OCTODONTID-LIKE ECHIMYIDAE (RODENTIA) : AN UPPER MIOCENE EPISODE IN THE RADIATION OF THE FAMILY

by

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ABSTRACT

Reigechimys octodontiformis gen. et sp. nov. and *R. plesiodon* sp. nov. are described. They represent the first record of the family Echimyidae for the Cerro Azul Formation (Huayquerian Age, Late Upper Miocene) at La Pampa Province, central Argentina. Both species have hypsodont cheek teeth with an eight-shaped occlusal design. This dental morphology represents a noticeable case of convergence to octodontids and indicates that these echimyids inhabited open environments.

RESUME

On décrit les espèces *Reigechimys octodontiformis* gen. et sp. nov. et *R. plesiodon* sp. nov. Elles représentent le premier signalement de la famille Echimyidae pour la Formation Cerro Azul (d'âge huayquérienne, Miocène superieure) de la Province de La Pampa, Argentine centrale. Les deux espèces ont des molaires hypsodontes avec un dessin occlusal en forme de huit. Cette morphologie dentaire représente un cas notable de convergence avec les octodontidés et montre que ces échimyidés habitaient des environnements ouverts.

INTRODUCTION

The family Echimyidae contains an assemblage of ancient, primitive and largely forest dwelling caviomorph rodents, now restricted to Central America and Northern South America.

During the Deseadan Age (?Lower-Upper Oligocene), from wich caviomorphs are first recorded, Echimyidae were present in Bolivia, Patagonia, and southern Brazil (Wood & Patterson, 1959; Patterson & Wood, 1982; Vucetich, 1986; Souza Cunha, 1983; Vucetich *et al.*, 1993). Their abundance and diversity in Patagonia until the Middle Miocene (Vucetich, 1986; Vucetich *et al.*, 1991) is in accordance with the tropical to subtropical climatic conditions then present throughout this area (Pascual, 1984a; 1986; Pascual & Ortiz Jaureguizar, 1990; Vucetich, 1986).

Beginning in the Upper Miocene, changes in mammal communities demonstrate an increasing aridity and the development of steppe biomass in meridional South America (Vucetich, 1984; Pascual, 1984a, 1984b, 1986; Pascual & Bondesio, 1982; Pascual *et al.*, 1985; Pascual & Ortiz Jaureguizar, 1990). These changes resulted in the restriction to the northern part of the continent of the areas in which the cladogenetic events, leading to the rich diversity of modern Echimyidae, occurred (Pascual, 1967). In Southern South America, however, the Echimyidae became rare and the few remainders were adapted to the new climatic and physiographic conditions (Kraglievich, 1965; Reig, 1986). Finally, they became extinct in this part of the continent during the Pleistocene.

In this report we described a new genus of Echimyidae which represents the first record of the family for the Huayquerian Land Mammal Age (Late Upper Miocene) of

central Argentina. It displays a dental morphology remarkably convergent with that of the Octodontidae. We analyze such a peculiar morphological type for an Echimyidae and discuss its paleoenvironmental significance.

Abbreviations and terminology: GHUNLPam: Cátedra de Geología Histórica, Universidad Nacional de La Pampa, Argentina; MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MLP: Museo de La Plata, Argentina; GEOBOL: Servicio Geologico de Bolivia. For cheek teeth terminology see Wood & Patterson (1959, fig. 1 B) and Fields (1957, fig. 2).

SYSTEMATICS

Order **RODENTIA** BOWDICH, 1821
Suborder **HYSTRICOGNATHI** TULLBERG, 1899
Infraorder **CAVIOMORPHA** WOOD & PATTERSON *in* Wood, 1955
Family **ECHIMYIDAE** GRAY, 1825
Subfamily **EUMYSOPINAE** RUSCONI, 1935

REIGECHIMYS gen. nov.

Type species: *Reigechimys octodontiformis* sp. nov.

Distribution: Upper Miocene of central Argentina.

Etymology: The genus is named in memory of Dr. Osvaldo A. Reig, who devoted a great part of his scientific research to the study of the echimyid and octodontid rodents.

Diagnosis: Eumysopinae similar in size to *Trichomys apereoides*. High, proto-hypsodont cheek teeth with a transitory figure-eight occlusal design; hypoflexid persistent, metaflexid less so, and mesoflexid reduced to a more or less ephemeral fossettid. Posterolophid broad; I_1 slender and high; masseteric crest barely projected outward due to the fact that the masseteric fossa is shallow.

Reigechimys octodontiformis sp. nov.

(Fig. 1 c, d and f)

Holotype: MLP 65-VII-29-107, partial right ramus with I_1 and DP_4–M_3.

Hypodigm: includes only the type.

Horizon and **locality**: Cerro Azul Formation (*sensu* Linares *et al.*, 1980) Huayquerian Age, Late Upper Miocene; Salinas de Hidalgo, Department of Atreucó, La Pampa Province (fig. 3).

Etymology: named for the figure-eight morphology of the occlusal surface.

Diagnosis: very hypsodont cheek teeth; mesoflexid only present as an ephemeral scar; metaflexid very persistent.

Description

The size of the mandible is similar to that of *Trichomys apereoides*. The diastema forms a gentle semicircular curve without an abrupt rebound in front of DP_4. The scar for the M. masseter medialis pars infraorbitalis (*sensu* Woods & Howland, 1979) is at the level of the middle of the mandibular height and almost continuous with the masseteric crest. Compared with other Eumysopinae such as *Eumysops*, *Euryzygomatomys*, *Trichomys* or *Proechimys*, the anterior part of the masseteric crest projects outward only slightly because the masseteric fossa is relatively shallow. The coronoid process, of which only the anterior part is preserved, diverges slightly in relation to the tooth row. Its anterior border forms a slope of about 140° with the mandibular body. The retromolar fossa is large and posterolateral to M_3.

The incisor is very slender and high. It crosses to the external wall of the mandible under the molariform series at the level of M_3 and there forms a bulbous projection at the base of the coronoid process (fig 1 c).

The cheek teeth show the greatest degree of hypsodonty known for the family, but form roots as was verified through an xray of the holotype (protohypsodonty *sensu* Mones, 1982). They are formed by two lobes separated by reentrant folds, one buccal and the other lingual. This results in a figure-eight transitory morphology. The lingual face of the anterior lobe is longer than in the posterior lobe. This suggests that the internal flexid is the metaflexid and that one or two anterior flexids have worn away.

The first tooth is a DP_4 because it is more worn than the molars (fig. 1 c and d). It is slightly smaller than M_{1-2} and similar to that one of "*Eumysops plicatus*" (Rovereto, 1914: 134, fig. 57) (*Eumysops plicatus* AMEGHINO, 1889 was based on a skull, while the material figured by Rovereto are two mandibular fragments). As in the latter, the lingual face of the anterior lobe is conspicuously longer than in the posterior lobe. The

	R. o.	R. p.		R. o.	R. p.
Diastema length	5.50	–	M_1 length	2.55	2.50
Ramus depth at DP_4–M_1	7.44	–	M_1 width ant.	2.10	2.30
Lower incisor width	1.15	–	M_1 width post.	2.20	2.15
Lower incisor depth	1.85	–	M_2 length	3.00	2.65
DP_4–M_3 length	10.50	–	M_2 width ant.	2.10	2.45
DP_4 length	2.35	–	M_2 width post.	2.20	2.25
DP_4 width ant.	1.80	–	M_3 length	2.20	–
DP_4 width post.	1.85	–	M_3 width ant.	1.65	–
			M_3 width post.	1.10	–

Table 1.— Measurements (in mm) of the type specimens of *Reigechimys octodontiformis* gen. et sp. nov. (MLP 65-VII-29-107) and *Reigechimys plesiodon* gen. et sp. nov. (GHUNLPam 306). The mandibular measurements were taken with mechanical calipers graduated to 0.02 mm. The measurements of the teeth were taken through the reticule eyepiece of a Zeiss stereomicroscope.
Abbreviations: ant.: anterior lobe; post.: posterior lobe; R.o.: *Reigechimys octodontiformis*; R.p.: *Reigechimys plesiodon*.

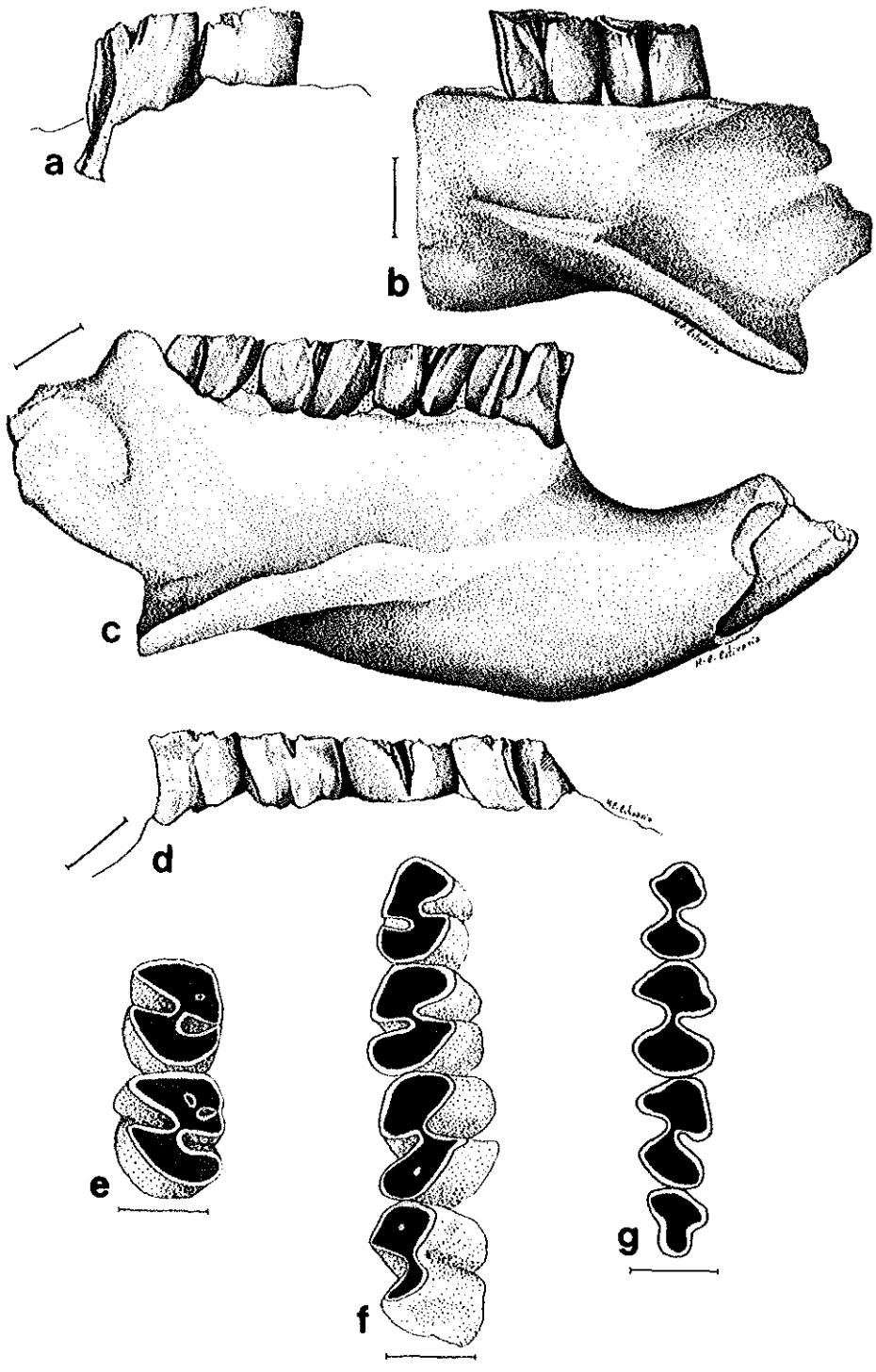

Figure 1.— Mandibles and cheek teeth of *Reigechimys octodontiformis* gen. et sp. nov., holotype MLP 65-VII-29-107 (**c**, **d** and **f**) and *Reigechimys plesiodon* gen. et sp. nov., holotype GHUNLPam 306 (**a**, **b** and **e**); **a** and **d**: internal view; **b** and **c**: external view; **e** and **f**: occlusal view; **g**: occlusal morphology of the extant octodontid *Octomys mimax* MACN 13765. Scale = 2 mm.

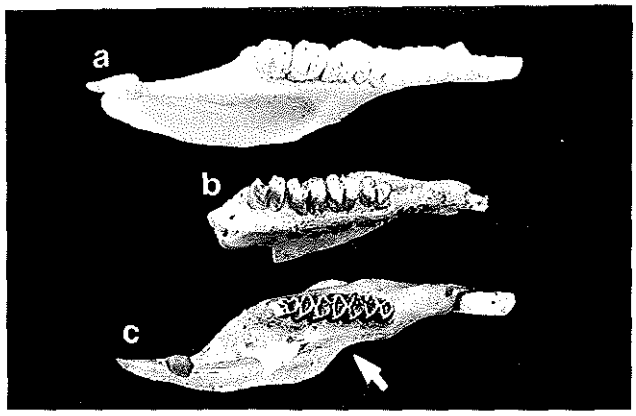

Figure 2.— Dorsal view of mandibles of: **a**, *Proechimys guyannensis* MLP 536; **b**, *Reigechimys octodontiformis* gen. et sp. nov., holotype MLP 65-VII-29-107; **c**, *Aconaemys sagei* MLP 17.II.92.10, topotype. Note the discontinuity between the masseteric notch and the masseteric crest in the jaw of the extant octodontid *Aconaemys* (arrow) (x 1.7).

metaflexid is posterior to the hypoflexid. The metastriid is very short, and with further wear it would close to form a metafossettid (fig. 1 d). On the other hand the hypoflexid is deeper, extending across three-fourths of the length of the labial wall. As in *"E. plicatus"*, the part of the anterior lobe adjacent to the metaflexid is set off.

The hypoflexid and metaflexid of M_{1-3} nearly face each other, but the latter is slightly posterior. From DP_4 to M_3 the posterior lobe becomes increasingly oblique distolingually, because the metaflexid has a wider lingual opening in less worn teeth.

In M_1 the metastriid extends through half of the crown while the hypostriid nearly reaches the base of the exposed crown (fig. 1 d).

The anterior lobe of the little worn M_3 bears the remnant of the mesofossettid (fig. 1 f). Furthermore, as we said above, the lingual face of this lobe is longer than that of the posterior lobe in all the cheek teeth. Thus, both characters together demonstrate that the anterior lobe of this species is formed by the combination of anterolophid and hypolophid.

Reigechimys plesiodon sp. nov.

(Fig. 1 a, b and e)

Holotype: GHUNLPam 306 fragmentary left mandible with M_{1-2}.

Hypodigm: includes only the type.

Horizon and **locality**: Cerro Azul Formation, Huayquerian Age, Late Upper Miocene; Laguna Chillhué, 15 Kms E from Cruce Padre Buodo, Department of Guatraché, La Pampa Province (fig. 3).

Etymology: *Plesio*, primitive, plus *odon*, tooth, indicating that it has a more primitive dental morphology than the type species.

Diagnosis: Protohypsodont cheek teeth, but with a lesser degree of hypsodonty than in the type species. This is also shown by the longer persistence of the mesoflexid.

Description

The mandibular masseteric configuration is similar to that of the type species, but the lateral crest (*sensu* Woods, 1972) is well developed in *R. plesiodon* and the furrow that runs dorsally to this widens anteriorly to form a subtriangular fossa.

Although M_{1-2} are protohypsodont, they are less hypsodont than those of *R. octodontiformis*, and probably much of the morphological differences between the molars of these species are due to this fact. For example, the depth, and thus the moment of closure, of the flexids are more similar to each other in *R. plesiodon* than in *R. octodontiformis*: therefore, the mesoflexid is comparatively more persistant. Because of this, a small mesofossettid is still present in M_1 when the metaflexid is already closed (see fig. 1 a, d, e and f).

The mesoflexid is represented by a small fossettid in M_1, and by two separated fossettids in M_2, of which the labial is the more anterior showing that the mesoflexid was anteriolabially oriented.

The closed ends of both hypo- and metaflexid are wider than in *R. octodontiformis*. The metaflexid is oriented more transversely and so it is less aligned with the hypoflexid than in the type species.

The lingual wall of the anterior lobe is less oblique than in *R. octodontiformis*.

DISCUSSION

THE AFFINITIES OF *REIGECHIMYS* GEN. NOV.

The dental morphology of the species described here is very similar to the Octodontidae. Indeed, this similarity is so remarkable that the type of *R. octodontiformis* was assigned by Zetti (1972, unpublished Thesis) to *Pseudoplataeomys*, an extinct octodontid of the Huayquerian (Late Upper Miocene) and Montehermosan (Lower Pliocene) Ages (Rovereto, 1914; Kraglievich, 1934). However, a more detailed study demonstrates that many of these resemblances are merely superficial and that the true affinities of *Reigechimys* are with the Echimyidae.

We propose these affinities for *Reigichimys* principally on the following two characters:

1.– Dental morphology: In *Reigechimys* the closure sequence of the lingual flexids is comparable to that one of the Eumysopinae (*sensu* Patton & Reig, 1989) *Trichomys* (see Petter, 1973, fig. 2), *Clyomys* and *Euryzygomatomys*, i.e., the mesoflexid closes earlier than the metaflexid. Notwithstanding, the diference in time between closure of the mesoflexid and metaflexid is exaggerated in *Reigechimys* due to the increased hypsodonty. Thus, the mesoflexid disappears so quickly with wear that in the holotype of *R. octodontiformis*, the most hypsodont

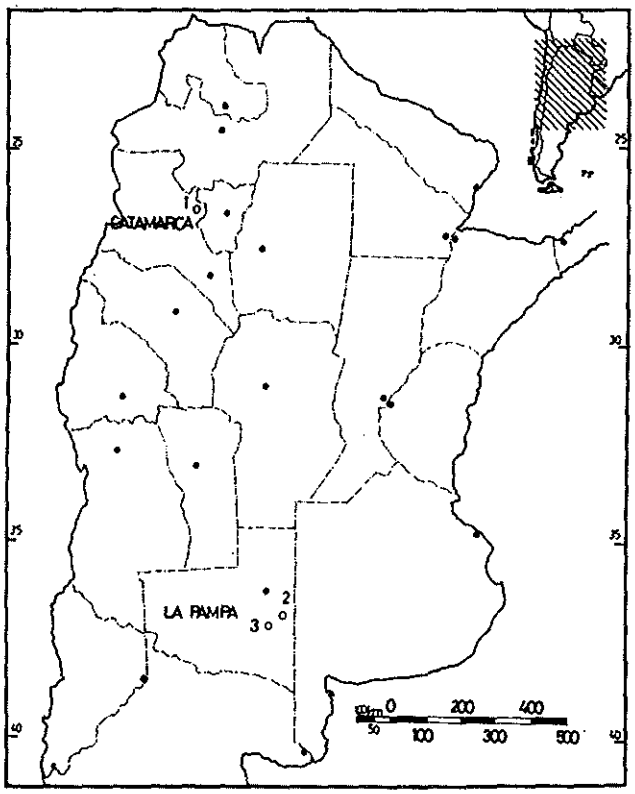

Figure 3.— Map showing the type localities cited in the text: **1**, Chiquimil, Department of Santa María; **2**, Salinas Grandes, Department of Atreucó; **3**, Laguna Chillué, Department of Guatraché.

species, it is represented by just a small fossettid in the little worn M_3.

In contrast, in fossil protohypsodont Octodontidae such as *Sciamys*, *Chasicomys* and *Pattersomys* (for the position of the latter, see Vucetich & Verzi, 1991), in which fossettid formation still occur, the closure of fossettids sequence is reversed. In this case, the metaflexid closes before the mesoflexid (see Pascual, 1967, plate).

Both types of closure of flexids can produce superficial similarity in occlusal morphologies, as can be seen comparing *R. octodontiformis* and the extant octodontid *Octomys mimax* (fig. 1 f and g). But in the latter the lingual flexid is anterior to the hipoflexid and no posterior as in *Reigechimys*, because it is the mesoflexid.

2.– Masseteric crest: In *Reigechimys*, the scar for the M. masseter medialis pars infraorbitalis is continuous with the masseteric crest. Such an arrangement is present in the Echimyidae. On the contrary, in the Octodontidae a discontinuity exists between the structures (fig. 2).

Among the currently recognized subfamilies of Echimyidae (see Reig, 1989), *Reigechimys* is referable to the Eumysopinae based on its dental morphology: their

cheek teeth does not develop into transverse plates (Patton & Reig, 1989: 82).

OTHER OCTODONTID-LIKE EUMYSOPINAE

Reigechimys octodontiformis is not the only Echimyidae that has been confused with the Octodontidae due to the superficial resemblances of their cheek teeth. Two other cases may be cited.

One of these is the unpublished new genus and species (from Chiquimil, Department of Santa María, Catamarca Province, Huayquerian Land Mammal Age, fig. 3) described by Spencer (1987: 27) as being an Octodontidae "Phtoramyinae". We have studied this material and, in accordance to its dental morphology, we consider that the holotype (MACN 8369) is an Echimyidae related to *Reigechimys*.

The other case is that represented by the material described by Villarroel & Marshall (1989: 39, figs. 8B-C) as cf. *Sciamys* (GEOBOL MH-441) from Bolivia, also assigned to the Huayquerian Age. It is evident from figure 8 C by Villarroel & Marshall that the secuence of fossettid closure is quite the same as that of *Reigechimys* and shows that this species must be assigned to the Eumysopinae. As the degree of hypsodonty of this specimen could not be ascertained, we are less confident in assigning this specimen to the same group of species here described.

These data show that the octodontid-like Echimyidae were widely distributed beyond La Pampa in western Argentina during the Late Upper Miocene. Moreover, if Villarroel & Marshall's species finally demonstrates to be related to *Reigechimys*, then the distribution of this peculiar group of Eumysopinae would extended at least to southern Bolivia.

PALEOENVIRONMENTAL SCENARIO

Vast and physiographically diverse plains developed through a great part of Argentina during the Upper Miocene (Pascual & Bondesio, 1982) accompained by a climatic deterioration (Pascual *et al.*, 1985; Vucetich, 1986; Gasparini *et al.*, 1986; Pascual & Ortiz Jaureguizar, 1990). Open environments were predominant in western and central Argentina during Huayquerian Land Mammal Age (Scillato-Yané, 1978: 456; Bondesio *et al.*, 1980: 119-120; Vucetich, 1986). Anyway, the existence of wooded areas such as gallery forest has also been postulated, and the presence of Echimyidae has been precisely considered an important evidence for this claim (Webb, 1978; Vucetich, 1986).

However, in the case of *Reigechimys* (and the related genus from Chiquimil) its very high cheek teeth suggest open environments more than wooded areas (see Pascual *et al.*, 1965). All extant caviomorph rodents inhabiting mesic to arid areas possess euhypsodont (*sensu* Mones, 1982) cheek teeth (except the semiaquatic *Myocastor*). The Echimyidae never developed euhypsodonty; but, among the extant Eumysopinae those inhabiting open environments have the highest and more simplified molars (*Trichomys, Carterodon, Clyomys* and *Euryzygomatomys*; see Alho, 1982; Reig,

1989). In this sense, *R. octodontiformis* represents an extreme case of this adaptive type.

Likewise, a detailed analysis of the remaining Upper Miocene Echimyidae of Argentina (Rovereto, 1914; Pascual, 1967; Bond, 1977; Zetti, 1972; Reig, 1989), show that most of the recorded species were probably associated with open biomass rather than to forested areas. None of them belong to the arboreal Echimyinae or Dactylomyinae, but undoubtedly belong to the Eumysopinae *sensu* Patton & Reig (1989), which are terrestrial rodents. Moreover, all of them have relatively hypsodont and simple cheek teeth similar to those of the above mentioned Eumysopinae inhabiting open environments.

In accordance with this analysis, the known Late Upper Miocene Echimyidae of central and western Argentina could not be used to support the existence of wooded areas.

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