A Miocene toxodontid (Mammalia: Notoungulata) from the sedimentary series of the Cura-Mallín Formation, Lonquimay, Chile

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ABSTRACT

Middle Miocene fluvo-lacustrine strata of the Río Pedregoso Member of the Cura-Mallín Formation are broadly exposed to the east and south of the town of Lonquimay, Chile. These strata accumulated in the extensional Cura-Mallín Basin, a basin which was subsequently inverted. The original depocenter is interpreted as a double half-graben, diachronic sub-basin system. A partial left mandible was collected from the Cura-Mallín Formation near the base of Cerro Tallón along the west bank of the Río Biobío. Morphological and morphometric comparisons permit referral of the specimen to the toxodontid notoungulate *Nesodon conspurcatus*. This represents the first report of *Nesodon conspurcatus* outside of Patagonia and one of the few well-documented occurrences of *Nesodon* outside of high latitude Argentina. The widespread geographic range of *Nesodon*, combined with its restricted temporal range, suggest it may be one of the most useful indicator taxa for Santacrucian age faunas. The absence of *Nesodon* in the type Friasian assemblage at Río Frías/ Cisnes in Chilean Patagonia strengthens the case for a faunal distinction between the Santacrucian and Friasian SALMAs.

Key words: Cura-Mallín Formation, Tectonics, Andes, Early Miocene, Santacrucian, Notoungulata, Toxodontidae, Lonquimay, Chile.

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RESUMEN

Un toxodonte (*Mammalia: Notoungulata*) del Mioceno de la serie sedimentaria de la Formación Cura-Mallín (Cuenca de Cura-Mallín, región de Lonquimay, Chile). Estratos fluvio-lacustres del Mioceno medio del Miembro Río Pedregoso de la Formación Cura-Mallín están ampliamente expuestos al este y al sur de la ciudad de Lonquimay, Chile. Estos estratos se acumularon en la cuenca extensional de Cura-Mallín, la cual posteriormente sufrió una inversión tectónica. En esta región esta cuenca se interpreta como un sistema de subcuencas diacrónico compuesto por dos half-graben. En estratos de la Formación Cura-Mallín expuestos en la ladera occidental del Cerro Tallón, en la orilla oeste del río Biobío se encontró una mandíbula izquierda incompleta de un notoungulado toxodontido. Comparaciones morfológicas y morfométricas indican que el ejemplar pertenece a *Nesodon conspurcatus*. Este es el primer hallazgo de *Nesodon conspurcatus* que se realiza fuera de Patagonia y una de las pocas ocurrencias bien documentadas de *Nesodon* en regiones de alta latitud fuera de Argentina. La amplia distribución geográfica de *Nesodon* y su restringido rango de distribución temporal, sugieren que este taxón podría ser uno de los indicadores más útiles para las faunas pertenecientes a la edad Mamífero Santacrucense. La ausencia de *Nesodon* en la fauna tipo de la Edad Mamífero Friasense en Río Frías/Cisnes, en la Patagonia chilena, parece confirmar lo anterior y sugiere la posibilidad de establecer una distinción faunística entre la Edad Mamífero Santacrucense y el Friasense.

Palabras claves: Formación Cura-Mallín, Tectónica, Andes, Mioceno temprano, Santacrucense, Notoungulata, Toxodontidae, Lonquimay, Chile.

INTRODUCTION

Only a single extensive pre-Holocene fossil mammal fauna was known from Chile prior to about 15 years ago (Río Frías/Cisnes, the type sequence of the Friasian SALMA; Roth, 1908; Marshall and Salinas, 1990; Flynn and Swisher, 1995), although Cenozoic faunas have been discovered in several parts of the Chilean Andes since then (Marshall *et al.*, 1990; Suárez *et al.*, 1990; Wall *et al.*, 1991; Wyss *et al.*, 1993, 1994; Flynn *et al.*, 1995, 1999, 2002a, 2002b, 2003, in press). The Lonquimay region, ~600 km south of Santiago (Fig. 1), is one of several parts of the country holding significant promise of producing additional such fossils. Remains of a variety of vertebrates (including fishes, mammals, and a bird) have been collected from exposures of the Cura-Mallín Formation near Lonquimay (Marshall *et al.*, 1990; Suárez *et al.*, 1990; Wall *et al.*, 1991; Rubilar, 1994; Azpelicueta and Rubilar, 1998). Preliminary identification of previously discovered mammal remains (Marshall *et al.*, 1990; Suárez *et al.*, 1990) suggested that the fossils were referable to the Santacrucian South American Land Mammal 'Age' (late early Miocene, 17.5-16.3 Ma, *sensu* Flynn and Swisher, 1995). Fossil leaves and pollen collected from the region suggest the area had a cool, wet climate at the time of deposition (Palma-Heldt, 1983; Palma-Heldt and Rondanelli, 1990).

In 2000, two of the authors (JPR, EZ) collected a large fossil mandible in the region of Cerro Tallón, approximately 15 km southeast of the town of Lonquimay. In March 2001, several of the authors returned to prospect for additional fossil mammal localities. Small collections were made from the Río Pedregoso Member of the Cura-Mallín Formation at several other sites, including: the east side of the Río Pedregoso; the north/northeast flank of Cerro Rucañanco; and the southwest flank of Cerro Los Tres Pinos. Preliminary identifications of the unprepared specimens suggest the presence of at least one rodent and one cingulate edentate, in addition to the large notoungulate specimen collected at Cerro Tallón described below. An updated taxonomic list of the mammals known from the Lonquimay region is presented in table 1.

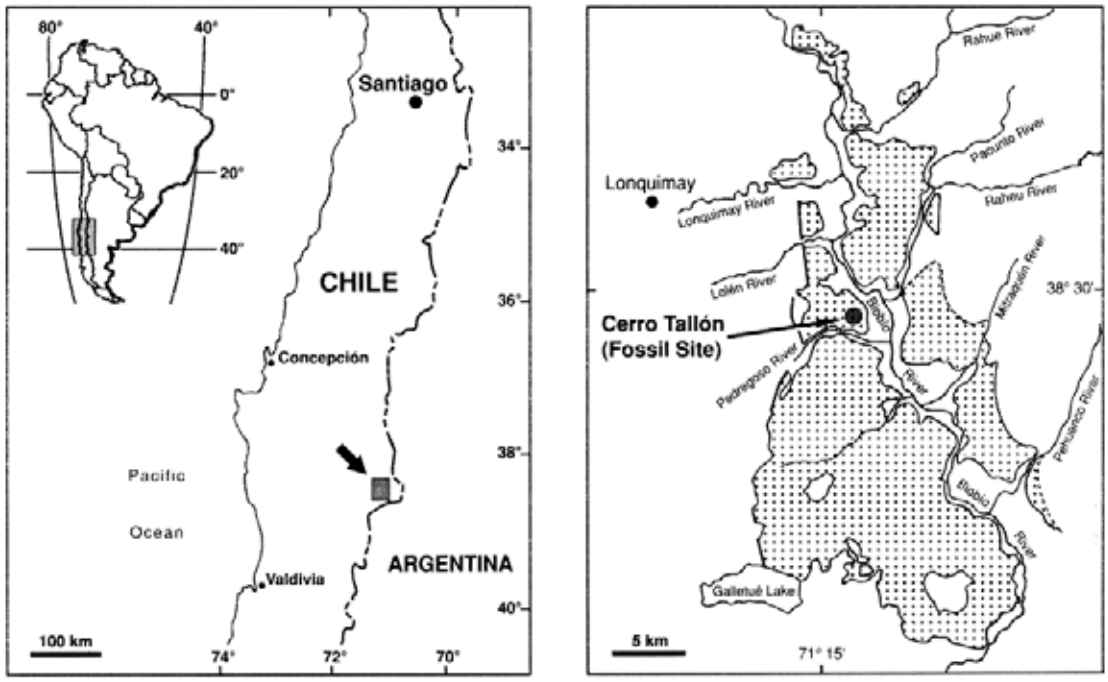


FIG. 1 Map view of the locality of *Nesodon conspurcatus* from Cerro Tallón. Shaded boxes represent inset maps. Stipple pattern in right inset represents surface outcrops of the Río Pedregoso Member of the Cura-Mallín Formation. Figure modified from Azpelicueta and Rubilar (1998) and Suárez and Emparan (1995).

TABLE 1. FOSSIL MAMMAL FAUNA OF THE RÍO PEDREGOSO MEMBER OF THE CURA-MALLÍN FORMATION NEAR LONQUIMAY, CHILE.

Taxon	Source
Edentata	
Glyptodontidae	
gen. et sp. indet.	Suárez *et al.*, 1990
?Rodentia	Suárez *et al.*, 1990
Notoungulata	
Interatheriidae	
Protypotherium sp.	Suárez *et al.*, 1990
?Mesotheriidae	Suárez *et al.*, 1990
Toxodontidae	
Nesodon conspurcatus	Present study
Litopterna	
Macraucheniidae	
gen. et sp. indet.	Suárez *et al.*, 1990
Astrapotheria	
Astrapotheriidae	
Astrapotherium sp.	Marshall *et al.*, 1990

MATERIALS AND METHODS

Upper tooth loci are indicated by upper case letters (*e.g.*, I1, P2, M1) and lower tooth loci by lower case letters (*e.g.*, i1, p2, m1). Terminology for toxodontid molar morphology follows Madden (1990). All measurements were taken to the nearest 0.1 mm using digital calipers. The coefficient of variation (CV) for dental measurements was calculated as: CV=100 x (standard deviation/mean) following Gingerich (1974).

Abbreviations - AMNH, American Museum of Natural History, New York; FMNH, The Field Museum, Chicago; PU, Princeton University Collection (now housed at Yale University, New Haven, Connecticut); SGOPV, vertebrate paleontology collections, Museo Nacional de Historia Natural, Santiago; Ma, megannum; mm, millimeter; cm, centimeter; m, meter; km, kilometer; *s.l.*, *sensu lato*; *s.s.*, *sensu stricto*; SALMA, South American Land Mammal 'Age', an informal biochronologic unit used for intracontinental correlation of fossil mammal faunas.

GEOLOGIC CONTEXT

Thick late Eocene through early-middle Miocene (Wyss *et al.*, 1993, 1994, 1996; Flynn *et al.*, 1995; Suárez and Emparan, 1995; Charrier *et al.*, 1996) volcanic, volcaniclastic, and sedimentary deposits are widely exposed (spanning at least 32.5-43°S) in the Andean Principal Cordillera and the Chilean eastern Central Depression. These deposits accumulated in extensional basins (probably trench-parallel), which subsequently became inverted (Fig. 2; Elgueta, 1990; Vergara *et al.*, 1997; Jordan *et al.*, 2001; Charrier *et al.*, 2002; Radic *et al.*, 2002).

Middle-late Cenozoic strata infilling the Cura-Mallín Basin between 36 and 39°S include the Cura-Mallín, Trapa-Trapa, and Mitrauquén formations in Chile (González and Vergara, 1962; Niemeyer and Muñoz, 1983; Muñoz and Niemeyer, 1984; Emparan *et al.*, 1992; Suárez and Emparan, 1995, 1997). Equivalent deposits on the Argentine side of the Principal Cordillera include the Estratos del Estero Tábanos and Estratos del Arroyo Carbón (Sarris, 1984). The basin is floored by the Jurassic Nacientes del Bio-Bío Formation (Suárez and Emparan, 1997), which correlates with the Cuyo Group of the Neuquén Basin at this latitude (de la Cruz and Suárez, 1997). Mid-late Cenozoic deposits make up two essentially north-south oriented swaths, separated by undeformed Plio-Pleistocene volcanic rocks.

Two contemporaneous, interfingering lithosomes or facies comprise the Cura-Mallín Formation (Burns, 2001; Radic *et al.*, 2002). The volcanic-volcaniclastic facies (Guapitrío and Río Queuco Members) consist of ashfall deposits, pyroclastics, and minor andesitic lavas and hypabyssal bodies (Suárez and Emparan, 1995). The sedimentary facies (Malla-Malla and Río Pedregoso Members) are composed of fluviatile-alluvial sandstones, conglomeratic sandstones and conglomerates, as well as lacustrine siltstones, sandstones, limestones, and coals (Suárez and Emparan, 1995). Based on depositional features, age, and inferred paleoenvironments, Radic *et al.* (2002) suggested the probable existence of at least two sedimentary half-grabens with opposite polarities. These sub-basins, one south of 38°S (with a single depositional cycle, at least 2,600 m thick, 22-8 Ma; Suárez and Emparan, 1995, 1997) and the other north of 38°S (two cycles, 400 m [western margin] to 3,000 m [eastern border] thick, ~26-22 Ma), were tectonically inverted during the late Miocene (Burns and Jordan, 2000; Carpinelli, 2000; Radic *et al.*, 2000), and are separated by an accommodation zone that coincides with Pliocene volcanic activity (Copahue and Callaqui Volcanoes) (Fig. 2). The mandible described here (SGOPV 5226), was collected from the western border of the southern sub-basin of the Cura-Mallín Basin, within the sedimentary facies of the Cura-Mallín Formation (Río Pedregoso Member). The sedimentary series from which the new fossil derives is described below (Fig. 3).

The lower part of the stratigraphic column consists of a 500 m thick series of fluviatile-alluvial sandstones, conglomeratic sandstones (with argillaceous matrix), and water-deposited tuffs. The

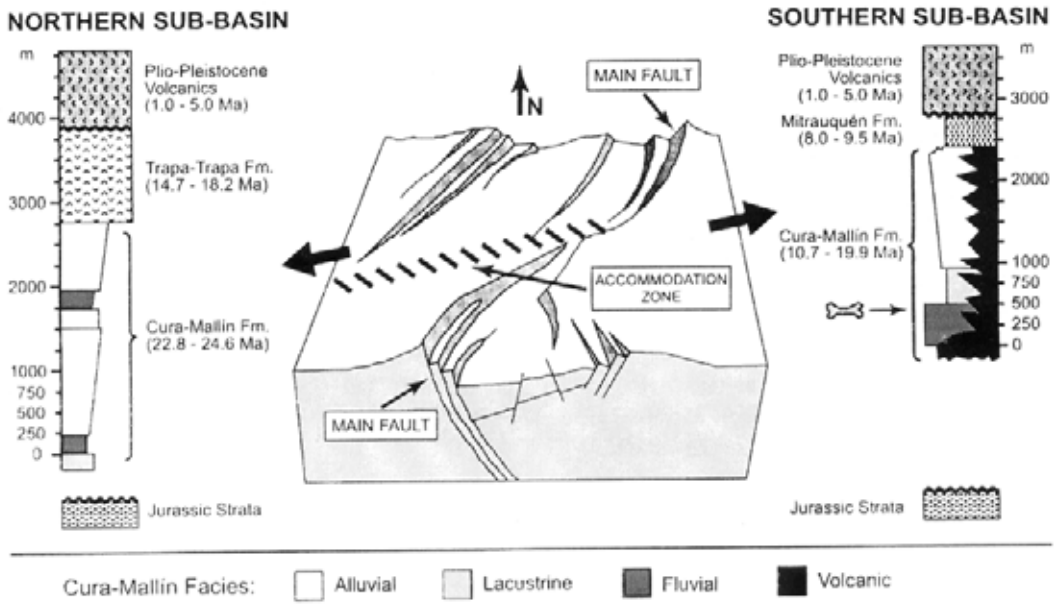
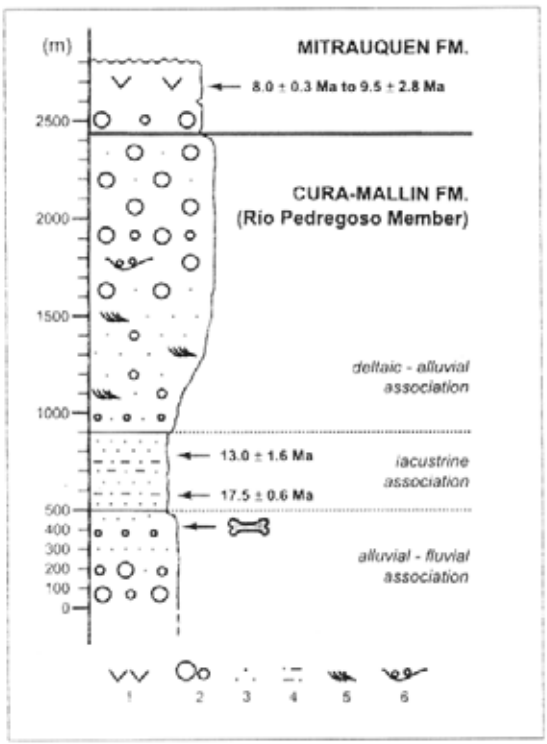


FIG. 2. Tectono-sedimentary model of the north-south trending Oligo-Miocene extensional basin between 37 and 39°S; two compartments are developed, separated by an oblique accommodation zone. Synthetic stratigraphic columns for each compartment are also represented. The volcanic facies of the Cura-Mallín Formation (corresponding to the Guapitrío Member; Suárez and Emparan, 1995, 1997), that underlies and laterally interfingers with the sedimentary facies from the west, has been dated near its base at 20.3, 19.9 and 19.1 Ma. The bone symbol indicates the stratigraphic position of the *Nesodon* mandible described in this paper (SGOPV 5226). The figure is based on Radic *et al.*, 2002.



volcanic composition of the clasts, and the argillaceous matrix, indicate that these sediments were transported by moderate energy rivers draining a volcanic source area. The mandible was collected near the top of this lower part of the section, in a 5 m thick series of green, fine to coarse-grained, montmorillonite-rich sandstones, with thin tuffaceous intercalations.

The middle part of the section is a 400 m thick lacustrine sequence, consisting of a series of 15-20

FIG. 3. Stratigraphy of the Río Pedregoso Member of the Cura-Mallín Formation based on exposures in the Río Pedregoso Valley (the eastern flank of the north-south oriented portion of the valley), and at Cerro Tallón (immediately north of the exposures in the Río Pedregoso Valley). Radiometric dates (K-Ar) are from Suárez and Emparan (1995, 1997). Dates for the Mitrauquén Formation represent the range of dates reported for the formation. The bone symbol indicates the stratigraphic position of the *Nesodon* mandible described in this paper (SGOPV 5226). Key to lithologic symbols: **(1)** lava; **(2)** conglomerate; **(3)** sandstone; **(4)** siltstone; **(5)** cross-bedding; **(6)** paleochannel.

cm thick, gray mudstone layers, alternating with thin tuffaceous, sandstone, and stromatolitic layers. Some sandstones are tuffaceous, whereas others are calcareous, bioclastic, stromatolitic, or oolitic (these latter sandstones contain brackish-water ostracodes, pelecypods, and gastropods).

The upper part of the stratigraphic column is 1,600 m thick; it coarsens upward, and can be subdivided into three portions. The lower portion consists of alternating sandstones and thin calcareous mudstones with gastropod remains; it is interpreted to have been deposited in a shallow lacustrine environment and in deltaic fans. The middle portion consists of lithic sandstones, with white vitroclastic tuffs, and tuffaceous sandstone intercalations. The sandstones are cross-bedded and some horizons contain carbonized vegetation, silicified logs, and gastropod fragments. The depositional environment corresponds to a delta prograding over lacustrine facies. The upper portion contains cross-bedded sandstones, tuffaceous breccias, tuffs, and conglomeratic sandstones (containing andesitic, and minor angular tuff, clasts). This interval was likely deposited in an alluvial channel system.

The Río Pedregoso Member is overlain (apparently conformably) by the late Miocene conglomeratic and volcanic Mitrauquén Formation (see Fig. 3).

SYSTEMATIC PALEONTOLOGY

Notoungulata Roth, 1903
Toxodontia Owen, 1853
Toxodontidae Gervais, 1847
Nesodontinae Murray, 1866
***Nesodon* Owen, 1846**

Nesodon conspurcatus Ameghino, 1887

Material: SGOPV 5226, a partial left mandible preserving the base of the third incisor and nearly complete p3-m3 (Fig. 4).

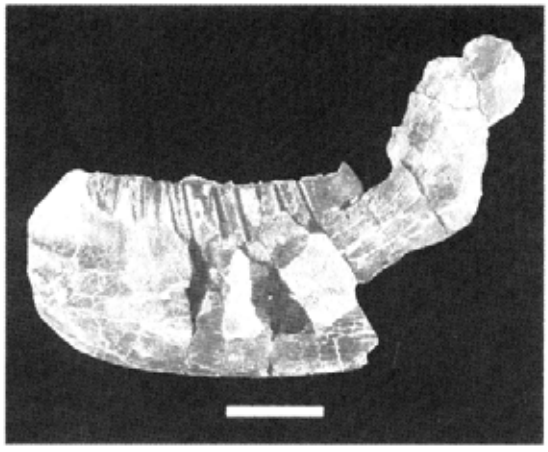


FIG. 4. Photograph of left mandible of *Nesodon conspurcatus* (SGOPV 5226) in lateral view. Scale bar equals 5 cm.

Locality: the northern slope of Cerro Tallón, above the western bank of the Biobío River, approximately 15 km southeast of Lonquimay (Fig. 1). Lower part of the Río Pedregoso Member, Cura-Mallín Formation, Cura-Mallín Basin, Chile. Santacrucian SALMA (see below).

Description: SGOPV 5226 consists of a partial left mandible that has been partially prepared. Most of the horizontal ramus is preserved in addition to part of the ascending ramus. The alveolar and inferior margins are roughly parallel, with the depth of the mandible averaging approximately 75 mm. The symphysis is short and unspecialized, bearing a shallow digastric fossa.

In anterior view, i3 is plainly visible in cross section (Fig. 5). It is a strongly procumbent, hypselodont (ever-growing) tooth, sub-triangular in shape. Its longitudinal axis is nearly aligned with that of the mandibular ramus. The greatest dimension of the tooth is 30 mm (as measured from the ventromedial to the dorsolateral corner); it measures 16 mm perpendicular to this maximum dimension. The mandible is expanded laterally at the base of the i3 to accommodate the tooth's large size, and a

FIG. 5. Camera lucida drawing of the root of i3 of *Nesodon conspurcatus* (SGOPV 5226) in anterior view. Scale bar equals 5 mm.

large mental foramen is present just posterior to this expansion. A smaller foramen is present directly below the juncture of p4 and m1 on the external surface of the mandible.

Five cheek teeth are preserved, the last two premolars and all three molars (Fig. 6). Although none is in perfect condition, most have lost only small sections of the occlusal surface, allowing occlusal outlines to be interpreted clearly. All teeth are fully erupted and have undergone moderate wear, indicative of a fully mature animal. The teeth are very hypsodont (Hypsodonty Index (HI = crown height / crown length) for m1 = 2.2) with thick labial enamel, thin to absent lingual enamel, and a very thin layer of cementum irregularly covering all external surfaces. Measurements are provided in table 2.

The cheek teeth exhibit simplified occlusal surfaces and prominent hypoflexids (buccal enamel folds). A central fossa is present in p4 and m1, the result of isolation of the lingual meta-entoconid fold. This area is not preserved in p3 nor in m2 and the fold is still patent in m3. A single talonid fossettid is present in m1, the remnant of the lingual ento-hypoconid fold. This fossettid and an additional accessory fossettid (located more anteriorly) are present in m2. Only the accessory fossettid is present in m3, the broad ento-hypoconid fold showing no indication of closure.

DISCUSSION

Based on the specimen's large size, procumbent and tusk-like i3, very high-crowned cheek teeth, limited cementum, and derived reduction of enamel along the lingual portions of the molars, the specimen can confidently be referred to the Toxodontidae (Madden, 1990; Cifelli, 1993; Nasif *et al.*, 2000). The unspecialized morphology of the mandibular symphysis and the presence of two lingual folds plus an accessory fossettid in the lower molars excludes the specimen from all traditional toxodontid 'subfamilies' other than the basal, likely paraphyletic, Nesodontinae (Madden, 1990, 1997; Nasif *et al.*, 2000).

Three major taxa are generally recognized within the Nesodontinae: *Proadinotherium*, *Adinotherium*, and *Nesodon* (Madden, 1990, 1997; Cifelli, 1993; Nasif *et al.*, 2000). The Cerro Tallón specimen differs from *Proadinotherium* in having more hypsodont cheek teeth (in *Proadinotherium* HI ranges from 0.5 to 1.0). Additionally, it is comparable to *Nesodon*, and differs from both *Proadinotherium* and *Adinotherium*, in having a reduced enamel band along the labial face of m1 (comprising 58% of crown length in the Tallón specimen versus more than 65% crown length in *Proadinotherium* and *Adinotherium*; Madden, 1990) and the external face of m1 talonid flattened and sharply angled posteriorly (it is smoothly convex in *Proadinotherium* and *Adinotherium*; Madden, 1990). Since both *Proadinotherium* and *Adinotherium* are small-bodied, the relatively large size of the Cerro Tallón specimen further supports its referral to *Nesodon*.

In his revision of *Nesodon*, Scott (1912) recognized three species: *N. imbricatus, N. cornutus,* and *N. conspurcatus*. *Nesodon imbricatus* is the most common of the three and numerous specimens (including nearly complete skeletons) have been referred to it. In contrast, *N. cornutus* is known only from its holotype, a nearly complete skull with heavily damaged teeth. It is distinguished from *N. imbricatus* by its unusually high occiput and the possible presence of a dermal horn. *N. conspurcatus* was

FIG. 6. Photograph (above) and camera lucida drawing (below) of left p3-m3 of SGOPV 5226 in occlusal view. Anterior is to the right. Scale bar equals 1 cm.

TABLE 2. MEASUREMENTS OF LOWER TOOTH DIMENSIONS FOR SELECTED SPECIMENS OF *NESODON* AND *ADINOTHERIUM* (TOXODONTIDAE: NESODONTINAE).

		p3		p4		m1		m2		m3	
Specimen	**Taxon**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SGOPV 5226 (Cerro Tallón)	Unknown	17.8	10.1	21.1	12.1	24.0	11.9	(28.8)	(12.2)	37.9	11.4
FMNH P13069	*N. imbricatus*	19.4	12.6	22.1	15.5	30.5	15.7	35.6	16.3	53.0	18.5
FMNH P13079	*N. imbricatus*	20.9	11.7	25.1	15.4	29.6	15.3	37.1	16.0	46.9	15.7
FMNH P13084	*N. imbricatus*	19.3	14.7	22.7	16.7	26.8	16.7	35.9	17.4	56.8	18.0
FMNH P13091	*N. imbricatus*	21.8	14.0	25.9	15.2	30.7-	14.9	35.3	15.6	45.8	14.7
FMNH UC1330	*N. imbricatus*	21.4	14.5	23.1	15.4	29.6	16.1	36.4	15.7	55.4	16.0
PU 15492*	*N. imbricatus*	18	15	21	16	27	15	34	16.5	52	17.5
PU 15000*	*N. imbricatus*	21	14.5	25	17	31	16.5	38	17	60	17
PU 15336*	*N. imbricatus*	23	12.5	25	14	31	15	34	15	49	14
PU 15969*	*N. imbricatus*	21.5	16	26	18	29	18.5	36	16	55	15
PU 15256*	*N. imbricatus*	22	16	26	18	29	18	38.5	19.5	66	20
PU 15487*	*N. imbricatus*	17	14	19	15.5	-	-	32	20	73	16
'Acrotherium patagonicum' **	*N. conspurcatus*	-	-	23.0	10.0	27.0	11.0	-	-	-	-
*Nesodon 'rutimeyeri'***	*N. conspurcatus*	18.0	8.5	24.0	9.5	25.0	9.7	-	9.0	-	-
*'Nesotherium carinatum'***	*N. conspurcatus*	18.0	9.0	20.8	8.0	25.0	11.7	29.0	12.0	34.0	11.5
*'Nesotherium elegans'***	*N. conspurcatus*	16.0	12.0	19.0	12.7	23.0	12.4	26.5	11.9	-	12.0
FMNH P12066	*A. ovinum*	11.8	6.1	12.5	6.5	14.2	6.5	17.2	7.1	23.1	7.2
FMNH P13104	*A. ovinum*	9.9	7.1	11.4	8.3	15.0	7.9	17.9	9.6	29.0	8.4
FMNH P13113	*A. ovinum*	12.0	6.4	13.2	6.9	17.2	6.8	19.9	8.0	21.5	7.0
FMNH P13229	*A. ovinum*	-	-	13.1	9.4	15.6	9.6	20.4	10.6	31.2	9.6
PU 15131*	*A. ovinum*	11	7	12.5	8	14	8	18.5	-	30	8
PU 15136*	*A. ovinum*	12	7.5	13.5	7	16	8	19	-	25	8
PU 15003*	*A. ovinum*	10	7	11.5	7.3	14.5	7	17	-	23.5	7
AMNH 9532*	*A. robustum*	-	-	-	-	-	-	21	-	31	9

* Data from Scott, 1912; ** Data from Mercerat, 1891.

originally described by Ameghino (1887) based on a single specimen, a series of five maxillary teeth. Subsequently, Scott (1912) considered ten other taxa junior synonyms of *N. conspurcatus*, significantly increasing the number of referred specimens. This species is distinguished from *N. imbricatus* and *N. cornutus* by its smaller size.

The question of how to distinguish sympatric fossil species based solely on size has been a topic of significant controversy, and no standard by which to do so has been generally recognized (Martin and Andrews, 1993). Two commonly employed methods are bivariate plots and the coefficient of variation (CV; Gingerich, 1974).

A bivariate plot of lower tooth dimensions for *N. imbricatus*, *N. conspurcatus*, and *Adinotherium* is presented in figure 7. The figure clearly demonstrates that specimens of all three species plot in distinct, non-overlapping clusters, thereby supporting Scott's recognition of at least two species of *Nesodon*. No tooth size data were available for the poorly preserved, single specimen of *N. cornutus*, but published descriptions suggest it to be similar to smaller specimens of *N. imbricatus* (Scott, 1912). The Cerro Tallón specimen plots within the cluster of specimens referred by Scott (1912) to *N. conspurcatus*, suggesting it pertains to that species.

Recognition of at least two species of *Nesodon* is further suggested by coefficients of variation calculated for a combined sample of *N. imbricatus* plus *N. conspurcatus*. Among modern taxa, single species CV values for m1 length rarely exceed 8.0 (Plavcan, 1993) and dental CV values in general rarely exceed 10.0 (Gingerich, 1974; Cope, 1993; Plavcan, 1993). The CVs computed for *Nesodon* are 9.1 for m1 length and 17.7 for m1 width, suggesting that the combined sample likely includes at least two species. Although the presence of high CVs at additional tooth positions would lend further support to a multiple-species hypothesis for *Nesodon* (Cope, 1993), the lack of necessary data for *N. conspurcatus* precludes such calculations for a combined sample. Based on the bivariate analysis and CV data, the specimen from Cerro Tallón is referred to *N. conspurcatus*.

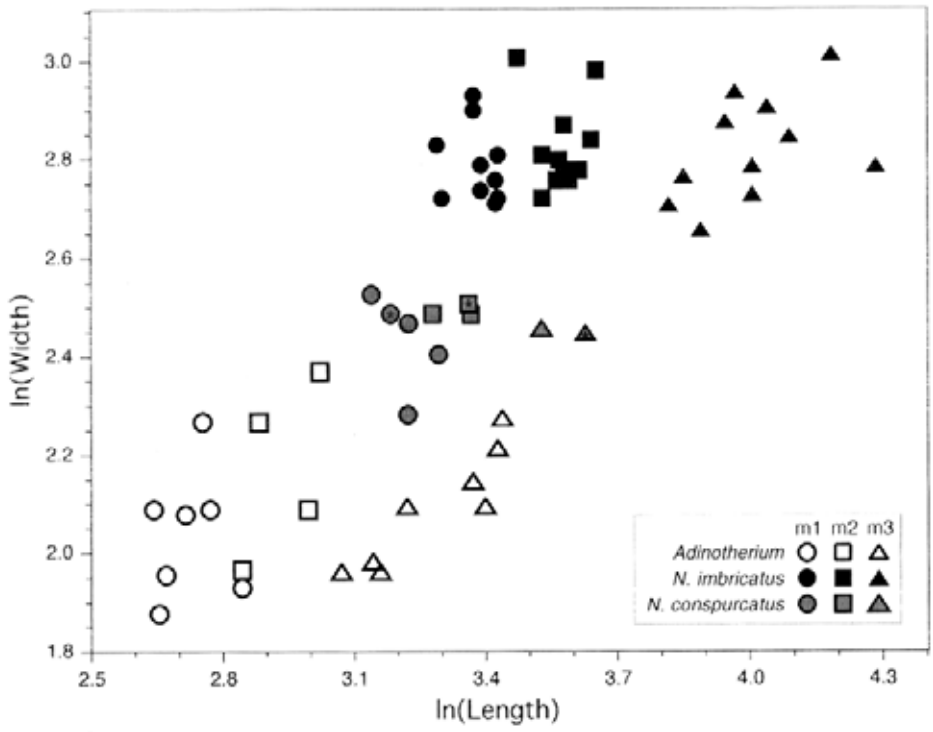


FIG. 7. Bivariate plot of log-transformed lower molar dimensions for various specimens of *Adinotherium*, *Nesodon imbricatus*, and *Nesodon conspurcatus*. Teeth from the Cerro Tallón specimen (SGOPV 5226) are denoted by an asterisk (*).

CONCLUSIONS

Nesodon is best known from the rich Santacrucian (late early Miocene) deposits along the Atlantic coast of Patagonia (Fig. 8; Scott, 1912). The taxon has also been listed as occurring at Río Frías (= Río Cisnes) in southern Chile (the type locality for the 'Friasian' SALMA, *sensu stricto*) and the Río Collón-Curá in Neuquén Province, Argentina (Colloncuran SALMA) (Bondesio *et al.*, 1980). In his detailed revision of *Palyeidodon* and other early to middle Miocene toxodontids, however, Madden (1990) lists *Nesodon* as restricted to the Santacrucian SALMA, and *Palyeidodon as* restricted to the middle Miocene 'Friasian' (*sensu stricto*; ?16.5-?15.5 Ma) and Colloncuran (15.5 -14.0 Ma) SALMAs.

Apart from the Chucal Fauna of northern Chile (Charrier *et al.*, 1994, 2000; Flynn *et al.*, 1999, 2002a; Croft *et al.*, in press), reports of *Nesodon* outside of Patagonia are poorly substantiated. Douglas (1914) collected a mandibular symphysis from the Bolivian Altiplano that was later identified by Dr. C.W. Andrews as *Nesodon*, but this fragmentary specimen was not figured and has not been conclusively relocated (R. Madden, oral communication, 2000). Schaub (1935) reported '?*Nesodon* spec.' from the 'La Vela Series' near San Juan, Venezuela, but the identification was based only on the semilunar notch of an ulna. C. de Paula Couto described *Nesodon imbricatus* from several localities along the Rio Juruá of Acre, Brazil based on isolated incisors, a partial upper M2, a partial ulna, and a portion of the occipital region of the skull (de Paula Couto, 1981, 1982). However, the partial M2, likely the most diagnostic of the specimens, differs significantly from typical *Nesodon imbricatus* from Patagonia; the molar is very narrow for its length (in spite being from an mature individual) and exhibits accessory fossettes, a feature that has not been previously recorded in *Nesodon*. The unusual morphology of M2 and the fragmentary nature of the other specimens do not convincingly support their assignment to *Nesodon imbricatus*.

Within Chile, *Nesodon* has been reported from the Altiplano Chucal Fauna (see above) and the Patagonian Pampa Castillo Fauna from the Meseta Guadal south of Lago General Carrera (Flynn *et al.*, 2002b), in addition to Cerro Tallón. All of these occurrences appear to be Santacrucian in age. The Chucal Fauna, in addition to including many typical Santacrucian taxa, is constrained by radioisotopic dates between approximately 21.5 and 17.5 Ma (Bond and García, 2002; Charrier *et al.*, 2002; Croft *et al.*, in press); it thus likely represents an early Santacrucian fauna, potentially extending the age range of that SALMA. Pampa Castillo, while not constrained by radioisotopic dates, includes a diverse mammal fauna (at least 36 species) permit-

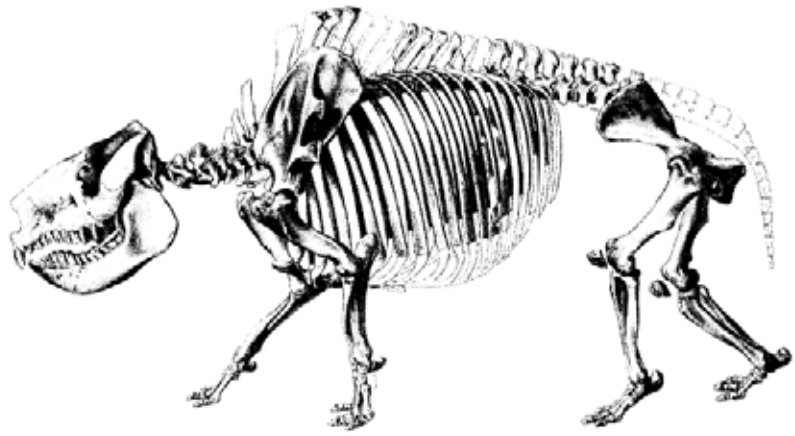


FIG. 8. Restoration of the skeleton of *Nesodon imbricatus* (from Scott, 1912, Plate XII), a close relative of *Nesodon conspurcatus*. In life, the animal would have been approximately the size of a domestic cow (*Bos taurus*).

ting a confident biostratigraphic correlation with Santacrucian faunas of Argentine Patagonia (Flynn *et al.*, 2002b). Fossil mammals previously collected from a variety of levels within the Cura-Mallín Formation near Lonquimay (*e.g.*, *Astrapotherium*; Marshall *et al.*, 1990) also suggested the fauna is referable to the Santacrucian SALMA.

At Lonquimay, the middle part of the Río Pedregoso Member (*i.e.*, lacustrine association; Fig. 3) ranges in age between 13 and 17.5 Ma (Suárez and Emparan, 1995, 1997). Although the base of the Río Pedregoso Member has not been dated directly, interfingering of this unit with the Guapitrío Member (a laterally equivalent facies) suggests that it extends no older than approximately 20 Ma (Suárez and Emparan, 1995, 1997). The Cerro Tallón specimen of *Nesodon conspurcatus* was collected from near the top of the lower part of the Río Pedregoso Member (*i.e.*, alluvial-fluvial association), suggesting an age slightly older than 17.5 Ma and younger than 20 Ma.

Flynn and Swisher (1995) estimated the Santacrucian SALMA to span approximately 17.5-16.0 Ma. The presence of *Nesodon* (a typical Santacrucian mammal; see below) in strata slightly older than 17.5 Ma both at Cerro Tallón and at Chucal suggests that the Santacrucian SALMA may extend slightly older than previously believed (see also Croft *et al.*, in press). Since no terrestrial mammal faunas have been shown to conformably underlie Santacrucian faunas, this age revision is not surprising.

Simpson (1980, p. 146) noted that Santacrucian faunas, although extremely rich and well-preserved, were 'known only from a limited region in southern Patagonia'. The series of new Chilean faunas greatly expands the geographic distribution and knowledge of assemblages assigned to this SALMA. The resemblance of the Pampa Castillo Fauna of southern Chile to traditional Santacrucian assemblages of Argentina suggests a relatively homogenous habitat across all of Patagonia in the late early Miocene; on the other hand, the unusual taxonomic composition of the Chucal Fauna of northern Chile suggests that significant South American provinciality had developed by this time (Flynn, 2002; Flynn *et al.*, 2002a, in press; Croft *et al.*, in press).

Nesodon does not occur in the type Friasian assemblage at Río Frías/Cisnes in the Chilean Patagonia; in contrast, *Palyeidodon* is present in both Friasian deposits in Chile and slightly younger Colloncuran SALMA deposits in northwest Argentina (Madden, 1990). The widespread geographic distribution of *Nesodon* during the Santacrucian SALMA (from 18 to 47° within Chile, and to higher latitudes within Argentine Patagonia), its restricted temporal range (Santacrucian SALMA only), and its general abundance ('by far the commonest [of Santa Cruz ungulates]'; Scott, 1912, p. 118) suggest that *Nesodon* may be one of the most useful indicator taxa for Santacrucian age faunas throughout much of South America. Moreover, the contrasting temporal occurrences of *Nesodon* (late early Miocene) and *Palyeidodon* (middle Miocene) provide further evidence for a faunal distinction between the Santacrucian and Friasian SALMAs, suggested by some workers (*e.g.*, Marshall, 1990, Marshall and Salinas, 1990) to be coeval. Although Bond and García (2002) reported ?*Palyeidodon* sp. from the Chucal Formation of northern Chile (Santacrucian SALMA), the specimen they describe does not appear to pertain to *P. obtusum*, the only species of *Palyeidodon* currently recognized (Madden, 1990; Bond and García, 2002; Croft *et al.*, in press). Until this specimen's specific identity and phylogenetic relationship to *P. obtusum* are determined, its bearing on the temporal range of *Palyeidodon* is uncertain.

The Cerro Tallón specimen thus represents the third report of *Nesodon* from Chile (and second definitive occurrence of the taxon outside of Patagonia), and the first identification of *N. conspurcatus* outside of high latitude Patagonia.

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