved skull lacking nasal bones, part of the basicranial region and the right zygomatic arch.

KU—University of Kansas

AMNH—American Museum of Natural History

KU9808 and KU9807 were collected by E. C. GALBREATH in 1951 and reported on by him in the year 1953 (p. 96).

KU9969 was found by R. R. CAMP in 1956 and has not previously been reported.

AMNH9043, the type of *Mylagaulus laevis*, was described and figured by MATTHEW in the year 1901 (p. 378-379).

AMNH17576 was described and figured by MATTHEW in the year 1924 (p. 75-82).

GEOLOGIC AGE OF FOSSILS

The geologic age of KU9808, KU9807 and KU9969 is late Miocene (late Barstovian); Pawnee Creek Formation (Kennesaw local fauna).

AMNH9043 also is from the late Miocene (Barstovian), Pawnee Creek Formation. AMNH17576 is from the latest middle Miocene (late Hemingfordian), lower Snake Creek beds.

RECENT SPECIMENS

Specimens of Recent fossorial rodents used in the study here reported are recorded as follows.

Materials		
Specimens(a)	Locality	Date Collected
<i>Aplodontia rufa rufa</i> (Rafnesque)		
KU14408 ♀	Seattle, King County, Washington	12 March 1944
KU14409 ♂	Seattle, King County, Washington	12 March 1944
KU32020 ♂	Seattle, King County, Washington	26 March 1949
KU32043?	North Cr., 20 mi. W. Olympia, Thurston County, Washington	21 May 1949
<i>Sciurus niger rufiventer</i> É. Geoffroy Saint-Hilaire		
KU9172 ♀	Denver County, Colorado (tag indicates specimen was intro- duced from Oklahoma)	17 August 1931
KU6206 ♂	Douglas County, Kansas	13 January 1928
<i>Thomomys bottae nigricans</i> Rhoads		
KU46468 ♂	Escondido, San Diego County, California	3 July 1929
<i>Thomomys townsendii elkoensis</i> Davis		
KU46480 ♂	3 mi. W. Halleck, Elko County, Nevada	19 May 1929
<i>Macrogeomys heterodus cartagoensis</i> Goodwin		
KU60664 ♀	Rancho Redondo, Volcán Irazú, San José, Costa Rica	3 June 1954

(a) Complete skeletons.

On the basis of size of the alveoli of P4 and M1, fossil specimens KU9807 and KU9808 are thought to be adults of approximately the same age; on the basis of the epiphyses, KU9969 is considered to be a younger individual, although nearly adult as judged by the development of processes for muscle attachment. The specimens of *Aplodontia rufa rufa* are considered to be adult because the tooth pattern is adult and sutures on the skull are obliterated.

Few good specimens of mylagaulid rodents have been reported in the literature. Use of only one species, *Mylagaulus laevis*, in the present study is hence a necessity,

but fortunately this species is typical of the family. The limitation to a single species and subspecies, *Aplodontia rufa rufa*, does not affect the comparisons which are thought to be valid on the generic level. For the same reason, generic names, rather than specific and subspecific combinations, are used throughout the comparisons and discussion except where another course seemed more to advantage.

For analysis and discussion of the structures observed the following Recent specimens (complete skeletons) were used.

Most of the comparisons are qualitative. Quantitative data were taken by using dial calipers on KU9807, KU9808 and where possible on KU9969 to supplement measurements from KU9808. The corresponding measurements were taken from *Aplodontia* KU32020 ♂, which was thought to be typical of the genus. The number and kinds of measurements were dictated by the condition of the fossils. These same specimens were used in the accompanying illustrations.

When the comparisons and analysis which follow were first done, use was made of published plates and descriptions of *Mylagaulus laevis* wherever possible to supplement and verify the conclusions reached on the basis of the University of Kansas material. These figured specimens, all from the American Museum of Natural History, have subsequently been examined personally. Unfortunately, direct comparisons of the University of Kansas and American Museum of Natural History specimens has not been accomplished.

The nomenclature used in the comparisons is patterned after that in REYNOLDS (1897). Certain terms from HILL (1935, 1937) are modified to accord with REYNOLDS' system.

MYLAGAULUS LAEVIS Matthew, 1924

Mylagaulus laevis Matthew, Bull. Amer. Mus. Nat. Hist., v. 16, art. 22, p. 298, Sept. 25, 1902

COMPARATIVE OSTEOLOGY

AXIAL SKELETON

SKULL

Plate 1, Table 1

Viewed dorsally, the skull is shorter, heavier and broader in *Mylagaulus* than in *Aplodontia*. The width across the zygomata (measured across widest part of the arches) of *Mylagaulus* is greater than the length of its skull (measured from tip of nasals to midpoint of the lambdoidal crest). The width of the zygomata in *Aplodontia* is subject to individual variation (TAYLOR, 1918, p. 443, pl. 28), but it is not so great as the length. The skull of *Mylagaulus* is only as long as the occiput is wide (measured across most lateral extensions of occiput). The skull of *Aplodontia* is longer than the occiput is wide.

Viewed laterally, the skull of *Mylagaulus* is more flattened dorsoventrally than that of *Aplodontia*. The basicranial region of *Mylagaulus* is bent more ventrally with respect to the palatal plane than in *Aplodontia*, which is variable in this character but seemingly does not form so large an angle with the palatal plane. The occiput of both genera is inclined anteriorly to the dorsoventral plane; in *Mylagaulus* the occiput forms a larger angle with this plane.

The nasals of both genera flare anteriorly and narrow posteriorly. The posterior suture of *Mylagaulus* (AMNH-17576) and *Aplodontia* is posterior to the anterior root of the zygomatic arch. The nasals constitute a greater part of the total dorsal length of the skull in *Mylagaulus* than in *Aplodontia*. The nasals of *Mylagaulus laevis*

(KU9807) are of special interest because they are thickened and rugose. The type specimen of *Mylagaulus laevis* (AMNH9043) is described (MATTHEW, 1902, p. 298) and figured (MATTHEW, 1901, as *M. monodon*, p. 378) as having smooth nasals but this was probably by contrast to the condition in horned mylagaulids. Personal observation of AMNH9043, which unfortunately is damaged in this critical region, reveals what might be a thickening and rugoseness similar to, but not as pronounced as, that of *Mylagaulus* KU9807. The nasals of *Aplodontia* are not thickened and are smooth.

The premaxillaries form the lateral and ventral surfaces of the rostrum in both genera. The premaxillaries bear the incisors. The incisive foramina of *Mylagaulus* are shorter than those of *Aplodontia*. A cross-section of the rostrum of both genera is circular; the rostrum as a whole is cylindrical in shape.

The anterior border of the orbit of *Mylagaulus* KU9807 is damaged but AMNH17576 and AMNH9043 do not show the little rounded notch visible on the anterior margin of the orbit of all specimens of *Aplodontia* examined. However, according to TAYLOR (1918, p. 443) this notch is variable in degree of development in *Aplodontia* and is nearly lacking in some specimens.

The sutures on the dorsal surface of skulls of *Mylagaulus* (KU9807, KU9808) are obliterated (except for the nasal suture mentioned above) but can be observed to some extent in AMNH17576, which is a better preserved but also a younger individual than either KU9807 or KU9808. Care has been taken in the comparisons to avoid emphasis on possible juvenile characteristics of KU17576, unless they serve to clarify some feature. Therefore, the discussion to follow will deal mainly with areas which will not be sharply delimited.

The frontal area of both *Mylagaulus* and *Aplodontia* is flattened transversely and in the midline is slightly concave anteroposteriorly. The frontals of *Mylagaulus*, unlike those of *Aplodontia*, are not constricted and bear strong postorbital processes. The postorbital processes of *Mylagaulus* are short, stout and blunt ended; they are but slightly curved ventrally, lying almost wholly in the horizontal plane. The frontals of *Aplodontia* are narrow behind the anterior zygomatic root and form a saddle-shaped interorbital constriction. Postorbital processes are lacking in *Aplodontia* but what possibly might be incipient postorbital processes are present on KU32020 ♂.

The parietal region of *Mylagaulus* continues the flattened plane of the frontals back to the interparietal region and lambdoidal crest; the parietal region of *Aplodontia* is slightly convex, rising above the flattened plane of the frontals. As recorded by MATTHEW (1924, p. 80), the parietal extended far enough forward to share in the postorbital process of the frontal of *Mylagaulus*, "... extending out on its postero-inferior surface almost to the tip of the process." Microscopic examination of KU9808 shows traces of what might be the suture in

question, but it cannot be definitively traced. The parietals of *Aplodontia* do not extend this far forward.

The temporal crests of KU9808 are weakly developed and far apart; the temporal crests of *Aplodontia* are variable in degree of development and in approach to one another (TAYLOR, 1918, p. 443). Although *Mylagaulus* AMNH17576 is a younger individual than KU9808, the temporal crests are well-developed and close together.

The interparietal of *Mylagaulus* KU9808 cannot be defined as a separate element; neither is the interparietal of *Aplodontia* clearly defined. The interparietal is visible in *Mylagaulus* AMNH17576 as a triangular element enclosed within the temporal crests and with its apex pointing anteriorly, which is in agreement with the traces of the anterior suture observed in *Aplodontia*. However, MATTHEW (1924, p. 81) terms this aspect of AMNH17576 as a "... supposed interparietal. . . ."

The zygomatic arch (measured from anterior to posterior root) encompasses the greater part of the skull in regard to length, and is more robust than that of *Aplodontia*. In *Mylagaulus* the anterior root of the zygomatic arch originates immediately anterior to P4 and forms a right angle with the axis of the skull, whereas, in *Aplodontia* the anterior root originates opposite P3 and forms an acute angle to the axis of the skull. The arch of *Mylagaulus* bends sharply posteriorly lateral to its origin so that the arch is parallel to the antero-posterior axis of the skull. At the posterior extremity it bends sharply medially to form almost a right angle with the expanded posterior region of the skull. The zygomatic arch of *Aplodontia* forms a slightly more acute angle with the anteroposterior axis of the skull posterior to its origin. Close to its posterior extremity the arch bends medially and posteriorly, then medially and anteriorly forming a V before joining the expanded posterior region of the skull.

In both *Mylagaulus* and *Aplodontia* the anterior surface of the zygomatic arch is pierced by the infra-orbital foramen. It is roughly circular and large enough to have transmitted a small slip of muscle, but not an appreciable part of the masseter medialis. If the infra-orbital foramen did transmit a slip of muscle there is no reflection of the condition evident on the rostrum anterior to the foramen.

The jugal region of the zygomatic arch of *Mylagaulus* bears a strong postorbital process which is directed dorsally toward the postorbital process of the frontal. Except for KU32043?, all University of Kansas specimens of *Aplodontia r. rufa* lack a postorbital process on the jugal area. The exception, KU32043?, exhibits what might be an incipient postorbital process of the jugal region. Specimens of the subspecies *Aplodontia rufa olympica* often exhibit "... prominent postorbital process on the jugals. . . ." (TAYLOR, 1918, p. 461).

The zygomatic plate of *Mylagaulus* is relatively

longer, wider and farther below the level of the infra-orbital foramen than is the zygomatic plate of *Aplodontia*. The zygomaseteric scar of *Mylagaulus* does not reach the inner base of the arch but is first developed on the undersurface of that part which bends posteriorly from the anterior root. The zygomaseteric scar of *Aplodontia* is first developed immediately external and ventral to the infraorbital foramen. The initial part of the zygomatic plate of *Mylagaulus* and of *Aplodontia* is separated from the anterior surface of the arch by a sharp angulation.

The internal surface of the arch in *Mylagaulus* tends to face somewhat dorsally in comparison with the internal surface in *Aplodontia* which is perpendicular to the horizontal plane. The undersurface of the posterior part of the zygomatic arch of *Aplodontia* exhibits a V-shaped plate which reflects the dorsal outline of the upper surface of the same part. This ventral V-shaped plate is present in the equivalent area of the arch of *Mylagaulus* but is not reflected in the dorsal outline; the apex of the V is pulled ventrally and anteriorly and the bony meatus is situated immediately behind it.

The squamosal of *Mylagaulus* is more nearly flat than the squamosal of *Aplodontia* which gently curves from the parietal over the braincase region; posteriorly, the squamosal of *Mylagaulus*, as well as in *Aplodontia*, is applied to the anterior surface of the lambdoidal crest. The post-zygomatic notch of *Mylagaulus* is in close association with the lambdoidal crest, being bounded by it posteriorly; the post-zygomatic notch of *Aplodontia* is bounded by an expansion of the squamosal anterior to the lambdoidal crest. The pre-lambdoidal or subsquamosal foramen of KU9808 is represented on the dorsal surface by a transverse series of three foramina along the base of the lambdoidal crest. Comparison, however, with AMNH17576 indicates this condition of KU9808 may be an artifact of preparation, for there appears to be but a single pre-lambdoidal foramen, amidst sculpturing, at the base of the crest. The pre-lambdoidal foramen of *Aplodontia* pierces the squamosal on the dorsal surface anterior to the crest.

The squamosal, in *Mylagaulus* and in *Aplodontia*, extends into the orbit. Immediately internal to the posterior root of the zygomatic arch of *Aplodontia* and marking the lateral limit of the braincase is a longitudinal sulcus. The coronoid process of the mandible hooks back over the skull between this sulcus and the posterior root of the arch. A shallow depression is present in the comparable area of *Mylagaulus*, but it is not clearly defined. The glenoid fossa of *Mylagaulus* and of *Aplodontia* is only partially external to the depression (sulcus) described above. The glenoid fossa of *Mylagaulus* is relatively longer than that of *Aplodontia* and is deeper because of a sharp ventral dip to the alisphenoid. The glenoid fossa of both genera is oblique to the axis

of the skull and is bounded posteriorly by the post-glenoid foramen.

The lambdoidal crest of *Mylagaulus*, as well as that of *Aplodontia*, is better developed laterally than in the midline. The crest of *Mylagaulus* is considerably better developed than that of *Aplodontia* and forms a flattened and transversely widened plate when viewed posteriorly. The occiput of *Mylagaulus* is more inclined forward and in posterior view is more nearly flat than in *Aplodontia*. The occiput of KU9808 is inclined so far forward that the median dorsal part of the transverse crest is opposite the posterior root of the zygomatic arch. The crest of *Mylagaulus* AMNH17576 is not inclined so far forward but the specimen is a younger individual and its crest is probably less developed than in an adult.

In *Mylagaulus* and *Aplodontia* the occipital region is remarkably similar in morphology. This region in KU9808 is damaged and the sutures are indistinct; therefore, the bulk of the comparisons utilize AMNH17576.

The mastoid plate of both *Mylagaulus* and *Aplodontia* is of the same shape. A comparison between KU9808 and AMNH17576 indicates that increased age is correlated with an increase in size of the mastoid plate, as in *Aplodontia* (TAYLOR, 1918, p. 444). The mastoid plate of AMNH17576 and of *Aplodontia* is continuous with the auditory bulla.

The supraoccipital sends out lateral extensions dorsal to the mastoid plate of both *Mylagaulus* and *Aplodontia*. The flange of bone forming the lateral extremity of the occiput is separated from the supraoccipital by a post-tympanic extension of the squamosal of both genera. This flange could be an extension of the supraoccipital or perhaps, as proposed by MATTHEW (1924, p. 80) for AMNH17576, an extension of the parietal (as in hystricomorph rodents). The condition has not been determined for *Aplodontia*.

A palatal view of AMNH17576 shows a flask-shaped auditory bulla with a long, outwardly directed neck or bony meatus, as in *Aplodontia*. The bony meatus is closely applied to the ventral, anterior surface of the occipital plate in both genera.

The foramen magnum and basioccipital of *Mylagaulus* cannot be described because of lack of material. Definite presphenoid, basisphenoid and basioccipital sutures cannot be seen either in KU9808 or in AMNH17576. The basicranial region of *Mylagaulus* dips underneath the secondary palate at a sharper angle than in *Aplodontia*, specimens of which exhibit this dip to varying but lesser degrees.

The alisphenoid is applied to a part of the anterior surface of the auditory bulla of *Mylagaulus*, AMNH17576, as in *Aplodontia*. An alisphenoid canal is present in both genera, having the same relationship to associated structures. Because of the basicranial plunge beneath the secondary palate, the alisphenoid of *Mylagaulus* dips more sharply ventrally than in *Aplodontia*.

It is not possible to make a detailed comparison of the bones within the orbit because those of *Mylagaulus* are either damaged or have the sutures obliterated. The conformation of the orbital region of *Mylagaulus* and of *Aplodontia* is strikingly similar. A comparison made by MCGREW (1941, fig. 2, p. 7, 8) of the foramina in the area anterior to the sphenoidal fissure reveals that the pattern is similar in *Mylagaulus* and *Aplodontia*. A difference that is of special interest is the presence of a foramen, anterior to the sphenopalatine foramen and above the enlarged P4 of *Mylagaulus*; this foramen is absent in the comparable area of *Aplodontia*.

The pterygoid wings of both KU9808 and AMNH-17576 are broken off but the condition of both suggests they were important elements, more so than in *Aplodontia*. The superior pterygoid fossa of *Mylagaulus* is relatively better developed than is this fossa in *Aplodontia*; it is longer and wider and tends to encompass the opening of the alisphenoid canal.

The posterior border of the secondary palate of *Mylagaulus* has a median projection; in *Aplodontia* it is V-shaped with the apex pointing anteriorly. The tooth-rows and secondary palate of *Mylagaulus* are compressed anteroposteriorly by comparison with *Aplodontia*. The tooth-rows are parallel in both genera but seem to diverge anteriorly in *Mylagaulus* because of the difference in size between the anterior and posterior cheek-teeth. A small foramen is situated medial and posterior to M3 in *Mylagaulus* (better developed in AMNH17576 than in KU9808) and in *Aplodontia*. The two palatine foramina of both genera are opposite M2 and are larger in *Mylagaulus*. A groove runs anteriorly from each palatine foramen, a condition which is better developed in *Mylagaulus*.

Anterior to the first cheek-tooth the maxillary region of *Mylagaulus* curves sharply dorsad and then horizontally before the maxillary-premaxillary suture; this creates an arched appearance immediately anterior to the secondary palate. This profile is faintly developed in some specimens of *Aplodontia* whereas in others the undersurface of the rostrum is almost level with the plane of the secondary palate.

MANDIBLE

Plate 1, Table 1

The mandible is deeper (depth measured below p4) and shorter (length measured from posterior border of incisive alveolus to posterior margin of tooth-row) in *Mylagaulus* than in *Aplodontia*. The depth of the mandible of KU9808 is three-fourths of its length; the depth of the mandible of KU32020 ♂ is two-fifths of its length. The diastema between the incisor and p4 of *Mylagaulus* is relatively deeper and relatively longer than in *Aplodontia*. The length of the diastema in KU9808 is two-fifths of the length of the mandible, whereas, in KU32020 ♂ it is three-eighths of the length. The mental

foramen in each genus is half-way down the external surface of the dentary. The mental foramen of *Mylagaulus* is opposite the midpoint of the diastema; the foramen of *Aplodontia* is opposite a point two-thirds of the length of the diastema posteriorly.

The coronoid process of *Mylagaulus* is oblique to the dentary and forms a 55- to 60-degree angle in KU9808 to the body of the mandible; the coronoid process of *Aplodontia* is perpendicular to the dentary. The coronoid process of KU9808 is slender and barely hooked backward. The coronoid process of *Aplodontia* is stout and in outline varies from being hooked backward strongly to one in which the hook is scarcely developed (TAYLOR, 1918, p. 444).

The condyloid process and condyloid tubercle of both genera are inclined medially; this inclination is more pronounced in *Mylagaulus*. The condyloid process of *Mylagaulus* is stouter as a whole. The angular process of *Aplodontia* may best be described by quoting from ELLERMAN (1941, p. 255): "Mandible with outer side of angular process pulled inwards to an abnormal degree; to such an extent that the posterior border is horizontal, and the two edges of this process form the base of a triangle which has for its apex the condylar process." This region in KU9808 is broken, but the remaining parts show this condition was present, although to a lesser degree than in *Aplodontia*.

The dorsal masseteric ridge of *Mylagaulus* does not extend anterior to the angular process on the external surface of the mandible as does that of *Aplodontia*. This ridge is pronounced in both genera and runs along the angular process toward the external base angle of the "triangle" described above. The masseteric fossa of *Mylagaulus* is deeper and better developed than that of *Aplodontia*. In relation to this better development of the masseteric fossa, the anterior border is formed by a ridge running ventrally from the posterior border of the condyloid process and perpendicular to the dorso-ventral plane. The comparable area of *Aplodontia* is thickened. In both genera, the fossa is bounded ventrally by the dorsal masseteric ridge.

The ventral masseteric ridge of *Mylagaulus* is nearly perpendicular to the long axis of the dentary, but at the ventral border the ridge curves backward and inward toward what would be the internal posterior tubercle of the medial border of the angular process (this area of KU9808 is missing). The ventral masseteric ridge of *Aplodontia* is at an acute angle to the dorsal masseteric ridge, approaches the ventral surface at an angle, and traverses it to join the posteromedial tubercle of the inflected angular process.

The inferior pterygoid depression, enclosed by the angular process, is better called a shelf than a depression. Because of damage to this area of KU9808 an exact comparison cannot be made but it would seem that the inferior pterygoid depression was of greater height but

not so deep anteroposteriorly as this depression in *Aplodontia*.

The sulcus ascendens of *Mylagaulus* is relatively larger than that of *Aplodontia*; in both genera it is separated from the inferior pterygoid depression by a ridge. The inferior mandibular foramen of *Mylagaulus* and of *Aplodontia* is situated on this ridge.

Inferiorly and posterior to the diastema, the dentary of both *Mylagaulus* and *Aplodontia* bulges outward; this bulge is less pronounced in *Mylagaulus*. Immediately posterior to this bulge in both genera the ventral masseteric ridge crosses onto the ventral surface of the mandible causing another, more pronounced, bulge.

TABLE 1. Comparative Measurements of Axial Skeleton, in Millimeters

	<i>Mylagaulus</i> (a) KU9807, KU9808	<i>Aplodontia</i> KU32020♂
SKULL		
Total length (measured from tip of nasals to median part of lambdoidal crest)	51.0(a,c)	70.0
Width across zygomata (measured across widest part of arch)	58.0(c)	56.0
Length of skull encompassed by zygomata	33.0(b)	39.0
Depth of zygomatic arch at anterior root	14.5(b)	7.5
Length of rostrum (measured from posterior border incisive alveolus to anterior border of alveolus of P4)	15.0(a)	20.0
Width across occiput	60.0(b)	50.0
MANDIBLE		
Length (measured from posterior border incisive alveolus to posterior margin tooth-row)	25.0(b)	32.0
Length of diastema	10.0(b)	13.0
Depth of mandible below p4	18.0(b)	12.5
VERTEBRAE		
Length of centrum of 11th thoracic	6.5(b)	7.0
Width of centrum of 11th thoracic (measured across anterior surface)	10.0(b)	7.5
Length of centrum of 5th lumbar	9.0(b)	10.0
Width of centrum of 5th lumbar (measured across anterior surface)	13.5(b)	8.5
Width across transverse processes of 5th lumbar	24.0(b,c)	17.0
Width across transverse processes of anterior free caudal	12.0(b,c)	6.5

(a) Measurements based on KU9807.

(b) Measurements based on KU9808.

(c) Measurements approximate because of damage.

DENTITION

The incisors of *Mylagaulus* and of *Aplodontia* are of the same absolute width. The cheek teeth of both genera are hypsodont. P3 of *Mylagaulus* is absent; P3 of *Aplodontia* is present as a functionless peg. P $\frac{4}{4}$ of both genera are important teeth and are larger than the succeeding molars. A highly specialized condition is developed in P $\frac{4}{4}$ of *Mylagaulus* which is not present in *Aplodontia*; these

teeth are greatly enlarged and increase in width below the occlusal surface.

The height of crown of P4 of *Mylagaulus* AMNH-17576, a young individual, is sufficient that the base of the tooth with its nearly-closed pulp cavities extends up into the orbit to a level above the infraorbital foramen, approaching the initial outflaring ventral surface of the postorbital process of the frontal; the basal one-third of the crown does not appear to have been covered with bone in life. There is less extreme crown height in P4 of the older individuals, *Mylagaulus* AMNH9043 and KU9808, this tooth in these having descended far enough because of wear for the orbital portion to be covered with bone. The available lower jaws of *Mylagaulus* (KU9808, AMNH9043) indicate only that p4 was enlarged and hypsodont. The height of crown of P $\frac{4}{4}$ of *Aplodontia* is not so extreme; in this genus the pulp cavities of the cheek teeth are open and the teeth ever-growing.

MATTHEW (1924, p. 79) suggests that as P $\frac{4}{4}$ of *Mylagaulus* erupts to compensate for wear, the molars behind them are progressively displaced from the jaw and the alveoli taken over by P $\frac{4}{4}$ so that in old age the dentition could possibly be functional without any molars; then, the dental formula of *Mylagaulus* could be expressed as $\frac{1.0.1.3-0}{1.0.1.3-0}$ (WILSON, 1949, p. 103). BLACK & WOOD (1956, p. 678) and DORR (1952) agree that, contrary to MATTHEW's idea (1924, p. 79) the molars of *Mylagaulus* are not progressively deciduous. Of possible pertinence to this debate, SHOTWELL (1958, p. 476) cites the dental formula $\frac{1.0.1.0}{1.0.1.0}$ in adult mylagaulids of the Hemphillian with young individuals, however, having small molars (SHOTWELL, 1958, fig. 15G, p. 467). The dental formula of *Aplodontia* is $\frac{1.0.2.3}{1.0.1.3}$.

There is some question about the homology of the small tooth immediately behind P $\frac{4}{4}$ in specimens of young mylagaulids. It has been identified as Dp $\frac{4}{4}$ by DORR (1952, p. 323) and as M $\frac{1}{1}$ by MATTHEW (1924), WILSON (1949), BLACK & WOOD (1956) and many others. The adult cheek dentition of *Mylagaulus* using DORR's interpretation (*op. cit.*) would be P $\frac{4}{4}$, M $\frac{1-2}{1-2}$; the alternate interpretation of MATTHEW (1924) would be P $\frac{4}{4}$, M $\frac{2-3}{2-3}$. Although the weight of opinion favors the latter interpretation, the studied specimens cannot settle this question of homology. *Mylagaulus* AMNH9043 and KU9808 each have in both upper and lower jaws two cheek teeth posterior to the enlarged P $\frac{4}{4}$ with no trace of the alveolus of the displaced cheek tooth; AMNH17576, the younger individual, also has this tooth missing but does show traces of the alveolus posterior to P4 (no mandible with this specimen).

The re-entrant folds and basins initially present in the tooth of *Mylagaulus* become worn and develop into a series of isolated enamel lakes, the number and disposi-

tion varying with the species as well as with the age of the individual, well-demonstrated by serial sectioning of selected teeth by McGREW (1941). Prior to wear the occlusal surface of the premolar of *Aplodontia* consists of several completely enclosed basins. With wear these enamel basins disappear and the pattern of the molars is simplified to an enamel ring which in the upper series has an externally directed mesostyle and in the lower series has an internally directed mesostylid.

A detailed comparison of the occlusal pattern of the specimens at hand would do little to further knowledge of the relationship of these two genera because of the pronounced dental specialization of *Mylagaulus*. McGREW (1941) deals with the question of dentition in the Aplodontioidea and by use of a series of fossil specimens of the families Mylagaulidae and Aplodontidae illustrates the relationship of the patterns of *Mylagaulus* and *Aplodontia*, and postulates that both patterns were derived from some common ancestral pattern.

VERTEBRAE

Table 1, Figures 1-4

CERVICAL VERTEBRAE

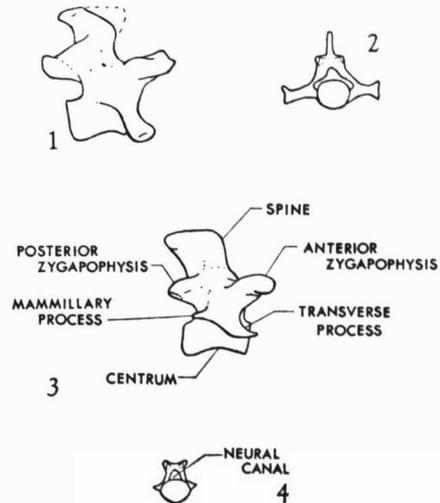
Since only fragments of the cervical vertebrae of KU9808 are remaining, a count is not possible. The fragments remaining of the cervical vertebrae of KU9808 are the lateral portions of the neural arches bearing the zygapophyses. The neural arch of *Mylagaulus* seemingly was more compressed anteroposteriorly than the neural arch of *Aplodontia*. The zygapophyses of *Mylagaulus*, unlike those of *Aplodontia*, are smoothly continuous with, rather than being extensions from, the neural arch. The anterior zygapophyses of *Aplodontia* are nearly horizontal, anteriorly directed projections from the neural arch with reciprocal posterior zygapophyses. The zygapophyses of *Mylagaulus* are longer, forming the entire lateral portion of the neural arch and overlap considerably on the same vertebra; there is little overlap of the zygapophyses of *Aplodontia* on the same vertebra. In both genera, the anterior zygapophysis is barely concave and the posterior zygapophysis is barely convex. The scant remaining part of the walls enclosing the vertebral canal of KU9808 suggests that the cervical vertebrae of *Mylagaulus* extended relatively more laterally than in *Aplodontia*.

THORACIC VERTEBRAE

No single thoracic vertebra of KU9808 is completely undamaged so the following description is incomplete and, moreover, is composite taking into account the possible variation along the vertebral column. Both *Mylagaulus* and *Aplodontia* have thirteen thoracic vertebrae. The centra of the thoracic vertebrae of *Mylagaulus* are relatively shorter and broader than the centra of *Aplodontia*. The anterior surfaces of the centra of both

genera tend to be flat and the posterior surfaces concave. This tendency is more pronounced in *Mylagaulus*.

On the anterior thoracic vertebrae the facet for the capitulum of the rib in both genera is situated partly on the posterior margin of one centrum and partly on the anterior margin of the succeeding centrum. The facet for the capitulum of the rib of *Mylagaulus* appears to shift caudally on the posterior thoracic vertebrae, as in *Aplodontia*, so that the articulation is no longer intercentral. The transverse process of *Mylagaulus* and *Aplodontia* is divided into ventral and dorsal parts; the ventral part bears a flattened facet for articulation with the tuberculum of the rib and decreases in development in posterior progression while the dorsal part becomes better developed in posterior progression, becoming the mammillary process of the lumbar vertebrae. The anterior thoracic vertebrae of *Mylagaulus* and of *Aplodontia* bear strong neural spines, which are heavier in *Mylagaulus*. Articulation of the posterior thoracics of both genera is like that of the succeeding lumbar.



FIGURES 1-4. *Mylagaulus laevis*, KU9808; *Aplodontia rufa*, KU32020 ♂. —1, Lateral view of fifth lumbar, KU9808. —2, Posterior view of anterior free caudal vertebra, KU9808. —3, Lateral view of fifth lumbar, KU32020 ♂. —4, Posterior view of anterior free caudal vertebra, KU32020 ♂. [All ×1.]

LUMBAR VERTEBRAE

The complete lumbar region of KU9808 is not present so the vertebral count must be given as 5+?. The lumbar region of *Aplodontia* consists of six vertebrae. The centra of *Mylagaulus* are shorter and broader than the centra of *Aplodontia*. The centra of KU9808 are about the same length as the centra of adult specimens of *Aplodontia* examined but are half again as wide. The centra of both genera have a ventral median ridge developed.

The transverse process of the fifth lumbar of *Mylagaulus* is a blade of bone directed more horizontally and less anteriorly than in *Aplodontia* and does not have any mammillary process. The comparable process of *Aplodontia* does not have a bladelike shape; it curves anteriorly and has a trace of a mammillary process on the posterior margin. The first lumbar of *Mylagaulus* exhibits a mammillary process which is relatively shorter and stouter than the comparable process of *Aplodontia*. The articular facet of the anterior zygapophysis in both genera faces mediad. The posterior zygapophysis in both genera is reciprocal to, and fits into a groove-like arrangement of, the anterior zygapophysis.

The neural spines in *Mylagaulus* and *Aplodontia* are elongated longitudinally and keeled on the dorsal surface. Although the extremities of the neural spines of the lumbar vertebrae of *Aplodontia* are not in contact, they may have touched together in *Mylagaulus*.

SACRUM

The sacrum of KU9808 is missing but part of the type material for the species *Mylagaulus laevis* (*M. monodon* MATTHEW, 1901) is a sacrum affixed to the ilia, which is used in the following comparisons.

The sacrum of *Mylagaulus* consists of at least four vertebrae but the broken posterior surface of the fourth sacral vertebra of AMNH9043 indicates that at least one more vertebra entered into the sacrum; the sacrum of *Aplodontia* consists of five vertebrae. Three of the sacral vertebrae of *Mylagaulus* are affixed to the ilia, whereas, only two sacral vertebrae of *Aplodontia* are affixed to the ilia.

The neural spines in both genera have fused into a plate, pierced by three foramina in *Mylagaulus* and by two foramina in *Aplodontia*. The zygapophyses in both have fused together and to the fused transverse processes, acting as a superior buttressing plate which is better developed in *Mylagaulus*. The anterior zygapophyses and posterior zygapophyses of the sacral complex in both have functional facets.

CAUDAL VERTEBRAE

A count of the caudal vertebrae of KU9808 is not possible. Of particular interest is a caudal vertebra of *Mylagaulus*, which is identified as the most anterior free caudal because of its well developed neural canal (relative to other caudals), well developed anterior zygapophyses and the presence of a neural spine. The transverse processes of this vertebra of *Mylagaulus* are directed horizontally and are perpendicular to the body of the vertebra. They are thickened at the distal extremity. The vertebra appears to be of the correct size to fit snugly between the dorso-medial borders of the ischia. None of the caudal vertebrae of *Aplodontia* has a neural spine, nor do any of them show the expansion and longitudinal

thickening at the end of the transverse process as described above.

The more posterior caudal vertebrae of *Mylagaulus* do not have a neural spine. They are wider relative to their length than posterior caudal vertebrae of *Aplodontia*.

RIBS

KU9808 has thirteen ribs; each specimen of *Aplodontia* examined had thirteen ribs. The anterior ribs of both genera are double-headed; the capitulum articulates with the centrum, and the tuberculum articulates with the transverse process. The heads come closer together in caudad progression. The angles of the dorsal part of the anterior ribs form right angles with the centra. The first rib of *Mylagaulus* and of *Aplodontia* is stouter than the succeeding ribs. The neck of the first rib of *Mylagaulus* is longer, the tuberculum better developed and the distal end is more flaring than is the first rib of *Aplodontia*.

PECTORAL GIRDLE AND FORELIMB SCAPULA

Table 2, Figures 5-8

The scapula of *Mylagaulus* appears to have the same outline—almost quadrangular with thickened borders—as in *Aplodontia* although part of the cranial border, cranial angle and adjoining area of KU9808 are missing. In KU9808 the scapula is approximately two-thirds again as wide anteroposteriorly (measured along anteroposterior midline of scapula), one-fourth again as long dorsoventrally (measured from point opposite origin of scapular spine on vertebral border to glenoid cavity) as the scapula of KU32020 ♂ and is considerably thicker.

TABLE 2. Comparative Measurements of Scapula, in Millimeters

	<i>Mylagaulus</i> KU9808	<i>Aplodontia</i> KU32020 ♂
Anteroposterior width (measured across mid-line perpendicular to axillary border)	32.0(a)	19.0
Dorsoventral length (measured from point opposite origin of spine on vertebral border to glenoid cavity)	43.5	35.0
Width supraspinous fossa (measured along mid-line described above)	14.0(a)	10.5
Width infraspinous fossa (measured along mid-line described above)	17.0	6.0

(a) Measurement approximate because of damage.

The vertebral border is thickened in both genera, but relatively more so in *Mylagaulus*. The spine arises dorsally from the thickened vertebral border at the same angle in both genera. Ventral to its origin, the spine of the scapula of both is perpendicular to the body of the scapula. The ventral two-thirds of the spine of KU9808 is missing.

The supraspinous fossa of KU9808 is no wider (width measured across anteroposterior mid-line), if as wide as, the infraspinous fossa (width measured across anteroposterior mid-line); in KU32020 ♂ the supraspinous fossa is nearly twice as wide as the infraspinous fossa. Nevertheless, the scapular notch of *Mylagaulus* reduces the size of the supraspinous fossa below that of the infraspinous fossa at the scapular neck.

The axillary border of *Mylagaulus* is relatively more thickened and turned more gently laterad, not forming the axillary ridge observed in *Aplodontia*. The infraglenoid tuberosity of *Mylagaulus* is better developed and more roughened than in *Aplodontia*.

The neck of the scapula of *Mylagaulus* is relatively thicker than the neck of *Aplodontia*. The long axis of the glenoid cavity in both genera is in the plane of the body of the scapula. The glenoid cavity of *Mylagaulus* is shorter anteroposteriorly and more nearly round than that of *Aplodontia*, which is more nearly ovoid in outline. The coracoid process of *Mylagaulus* forms the anterior part of the glenoid cavity and is relatively shorter and stouter than that of *Aplodontia* in which there is a slender hook situated on the anterior border of the glenoid. The coracoid process of both genera is strongly hooked anteromedial, the medial hooking being more pronounced in *Mylagaulus*.

The medial surface of the scapula of both genera is slightly concave. The medial surface of the scapula of *Aplodontia* is marked by three muscular lines or ridges, of which the two outer merge with the cranial and axillary borders respectively at the neck of the scapula. In KU9808 two muscular lines (area of third ridge is in the missing cranial angle region) converge toward, but fade before reaching, the neck of the scapula.

CLAVICLE

The clavicle of KU9808 is seemingly articulated with the sternum, as in *Aplodontia*; the lateral half of the clavicle of KU9808 is missing. The sternal articulation of the clavicle of *Mylagaulus* is nearly circular in cross section and is relatively better developed than in *Aplodontia* which has an articular area that is oval in cross section. The shaft of the clavicle of KU9808 is thicker and less flattened than is the transversely flattened shaft of *Aplodontia*.

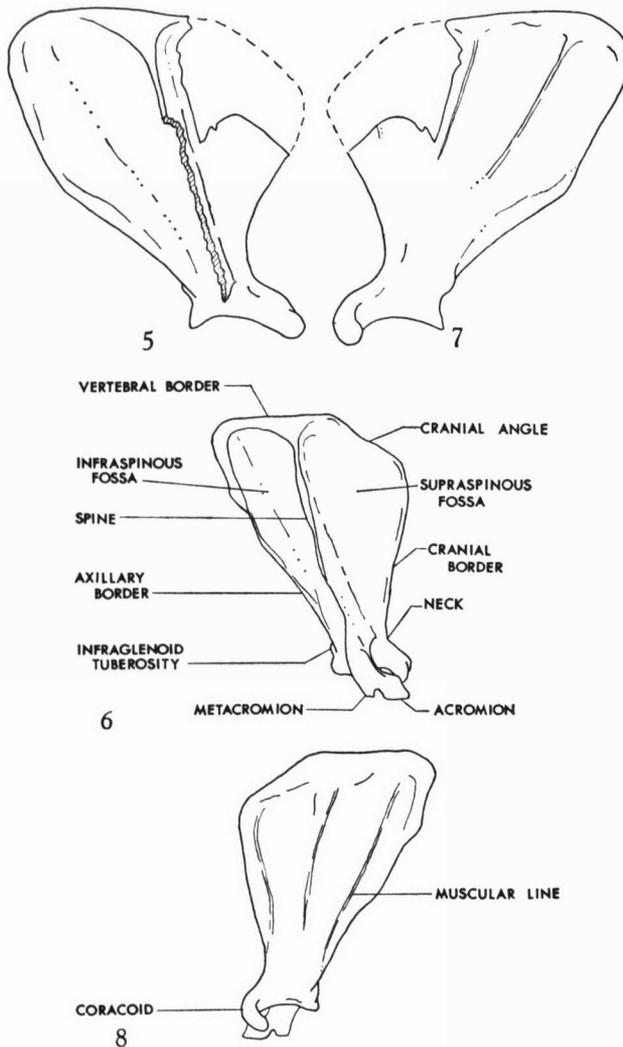
HUMERUS

Table 3, Figures 9-12

The humerus in *Mylagaulus* (KU9808, KU9969) is longer (length measured from most proximal surface of head to center of distal articulation) and relatively stouter than the humerus of KU32020 ♂. The humerus is more curved in *Mylagaulus* than in *Aplodontia*. In *Mylagaulus*, the humerus bends medially in its proximal half; the remaining part of the humerus is almost straight.

In both genera, the head is in line with the body of the element. All of the greater tuberosity and most of the lesser tuberosity of KU9808 is missing; consequently, comparisons involving this region are made mainly with KU9969. The greater tuberosity of KU9969 is about half again as large as the lesser tuberosity and bears two clearly marked depressions, as in *Aplodontia*. One of these depressions is dorsal and the other is lateral.

Anteriorly, the intertubercular sulcus of KU9969, unlike that in *Aplodontia*, is not defined, although there is a deep groove running obliquely across the lesser tuberosity which is not present in *Aplodontia*. Between



FIGURES 5-8. *Mylagaulus laevis*, KU9808; *Aplodontia rufa*, KU32020 ♂. —5, Lateral view of right scapula, KU9808. —6, Lateral view of right scapula, KU32020 ♂. —7, Medial view of right scapula, KU9808. —8, Medial view of right scapula, KU32020 ♂. [All ×1.]

the lesser tuberosity and head of both genera is a roughened surface, which is relatively more widespread in *Mylagaulus*. Below the lesser tuberosity of *Mylagaulus*, in a region comparable to a roughened area in *Aplodontia* for muscle attachment, is developed a median ridge which persists to immediately above the level of the deltoid tuberosity.

TABLE 3. *Comparative Measurements of Humerus, in Millimeters*

	<i>Mylagaulus</i> KU9969	<i>Mylagaulus</i> KU9808	<i>Aplodontia</i> KU32020♂
Length (measured from proximal surface head to center of distal articulation)	52.0	51.0	43.0
Distance from proximal surface head to lower margin deltoid process	33.5	33.5	19.5
Transverse width of proximal epiphysis	15.5	?	12.5
Transverse diameter of shaft at mid-line	9.0	9.5	5.0
Width across epicondylar processes	23.0	22.0	16.0

Anteriorly, the greater tuberosity of KU9969 is continuous with the deltoid crest, as in *Aplodontia*. The deltoid crest of *Mylagaulus* is close to the shaft, flattened, and terminates in a lobate deltoid process; the deltoid crest of *Aplodontia* rises abruptly from the shaft of the humerus, is a sharp ridge, and terminates in a sharp deltoid process. The deltoid crest of *Mylagaulus* is less lateral in position than is the crest of *Aplodontia*. The long axis of the deltoid tuberosity in both genera is in line with the shaft of the humerus. The deltoid tuberosity of *Mylagaulus*, the major part of which is below the midpoint, is relatively farther down the shaft of the humerus than in *Aplodontia* where the major part is above the midpoint. In *Mylagaulus*, a minor ridge from the deltoid tuberosity blends ventrally into the medial epicondyle. The same condition is present to a greater extent in *Aplodontia*.

Below the level of the deltoid tuberosity the humerus in both genera flares out laterally and medially to form the ectepicondylar process and external epicondyle, and internal epicondyle respectively. The ectepicondylar process of both genera is a broad, winglike plate of bone; that of *Mylagaulus* is better developed. The internal epicondyle of *Mylagaulus* and of *Aplodontia* is pierced by the entepicondylar foramen, which in *Mylagaulus* is smaller. The medial surface of the medial epicondyle of both genera is roughened. The medial extremity of the medial epicondyle has a tendency, more pronounced in *Mylagaulus*, to bend posteriorly. On the posterior surface of the medial epicondyle of *Mylagaulus* and of *Aplodontia* is situated a deep fossa; this is relatively deeper in the former.

The trochlea and capitulum of both genera are not distinct from each other. The radial fossa of *Mylagaulus*

is a more distinct entity than in *Aplodontia* where it is not sharply separated from the ectepicondylar fossa.

The olecranon fossa of *Mylagaulus* is shallower than in *Aplodontia*. In *Mylagaulus*, the olecranon fossa is as wide as the articulating facet above which it is situated; in *Aplodontia* this fossa is not so wide as the articulating facet. The distal articulating facet of *Mylagaulus* is widened in proportion to the increase in size of the humerus over that in *Aplodontia* but its height has not increased to the same degree.

ULNA

Table 4, Figures 13, 14

In both *Mylagaulus* and *Aplodontia* the ulna is the longest bone of the forelimb. The ulna of *Mylagaulus* is longer than that of *Aplodontia*, the total length being in proportion to the increase in size of the humerus in *Mylagaulus*. However, the proportions of the ulna proper are different in the two genera. From the posterior edge of the semilunar notch to the tip of the styloid process the ulnae of KU9808 and KU32020♂ are of the same absolute length. The difference in total length of the ulna is due to an increase in length of the olecranon of KU9808. The ulna of *Mylagaulus* is more robust than that of *Aplodontia*.

The shaft of the ulna of *Mylagaulus* is gently curved in one plane and that of *Aplodontia* is curved in two planes. Viewed laterally, the ventral margin of the ulna of *Mylagaulus* curves first ventrally and then dorsally, tapering to a styloid process. Viewed laterally, the ventral margin of the ulna of *Aplodontia* follows the path described above; viewed dorsally, the central third of the shaft is bowed outward slightly.

From both lateral and dorsal aspects, the olecranon of *Mylagaulus* is broader than is that of *Aplodontia*. The dorsal edge of the olecranon of *Mylagaulus* is blunt; the edge in *Aplodontia* is sharp and narrow. The tip of the olecranon of *Mylagaulus* is bent mediad and expanded more than in *Aplodontia*. In both, the ventral margin of the ulna is expanded into a flattened ridge sometimes

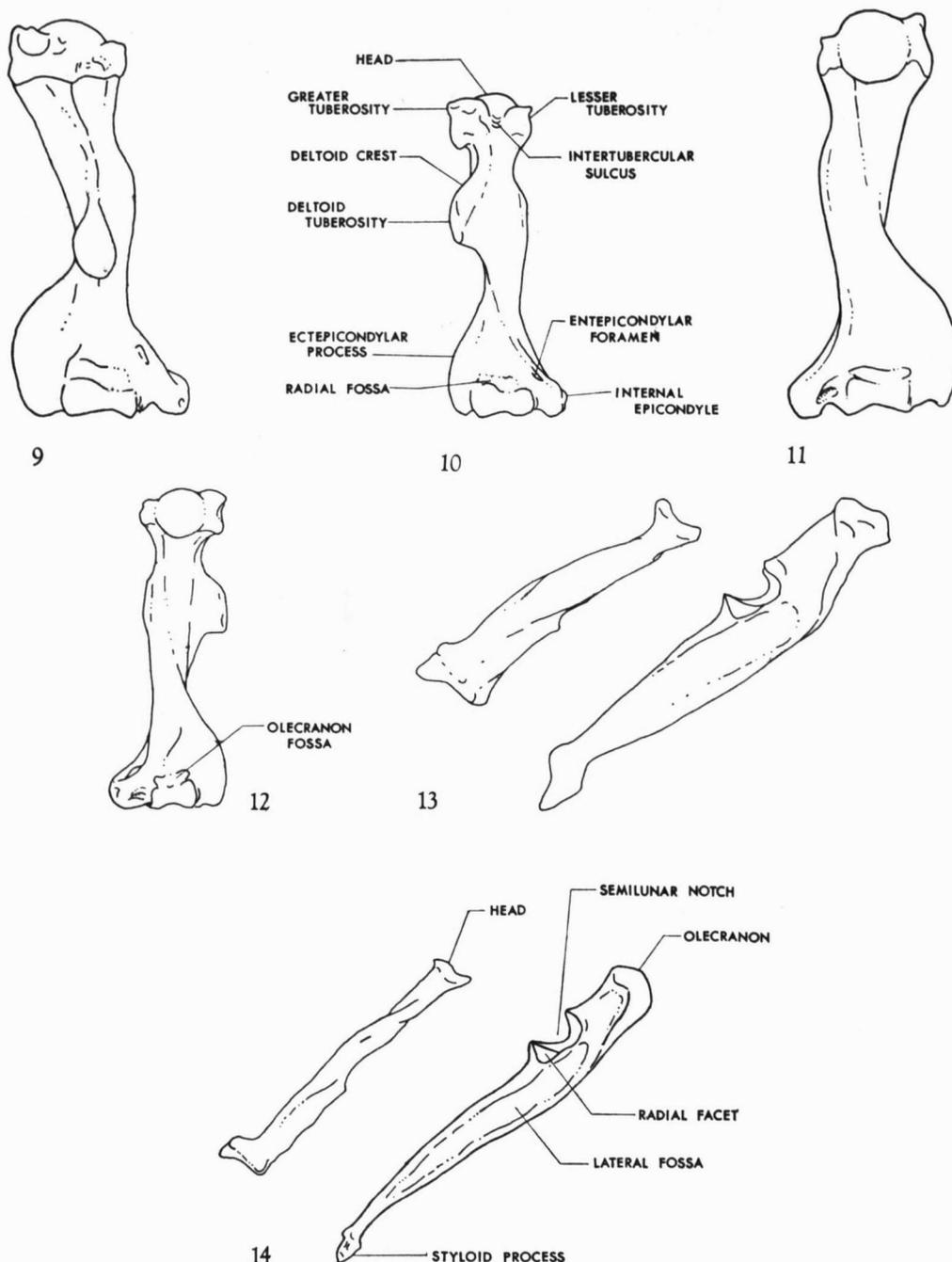
TABLE 4. *Comparative Measurements of Ulna and Radius, in Millimeters*

	ULNA		
	<i>Mylagaulus</i> KU9808	<i>Mylagaulus</i> KU9808	<i>Aplodontia</i> KU32020♂
Length of ulna (measured from posterior end of olecranon to tip of styloid process)	62.5		55.0
Length from posterior lip of semilunar notch to tip of styloid process	46.0		46.0
Dorso-ventral depth immediately distal to radial facet	8.5		5.0
	RADIUS		
	<i>Mylagaulus</i> KU9969	<i>Mylagaulus</i> KU9808	<i>Aplodontia</i> KU32020♂
Length	?	38.0	39.5
Transverse width across head	7.7	7.5(a)	6.0
Width across distal end	?	10.0(a)	7.5

termed the bicipital ridge (Howell, 1926); the bicipital ridge of *Mylagaulus* is better developed.

Dorsally, the coronoid process and the dorsal lip of

the semilunar notch are in line with each other and set at an angle to the body of the ulna in *Mylagaulus*; the same is true of *Aplodontia*. The radial notch of KU9808



FIGURES 9-14. *Mylagaulus laevis*, KU9808; *Aplodontia rufa rufa*, KU32020 ♂.

- 9, Anterior view of right humerus, KU9808. ——— 10, Posterior view of right humerus, KU32020 ♂. ———
 Anterior view of right humerus, KU32020 ♂. ——— 13, Lateral view of left radius and ulna, KU9808. ———
 11, Posterior view of right humerus, KU9808. ——— 14, Lateral view of left radius and ulna, KU32020 ♂.

[All ×1.]

has been damaged but the radial notch of KU9969 is a distinct facet and has the same shape as in *Aplodontia*. Below the radial notch which is situated laterally in both genera, the line of articulation with the radius can be traced to the styloid process. In *Mylagaulus* it is a relatively broader line than in *Aplodontia*, curves to the dorsal edge, and at the styloid process is barely over onto the internal surface of the ulna; in *Aplodontia*, the radius curves to the dorsal edge but does not reach the internal surface. The distal third of the radial line in both genera is a groove, considerably deeper in *Mylagaulus*.

The lateral and medial concavities in *Mylagaulus* appear to be less developed than in *Aplodontia*. The body of the ulna of *Mylagaulus* is less tapered anteriorly (toward styloid process) than this element in *Aplodontia*. The styloid process of *Mylagaulus* is disproportionately better developed than that of *Aplodontia*, although it maintains the same shape.

RADIUS

Table 4, Figures 13, 14

In both KU9808 and KU32020 ♂ the radius is of approximately the same absolute length and is shorter than the ulna by the length of the olecranon process and semilunar notch. Viewed dorsally, the curvature of the shaft of the radius is similar in *Mylagaulus* and *Aplodontia*; the shaft is gently bowed laterally over the distal two-thirds of its length. Viewed laterally, there is a gentle dorsal bowing of the shaft in both genera. The radius of *Mylagaulus* is more robust than that of *Aplodontia*. In both genera, the shaft is elliptical in cross section.

The head of the radius of *Mylagaulus* is relatively more expanded than that of *Aplodontia*. Despite some damage to the external edge of the head in KU9808 the shape is judged to be ovoid and is definitely ovoid in KU9969, as in *Aplodontia*. The radius in both genera is in contact along most of its length with the ulna. On the ulnar side of the radius of both genera for the distal third of its length, a narrow ridge is developed which fits into a groove on the ulna; this ridge in *Mylagaulus* is considerably better developed. On the lateral surface of the distal end of the radius of both genera there is a deep groove, terminating in the carpal articulation.

The distal articulating facet of *Mylagaulus* is relatively more expanded than the facet of *Aplodontia*. The distal facet of *Mylagaulus* has undergone rotation in comparison to that of *Aplodontia*. Viewed anteriorly, the distal articulating facet of *Mylagaulus* has been rotated 25 to 30 degrees externally with relation to the shaft. The carpal articulating surface in both genera has a styloid process developed on the dorsal edge which is concave.

MANUS

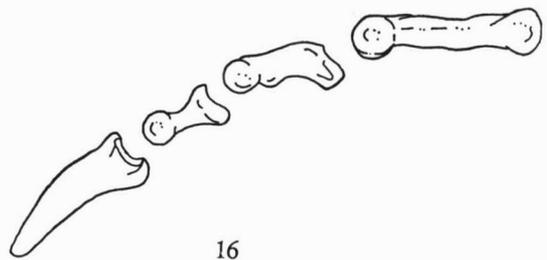
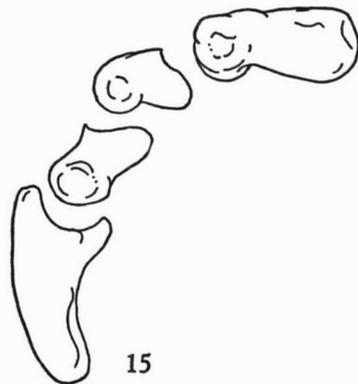
Table 5, Figures 15, 16

CARPALS

None of the carpal elements of KU9808 are present.

METACARPALS

The metacarpals of *Mylagaulus* are approximately the same length as but are thicker than those of *Aplodontia*. In both genera, distal articulations are limited to the anterior and ventral surfaces and the ventral surfaces of the distal articulations are keeled. In relation to the length of the metacarpal, the distal articulation is larger in *Mylagaulus* than in *Aplodontia*. In each genus there are two fossae, one on each side of the distal end of the metacarpal, which are relatively deeper in *Mylagaulus*.



FIGURES 15-16. *Mylagaulus laevis*, KU9808; *Aplodontia rufa rufa*, KU32020 ♂. ————15, Third metacarpal and digit, KU9808. ————16, Third metacarpal and digit, KU32020 ♂. [All $\times 2$.]

PHALANGES

What appears to be the third digit of KU9808 has been preserved in an articulated state and has been utilized for the following comparisons. The proximal phalanx is shorter (length measured along lateral longitudinal axis) and all three phalanges stouter in *Mylagaulus* than in *Aplodontia*. The proximal articulation in both genera is concave and notched inferiorly. The proxi-

mal articulation in *Mylagaulus* is relatively deeper and inclined forward; consequently, the dorsal border is more

fossae on the lateral surfaces of the distal ends of the phalanges in *Mylagaulus* are relatively deeper than those in *Aplodontia*.

TABLE 5. Comparative Measurements of Manus, in Millimeters

	<i>Mylagaulus</i> KU9808	<i>Aplodontia</i> KU32020 ♂
Total length third metacarpal	13.0	12.0
Length of head of third metacarpal	4.5	3.0
Breadth of head of third metacarpal	5.0	3.5
Length third proximal phalanx (along lateral long axis)	6.5	7.0
Breadth of distal articulation third proximal phalanx	4.5	3.0
Length of second phalanx, third digit (measured along lateral long axis)	6.5	4.5
Breadth of distal articulation second phalanx, third digit	4.5	2.5
Length of third ungual phalanx	11.5	8.5
Breadth of third ungual phalanx (measured across proximal end)	3.5	2.0

The ungual phalanx in both genera is elongated and blade-shaped, being flattened transversely. The proximal articulation of the ungual phalanx is concave and so shaped that it covers the anterior and dorsal parts of the preceding phalanx. The ungual phalanx of *Mylagaulus* is longer, deeper, and considerably heavier than that of *Aplodontia*.

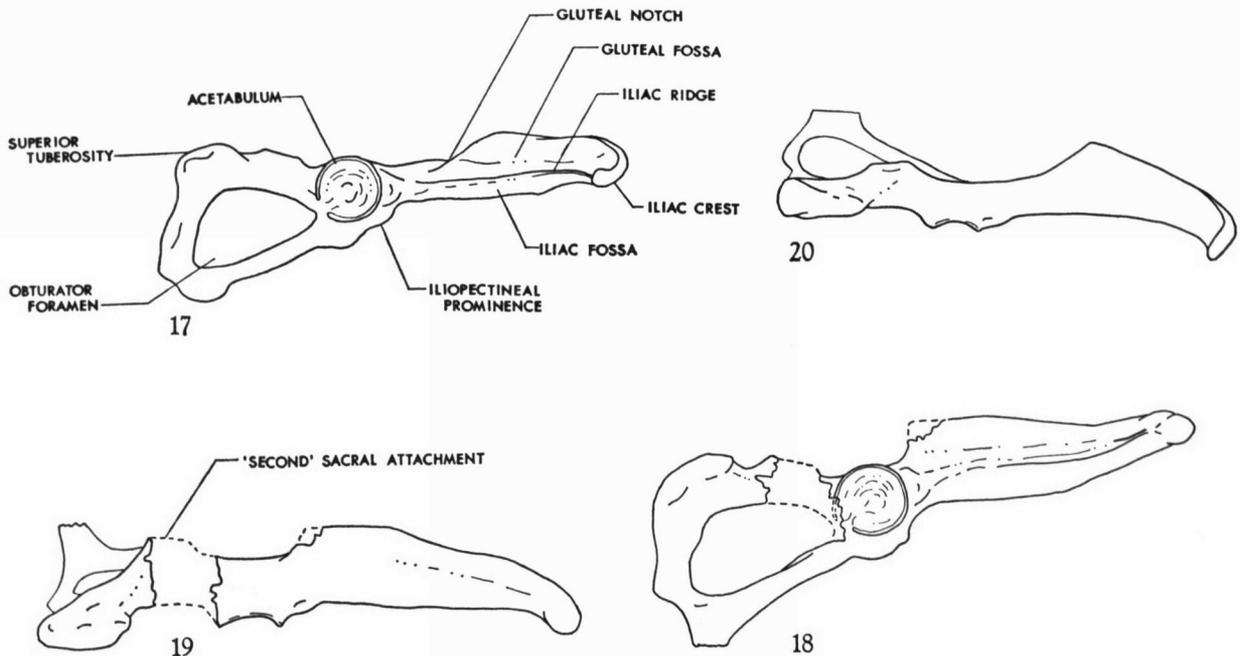
PELVIC GIRDLE AND HIND LIMB
PELVIS

Table 6, Figures 17-20

The pelvis of *Mylagaulus* is larger and more robust than that of *Aplodontia*, but not to the same degree as the pectoral girdle. Measured from the mid-point of the acetabulum, the pelvis of *Mylagaulus* is one-fifth again as long in its anterior part and one-third again as long in its posterior part as the pelvis of *Aplodontia*. There has been some increase in depth of the pelvis of *Mylagaulus* posterior to the acetabulum. The pelvis of *Mylagaulus* forms more of an angle with the vertebral column than does the pelvis of *Aplodontia*.

Superiorly, the ilia of *Mylagaulus* are more divergent than those of *Aplodontia*. The anterior part of the ilium in both bears an iliac crest which has less of a medial

anterior than in *Aplodontia*. The distal articulations of the proximal and middle phalanges of *Mylagaulus* are relatively enlarged by comparison with *Aplodontia*. The distal articulation in both genera is limited dorsally, being more pronounced in *Mylagaulus*; the distal articulation of the middle phalanx in both genera is not so limited superiorly as in the proximal phalanx. The



FIGURES 17-20. *Mylagaulus laevis*, KU9808; *Aplodontia rufa rufa*, KU32020 ♂.

17, Lateral view of right innominate bone, KU32020 ♂. ———18, Lateral view of right innominate bone, KU9808. ———19, Dorsal view of right innominate bone, KU9808. ———20, Dorsal view of right innominate bone, KU32020 ♂. [All ×1.]

extension in *Mylagaulus*. The iliac ridge in *Mylagaulus* and in *Aplodontia* extends from the iliac crest to the acetabulum on the lateral surface of the ilium, dividing it into a gluteal fossa superiorly, and an iliac fossa inferiorly. The iliac ridge in both genera is roughened and expanded immediately anterior to the acetabulum. The gluteal fossa of *Mylagaulus* is less excavated than that of *Aplodontia*; the iliac fossa of *Mylagaulus* is better developed than the iliac fossa of *Aplodontia*.

TABLE 6. Comparative Measurements of Pelvis, in Millimeters

	<i>Mylagaulus</i> KU9808	<i>Aplodontia</i> KU32020♂
Length of iliac crest to mid-point of acetabulum	42.5	35.0
Length from posterior margin of superior tuberosity to mid-point of acetabulum	28.5	22.0
Depth of ilium through posterior part of sacral attachment scar	11.5(a)	5.0
Anteroposterior length of sacral scar	21.0	17.0
Depth measured from dorsal border of superior tuberosity to level of pubic symphysis	29.0(a)	24.5
Anteroposterior length of pubic symphysis	4.0(a)	6.0
Transverse depth of pelvis at acetabulum (measured from dorsal lip to medial border)	9.0	6.5

(a) Measurement approximate because of damage.

The ventral border of the ilium of *Mylagaulus* is parallel to and close to the plane of the iliac ridge anteriorly, but diverges from it posteriorly in a gentle curve toward the iliopectineal prominence. The inferior border of the ilium of *Mylagaulus* is more ventral than that of *Aplodontia*, as well as more lateral.

The sacroiliac joint of *Mylagaulus* is lengthened posteriorly and has been shortened anteriorly compared to the sacroiliac joint of *Aplodontia*. The more ventral and less medial position of the inferior border of the ilium of *Mylagaulus* and a more posterior position of the gluteal notch offers a deeper surface dorsoventrally for the sacroiliac joint than is present in *Aplodontia*.

Although the dorso-medial border of the ischium of KU9808 is damaged, there is a medial inflection toward the vertebral column posterior to the acetabulum, as in *Aplodontia*. Articulation of the ischium with the caudal vertebrae cannot be definitely ascertained from KU9808 but the pelvis of *Mylagaulus* does suggest that the inflection was greater than that observed in *Aplodontia* where, in the specimens examined, there is no indication of a union of the ischium with the caudal vertebrae.

The superior tuberosity of *Mylagaulus* is relatively longer and higher above the dorsal lip of the acetabulum than in *Aplodontia*. The posterior (ischial) part of the obturator foramen in both *Mylagaulus* and *Aplodontia* is at a right angle to the horizontal.

The pubic rami of both genera are inclined postero-ventrad to the acetabulum. The pubic symphysis, formed by medial extensions of the rami, is well caudad in both.

Allowing for damage to KU9808, it seems that the pubic symphysis is shorter anteroposteriorly in *Mylagaulus* than in *Aplodontia*. The obturator foramen is of the same shape in both genera.

The acetabulum of *Mylagaulus* is relatively deeper and of greater diameter than the acetabulum of *Aplodontia*. The parts of the innominate elements bordering on, and incorporated into, the acetabulum of *Mylagaulus* are relatively thicker, to accommodate the increased depth, than in *Aplodontia*. Judging from what remains of the inferior border of the acetabulum of KU9808, the acetabular notch was in the same relative position—posteroventrad—as in *Aplodontia*.

FEMUR

Table 7, Figures 21-24

The femur in *Mylagaulus* is longer (measured from proximal surface of head to distal surface of patellar groove) and thicker (measured at midpoint) than in *Aplodontia*. The length and thickness of the femur of *Mylagaulus* is less than would be expected by comparison with its forelimb, although in keeping with the size of the pelvis. The femur of *Mylagaulus* is longer than its humerus on an absolute scale. However, the femur of *Aplodontia* is relatively longer in relation to its humerus than is the femur of *Mylagaulus* in relation to its humerus. The head of the femur in both genera is spherical and is shifted cranially and comparatively better developed in *Mylagaulus*; the greater development is in proportion to the depth of the acetabulum. The fossa for the ligamentum teres in *Mylagaulus* is relatively deeper than in *Aplodontia*.

The greater trochanter in both genera occupies the same relative position on the lateral side of the proximal epiphysis. The greater trochanter does not extend dorsally above the level of the head of the femur in *Mylagaulus*; it does extend slightly above the level of the head in *Aplodontia*. The lesser trochanter is on the medial side of the femur, beneath the level of the head of the femur, and has the same shape and same relative degree of development in both genera. The two trochanters are not connected posteriorly by a trochanteric ridge. The

TABLE 7. Comparative Measurements of Femur, in Millimeters

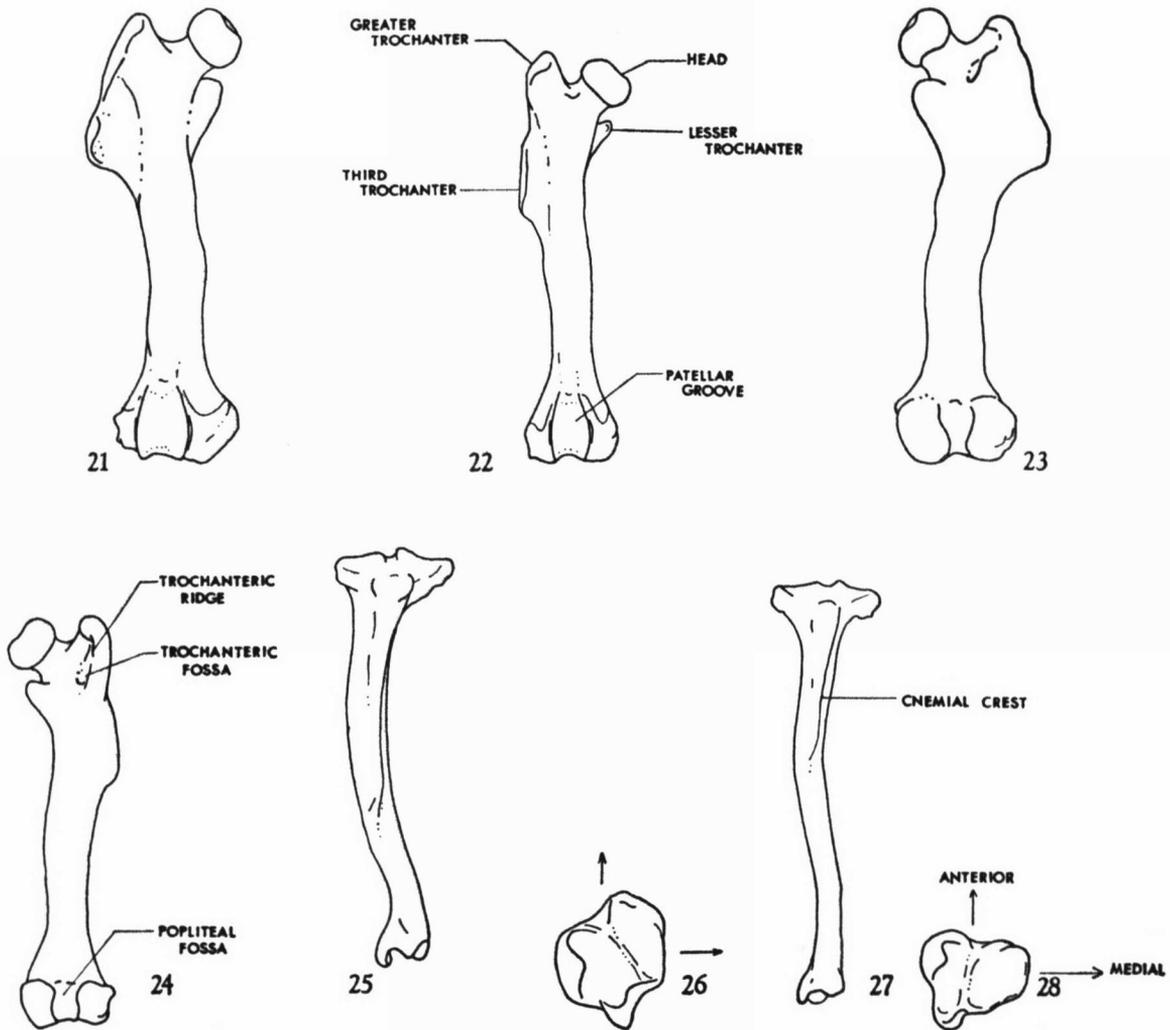
	<i>Mylagaulus</i> KU9808	<i>Aplodontia</i> KU32020♂
Length (measured from proximal surface of head to distal surface of patellar groove)	56.5	53.0
Anteroposterior diameter of head	8.5	6.5
Transverse width of shaft at mid-point	8.0	6.0
Transverse width through widest part of lateral crest perpendicularly through shaft	14.0	9.0
Anteroposterior width at mid-line	5.5	4.0
Transverse width of distal epiphysis	7.0	5.0
Breadth of patellar groove	14.5	12.5

trochanteric fossa of *Mylagaulus* is shallower than that of *Aplodontia*.

The lateral crest of *Mylagaulus* is well developed and is continuous with the external margin of the greater trochanter. The lateral crest in *Aplodontia* is not so well developed and is not continuous with the greater trochanter. The lateral border of the lateral crest in *Mylagaulus* is bent anteriorly forming a deep, broad fossa between the lateral limit of the crest and the shaft of the femur. This character is only suggested in *Aplodontia*. The lateral crest in both genera extends one-third of the length of the femur.

The patellar groove in *Mylagaulus* is broader and

more external than the groove of *Aplodontia* which is centered on the distal end of the femur. The fossae on the external surface of the lateral epicondyle of *Mylagaulus*, which probably represents attachments of the lateral head of the gastrocnemius and ligaments, are relatively better developed than those in *Aplodontia*, but have the same conformation. Fossae on the internal surface of the medial epicondyle are better developed in *Mylagaulus* but have the same arrangement as in *Aplodontia*. They probably represent the origin of the medial head of the gastrocnemius and attachments of ligaments. The popliteal fossa of *Mylagaulus* is deeper than in *Aplodontia*.



FIGURES 21-28. *Mylagaulus laevis*, KU9808; *Aplodontia rufa rufa*, KU32020 ♂.

- 21, Anterior view of right femur, KU9808. ———— 22, Anterior view of right femur, KU32020 ♂.
- 23, Posterior view of right femur, KU9808. ———— 24, Posterior view of right femur, KU32020 ♂.
- 25, Anterior view of right tibia, KU9808. ———— 26, Ventral view of tarsal articulating surface of tibia, KU9808.
- 27, Anterior view of right tibia, KU32020 ♂. ———— 28, Ventral view of tarsal articulating surface of tibia, KU32020 ♂. [Figs. 21-25, 27 ×1; figs. 26, 28 ×2.]

TIBIA

Table 8, Figures 25-28

The tibia of *Mylagaulus* is shorter than its femur; in *Aplodontia* the tibia is approximately equal to the length of the femur. The tibia in both genera exhibits torsion in the anteroposterior plane and in the transverse plane. Torsion in the transverse plane is more pronounced in *Mylagaulus*. The articular arm for the femur of *Mylagaulus* is relatively more expanded, but does not have the rounded triangular shape of proximal epiphysis of *Aplodontia*. This expansion in *Mylagaulus* is evident in the greater external extent of the proximal epiphysis compared to that in *Aplodontia*. The medial and lateral condyles in both genera are concave in the transverse plane and convex in the anteroposterior direction. The tuberosity is part of the epiphysis of *Mylagaulus* and of *Aplodontia*. Articulation of the fibula in *Mylagaulus* and in *Aplodontia* is at the external underside of the proximal epiphysis and the contact area is relatively larger in *Mylagaulus*.

Although the proximal end of the cnemial crest of *Mylagaulus* is situated at the same position with respect to the condyles as the crest of *Aplodontia*, it is more lateral with respect to the shaft because of a greater lateral extension of the epiphysis of *Mylagaulus*. The cnemial crest of *Mylagaulus* is twice as high as the crest of *Aplodontia*, which is a thin, sharp blade of bone. In *Mylagaulus*, the crest probably curves medially to run along the anterior surface before blending with the shaft below the mid-point; in *Aplodontia* it is on the anterior surface of the shaft and extends half the length of the

TABLE 8. Comparative Measurements of Tibia, in Millimeters

	<i>Mylagaulus</i> KU9808	<i>Aplodontia</i> KU32020♂
Length (measured from dorsal surface proximal epiphysis to ventral surface distal epiphysis)	50.0	53.5
Anteroposterior diameter of shaft at point one-third of way down shaft	11.0	8.0
Transverse diameter of shaft at point one-third of way down shaft	5.0	3.5
Transverse diameter of distal epiphysis	7.5	6.5

shaft. Consequently, the lateral fossa of *Mylagaulus* is better developed.

The interosseous crest of *Mylagaulus* is sharper and more clearly defined than this crest in *Aplodontia*. The medial crest of both genera follows the line of the shaft from the external limit of the medial epicondyle for two-thirds of the length of the element. The medial crest of *Mylagaulus* does not project so far from the shaft as in *Aplodontia*. Between the medial and interosseous crests of both is the caudal fossa which in *Mylagaulus* is a deep, narrow furrow and in *Aplodontia* is a broad, shallow fossa.

The tarsal articulating surface of *Mylagaulus* is relatively more expanded than that of *Aplodontia*, although in both genera the surface consists of two valleys separated by a ridge, which fits the trochlea or groove of the astragalus. The median valley is bounded by median and posterior malleoli which are relatively longer and more incurved in *Mylagaulus*. The lateral valley, bounded by an anterior malleolus of the tibia, is deeper in *Mylagaulus*. The entire distal articulation of the tibia of *Mylagaulus* has been rotated approximately 45 degrees with respect to the shaft when compared with the tibia of *Aplodontia*; consequently, the medial malleolus is more posterior and the lateral malleolus is more anterior. The posterior and lateral surfaces of the posterior malleolus of both genera are grooved dorsoventrally.

FIBULA

The fibula of KU9808 is represented only by fragments but much can be told from these, and from its reflection on the tibia, about its structure. The proximal epiphysis of the fibula of *Mylagaulus* and of *Aplodontia* is a separate entity from the epiphysis of the tibia. The shaft in *Mylagaulus* is relatively heavier than that of *Aplodontia* and has an interosseous crest developed in response to the interosseous crest of the tibia. Because of greater transverse bowing medially, and the anterior shift of articulation of the styloid process (lateral malleolus) of the fibula of *Mylagaulus*, the interosseous space is larger and the distal part of the fibula makes a shorter contact with the tibia than was observed in *Aplodontia*, where the fibula is in contact for one-third of its distal length. The internal surface of the styloid process of *Mylagaulus* and of *Aplodontia* bears a facet for articulation with the external surface of the astragalus.

PES

Table 9, Figures 27-30

The proportions of the pes of KU9808 are more delicate and the pes approaches in pattern that of *Aplodontia* more closely than does the manus.

TARSALS

The only tarsals present in KU9808 are the calcaneum and astragalus.

Astragalus. The shape and proportions of the astragalus of *Mylagaulus* and of *Aplodontia* are similar except for a slightly larger head in the former. The body of the astragalus in each is broader than high. The external condyle is wider than the internal condyle and is separated from it by the trochlea. The trochlea is pulley-like and extends over the dorsal surface and complete posterior surface of the astragalus of both genera. Two facets for articulation with the calcaneum are situated on the inferior surface of the body of the astragalus. The ex-

ternal facet is concave and articulates with the dorsal process of the calcaneum; the internal facet is smaller, separated from the external facet by a groove, and articulates with the dorsal surface of the sustentaculum of the calcaneum. The neck is short and the head roughly rounded.

TABLE 9. Comparative Measurements of *Pes*, in Millimeters

	<i>Mylagaulus</i> KU9808	<i>Aplodontia</i> KU32020 ♂
Proximodistal length astragalus	8.9	8.3
Mediolateral width astragalus	6.0	6.0
Dorsoventral depth astragalus	4.5	4.5
Anteroposterior length calcaneum	16.5	13.5
Internoexternal length of sustentaculum	9.5	18.5
Dorsoventral depth of shaft of calcaneum at midpoint	6.0	5.0
Dorsoventral depth of posterior extremity of shaft of calcaneum	8.0	5.5
Length of third metatarsal	17.0	15.5
Length of head of third metatarsal	3.5	2.5
Breadth of head of third metatarsal	3.5	3.0

Calcaneum. The calcaneum in both genera is T-shaped, the main shaft oriented anteroposteriorly and the sustentaculum oriented internoexternally. The calcaneum of *Mylagaulus* is more robust and relatively larger in comparison with its astragalus than in *Aplodontia*. The main shaft is relatively deeper, the posterior extremity of the shaft more rounded, the keel of the shaft more pronounced, and the sustentaculum broader in an anteroposterior direction in *Mylagaulus*. A groove situated on the lateral surface of the external part of the sustentaculum is more pronounced in *Mylagaulus* than in *Aplodontia*. Another groove runs along the dorsal root of the internal part of the sustentaculum of both genera. The anterior articulating surface of both *Mylagaulus* and *Aplodontia* is concave.

METATARSALS

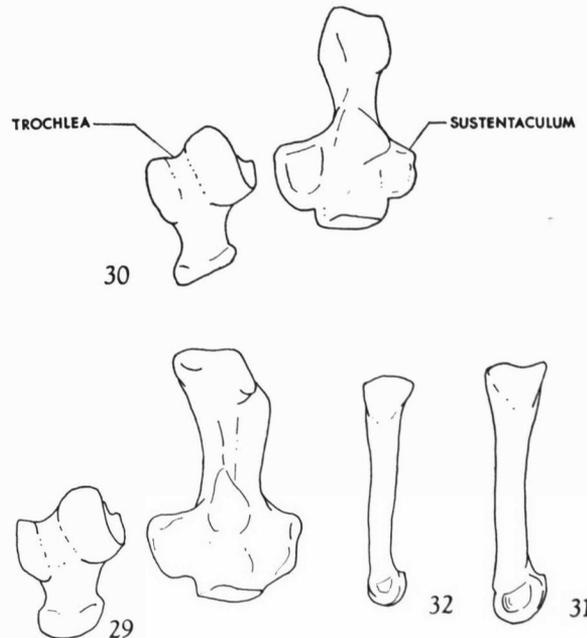
Because of the fragmentary nature of the remains of the metatarsals of KU9808, discussion will concern proportions and articulations only.

The metatarsal of *Mylagaulus* is slightly longer on an absolute scale than in *Aplodontia*, but is relatively more heavily developed. The head of the metatarsal in both bears a keel on the inferior surface, which is more pronounced in *Mylagaulus* and ends almost in a hook. The depressions on the lateral surfaces of the metatarsal are deeper in *Mylagaulus*. In comparison with *Aplodontia*

the head of the metatarsal of *Mylagaulus* is enlarged in relation to length and breadth.

PHALANGES

The phalanges of *Mylagaulus* are barely longer, but are considerably heavier than those of *Aplodontia*. The proximal articulation of the proximal phalanx of both genera is concave and notched on the inferior border, both conditions being exaggerated in *Mylagaulus*. The distal head of the proximal phalanx of both is bipartite with the greater part of the articulation limited to the inferior surface. The proximal articulation of the middle phalanx in both genera is concave and set at an angle to the body of the phalanx with the superior margin more anterior than the inferior margin. The head is deeply grooved, not so limited superiorly as in the proximal phalanx, and is more superior in *Mylagaulus* than in *Aplodontia*.



FIGURES 29-32. *Mylagaulus laevis*, KU9808; *Aplodontia rufa rufa*, KU32020 ♂. ————29, Dorsal view of left astragalus and calcaneum, KU9808. ————30, Dorsal view of left astragalus and calcaneum, KU32020 ♂. ————31, Lateral view of third metatarsal, KU9808. ————32, Lateral view of third metatarsal, KU32020 ♂.

[All ×2.]

DISCUSSION

Many of the similarities between the skeletons of *Aplodontia* and *Mylagaulus* are explicable on the basis of common habitat as well as on the basis of

phyletic relationship. A difference in degree of adaptation to this common habitat serves to explain many of the differences observed.

For progression through the dense medium of earth *Aplodontia* and *Mylagaulus* have developed a wedge-shaped head, which is flattened dorsally. The more flattened skull of *Mylagaulus* shows greater fossorial modifications than the skull of *Aplodontia* but the two are elaborations of the same pattern (Pl. 1). The greater tilting forward of the occiput, the greater flattening of the roof of the skull and the heavier zygomata all are reflections of its greater adaptation to underground existence. These greater fossorial modifications of *Mylagaulus* have led to a change in proportions of the skull as compared to those in *Aplodontia*; in many respects, *Mylagaulus* actually brings closer to a culmination the fossorial adaptations of *Aplodontia*.

The rostral region of a fossorial animal is important as the leading part of the axial skeleton in forward motion. Importance of the rostrum is shown by the ratio of length of rostrum to length of skull in *Aplodontia* in comparison with a nonburrowing animal such as *Sciurus*. The rostrum of *Mylagaulus* is relatively longer than the rostrum of *Aplodontia*, because of the greater specialization of the former. The shape of the rostrum of *Aplodontia* and of *Mylagaulus* is similar, but this may be due in part to a lack of masseter specialization onto the rostrum.

The skull of *Mylagaulus* is more nearly flat than the skull of *Aplodontia*, which in turn is more nearly flat than the skull of a non-fossorial mammal such as *Sciurus*. The flat skull and thick roof of the skull of *Mylagaulus* is an exaggeration of the trend seen in *Aplodontia*.

The presence of postorbital processes on the frontals and jugals of *Mylagaulus* does not exclude it from relationship with *Aplodontia*. The pre-Arikarean genera and some of the Arikarean genera of the Aplodontidae possessed these processes (WILSON, 1949, p. 102). They are still exhibited in some forms of *Aplodontia* as incipient processes. This is probably a phyletic divergence for while it could be postulated that these processes of *Mylagaulus* serve to protect the eye by ringing it with bone, typically fossorial rodents such as *Thomomys* and *Macrogeomys* do not possess them and a non-fossorial form, *Sciurus*, does. They do serve to show that the eye of *Mylagaulus* was small, as is the eye of *Aplodontia* (CAMP, 1918). Reduction of the eyes in both genera probably indicates lack of function underground.

A well-developed lambdoidal crest, shortening of the posterior region of the skull, lateral expansion of the occiput and tilting forward of the occiput of

Mylagaulus and of *Aplodontia* compared to *Sciurus* are all responses to fossorial existence. These developments provide firm attachments for some masticatory muscles and for muscles from the trunk region to hold the skull rigidly and solidly under stress of forward motion. The pattern of this region in *Aplodontia* and *Mylagaulus* is similar, but the latter shows greater expansion and development of areas where muscles attach and greater shortening of the skull.

The tendency of the zygomatic arch to become thin and even for a part of the arch to disappear in some fossorial mammals has been interpreted as a means of reducing friction (SHIMER, 1903, p. 822). This tendency is not evident in *Mylagaulus* and *Aplodontia*, for both have the primitive sciuriform musculature; the origins of the masseter medialis and masseter lateralis are on the zygomatic arch in each genus. A fossorial mammal such as a mole (insectivore) does not have this complicated musculature and the arch therefore can be reduced and in the related shrews disappears. Such reduction would decrease the efficiency of the masticatory mechanism of *Mylagaulus* and of *Aplodontia*; this illustrates that adaptation can take place only within the framework of the anatomy of the forms involved. Probably in connection with reducing friction, the arches of *Aplodontia* do not project far beyond the lateral limits of the occiput and the arches of *Mylagaulus* not at all.

The greater heaviness of the zygomatic arches, broader and more posterior extension of the zygomatic plate and the deeper internal surface of the arch of *Mylagaulus* suggests an increase in importance of masticatory muscles. The glenoid fossa of *Mylagaulus* indicates less lateral movement of the mandible was possible than in *Aplodontia*.

The mandible of *Mylagaulus* is deeper and more robust than the mandible of *Aplodontia*. To some extent this depth in *Mylagaulus* may be related to the enlargement of p4. The peculiar development of the angular process in *Mylagaulus* and in *Aplodontia* is probably due to inheritance from a common pattern which tended in this direction, and for other reasons one of which could be importance of the inferior pterygoid muscles. The various ridges and fossae in the mandible of *Mylagaulus* are better developed than those of *Aplodontia*, in agreement with the evidence of the importance of masticatory muscles on the skull.

The increased importance of the masticatory

muscles and the greater number of cutting lakes of enamel on the occlusal surfaces of the cheek-teeth of *Mylagaulus* might indicate that its diet was harsher than that of *Aplodontia*. Careful examination of the skull and mandible of *Mylagaulus*, however, suggests an alternative. The deepened diastema, turned-up anterior part of the mandible, and arched appearance immediately anterior to the palate of *Mylagaulus* are reminiscent of the condition in pocket gophers. *Mylagaulus* probably used its incisors to aid in digging its burrow. The reduced lateral motion of the mandible of *Mylagaulus* would aid in delivering a sharp, steady thrust. So far as the author knows, this habit has not been reported in *Aplodontia* and, if present, is not reflected in the osteology of the skull and mandible to any appreciable extent.

The means of operating the incisor digging-apparatus of *Mylagaulus* would be different from that in *Thomomys* and *Macrogeomys* because of the difference in masticatory musculature and difference of articulation of the jaw in the glenoid fossa. The articulation of the jaw in *Thomomys* permits digging without excessive motion of the skull upward; the anterior part of the skull of *Mylagaulus* would have had to be raised more than in *Thomomys* if it did burrow in the manner suggested. This need for lifting the skull might be yet another explanation for the development of the lambdoidal crest and occipital region of *Mylagaulus*, which is even greater than that observed in *Thomomys* and *Macrogeomys*.

That the biomechanical limit for increasing the height of crown of P4 has been approached or reached is apparent from the observations on a young *Mylagaulus* (subadult) in which this tooth almost reaches the postorbital process of the frontal. As SHOTWELL (1958, p. 470) states, "Hypsodonty in small mammals with non-ever-growing teeth can only be developed to the limit presented by the depth of jaw in which the tooth rests. In a form which has an enlarged premolar this is even more limiting." The development of an ever-growing tooth in *Aplodontia* has avoided this limitation on crown development. The small foramen above P4, reported by MCGREW (1941) as characteristic of mylagaulids is almost certainly related to the maintenance of a blood and nerve supply to the enlarged P4 as it descends to compensate for wear. The fourth premolar is an important tooth in both genera, but the displacement of cheek teeth by $P\frac{4}{4}$ in *Mylagaulus* has never been duplicated in the closely related aplodontids.

The compression of the tooth-rows of *Mylagaulus*

in comparison with *Aplodontia* is in keeping with the compressed skull posterior to the anterior root of the zygomatic arch. As mentioned previously, the pattern of the cheek-teeth of *Mylagaulus* and of *Aplodontia* has been shown by MCGREW (1941) and others to be related. The evolutionary sequences of the cheek teeth within the aplodontid and mylagaulid rodents of the Great Basin is illustrated by SHOTWELL (1958).

The beds on the modern high plains in which remains of *Mylagaulus* are found are probably deposits of a past plains environment, and do not usually contain aplodontids. Farther to the west are deposits in which both fossil mylagaulids and aplodontids are associated. SHOTWELL (1958) has linked the past distribution of the mylagaulids and aplodontids and the present limited range of *Aplodontia* to a time-changing distribution of geofloras; the mylagaulids are probably associated with a grasslands or grassland-woodland ecotone, or both. The grasses of this area would be considerably tougher and harsher than the grasses of the damp areas in which the modern *Aplodontia* lives. The enamel lakes of the cheek teeth of *Mylagaulus* would be effective cutting and grinding mechanisms for the harsh diet.

The shape of the auditory bullae is probably attributable to both relationship and similar adaptation. The bony meatus of *Thomomys* has an outwardly directed neck, but the resemblances between *Mylagaulus* and *Aplodontia* are more than in just this respect. The bullae bear the same relationship to other bones of the ventral surface of the skull, such as the alisphenoid, and this similarity of pattern is due to more than similar habitat.

The postcranial skeleton of *Mylagaulus* has undergone a change of proportions, as has the skull, in relation to *Aplodontia*. The comparisons are, for the most part, comparisons of degree of exaggeration of adaptation.

A shortening anteroposteriorly and broadening transversely of the vertebrae seems to be a fossorial character, for the vertebrae of *Aplodontia* and *Thomomys* are broadened and shortened compared to those of *Sciurus*; the cervical vertebrae of *Mylagaulus* are relatively shorter and broader than those of either *Aplodontia* or *Thomomys*. This condition makes for a sturdy axis for the body.

Compression of the cervical vertebrae of *Mylagaulus* and overlap of the zygapophyses on the same vertebra makes for a sturdy neck with the head drawn relatively closer to the trunk than in *Aplo-*

dontia. If *Mylagaulus* used its incisors for digging, shortening of the neck would have brought the occipital region closer to the origin of muscles which help to lift the skull.

The articulating surfaces of the centra of the thoracic vertebrae of *Mylagaulus* and of *Aplodontia* do not permit much movement of the thoracic region. The articulations of the posterior thoracics and lumbaris in *Mylagaulus* are the same as these articulations in *Aplodontia*, in which there is some flexibility; however, the proximity of the spines of successive lumbaris of *Mylagaulus* would serve to restrict, if not prevent, dorsoventral movement and might indicate greater curvature of the back.

The greater development of the transverse processes of the cervical vertebrae, more pronounced angle of the ribs, and thicker vertebral border of the scapula of *Mylagaulus* all suggest that stronger fixing or movement of the scapula, or both, was needed than in *Aplodontia*.

The expansion of the sternal end of the clavicle of *Mylagaulus* compared with that of *Aplodontia* may mean an increased importance of the muscles arising from the clavicle, necessitating firm articulation of the clavicle with the manubrium of the sternum, increase in importance of muscles arising from the sternal end proper of the clavicle, or increase in size of the manubrium and associated pectoral musculature, or both. Considering the general increase in areas of muscle attachment on the skeleton of *Mylagaulus*, all three causes are probably involved in the observed expansion. Also, a relative increase in size of the manubrium, if not accompanied by a shortening of the clavicle would have rotated the scapula into a more horizontal position and shifted the forelimb more craniad.

The relatively greater width of the infraspinatus fossa of the scapula of *Mylagaulus* compared with the scapula of *Aplodontia* suggests an increase in importance of the musculature arising from this area which would produce greater downward extension of the forelimb. Despite this exaggeration the overall pattern of the scapula of the two is quite similar.

The entire forelimb of *Mylagaulus* is more heavily developed and is capable of delivering more force and withstanding more stress but is, in most respects, an exaggeration of the forelimb of *Aplodontia*. The deltoid crest of the humerus of *Mylagaulus* is more nearly centered on the anterior surface, a much more effective arrangement for a downward extension of the forelimb from a forward position. In this re-

spect *Mylagaulus* is more fossorially adapted than *Thomomys* for in the latter the deltoid process and crest are not so centered on the anterior surface of the humerus. The distal growth and enlargement of the crest and process reflect need of the more powerful muscles of *Mylagaulus* for a greater area of attachment.

The shallowness of the olecranon fossa of the humerus of *Mylagaulus* and the depth of the radial fossa indicate that the antebrachium was probably carried in a flexed position with the result that the distal end was well craniad; the antebrachium was probably capable of great flexion upward and limited extension downward. The antebrachium of *Aplodontia* is capable of greater extension and less flexion. The arrangement in *Mylagaulus* brings the path of movement of the forearm into an anteroposterior arc. Both *Mylagaulus* and *Aplodontia* have exaggerated muscle processes but are still similar in form if compared with *Thomomys*. The relatively greater exaggeration of the distal end of the humerus of *Mylagaulus* suggests an increased importance in forearm musculature.

The ulna of *Aplodontia* from the semilunar notch to the distal extremity is relatively shorter in comparison with its humerus than the ulna of *Sciurus* with its humerus. The ulna of *Mylagaulus* distal to the semilunar notch is even shorter in relation to its humerus. Correlated with the decrease in length of the distal part of the ulna of *Mylagaulus* and of *Aplodontia* has been an increase in length of the olecranon. This relationship means that the same force upward on the end of the olecranon will deliver a greater force downward at the distal end of the ulna, and is of greater effect in digging.

Almost no rotation is possible in the radius-ulna of *Mylagaulus* where the union of these has been reinforced by development of a ridge on the radius and a groove on the ulna which, interestingly enough, is the opposite of the condition in pocket gophers. The immovability of the radius-ulna articulation means that muscle power is not lost through rotation, but is directed in a single plane. There is some rotational movement possible in the radius-ulna of *Aplodontia* but it is limited compared with that in *Sciurus*.

The rotation of the distal end of the radius of *Mylagaulus* in comparison with the distal end of the radius of *Aplodontia* indicates a manus which has the palm facing inward and downward and all of the weight placed on the outer edge of the manus, as in ground sloths. The manus of *Aplodontia* has

a tendency for the greatest amount of weight to be placed on the external digits and for a part of the palm nearest to the midline of the body to be lifted off the ground.

The metacarpals and phalanges of *Mylagaulus* are sturdier than those of *Aplodontia* and better capable of carrying through the extra force delivered by specializations of the forelimb. The phalanges (except unguals) and metacarpals of *Mylagaulus* and of *Aplodontia* are relatively shortened with respect to length of the ulna, and distal articulations are limited superiorly, in comparison with *Sciurus*. These trends are more pronounced in *Mylagaulus* and, together with inclination of the proximal articulation of the middle phalanx, indicate a manus which was flexed and could not be extended, even under stress of digging, forming an efficient rake or shovel pushing loosened earth underneath the body. The better fossorial adaptation of the manus of *Mylagaulus* over that of *Aplodontia* is also reflected in the relatively longer and stouter ungual phalanges despite shortened proximal and middle phalanges. The exaggeration of the distal portion of the humerus, from which arise flexors and extensors of the manus, attests to the importance of the manus in digging.

Using the terms of REED (1951, p. 522), the method of digging of *Mylagaulus* was of the "terrier type" in which the animal digs by a series of running motions with the forelegs, rather than the "lateral thrust" or swimming mechanism of the mole. As a result of the possible forward shift of the shoulder and flexed position of the antebrachium of *Mylagaulus* these running motions would not be under the body but would describe an arc anterior to the girdle, somewhat oblique to but most nearly in the dorsoventral plane. The flexed digits and the tendency for the plantar surface of the manus to be turned medially would rake the dirt from in front of to beneath the axis of the body. The extreme specializations for fixing the shoulder and elbow joints of the mole (REED, 1951) are not present in *Mylagaulus*, probably related to the need for greater flexibility in the mylagaulid method of digging, and its additional use of the forelimb for support.

As pointed out by SHIMER (1903) and CHAPMAN (1919), the pelvis of a burrowing mammal must be strengthened for the hind limbs to push the body forward through the earth and to brace the body while the forelimbs are actively engaged in digging. The pelvis of *Mylagaulus* is heavier than that of *Aplodontia* which is heavier than the pelvis of *Sciurus*.

Yet the pelvis of *Mylagaulus* and of *Aplodontia* resemble each other by more than fossorial modifications, as evidenced in comparisons with *Thomomys*.

Three of the sacral vertebrae of *Mylagaulus* enter into the sacroiliac joint, making it a large and strong articulation; in contrast, only two of the sacral vertebrae of *Aplodontia* enter into the sacroiliac articulation. The sacrum proper of *Mylagaulus* is sturdier than the sacrum of *Aplodontia* because of greater development of a buttressing plate formed by fusion together of zygapophyses and transverse processes.

The greater angle formed by the pelvis of *Mylagaulus* with the vertebral column could be interpreted to mean that the force delivered along the ilia from the hind limbs would be diminished when transmitted to the vertebral column. However, the posterior migration of the sacroiliac joint brings it closer to the source of power from the hind limb. The force need not be directed forward along the ilia for any distance before transmitted to the vertebral column. This arrangement makes for strength, but not for speed. The decrease in importance of the gluteal fossa, increase in importance of the iliac fossa, and relatively larger posterior part of the pelvis in *Mylagaulus* compared to the condition in *Aplodontia* indicates a de-emphasis of quick, long movements and an emphasis on power.

The inflection of the dorsal borders of the ischia of *Aplodontia* toward the vertebral column foreshadows what has been termed a second sacrum (CHAPMAN, 1919). This "second sacrum" was probably developed in *Mylagaulus*, judging from the greater inflection of the dorsal borders of the ischia, and the expansion of the first free caudal vertebra (Fig. 2). This second sacrum is also developed in *Thomomys*. The relative shallowness of the part of the pelvis caudal to the acetabulum, and the reduction of the pubic symphysis may be indicative of a decrease of adduction of the hind limb. The relatively greater depth of the acetabulum of *Mylagaulus* and of *Aplodontia* over the condition in *Sciurus*, and of *Mylagaulus* over the condition in *Aplodontia*, undoubtedly strengthens the femoro-pelvic joint.

That hind limb and forelimb are adapted differently to perform different functions in fossorial mammals (SHIMER, 1903) is revealed by comparison of the development of forelimb and hind limb of *Mylagaulus*, the forelimb being considerably better developed. The pattern of the bones of the hind limb of *Mylagaulus* and of *Aplodontia* is surprisingly similar because of less exaggeration from the basic

pattern by *Mylagaulus* than is true of the forelimb. The hind leg of *Mylagaulus* and of *Aplodontia* is shortened relatively to the foreleg if compared with the legs of such an arboreal rodent as *Sciurus*. This shortening makes for a set of levers adapted for delivering more power, although with loss of distance covered, and brings the level of the back part of the body down closer to the ground. The rump is hence not much elevated above the level of the forebody.

As in the forelimb, the processes of the hind limb for muscle attachment are exaggerated and developed to an extreme in *Mylagaulus*, attesting to greater muscular development compared with *Aplodontia*. The anteroad shift of the head of the femur and the external shift of the patellar groove of *Mylagaulus* in comparison with *Aplodontia* suggest that the thigh was carried well forward and was directed somewhat towards the midline as well. The relative shortness of the crus in comparison with the thigh in *Mylagaulus* is the same trend as in the pectoral limb, that is to say, more force at the distal end of the crus for the same force exerted on the proximal end.

The rotation of the distal articulation of the fibula of *Mylagaulus* would cause the feet to toe inward as well as forward and is similar to the arrangement in *Thomomys*. The earth thrown underneath the body by the forelimbs was probably pushed behind the body by the hind feet. The greater extent of the trochlea of the astragalus of *Mylagaulus* and of *Aplodontia* over that seen in *Sciurus* permits the tarsals to be rotated to form an angle of 180 degrees with the crus. The metatarsals and phalanges of *Mylagaulus* and of *Aplodontia* are relatively shortened compared with *Sciurus* and are most shortened in *Mylagaulus*. The relative shortening of the pes and lengthening of the calcaneum of *Mylagaulus* means more force could be delivered by the pes than in *Aplodontia*. *Mylagaulus* was capable of disposing of more earth backward, and exerting more force upward through the limb against the body than *Aplodontia*. The flexed phalanges of *Mylagaulus* form an effective scoop or shovel.

The complete skeleton of *Mylagaulus* demonstrates that it was more fossorially developed than that of *Aplodontia*, which with its degree of modification, is slow and lumbering but does spend some time above ground (CAMP, 1918, p. 528). *Mylagaulus* may not have come to the surface often, if at all; its extreme limb proportions ill-suited it for terrestrial locomotion.

When two related genera such as *Mylagaulus* and *Aplodontia* have taken up the same mode of life,

similarities are developed which are directly attributable to the environment. However, as the foregoing comparisons and analysis have shown, these adaptations can mask a genetic relationship when there is a pronounced difference in degree of adaptation. The adaptive expression for the same mode of life of animals of a similar basic plan can vary, but can usually be recognized if the demands of the environment and effects of adaptation on the body are understood. Without recourse to the fossil record in certain instances the relationship of these two genera might have been obscured. Such instances are the presence of postorbital processes in *Mylagaulus* and absence of them in *Aplodontia*, and the difference in tooth pattern between *Mylagaulus* and *Aplodontia*. *Mylagaulus*, in certain respects, such as limb proportions and development of crests and processes for muscle attachment, is even better adapted for underground existence than is *Thomomys*.

A geologically younger genus, and last genus as the record now stands, of the *Mylagaulidae* is *Epigaulus* which has been well described and figured (GIDLEY, 1907). A brief comparison of *Mylagaulus* with *Epigaulus* to observe how the trends already discussed are maintained might yield an even better understanding of fossorial adaptation and its effect on basic rodent morphology.

The proportions of the skull of *Epigaulus* (GIDLEY, pl. 57-60) exaggerate the broadening and shortening already observed in *Mylagaulus*. The lambdoidal crest of *Epigaulus* is better developed and forms a collar about the head when viewed from in front. The zygoma do not extend beyond the lateral limits of the lambdoidal crest, as they did in *Mylagaulus*, and do not even equal the greatest width of the skull.

A startling difference between *Epigaulus* and *Mylagaulus* is the presence of paired horns on the nasals of *Epigaulus*. It has been proposed that these horns were associated with digging (GIDLEY, 1907; MATTHEW, 1902). *Mylagaulus*, KU9807 and AMNH 9043, show callosities on the tips of the nasals and these may hint how horns arose in related members of the family.

The masticatory muscles of *Epigaulus* were more developed than in *Mylagaulus* as is evidenced by an even greater depth of the zygomatic arch, lengthening of the zygomatic plate, and increase in areas for muscle attachment on the mandible. The arched rostrum anterior to the secondary palate, depth of the diastemal profile and compression of the lower jaw observed in *Mylagaulus* are better developed in

Epigaulus and lend weight to the thought that the incisors were used in digging.

A reconstruction of the vertebral column of *Epigaulus* (GIDLEY, 1907, pl. 65) shows the head carried low in relation to the rest of the body. If the anterior part of the skull of *Epigaulus* is raised to open the jaws the horns would act upward and backward to loosen the earth; in closing the jaws, the incisors of the upper jaw would act forward and downward. This habit in *Mylagaulus*, of digging with the incisors, or possibly packing earth with the snout as has been observed in *Cynomys*, would have abraded the rostrum against the top of the burrow and possibly acted as a selective force in directing evolution of paired horns in *Epigaulus*. This is offered as an additional thought since most, if not all, workers believe the presence of horns to be a secondary sexual characteristic. This view was expressed as early as 1907 by GIDLEY (p. 635) who, at this time, also considered the possibility of their usefulness in burrowing (*loc. cit.*).

A ventral view of the skull of *Aplodontia* and of *Epigaulus* (GIDLEY, 1907, pl. 60) shows the basic similarity of pattern to be still recognizable, though heavily masked by the extreme specialization of *Epigaulus*. The relationship of the alisphenoid and bulla of *Epigaulus* is the same as in *Mylagaulus* and *Aplodontia*, despite the lengthened bony meatus necessitated by the great lateral expansion of the occiput. The angle of the jaw in *Epigaulus* is inflected, but less so than in *Aplodontia*; the degree of inflection in comparison with *Mylagaulus* could not be determined from the figures.

The pelvic and pectoral girdles of *Epigaulus* are exaggerations of the trends seen in *Mylagaulus*. The processes for attachment of muscles on the limb bones of *Epigaulus* have been enlarged over those of *Mylagaulus*, and the shortening of the distal parts of the limbs has been carried farther. The mechanisms for increasing mechanical advantage at the distal segments of the limbs (e.g. lengthening of the olecranon relative to the body of the ulna) have also been further developed. The forefoot has the palm turned more mediad and the hind foot has been rotated inward more than in *Mylagaulus*—so much so that the side of the foot faces forward.

The extreme fossorial adaptation observed in *Epigaulus* would tend even more than in *Mylagaulus* to obscure the relationship of mylagaulids to aplodontids. The presence of just a single preceding form such as *Mylagaulus* aids in interpretation and helps

to show affinities. Without the presence of antecedent forms, the true position of a genus like *Epigaulus* would be most difficult to determine.

SUMMARY AND CONCLUSIONS

A bone by bone comparison of the skeleton of *Mylagaulus* with the skeleton of *Aplodontia* followed by an analysis of the observed structures leads to the following conclusions.

- I. Resemblances between *Mylagaulus* and *Aplodontia* probably due to common inheritance are summarized as follows.
 1. Arrangement of cranial foramina.
 2. Primitive sciuriform masseter musculature.
 3. Relationship of component elements of occiput.
 4. Relationship of auditory bulla and alisphenoid.
 5. Inflected angle of mandible.
 6. Morphology of scapula.
 7. Morphology of pelvis and hind limb (because of less exaggeration than in forelimb).
- II. Resemblances between *Mylagaulus* and *Aplodontia* judged to be the result of similar fossorial adaptations are the following.
 1. Flat dorsum of skull.
 2. Transverse expansion of posterior part of skull.
 3. Well developed lambdoidal crest.
 4. Inclined occiput.
 5. Strong centra of vertebrae.
 6. Strong limb girdles.
 7. Great development of processes for attachment of muscles on limbs.
 8. Shortness of elements in antebrachium and crus.
 9. Torsion of manus and pes.
 10. Short and flexed manus and pes.
- III. The skeleton of *Mylagaulus* is better adapted fossorially than the skeleton of *Aplodontia* in the following respects.
 1. Heavier development of skull and skeleton.
 2. Greater flattening, near concavity of dorsum of skull.
 3. Longitudinal shortening of dorsum of skull posterior to anterior root of zygomatic arch.
 4. Greater transverse expansion of posterior part of skull.
 5. More inclined occiput.
 6. Arching of inferior surface of rostrum.
 7. Longitudinal compression of mandible and deepening of its diastemal profile.
 8. Greater longitudinal compression and transverse expansion of vertebrae.
 9. Greater strengthening of limb girdles.
 - a. Broadening of scapula.
 - b. Posterior migration of true sacrum and probable development of "second sacrum."

10. Extreme development and exaggeration of forelimb in comparison to hind limb.
 11. Greater development of processes for attachment of muscles on limbs.
 12. Greater relative shortening of elements of antebrachium and crus.
 13. Greater torsion of manus and pes.
 14. Greater shortening and flexion of manus and pes.
- IV. Inferences based on observed structures warrant the probability of the following conclusions with respect to *Mylagaulus*.
1. Individuals hardly, if ever, came above ground.
 2. They used incisors for digging, a habit which

may show how horns arose in related members of the family.

3. These animals used the "terrier" method of digging, with forelimbs displacing dirt from in front of the body to beneath its axis.
4. They used the hind limbs to dispose of soil loosened by means of the forelimbs and incisors.
5. They may have eaten a harsher diet than did *Aplodontia*.

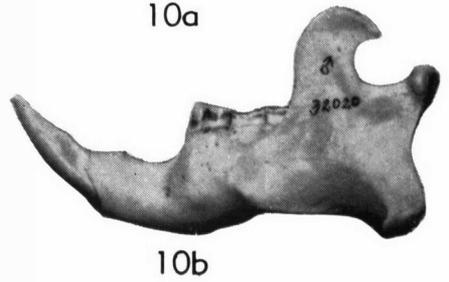
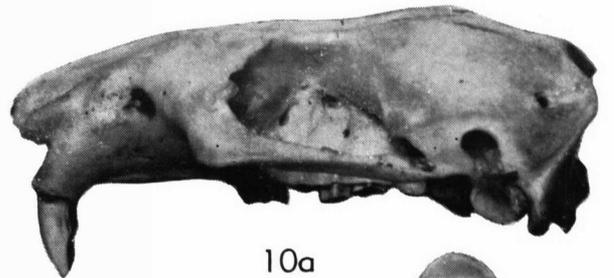
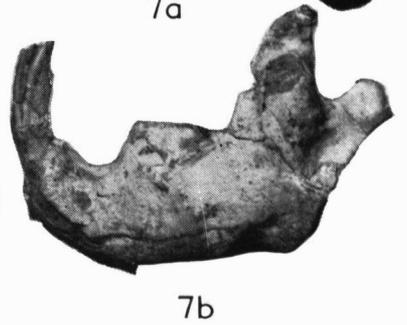
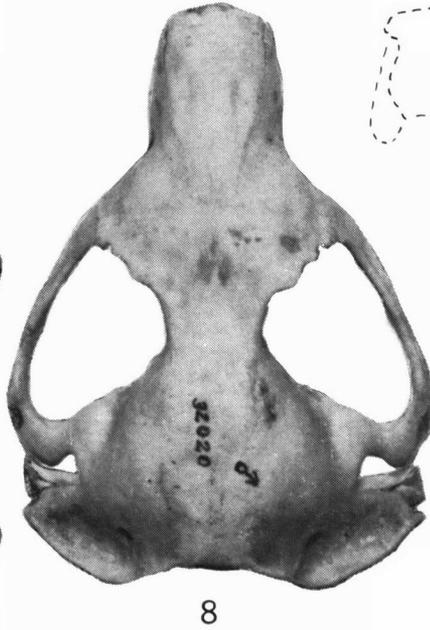
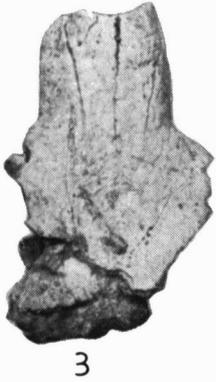
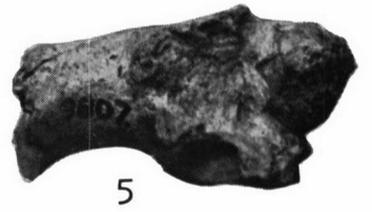
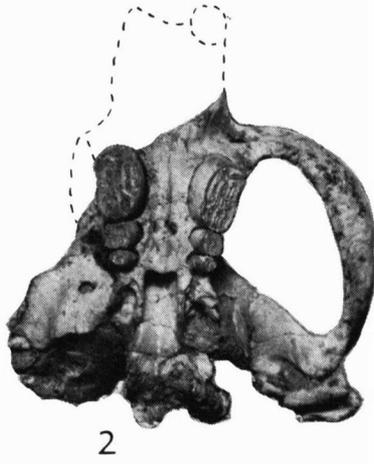
The fossorial trends and exaggerations observable in *Mylagaulus* over those in *Aplodontia* are amplified still further in *Epigaulus*.

EXPLANATION OF PLATE 1

1-7. *Mylagaulus*.—1,2. Dorsal and ventral views of skull, KU9808.—3,5. Dorsal, ventral, and lateral views of skull, KU9807.—6. Dorsal view of mandible, KU9808.—7a,b. Lateral views of skull and mandible, KU9808.

8-11. *Aplodontia*, all specimen KU32020 ♂.—8,9. Dorsal and ventral views of skull.—10a,b. Lateral views of skull and mandible.—11. Dorsal view of mandible. [All $\times 1$.]

PLATE 1



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