

Systematics and biogeographic significance of *Drytomomys typicus* (SCALABRINI in AMEGHINO, 1889) nov. comb., a Miocene Dinomyidae (Rodentia, Hystricognathi) from Northeast of Argentina

Adriana Candela, La Plata and **Norma L. Nasif**, San Miguel de Tucumán

CANDELA, A. & NASIF, N. L. (2006): Systematics and biogeographic significance of *Drytomomys typicus* (SCALABRINI in AMEGHINO, 1889) nov. comb., a Miocene Dinomyidae (Rodentia, Hystricognathi) from Northeast of Argentina. - N. Jb. Geol. Paläont. Mh., **2006**: 0-0; Stuttgart.

Abstract: Extinct dinomyids (Rodentia, Hystricognathi) are yet poorly known. Among them, *Drytomomys* ANTHONY, 1922 has a particular interest from a bio-geographical perspective, since it is one of the few extinct mammal genera recorded both in the "Mesopotamian" (= "Conglomerado osífero". Late Miocene, Northeast of Argentina) and Laventan (Middle Miocene, La Venta, Colombia) faunas. The comparative study of the holotype of "*Olenopsis*" *typicus* SCALABRINI in AMEGHINO, 1889, coming from the "Conglomerado osífero", enables the allocation of this species to genus *Drytomomys*. The assignment of specimens recovered from La Venta fauna to *D. aequatorialis* is confirmed. The geographical distribution of *Drytomomys* suggests a biogeographical relationship of the Northeast of Argentina with the North of South America during the Miocene.

Zusammenfassung: Trotz ihrer hohen Diversität, Häufigkeit und weiten Verbreitung in Südamerika sind die ausgestorbenen Dinomyiden (Rodentia, Hystricognathi) immer noch schlecht verstanden. Unter ihnen ist *Drytomomys* ANTHONY, 1922, aus biogeografischer Sicht von besonderem Interesse, da es eine der wenigen ausgestorbenen Mammalia-Gattungen darstellt, die sowohl aus den „Mesopotamian“-Faunen (= „Conglomerado osífero“, Basis der Ituzaingó-Formation, Ober-Miozän, Provinz Entre ríos, Argentinien) als auch den Laventan-Faunen (Mittel-Miozän, Kolumbien) beschrieben wurde. In dieser Arbeit wird eine Analyse des Holotypus von *D. typicus*

(SCALABRINI in AMEGHINO, 1889) comb. nov. aus dem ..Conglomerado osífero" präsentiert, die eine Klärung der Systematik und der Verbreitung dieser Gattung ermöglicht. Die Zuordnung von Exemplaren aus La Venta in Kolumbien zu *Drytomomys* wird bestätigt, was somit auf eine große geographische Verbreitung der Gattung im Miozän Südamerikas sowie auf faunistische Beziehungen zwischen der Mesopotamischen Región Argentinien und der Brasilianischen Unterregion hin-deutet.

Key words: *Drytomomys*, Dinomyidae, Hystricognathi, Rodentia, Systematics, Bio-geography, Late Miocene, NE Argentina.

1. Introduction

Dinomyidae are represented by a single extant species, *Dinomys branickii* PETERS, dwelling in forest areas of eastern Andes of Brazil, Perú, Ecuador, Bolivia, Venezuela, and Colombia (WHITE & ALBERICO, 1992). The family is known since Middle Miocene of Argentina (AMEGHINO, 1904), and attained its highest diversity during the Late Miocene (AMEGHINO 1883, 1885, 1886;

KRAGLIEVICH 1926, 1931, 1932; NASIF et al. 2004). Despite its important South American Neogene record (MONES 1981; LATRUBESSE et al. 1997;

LINARES, 2004), the systematics and evolutionary history of extinct dinomyids are still poorly understood. Among them, *Drytomomys* ANTHONY, 1922, deserves particular attention from biogeographic perspective since it is recovered from the "Conglomerado osífero" (= "Mesopotamian" sensu FRENGUELLI 1920, basal levels of the Ituzaingó Formation, Late Miocene, Northeast of Argentina; CIONE et al. 2000; Fig. 1), and from the La Venta fauna (Laventan Age, Honda Group, Middle Miocene, Colombia; MADDEN et al. 1997), being one of the few extinct mammal genera registered in both units.

In this contribution we analyze the holotype of the Miocene dinomyid "*Olenopsis*" *typicus* SCALABRINI in AMEGHINO 1889, coming from the "Mesopotamian", which remained lost until now. Its comparative study allows the clarification of taxonomic status of "*O.*" *typicus*, herein assigned to *Drytomomys*. The presence of this genus in La Venta fauna is confirmed. The record of *Drytomomys typicus* in the Northeast of Argentina suggests a biogeographic relationship between this area and northern South America, as indicated by other fossil mammals (CIONE et al. 2000).

Drytomomys typicus (SCALABRINI in AMEGHINO, 1889) nov. comb.

3

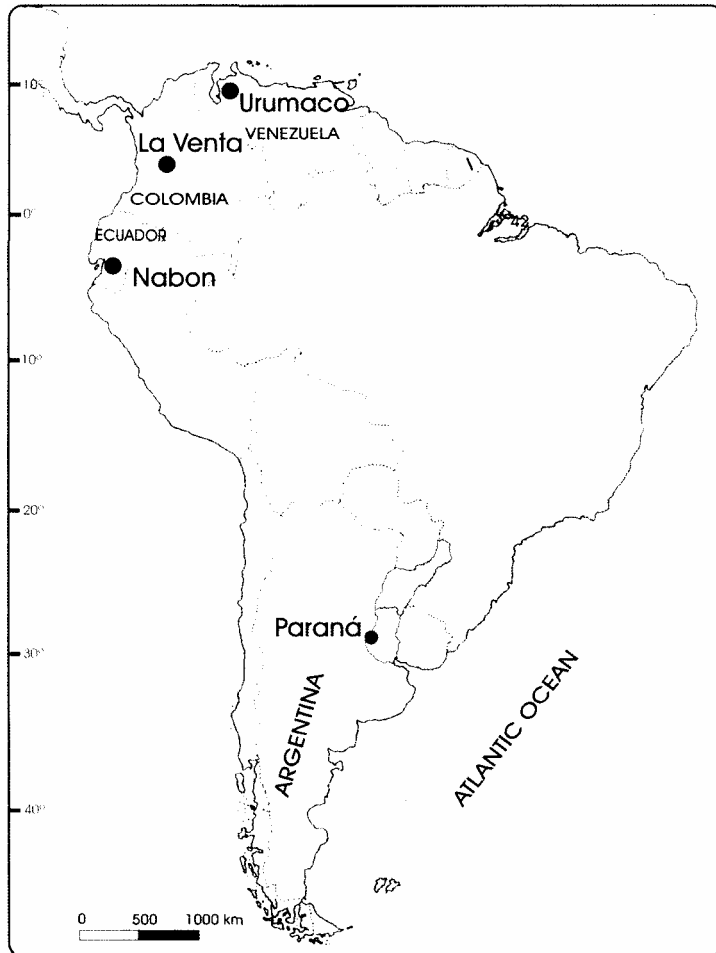


Fig. 1. Location map of South América showing the distribution of *Drytomomys* ANTHONY, 1922; shaded área shows the Mesopotamia región in Argentina.

Repositorios and abbreviations: AMNH, American Museum of Natural History, New York; INGEOMINAS (IGM), Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Museo Geológico, Bogotá, Colombia; MACN,

Museo de Ciencias Naturales "Bernardino Rivadavia", Argentina; MASP, Museo de Ciencias Naturales y Antropológicas Profesor Antonio Serrano de Paraná, Argentina; MLP, Museo de La Plata, Argentina; OMNH, San Noble Oklahoma Museum of Natural History; UCMP, University of California Museum of Natural History, United States; mi-3, lower molars; DP4/dp4, upper and lower deciduous premolar; p4, lower permanent premolar; APD, anteroposterior diameter; TD, transverso diameter.

2. Taxonomic history

Olenopsis typicus SCALABRINI in AMEGHINO, 1889, coming from the "Conglomerado Osífero" (= "Mesopotamian" sensu FRENGUELLI 1920; Late Miocene, Northeast of Argentina), presents a complex taxonomic history. According to AMEGHINO (1889: 901 f.), this species had been previously identified by SCALABRINI (in AMEGHINO 1889), who would have included it in the genus *Paranomys*. In that opportunity, AMEGHINO (1889), following the thought of SCALABRINI, recognized the validity of this species, but included it in the genus *Olenopsis* AMEGHINO.

O. uncinus AMEGHINO, the type species of this genus, recovered from the Santa Cruz Formation (Early-Middle Miocene, Santacrucian Age, Patagonia, Argentina), was erected on the basis of three syntypes (AMEGHINO 1889, pl. 6, figs. 14-16; WOOD & PATTERSON 1959): MACN A 17 (a left mandibular fragment with the series dp4-ml and m2 in eruption, hitherto lost), MACN 1613 (a lower cheek tooth), and MACN 1614 (a single DP4). *O. typicus* was recognized on the basis of a mandibular fragment of a juvenile specimen (AMEGHINO 1889, pl. 32, fig. 4a-c) which remained lost until now.

Within *Olenopsis*, SCOTT (1905) recognized both species described by AMEGHINO (1889), *O. uncinus* and *O. typicus*. Noteworthy that in this occasion he pointed out that he only had access to a cast of the holotype of *O. typicus*.

KRAGLIEVICH (1934) recognized the genus *Paranomys* [sic] SCALABRINI as a valid one, writing: "*Paranomys* (SCAL.) KRAGL" (MONES, unpubl.). Thus KRAGLIEVICH included in this genus to *O. typicum* (= *Olenopsis typicus*). He indicated that this species "nada tiene que ver con *Olenopsis uncinus*.." (KRAGLIEVICH 1934: 73), remarking that "Ya el mismo Ameghino dudó de esta identidad genérica..." (KRAGLIEVICH 1934: 73). In this way, KRAGLIEVICH (1934) only included in *Olenopsis* the Patagonian *O. uncinus*.

The genus *Drytomomys* ANTHONY, 1922, was erected to include *D. aequatorialis* ANTHONY, 1922, coming from sediments of the Nabon region of Ecuador, probably Miocene in age (see FIELDS 1957: 324; PATTERSON & WOOD 1982: 447). This genus was posteriorly synonymized by FIELDS (1957) with *Olenopsis*. In this opportunity, FIELDS (1957) assigned several

specimens coming from Middle Miocene of La Venta to *O. aequatorialis* (ANTHONY, 1922). This way, FIELDS (1957) recognized ANTHONY'S specific name, *aequatorialis*, as valid, extending his diagnosis on the basis of La Venta specimens. Note that his study on *O. typicus* was based exclusively on AMEGHINO'S (1889) illustrations. WOOD & PATTERSON (1959) put in question the generic assignment of *aequatorialis* (ANTHONY, 1922) to *Olenopsis*, previously proposed by FIELDS (1957). These authors pointed out that: "there is doubt as to whether the Santacruzan species of *Olenopsis* is congeneric with the Colombian one described by FIELDS" (WOOD & PATTERSON 1959: 328). Besides, they remarked the similarity between the syntype MACN 1614 (DP4) of *O. uncinus* and the DP4 of *Neoreomys* AMEGHINO, a dasyproctid widely represented at the Miocene of Patagonia (AMEGHINO 1887), genus to which these authors assigned this specimen (WOOD & PATTERSON 1959: 361, 21 footnote). PATTERSON & WOOD (1982: 447) pointed out that the syntype material of *O. uncinus* is partly lost, in part referable to *Neoreomys*, and differs from the material described by FIELDS (1957). In this context, they retained the generic name of *Drytomomys* to *aequatorialis* and, following FIELDS (1957), assigned La Venta specimens to this species (PATTERSON & WOOD 1982:447). Likewise, PATTERSON & WOOD (1982) stated that *Olenopsis typicus* is congeneric neither with *O. uncinus* nor with *D. aequatorialis*, and referred the "Mesopotamian" species to *Paranamys* KRAGLIEVICH, 1934. MONES (1981) assigned *typicus* to *Paranamys*. He considered this species as a Dinomyidae, while included *Olenopsis*, represented by *O. uncinus*, in Dasyproctidae. Later, MONES (1986) assigned *P. typicus* to Dasyproctidae. More recently, WALTON (1990) questioned the synonymy of *Olenopsis* with *Drytomomys* and the La Venta dinomyids. Among the latter, WALTON (1997) identified "*Olenopsis*", pointing out that this would be recognized as a new genus, represented by two species differing mainly in size. Thus far, these species were neither formally nominated nor described. In summary, according to WOOD & PATTERSON (1982) and WALTON (1997), *O. uncinus* is assigned, at least partially, to *Neoreomys*; *O. typicus* is assigned to *Paranamys*; the genus *Drytomomys* would be valid and retained for the species *D. aequatorialis* of ANTHONY (1922), while dinomyids from La Venta would be provisionally referred to "*Olenopsis*" (FIELDS 1957; WOOD & PATTERSON 1982; WALTON 1997). This systematic hypothesis gets clearer through the study of the holotype of "*Olenopsis*" *typicus* herein reported.

3. Systematic paleontology

Order Rodentia BOWDICH, 1821 Suborder Hystricognathi
TULLBERG, 1899 Family Dinomyidae PETERS, 1873 Subfamily
Potamarchinae KRAGLIEVICH, 1926 Genus *Drytomomys*
ANTHONY, 1922

Type species: *Drytomomys aequatorialis* ANTHONY, 1922: 2, pl. 2.

Drytomomys typicus (SCALABRINI in AMEGHINO, 1889)
nov. **comb.** **Figs. 2, 3.a**

1889 *Paranomys typicus*. - SCALABRINI in AMEGHINO, p. 901-902.

1889 *Olenopsis typicus*. - SCALABRINI in AMEGHINO, p. 901-902, pl.
32, fig.

4a-c.

1981 *Paranomys typicum* KRAGLIEVICH, 1934. - MONES, p.

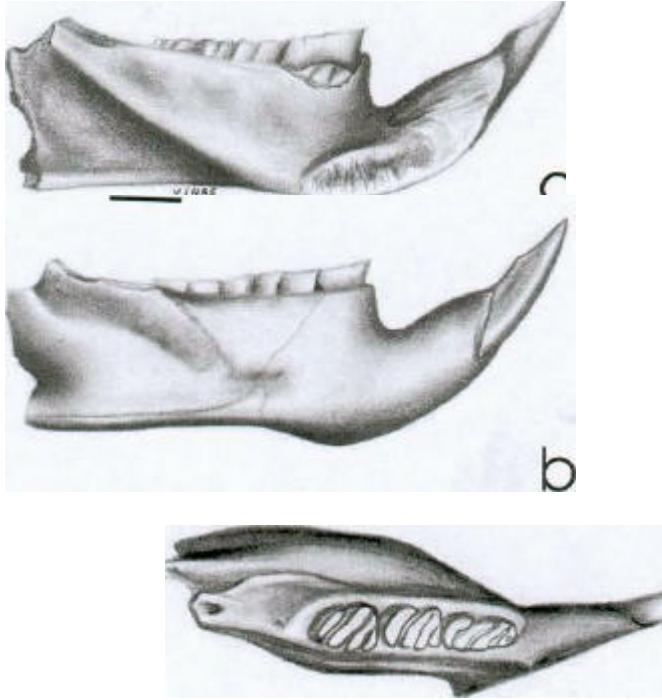
613. 1986 *Paranomys typicus*. - MONES, p. 206.

Holotype: MASP 6, left mandibular fragment with incisor and dp4-m2.

Diagnosis: Mandible slender, well developed posterior fossa for the masseteric medialis posterior muscle, shallow masseteric fossa, poorly developed masseteric crest, masseteric notch for the medial masseter tendon located at level of mi and below the half of the mandibular height, posterior margin of the diastema forming an almost right angle with the alveolar edge, mandibular foramen dorsally located respect to the alveolar lingual margin; pentalophodont dp4, mi-2 long in relation to the incisor APD.

Geographical and stratigraphic provenance: "Conglomerado osífero" (= "Mesopotamian" sensu FRENGUELLI 1920), outcropping at the base of the Ituzaingó Formation (DE ALBA 1953; HERBST 2000), nearby Paraná city. Entre Ríos Province, Northeast of Argentina (Fig. 1). Note that the Ituzaingó Formation, considered of Late Miocene-Pliocene age (ACEÑOLAZA 1976; DE ALBA 1953; HERBST 2000), has a wide distribution in northeastern Argentina (Mesopotamia región). However, the "Mesopotamian" or "Conglomerado osífero" unit is restricted to the basal levels of the Ituzaingó Formation at the Entre Ríos Province. This fossiliferous unit is represented by discontinued outcroppings at the left margin of Paraná river since the Paraná city (e.g. La Toma Vieja, La Celina localities) to the north. The "Conglomerado osífero" has been considered Tortonian (Late Miocene) or Huayquerian (Late Miocene) in age, according to the local chronology (e.g., PASCUAL & ODREMAN RIVAS 1971; MARSHALL et al. 1983; CIONE et al. 2000).

Comparative description: The holotype (MASP 6) of *Drytomomys typicus* nov. comb. is a juvenile specimen, having few worn dp4-m2, probably intra-alveolar m3,



c

Fig. 2. *Drytomomys typicus* (SCALABRINI in AMEOHINO, 1889) nov. comb., MASP6 (holotype), left mandibular fragment with incisor and dp4-m2 in lingual (a), labial (b), and dorsal (c) views. Scale 1 cm.

and the p4 in eruption, which is visible arising below dp4 (Fig. 2.a). The mandible is less robust and massive than that of the holotype of *D. aequatorialis* ANTHONY (1922: 3, fig. 2b, d) (Table 1), and than those of specimens of La Venta referred to this species (e.g., UCMP 41636 and 40055, see FIELDS 1957: 328, fig. 16a-d). It should though be remembered that this trait could be modified during ontogenetic

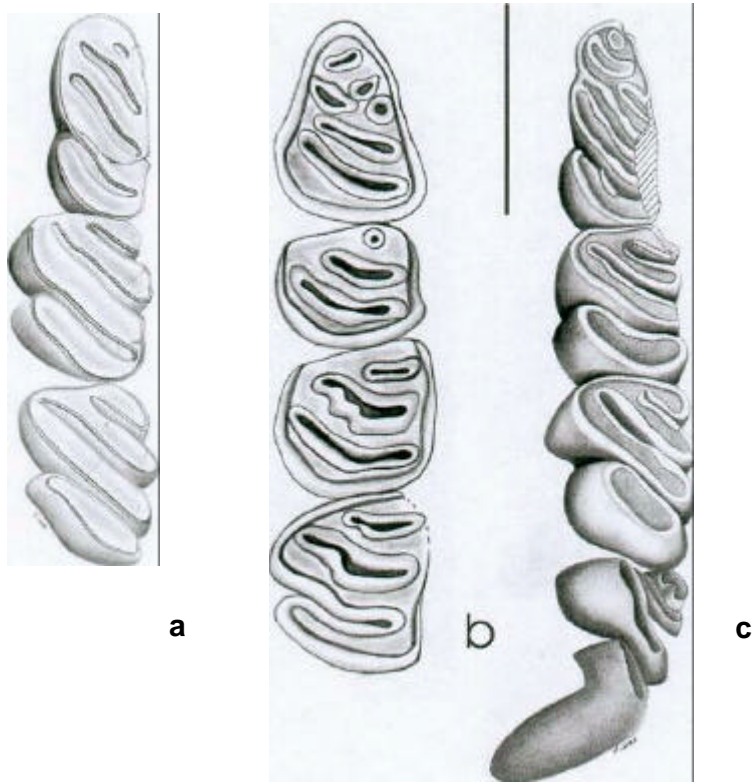


Fig. 3. a - *Drytomomys typicus* (SCALABRINI in AMEGHINO, 1889) nov. comb., MASP6 (holotype), left dp4-m2; **b-c** - *D. aequatorialis* ANTHONY, 1922, (b) AMNH 13219 (holotype), left p4-m3 (modified from ANTHONY 1922, fig. 2), (c) IGM 87.067, left dp4-m3. Scale 1 cm.

development. However, it unlike the mandible of holotype of *D. typicus* had to reach the robustness that of holotype of *D. aequatorialis*. *D. typicus* has an elongated symphysis, extending posteriorly to the middle pair of dp4, a similar condition to that of *D. aequatorialis* (ANTHONY, 1922, fig. 2; FIELDS 1957, figs. 16-17). The diastema is shorter than the length of dp4-m2. Its posterior border ascends abruptly at an almost right angle with the alveolar edge. In *D. aequatorialis* and *Dinomys branickii* this border ascends smoothly, describing a gentle curve. The masseteric notch for the tendón of medial masseter muscle is located below mi, and somewhat

***Drytomomys typicus* (SCALABRINI in AMEQHINO, 1889) nov. comb. 9**

below the half of the mandibular height (Fig. 2.b), while in *D. aequatorialis* and *D. branickii* this notch is located at the level of p4-m1 and closer to the alveolar edge. The masseteric crest is poorly developed and defines a very shallow masseteric fossa, which is convex in its anterior portion. The fossa for the insertion of the medial posterior masseter is well developed, a trait not present in *D. branickii*. The existence of this fossa in *D. aequatorialis* is difficult to evaluate since the poor state of preservation of this mandibular region in the available specimens. The lateral crest is well defined, extending from the masseteric notch to the coronoid process, of which only the basal portion is preserved. This indicates that the coronoid process was more developed than in *D. branickii* and other extinct dinomyids (e.g., *Tetrastylus* AMEGHINO, *Eumegamys* KRAGLIEVICH), and that it would cover laterally the m3 in labial view. The mandibular foramen is located posteriorly to the m3, opening dorso-labially respect to the alveolar lingual edge (Fig. 2.c). The incisor is very narrow (Table 1), a character probably related, at least partially, to the early ontogenetic stage of the specimen. The degree of curvature of the incisive suggests that its base would reach the intra-alveolar bases of m2-3. Cheek teeth are protohypsodont (*sensu* MONES, 1982), with a laminar design, narrow flexids/fossetids, and the hypoflexid connected to the metaflexid/metafossetid (lingual posterior fossetid) (Fig. 3.a). The dp4 is longer than wide and longer than mi-2 (Table 1). The dp4 shows a pentalophodont design, with all lophids lingually joined, and the first four lophids labially joined. These lophids are separated by elongated and obliquely oriented fossetids, the most anterior of them is very small and would disappear with more wear. Like in *D. aequatorialis* (e.g. IMG 87.0767, Fig. 3.c; FIELDS, 1957, fig. 18b), the hypoflexid is continuous with the metafossetid. Note that the first cheek teeth of the holotype of *D. aequatorialis*, with a hexalophodont design (Fig. 3.b), was considered by ANTHONY (1922) and FIELDS (1957) as a p4. WALTON (1997: 399) pointed out the possibility that it would be a dp4. Note that this tooth has all lophids labially joined. This suggests a higher wear than that of m3, which would support its assignment to dp4. However, we prefer to maintain the original assignment of Anthony until a larger sample is available. The m1-2 are longer in relation to the incisor DAP than those of *D. aequatorialis* (Table 1), a trait that cannot be attributed to ontogenetic variability. Like in this species both molars show a tetralophodont design, with the three first lophids (metalophid, mesolophid? and hypolophid, *sensu* CANDELA 2002) labially joined, and the posterior lophid (posterolophid) disconnected from the remaining lophids. The hypoflexid is continuous with the metaflexid/metafossetid (Fig. 3.a). In mi the two anterior lingual flexids remain open, while the posterior has become a metafossetid due to the union of the hypolophid and the posterolophid. The m2 is longer than mi and all its lingual flexids remain open. This pattern is similar to that of *D. aequatorialis* (FIELDS 1957, fig. 16-17; Fig. 3.c). Measurements are given in Table 1. Comments: In the context of the dinomyids systematics, an interesting aspect is the probable change in tooth size during ontogenetic development. FIELDS (1957:354) pointed that the difference in anteroposterior diameter in teeth between juveniles and adults of "*Olenopsis*" *aequatorialis* is probably not only due to wear. He

10 A. Candela and N. L Nasif

Table 1.	Meas	remens	(iii)	i)	of the	ible	lower	cheek	teeth	of
<i>Drytor noi</i>	<i>mys</i>	(SCAI	.ABR	in	AMEGHI	889)	<i>r.</i>	<i>aequ</i>	;	
	<i>typil</i>	i, md	INI	NO, 1.			comb.	<i>Dino</i>		
	<i>typicu</i>	<i>D.</i>	<i>atori</i>					<i>brani</i>	<i>i</i>	
	MAS	IGM	UCM	UCMP	UCM	AMN	OMN	MACN		
	juveni	87.06	39969*	39928*	4005	13219	7409	12961	adult	
	le	7	37928*	juvenile	5	**	sub-			
		(cast)	juvenile	adult	adult	adult				
APDof	5.03	-	5.5	6.4	9.8	10.8	11.7	12.4		
incisor										
TDof	4.02	5.20	4.7	5.2	7.6	8.4	6.0	7.4		
incisor										
p4-m3	-	-	28.7	31.8	32.8	31.5	27.0	31.4		
length										
dp4-	27.08	26.13	-	-	-	-	-	-		
m?										
APDd	9.50	9.88	-	9.5	-	-	-	-		
TDdp4	4.70	-	-	4.5	-	-	-	-		
APDp	-	-	6.9	7.4	9.6	9.5	6.3	6.4		
TDp4	-	-	5.0	5.5	7.3	6.7	4.8	5.6		
APDm	8.20	7.14	6.4	7.7	7.6	6.5	6.2	6.5	7.0	
TDml	6.70	6.60	5.6	5.8	6.9	6.8	7	6.3	6.0	
APDm	9.22	8.40	8.0	8.0	8.3	7.5	7.5	6.5	8.6	
TDm2	6.70	7.16	5.9	6.2	7.8	7.8	7.4	6.2	7.0	
APDm	-	-	7.4	8.5	9.2	8.8	7.0	8.4		
DTm3	-	-	4.9	6.8	7.2	7.5	5.7	6.8		
Depth	19.21	-	19.0	25.5	29.8	29.7	27.0	29.0		
below										
dp4/p4										
Depth	18.25	-	18.3	23.6	27.8	28.2	25.0	27.0		
below										
dp4/p4										
Length	15.60	~	16.5	~	18.0	16.0	11.4	20.0		
of										

* From FIELDS (1957), ** From ANTHONY (1922).

Drytomomys typicus (SCALABRINI in AMEGHINO, 1889) nov. comb.

11

noted a difference in teeth size between juveniles and adults of *Dinomys branickii* and suggested that in this genus tooth may grow in diameter during eruption. He stated that: "... the process of diametric growth is possible, as the enamel organ supplies new enamel to the base to the column throughout at least part of the life of the individual. Since the enamel organ remains active, expansion of the teeth is possible as the gross proportions of the skull increase. This factor could account for the differences in size of teeth in juvenile and adult *Dinomys*" (FIELDS 1957: 354). It is possible that in *Drytomomys*, according to its protohypsodont condition, teeth have grown in diameter during a shorter period, stopping when roots and fossae close. This would explain the differences in diameter between juvenile and adult teeth pointed by FIELDS (1957). It should be remarked that WALTON (1997) claimed the difficulty in identifying species among La Venta specimens because of their wide variability in size, relative size of incisors, crown height and shape, and enamel infolding at different state of wear (WALTON 1997, fig. 24.3.I-K).

Drytomomys cf. typicus

Fig. 4 Referred

material: MLP 15-250, one left m1 or 2.

Geographical and stratigraphic provenance: Same as the holotype of *Drytomomys typicus*.

Measurements: APD: 9.34 mm (at occlusal level); TD: 7.66 mm; crown height (at the level of hypoconid): 15.90 mm.

Description: Specimen MLP 15-250 is tetralophodont, very similar to, but somewhat wider than m2 of the holotype of *Drytomomys typicus* (Table 1). Its three first lophids are labially joined in the protoconid region. The enamel thickness very close to the first lophid suggests a small vestigial lophid. In each lophid, the anterior edge of enamel is notably crenulated, thinner and lower than the posterior edge. The first lingual flexids remain open but near to close, while the posterior flexid has become a metafossetid. The hypoflexid extends towards the base of the tooth. At this level, the crown gets narrower. The bottom of the lophids is visible at the base of the tooth, resembling cheek teeth of other protohypsodont dinomyids, such as *Potamarchus* BURMEISTER. In euhypsodont dinomyids, such as *Tetrasylus* and *Dinomys*, the bases of cheek teeth are open.

Comments: MLP 15-250 is very similar to the m1-2 of the holotype of *Drytomomys typicus*. It differs from the latter in the presence of an enamel thickness very close to the first lophid, and of crenulations of the anterior enamel edges in each lophid. It should be noted that this latter trait is also present in the genus *Potamarchus*. MLP 15-250 is larger than the molars of

a



Fig. 4. *Drytomomys* cf. *typicus* (SCALABRINI in AMEQHINO, 1889) nov. comb., MLP 15-250, lower m1 or m2 in occusial (a) and labial (b) views. Scale 1 cm.

the holotype of *D. typicus*, although this may be due partially to different ontogenetic stages. In fact, taking into account the probable size enlargement of the teeth of *Drytomomys* during growth (see above), MLP 15-250 could correspond to an adult *D. typicus*. Therefore, we tentatively refer MLP 15-250 to this species, until a comprehensive review of extinct dino-myids (NASIF, in prep.) allows to determine its more precise taxonomic status.

4. Discussion

Systematics: In agreement with WOOD & PATTERSON (1959) and PATTERSON & WOOD (1982), the study of the syntypes of *Olenopsis uncinus* (AMEGHINO 1889, pl. 4, figs. 16-17) indicates that this species should be assigned to the genus *Neoreomys*, tentatively to *N.-australis* Ameghino. Because *Olenopsis uncinus* is the type species and hence the name-bearing species of *Olenopsis*, this genus has to be considered as a junior synonym of *Neoreomys*.

On the other hand, the traits of the holotype (MASP 6) of "*Olenopsis*" *typicus* indicate that this species is not congeneric with *O. uncinus*. As was noted above, the holotype of "*O.*" *typicus* shares several traits with the holo-

***Drytomomys typicus* (SCALABRINI in AMEGHINO, 1889) nov. comb. 13**

type (AMNH 13219) of *D. aequatorialis* ANTHONY, 1922, with La Venta specimens assigned by FIELDS (1957) to this species, and with IGM 87.067, coming also from that locality (Fig. 3.c). The occlusal design of cheek teeth of *D. aequatorialis*, with three lophids labially joined and a fourth separated lophid, is essentially identical to that of the holotype of "*O.*" *typicus*. Like-wise, the general size and occlusal designs of m1-2 of La Venta specimens studied by Fields (1957, fig. 16-17) are very similar to those of the holotype of "*O.*" *typicus*. Note that IGM 87.067 (Fig. 3.c), a juvenile with m3 in eruption, is very similar to the holotype of "*O.*" *typicus*. Both specimens show a same occlusal design and similar molar size, though, in IGM 87.067 m1-2 are somewhat shorter (Table 1). Nevertheless, these differences lie within the interspecific variability found in La Venta specimens (FIELDS, 1957; WALTON, 1997). Unlike the holotype of "*O.*" *typicus*, IGM 87.067's dp4 is hexalophodont. Nevertheless, both the number and distribution of lophids of dp4 in Hystricognathi are variable features within a genus (CANDELA 2002).

In this context, traits shared by La Venta specimens, the holotype of *D. aequatorialis*, and the holotype of "*O.*" *typicus* justify their inclusion in the same genus. According to priority rules, both species, *aequatorialis* and *typicus*, have to be referred to the genus *Drytomomys* (see taxonomic history). Hence, the proper combination for the latter species is *Drytomomys typicus*. *Paranomys* has to be considered as a junior synonym of *Drytomomys*. The inclusion of *typicus* and *aequatorialis* in the same genus (FIELDS 1957) has been questioned (PATTERSON & WOOD 1982; WALTON 1996) probably because the holotype of *typicus* was unavailable for comparison with La Venta specimens. The study of *typicus* strengthens the assignment of La Venta specimens studied by FIELDS (1957) and of IGM 87.067 to *Drytomomys*. Note that specimens from La Venta studied by WALTON (1997) have neither been formally recognized nor taxonomically assigned yet. Until this review is carried out, we propose to maintain La Venta specimens studied by FIELDS (1957) and IGM 87.067 in the species *D. aequatorialis*. *Drytomomys* shows a mandibular and tooth morphology more generalized than those of other Miocene dinomyids (e.g., *Tetrastylus*, *Eumegamys*; NASIF in preparation). *D. typicus*, included in Potamarchinae (KRAGLIEVICH 1926; MCKENNA & BELL 1997), has protohypsodont cheek teeth, with "roots" that arose earlier than in other dinomyids, with a tetralophodont design, and a pentalophodont dp4 (a design that has been proposed as primitive for Hystricognathi; CANDELA 2002). Their generalized condition has probably been the main reason for their alternative inclusion in Dasypsectidae (MONES 1986) and Dinomyidae (SCOTT 1905; KRAGLIEVICH 1934; FIELDS 1957; PATTERSON & WOOD 1982; WALTON 1997; MCKENNA & BELL 1997).

In tum, *Drytomomys* (= *Olenopsis*) has been related to *Scleromys* AMEGHINO 1887 (Miocene from Patagonia and La Venta; FIELDS 1957; WALTON 1997;

MCK.ENNA & BELL 1997), which has also been referred to both families (e.g., MONES 1981; WALTON 1997). In fact, *Drytomomys* and *Scleromys* share a set of characters, being it difficult to distinguish between both taxa (WALTON 1997). This reveals the difficulty to diagnose both families when fossil taxa are considered. A phylogenetic analysis of Hystricognathi including these taxa is necessary to diagnose Dasyproctidae and Dinomyidae on the basis of their tooth characters and to clarify the taxonomic status of fossil taxa traditionally included in these families.

Biogeographic significance: Caviomorph rodents *Drytomomys* and *Prodolichotis* Kraglievich, and the Xenarthra *Scirrotherium* EDMUND & THEODOR are the single extinct mammal genera present both in the "Mesopotamian" (= "Conglomerado osífero", Late Miocene, Northeast of Argentina) and Laventan (Middle Miocene, La Venta, Colombia) faunas. Vertebrates recovered from the "Mesopotamian" comprise many endemic taxa, as well as several taxa in common with other biogeographic areas of Argentina (Northwestern, Patagonia, and Pampean Región), and with other Neogene faunas of the rest of South América (e. g. Acre; CIÓME et al. 2000). The biogeographic history of this particular faunistic assemblage is poorly understood. The Miocene record of *Drytomomys*, suggests a biogeographical connection between the Northeast of Argentina with North of South América, as suggested by the distribution of other fossil mammals (CIONE et al. 2000).

Drytomomys is one of the oldest dinomyids and, together with *Potamarchus*, one of the more widely distributed in South América (LATRUBESSE et al. 1997; LINARES 2004). Recently, LINARES (2004) identified the presence of "*Olenopsis*" I in the lower part of the Lower Member (level 9) of Urumaco Formation (Venezuela; Laventan Age). According to this author, the taxon is similar to one of La Venta species recognized by WALTON (1997). Its affinities with *Drytomomys* should not be discarded.

Acknowledgements

We are grateful to M. REGUERO for giving permission to study of fossil dinomyids of MLP; A. KRAMARZ for giving access to collections of MACN; G. BAHLER and J. PEÑA for giving permission to study materials from MASP; J. NORIEGA for his useful information on the "Mesopotamian" and for facilitating of material that motivated this study; to the reviewers A. MONES and J. NORIEGA for their useful comments that contributed to improve the manuscript. A. VIÑAS made the illustrations of studied specimens. This work is a contribution to PICT 11928, PICT 8395 (ANPCYT) and CIUNTG316.

References

- ACEÑOLAZA, F. G. (1976): Consideraciones bioestratigráficas sobre el Terciario marino de Paraná y alrededores. - Acta geol. Lilloana, **13** (2): 91-118.
- AMEGHINO, F. (1883): Sobre una nueva colección de mamíferos fósiles recogidos por el Profesor Scalabrini en las barrancas del Paraná. - Bol. Acad. Nac. Cieñe. Córdoba, **5**: 112-113.
- (1885): Nuevos restos de mamíferos fósiles oligocenos recogidos por el profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la Ciudad de Paraná. - Bol. Acad. Nac. Cieñe. Córdoba, **8** (I): 5-207.
- (1887): Enumeración sistemática de las especies de mamíferos fósiles colectados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. - Bol. Mus. La Plata, **1**: 1-26.
- (1889): Contribución al conocimiento de los mamíferos fósiles de la República Argentina. - Actas. Acad. Nac. Cieñe. Córdoba, **6**: xxxii + 1027 pp.
- (1904): Nuevas especies de mamíferos cretácicos y terciarios de la República Argentina. - An. Soc. cient. Argent, **57**: 162-175, 327-341.
- ANTHONY, E. H. (1922): A new fossil rodent from Ecuador. - Amer. Mus. Novit., **35**: 1-4.
- CANDELA, A. M. (2002): Lower deciduous tooth homologies in Erethizontidae (Rodentia, Hystricognathi): evolutionary significance. - Acta Palaeont. Polon., **47**(4): 117-723.
- CIONE, A. L., AZPÉLICUETA, M., BOND, M., CARLINI, A. A., CASCIOTTA, J. R., COZZUOL, M. A., DE LA FUENTE, M., GASPARINI, Z., GOIN, F. J., NORIEGA, J., SCILLATO-YANÉ, G. J., SOILBELZON, L., TONNI, E. P., VERZI, D. & VUCETICH, M. G. (2000): Miocene vertebrales from Entre Ríos province, eastern Argentina. - In: ACEÑOLAZA, F. G. & HERBST, R. (Eds.): El Neógeno de Argentina. - Serie de Correlación Geológica (Insugeo), **14**: 191-237; Tucumán.
- DE ALBA, E. (1953): Geología del Alto Paraná, en relación con los trabajos de derrocamiento entre Ituzaingó y Posadas. - Rev. Asoc. geol. Argent., **8**: 129-161.
- FIELDS, R. W. (1957): Hystricomorph rodents from the Late Miocene of Colombia, South América. - Univ Calif Public. Geol. Sci, **32** (5): 207-403.
- FRENGUELLI, J. (1920): Contribución al conocimiento de la geología de Entre Ríos. - Bol. Acad. nac. Cieñe. Córdoba, **24** (1-2): 55-256.
- HERBST, R. (2000): La Formación Ituzaingó (Plioceno). Estratigrafía y distribución. - In: ACEÑOLAZA, F. G. & HERBST, R. (Eds.): El Neógeno de Argentina. - Serie de Correlación Geológica (Insugeo), **14**: 181-190; Tucumán.
- KRAOLIEVICH, L. (1926): Los grandes roedores Terciarios de la Argentina y sus relaciones con ciertos géneros pleistocenos de las Antillas. - An. Mus. Nac. Hist. Nat. Buenos Aires, **34**: 122-135.
- (1931): Nuevos géneros de roedores eumegámidos. - Physis, **10** (37): 392-399.
- (1932): Diagnósis de nuevos géneros y especies de roedores cávidos y eumegámidos fósiles de la Argentina. Rectificación genérica de algunas especies conocidas, y adiciones al conocimiento de otras. - An. Soc. cient. Argent., **115** (4): 155-181, (5-6): 211-237.

KRAGLIEVICH, L. (1934): La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron. - 136 pp.; Montevideo (El Siglo).

LATRUBESSE, E. M., BOCQUENTIN, J., SANTOS, J. C. R. & RAMONELL, C. G. (1997): Paleoenvironmental model for the Late Cenozoic of Southwestern Amazonia. *Paleontology and Geology*. - *Acta amazon.*, 27 (2): 103-118.

LINARES, O. J. (2004): Bioestratigrafía de la fauna de mamíferos de las formaciones Socorro, Urumaco y Codore (Mioceno medio-Plioceno temprano) de la región de Urumaco, Falcon, Venezuela. - *Paleobiol. Neot.*, 1: 1- 26; Caracas.

MADDEN, R. H., GUERRERO, J., KAY, R. E., FLYNN, J. J., SWISHER III, C. & WALTON, A. H. (1997): The Laventan Stage and Age. - In: KAY, R. E., MADDEN, R. H., CIFELLI, R. L. & FLYNN, J. J. (Eds.): *Vertebrate Paleontology in the Neotropics. The Miocene fauna of La Venta, Colombia*, p. 499-519; Washington (Smithsonian Inst. Press).

MARSHALL, L. G., HOFFSTETTER, R. & PASCUAL, R. (1983): Mammals and stratigraphy. Geochronology of the continental mammal-bearing Tertiary of South America. - *Palaeovertebrata, Mém. Extraord.*, 193; Montpellier.

MCKENNA, M. C. & BELL, S. K. (1997): *Classification of Mammals Above the Species Level*. - 631 pp.; New York (Columbia Univ. Press).

MONES, A. (1981): Sinopsis sistemática preliminar de la familia Dinomyidae (Mammalia: Rodentia: Caviomorpha). - *Anais do II Congresso Latino-Americano de Paleontología*, 2: 605-619; Porto Alegre.

- (1982) An equivocal nomenclature: What means hypsodonty? - *Paläont. Z.*, 56:107-111.- (1986): *Paleovertebrata Sudamericana. Catálogo sistemático de los Vertebrados fósiles de América del Sur. Parte I. Lista preliminar y bibliografía*. - *Cour.Forsch.-Inst. Senckenberg*, 82: 1-625.
NASIF, N. L., ACEÑOLAZA, E. G. & ESTEBAN, G. I. (2004). Nuevo material dextrócaros y roedores para la Formación Ituzaingó (Mioceno superior), provincia de Entre Ríos, Argentina. - *Ameghiniana*, 41 (4, Suplemento): 4R.

PASCUAL, R. & ODREMAN RIVAS, E. O. (1971): Evolución de las comunidades de los vertebrados del Terciario argentino. Los aspectos paleozoogeográficos y paleoclimáticos relacionados. - *Ameghiniana*, 8 (3-4): 372-412.

PATTERSON, B. & WOOD, A. E. (1982): Rodents from the Desadan Oligocene of Bolivia and the relationships of the Caviomorpha. - *Bull. Mus. Comp. Zool.*, 149(7): 371-543.

SCOTT, W. B. (1905): Mammalia of the Santa Cruz beds. III. Glires. - *Reports of the Princeton University Expeditions to Patagonia, 1896-1899*, 5 (Paleontology): 384-489; Princeton.

WALTON, A. (1990): Rodents of the La Venta fauna, Miocene, Colombia: Bio-stratigraphy and paleoenvironmental implications. - Unpublished Ph. D. dissertation, Southern Methodist University, Dallas, Texas.

- (1997): Rodents. - In: KAY, R. F., MADDEN, R. H., CIFELLI, R. L. & FLYNN, J. J. (Eds.): *Vertebrate Paleontology in the Neotropics. The Miocene fauna of La Venta, Colombia*, p. 393-409; Washington (Smithsonian Inst. Press).

***Drytomomys typicus* (SCALABRINI in AMEGHINO, 1889) nov.
comb. 17**

WHITE, T. G. & ALBERICO, M. S. (1992): *Dinomys branickii*. -
Mammalian Species,

410: 1-4. WOOD, A. E. & PATTERSON, B. (1959): The rodents of the
Desierto of Patagonia and
the beginning of South American rodent evolution. - Bull. Mus. Comp.
Zool.,
120(3): 281-482.

Manuscript received: October 17th, 2004. Revised versión
accepted by the Stuttgart editor: January 9th, 2006.

Addresses of the authors:

ADRIANA CANDELA, Departamento de Paleontología Vertebrados,
Facultad de Ciencias Naturales y Museo de La Plata, Paseo del Bosque,
1900 La Plata, Argentina;
e-mail: acandela@museo.fcnym.unlp.edu.ar

NORMA L. NASIF (corresponding author). Facultad de Ciencias Naturales
e IML, Universidad Nacional de Tucumán, Miguel Lillo 205,4000, San
Miguel de Tucumán, Argentina;
e-mail: norma_nasif@yahoo.com.ar