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1992. *Transactions of the Nebraska Academy of Sciences*, XIX: 75–82

CYLINDRODONTS (CYLINDRODONTIDAE, RODENTIA) AND A NEW GENUS OF EOMYID, *PARANAMATOMYS*, (EOMYIDAE, RODENTIA) FROM THE CHADRONIAN OF SIOUX COUNTY, NEBRASKA

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ABSTRACT

Cylindrodon galbreathi Ostrander is shown to be a junior synonym of *C. nebraskensis* Hough and Alf, and the first specimen of *Ardynomys occidentalis* is reported from the Chadronian of Nebraska. A restudy of the holotype of *Cupressimus storeri* Ostrander has revealed that this species is not referable to *Cupressimus* Storer but is referred to a new genus, *Paranamatomys,* which is referred to a new tribe of eomyids, the Namatomyini. Only six species of rodents have been documented from the Chadronian of Nebraska, far fewer than other faunas of the same age.

† † †

Although the rodents of the "White River" fauna (Chadronian to Whitneyan) of North America have been thoroughly reviewed (Wood, 1937, 1980), little of the Chadronian rodent fauna of Nebraska has been fully described. Descriptions of rodents from the Chadronian of Nebraska have been limited to reports of small micromammal faunas (Hough and Alf, 1956; Ostrander, 1983a; Wood, 1969) or descriptions of single species (Alf, 1962), limiting the number of known species to far fewer than other known Chadronian faunas (for example, see Black, 1965). Two of these micromammal faunas from Nebraska have been shown to be a mixture of Chadronian and Orellan elements (Guthrie and Allen, 1974; Ostrander, 1985). Recently, Ostrander (1985) listed nearly 30 species of rodents as occurring from Chadronian faunas in Nebraska (including several new species and at least two new genera), but very few of these species have been documented in the literature (Ostrander, 1983a). The total number of rodent species described from the Chadronian faunas of Nebraska is probably fewer than ten if species of possible Orellan age are eliminated. A review of some of the described species of rodents from the Chadronian of Nebraska, including some new material, allows for better understanding of the systematics of these species compared with other Chadronian faunas and includes a previously unreported species.

Abbreviations for institutions used throughout text: CM, Carnegie Museum, Pittsburgh; SDSM, South Dakota School of Mines and Technology, Rapid City; SMNH, Saskatchewan Museum of Natural History, Regina; UNSM, University of Nebraska State Museum, Lincoln; WSAM, Alf Museum, Webb School. Dental terminology used follows Wood and Wilson (1936).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family Cylindrodontidae Miller and Gidley, 1918
Genus ***Cylindrodon*** Douglass, 1901

Cylindrodon nebraskensis Hough and Alf, 1956
(Figs. 1A–D)

Cylindrodon fontis Douglass (in part), Galbreath, 1969; *Cylindrodon galbreathi* Ostrander, 1983a

Type specimen: WSAM 1908, mandible with LI_1 and P_4-M_2. **Locality and horizon**: Type and UNSM specimens from ant hills in the Chadron Formation, SE1/4, sec. 5, T33N, R53W, Sioux County, Nebraska.

Other referred specimens from Raben Ranch Local Fauna, Sioux County, Nebraska, and various localities in northeastern Colorado (see Galbreath, 1969; Ostrander, 1983a). **Age**: Middle Chadronian (early Oligocene of Berggren et al., 1985; latest Eocene of Swisher and Prothero, 1990). **Topotypic specimens**: UNSM 81089, eight isolated cheek teeth; and UNSM 26535, partial mandible with I_1 and P_4-M_1. **Emended diagnosis:** Larger than *C. fontis* and *C. collinus*, especially in anteroposterior length of cheek teeth (see Galbreath, 1969, *table 2*; Ostrander, 1983a, *table 3*); cheek teeth maintain squared occlusal outline until very late in wear; short, posteriorly-oriented spur on protoloph or metaloph of upper molars and metalophid of lower molars.

Discussion. Hough and Alf (1956) described an anthill fauna from Sioux County, Nebraska, which contained a single specimen of a cylindrodont rodent, the holotype of *Cylindrodon nebraskensis*. They identified the fauna as Chadronian even though some genera present were more typically Orellan (such as *Eumys*, *Diplolophus*). Guthrie and Allen (1974) demonstrated that specimens from nearby exposures of Orellan strata had been mixed into this fauna by the ants. It is most likely that the cylindrodonts in the fauna are Chadronian species because all of the referred specimens lack the superficial wear that Guthrie and Allen noticed on the reworked Orellan specimens and no Orellan cylindrodonts have ever been reported.

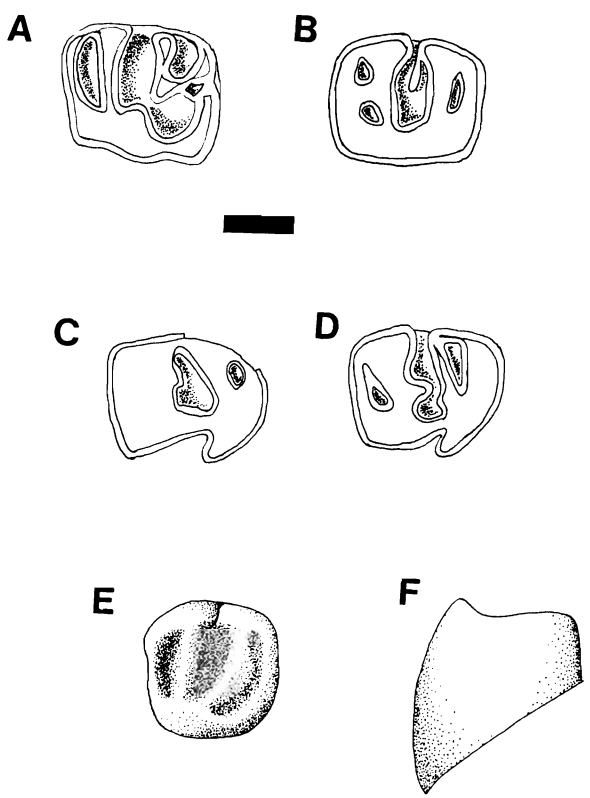

Figure 1. Cheek teeth of cylindrodonts from Sioux County, Nebraska. A–D, *Cylindrodon nebraskensis*, UNSM 81089. A, LM^1 or M^2. B, RM^1 or M^2. C, LM_1 or M_2. D, LM_1 or M_2. E–F, *Ardynomys occidentalis*, UNSM 81090, LM^1 or M^2. E, occlusal view. F, posterior view, occlusal surface toward top of page. Bar scale represents 1 mm.

Cylindrodon nebraskensis was diagnosed as being larger than other species of the genus and having a more squared outline of the lower cheek teeth and deeper (dorsoventrally) mandible (Hough and Alf, 1956:133). Despite these diagnostic characteristics, nearly all authors who discussed cylindrodont rodents since the original description of *C. nebraskensis* have failed to recognize or mention it (Black, 1965; Wood, 1974; Storer, 1978). Wood (1980: *8*), the only author to cite the Nebraska species, suggested that *C. nebraskensis* was just a population of *C. fontis*.

Ostrander (1983a) named a new species, *C. galbreathi*, from the Chadronian of Sioux County, Nebraska, and northeastern Colorado (also see Galbreath, 1969). This species was diagnosed as being larger than other species of the genus and having an antero-posteriorly directed spur on all the cheek teeth. Again, no reference was made to *C. nebraskensis*, though Ostrander's referred material was from the same horizon and in the geographic vicinity of the type locality of *C. nebraskensis*. All of the specimens collected from anthills in the area from which the type of *C. nebraskensis* was recovered (both upper and lower cheek teeth) show the characteristic "spur" of *C. galbreathi* (Fig. 1). The holotype of *C. nebraskensis* (WSAM 1908) consists of a mandible with heavily-worn cheek teeth. It is evident that the holotype of *C. nebraskensis* lacks this feature only because it represents a very old individual whose cheek teeth are in a late stage of wear. Therefore, *C. galbreathi* should be considered a junior synonym of *C. nebraskensis*.

Wood (1937) cited *Cylindrodon* n. sp. from the Chadronian Beaver Divide area of Wyoming that differed from the type species *C. fontis* in the relative size and shape of the cheek teeth and lower incisor. Later this species was listed as unnamed but distinct from *C. fontis* (Wood, 1980). It is quite possible that this species is synonymous with *C. nebraskensis*. Hough and Alf (1956) first noticed the similarity in the shape of the lower incisor between *C. nebraskensis* and the Wyoming species and they suggested such a synonymy.

Ostrander (1983a, *fig. 3B*) figured and described the posterior spur that arose from the protoloph of an upper molar. However, on all the topotypic specimens from Nebraska and those figured by Galbreath (1969, *fig. 2*) a distinct spur arises from the metaloph and

Table I. Dental measurements of referred specimens of *Cylindrodon nebraskensis* from Sioux County, Nebraska. Abbreviations: a-p, anteroposterior length; tr, transverse width (upper molars only); tra, anterior transverse width; trp, posterior transverse width. Measurements in millimeters.

		UNSM 81089		
M^1 or M^2	a-p	2.17	2.14	2.26
	tr	2.19	1.98	2.07
M^3	a-p	1.85	1.67	
	tr	1.67	1.64	

		UNSM 81089		UNSM 26535
I_1	a-p			2.54
	tra			2.06
P_4	a-p	2.04		2.47
	tra	1.53		1.31
	trp	1.81		2.05
M_1 or M_2	a-p	2.21	2.11	2.39
	tra	1.96	1.69	2.07
	trp	2.30	2.09	2.24
Depth of mandible below M_1				6.75

joins the posterior cingulum.

Genus ***Ardynomys*** Matthew and Granger, 1925
Ardynomys occidentalis Burke, 1936
(Figs. 1E, F)

Referred specimen: UNSM 81090, LM^1 or M^2. **Locality and horizon**: Chadron Formation, SE1/4, sec. 5, T33N, R53W, Sioux County, Nebraska. **Age**: Middle Chadronian. **Description**: M^1 or M^2 nearly as long as wide (a-p, 2.0 mm; tr, 2.2 mm; see Table I for abbreviations); unilaterally hypsodont; squared occlusal outline; anterior and posterior cingula continuous for entire width of tooth joining buccal cusps and blocking transverse valleys buccally; buccal cusps transversely compressed into continuous ridge; central transverse valley blocked by ridge connecting metacone and paracone with minute valley near center; metaconule distinct swelling on metaloph, may fuse after moderate wear to posterior cingulum.

Discussion. Previously, *Ardynomys occidentalis* was reported from the early Chadronian of McCarty's Mountain, Montana (Burke, 1936), and Vieja Group, Texas (Wood, 1974). Both of these occurrences are slightly older than the Nebraska specimen which is middle Chadronian (Ostrander, 1985). This is the first record of *Ardynomys* from Nebraska. Altough Ostrander (1985) listed as many as four species of cylindrodonts from his many Chadronian localities in Nebraska, he never cited *Ardynomys*.

There is no difference between UNSM 81090 and the upper molars of the type specimen of *A. occidentalis* from Montana (CM 12010). However, the specimens from Texas are slightly larger (Wood, 1974: *table 8*) and relatively wider than UNSM 81090 and the holotype. Also, the valleys between the cingula and the major lophs of the upper molars (proto- and metalophs) are not buccally blocked in the Texas specimens as in the Nebraska and Montana specimens.

Wood (1974) also cited some differences between the skulls of *A. occidentalis* from Texas and the holotype but noted that these were the more primitive condition in the former, which indicated only a slightly older age of the specimens. This also appears to be the case with the dentition. The Texas specimens more closely approach the condition in *Pseudocylindrodon*, as do the differences in the skull.

Family EOMYIDAE Depéret and Douxami, 1903
Subfamily Eomyinae Depéret and Douxami, 1903
Tribe NAMATOMYINI new

Diagnosis: Small eomyids; cheek teeth brachydont with increase in crown height due to increase in cusp height; cusps of cheek teeth uninflated, anteroposteriorly compressed; anteroconid primitively present on P_4; buccal extension of mesoconid primitively retained on lower cheek teeth. **Included genera**: *Namatomys* Black (1965); *Montanamus* Ostrander (1983b); *Paranamatomys* new genus; and species referred previously to "*Namatomys*".

Discussion. The genera included in Storer's (1987) "*Namatomys* group," along with the new genus described below, all share the unique characters of increased crown height of the teeth by increased height of the cusps and the presence of an anteroconid on P_4 (at least primitively). These derived features separate these genera from the remainder of the Eomyinae. These genera also retain a number of primitive dental characters (cusps uninflated and compressed, buccal extension of the mesoconid primitively retained). The remainder of the eomyines have cheek teeth that have: 1) rounded, inflated cusps; 2) lack of an anteroconid on P_4(developed convergently in *Cupressimus*); and 3) increased crown height through increase in the base of the crown.

This unique combination of derived and primitive features of the dentition of the genera of the "*Namatomys* group" indicates a distinct group of eomyids that should be contained in a supergeneric taxon. Such a taxon is proposed here as the Tribe Namatomyini.

Paranamatomys new genus

Type and only species: *Cupressimus storeri* (Ostrander, 1983). **Range**: Middle Chadronian of Nebraska. **Diagnosis**: Small eomyid, near size of *Adjidaumo*; masseteric scar on mandible low ridge extending anterior to P_4; mental foramen high on mandible; cheek teeth brachydont; cusps on cheek teeth not inflated with some anteroposterior compression; small anteroconid on P_4 connecting with protoconid; anterior cingulum on lower molars buccally attached to protoconid; mesolophid of lower cheek teeth noncentral, oriented slightly obliquely. **Etymology**: *Para* (Greek), near; and *Namatomys* probable closely related genus of eomyine.

Discussion. The genus *Cupressimus* was first described by Storer (1978) from the Chadronian of Saskatchewan and limited to the type species *C. barbarae*. Later, Wood (1980) synonymized this genus with *Viejadjidaumo*, otherwise known only from the Chadronian of Texas (Wood, 1974), based on dental similarities of the lower cheek teeth. Both Ostrander (1983a) and Storer (1987) pointed out differences between *Cupressimus* and *Viejadjidaumo* thus recognizing different genera.

A second species of *Cupressimus*, *C. storeri*, was described from the Chadronian of Nebraska by Ostrander (1983a). However, a number of differences in the dental morphology of *C. storeri* and the type species indicate that the former is not referable to this genus. Unfortunately, the figures of the holotypes of both *C. barbarae* (Storer, 1978: *fig. 5B*) and *C. storeri* (Ostrander, 1983a: *fig. 4*) do not show enough detail of the occlusal surface of the cheek teeth to see many of the details of occlusal morphology that separate these two species.

Perhaps the most diagnostic feature of the genus *Cupressimus* (based on the type species) is the shallowness of the talonid basin coupled with the large size and roundness of the major cusps. The four major cusps of the lower molars of *C. barbarae* (protoconid, metaconid, entoconid, hypoconid) are quite large and the cusps that are directly buccal or lingual to each other nearly meet centrally with only a very short loph between them. It is also evident that the lophs will disappear with relatively little wear because they rise only slightly above the base of the talonid basin. The molars are also nearly as wide as they are long.

As discussed by Ostrander (1983a) and Storer (1987), the lower cheek teeth of *Viejadjidaumo* differ greatly in having a more typical eomyine molar morphology with the molars longer than wide and the cusps proportionately smaller and the lophs better developed. *Cupressimus* and *Viejadjidaumo* are clearly not synonymous.

The features of *Cupressimus storeri* that separate it from *C. barbarae* are: 1) smaller size; 2) lower crowned cheek teeth; 3) cusps not as large and lophs better developed; 4) buccal attachment of the anterior cingulum to the protoconid; 5) longer mesolophid that does not taper into the talonid basin; 6) metalophid on M_1 joins the protoconid at its anterolingual corner (rather than posterolingual in *C. barbarae*); and 7) longer posterior cingulum on M_1. Clearly, *C. storeri* belongs in a new genus of eomyid, and cannot be referred to any existing genus. The new genus named here contains only the type species, *P. storeri*.

Among other North American eomyids, *Paranamatomys* shares more dental features in common with the "*Namatomys* group" as defined by Storer (1987) than with any other group. The cusps of the teeth of

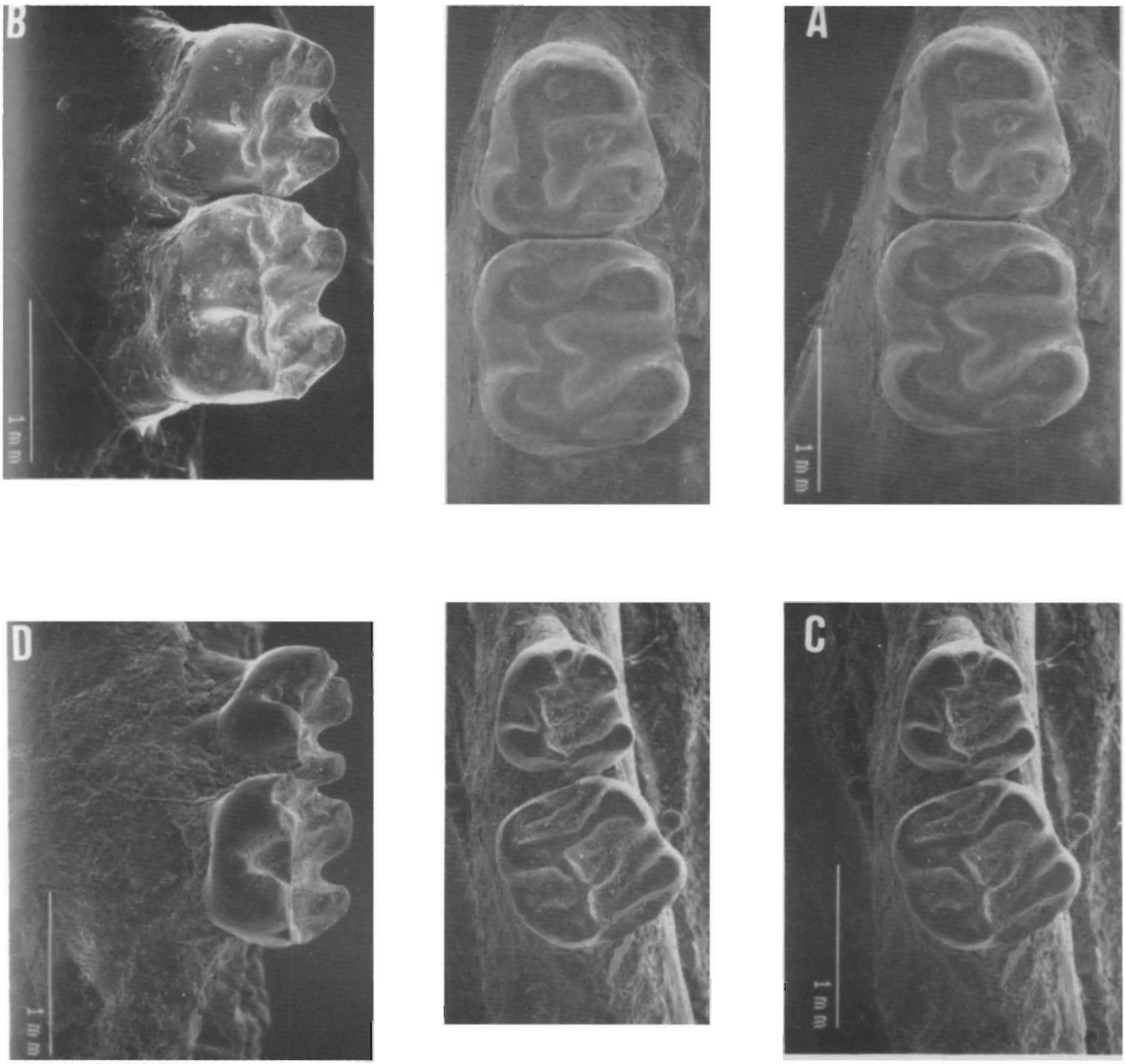

Figure 2. Scanning electron micrographs of the holotypes of *Cupressimus barbarae* (SMNH P661.101) and *Paranamatomys storeri* (SDSM 10139). A, *C. barbarae*, LP_4-M_1 occlusal view (stereo). B, same as A, oblique lateral view. C, *P. storeri*, LP_4-M_1 occlusal view (stereo). D, same as C, oblique lateral view.

Paranamatomys are anteroposteriorly compressed as in *Namatomys*, unlike the cheek teeth of other eomyines ("*Adjidaumo-Paradjidaumo* group") which have enlarged and rounded cusps. The crown height of the cheek teeth of *Paranamatomys* is attained by the heightening of the cusps, also as in *Namatomys*, rather than by an increase in the height of the base of the crown as in the Eomyini. *Paranamatomys* does not have the degree of lophodonty, elongation of the lower molars, and nearly central ectolophid of *Yoderimys*, so it cannot be considered a yoderimyine.

Paranamatomys differs from the other members of the Namatomyini mainly in the attachment of the anterior cingulum on the lower molars and the lack of a buccal extension of the mesoconid. In all other genera of this tribe (*Namatomys*, *Montanamus*, "*Namatomys*") the anterior cingulum of the lower molars is free buccally and attached to the metalophid by an anterior arm of the protoconid. In *Paranamatomys* the buccal end of the anterior cingulum attaches directly to the protoconid with no free end. Storer (1987) defined the "*Namatomys* group" as maintaining the primitive sciuravid feature of a mesoconid in the lower cheek teeth that had at least a small buccal extension. This is lacking in *Paranamatomys*. *Paranamatomys* differs from *Montanamus* by the presence of a posterior cingulum on M_1 and an anteroconid on P_4 (Ostrander, 1983b). The lower molars of *Namatomys lloydi* and those referred to "*Namatomys*" (Korth, 1989; Lindsay, 1968; Storer, 1984, 1987) are proportionally longer than M_1 of *Paranamatomys*. Both *N. lloydi* and "*N.*" *lacus* possess a second posterior arm of the protoconid (= mesoconid) on the lower molars not present in *Paranamatomys*. The mesolophid on the cheek teeth of *Paranamatomys* originates from the ectolophid posterior to its center and angles slightly in an anterolingual direction. This type of mesolophid is seen in the species referred to "*Namatomys*". Korth (1989) suggested that a number of specimens from Nebraska previously referred to *Adjidaumo minutus* by Wood (1969) might well represent an Oligocene species of "*Namatomys*." These specimens have a more lingual attachment of the anterior cingulum on the lower molars than does *P. storeri* and cannot be referred to this genus.

The masseteric scar on the mandible of *Paranamatomys* is very heteromyid-like (a low shelf extending anteriorly to a point anterior to P_4). The only other eomyids with this same muscle scar on the mandible are the Chadronian *Meliakrouniomys* (Emry, 1972; Harris and Wood, 1969) and Orellan *Metadjidaumo* (Korth and Tabrum, in press). Both of these latter genera clearly belong the "*Adjidaumo-Paradjidaumo* group" of eomyids (=Eomyini) and are not closely related to *Paranamatomys*. The mandible for two namatomyines, *Namatomys* and *Montanamus*, are known and both have the more typical eomyid pattern of a U-shaped masseteric fossa that terminates anteriorly below P_4.

Paranamatomys storeri (Ostrander, 1983a)
(Figs. 2C, D)

Cupressimus storeri Ostrander, 1983a

Type specimen: SDSM 10139, partial mandible with LI_1, P_4-M_1. **Locality and horizon**: "Raben Ranch, 2 miles southwest of Orella, Sioux County, Nebraska SDSM (locality) V772." (Ostrander, 1983a: 134). **Age**: Medial Chadronian. **Diagnosis**: Same as for genus.

Discussion. Ostrander (1983a) fully described the dentition of *P. storeri*. However, one observation that appears incorrect is the attachment of the anterior cingulum on the lower molars. Ostrander noted that the attachment of the cingulum was lingual to the buccal end, leaving the buccal end free. On the holotype the buccal end of the anterior cingulum is clearly attached to the protoconid.

The attachment of the anterior cingulum on the lower molars of *Paranamatomys storeri* is seen elsewhere among the eomyids in *Metadjidaumo*, *Paradjidaumo* and *Centimanomys*. Both *Metadjidaumo* and *Paradjidaumo* have mesodont cheek teeth unlike *P. storeri*, and *Centimanomys* is much larger (Galbreath, 1955) and has well-pronounced elongate lophs and reduced cusps on the cheek teeth. These three genera are also members of the "*Adjidaumo-Paradjidaumo* group" (Storer, 1987) and cannot be closely related to *Paranamatomys*.

Relationships of *Paranamatomys* among the rest of the genera included in the Namatomyini, based on dental morphology, appear relatively simple. The proportions of the lower molars of *Paranamatomys* (relatively wider than *Namatomys*) and the lack of a posterior cingulum on P_4 are derived features that are shared with *Montanamus*, suggesting closer relationship than with *Namatomys*. However, the attachment of the anterior cingulum and masseteric fossa on the mandible of *Paranamatomys* make it clearly distinct from *Montanamus* which separately derives a much reduced premolar (loss of anteroconid) and loss of a posterior cingulum on the lower molars. *Namatomys*, *Paranamatomys* and *Montanamus* all have higher crowned cheek teeth than the species referred to "*Namatomys*" and all have a better developed ectolophid on the lower cheek teeth which is often incomplete in species of "*Namatomys*" (see Lindsay, 1968). A cladogram of these relationships is presented in Fig. 3.

IMPLICATIONS FOR THE CHADRONIAN RODENT FAUNA OF NEBRASKA

Including the descriptions presented here, only six species of rodents have been described from the Chadronian of Nebraska: *Ischyromys veterior*, *Cylindrodon nebraskensis* (= *C. galbreathi*), ?*Pseudocylindrodon* sp., *Ardynomys occidentalis*, *Paranamatomys storeri* and *Pipestoneomys pattersoni* (possibly = *P. bisulcatus*). Four additional species have been described from Chadronian faunas in Nebraska but are not definitely known to occur in the Chadronian outside of these faunas. The specimens representing these species may have been introduced by mixing with elements of the overlying Orellan strata: *Adjidaumo minutus*, *Paradjidaumo trilophus*, *Eumys elegans* and "*Namatomys*" *sp.* (= *Adjidaumo minutus*, in part)

Although the Chadronian rodent fauna from Nebraska may contain as many as thirty species (see lists in Hough and Alf, 1956; Ostrander, 1985) very few of these species have been documented. Clearly, a much more thorough description of the Chadronian rodent fauna is necessary to verify the occurrence of species listed elsewhere. Such a review would give a better insight into the relationship of the Nebraska Chadronian to that of other areas in North America.

ACKNOWLEDGMENTS

Assistance in the collection and sorting of topotypic material of *Cylindrodon nebraskensis* was provided by A. Hermanson, J. Hageman, G. Larson, and D. Ellis of Doane College, Crete, Nebraska. The holotype of

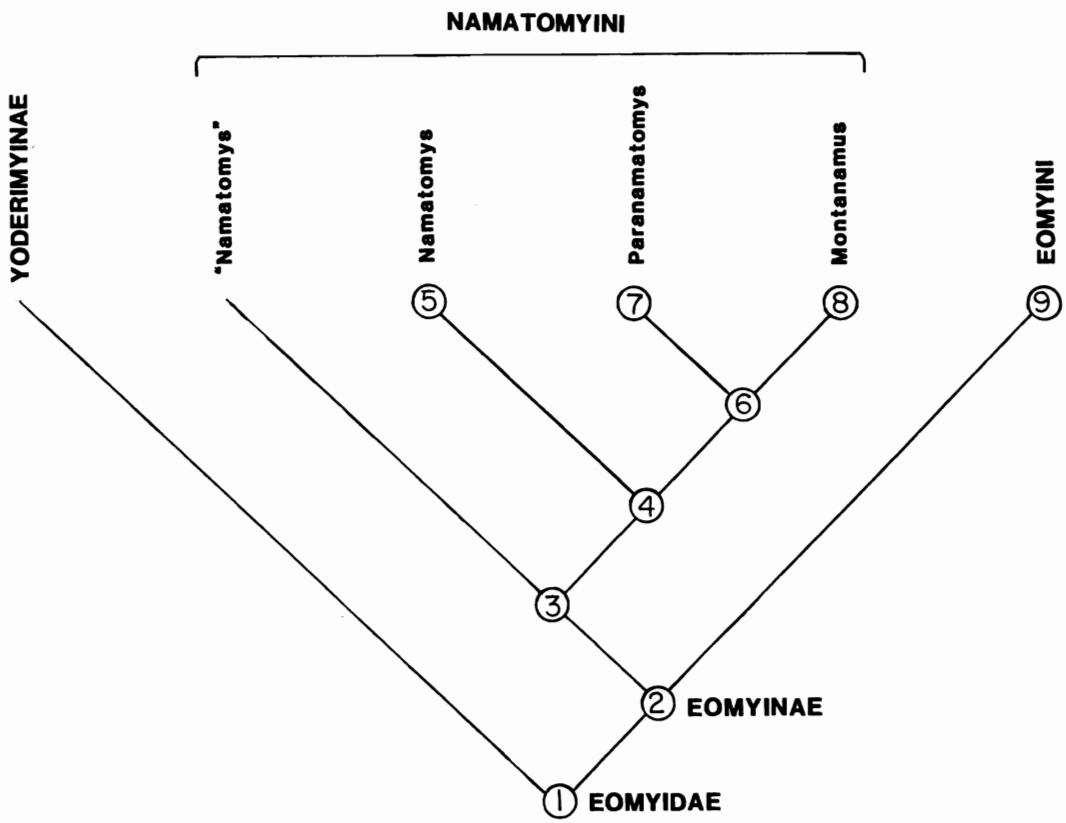

Figure 3. Cladogram of the relationships of Namatomyini within the Eomyidae.
Definition of nodes:

1. Eomyidae. "Omega" occlusal dental pattern of cheek teeth; two-part portio interna of incisor enamel.
2. Eomyinae. Loss of P^3.
3. Namatomyini. Anteroconid on P_4; crown height increased through increase in cusp height.
4. Higher crowned cheek teeth; ectolophid of lower cheek teeth more strongly developed.
5. Mesolophid doubled.
6. Lower molars relatively wider; loss of posterior cingulum on P_4.
7. Loss of buccal extension of mesoconid on lower cheek teeth; buccal attachment of anterior cingulum on molars; anteriorly extended masseteric scar on mandible.
8. Loss of posterior cingulum on lower molars; loss of anteroconid on P_4; decreased lophodonty.
9. Eomyini. Cusps of cheek teeth bulbous, inflated; loss of buccal extension of mesolophid; crown height attained by increase in height of base of crown.

Cupressimus barbarae was borrowed by permission of J. E. Storer (SMNH) and a cast of the holotype of *C. storeri* was provided by P. Bjork and J. E. Martin (SDSM). SEM photos were taken by Brian Terhune of the Barton Laboratory, Cornell University-Geneva Campus. An earlier version of this manuscript was reviewed by Dr. Storer of the Saskatchewan Museum of Natural History.

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