

Chapter 12

Skull and Dentition of *Willeumys korthi*, nov. gen. et sp., a Cricetid Rodent from the Oligocene (Orellan) of Wyoming

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ABSTRACT

The skull and mandible, with complete dentitions, of an Orellan rodent are described as a new genus and species of Eumyinae (Rodentia, Muroidea, Cricetidae) based on a combination of unique and shared features: small molar series compared to skull size, featherlike diagonal ridges on surface of lower incisor enamel, rounded triangular shape of M3, and flat interorbital roof and separate temporal crests.

INTRODUCTION

Eumys elegans, the common North American cricetid from the Orellan (early Oligocene), is known from thousands of partial specimens. Only recently did a complete, well-preserved skull come to light (Wahlert, 2004). Another Orellan rodent skull, embedded in matrix and thought to be the eomyid *Paradjidaumo*, was prepared by Otto Simonis at the American Museum of Natural History in the 1970s. This specimen, the new cricetid (F:AM 97815) described here, displays a unique combination of osteological and dental characters: it is nearly complete and retains both mandibles; the lightly worn teeth are fully occluded. Simonis perfectly separated upper and lower dentitions on the left side and removed the mandible. Martin (1980: 17) mentioned this specimen, associated it with *Eoeumys vetus*, and stated that it was of Chadronian age, an error based on the specimen label that has been corrected by referring to the original Frick field notes.

METHODS AND MATERIALS

A list of specimens used for comparison is presented in the appendix. Photographs of the dentitions of the new taxon were taken with a Zeiss EVO 60 Variable Pressure SEM

at the American Museum of Natural History. Line drawings are based on digital photographs of the specimen; the photographs in this publication are a different set. Masseteric muscle nomenclature, as in my previous publications, is from Tullberg (1899), and dental terminology is from Reig (1977). I have reinstated Cricetidae in the modern classification system (e.g., McKenna and Bell, 1997) since paleontologists still recognize the term as a signpost for native North American muroids.

Measurements were taken with a Mitutoyo digital caliper to the nearest hundredth of a millimeter. Definitions of cranial measurements: condylobasilar length, distance between lines tangent to the posterior edges of the incisor alveoli and to occipital condyles; diastemal length, shortest line from posterior margin of the incisor alveolus to anterior margin of upper first molar; incisive foramen length, anteroposterior dimension of those apertures; palatal length, from a line tangent to the back of the incisor alveoli to the most posterior point of the palatine bones at midline; length of zygomatic plate (oblique), from anteriormost point on the posterior edge to anterior edge in front of anteriormost curve of the muscle origin; anterior and posterior palatal widths, shortest distances between alveoli of upper first and third

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molars, respectively; rostral width, shortest dorsal measurement between the origins of the infraorbital parts of the medial masseter; interorbital width, minimum expanse between orbits. Length of the molar series is the most reliable dental measurement because the caliper jaws bracket the series. Length measurements of individual teeth are along the median axis of the tooth, but, at best, they are good estimates; where possible, I have calculated lengths from SEM photos based on measured length of entire tooth row. Width of teeth is measured at right angles to length, but the measurement depends on the orientation at which the tooth is measured, and it may differ on the two sides of a specimen; SEM photos provide no solution to this problem. Incisor width is the maximum transverse width, depth is taken from the enamel face to the posterior-most surface of the dentine. Many of my measurements differ from those that are published for the same specimens.

SYSTEMATICS

SUBORDER MYOMORPHA

SUPERFAMILY MUROIDEA Miller and Gidley, 1918

FAMILY CRICETIDAE G. Fischer, 1817

SUBFAMILY EUMYINAE Simpson, 1945

Willeumys, new genus

TYPE SPECIES: *Willeumys korthi*.

ETYMOLOGY: For William W. Korth in recognition of his contributions to paleoglimnology.

DIAGNOSIS AND DESCRIPTION: As for the single included species, below.

Willeumys korthi, new species

TYPE SPECIMEN: FAM 97815, skull with associated lower jaws (teeth originally in occlusion); cervical vertebrae, scapula, and forelimb in matrix. Field number DOUG 22 719; south of Tower Area, Reno Ranch, top of nodules, 5 mi SE of Douglas, Converse County, Wyoming.

DIAGNOSIS: *Unique features*—cricetid rodent with narrow rostrum, sides of nasal bones straight—nearly parallel—and tapering posteriorly, short molar series length

(5.2 mm), optic foramen posterodorsal to M3, anterior margin of hypoflexus in M1 straight and perpendicular to tooth axis, upper incisor narrow, lower incisor with featherlike diagonal ridges on enamel surface. *Features shared with other taxa*—slight zygomatic plate not constricting ventral part of infraorbital foramen, interorbital roof relatively flat with angular transition to orbital wall, temporal crests widely separated, upper molar series approximately parallel, hypcone lacking on M3 (its position marked by a ridge), resulting in rounded triangular rather than semirectangular shape; coronoid process of mandible rising lateral to m3, alveolus of lower incisor ending below m3 and not forming a bulge on the lateral side of the jaw. See table 1 for comparison of diagnostic characters and tables 3 and 4 for dental dimensions.

CRANIAL ANATOMY

DORSAL VIEW

In dorsal view (figs. 1A, 2A) the skull appears slender and the rostrum long and narrow (table 2). The width between the indenting curves on each side of the snout anterior to the root of the zygoma is 3.94 mm; these curves mark the dorsal edge of the origin of the infraorbital part of the medial masseter muscle, which penetrated the infraorbital foramen and arose on the side of the rostrum. The premaxillae have only narrow exposure on the dorsal surface of the rostrum. A tiny dorsal rostral foramen is present in the premaxilla at the suture with the maxilla just anterodorsal to the infraorbital canal.

The nasal bones are widest anteriorly where they wrap ventrally onto the sides of the rostrum. Otherwise, they are almost parallel sided and become narrower posteriorly; the premaxillae do not constrict the midpart of the nasal bones, which have straight edges. The suture of the nasals with the frontal is somewhat posterior to the maxillary-frontal suture adjacent to the lacrimal bone. The frontal does not project in a V between the nasals. The posterior ends of the premaxillae terminate slightly posterior to the maxillary-frontal suture and a little

TABLE 1
Comparison of Diagnostic Characters among Five Fossil Cricetids

	<i>Willeumys korthi</i> (F:AM 97815)	<i>Eoemys vetus</i> (AMNH 8742)	<i>Leidyomys lockingtonianus</i> (AMNH 7028)	<i>Leidyomys nematodon</i> (AMNH 7018)	<i>Emys elegans</i> (Chalky Buttes)
Rostral width at masseter indents	3.94 mm	4.10 mm	6.32 mm	no data	4.53–5.35 mm
Sides of nasal bones	straight	slightly curved	curved	no data	strongly curved
Transition skull roof to orbital wall	obtuse angle with sharp transition	obtuse angle with rounded transition	obtuse angle with sharp transition	nearly right angle with sharp transition	gradual and curved
Temporal crests	widely separated	no data	widely separated	widely separated	single median
Zygomatic plate and infraorbital foramen	slight, does not constrict foramen	slight, does not constrict foramen	slight, does not constrict foramen	no data	broad, constricts foramen ventrally
Optic foramen	posterior to M3	dorsal to M3	just posterior to M3	no data	dorsal to M3
Upper molar series	approximately parallel	slight anterior convergence	parallel	parallel	strong anterior convergence
M1 hypoflexus anterior edge	straight and transverse	curves around protocone	no data	curves around protocone	curves around protocone
Hypocone on M3	none, mure meets posteroloph	none, mure meets posteroloph	present	present	none; mure meets posteroloph
M3 shape in crown view	Semi triangular (narrower lingually)	semi-triangular	semi-rectangular	semi-rectangular	semi-triangular
Coronoid process	rises lateral to m3	mandible absent	mandible absent	mandible absent	rises lateral to m2
Lower incisor enamel surface	feather-like diagonal ridges	mandible absent	mandible absent	mandible absent	almost smooth
Alveolus of lower incisor ending	below m3, no bulge on ramus	mandible absent	mandible absent	mandible absent	posterodorsal to m3, bulge present

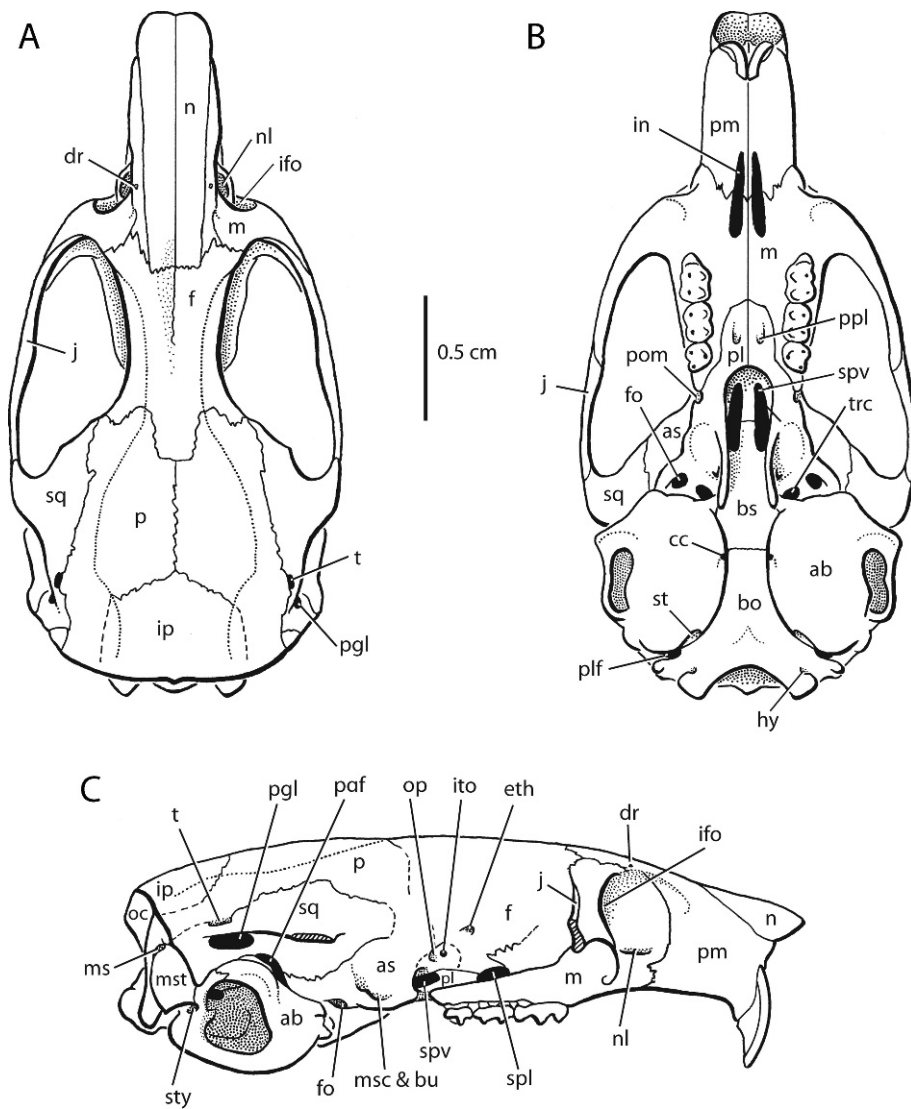


Fig. 1. Diagrams of *Willeumys korthi* skull, F:AM 97815; outline restored to eliminate effect of crushing, rotation, and breakage; molar series in ventral view were probably parallel in life. A. Dorsal view. B. Ventral view. C. Lateral view. *Abbreviations (bones)*: **ab** auditory bulla; **as** alisphenoid; **bo** basioccipital; **bs** basisphenoid; **f** frontal; **ip** interparietal; **j** jugal; **m** maxilla; **mst** mastoid; **n** nasal; **oc** occipital; **p** parietal; **pl** palatine; **pm** premaxilla; **sq** squamosal; (*foramina*): **bu** buccinator; **cc** carotid canal entrance; **dpl** dorsal palatine; **dr** dorsal rostral; **eth** ethmoid; **fo** foramen ovale; **hy** hypoglossal; **icf** internal carotid foramen; **ifo** infraorbital; **in** incisive; **ito** interorbital (in orbitosphenoid bone); **ms** mastoid; **msc** masticatory; **nl** nasolacrimal; **op** optic (in orbitosphenoid bone); **paf** postalar fissure; **pgl** postglenoid; **plf** posterior lacerate; **pom** posterior maxillary; **ppl** posterior palatine; **spl** sphenopalatine; **spv** sphenopalatine vacuity (partly hidden in lateral view by edge of anterior alar fissure); **st** stapedial; **sty** stylomastoid; **t** temporal; **trc** transverse canal.

anterior to the ends of the nasals. There is no distinct zygomatic notch between the rostrum and the zygomatic plate, since the zygomatic plate does not extend far forward or dorsally.

The lacrimal bones are missing. They were small, and their positions can be determined from a facet at the dorsomedial end of the maxillary root of the zygoma and a small

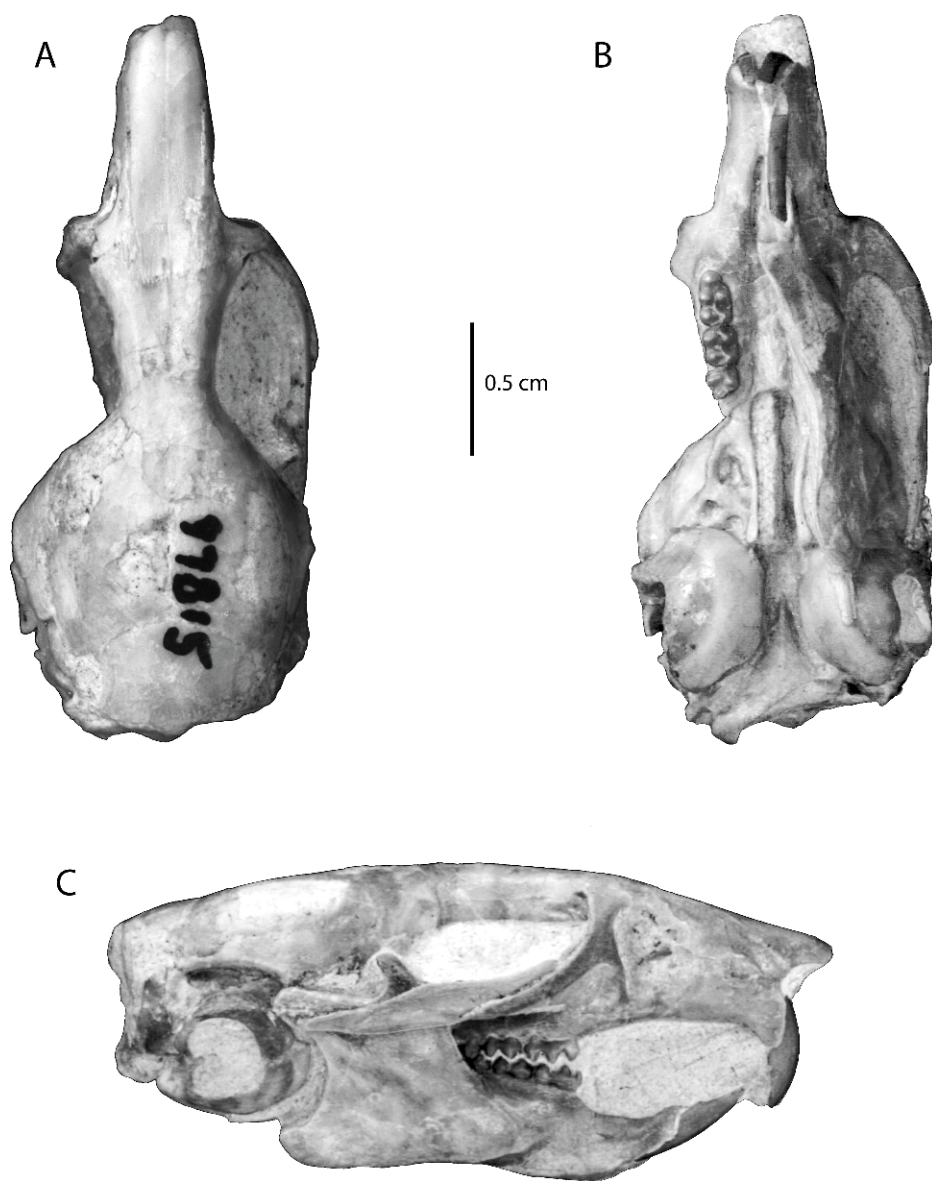


Fig. 2. Photographs of the skull of *Willeumys korthi*, F:AM 97815. A. Dorsal view. B. Ventral view (reversed). C. Lateral view.

adjacent part of the frontal bone. The jugal bone ascends the maxillary root, and its pointed tip probably touched the lacrimal bone. The frontal bone has a median suture in its anterior half but is single (fused) posteriorly.

The interorbital width is narrowest posteriorly and measures 3.9 mm. It widens

gradually toward the lacrimal region and more steeply around the cranium. A shallow, median trough depresses the center of the frontal and posterior parts of the nasals so that the bone surface rises laterally toward the orbits. There is a sharp transition from the dorsal surface of the frontal to the curved surface that continues lateroventrally and

TABLE 2
Cranial Dimensions of Specimens (in millimeters)*

Taxon	Specimen #	Length					Width			
		Cd-Bas	Diast	Incis	Palat	Zy Pl	Pal M1	Pal M3	Rostral	Interorb
<i>Willeumys korthi</i>	F:AM 97815	26.3	7.6	3.6	12.3	2.9	~3.0	?	3.7	3.9
<i>Eumys elegans</i>	AMNH 94108	27.8	7.8	3.9	13.9	4.4	2.4	43.8	4.5	4.2
<i>Eoeumys vetus</i>	AMNH 8742	?	6.7	3.9	11.5	3.4	2.4	2.8	4.2	4.1
<i>Leidymys nematodon</i>	AMNH 7018	?	?	?	?	?	4.7	4.7	?	4.8
<i>Leidymys</i>										
<i>lockingtonianus</i>	AMNH 7028	~36.1	~10.4	7.9	~16.0	3.3	?	?	6.2	6.4
<i>Pacculus insolitus</i>	AMNH 7022	?	?	?	?	?	?	?	?	?
<i>Scottimus exiguus</i>	AMNH 12261	?	?	?	?	?	2.3	3.0	?	?

Abbreviations: Cd-Bas, condylobasilar; Diast, diastemal; Incis, incisive foramen; Palat, palate; Zy Pl, zygomatic plate; Pal M1, width of palate between alveoli of M1's; Pal M3, width of palate between alveoli of M3's; Interorb, interorbital.

* See Measurements section of text for information on how measurements were taken.

descends as the orbital wall. In cross section the transition from dorsal to curved lateral surfaces would make an obtuse angle. The effect is of a pair of very low interorbital ridges that spread apart anteriorly and disappear close to the lacrimal bones. The transition in surface orientation can be followed a short distance posteriorly onto the cranium. The medial part of the frontal extends farthest posterior and forms a U-shaped suture with the parietals. Weak lyrate crests on the parietal bones mark the dorsal extent of the temporal muscles, which were widely separated and limited to the sides of the cranium. Hence, there is no median sagittal crest. The interparietal bone is single and wide; and the origin of the temporal muscle extended onto its lateral parts.

ANTERIOR VIEW

In anterior view (fig. 3), the infraorbital canal is shaped a bit like the letter D. It measures about 3.5 mm dorsoventrally and is broad and widest above the middle. The short zygomatic plate flattens the ventrolateral side of the infraorbital canal; the lacrimal canal, which is squashed, would have constricted the rostroventral side. The lacrimal foramina are not clearly preserved because the rostrum is narrowed somewhat by lateral crushing.

LATERAL VIEW

When positions are described in lateral view, the skull is held with occlusal side of cheek teeth horizontal. In lateral view (figs. 1C, 2C), the nasal bones project a short distance beyond the incisors, which are orthodont. The damaged sides of the rostrum reveal that the incisor alveolus ends posteriorly at the base of the infraorbital foramen. A curved edge of bone, which marks the bony entrance to the lacrimal canal, is preserved on the left side of the rostrum; it is anterior to the ventral part of the infraorbital canal. A slight depression extends from the dorsal part of the infraorbital foramen anteriorly for about half the rostral

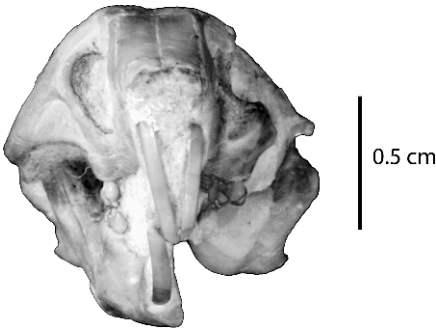


Fig. 3. Photograph of the skull of *Willeumys korthi*, F:AM 97815, anterior view.

length of the premaxilla; this marks the origin of the infraorbital part of the medial masseter. This muscle division reached much farther forward than did the anterior part of the lateral masseter on the zygomatic plate.

The anterior origin of the lateral masseter extended anterodorsally on the maxillary root of the zygoma, which forms the zygomatic plate. The plate extends antero-medially to such a small degree that its margin below the infraorbital foramen has only a slight anteriorly convex curvature. A low boss at the anteroventral edge of the plate, anterior and dorsal to the root of M1, marks the origin of the superficial masseter. The anteroposterior length of the zygomatic plate is about 2.9 mm. The zygomatic arch is complete. The maximum height of the jugal in the middle is about 1.6 mm. The jugal tapers posteriorly to a rounded point beneath the squamosal root of the zygoma.

In the orbit, the sphenopalatine foramen is dorsal to the entire length of M2; the maxilla forms its anterior and ventral borders; a sliver of the palatine reaches the foramen posteriorly. Damage to the orbital wall makes it impossible to see the relationship of the frontal and orbitosphenoid bones to the foramen. The ethmoid foramen faces ventrally and is above the anterior half of M3. The relationship of sutures in its vicinity cannot be determined. The optic foramen faces anteriorly and is posterior to M3; its diameter is about 0.9 mm. Anterior to it, a small interorbital foramen pierces the orbitosphenoid bone. There is no trace of a dorsal palatine foramen in or near the maxillary-palatine suture; the foramen may have been located in the back of the sphenopalatine foramen. The anterior alar fissure is posterior to the optic foramen and extends posteroventral to it. The anterior end of the sphenopalatine vacuity is medial to the fissure and extends almost as far as the posterior margin of M3. The posterior wall of the orbit is smooth and without ridges; the sphenofrontal foramen was not found, but the region is somewhat damaged and a small aperture could be easily missed. The ventral extent of the parietal bone and the relationship of frontal, squamosal, and alisphenoid bones could not be determined.



Fig. 4. Photograph of the skull of *Willeumys korthi*, F:AM 97815, left auditory region.

Masticatory and buccinator foramina share a curved groove in the side of the alisphenoid bone. A bulge of the cranial wall may separate the two foramina. A window onto the alisphenoid canal might be present medial to the anterior end of the groove. A strut of the alisphenoid bone separates these foramina from the foramen ovale; the strut protrudes ventrally and thus the accessory foramen ovale is absent. A postalar fissure is present between the alisphenoid and squamosal bones and the anterior surface of the auditory bulla; the fissure widens dorsally. There is a large, oval postglenoid foramen in the squamosal below the ridge extending posteriorly from the zygomatic root. The ventral margin of the postglenoid foramen is missing, but the squamosal appears to have continued around the foramen. A small temporal foramen is present in the squamosal-parietal suture dorsal to the posterior half of the postglenoid foramen.

The small ectotympanic bulla (fig. 4) forms a posteriorly facing C that is closed posteriorly. The opening of the bony meatus is large with its long axis dorsoventral; the meatus is not tubular, but the anterodorsal rim is thick and projects laterally. The ventral limb of the ectotympanic curves upward around the meatus, and its posterior lamina forms a hook that bends anteromedially into the ear chamber. What may be a tubercle of the mastoid continues the posterior lamina dorsally and has a short suture with the

dorsal limb of the ectotympanic. A descending process of the squamosal abuts this region. The stylomastoid foramen is enclosed at the junction of dorsal and ventral parts of the ectotympanic ring and the ventrolateral part of the mastoid portion of the periotic.

VENTRAL VIEW

In ventral view (figs. 1B, 2B), the incisive foramina occupy close to half of the diastemal length, but they do not extend as far posteriorly as the front of the first molar. The premaxillary-maxillary suture intersects their lateral margins at about midlength. The anteriormost part of the posterior margin of the zygomatic plate is approximately even with the anteroloph of M1.

The molar rows are nearly parallel; slight crushing makes them appear somewhat closer together posteriorly. The palate is flat, and the maxillary-palatine suture crosses the palate medial to the M1/M2 junction. The posterior palatine foramina appear to be medial to M2; their full extent cannot be determined due to compression damage of the posterior part of the palate. The palate ends a slight distance anterior the level of the posterior margin of M3. The maxilla ends behind the cheek teeth in a point, and, just behind it, the posterior maxillary notch indents the palatine bridge to the pterygoid region.

The walls of the mesopterygoid fossa, the portion of the nasal passage bounded laterally by the posterior part of the palatine bones and by the pterygoid region, form a horseshoe shape; the fossa is widest anteriorly (medial to the palatine bridge between pterygoid fossa and maxilla) and narrower between the hamular processes medial to the pterygoid fossa. The ends of the hamular processes curve slightly laterally to meet the styliiform processes of the bullae. The sphenopalatine vacuities in the mesopterygoid fossa indent the anterior edge of the basisphenoid and run alongside the presphenoid into the floor of the orbit.

The pterygoid fossa is excavated but not as deeply as the roof of the mesopterygoid fossa for the nasal passage. A strong crest forms the lateral edge of the anterior part of pterygoid fossa; the crest decreases posteri-

orly to a mere change in angle where the alisphenoid extends between masticatory foramen from the foramen ovale. A rounded surface, alongside the foramen ovale, marks the passage of the mandibular branch of the trigeminal nerve, and no accessory foramen ovale is formed. The pterygoid fossa is divided into two parts that are separated by a diagonal swelling that runs posteromedially from the lateral edge. The internal pterygoid muscle took its origin in the narrower, rounded anterior part. A foramen of unknown function faces anterolaterally at the posteromedial end of the swelling. Posterior to the swelling is a triangular surface that slopes gradually upward toward the auditory bulla. The foramen ovale occupies most of the lateral part; the posterior entrance to the alisphenoid canal is within its anterior end. A large foramen medial to the foramen ovale is probably the entrance into the transverse canal. The piriform fenestra is absent.

The basioccipital and basisphenoid are swollen laterally at their junction, but there is no change in angle or flexion of the skull base. A triangular keel extends anteriorly from the condyles between the auditory bullae to the suture with the basisphenoid. Its greatest relief is between the bullae where depressions flank it; these are the insertion sites for the longus capitis and rectus capitis anterior muscles in rodents (Wahlert and Sawitzke, 1988: 129; Howell, 1926: fig. 23B).

The auditory bulla is inflated anteriorly and medially. The course of the internal carotid artery is marked by a groove that indents the medial surfaces of the bulla and petrosal and slopes anterodorsally to a foramen that lies just posterior to the basioccipital-basisphenoid suture. The foramen leads into a carotid canal between the bulla and median cranial bones. The artery probably entered the cranium at the antero-medial end of the bulla. A stapedial foramen is present in the posteromedial curve of the bulla between the ectotympanic and the petrosal. The aperture makes a circular indentation in the bulla and a slight dip in the petrosal margin. The course of the stapedial artery is marked by a groove across the promontorium to the fenestra vestibuli. It would have passed between the crura of the stapes and exited from the middle ear via a

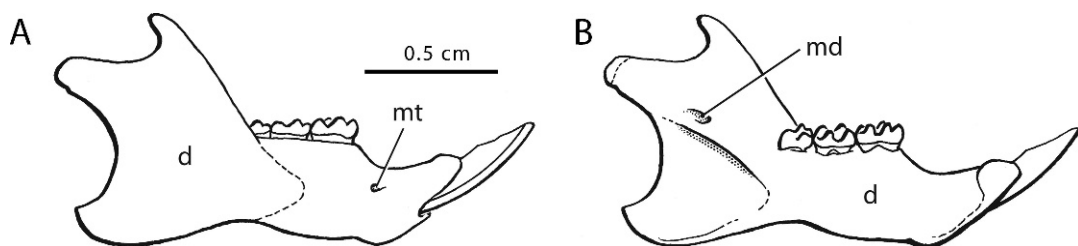


Fig. 5. Diagrams of the mandible of *Willeumys korthi*, F:AM 97815. A. Lateral view. B. Medial view. Abbreviations: **d** dentary; **md** mandibular foramen; **mt** mental foramen.

foramen in the medial wall of the fallopian canal. The fallopian canal for the facial nerve appears as a curved bony tube that forms the medial side of the epitympanic recess.

The posterior lacerate foramen is posterodorsal to the stapedial foramen; it ends laterally at the junction of the mastoid and the occipital, where a short paroccipital process descends. The hypoglossal foramen is between the posterior lacerate foramen and the lateral condyle of the occiput.

MANDIBLE

Both mandibles are present with upper and lower dentitions in near occlusion; the mandible on the left side has been taken off. Specimens on hand of *Eumys elegans* have no associated mandibles, and I have selected a group of lightly worn lower dentitions from the Chalky Buttes sample of *Eumys elegans* (Wahlert, 2004) for comparison.

Paleontologists routinely refer to any tooth-bearing mandibular fragment as a "ramus," but this differs from current anatomical usage (Evans, 1993, Bezuidenhout and Evans, 2005). The mandible (figs. 5, 6) is divided into two regions, the anterome-

dial body, which bears the dentition, and the posterolateral ramus, which has muscle insertions and articulates with the skull. It is dorsoventrally short and bucco-lingually narrow in comparison to *E. elegans*. In lateral view the single mental foramen opens in the body of the mandible a little posterior to the middle of the diastema, dorsal to its midheight and above the incisor alveolus.

The ramus of the mandible is thick at the condyle and in three linear zones: the anterior edge of the coronoid process, the ventral edge of the angular process, and a buttress that extends from the posteroventral part of the condyle into the bone of the body in which the molar teeth are rooted. The buttress makes a ridge on both the medial and lateral sides of the ramus. The posterior end of the incisor alveolus does not form a bulge on either side of the mandible; shining a bright light through the mandible indicates that the alveolus may end below or just posterior to m3.

In lateral view, the coronoid process of the ramus rises alongside the molar series and obscures the posterior part of m3; it slopes posteriorly in a gentle curve. With the tooth row horizontal, the tip of the coronoid process is higher than the condyloid process.

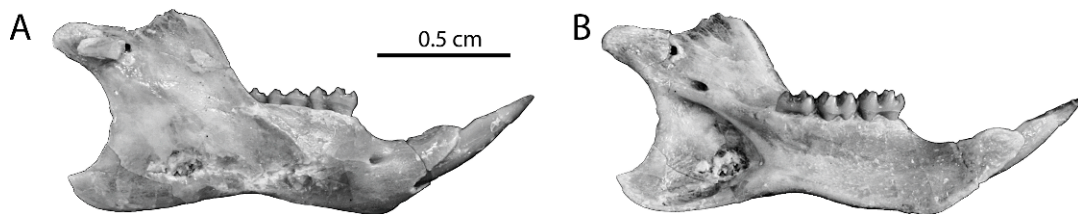


Fig. 6. Photographs of the mandible of *Willeumys korthi*, F:AM 97815. A. Lateral view (reversed). B. Medial view.

The condyloid process extends slightly farther posteriorly than the angular process, and the semilunar notch between them is nearly symmetrical, like the arc of a circle. The masseteric fossa of the ramus is a broad, semitriangular surface on the lateral side of the mandible where divisions of the masseter muscle insert. Its dorsal boundary, the superior masseteric crest, continues antero-ventrally from the leading edge of the coronoid process. The relief of this crest is little more than a change of angle from the area of muscle insertion to the dental portion of the body medial to it. The crest turns ventrally beneath the m1–m2 junction to join the ventral masseteric crest. The posterior part of the ventral masseteric crest descends from the tip of the angular process; it curves anteriorly into the ascending ventral edge of the mandible. Beneath the m2–m3 junction, it separates from the margin of the jaw and ascends to meet the descending superior ridge. The ventral crest continues a short distance anterior to the upper crest and forms a low boss beneath the posterior part of m1.

On the medial surface of the mandible, a buttressing ridge of bone descends anteriorly from the posteroventral part of the condyle to the thick bone of the body that houses the molar roots; the rest of the ramus above and below this ridge is very thin. The mandibular foramen enters the dorsal side this ridge at a point ventral to the posterior part of the coronoid process. The in-turned edge of the angle of the mandible mirrors the descending ridge, and together they define a deep, triangular fossa where the internal pterygoid muscle inserted.

DENTITION

The dentition is lightly worn with only small areas of exposed dentine in the centers of cusps; connecting ridges are not broadened as they would be with deep wear. Dental variation in *Eumys elegans* and many other Oligocene murids is known to be very high (Alker, 1967; Rosser, 1978; Dienemann, 1987; Wahlert, 2004); thus, the dental morphology of this one specimen cannot be taken as diagnostic for the taxon to which it belongs. Aside from differences in proportion, the upper and lower dentitions are

nearly the mirror images of each other even in some small details. Stereo images are presented in figure 7 and a labeled diagram of cusps in upper and lower second molars in figure 8. Dimensions of the upper and lower dentitions are given in tables 3 and 4.

UPPER DENTITION

The upper incisor, seen in cross section, is broadest in the anterior third. The anterior face of the enamel is relatively flat; it has an abrupt angle at the medial edge of the tooth but curves around onto the lateral side of the tooth. The anterior surface of the enamel is lightly ornamented, as if vertical brush-strokes were left in thick wet paint.

Although I am describing upper teeth, I portray them as if the cusps were up and the basins and flexi down. The upper molar dentition measures approximately 5.2 mm in length; M1 occupies 44% of the total, and the length of the molars declines to a low in M3. M1 and M2 are longer than wide; M3 has equal dimensions. An anteroloph is present in each molar. In M1 it takes the form of a single, large cusp or anterocone. A swelling descends from the cusp apex in the direction of the paracone; it does not reach the paracone, and the protoflexus and paraflexus form a continuous valley. In M2 and M3 the anterior cingulum makes a low ridge that brackets the front of the tooth; it is highest a short distance lingual to its midpoint, and an anterior mure extends from there to the anterior arm of the protocone.

In M1 and M2, the four main cusps are of nearly equal size at the base, but lingual (protocone and hypocone) and buccal (paracone and metacone) pairs differ in height and shape. In M3 the protocone and paracone are similar in size, but the metacone is small and there is no hypocone. The hypoflexus indents the lingual side of each molar between protocone and hypocone. In M1 it forms the flat posterior surface of the protocone; in M2 the hypoflexus curves medially around the protocone and slightly indents its connection with the mure; in M3 it curves medially around the protocone and strongly indents its connection with the mure, thus making the protocone appear as a posteriorly projecting peninsula. In M1 the paraloph has



Fig. 7. SEM stereo photographs of the dentition of *Willeumys korthi*, F:AM 97815. A. Upper left molars. B. Lower left molars (reversed).

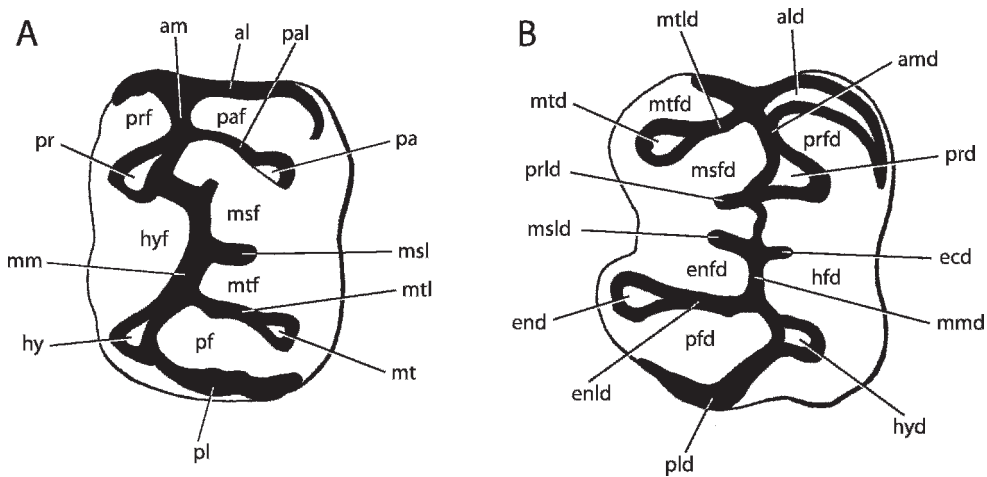


Fig. 8. Diagrams of the second molars of *Willeumys korthi*, F:AM 97815; anterior is at the top, lingual to the left. A. Upper left M2. B. Lower left m2 (reversed).

Abbreviations, upper molars: al anteroloph; am anterior mure; hy hypocone; hyf hypoflexus; mm median mure; msf mesoflexus; msl mesoloph; mt metacone; mtf metaflexus; mtl metaloph; pa paracone; paf paraflexus; pal paraloph; pf posteroflexus; pl posteroloph; pr protocone; prf protoflexus; lower molars: alld anterolophid; amd anterior murid; ecd ectolophid; end entoconid; enfd entoflexid; enld entolophid; hfd hypoflexid; hyd hypoconid; mmd median murid; msfd mesoflexid; msld mesolophid; mtd metaconid; mtfd metaflexid; mtlld metalophid; pfd posteroflexid; pld posterolophid; prd protoconid; prfd protoflexid; prld protolophulid.

TABLE 3
Dimensions of Upper Dentitions (in millimeters)

Taxon	Specimen #	M1-3	M1	M1	M2	M2	M3	M3	I1	I1
		a-p	a-p	max w	a-p	max w	a-p	max w	width	depth
<i>Willeumys korthi</i> *	F:AM 97815	5.20	2.27	1.34	1.66	1.34	1.26	1.26	0.60	1.25
<i>Eumys elegans</i> *	AMNH 94108	6.36	2.85	1.87	2.05	1.86	1.44	1.6	1.56	1.90
<i>Eoeumys vetus</i> *	AMNH 8742	5.93	2.49	1.72	1.79	1.66	1.67	1.63	0.96	1.20
<i>Leidymys nematodon</i> *	AMNH 7018	6.47	2.67	1.72	1.93	1.93	1.90	1.76	?	?
<i>Leidymys lockingtonianus</i>	AMNH 7028	6.86	2.77	1.98	2.09	2.17	1.84	1.84	1.34	?
<i>Pacculus insolitus</i>	AMNH 7022	?	2.44	2.03	1.84	1.99	?	?	?	?
<i>Scottimus exiguus</i>	AMNH 12261	5.73	2.54	1.73	1.72	1.55	1.38	1.38	?	?

Abbreviations: a-p, antero-posterior length; max w, maximum transverse width. Teeth of *Leidymys lockingtonianus* are extremely worn and dimensions are smaller than at a younger age.

* Individual tooth lengths calculated from SEM photographs.

a posteromedial orientation and it joins the posterior arm of the protocone; the basin between the two cusps is terminated posteriorly (open anteriorly), and it is not part of the mesoflexus. In M2 and M3 the paraloph has an anterolingual orientation and meets the anterior arm of the protocone; the intervening basin is terminated anteriorly and adds to the length of the mesoflexus. This basin is far lingual in the crown and strongly indents the protocone; in M3 it overlaps with the anterior tip of the hypoflexus. In both M2 and M3 a low projection from the posterior arm of the protocone toward the paracone marks the position of the posterior connection seen in M1.

In M1 and M2, the mure extends posteriorly from the protocone, curves around the

hypoflexus, and continues to the hypocone. In M1 and M2, a short mesoloph extends anterobuccally from the mure and crosses about one-third the distance from the mure to the edge of the tooth. The buccal flexus between the paracone and metacone is thus divided in the interior of the crown into mesoflexus and metaflexus. The hypoflexus makes a deeper valley in the crown than does the buccal flexus. In M1 and M2 the metaloph intersects the mure where it joins the anterior arm of the hypocone; the intersection is similar in M3 although there is no hypocone and the mure continues to the posteroloph. M3 lacks a mesoloph. In crown view, M3 has a rounded, triangular shape since the lingual side, which lacks a hypocone, is narrower than the buccal side. All

TABLE 4
Dimensions of Lower Dentitions (in millimeters)

Taxon	Specimen #	m1-3	m1	m1	m2	m2	m3	m3	il	il
		a-p	a-p	max w	a-p	max w	a-p	max w	width	depth
<i>Willeumys korthi</i> *	F:AM 97815	5.34	2.03	1.24	1.71	1.45	1.61	1.36	0.68	1.16
<i>Eumys elegans</i>	F:AM 133695	7.16	2.41	1.84	2.36	2.06	2.32	1.96	1.80	2.14
<i>Scottimus exiguus</i>	AMNH 12261	5.98	2.09	1.40	1.92	1.56	1.80	?	?	?

Abbreviations: a-p, antero-posterior length; max w, maximum transverse width.

* Individual tooth lengths calculated from SEM photographs.



Fig. 9. SEM photograph of anterior surface of right lower incisor.

molars have a posteroloph that encloses a long transverse basin, the posteroflexus, which indents the buccal side of the hypocone; the metaloph forms the anterior side of the posteroflexus.

LOWER DENTITION

The lower incisor is slightly broader than the upper, its greatest breadth near the middle; both upper and lower incisors have about the same depth. Interdental wear has flattened the medial surface of the incisor tip; in front view the incisor ends in a rounded point. The enamel of the lower incisor has an abrupt angle at the medial edge of the tooth; the anterior face is curved rather than flat. The enamel surface (fig. 9) is unusual because it bears a combination of longitudinal and pinnate ridges on the anterior face and pinnate ridges curving onto the lateral side. The medial edge of the enamel has a single longitudinal ridge; weaker ridges feather out from it at a steep angle buccally and climb toward the worn apex of the incisor. In the middle of the enamel face, they meet a few nearly longitudinal ridges that have a slight lingual inclination. Lateral to these, tiny

ridges curve outward and apically and nearly reach the lateral edge of the enamel. Both the inner and outer sets of ridges are directed apico-buccally.

The lower molar dentition measures approximately 5.34 mm in length, similar to the upper dentition; m1 occupies 38% of the total. Although the length of the lower molars declines to a low in m3, the three molars are more nearly equal in length than are the uppers, with m1 occupying less of the total dental length. The lower dentition tapers somewhat at both ends; the protoconid and metaconid of m1 and the hypoconid and entoconid of m3 are closer together than are the transverse pairs of cusps between them.

An anterolophid is present in each molar. In m1 it takes the form of a single, large anteroconid separated from the posterior cusps by a crescent valley. A crest from the lingual end of the cusp curves to the base of the metaconid; a similar buccal crest extends to the base and almost to the side of the protoconid. In m2 and m3, the anterior cingulum makes a low ridge that brackets the front of the tooth. It is highest a short distance buccal to its midpoint, and a short anterior murid extends from here to the anterior arm of the protoconid.

In m1 and m2 the four main cusps are of nearly equal size at the base, but lingual (metaconid and entoconid) and buccal (protoconid and entoconid) pairs differ in height and shape. In m3 the protoconid and metaconid are similar in size, but the entoconid is small, and the hypoconid is at the buccal end of the stout posterior cingulid. The hypoflexid indents the buccal side of each molar between the protoconid and hypoconid; it does not curve around the protoconid but curves around the hypoconid. In m1 the metalophid is a very slight ridge that meets the posterior arm of the protoconid; the basin between the two cusps is terminated posteriorly (open anteriorly), and it is not part of the mesoflexid. In m2 and m3 the metalophid has an anterobuccal orientation and meets the anterior cingulid; the intervening basin is terminated anteriorly and adds to the length of the mesoflexid. In m2 the posterior arm of the protoconid extends toward but does not reach the

posterobuccal side of the metaconid. In m3 the posterior arm of the protoconid extends posterolingually to the margin of the tooth between the metaconid and entoconid.

In m1 the murid begins on the posterior side of the protoconid; in m2 and m3, from the back of the posterior arm of the protoconid. In all molars, the murid extends into the anterior arm of the hypoconid. A thickening in the murid creates a subtle division of the head of the hypoflexid. On the side opposite this thicker part in m1 and m2, there is a mesolophid that extends about half way to the margin of the tooth. It partially divides the lingual flexid into a mesoflexid (anterior) and entoflexid (posterior). The mesolophid is lacking in m3. The entolophid connects the entoconid to the murid at its junction with the hypoconid. All molars have a posterolophid that encloses a broad transverse basin, the posteroflexid.

OCCCLUSION AND WEAR

This specimen presents a rare look at molar occlusion and early wear that are comparable to *Eumys*, as described by Butler (1980). Moderate wear obliterates the pattern and reduces the crown to a relatively flat system in which enamel merely forms outlines, and the enclosed dentine is scooped out by wear. This raises a question as to whether complex occlusion is important in young individuals and not as important in older individuals. It is also possible that older individuals with flattened crowns have more freedom in occlusal movement.

Transverse pairs of high cusps in the molars alternate with low transverse valleys. As lower molars engage and move medially across uppers, the high cusps of one set of teeth occlude with the low features of the opposing set. Cusps of the lower molars bite on the anterior side of corresponding cusps in the uppers. Thus the anterior cingulid of m1 occludes with the anteroventral surface of the anterior cingulum in M1, and the protoconid and metaconid fit in the flexus between the cingulum and the paracone and protocone of the upper molars. In m2 and m3 the protoconid and metaconid bite against the low, paired cingula of adjacent upper molars anterior to the paracone and protocone.

Hypoconids fit into metaflexi between the paracones and metacones of upper molars and entoconids fit into the hypoflexi between protocones and hypocones of the upper molars. Pairs of cusps in the upper molars bite into low features of the lower teeth: paracones and protocones bite into the hypoflexids and entoflexids posterior to the protoconids and metaconids; metacones and hypocones occlude with the low cingulids of adjacent lower molars posterior to the hypoconids and entoconids. Sets of wear facets can be matched to those diagrammed by Butler (1980).

DISCUSSION

Willeumys korthi differs from other North American Oligocene and later cricetids in a mixture of primitive, ambiguous, and derived characters. This assessment is based only on my experience with paramyid, sciuravid, and extinct cricetid rodents and not on an exhaustive character study. Primitive characters include the posterior position of the optic foramen and anterior edge of the coronoid process relative to M3, slight zygomatic plate, roughly parallel molar series, and short alveolus of lower incisor. Ambiguous characters include narrow skull, paired temporal crests, narrow incisors, small molars, and roughly triangular shape of M3. The pattern of featherlike ridges on the enamel of the lower incisors is unique and derived. Korth (personal commun.) examined the specimen and said that the pattern of ridges is different from any he has seen; on lower incisors of *W. korthi* the medial and lateral sets of inclined ridges slant bucco-apically, whereas on incisors attributed to *Eoeumys vetus* (Martin, 1980: fig. 26B) the ridges ascend in opposite directions and converge medially. Kalthoff (2000: fig. 42) diagrammed incisor enamel surface patterns of fossil Eurasian cricetids; none matches the pattern in *W. korthi*. The specimen includes cervical vertebrae, a partial scapula, and fragments of limb bones still embedded in rock matrix. Such remarkable preservation suggests death in a burrow, protected from predators, scavengers, and weathering, but not from physical deformation. Analysis of the postcranial remains might indicate whether *Willeumys* was a

burrowing rodent. The locality, Reno Ranch, 5 miles SE of Douglas Wyoming, is very close to the mammalian burrows described by Sundell (1996) from the mid-Orellan, 2–3 miles southeast of Douglas. Sundell's rodent fauna consisted of *Heliscomys*, *Ischyromys*, *Paradjidaumo*, and *Prosciurus*, but lacked cricetids.

Other North American eumyines, *Eumys* and *Coloradoeumys* (Martin, 1980: fig. 6), have a median sagittal crest, and broad skulls and rostra. *Eoeumys vetus*, *Leidymys lockingtonianus*, and *Leidymys nematodon* share several features with *W. korthi*: upper molar series roughly parallel, slight zygomatic plate, interorbital region flat, and temporal crests paired. *Eoeumys vetus* differs in that the flat interorbital surface has a curved, not angular, continuity with the orbital wall, the rostrum is broad, the teeth large, and the upper incisors broad. *Leidymys*, from the Miocene John Day beds, has a flat interorbital roof and angular transition to the orbital surface, but the skulls are broader, and M3 roughly rectangular with a full hypocone; *L. lockingtonianus* also preserves narrow, deep upper incisors. Other fossil cricetids, known primarily from dentitions, differ greatly from *W. korthi*. Transverse crests are much more prominent in several other taxa (see figs. in Martin, 1980) including *Wilsonium planidens*, *Leidymys blacki*, *Pacculus woodi*, *Pacculus insolitus*, and *Geringia mcgregori*. In *Scottimus exiguus*, the molar series converges anteriorly, and extra anteroposterior crests are present in the crowns (see figs. in Korth, 1981).

Willeumys korthi is distinct from all other known Oligocene and Miocene cricetids from North America, and its mixture of characters do not fit into any named genus. Placing *Willeumys* in the Eumyinae rather than the Eucricetodontinae—including *Leidymini* L.D. Martin, 1980—reflects my uncertainty about the definition of the latter taxon. Mein and Freudenthal (1971: 3) said that the Eucricetodontinae is a heterogeneous group, and remains of most species are insufficient for analysis of phylogenetic relationships. This was also true for most early North American cricetids. Taxonomic groups of North American Oligocene cricetids are not based on unique derived charac-

ters. Martin (1980) differentiated Eumyinae from the eucricetodontine Leidymini, pointing out that the Eumyinae have a single sagittal crest and smaller infraorbital foramen. The sagittal crests mark the dorsal extent of the temporalis muscles, a part of the masticatory system; it is likely that similar states may have been derived multiple times in rodent phylogeny and that either state might be primitive. Landry (1999: 312) suggested that the “ancestral sciurognath had some features very different from those of *Paramys*. Specifically ... its skull must have been more like that of *Rattus* than *Paramys*.” Landry (personal commun.) described the primitive *Rattus*-like skull as “box-shaped” with paired temporal crests. The size of the infraorbital canal (anterior view) is influenced by many different systems: the canal must be big enough to transmit the vessels, nerves, and muscle that pass through it; the bulge of the lacrimal foramen and canal on its medial side constrict it ventromedially; the size and position of the zygomatic plate, which extends the origin of the lateral masseter anteriorly, constricts it ventrolaterally. A small zygomatic plate, which does not constrict the infraorbital foramen, is primitive in cricetid or muroid rodents.

The current classification of North American fossil cricetids needs revision. In large part it is based on dental characters. Dental variation is so high in *Eumys* and in Old World cricetids that the phylogenetic signal from dental morphology can be determined only from a large sample of specimens; for most taxa the sample size is too small. As fossil cricetid specimens were collected and described, they were usually put into existing taxa, and the definitions of these taxa become ever broader and less meaningful. The relation of morphology to function also needs to be considered. In rodents gnawing and mastication are uncoupled, and the skull must bear the stress of both activities. How do paired and temporal crests or a single sagittal crest relate to these activities? Perhaps there is sufficient cranial material of extinct North American cricetids that a new phylogenetic study is warranted. *Willeumys* is a unique specimen, and I have relied very little on dental morphology for comparison. I rated the state of many cranial characters as

ambiguous. A reviser must select one or more outgroups to determine their polarity. One could look back to the Eocene sciuravids for primitive characters, to the distant sister taxa, such as the eomyoids, glirids, or dipodoids. The North American cricetids are presumed to be immigrants from Asia, and they may represent twigs of a tree based elsewhere.

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logical Sciences. Annals of the New York Academy of Sciences 529: 128–130.

APPENDIX

Comparative sample of specimens examined

Eumys elegans: Chalky Buttes specimens of crania and dentitions studied by Wahlert (2004). AMNH 1430, skull, Oligocene, White River Formation, Metamynodon beds. Cheyenne River, SD. AMNH 5500, front of skull, Oligocene, White River Formation, Oreodon beds, Cedar Creek, Col. AMNH 5501, front of skull, Oligocene, White River Formation, Oreodon beds, Cedar Creek, Col. AMNH 38872, front of skull, two lower jaw fragments, White River Formation, Lower Oreodon Beds, South of Scenic, SD. AMNH 38873, palate, White River Formation, Lower Oreodon Beds, South of Scenic, SD. F:AM 103377, snout with right M1–2, L M1, north of Old Woman in a Boat Butte, 50 to 60 feet above PW, Parsons Ranch, Sioux Co., SD. F:AM 103378, partial skull and left mandible, 6 miles east of Grover, Weld Co., Col. F:AM 94929, snout and palate with dentition, Dickinson Member, Brule Formation, Fitterer Channel, Fitterer Ranch, SW of Dickinson, Stark Co., ND.

OTHER GENERA: Text following specimen number appears on catalog cards, additions by the author are in brackets:

Eoeumys vetus (Wood, 1937), AMNH 8742, holotype, front of skull. [Probably Orellan, Oligocene] Horizon: White River, Martin Canyon, Logan Co., Colorado. Martin, AM Exped., 1898, Field No. 107 [specimen label adds: Oreodon Beds., Loc. Cedar Crk., Logan Co., Colo.]

Leidymys nematodon (Cope, 1879), AMNH 7018, geno-holotype, palate. [Probably late early Arikarean, Miocene] Horizon: John Day, John Day Basin [specimen label adds: Miocene, John Day R.], Oregon, Coll. T. Condon, Cope Collection.

Leidymys lockingtonianus (Cope, 1881), AMNH 7028, holotype, skull. [Late early Arikarean, Miocene] Horizon: John Day, the Cove, John Day River, Oregon. Coll. Wortman, Cope Collection.

Pacculus insolitus Cope, 1879, AMNH 7022, geno-holotype, palate and fragments. [Late early Arikarean, Miocene] Horizon: John Day, [specimen label adds: Diceratherium Beds,] "The Cove," John Day R., Oregon. Coll. Wortman 1879, Cope Collection.

Scottimus exiguus, (Wood, 1937). AMNH 12261, holotype, palate and left ramus. [Latest Orellan, Scenic Member, Brule formation, Oligocene] Horizon: White River, Mid. Oreodon Beds, Sheep Mountain [specimen label adds: Badlands], SD. Coll. Mrs. Thomson, Exp. 1904, Field No. 4.