STRANGE EOCENE RODENTS FROM SPAIN

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ABSTRACT

A new European rodent from the middle Eocene of Spain, *Zamoramys extraneus* n. gen., n. sp., appears to be closely related to the middle Eocene chapattimyid rodents of Indo-Pakistan. This contradicts the generally accepted paleobiogeographic hypothesis of a Tethyian barrier between Europe and Asia isolating Europe during the middle Eocene. Because of this barrier, some authors have proposed that European and Asian rodents were not closely related, their similarity being the result of morphological convergence. Here monophyly has been tested, using the parsimony criterion, based on an analysis of dental characters (including discussing of homology and the validity of some characteristics). Our results indicate a phylogenetic relationship among the Asiatic Ctenodactyloidea, *Zamoramys* from Spain, and the European endemic Theridomyoidea. We also conclude from our analysis that theridomyoids and European ischyromyoids are probably not closely related phylogenetically.

RESUMEN

Zamoramys extraneus n. gen., n. sp., un nuevo roedor del Eoceno medio de España, presenta una morfología muy cercana a la de los Chapattimyidos del Eoceno medio Indo-pakistani. Esto contradice la hipótesis paleobiogeográfica, generalmente admitida, de la existencia de una barrera, el Tethys, entre ambos continentes, así como el aislamiento de Europa durante el Eoceno medio. A causa de esta hipótesis algunos autores han propuesto que estos roedores no están relacionados filogenéticamente sino que sus similitudes son debidas a convergencia morfológica. La monofilia ha sido testada usando el criterio de parsimonia, sobre criterios de morfología dental, discutiéndose además la homología y validez de algunos de ellos. Los resultados obtenidos implican una relación filogenética entre los ctenodactyloideos asiáticos, estos roedores españoles y los theridomyoideos endémicos europeos. De este análisis también se desprende que theridomyoideos e ischyromyoideos europeos probablemente no tienen relación filogenética directa.

RESUME

Un nouveau rongeur de l'Eocène moyen d'Espagne, *Zamoramys extraneus* n. gen. n. sp., ressemble morphologiquement et paraît étroitement apparenté aux Chapattimyidae indo-pakistanais de l'Eocène moyen. Ceci contredit l'hypothèse paléogéographique, généralement admise, d'une barrière entre les deux continents, la Téthys, et de l'isolement de l'Europe pendant l'Eocène moyen. Pour ces raisons, certains auteurs ont proposé que ces rongeurs n'étaient pas apparentés, mais que leur ressemblance résultait d'une convergence morphologique. Leur monophylie a été testée en utilisant le critère de parcimonie, après analyse des caractères dentaires, et discussion de l'homologie et de la validité de certains d'entre eux. Les résultats montrent une relation de parenté entre les Ctenodactyloidea asiatiques, ces rongeurs d'Espagne et les Theridomyoidea endémiques d'Europe. Il résulte aussi de cette analyse que les theridomyoïdés et les ischyromyoïdés européens ne sont probablement pas étroitement apparentés.

INTRODUCTION

Unusual mammalian faunal associations were discovered some years ago from early-middle Eocene continental beds at the localities of Santa Clara and Sanzoles,

province of Zamora, Duero Basin, central-western Spain (Peláez-Campomanes *et al.* 1989). In these associations, rare remains of rodent teeth represent a strange new group for the European fossil record. The morphology of these rodents (Pl. 1, figs. 1-6) is different from the European Eocene rodent groups Ischyromyoidea and Theridomyoidea, and surprisingly close to that of the middle Eocene rodent family Chapattimyidae described by Hussain *et al.* (1978) from Pakistan and by Sahni and Khare (1973) and Sahni and Srivastava (1976, 1977) from India. When first studied, the new specimens were designated cf. Chappatimyidae by Peláez-Campomanes *et al.* (1989).

Morphological similarity between Spanish and Indo-Pakistan rodent groups might indicate a phylogenetic relationship, which would require some kind of faunal exchange between Western Europe and Indo-Pakistan. A Tethyian oceanic barrier is claimed to separate both regions during early Eocene times, and Europe is supposed to be isolated during most of the middle and late Eocene (Dawson 1977, Hartenberger 1982).

Since there was a high degree of provincialism in Europe during the Eocene (Crusafont 1961, Schmidt-Kittler 1977, Hartenberger 1973, Casanovas & Moya 1992), French authors have indicated that similarities between the Spanish and Indo-Pakistan rodents are all plesiomorphic and might represent a case of parallel evolution (Hartenberger 1990, 1993; Hugueney & Adrover 1991, Vianey-Liaud 1991).

The aim of the present work is to carry out a phylogenetic analysis of this Spanish rodent and their Eocene relatives using the cladistic method of parsimony, which has not previously been applied to these taxa. The parsimony criterion may distinguish between convergence and monophyly, and thus may help to clarify the relationships of the new Spanish rodent.

DESCRIPTION OF THE
NEW SPANISH EOCENE RODENT

The two localities that have yielded the fossil material named here correspond to sandy and clayish beds at the top of a mainly fluvial formation classically dated as middle Eocene (Roman 1923, Crusafont *et al.* 1960). One and one-half tons of sediment have been processed to obtain micromammalian remains. The assemblage of fossil microvertebrates includes remains of large percoid fishes (*Vixperca corrochani* DE LA PEÑA, 1989), turtles, crocodiles, and mammals other than rodents (*Peratherium matronense, Anchomomys* sp., Palaeoryctidae, Dichobunidae, cf. Anagalida; Peláez-Campomanes *et al.* 1989). Large mammals have been recorded from the nearby locality of Corrales (*Lophiodon isselense, Chasmotherium minimum*).

The rodents belong to two species. One isolated tooth may be assigned to *Microparamys* sp. The remaining teeth deserve a new name since they represent a new type not previously recorded in Europe.

<center>Family indet.</center>

<center>Genus *ZAMORAMYS* n. gen.</center>

Derivatio nominis: From Zamora, the province where this rodent has been found.

Type species: *Zamoramys extraneus* n. sp.

Diagnosis, Distribution: See below.

<center>*Zamoramys extraneus* n. sp.</center>

<center>(Pl. 1, figs. 1-6)</center>

Cf. Chapattimyidae indet. Peláez-Campomanes *et al.*, 1989, p. 140, Pl. 1, figs. 1-5.
Aff. Chapattimyidae indet. Peláez-Campomanes *et al.*, 1989, p. 141, Pl. 1, fig. 6.

Derivatio nominis: From the Latin word *extraneus*, meaning strange, unusual, foreign.

Diagnosis: Small, bunodont cheek teeth. Very small premolars. Upper teeth with the metaloph and paraloph convergent toward the protocone; hypocone well developed, lingually situated. Lower teeth with a strong, globular hypoconulid and small
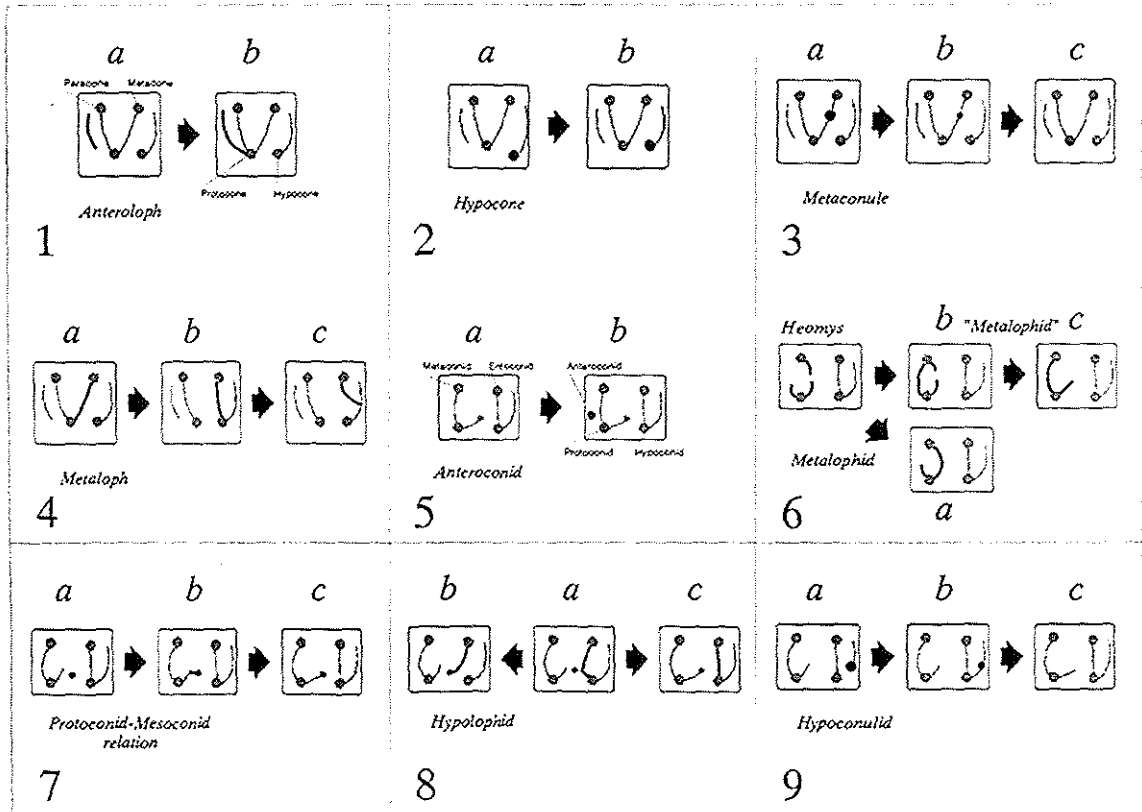

Figure 1.— Dental characters used in this analysis and their evolutionary polarity. Upper teeth, characters 1-4; lower teeth, characters 5-9 (see text).

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anteroconid; mesoconid either isolated or linked with a small crest to the posterior arm of the protoconid.

Differential diagnosis: *Zamoramys extraneus* n. gen. n. sp. differs from true chapattimyids in having a small anteroconid on lower cheek teeth. It differs from theridomyids and ischyromyids in having smaller premolars relative to molars, a hypocone more lingual than the protocone, a large hypoconulid isolated from the hypoconid, and a poorly developed ectolophid on the lower molars. It further differs from theridomyids in having the metaloph directed toward the protocone.

Holotype: Left M_2 (Pl. 1, fig. 2), preserved in the Department of Paleontology, University Complutense of Madrid.

Paratypes: P^4, M^1, M_1, and M_3 (Pl. 1, fig. 1; Pl. 1, figs. 3-6).

Type locality: Santa Clara de Avedillo, Zamora, Spain.

Type level: Middle Eocene.

Other localities: Sanzoles, Zamora, middle Eocene.

A more detailed description, measurements, and comparison is published in Peláez-Campomanes *et al.* (1989).

COMPARATIVE MATERIAL AND METHODS

The taxa included in our phylogenetic study comprise nine genera from the Eocene of Europe, America, and Asia, including the oldest representatives of several rodent families. In the case of genera with long stratigraphic ranges, only their Eocene species have been used to characterize their morphology.

The eight genera compared with the material from Santa Clara-Sanzoles are: (1) *Cocomys*, the oldest ctenodactyloid from China (Dawson *et al.* 1984, Li *et al.* 1989); (2) *Birbalomys*, a true chapattimyid from Pakistan and India (Hussain *et al.* 1978, Sahni 1980, Hartenberger 1982); (3) and (4) the ischyromyids *Paramys* from North America (Wood 1962) and Europe (Michaux 1968), and *Microparamys* from North America (Wood 1962) and Europe (Hartenberger 1971); (5) *Eogliravus*, the oldest glirid from Europe (Hartenberger 1971, Peláez-Campomanes 1993); (6) *Protadelomys*, the oldest theridomyoid from Europe (Hartenberger 1969, Peláez-Campomanes 1993); and (7) and (8) the theridomyids *Elfomys* (Hartenberger 1990); and *Theridomys* from Europe (Hartenberger 1973, Hartenberger & Louis 1976).

Morphological and structural characters of the teeth are the main data for phylogenetic purposes, since cranial and other skeletal characters are poorly known in most Eocene rodents. We have chosen in this study nine dental features, four from the upper cheek teeth and five from the lower ones. The following paragraphs contain a detailed description of these morphological characteristics, as well as the polarity assigned for each one using primitive Paleocene mammals as an outgroup. The character matrix has been analyzed with the computer programs PHYLIP 3.0 of

Felsenstein (1983; using the mixed parsimony algorithm MIX), and PAUP 3.3 of Swofford (1989), to obtain the most parsimonious phylogenetic tree (that containing the least number of steps or changes).

CHARACTER ANALYSIS

In the upper check teeth we consider four characters (Figs. 1.1-1.4):

1.— Anteroloph (Fig. 1.1). We distinguish two main morphotypes in the genera studied: (a) Anteroloph isolated from the protocone, lower than the protoloph; and (b) Anteroloph connected with the protocone, approximately as high as the protoloph. The primitive morphotype corresponds to the first type, a low isolated anteroloph.

Legend:
- □ Primitive
- ◪ Intermediate
- ■ Derived 1
- ▦ Derived 2

		Paramys	Microparamys	Eogliravus	Cocomys	Birbalomys	Zamoramys n. gen.	Protadelomys	Elfomys	Theridomys
1	Anteroloph	□	□	□	□	□	□	■	■	■
2	Hypocone position	■	■	■	□	□	□	■	■	■
3	Metaconule	◪	◪	■	□	□	□	□	◪	■
4	Metaloph	□	□	□	□	□	□	◪	◪	■
5	Anteroconid	□	□	□	□	□	■	■	■	■
6	Metalophid	▦	▦	▦	◪	◪	■	■	■	■
7	Protoconid-Mesoconid relation	□	□	□	□	□	□	◪	■	■
8	Hypolophid	▦	▦	▦		□	□	□	■	■
9	Hypoconulid	◪	■	■	□	□	□	◪	■	■

Figure 2.— Matrix of taxa and characters. The code differentiates between cases with linear polarity (morphotypes primitive, intermediate, derived 1) and those with divergent polarity (primitive, derived 1, derived 2).

2.— H y p o c o n e (Fig. 1.2). Two different morphotypes can be distinguished: (a) the hypocone has a more labial position than the protocone; or (b) its position is almost at the same level as the protocone. The hypocone is absent in primitive mammals, and it first appears labially to the protocone. The most primitive rodents have also this morphology (Dashzeveg 1990, Meng *et al.* 1994). The morphotype (a) is thus considered as the primitive one.

3.— M e t a c o n u l e (Fig. 1.3). There are three different cases: (a) metaconule large and globular; (b) metaconule small; and (c) metaconule absent. The presence of a well-developed metaconule is the rule in Paleocene mammals, thus we consider morphotype (a) as primitive, (b) as intermediate, and (c) as derived.

4.— M e t a l o p h (Fig. 1.4). Three morphotypes are found: (a) metaloph directed toward the protocone; (b) metaloph directed toward the hypocone; and (c) metaloph joining the posteroloph. The metaloph directed toward the protocone is considered as primitive, and the other two morphotypes as linearly derived. This polarity can be observed in the oldest Theridomyoidea such as *Protadelomys* from Casa Ramón, Spain (Peláez-Campomanes 1993, 1995), with some specimens showing the primitive pattern, metaloph directed towards the protocone. The most derived morphology is present in the theridomyid species. The change from morphology (b) to (c) may be seen in the Phiomyidae from North Africa as well (Wood 1968, Jaeger *et al.* 1985).

The lower check teeth bear five characters (Figs. 1.5-1.9):

5.— A n t e r o c o n i d (Fig. 1.5). This character shows two morphotypes: (a) anteroconid absent, and (b) anteroconid present. The absence of anteroconid is considered the primitive pattern.

6.— M e t a l o p h i d (Fig. 1.6). The morphotype (a) shows the metalophid formed by the posterior arm of the protoconid; (b) has a "metalophid" formed by the anterior arm of the protoconid, the posterior arm having a transverse direction; and in (c) the "metalophid" is, as in type (b), formed by the anterior arm of the protoconid but the posterior one is diagonal. Thus, these structures present a problem of homology, since they seem formed by two different arms of the protoconid: the posterior arm, type (a), is here considered as a true metalophid, and the anterior one represented by types (b) and (c) is here designed as a nonhomologous "metalophid." Thus, the metalophid seen in the more primitive glires such as *Heomys* (Mixodonta; Dashzeveg & Russell 1988) in Fig. 1.6, *Alagomys* (Dashzeveg 1990) and the ischyromyids of type (a) in Fig. 1.6a seem to be nonhomologous to the crest called "metalophid" in ctenodactyloids of type (b) in Fig. 1.6b and theridomyoids of type (c) in Fig. 1.6c. The latter crest may be homologous in fact to the anterolophid of ischyromyids. Both kinds of crests may have evolved in two independent ways from a primitive form like *Heomys*; the polarity is represented in Fig. 1.6. We consider the morphotype (c) derived from (b) without any direct relationship to the independently derived morphotype (a).

7.— M e s o c o n i d (Fig. 1.7). This character shows three steps in its evolution: (a) the mesoconid is isolated, far from the posterior arm of the protoconid; (b) the mesoconid is connected by a longitudinal crest to the posterior arm of the protoconid; and (c) the posterior arm of the protoconid is directly connected with the mesoconid. Here (a) is

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primitive and (b) and (c) linearly derived.

8.— H y p o l o p h i d (Fig. 1.8). Three morphotypes have been observed: (a) the hypolophid reaches the anterior arm of the hypoconid; (b) the hypolophid reaches the mesoconid; and (c) the hypolophid reaches the hypoconid. The morphotype (a) is considered as primitive, with (b) and (c) independently derived from (a). This structure is not yet developed in *Cocomys*, where the hypolophid is still incipient and not well defined.

9.— H y p o c o n u l i d (Fig. 1.9). This structure has three morphotypes: (a) hypoconulid large and isolated from the hypoconid; (b) hypoconulid small, connected to the hypocone; and (c) hypoconulid absent. Hartenberger (1990) considered the morphotype (a) as primitive, although the hypoconulid is rarely developed in Paleocene mammals. According to the outgroup criterion, we took at first glance the type (c) as the primitive one (Peláez-Campomanes & López-Martínez 1993), but we follow here the opinion of Hartenberger (1990) to test the differences in the results. Thus, the type (a) is here taken as primitive and the other two types are considered successive steps in a claimed process of hypoconulid reduction.

OTHER CHARACTERS
NOT INCLUDED IN THE ANALYSIS

Other dental characters have not been used in this study because *Zamoramys* is only known by a few teeth. However, since some relationships among rodent superfamilies may be inferred from our phylogenetic analysis, we will discuss the distribution of several other characters used by other authors, such as the enamel structure and the size ratio between different dental elements.

The enamel structure has largely been used to establish phylogenetic relationships among rodents since Korvenkontio's (1934) study. Discrepancies on the definition among the different types of enamel structure (pauciserial, uniserial and multiserial; see Wahlert 1968, 1989; Sahni 1985, Koenigswald 1985, Hussain *et al.* 1978, Li *et al.* 1989, Dauphin 1988) and disagreement on the evolutionary polarity of the enamel types (Sahni 1985, Koenigswald 1985) have been resolved by Martin (1992, 1993). According to this author the pauciserial enamel pattern found in Eocene rodents (Meng *et al.* 1994) is primitive. The multiserial type found in Hystricognathi, Ctenodactylidae, and *Pedetes* is derived (Martin 1993). The uniserial enamel pattern is considered independently derived in several lineages (Ischyromyoidea, Anomaluridae, Theridomyoidea) according to this author.

The incisors of *Zamoramys* have not been found, and the enamel type is unknown. Nevertheless, a pauciserial type may be predicted since all the early-middle Eocene rodents share this primitive enamel condition.

The relative sizes of different dental elements differentiate the Ctenodactyloidea from other rodent groups, such as the ischyromyids (Hussain *et al.* 1978, Dawson *et al.* 1984). According to these authors, molars increase in size from M^1 to M^3 in the

Ctenodactyloidea. On the contrary, the molar size decreases in ischyromyids from M^1 to M^3. This character is not available in *Zamoramys* because we do not have all of these teeth. The size ratios of M_1, M_2 and M_3 of the Santa Clara assemblage agree with those of ctenodactyloids. In the case of middle Eocene Theridomyoidea, the molars increase from M^1 to M^3 as it has been shown by Hartenberger (1969) and Peláez-Campomanes (1993). So, theridomyoids share this feature with ctenodactyloids, but not with ischyromyids.

RESULTS AND DISCUSSION

A parsimony analysis of the nine characters described for the nine genera (Fig. 2) has been performed using the Mixed Parsimony Algorithm (MIX) of the PHYLIP 3.0 (Felsenstein 1983) and PAUP 3.3 (Swofford 1989) computer programs. A unique tree is obtained in both cases (Fig. 3) that needs 21 steps, with a rather high Consistency Index (CI = 0.762). In this tree, ischyromyids and glirids cluster independently from ctenodactyloids and theridomyoids; the chapattimyid (*Birbalomys*) groups with the ctenodactyloid *Cocomys* and the theridomyoids. The Spanish *Zamoramys extraneus* clusters with Theridomyoidea after this trichotomy.

The tree bears four convergences in three characters (Fig. 3, square symbols): (1) the external position of the hypocone (character 2); (2) the reduction of the hypoconulid (character 9), both independently attained by ischiromyids + glirids and theridomyoids, and (3) the metaconule reduction (character 3), independently attained by glirids and theridomyids. The reduction of metaconule and hypoconulid may be related to the development of the lophodont tooth morphology, which is independently attained by many ischyromyids, glirids and theridomyoids, as well as more derived ctenodactyloids not included in the analysis.

Any other phylogenetic hypothesis bears a larger number of convergences in unrelated characters. For example, if the character 9a (large hypoconulid) is considered as derived, the Ctenodactyloidea and *Zamoramys* cluster together (Peláez-Campomanes *et al.* 1993), but two additional convergences appear (characters 5 and 6). Within the strict parsimony criterion, *Zamoramys extraneus* cannot be considered as a true chapattimyid in the cladistic sense (Fig. 3). However, the parsimony criterion cannot be taken as an absolute one, since many homoplasies are often recognized in mammalian evolution. Using the phenetic criterion (Fig. 4), *Zamoramys* clusters with the Ctenodactyloidea, instead of the Theridomyoidea.

Some inferences may be made from this cladogram. First, the early differentiation of ischyromyids and ctenodactyloids agrees with the basal dichotomy proposed by Luckett and Hartenberger (1985). Two derived characters, the metalophid and hypolophid (numbers 6 and 8) separate both clusters. In the case of the metalophid, the ischyromyids strengthened the primitive connection between the posterior wall of the metaconid and protoconid (character state 6a), whereas the Ctenodactyloidea developed an anterior connection between both cusps (character state 6b).
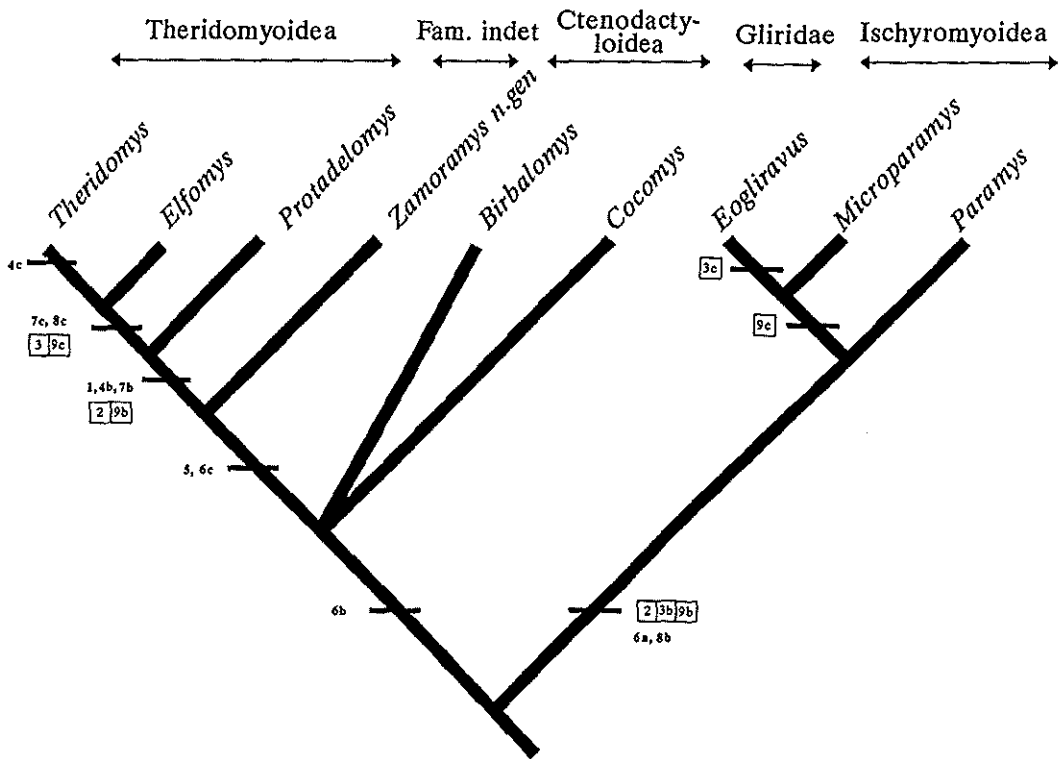
Figure 3.— Phylogenetic tree for the nine Eocene rodents analyzed using parsimony. This is the shortest cladogram obtained by the computer packages PHYLIP and PAUP (see text). It requires 21 steps and has 4 convergences. Transverse bars and numbers indicate the codes of the characters derived in each branch. Square symbols mark convergences.

The interpretations of rodent enamel pattern proposed by Martin (1992, 1993) support this hypothesis: parallel evolution towards uniserial type in the former linage, whereas multiserial enamel evolved once in the latter linage.

Secondly, the phylogenetic position of *Zamoramys* lies between the ctenodactyloids and the theridomyoids. The Asiatic ctenodactyloids *Cocomys* and *Birbalomys* do not share any synapomorphy among the analyzed characters. *Zamoramys extraneus* shares with Theridomyoidea the presence of an anteroconid (character state 5b) in the lower molars, and the same type of "metalophid": an anterior connection between the metaconid and protoconid, and complete absence of the posterior connection (character state 6c).

Thirdly, most of the characters from the upper molars distinguish the Theridomyoidea clearly from the rest of the genera. *Protadelomys* is derived 5 out of 9 characters (numbers 1, 2, 4, 7, 9), showing the highly derived condition of the superfamily it represents. *Zamoramys*, which has a very primitive dental morphology, cannot be included in this taxon without a large modification of the diagnosis. The phylogenetic position of *Zamoramys* between Ctenodactyloidea and Theridomyoidea bears on the controversial problem of the origin of theridomyoids.
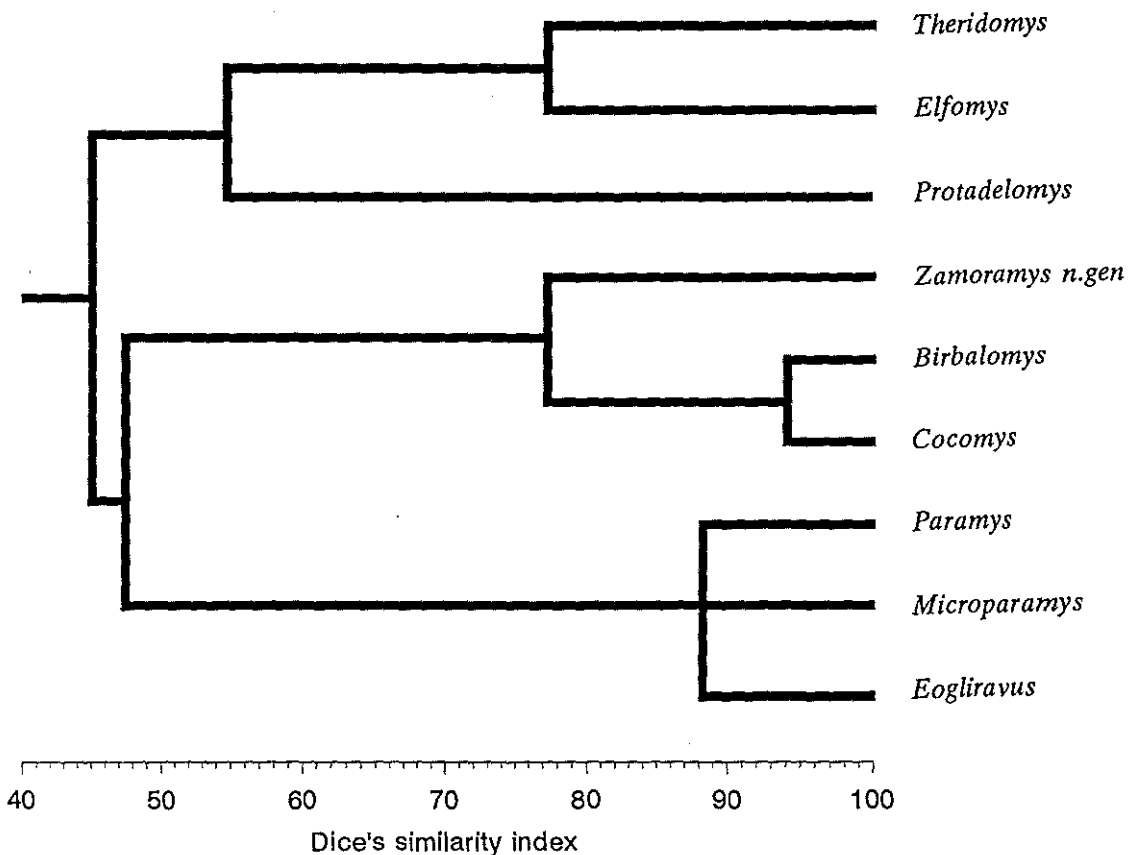
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Figure 4.— Phenogram showing the overall morphological similarity among the nine rodent genera on the basis of the nine dental characters considered in this paper. The Dice index has been used for calculations. Three main clusters are clearly differentiated. *Zamoramys* groups with Cocomyidae and Chapattimyidae. The three clusters have approximately the same similarity index (44-47%).

A possible phylogenetic relationship between theridomyids and ischyromyids has been proposed (Wood 1962, Thaler 1966). The enamel microstructure of the theridomyoids seems more related to that of the ischyromyoid group than to the ctenodactyloid one (Martin 1992, 1993). Early representatives of the theridomyoids show a pauciserial enamel pattern (the primitive type), but Oligocene members have uniserial enamel, just as Ischyromyoidea do (Martin 1993).

However, Hartenberger (1990) related the theridomyoids (and the anomalurids) with the phiomyids, in disagreement with the results of Martin (1993). Our analysis shows the theridomyoids to be closer to the ctenodactyloids, instead of to the ischyromyoids. The relationships between theridomyoids and ctenodactyloids is mainly supported by the synapomorphy of the "metalophid". The crest named "metalophid" in theridomyoids would correspond with the anterior metalophid (also called "metalophulid I") of the Ctenodactyloidea, whereas the true metalophid is lost, the posterior arm of the protoconid being a relict.

If the theridomyoids are related to ctenodactyloids or phiomyids, the uniserial

enamel type must be convergent in the two independent clades. This may be the case, since Martin (1993) recognized the independent acquisition of uniserial enamel from pauciserial enamel in different clades.

Hartenberger (1993) hypothesized that the theridomyoids migrated to Europe near the end of the middle Eocene. Now *Zamoramys* shows the dental morphology that would be expected for a hypothetical ancestor of the theridomyoids, with a mainly primitive dental pattern and two derived characters shared with them. *Zamoramys* thus appears to represent a stem group of Theridomyoidea, and consequently this superfamily might have its origin in Europe.

In our analysis, theridomyoids and *Zamoramys* are related to the Asiatic and Indo-Pakistan ctenodactyloids in sharing the derived character 6b. Accordingly, some biogeographical relation between southern Europe and Asia can be expected. Since other mammalian groups from Asiatic, Indian, and European sides of Tethys are also closely related (Krause & Maas 1990), the alternative hypothesis of long-range dispersal events across an oceanic barrier seems less probable. Hartenberger (1993) argued that the center of origin of theridomyoids might be Africa, on the basis of a proposed phylogenetic relationship with anomalurids (Luckett & Hartenberger 1985, Hartenberger 1990). So, accepting this hypothesis and the possible relationship between theridomyoids and *Zamoramys* inferred here, we expect to find rodents in Africa with the primitive dental pattern of the latter.

CONCLUSIONS

From our phylogenetic analysis we infer a close relationship between Ctenodactyloidea and Theridomyoidea. The new genus and species *Zamoramys extraneus* from the middle Eocene of Santa Clara and Sanzoles lies in an intermediate position between Asiatic Ctenodactyloidea and European Theridomyoidea. It shares with the ctenodactyloids and the true chapattimyids the same type of "metalophid" and presence of a large hypoconulid. It does not share most of the synapomorphies of the Theridomyoidea (diagnostic characters such as the linked anteroloph, internal hypocone, posterior metaloph, mesoconid connection, transverse hypolophid, etc.). *Zamoramys* shares some apomorphic characters with theridomyoids, such as the presence of an anteroconid and the same "metalophid" type. Thus, the monophyly of the theridomyoid rodent taxa and the Spanish one is proposed.

Secondly, an early differentiation between Ischyromyidae and Ctenodactyloidea is supported by their different metaconid and hypolophid types, and different tooth size relationships. Three derived characters shared by ischyromyids and theridomyoids appear to be convergent, related to the lophodont dental type attained independently in different groups. According to the parsimony criterion, the European endemic Theridomyoidea is closer to the Asiatic Ctenodactyloidea, instead of to the North American and European Ischyromyidae.

Thirdly, this phylogenetic hypothesis provides new evidence for some early-

middle Eocene biogeographic interchange between Eurasian faunas separated by Tethys, which is in disagreement with the paleogeography usually envisaged.

ACKNOWLEDGEMENTS

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LEGEND OF THE PLATE

PLATE 1

Cheek teeth of *Zamoramys extraneus* n. gen. n. sp. from Santa Clara (1-5) and Sanzoles (6)

Fig. 1.— Right M_3 SCL-24.
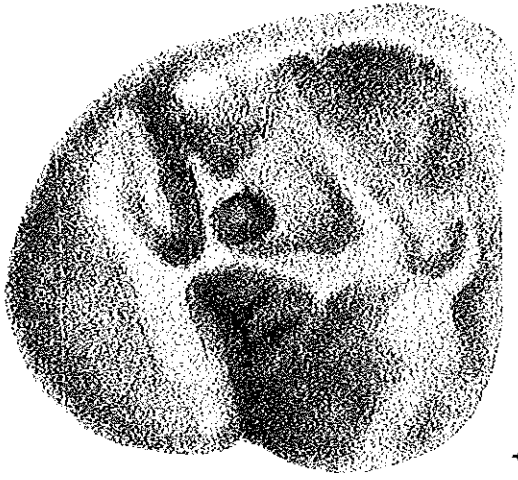
Fig. 2.— Left M_2, holotype, SCL-10.

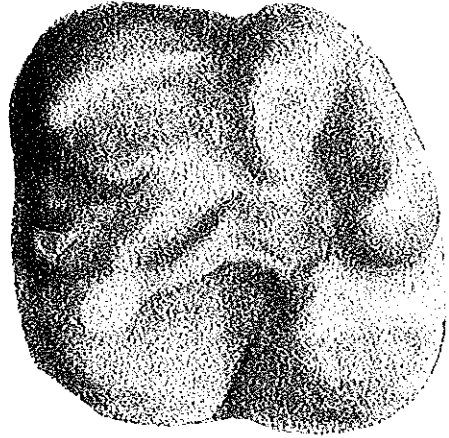Fig. 3.— Right M_1 SCL-20.

Fig. 4.— Right P^4, SCL-22.

Fig. 5.— Left M^{1-2}, SCL-11.

Fig. 6.— Right M_2, SZ-1.

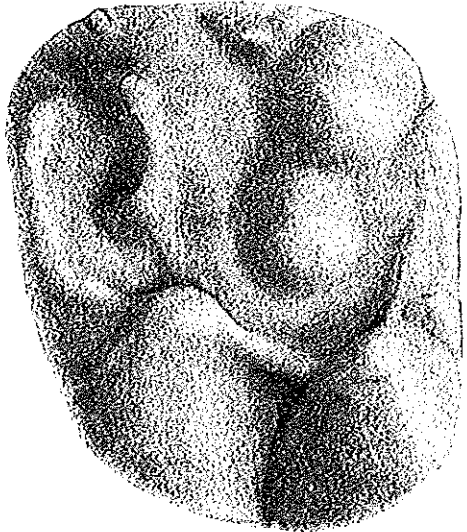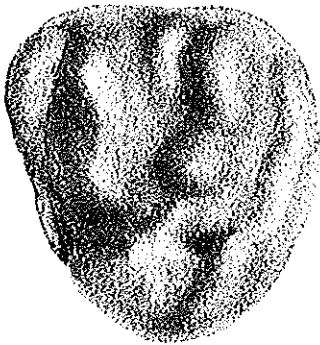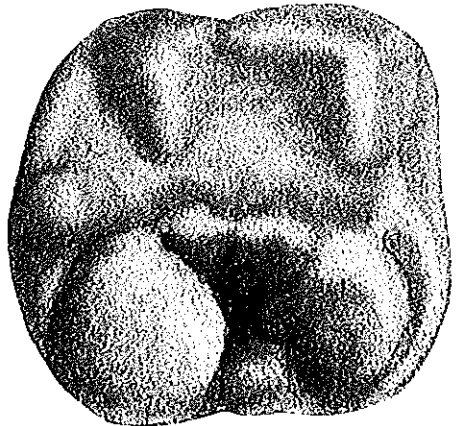Stored in the Department of Paleontology, Universidad Complutense de Madrid.

PLATE 1