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A NEW GENUS OF PRAIRIE DOG (SCIURIDAE, RODENTIA) FROM THE MIOCENE (BARSTOVIAN OF MONTANA AND CLARENDONIAN OF NEBRASKA) AND THE CLASSIFICATION OF NEARCTIC GROUND SQUIRRELS (MARMOTINI)

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ABSTRACT

A new genus of sciurid, *Cynomyoides*, is named. The new genus includes a new species from the late Clarendonian of Nebraska, *C. vatis* (type species), and an unnamed species from the early Barstovian of Montana. The dental and mandibular morphology of *Cynomyoides* is reminiscent of that of the latest Tertiary to Recent prairie dog *Cynomys* and is believed to be part of the lineage leading to *Cynomys*. The recognition of a Miocene genus of prairie dog extends the known record of these ground squirrels well back into the Tertiary and makes it much less likely that *Cynomys* was derived from a species of the ground squirrel *Spermophilus* in the latest Tertiary, as has been suggested by previous authors. A new scheme for the classification of nearctic marmotines is proposed.

† † †

Previously, the earliest recognized occurrence of a fossil prairie dog was from the late Blancan (Eshelman, 1975; Hibbard, 1942). All previous authors have believed that prairie dogs (genus *Cynomys*) evolved from a *Spermophilus*-like ancestor in the latest Hemphillian or Blancan (Black, 1963; Bryant, 1945; Eshelman, 1975; Hafner, 1984).

Sutton and Korth (1995) recently described two teeth from the early Barstovian of Montana that resembled *Cynomys* and placed them questionably in the genus, suggesting that additional specimens of *Cynomys*-like squirrels might be found in deposits intermediate between the Barstovian and Blancan. Recently, a specimen has been recovered from the late Clarendonian of Antelope County, Nebraska, that has the dental characteristics of prairie dogs that clearly separate it from other ground squirrels (Tribe Marmotini). The genus represented by this specimen is the same as that for the Barstovian specimens from Montana. This extends the record of prairie dogs back into the early Barstovian, approximately ten million years earlier than previously believed.

Dental terminology follows that of Wood and Wilson (1936). Lower cheek teeth are denoted by lower case letters (e.g. p4, m1). Abbreviations for institutions: CM, Carnegie Museum, Pittsburgh; UNSM, University of Nebraska State Museum, Lincoln.

SYSTEMATICS

Order Rodentia Bowdich, 1821
Family Sciuridae Gray, 1821
Subfamily Sciurinae Gray, 1821
Tribe Marmotini Pocock, 1923
Genus ***Cynomyoides*** new

?*Cynomys* Sutton and Korth, 1995

Type species: *Cynomyoides vatis* n. sp. **Referred species**: *Cynomyoides* sp. (Sutton and Korth, 1995). **Range**: Early Barstovian of Montana and late Clarendonian of Nebraska. **Diagnosis**: Cheek teeth highly lophate and anteroposteriorly compressed as in *Cynomys* (greater than in *Spermophilus* or *Marmota*), but lower crowned; trigonids of lower molars small and elevated as in *Cynomys* but have only weak or incomplete metalophulid II (strongly developed, elevated and enclosing trigonid basin in *Cynomys*); m3 posteriorly enlarged with broad, curved central loph as in *Cynomys*; mesostylids strongly developed on lower molars and attached to metaconid (lacking in *Cynomys*); accessory cusps in talonid basins of p4-m2 present, but smaller than those of *Cynomys* molars. **Etymology**: *Cynomys*, the genus of prairie dog, and the suffix *-oides*, Greek, like.

Discussion. *Cynomyoides* is distinguishable from any species of *Spermophilus* or *Marmota* by its highly

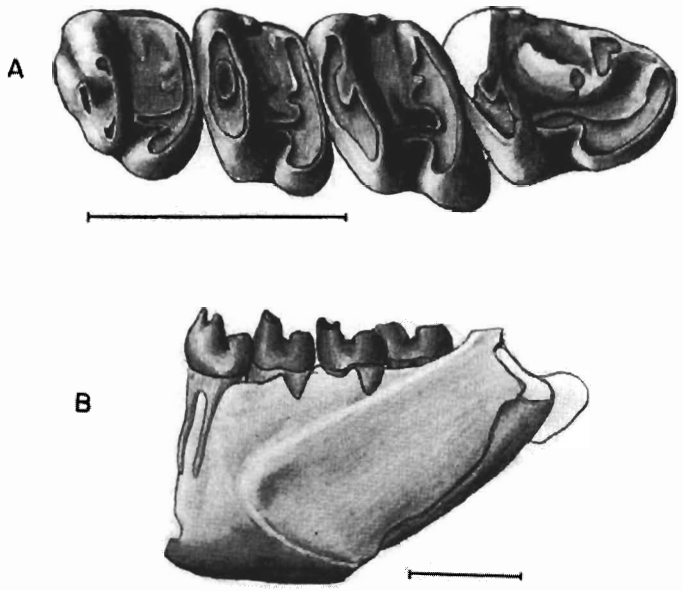

Figure 1. Holotype of *Cynomyoides vatis*, UNSM 101817. A, left p4-m3 (occlusal view). B, lateral view of mandible. Bar scale below each figure = 5 mm.

lophate, anteroposteriorly compressed cheek teeth, and heavily built mandible. The irregularities of the talonid basins of the cheek teeth are also as in *Cynomys*. *Cynomyoides* differs from the latest Tertiary to Recent *Cynomys* in having cheek teeth less high crowned, the trigonid basin on lower molars less well defined, and having the accessory cuspules in the talonid basins of the lower cheek teeth less well developed. The large crescentic lophid in the center of the talonid basin of m3 of *Cynomys* is present in the species described below from the late Clarendonian of Nebraska as well as an early Barstovian specimen from Montana questionably referred to *Cynomys* (Sutton and Korth, 1995).

Cynomyoides vatis n. sp.
(Fig. 1; Table 1)

Type and only specimen: UNSM 101817, left mandible with p4-m3. **Horizon and locality**: Blue Jay Quarry (UNSM locality Ap-112), NW 1/4, SW 1/4, NW 1/4, NE 1/4, sec. 22, T28N, R7W, Antelope County, Merritt Dam Member, Ash Hollow Formation. **Age**: Late Clarendonian. **Diagnosis**: Cheek teeth larger and higher crowned than Barstovian *Cynomyoides* sp. **Etymology**: Latin, *vatis*, seer or prophet. **Description**: Little is observable about the mandible except that it is more robust and transversely thick than in species of *Spermophilus*. The masseteric scar is a raised ridge that ends anteriorly in a broad U-shape, reaching a point even with the posterior margin of p4. The ascending ramus originates at the posterior end of the tooth row. Due to breakage, the position of the mental foramen and morphology of the diastema cannot be determined. The lower incisor is broad and strongly convex anteriorly with a flat medial surface.

The lower cheek teeth are mesodont (higher crowned than those of species of *Spermophilus*, lower crowned than those of *Cynomys*), and strongly anteroposteriorly compressed (except m3), being much shorter than wide. The trigonids of the lower cheek teeth are elevated well above the level of the talonid basins. The trigonid basin is small and oval. It is enclosed anteriorly and posteriorly on p4 and m1, and open posteriorly on m2 and m3. The ectolophid is strongly developed on all the lower cheek teeth and runs from the hypoconid into the posterior wall of the trigonid posterior to the protoconid. There is no indication of a mesoconid.

The lower premolar is molariform and nearly equal in size to the first two molars, differing only in having the metalophid slightly more narrow (buccolingually) than the talonid. On m1 and m2, the metalophid is also narrower than the talonid, but not proportionally as much as in p4. The molars all have a pronounced mesostylid attached to the posterior wall of the metaconid that is lacking on p4. In the talonid basins of p4-m2 there is an indication of at least one large, low cusp that has been all but worn away, similar to the cusps in the talonid basins of *Cynomys* that are much larger and often multiple. This accessory cusp on the cheek teeth of *C. vatis* is most pronounced on m2 and smallest on p4.

The last lower molar is, by far, the largest of the cheek teeth. The trigonid is elevated and small but open posteriorly as in m2. The talonid is widely expanded posteriorly. The talonid basin contains a large, low crescentic loph near its center that is attached at its posterior end to a partial hypolophid that runs buccally from the entoconid. Posteriorly, the tooth is rounded.

Discussion. The holotype of *Cynomyoides vatis* differs from the Barstovian specimen of m3 from Montana (CM 27842) by its larger size and slightly higher crown height (Sutton and Korth, 1995: p. *282*, fig. 2J). The central, crescentic loph in the talonid basin and elevated trigonid of m3 is nearly identical for the two species, making the Barstovian specimen clearly referable to *Cynomyoides*.

Table 1. Dental measurements of *Cynomyoides vatis*, UNSM 101817 (holotype). Measurements in mm. Abbreviations: a-p, anteroposterior length; tra, anterior transverse width; trp, posterior transverse width.

p4			m1			m2			m3			alveolar length
a-p	tra	trp	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp	p4-m3
2.69	2.84	3.24	2.26	3.31	3.32	2.58	3.50	3.56	4.06	3.57	2.62	11.88

All species of *Cynomys* have higher crowned cheek teeth, and the accessory cusps in the talonid basins of the lower molars are much larger than in those of *C. vatis*. No species of *Spermophilus* or *Marmota*, either contemporary or later than *Cynomyoides*, has the compression, elevated trigonids, and irregularities in the talonid basins present in the lower cheek teeth of *Cynomyoides* or *Cynomys*. The mandibles of both these later genera are also much more robust than any species of *Spermophilus*.

CONCLUSIONS

Previously, the origin of prairie dogs was believed to be from an ancestral ground squirrel sometime in the latest Tertiary (Black, 1963; Bryant, 1945; Eshelman, 1975; Hafner, 1984). It was even suggested that the ancestor of *Cynomys* was to be found within *Spermophilus* (*Spermophilus*) (Eshelman, 1975; Hafner, 1984). Since the earliest definite occurrence of the former subgenus was the Hemphillian (Shotwell, 1956) and only possibly Clarendonian (Black, 1963), and the first occurrence of the only previously known genus of prairie dog *Cynomys*, was late Blancan (Hibbard, 1942; Eshelman, 1975), the ancestor of the prairie dogs was naturally suspected to have existed sometime in the late Hemphillian or early Blancan. Hafner (1984) even suggested that the genus *Spermophilus* might even be paraphyletic because of the similarity of the subgenus *Spermophilus* to *Cynomys*.

However, the recognition of a Barstovian and Clarendonian species with dental morphology similar to that of *Cynomys* suggests that the origin of the prairie dogs was much earlier than previously believed and the relationship between prairie dogs and *Spermophilus* is not as close. The distinct dental and mandibular morphology of prairie dogs appears in the fossil record as *Cynomyoides* in the Barstovian, about the same time as the first occurrence of *Spermophilus* (see Korth, 1994: *123*). This suggests that the prairie dog lineage and *Spermophilus* have been separate since their respective origins. It is not unlikely that the *Cynomyoides-Cynomys* lineage evolved from a primitive marmotine. The earliest marmotine is *Miospermophilus* from the Hemingfordian (Black, 1963) and has been suggested as the ancestor of all later marmotines (Hafner, 1984). However, these early spermophiles did not have any indication of the amount of compression of the cheek teeth with elevated trigonids and deep mandible present in the prairie dogs.

Hafner (1984), in a study of Nearctic sciurids, included *Cynomys* in a subtribe of marmotines, the Spermophilina, along with *Spermophilus* and the Hemingfordian *Miospermophilus*, separate from all other marmotines. He also recognized two other subtribes, the Marmotina (including *Marmota* and the fossil forms *Palaearctomys* and *Paenemarmota*) and the Ammospermophilina (including *Ammospermophilus* only). With the first occurrence of a prairie dog now known to be from the early Barstovian, it is clear that *Spermophilus* and the prairie dogs have been separate throughout their known records of existence. The subgenus *Spermophilus* is not a likely ancestor of the prairie dogs based on the fossil record because the earliest record of this subgenus is questionably Clarendonian (Black, 1963), much later than the early Barstovian occurrence of *Cynomyoides*.

Based on first occurrences as the major factor of separation between the lineages of marmotines, it appears that the prairie dogs were the first to appear along with *Spermophilus* and the lineage leading to *Marmota* represented by *Palaearctomys* in the early Barstovian. The next separation was that of *Ammospermophilus* in the Clarendonian along with the probable first occurrence of the subgenus *Spermophilus*.

Based on this criterion, the prairie dogs are as distinct phylogenetically from *Spermophilus* as is *Marmota*. This implies that, based on the fossil record, the inclusion of *Spermophilus* and *Cynomys* into a single subtribe that excludes *Marmota* and its relatives is not warranted. In fact, the separation of *Cynomyoides* and *Cynomys* into their own separate subtribe is more likely. The fossil record also suggests that *Ammospermophilus* is more closely related to *Spermophilus* and does not warrant a separate subtribe. With the recognition of a Barstovian to Clarendonian prairie dog, Hafner's (1984) classification of the subtribes of the nearctic marmotines should be amended as follows (see Fig. 2):

Tribe Marmotini Pocock, 1923

Subtribe Marmotina Pocock, 1923

Included genera: *Marmota* Frisch, *Palaearctomys* Douglass, *Paenemarmota* Hibbard and Schultz.

Subtribe Spermophilina Moore, 1959

Included genera: *Spermophilus* Cuvier, *Ammospermophilus* Merriam, *Miospermophilus* Black.

Subtribe Cynomyina Gromov et al., 1965

Included genera: *Cynomys* Rafinesque, *Cynomyoides* n. gen.

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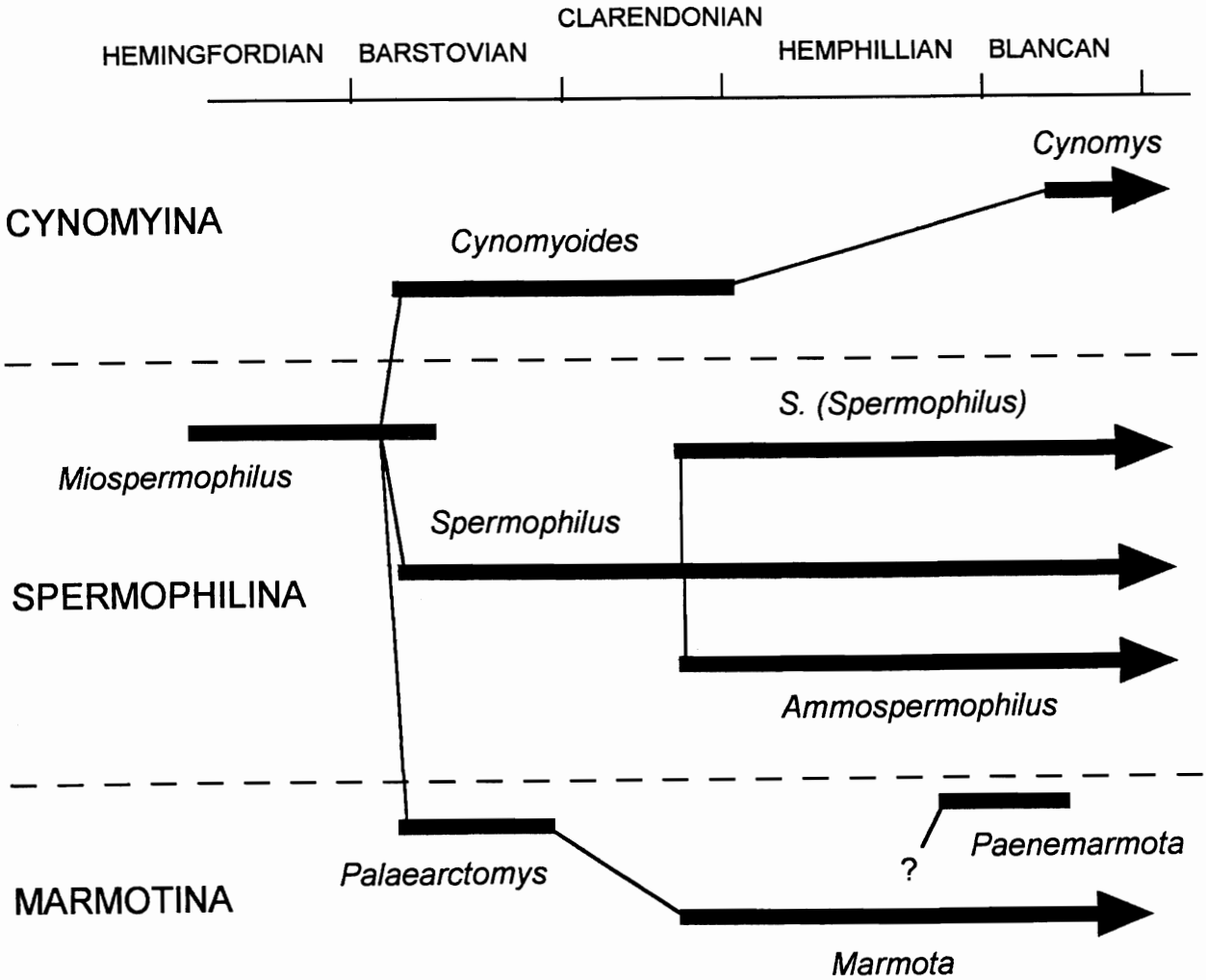

Figure 2. Proposed phylogeny of Nearctic marmotines (modified from Hafner, 1984, fig. 1.4). Heavy vertical lines represent known occurrences, thin horizontal lines represent proposed relationships.

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