

## Recent Additions to Knowledge of Tertiary Mammals from the Chilean Andes

Darin A. Croft<sup>a</sup>, Reynaldo Charrier<sup>b</sup>, John J. Flynn<sup>c</sup>, and André R. Wyss<sup>d</sup>

<sup>a</sup>Dept. of Anatomy, Case Western Reserve U., Cleveland, Ohio, [dcroft@case.edu](mailto:dcroft@case.edu); <sup>b</sup>Dpto. de Geología, U. de Chile, Santiago, [rcharrie@cec.uchile.cl](mailto:rcharrie@cec.uchile.cl); <sup>c</sup>Div. of Paleontology, American Museum of Natural History, New York, [jflynn@amnh.org](mailto:jflynn@amnh.org); <sup>d</sup>Dept. of Earth Science, U. of California – Santa Barbara, California, [wyss@geol.ucsb.edu](mailto:wyss@geol.ucsb.edu)

### Background

The physiognomy of Chile is dominated by the Andes, the longest terrestrial mountain chain on Earth. In hindsight, given the vast exposures of stratified rocks across the range, it is remarkable that the rich fossil record of mammals in Chile remained virtually unrecognized until about 20 years ago. Our ongoing US-Chilean collaboration continues to dramatically correct this oversight, the record of Tertiary mammals now known from Chile being among the best in South America. In total we have recovered more than 2,300 specimens from some two dozen localities, spanning some 30 degrees of latitude and ranging in age from approximately 10 to 40 million years (late Eocene through late Miocene, Casamayoran through ?Chasicuan South American Land Mammal “Ages” – SALMAs; Fig. 1). Most of these specimens have been recovered from volcanoclastic sediments of the Abanico (= Coya-Machali) Formation that were deposited as distal ignimbrites or debris flows. Because of this unusual mode of preservation, these fossils are generally exceptionally well-preserved in terms of completeness and anatomical detail. We here provide an overview our fieldwork, highlighting some of our most significant past and ongoing investigations.

### Late Eocene (Casamayoran and Mustersan SALMAs)

One of the oldest Tertiary mammal faunas from Chile is that of Tapado, originating from the Tinguiririca River Valley ca. 14 km northwest of localities that produced the earliest Oligocene Tinguiririca Fauna<sup>1,2</sup>. No associated radioisotopic dates have yet been reported for this locality, but samples are currently being analyzed. Most of the several dozen specimens collected from this area have now been prepared and only endemic ungulates have been identified. These include cf. *Ernestokokenia* (a didolodontid “condylarth”), cf. *Notonychops* (potentially a basal notoungulate), and four notoungulates: *Notostylops* sp. (Notostylopidae), *Ignigena minisculus*, (Interatheriidae), *Eohyrax* sp. (Hegetotheria), and *Pleurostylodon* sp. (Isotemnidae). These indicate a general correspondence to the Casamayoran SALMA, suggesting a late Eocene age of at least 38 Ma and possibly substantially older, as the extent of the Casamayoran is currently poorly constrained<sup>3-6</sup>. Numerous additional specimens that likely pertain to the Tapado Fauna were recovered in 2006, ~1-2 km northwest of and slightly higher stratigraphically than the localities originally producing this fauna.

An interatheriid notoungulate rostrum assignable to *Antepithecus brachystephanus* was recovered from the Azufre River valley, a major northern tributary of the Tinguiririca, in the 1990s<sup>1,2</sup>. This taxon otherwise is known only from the Casamayoran of Argentina, suggesting that some Azufre strata temporally overlap those from Tapado, at least in part. The recovery of many additional specimens from several sites in the Azufre region in 2008 will permit a refined age assessment of this newly identified fauna.

A remarkably thick and fossiliferous sequence occurs in the western reaches of Río Teno (the major drainage immediately south of Tinguiririca), with at least three stratigraphically superposed faunas represented<sup>7</sup>. Although collected only recently (and thus not yet studied), it is clear that the oldest of these faunas predates the Tinguirirican SALMA, and thus too is Eocene in age.

## Oligocene (Tinguirirican and Deseadan SALMAs)

One of the most important – and certainly the best known – Chilean fossil mammal assemblage is the Tinguiririca Fauna from near Termas del Flaco (35° S, 70° W)<sup>5, 8-10</sup>. More than 350 specimens have been collected from the locality since its discovery in 1988, representing two dozen species of native ungulates, marsupials, xenarthrans, and rodents. The two rodent species are noteworthy in being the earliest recorded members of that clade in South America<sup>5, 8, 10, 11</sup>. Approximately half of the species from this locality have been described in detail<sup>12-17</sup>; current systematic efforts focus on the fauna's four notohippids, including two hypsodont (high crowned) and two brachydont (low crowned) forms<sup>18</sup>.

The Tinguiririca Fauna differs dramatically from geologically older South American faunas in its high proportion of hypsodont mammals; such a transition does not occur on other continents until 10-15 million years later<sup>5, 11</sup>. The well-preserved specimens from Tinguiririca have permitted a variety of analyses focused on habitat inference, and these suggest that the mammals of Tinguiririca were living in an environment with relatively few trees and abundant open areas<sup>5, 10, 19</sup>.

*Johnbell hatcheri*, a recently described interatheriid notoungulate, occurs both at Tinguiririca and in a fauna from the Río Cachapoal, approximately 100 km to the north<sup>2</sup>. The presence of the Tinguirirican archaeohyracids *Archaeotypotherium* and *Protarchaeohyrax*<sup>10</sup>, in addition to *Johnbell hatcheri*, suggests that the fossils from Cachapoal are Tinguirirican in age – at least in part. Other taxa recorded at Cachapoal include the marsupial *Polydolops mckennai*<sup>20</sup>, additional notoungulates, several xenarthrans, and at least one rodent. A trachytheriine mesotheriid from Cachapoal – along with another from Rocas Bayas in Argentina – represents the earliest record of this notoungulate clade<sup>10</sup>.

Two assemblages from the Río Maipo drainage (east of Santiago and north of Río Cachapoal) likely are Tinguirirican and/or Deseadan in age. The earlier discovered of these includes the interatheriid *Santiagorothia* and an archaeohyracid. Few specimens from the more recently discovered assemblage have been prepared, but it is clear that typothere notoungulates and rodents predominate, and that armadillos are also present; the abundance of rodents suggests a post-Tinguirirican age.

## Miocene (Colhuehuapian, Santacrucian, and younger SALMAs)

More than two hundred specimens (mostly typothere notoungulates and rodents) have been collected from the Las Leñas region, approximately 60 km north-northeast of Termas del Flaco. Notable among these is the platyrrhine primate *Chilecebus carrascoensis*, represented by a complete skull<sup>21</sup>. An associated <sup>40</sup>Ar/<sup>39</sup>Ar radioisotopic date of 20.09 +/- 0.27 Ma indicates a Colhuehuapian age for *Chilecebus*, making this specimen the oldest well-preserved and well-dated South American primate cranium. Using new platyrrhine-specific equations, the body mass of *Chilecebus* is now estimated to be slightly less than 600 g, giving *Chilecebus* an EQ of 1.11, smaller than any living anthropoid and indicating independent brain expansion for the Old and New World anthropoid clades<sup>22</sup>. The bulk of the Las Leñas fauna is likely Colhuehuapian in age, although a component may be slightly older.

Colhuehuapian mammals also have been collected from several localities from the Cura-Mallín Formation in the Laguna del Laja region of Biobío province (37.5° S, 71° W). These are the oldest fossils from the area, with Santacrucian through ?Chasicuan taxa having been recovered from younger levels. SALMA assignments for these faunas are supported by a detailed stratigraphic framework<sup>23</sup> and a series of <sup>40</sup>Ar/<sup>39</sup>Ar dates spanning 20-9 Ma<sup>24</sup>. In total, more than 250 specimens have been collected from the nearly 2 km thick stratigraphic sequence. Laguna del Laja thus records a nearly unparalleled succession of mammal faunas from a continuous stratigraphic sequence spanning at least 4-5 SALMAs<sup>24</sup>.

Among the mammals from Laguna del Laja, rodents have received the greatest attention. They are notable for their high degree of endemism, with all twenty taxa representing new species<sup>25, 26</sup>. Notoungulates are also common, with four families represented: Hegetotheriidae (including both Hegetotheriinae and Pachyrukhinae), Intertheriidae, Toxodontidae, and Leontiniidae. Several dasypodid specimens have been collected, as well as a pair of mandibles of the mylodontid sloth *Nematherium*. Marsupials are relatively rare, with only a sparassodont (aff. *Sipalocyon*) and an abderitid identified thus far.

A small number of early Miocene mammals, birds, and other vertebrates have been collected from the Cura-Mallín Formation about 100 km south of Laguna del Laja in the area of Lonquimay<sup>27</sup>. The presence of *Nesodon conspurcatus* suggests a Santacrucian age for fossils derived from the lower part of the Río Pedregoso Member<sup>27</sup>, and a radioisotopic date of 17.5 +/- 0.6 Ma just above the site where this fossil was collected suggests an absolute age similar to that of Chucal (see below). Other mammals from various localities across the region include an astrapothere (?*Astrapotherium*<sup>28</sup>), the intertheriid *Protypotherium*, a glyptodontid, and a macraucheniid litoptern<sup>29</sup>.

Pampa Castillo, our southernmost fossiliferous locality (47° S, 72-73° W), derives from a thick sequence of fluvial beds in the southern Andes south of Lago General Carrera. These strata contrast with the primarily volcanoclastic layers of the Abanico and Cura-Mallín formations in central Chile, and in this regard the fauna is more similar to classic mammal-bearing localities in Patagonian Argentina than to most other Chilean faunas. The softer fossil-bearing sediments have allowed many of the nearly 300 specimens from there to be prepared, and 36 species have been identified<sup>30</sup>. The fauna is Santacrucian in age, and it is broadly similar to late early Miocene faunas from the coast of Santa Cruz province, Argentina.

The Chucal Fauna from the Chilean Altiplano resembles that of Pampa Castillo in being derived from fluvo-lacustrine rather than volcanoclastic strata<sup>31</sup> and in pertaining to the Santacrucian SALMA. It contrasts with Pampa Castillo in its high degree of endemism; approximately 50% of species are new<sup>32-34</sup>. This endemism no doubt is partly attributable to its location in extreme northern Chile (19° S, 69° W), more than 3,000 km north of Pampa Castillo and classic Santacrucian localities. The fauna is bracketed by radioisotopic dates indicating an age of between 17.5 and 18.8 Ma. Most of the 18 species present in the fauna now have been described, including seven notoungulates (toxodontids, mesotheriids, and a hegetotheriid), a litoptern (*Theosodon*), and three cingulate xenarthrans (a dasypodid, a peltephilid, and a glyptodontid)<sup>33-35</sup>. The three mesotheriids and the glyptodontid (*Parapropalaeohoplophorus septentrionalis*) are basal members of their respective clades, suggesting that the intermediate latitudes might have been important centers of origin/diversification for these groups<sup>33, 34</sup>. The rodents are currently under study, but the most abundant species – a chinchilline chinchillid – extends the fossil record of this subfamily back some 15 million years and also underscores this region as a center of diversification for major groups<sup>32</sup>.

Mesotheriids are the only Tertiary fossil mammals known from the Precordillera of northernmost Chile, being represented by *Caragatypotherium munozi* from the mid-late Miocene (~10-12 Ma) Huaylas Formation near Caragua<sup>36</sup>. Their rarity in coeval higher latitude and tropical assemblages, but commonness in the Bolivian and Chilean Altiplano, further emphasizes the biogeographic distinctiveness of this region.

Several faunas from the Abanico Formation south of Termas del Flaco may pertain to the Colhuehuapian and/or Santacrucian SALMAs. Investigations are ongoing, but preliminary study has revealed that small marsupials, several notoungulates clades, a litoptern, several species of rodents, various armadillos, and sloths are present.

Summary

In the span of two decades, the Andean Main Range of Chile – once regarded as barren of terrestrial vertebrate fossils – is now recognized as one of the continent’s greatest archives of Cenozoic mammal evolution. Recent discoveries have filled numerous geographic and temporal gaps in the South American mammal record, and have permitted the recognition of a new SALMA (the Tinguirirican). These paleontological discoveries also have greatly clarified the chronology of the post-Neocomian Andean cover rock sequences, thus illuminating the geologic history of this intensively studied mountain range in the process. Moreover, the volcanic nature of these sequences provides an unparalleled opportunity to calibrate the SALMA succession.

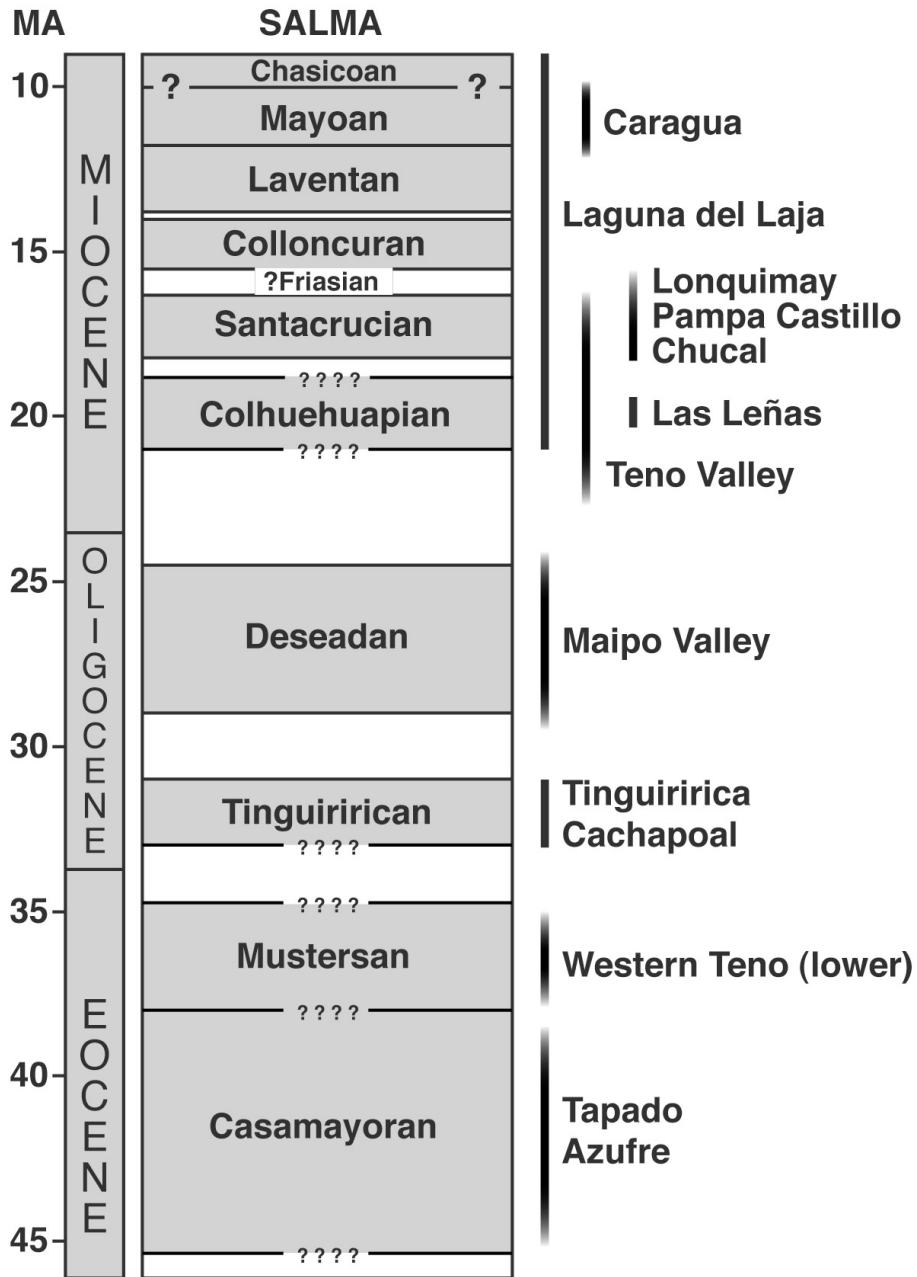


Figure 1: Ages of fossil mammal assemblages discussed in the text. SALMA sequence is based on (3) as modified by (10).

## REFERENCES

1. Flynn, J. J., D. A. Croft, R. Hitz, and A. R. Wyss. 2005. The Tapado Fauna (?Casamayoran SALMA), Abanico Formation, Tinguiririca Valley, central Chile. *Journal of Vertebrate Paleontology* 25:57A.
2. Hitz, R., J. J. Flynn, and A. R. Wyss. 2006. New basal Interatheriidae (Typotheria, Notoungulata, Mammalia) from the Paleogene of central Chile. *American Museum Novitates* 3520:1-32.
3. Flynn, J. J., and C. C. Swisher, III. 1995. Cenozoic South American Land Mammal Ages: Correlation to global geochronologies; pp. 317-333 in W. A. Berggren, D. V. Kent, M.-P. Aubry and J. Hardenbol (eds.), *Geochronology, Time Scales, and Global Stratigraphic Correlation*. SEPM (Society for Sedimentary Geology) Special Publication No. 54.
4. Kay, R. F., R. H. Madden, M. G. Vucetich, A. A. Carlini, M. M. Mazzoni, G. H. Re, M. Heizler, and H. Sandeman. 1999. Revised geochronology of the Casamayoran South American land mammal age: Climatic and biotic implications. *Proceedings of the National Academy of Sciences of the United States of America* 96:13235-13240.
5. Flynn, J. J., A. R. Wyss, D. A. Croft, and R. Charrier. 2003. The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal "Age". *Palaeogeography, Palaeoclimatology, Palaeoecology* 195:229-259.
6. Kohn, M. J., A. A. Carlini, J. A. Josef, R. F. Kay, R. H. Madden, and M. G. Vucetich. 2004. Climate stability across the Eocene-Oligocene transition, southern Argentina. *Geology* 32:621-624.
7. Wyss, A. R., R. Charrier, D. A. Croft, and J. J. Flynn. 2004. Paleontological reconnaissance of the central Andean Main Range by helicopter: additional new Cenozoic mammal faunas from Chile. *Journal of Vertebrate Paleontology* 24:133A.
8. Wyss, A. R., J. J. Flynn, M. A. Norell, C. C. Swisher, III, M. J. Novacek, M. C. McKenna, and R. Charrier. 1994. Paleogene mammals from the Andes of central Chile: a preliminary taxonomic, biostratigraphic, and geochronologic assessment. *American Museum Novitates* 3098:1-31.
9. Flynn, J. J. 2002. Cenozoic Andean paleoenvironments and tectonic history: evidence from fossil mammals. 5th International Symposium of Andean Geodynamics: 215-218.
10. Croft, D. A., J. J. Flynn, and A. R. Wyss. 2008. The Tinguiririca Fauna of Chile and the early stages of "modernization" of South American mammal faunas. *Arquivos do Museu Nacional, Rio de Janeiro* 66:191-211.
11. Flynn, J. J., and A. R. Wyss. 1998. Recent advances in South American mammalian paleontology. *Trends in Ecology and Evolution* 13:449-454.
12. Flynn, J. J., and A. R. Wyss. 1999. New marsupials from the Eocene-Oligocene transition of the Andean Main Range, Chile. *Journal of Vertebrate Paleontology* 19:533-549.
13. Hitz, R., M. Reguero, A. R. Wyss, and J. J. Flynn. 2000. New interatheriines (Interatheriidae, Notoungulata) from the Paleogene of central Chile and southern Argentina. *Fieldiana: Geology (New Series)* 42:1-26.
14. Croft, D. A., M. Bond, J. J. Flynn, M. A. Reguero, and A. R. Wyss. 2003. Large archaeohyracids (Typotheria, Notoungulata) from central Chile and Patagonia including a revision of *Archaeotypotherium*. *Fieldiana: Geology (New Series)* 49:1-38.
15. Reguero, M. A., D. A. Croft, J. J. Flynn, and A. R. Wyss. 2003. Small archaeohyracids from Chubut Province, Argentina and central Chile: implications for trans-Andean temporal correlation. *Fieldiana: Geology (New Series)* 48:1-17.

16. McKenna, M. C., A. R. Wyss, and J. J. Flynn. 2006. Paleogene pseudoglyptodont xenarthrans from central Chile and Argentine Patagonia. *American Museum Novitates* 3536:1-18.
17. Carlini, A., M. B. Cianco, J. J. Flynn, G. J. Scillato-Yané, and A. Wyss. In review. The phylogenetic and biostratigraphic significance of new armadillos (Mammalia, Xenarthra, Dasypodidae, Euphractinae) from the Tinguiririca (Early Oligocene) of Chile. *Journal of Systematic Palaeontology*.
18. Wyss, A. R., J. J. Flynn, and D. A. Croft. 2005. New notoungulates (Notoungulata, Eutheria) from the central Chilean Andes. *Journal of Vertebrate Paleontology* 25:132A.
19. Croft, D. A. 2001. Cenozoic environmental change in South America as indicated by mammalian body size distributions (cenograms). *Diversity and Distributions* 7:271-287.
20. Flynn, J. J., and A. R. Wyss. 2004. A polydolopine marsupial skull from the Cachapoal Valley, Andean Main Range, Chile. *Bulletin of the American Museum of Natural History* 285:80-92.
21. Flynn, J. J., A. R. Wyss, R. Charrier, and C. C. Swisher. 1995. An early Miocene anthropoid skull from the Chilean Andes. *Nature* 373:603-607.
22. Sears, K. E., J. A. Finarelli, J. J. Flynn, and A. R. Wyss. 2008. Morphometric estimators of body mass and diet in New World monkeys (Platyrrhini, Anthropoidea, Primates), with consideration of the Miocene-aged *Chilecebus carrascoensis*. *American Museum Novitates* 3617:1-29.
23. Herriott, T. M. 2006. Stratigraphy, structure, and  $^{40}\text{Ar}/^{39}\text{Ar}$  geochronology of the southeastern Laguna del Laja area: Implications for the mid-late Cenozoic evolution of the Central Chilean Andes near  $37.5^\circ\text{S}$ , Chile. University of California, Santa Barbara, 97 pp.
24. Flynn, J. J., R. Charrier, D. A. Croft, P. B. Gans, T. M. Herriott, J. A. Wertheim, and A. R. Wyss. in press. Chronologic implications of new Miocene mammals from the Cura-Mallín and Trapa Trapa formations, Laguna del Laja area, south central Chile. *Journal of South American Earth Sciences*.
25. Wertheim, J. A., T. M. Herriott, D. A. Croft, J. J. Flynn, and P. B. Gans. 2006. Unusual fossil rodent faunas from south central Chile. *Journal of Vertebrate Paleontology* 26:137-138A.
26. Wertheim, J. A. 2007. Fossil rodents from Laguna del Laja, Chile: a systematic, phylogenetic, and biochronologic study. University of California, Santa Barbara, 366 pp.
27. Croft, D. A., J. P. Radic, E. Zurita, R. Charrier, J. J. Flynn, and A. R. Wyss. 2003. A Miocene toxodontid (Mammalia: Notoungulata) from the sedimentary series of the Cura-Mallín Formation, Lonquimay, Chile. *Revista Geológica de Chile* 30:285-298.
28. Marshall, L. G., P. Salinas, and M. Suárez. 1990. *Astrapotherium* sp. (Mammalia, Astrapotheriidae) from Miocene strata along the Quepuca River, central Chile. *Revista Geológica de Chile* 17:215-223.
29. Suárez, M., C. Emparán, R. Wall, P. Salinas, L. G. Marshall, and A. Rubilar. 1990. Estratigrafía y vertebrados fósiles del Mioceno del Alto Biobío, Chile Central ( $38^\circ\text{-}39^\circ\text{S}$ ). Segundo Simposio sobre el Terciario de Chile:311-324.
30. Flynn, J. J., D. A. Croft, R. Charrier, G. Hérail, and A. R. Wyss. 2002. The first Cenozoic mammal fauna from the Chilean Altiplano. *Journal of Vertebrate Paleontology* 22:200-206.
31. Charrier, R., A. Chávez, S. Elgueta, G. Hérail, J. J. Flynn, D. A. Croft, A. Wyss, R. Riquelme, and M. García. 2005. Rapid tectonic and paleogeographic evolution associated with the development of the Chucal anticline and the Chucal-Lauca Basin in the Altiplano of Arica, northern Chile. *Journal of South American Earth Sciences* 19:35-54.
32. Flynn, J. J., M. J. Novacek, H. E. Dodson, D. Frassinetti, C. McKenna, M. A. Norell, K. E. Sears, C. C. Swisher, III, and A. R. Wyss. 2002. A new fossil mammal assemblage from

the southern Chilean Andes: implications for geology, geochronology, and tectonics. *Journal of South American Earth Sciences* 15:285-302.

33. Croft, D. A., J. J. Flynn, and A. R. Wyss. 2004. Notoungulata and Litopterna of the early Miocene Chucal Fauna, northern Chile. *Fieldiana: Geology (New Series)* 50:1-52.
34. Croft, D. A., J. J. Flynn, and A. R. Wyss. 2007. A new basal glyptodontid and other Xenarthra of the early Miocene Chucal Fauna, northern Chile. *Journal of Vertebrate Paleontology* 27:781-797.
35. Bond, M., and M. García. 2002. Nuevos restos de toxodonte (Mammalia, Notoungulata) en estratos de la Formación Chucal, Mioceno, Altiplano de Arica, norte de Chile. *Revista Geológica de Chile* 29:81-91.
36. Flynn, J. J., D. A. Croft, R. Charrier, and A. R. Wyss. 2005. New Mesotheriidae (Mammalia, Notoungulata, Typotheria), geochronology and tectonics of the Caragua area, northernmost Chile. *Journal of South American Earth Sciences* 19:55-74.