

# A PREDICTIVE DISTRIBUTION MODEL FOR *Andinomys edax* (RODENTIA: CRICETIDAE) IN ARGENTINA

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**ABSTRACT:** We studied the distribution of *Andinomys edax* (Rodentia, Cricetidae, Sigmodontinae) in northwestern Argentina. Presence data obtained from field records, museum specimens and literature were used to model the potential distribution of this species. *Andinomys edax* was known in Argentina from only 41 occurrence localities, most of them restricted to Jujuy province. Here we add new localities from Catamarca, Jujuy, Salta and Tucumán provinces. We used the maximum entropy method (Maxent) and seven environmental variables to produce a potential distribution map of the species. The 7.015 cumulative threshold (corresponding to the equal test of sensitivity and specificity) was the most efficient hypothetical distribution according to the omission rate. The area under the curve (AUC) was of 0.987 for training data. The model indicates that *A. edax* is mainly distributed on the more humid eastern montane ranges in the region, associated to high altitude grasslands and ecotonal zones between 1500 and 4000 m in Yungas, Prepuna, Puna and High Andean environments. These results, as well as the known fossil record for the species in Argentina, indicate the ecological plasticity of *A. edax*, present in the region at least since Middle-Upper Pleistocene times.

**RESUMEN:** Un modelo predictivo de distribución para *Andinomys edax* (Rodentia: Cricetidae) en Argentina. Se estudió la distribución de *Andinomys edax* (Rodentia, Cricetidae, Sigmodontinae) en el noroeste de Argentina. Para modelar la distribución potencial de la especie se usaron datos de presencia obtenidos a partir de registros de campo, de especímenes depositados en colecciones y de la literatura. *Andinomys edax* se conocía en Argentina por sólo 41 localidades, la mayoría de ellas en la provincia de Jujuy. En este trabajo se adicionan nuevas localidades para las provincias de Catamarca, Jujuy, Salta y Tucumán. El mapa de distribución potencial de la especie fue modelado utilizando el método de máxima entropía (Maxent) y siete variables ambientales. De acuerdo con la tasa de omisión, el umbral acumulativo de 7.015 (correspondiente al test de igualdad de sensibilidad y especificidad) determinó la distribución hipotética más eficiente. El área bajo la curva (AUC) para el test ROC fue de 0.987 para los datos de entrenamiento. De acuerdo con el modelo, *A. edax* se distribuye principalmente sobre las laderas orientales húmedas de los cordones montañosos de la región, asociada a pastizales de altura y sus ecotonos entre 1500 y 4000 m, en ambientes de Yungas, Prepuna, Puna y Altos Andes. Estos

resultados, así como el registro fósil de la especie en Argentina, indican una gran plasticidad ecológica de *A. edax*, presente en la región al menos desde el Pleistoceno medio-superior.

**Key words.** Maxent. Northwestern Argentina. Potential distribution. Sigmodontinae.

**Palabras clave.** Distribución potencial. Maxent. Noroeste de Argentina. Sigmodontinae.

## INTRODUCTION

Among Neotropical mammals, the subfamily Sigmodontinae (Rodentia, Cricetidae) is one of the most diversified and complex groups, with approximately 380 species (Musser and Carleton, 2005). In the last decade, phylogenetic analyses based on molecular characters have identified several sigmodontine genera that cannot be placed into any of the previously recognized suprageneric groups (Smith and Patton, 1999; D'Elia, 2003; D'Elia et al., 2003). Smith and Patton (1999) treated these genera as "unique lineages" and D'Elia (2003) referred to them as genera without clear phylogenetic relationships, as Sigmodontinae incertae sedis. One of these unique lines is the monotypic genus *Andinomys* Thomas (D'Elia et al., 2005, 2006), previously assigned to the tribe Phyllotini based on its morphology (e.g. Hershkovitz, 1962; Olds and Anderson, 1989; Steppan, 1995). *Andinomys edax* Thomas 1902, the only species of the genus, is a very distinctive species among sigmodontines by its particular cranial, dental (Hershkovitz, 1962; Steppan, 1995), and molecular characters (D'Elia et al., 2005).

*Andinomys edax* has a broad distribution in the Central Andean region of South America, from southeastern Peru, through southwestern Bolivia and northernmost Chile to northwestern Argentina (Pine et al., 1979; Redford and Eisenberg, 1992; Anderson, 1997; Eisenberg and Redford, 1999; D'Elia et al., 2006). In Argentina *A. edax* is known from a few records and, as most sigmodontine species, no potential distribution map has been built for the species. The aim of this contribution is to model the potential distribution for *Andinomys edax* and provide new occurrence localities in Argentina.

## MATERIAL AND METHODS

For the ecoregions nomenclature we followed Burkart et al. (1999) and for the belts of the Yungas ecoregion we followed Brown et al. (2001). Distributional data of *A. edax* were obtained from field work through captured specimens (JPJ, PEO) and owl pellets samples (PEO-e), study of museum specimens and bibliographic revision. The new specimens studied, here informed with their field numbers, will be deposited at the Colección de Mamíferos Lillo (CML), San Miguel de Tucumán, Tucumán, Argentina. The studied collections were CML and Museo de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina. Information on all specimens examined is provided in the **Appendix**. Geographic coordinates were obtained with a GPS and from maps of the Instituto Geográfico Militar (IGM, Argentina, scales 1:250 000 and 1:500 000) with five decimal degrees precision.

We used seven environmental variables to build the distribution model. These variables constitute a subset of 16 climatic, six vegetation and three topographic variables analyzed, that were selected with the object of avoid multicollinearity. All seven variables had Pearson correlation values ( $r$ ) lower than 0.7 for  $P = 0.05$ . The spatial resolution of variables was 30 arc seconds, approximately equal to 0.72 km<sup>2</sup> in the study area (Hijmans et al., 2004). Climatic variables were obtained from the web page of WORLDCLIM (<http://biogeو.berkeley.edu/worldclim>) and included temperature mean diurnal range, maximum temperature of the warmest month, temperature annual range, and annual precipitation. The topographic variable (altitude) was obtained from the digital elevation model (DEM) produced by NASA (Shuttle Radar Topographic Mission [SRTM]), available from <http://glcfapp.umiacs.umd.edu:8080/esdi/index.jsp>. Vegetation variables consist of two estimates of the Normalized Difference Vegetation Index (NDVI), available from <http://edcdaac.usgs.gov/1KM/1kmhomepage.html>. These variables were calculated from maximum monthly values (sensu Parra

et al., 2004) and are: medium “greenness” (number of months where each pixel had a value between 109 and 150; Holben, 1986) and annual seasonality ( $100 \times [\text{overall maximum} - \text{overall minimum}] / \text{overall maximum}$ ; Hurlbert and Haskell, 2003). We used NDVI data from two years, April 1992 to March 1993 and February 1995 to January 1996.

We used Maxent (Phillips et al., 2006) to model the *Andinomys edax* distribution. This general-purpose method estimates a target probability distribution by finding the probability distribution of maximum entropy, subject to a set of constraints representing the incomplete information about the target distribution (Phillips et al., 2006; Phillips and Dudík, 2008). When applied to presence-only species distribution, the pixels of the study area make up the space on which the Maxent probability distribution is defined, pixels with known species occurrence records constituted the sample points, and the constraints are expressed in terms of functions of the environmental variables (Phillips et al., 2006; Phillips and Dudík, 2008). The best threshold, which defines the species distribution, can be determined through the performance of the omission rate and predicted area as a function of the cumulative threshold (Phillips et al., 2006). The Maxent procedure randomly selects 75% of the presence data to build the model (**Appendix**). We validated the model by a threshold-independent test, the receiver operating characteristic (ROC) analysis (Fielding and Bell, 1997; McPherson et al., 2004). The ROC characterizes the performance of the model at all possible thresholds by a single number, the area under the curve (AUC).

## RESULTS

### Distributional records

We obtained 41 records from the literature, for Jujuy, Salta, Tucumán and Catamarca provinces (**Fig. 1a** and **Appendix**; Thomas, 1913, 1921; Yepes, 1935; Hershkovitz, 1962; Heinonen Fortabat and Bosso, 1994; Mares et al., 1997; Díaz, 1999; Díaz and Barquez, 1999, 2007; Díaz et al., 2000; Jayat et al., 2008). In this contribution we add five new localities from Catamarca, Jujuy, Salta and Tucumán provinces (**Fig. 1a** and **Appendix**).

### Potential distribution

The performance of the omission rate and predicted area as a function of the cumulative threshold indicates that the equal test of sensitivity and specificity threshold (7.015) represents the best distributional hypothesis for the distributional record data and environmental variables considered in our study. Additionally, the ROC analysis, with an AUC of 0.987 for training data, indicates a good performance of the model.

The potential distribution map indicates that *A. edax* is mainly distributed between 1500 and 4000 m elevation on the more humid eastern montane ranges in the region, on Cordillera Oriental, Sierras Centrales and northernmost Sierras Pampeanas. The species seems mainly associated with high altitude grasslands and related ecotonal areas of Altos Andes and Yungas ecoregions (sensu Burkart et al., 1999). Moreover, on western slopes the distributional hypothesis indicates that it occurs in grassy areas of Monte de Sierras y Bolsones through the entire region and in the most humid places of Puna in Jujuy province (**Fig. 1b**). A few pixels in the model also indicate the potential presence of *A. edax* for the Chaco Seco ecoregion in northeastern Salta and in lower belts of Yungas forest in central Tucumán (**Fig. 1b**).

The diverse environmental conditions where *A. edax* lives, from Puna (mean annual rainfall <350 mm; mean annual temperature <10°C) to Yungas (mean annual rainfall >1500 mm; mean annual temperature >16 °C), suggests that this species has a high ecological plasticity. This can also be inferred from the fossil record. *Andinomys edax* has been an ubiquitous sigmodontine in northwestern Argentina since, at least, the Late Pleistocene times (Ortiz and Jayat, 2007a), and all the small mammal fossil assemblages where it has been found suggest a wide range of paleoenvironmental conditions (Ortiz, 2001; Ortiz and Pardiñas, 2001; Teta and Ortiz, 2002; Ortiz and Jayat, 2007a,b).

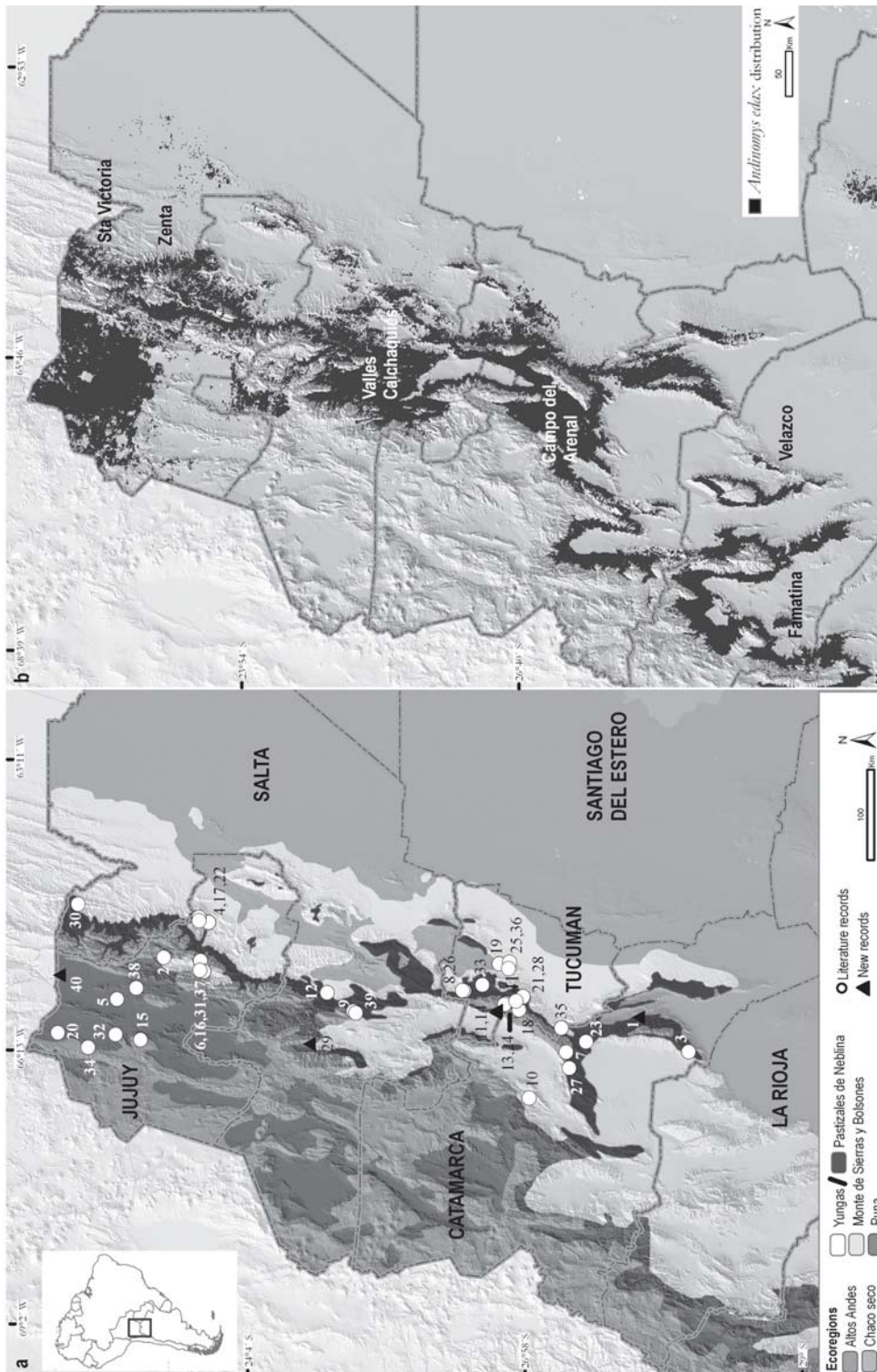


Fig. 1. a) Recording localities of *Andinomyx edax* in the ecoregions of northwestern Argentina; b) Potential distribution of *Andinomyx edax* in Argentina.



## DISCUSSION AND CONCLUSION

With a few outstanding exceptions (e.g., *Akodon lutescens*, *A. simulator*, *Phyllotis osilae*, and *P. xanthopygus*), most of northwestern sigmodontine species are known by a few occurrence localities. Until recently, the distributional information for *Andinomys edax* was scarce and concentrated to the northern extreme of this region, with almost 60% of the distributional records in Jujuy province (Díaz, 1999; Díaz and Barquez, 2007). Recently, we added several records for the species in high altitudinal grassland environments, most of them for the south of northwestern Argentina (Jayat et al., 2008). Here we offer all the records at hand for the species in the region, filling a noteworthy gap of information.

Predictive modelling of species occurrences has become an important tool in biogeographical and ecological studies, with many contributions in the last 20 years (Scott et al., 2002; Guisan and Thuiller, 2005; Guisan et al., 2006). The proliferation of new technologies, such as Geographic Information Systems, new statistical packages and specific programs dedicated to prediction of distributions, as well as the growing accessibility to global databases, have successfully promoted the development of this topic. Among several available modelling techniques, Maxent has proved to be a good tool for determining distributional areas without absence data, few recording localities, limited environmental data and for a number of taxonomical groups and geographic areas (Phillips et al., 2006; Benito de Pando and Peñas de Giles, 2007; Guisan et al., 2007a,b; Giovanelli et al., 2008; Ortega-Huerta and Townsend Peterson, 2008). Many additional advantages for Maxent procedure have been delineated in Phillips et al. (2006).

We use a “correlative approach” to ecological niche modeling (Soberón and Peterson, 2005). In this approach, the algorithm (in this case Maxent) searches the map for areas that are “similar” ecologically (often climatic) to those where the species is known to occur,

and so, the resulting model constitute a geographic representation of the fundamental ecological niche (FN) and not the distributional area of the species (Soberón and Peterson, 2005). This last area is determined by a mixture of biotic and abiotic factors in a complex spatial context. Notwithstanding, we tried to approach to the distributional area of *A. edax* using our own knowledge about areas in northwestern Argentina where the species is absent and taking advantage of the spatial scale of our study. In this way, although the distribution of *A. edax* extends northward to southern Peru, we choose to model its distribution only in Argentina. We have much more information for their distribution in this country (presence and absence data), we examined most of the cited specimens, and we know in detail the geographic features and environmental characteristics of northwestern Argentina, which allowed us to interpret and evaluate the performance of the model. The regional scale of this analysis indicates, at least theoretically, a low influence of biotic factors on the resulting model (Soberón and Peterson, 2005).

The model obtained for *A. edax* in the study area is a good approximation according to our field experience and has relatively sound validation values. Notwithstanding, new occurrence records could improve the distributional hypothesis obtained here. In our model building we used seven environmental variables related to climatic, topographic and vegetation characteristics of the area; however, better results can be obtained by using more related species life requirements variables (e.g. food resources availability). Unfortunately, as for many sigmodontine species of northwestern Argentina, there is not enough information about habitat requirements for *A. edax*.

Albeit all the *A. edax* records in Argentina come mainly from highland grasslands of Jujuy, Salta, Tucumán and Catamarca provinces, the potential distribution indicates its presence in several mountainous areas in La Rioja and Córdoba provinces, such as Sierras de Velazco, Famatina, Sierras Grandes and Sierras Chicas (**Fig. 1b**). Until now, there were no known records for the species in these ar-

east, despite environmental similarities with nearby areas situated northward in Catamarca province. This absence can be explained by the lack of sampling in Sierra de Velazco and Famatina ranges, both large and unexplored areas. However, the absence of *A. edax* in Sierras Grandes could be related to historical causes, being the species unable to colonize these areas across regions occupied by extensive dry and warm Chaco environments. Alternatively, a possible colonization of Sierras Grandes during Quaternary times followed by local extinction can not be ruled out. It is necessary to highlight that many surveys were accomplished in this hilly area but *A. edax* has never been registered (Polop, 1989, 1991; Priotto et al., 1996; Altrichter et al., 2001, 2004; Kufner et al., 2004).

The model predicts the presence of the species for extensive areas of Monte de Sierras y Bolsones environments in all the study area. We think that the more xeric areas in this ecoregion are not a good environment for *A. edax*. The presence of the species in areas such as Campo del Arenal (Catamarca) and low elevation places of the Valles Calchaquíes (Tucumán and Salta) constitutes probably an overestimation of the real distribution. Most of locations in Monte de Sierras y Bolsones where *A. edax* was registered are associated to humid microenvironments, with nearby watercourses flanked by dense bunch grasses. Probably, the prediction of the species presence in xeric areas of the Monte is consequence of the use of owl pellets records (localities 10, 14 and 29). We think that using owl pellets samples for predicting species distribution in areas with high environmental heterogeneity, and sharply contrasting conditions in short distances, must be taken with caution.

A few low elevation areas (below 1000 m) are considered as an adequate environment for *A. edax* by the Maxent model. One of these areas is located in Selva Montana of Yungas, around the Sierra de San Javier, Tucumán (Fig. 1). From this area there is one record for Horco Molle, a noticeably different locality from the rest of sites where *A. edax* has been trapped,

with more humid and warmer climatic conditions and a very different vegetation structure. This apparently incongruent record, as well as the distributional prediction, is probably the result of inadequate sampling in this intermediate altitudinal belt. The sigmodontines of the Yungas ecoregion in northwestern Argentina have been relatively well surveyed at low (Selva Pedemontana) and high (Bosque Montano and Pastizales de Neblina) elevations (Jayat et al., 2008, in press), but there are very few collecting localities in Selva Montana, between 700 and 1400 m elevation. The second low elevation area includes very small patches of Chaco environments in northeastern Salta (Fig. 1b). Our field experience and all the available distributional evidence indicate that this is clearly an overestimation of the real distribution, and we think the species is not present in the Chacoan region. In spite of more than 100 localities until now surveyed, *Andinomys edax* was not registered in this xeric ecoregion.

In Salta province the present record of the species is very poor, restricted to only five localities in central and northernmost areas. In spite of these few records, the potential distribution map predicts the presence of *A. edax* for large areas in the eastern slopes of Sierra de Santa Victoria and Sierra de Zenta, in the northern part of the province, where we think the species is indeed present (Fig. 1b).

The model also indicates the *A. edax* presence in highland grasslands of isolated eastern mountain systems of all the region, such as Sierra de Santa Bárbara, Sierra del Centinela (Jujuy), Sierra de Metán, Sierra de la Candelaria (Salta), Sierra de Medina, Sierra del Campo (Tucumán), and Sierra de Ancasti (Catamarca) (Fig. 1b). In these systems we recorded other two sigmodontine species (*Necomys lactens* and *Phyllotis osilae*) restricted to highland grassland environments through most of Northwestern Argentina and usually registered sympatrically with *A. edax* (Jayat and Pacheco, 2006; Jayat et al., 2006, 2008). This similar distributional pattern together with the proximity of these systems

respect to areas of proved presence, suggest that *A. edax* is also present in these areas.

Although *A. edax* is mainly a dweller of high altitude grasslands and related ecotonal highland systems, it inhabits humid places of very dissimilar ecoregions, being part of very different micromammal assemblages from the Middle-Upper Pleistocene to present time. Notwithstanding the noteworthy Quaternary environmental changes that have impacted on small mammal communities in northwestern Argentina (Ortiz et al., 2000a; Ortiz and Pardiñas, 2001; Pardiñas et al., 2002; Teta and Ortiz, 2002; Ortiz and Jayat, 2007a, b), *A. edax* is present in most of the studied fossil assemblages in this region.

Clearly, the distributional hypothesis obtained here can be improved with additional field data coming from northwestern Argentina, including all its distributional area in South America, and with a better knowledge on the ecological requirements of the species. However, this hypothesis represents the best available approximation and constitutes an objective tool for conservation planning in Argentina. This distributional model, and those obtained for other species in this region (e.g. Porcasi et al., 2005; Jayat and Pacheco, 2006), can constitute the base for further studies on ecology and biogeography of the sigmodontines in northwestern Argentina and the foundations for the development of appropriate conservation policies based on areographic characteristics such as size of total area, shape and connectivity, hot spot areas, and endemism.

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## APPENDIX

List of the presence localities and data sources for *Andinomys edax* in Argentina. Asterisks indicate the localities representing new records for the species.

N°	Presence localities	Province	Lat. S	Long. W	Sources
1*	3 km S Las Juntas, 1654 m	Catamarca	28.13555°	65.88722°	PEO-e 250, 260
2	11 km E Humahuaca, 2 km E Pucará on road to Cianzo	Jujuy	23.20000°	65.26600°	Díaz, 1999; Díaz and Barquez, 2007
3	45 km west of Chumbicha, about 3000 m (= Otro Cerro, 3000 m)	Catamarca	28.65541°	66.24708°	Thomas, 1919; Hershkovitz, 1962
4	Abra de Cañas (= Abra de Cañas, 1700 m, Abra de Cañas, app. 30 km NW of Calilegua on Valle Grande Rd, 1700 m; Abra de Cañas, El Monolito, 1700 m)	Jujuy	23.66600°	64.90000°	CML 1805; Heinonen and Bosso, 1994; Díaz, 1999; Díaz and Barquez, 2007
5	Abra Pampa	Jujuy	22.71600°	65.70000°	CML 1220; Díaz, 1999; Díaz and Barquez, 2007
6	Alfarcito, 2600 m (= Alfarcito, near Maitamará, 2600 m)	Jujuy	23.60208°	65.36875°	Thomas, 1921; Hershkovitz, 1962
7	Andalgalá, confluence of the rivers Minas and Candado, 2600 m	Catamarca	27.38333°	66.25000°	CML 4814; Jayat et al., 2008
8	App. 10 km S Hualinchay, on road to Lara, 2300 m	Tucumán	26.32227°	65.61263°	JPJ 752, 1221, 1226, 1227; Jayat et al., 2008
9	App. 15 km W Escoipe, on highway 33, 2680 m	Salta	25.17410°	65.82536°	JPJ 1045, 1061, 1062; Jayat et al., 2008
10	Barranca Larga, Los Viscosos cave, 2400 m	Catamarca	27.01885°	66.74517°	Ortiz et al., 2000b
11*	On road to Amaicha, km 98, highway 307	Tucumán	26.65958°	65.81791°	CML 2221, 2406
12	Campo Quijano	Salta	24.90000°	65.63333°	MACN 17565; Díaz et al., 2000
13	Carapuncu, km 81 of highway 307, 2960 m	Tucumán	26.75526°	65.74408°	JPJ 1064; Jayat et al., 2008
14*	Castillo de las Brujas, 15 km SE Amaicha del Valle	Tucumán	26.64958°	65.84291°	PEO-e 50
15	Cerro Casabindo, 4000-4800 m (= Cerro Casabindo, 4500 m; Cerro Casabindo, 4800 m)	Jujuy	22.95791°	66.12041°	Thomas, 1919; Hershkovitz, 1962; Díaz and Barquez, 2007

N°	Presence localities	Province	Lat. S	Long. W	Sources
16	Cerro de La Lagunita (= Cerro de Lagunita, E Maimará, 4500 m; Cerro de Lagunita, Maimará, 4500 m; Cerro Lagunita, Maimará, 4500 m; La Laguna 4500 m, Sierra de Tilcara, E Maimará; La Laguna, Sierra de Zenta (=Tilcara), 4500 m; Sierra de Tilcara, 4500 m; Sierra de Zenta (=Tilcara); Sierra de Zenta, 4500 m; La Laguna, Sierra de Zenta, 4500 m)	Jujuy	23.58300°	65.30000°	Thomas, 1913, 1921; Yepes, 1935; Hershkovitz, 1962; Díaz, 1999; Díaz and Barquez, 2007
17	Cerro Hermoso (= Cerro Hermoso (surroundings), 2800 m)	Jujuy	23.56666°	64.85000°	MACN 19.554; Heinonen and Bosso, 1994; Díaz and Barquez, 1999
18	Cerro Muñoz, near Ibáñez's house, for the path from Santa Cruz, 3300 m	Tucumán	26.89334°	65.80904°	PEO 37; Jayat et al., 2008
19	Cerro San Javier, 2000 m (= Sierra de Tafí Viejo, 2000 m; Taficillo; Sierra de Tafí Viejo, Tucumán, 2000 m)	Tucumán	26.68705°	65.33233°	MACN 33.85, 26.147, 26.148; Yepes, 1935; Capllonch et al., 1997
20	Cuesta del Hurón, 29 km W Cieneguillas on highway 64, 3835 m	Jujuy	22.10000°	66.05000°	Díaz, 1999; Díaz and Barquez, 2007
21	Drain of La Angostura dam	Tucumán	26.93708°	65.68291°	PEO-e 21
22	Duraznillar, 2500 m	Jujuy	23.56666°	64.88333°	Heinonen and Bosso, 1994
23	El Espinillo, Campo del Pucará, Las Estancias	Catamarca	27.59043°	66.14291°	PEO-e 123; Jayat et al., 2008
24	El Infiernillo (= Infiernillo, 3000 m; on highway to Amaicha, km 83)	Tucumán	26.74375°	65.75541°	CML 670, 688, 689; MACN 17566; Dalby and Mares, 1974
25	Horco Molle, 650 m (= Horco Molle, 15 km W San Miguel de Tucumán)	Tucumán	26.79400°	65.31600°	CM 43505; Capllonch et al., 1997
26	Hualinchay, on road to Cafayate, 1861	Tucumán	26.30591°	65.61021°	JPI 254; Jayat et al., 2008
27	km 33 of highway 47, S Capillitas, 2500 m	Catamarca	27.41666°	66.41666°	JPI 718; Jayat et al., 2008
28	La Angostura, 1900 m	Tucumán	26.94041°	65.70271°	Ortiz and Pardiñas, 2001
29*	La Poma, 3 km E	Salta	24.71375°	66.16625°	PEO-e 201
30	App. 5 km (by road) S Los Toldos, on road to Vallecito, 1705 m	Salta	22.30854°	64.71083°	PEO-e 271; Jayat et al., 2008

(Appendix cont.)

Nº	Presence localities	Province	Lat. S	Long. W	Sources
31	Maimará (= Maimará, 2200 m; Maimará, 2230 m; Maimará, 2328 m; Maimará, 2500 m)	Jujuy	23.61600°	65.46600°	CML 111, 279, 372, 373; Thomas, 1913; Yepes, 1935; Díaz, 1999; Díaz and Barquez, 2007
32	Pan de Azúcar Mine, 13 km S, on Río Cíncel	Jujuy	22.70000°	66.06600°	Díaz, 1999; Díaz and Barquez, 2007
33	Ñorco, Vipos, 2500 m	Tucumán	26.51208°	65.54958°	Hershkovitz, 1962
34	Rinconada, 6 km N, on road to Timón Cruz, 4286 m	Jujuy	22.41600°	66.20000°	Díaz, 1999; Díaz and Barquez, 2007
35	Río Vallecito, 1500 m (= Río Vallecito)	Catamarca	27.33333°	66.00000°	Hershkovitz, 1962; Mares et al., 1997
36	San Javier	Tucumán	26.78300°	65.38300°	Capllonch et al., 1997
37	Tilcara (= Tilcara, 2400 m)	Jujuy	23.55000°	65.33300°	Steppan, 1995; Díaz, 1999; Díaz and Barquez, 2007
38	Tres Cruces (= Tres Cruces, 4000 m)	Jujuy	22.91600°	65.58300°	CML 380; Díaz, 1999; Díaz and Barquez, 2007
39	Valle Encantado, Los Cardones National Park, 3000 m	Salta	25.19680°	65.84276°	Ortiz et al., 2000b
40*	Yavi	Jujuy	22.11600°	65.45000°	PEO-e 98
41	Zanjón de Tafí, 2 km SW Tafí del Valle	Tucumán	26.86194°	65.71833°	PEO-e 182; Jayat et al., 2008
<b>Localities not precisely located</b>					
	Jujuy	Jujuy			Díaz, 1999; Díaz and Barquez, 2007
	Mountains W of Yala (= W of Yala; Yala mountain west of)	Jujuy			Hershkovitz, 1962; Steppan, 1995; Díaz, 1999; Díaz and Barquez, 2007
	Aconquija, 3000 m	Tucumán			MACN 33.178, 29.250-29.253, 30.72; Yepes, 1935