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PROSIGMODON OROSCOI, A NEW SIGMODONT RODENT FROM THE LATE TERTIARY OF MEXICO

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ABSTRACT—The age and morphology of *Prosigmodon oroscoi* n.gen., n.sp., from early Pliocene (late Hemphillian and early Blancan) deposits in Chihuahua, Mexico, support the hypothesis of North American origin for sigmodontine rodents, and subsequent entry into South America about 4 Ma.

INTRODUCTION

EXTANT cricetid rodents of the New World comprise two major groups. The peromyscines are mainly North American in distribution and are characterized by having a simplified glans penis without lateral digits. The sigmodontines are mainly South American in distribution and have a complex penis. Peromyscines are poorly represented but present in South America, while sigmodontines are poorly represented but present in North America. The extreme diversity of recent South American sigmodontines (about 40 genera and 180 species) has suggested to some students (e.g., Hershkovitz, 1972) a relatively early (Miocene) origin of the group in South America, with subsequent late Pliocene and Pleistocene northward migration of a few forms to Middle and North America. Other students maintain that sigmodontines entered South America rather late (Pliocene; Montehermosan) via waif dispersal or the Panamanian land bridge from the north where diversification was beginning, and then radiated producing the present South American diversity (Simpson, 1950; Marshall et al., 1979). Baskin (1978) has reported the sigmodontine genus Calomys, now living only in South America, from late Miocene (Hemphillian) deposits at White Cone, Arizona. This record is older than any South American record of sigmodontines and, therefore, supports the hypothesis of a northern center of origin for the group.

The sudden appearance of North American mammals, including four genera of sigmodontines (Reig, personal commun.), at the beginning of the Chapadmalalan Land Mammal Age in South America, and the appearance in North America of several South American mammals in the late Blancan Land Mammal Age support the existence of a Panamanian land bridge about 2.5 to 3.0 Ma (Webb, 1978; Marshall et al., 1979).

We report here a new genus of sigmodontine rodent from Pliocene deposits near Yepómera, Chihuahua, Mexico. The new taxon reported here was found in association with at least five other cricetid species. Large mammals from the Yepómera fauna (also known as the Rincon fauna) have been described (Lance, 1950), and establish a late Hemphillian age for the Yepómera assemblage. A diverse rodent fauna has been recovered from the Hemphillian localities (Wilson, 1949; Lindsay & Jacobs, in prep.) and from newly discovered Blancan localities in strata that overlie the Hemphillian localities. South American mammals are unknown from the superposed strata that have yielded the Yepómera (late Hemphillian) and Concha (early Blancan) faunas in Chihuahua. Absence of South American mammals in these strata suggest that they were deposited prior to the Panamanian land bridge and the South American Chapadmalalan Land Mammal Age.

Diversity of the Chihuahua cricetids and absence of mammals with South American ancestry from the same deposit supports the hypothesis of late Miocene and early Pliocene (Hemphillian) origin and diversification of sigmodontine cricetids in southwestern North America (Jacobs, 1977a).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821 Family CRICETIDAE Rochebrune, 1883 PROSIGMODON n. gen. Text-fig. 1, Table 1

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425

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TEXT-FIG. 1.—Upper teeth of sigmodont rodents: A, left upper first molar of Sigmodon medius of Blancan (Pliocene) age from 111 Ranch, Arizona; B, left upper first molar of Prosigmodon oroscoi (holotype, IGCU 1217) of Hemphillian and Blancan (Pliocene) age from Yepomera, Chihuahua, Mexico; C, left upper first molar of Calomys (Bensonomys) gidleyi of middle Hemphillian (late Miocene) age from White Cone, Arizona; D, labial view of left upper first molar of Prosigmodon oroscoi (holotype, IGCU 1217) showing root structure; E, left upper third molar of Prosigmodon oroscoi (reversed illustration of IGCU 1180). Type-species.—Prosigmodon oroscoi, known from several superposed Pliocene (Hemphillian and Blancan) localities near Yepómera, Chihuahua, Mexico. The holotype (Text-fig. 1) is a left M^1 (Instituto de Geologia Ciudad Universitaria 1217) from University of Arizona Laboratory of Paleontology locality Y-39 (=Ch-15 of IGCU). A larger species (undescribed) has been recovered with *P. oroscoi*.

Diagnosis.—A genus of cricetid rodent with rooted, moderately high-crowned and moderately robust cheek teeth with accessory roots often developed, especially on M^1 . The anterocone of M¹ is wide, weakly bilobed when unworn, and expanded anterolingually at the base. The anteroconid of M_1 is wide and strongly bilobed. The M³ has a narrow anterior cingulum, and a metacone that is indistinct or absent; the median valley is deep, but the anterior and posterior valleys are shallow. The M³ is not lophate. The dentary is moderately deep with a prominent lower masseteric crest; the mental foramen is dorsally placed on the diastema, anterior to but lower than the M_1 .

Etymology.—The generic name is from pro-, a prefix meaning before, and Sigmodon, the cotton rats, alluding to the close relationship of the two and the primitive nature of Prosigmodon with respect to Sigmodon. The species is named for Francisco Orosco, a rancher native to the area, who worked for California Institute of Technology parties in the original excavations at Yepómera and guided us to many localities.

Comparisons.—Prosigmodon is most similar to Calomys (Bensonomys) and Sigmodon (Text-fig. 1; Table 1). It is distinct from Calomys (Bensonomys) in its more robust cheek teeth that are higher crowned, and have less strongly bilobed anterocone and anteroconid. The M^1 and M_1 of *Prosigmodon* are relatively shorter and wider than in Calomys (Bensonomys). The masseteric crest of Calomys (Bensonomys) terminates high on the side of the dentary, well above the level of the mental foramen; whereas the masseteric crest of Prosigmodon terminates at about the level of the mental foramen, as it does in fossil species of Sigmodon. Prosigmodon differs from Sigmo*don* in being less robust, slightly lower crowned, and in having a slightly bilobed anterocone on M¹ and a strongly bilobed anteroconid on M_1 . Union of the anterocone and

		Num- ber	Mean	Observed range	Туре
M1	length width	6 6	1.93 1.37	1.80-2.08 1.23-1.48	1.96 1.38
\mathbf{M}^2	length width	3 3	1.43 1.37	1.36–1.52 1.28–1.44	
M ³	length width	2 2	1.14 1.18	1.12–1.16 1.16–1.20	
M ₁	length width	0 1	1.33		
M_2	length width	2 2	1.47 1.29	1.45–1.48 1.26–1.32	
M ₃	length width	1 1	1.22 1.05		

TABLE 1—Measurements (mm) of Prosigmodon oroscoi.

protocone is more lingual, and cusps in the upper molars of *Prosigmodon* are not so posteriorly inclined as in those of *Sigmodon*. The M^3 of *Prosigmodon* is cuspate with paracone, protocone, and hypocone distinct; the M^3 of *Sigmodon* is lophate, with the three lophs terminating at the anterior cingulum, paracone, and posterior cingulum (based on homologous structures in *Prosigmodon*). The anterior cingulum on M^3 of *P. oroscoi* is short, whereas it is long on *Sigmodon*. Modern *Calomys* has a bilophate M^3 with smaller anterior cingulum compared to *Sigmodon*, but *Calomys* (*Bensonomys*) has a cuspate M^3 .

In his thorough review of fossil and extant species of Sigmodon, Martin (1979) recognized Sigmodon medius medius as the earliest and most primitive species of the genus. Martin noted (1979, p. 19) that reentrant folds (termed "valleys" in our diagnosis) are relatively shallow, and the dentition is more brachydont (termed "lower crowned" in our diagnosis) in S. medius than in other species of Sigmodon. He also noted that accessory rootlets on M_1 of S. medius are usually only tiny pegs, with the labial rootlet better developed than the lingual. Accessory rootlets are developed in *Cal*omys (Bensonomys), Prosigmodon, and Sigmodon; however, they are not as well developed in Calomys and are better developed in Sigmodon, compared to Prosigmodon. Prosigmodon has an accessory rootlet on the upper molars (commonly on M^1 and less commonly on M²) but never observed in the present sample on lower molars, as is common in Sigmodon.

A second (unnamed) species of *Prosigmodon*

occurs with *P. oroscoi* in Chihuahua. The second species has larger, higher crowned, and more robust molars than *P. oroscoi*, but retains the bilobed anterocone and anteroconid on M_1^1 plus a cuspate M^3 ; accessory rootlets are slightly better developed on the unnamed species of *Prosigmodon* than on *P. oroscoi*.

CONCLUSIONS

Prosigmodon is closely related to Calomys (Bensonomys) on the one hand, and Sigmodon on the other. It is more advanced than Calomys (Bensonomys) while being more primitive than Sigmodon in height of crown, strength of connections between cusps, robustness, and development of accessory rootlets. The age of **Prosigmodon** is late Hemphillian and early Blancan. It is morphologically and temporally suited to represent a descendant of Calomys (Bensonomys). The more lingual connection of the anterocone and protocone in Prosigmodon relative to *Calomys* and *Sigmodon* precludes Prosigmodon (at least P. oroscoi) from direct ancestry of Sigmodon. However, overall similarity of Prosigmodon and Sigmodon suggests that Prosigmodon is near the ancestral stock of Sigmodon and supports the derivation of Sigmodon from North American cricetids, rather than Old World cricetodontines as suggested by Jacobs (1977a), or from South American cricetids as suggested by Hershkovitz (1972).

Baskin (1978) suggested that Calomys was derived from Copemys. Copemys is known from the Miocene of North America, Europe (Fahlbusch, 1967) and southern Asia (Jacobs, 1977b), although some students (e.g., Engesser, 1979) place the European species in a distinct genus. A similar (perhaps congeneric) form, Spanocricetodon, has been reported from the Miocene of China (Li, 1977). The significant point is that Miocene Holarctic forms are closely related. Copemys entered North America from Asia in the Miocene (Barstovian) (Lindsay, 1972). It has not been reported from southern continents. Therefore, if Baskin is correct in considering Calomys derived from Copemys, and if the fossil record as now known accurately reflects the distribution of *Copemys*, then the place of origin of Calomys is in the Nearctic.

Prosigmodon probably evolved in Nearctica as well, considering that it may be derived from *Calomys*, and the earliest record of *Cal*- omys is in North America. Fossil sigmodontines appear in South America in the late Pliocene (Montehermosan) (Marshall et al., 1979; Reig & Linares, 1969). This being the case, *Calomys* from Arizona of middle Hemphillian age is older than *Prosigmodon* (late Hemphillian and Blancan) of Mexico, and both are probably older than the earliest records of sigmodontines in South America.

The presence of a complex penis in sigmodontines (Hershkovitz, 1972) and host-ectoparasite relationship (Wenzel & Tipton, 1966) have been considered evidence for a South American origin of the group. However, a complex penis may be a primitive character (Hooper & Musser, 1964; Hershkovitz, 1966) present in the common ancestor of peromyscines and signodontines, which was later simplified in the former but retained in the latter. There are no relevant data provided by fossils regarding the penis morphology of extinct peromyscines and sigmodontines.

Most ectoparasites of sigmodontine rodents are either restricted to or centered in South American (Wenzel & Tipton, 1966), and this relationship has been cited as evidence for a South American origin for these rodents. However, the infestation of a mainly South American group of rodents by parasites presently restricted to or centered in South America does not demonstrate a center of origin for either.

The high diversity of sigmodontines in South America intuitively may imply unreasonably fast rates of evolution to develop such diversity since the late Pliocene. However, as reflected by the fossil record, there is absolutely no physical evidence yet known which places sigmodontines or their possible ancestors in South America earlier than the late Pliocene (Montehermosan). In addition, Gardner & Patton (1976), in connection with their study of karyotypic variation in Neotropical cricetids, suggested that "chromosomal re-organization may have played a major causal role in the speciation process during what clearly appears to have been an explosive phase of radiation within the group."

We consider that sigmodontines originated and initially diversified in North America (possibly Central America as well, but data there are lacking). By the late Pliocene (Montehermosan) sigmodontines entered South America during a period of expanded savanna (Webb, 1978; Baskin, 1979), and then radiated to achieve their present diversity. This hypothesis is essentially the same as that advocated by Simpson (1950, 1980), Patterson & Pascual (1972), and Baskin (1978). It is consistent with the fossil record as now known.

The time of major diversification of sigmodontines in North America included late Hemphillian and Blancan Land Mammal Ages. Neville et al. (1979) note the appearance of Equus along with the occurrence of the Eurasian immigrants Trigonictis and Castor occurred at about 3.7 Ma in the Hagerman fauna of Idaho. These taxa along with others, characterize the beginning of the Blancan Land Mammal Age. Resolution of the Blancan/Hemphillian boundary remains uncertain, but the boundary occurs in the interval of 4 to 5 Ma [that is, between the appearance of unequivocal Blancan mammals at Hagerman at slightly less than 4 Ma and Hemphillian mammals beneath an ash dated 5.3 Ma at Coffee Ranch, Hemphill County, Texas (Boellstorff, 1976)].

If the late Hemphillian and Blancan diversification of sigmodontines documented in southwestern North America accurately reflects the history of these rodents, then sigmodontines probably entered South America between 4 and 5 million years ago. This may be somewhat later than the "Messinian Low" (7-5 Ma) which Marshall (1979) suggested as the time when sigmodontines entered northern South America. The introduction of sigmodontines into South America at 4 Ma rather than 5–7 Ma would not contradict the paleobiogeographic model proposed by Marshall (1979) for the spread of sigmodontines along savanna-grassland habitats after 4 Ma.

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