HILARCOTHERIUM CASTANEDAII, GEN. ET SP. NOV., A NEW MIOCENE ASTRAPOTHERE (MAMMALIA, ASTRAPOTHERIIDAE) FROM THE UPPER MAGDALENA VALLEY, COLOMBIA

M. C. Vallejo-pareja, J. D. Carrillo, J. W. Moreno-bernal, M. Pardo-jaramillo, D. F. Rodriguez-gonzalez, and J. Muñoz-duran

QUERY SHEET

This page lists questions we have about your paper. The numbers displayed at left can be found in the text of the paper for reference. In addition, please review your paper as a whole for correctness.

Q1. Au: Please check and confirm that all author names, affiliations, and corresponding author information are correct

Q2. Au: If you have registered and received a ZooBank ID (LSID) for this manuscript, please provide it to the Production Editor. If you have yet to register your paper and you are sure that a Zoobank ID is required, you must do so now at http://www.zoobank.org/register and provide the information to the Production Editor.

Q3. Au: Jose Royo y Gómez is inside quotation marks in Affiliation, but not in all mentions in the text. OK?

Q4. Au: The next series of level 3 heads has 'Etymology' before 'Diagnosis.' Use the same sequence for both series?

Q5. Au: Which matches your meaning: 'The roots of right p4 and [the roots of] right m1–m3 are...' [delete comma] or 'The roots of right p4, and right m1–m3, are...' [add second comma]/'Right m1–m3 and the roots of right p4 are...'?

Q6. Au: Cabrera, 1929. 'Astrapotherido' [first letter A uppercase] correct?

Q7. Au: Kingdon, 1997. Number of pages?

Q8. Au: Kraglievich, 1928. Publisher in Buenos Aires?

Q9. Au: Kramarz, 2009. Please delete the issue number unless every issue starts with page 1.

Q10. Au: Simpson, 1967. Please verify the page range.

Q11. Au: Appendix 1. The specimen number for *C. snorki* is UCMP 40017 in the first three sections and UCMP 40358 in the last section. Correct?

Q12. Au: Appendix 3. log BM. Also $\log_{10}$?

TABLE OF CONTENTS LISTING

The table of contents for the journal will list your paper exactly as it appears below:

HILARCOTHERIUM CASTANEDAII, GEN. ET SP. NOV., A NEW MIOCENE ASTRAPOTHERE (MAMMALIA, ASTRAPOTHERIIDAE) FROM THE UPPER MAGDALENA VALLEY, COLOMBIA

M. C. VALLEJO-PAREJA,*,[1] J. D. CARRILLO,[2] J. W. MORENO-BERNAL,[3] M. PARDO-JARAMILLO,[4]
D. F. RODRIGUEZ-GONZALEZ,[5] and J. MUÑOZ-DURAN[5]

[1]Smithsonian Tropical Research Institute, Panama, Republic of Panama, P.O. Box 0843–03092, Panama, vacama@gmail.com;
[2]Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Strasse 4, CH-8006, Zürich, Switzerland,
juan.carrillo@pim.uzh.ch;
[3]Department of Earth and Atmospheric Sciences and Nebraska State Museum of Natural History, University of Nebraska–Lincoln,
Lincoln, Nebraska 68588–3040, U.S.A., jwmorenob@huskers.unl.edu;
[4]Museo Geológico Nacional 'José Royo y Gómez,' Servicio Geológico Colombiano, Diag. 53 No. 34–53, Bogotá D.C., Colombia,
mpardo@sgc.gov.co;
[5]Departamento de Biología, Universidad Nacional de Colombia, Cra. 30 No. 45-03, Bogotá D.C., Colombia, dfrodriguezgo@unal.
edu.co; jvmunozd@unal.edu.co

ABSTRACT—Astrapotheria are an order of extinct South American herbivores recorded throughout the continent, from the late Palaeocene to middle Miocene. Here we describe *Hilarcotherium castanedaii*, gen. et sp. nov., an Uruguaytheriinae astrapothere from sediments of La Victoria Formation (middle Miocene) in the Tolima Department, Upper Magdalena Valley, Colombia. *H. castanedaii*, represented by a partial skull, mandible, and some postcranial remains, is characterized by (1) unique dental formula, with 0/3i, 1/1c, 1/1p, and 3/3 m; and (2) lower canines with subtriangular transversal section at the base. *Hilarcotherium* differs from the equatorial Uruguaytheriinae genera *Xenastrapotherium* and *Granastrapotherium* in (1) having three lower incisors; (2) the diagonal implantation of the lower canines; (3) lower molars with lingual cingulid; (4) the presence of the hypocone in the third upper molar; and (5) the presence of anterolingual pocket in the fourth upper premolar. Our phylogenetic analysis supports the monophyly of the subfamilies Astrapotheriinae and Uruguaytheriinae. Within the latter, we confirm the monophyly of the neotropical clade (*Hilarcotherium*, *Xenastrapotherium*, and *Granastrapotherium*). *H. castanedaii* shows some plesiomorphic features such as the aforementioned presence of the i3 and the developed hypocone in the last upper molar. Its estimated body mass (1303 kg) is intermediate among Astrapotheriidae.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Astrapotheria, a lineage of South American extinct herbivores, are recorded from late Paleocene–early Eocene Itaboraian South American Land Mammal Age (SALMA; Oliveira and Goin, 2011) to middle Miocene Laventan SALMA (Paula Couto, 1952; Simpson, 1967; Johnson, 1984; Cifelli, 1985, 1993; Johnson and Madden, 1997; Weston et al., 2004; Goillot et al., 2011). The group attained great size variation, with body mass estimates ranging from 60.28 kg in some primitive genera (Vizcaíno et al., 2012) to 4120 kg in more derived genera (Kramarz and Bond, 2011). Astrapotheres exhibit several characteristic cranial, postcranial, and dental traits, including well-developed tusks separated from the premolars by a diastema, flattened astragalus, and calcaneus with secondary ectal facet and enlarged peroneal tubercle (Cifelli, 1993). The more derived genera have strongly retracted nasals indicating the presence of a proboscis (Johnson, 1984). According to Cifelli (1993), there are two families within Astrapotheria: the paraphyletic Trigonostylopidae, which was the first to radiate and has a fossil record that extends from the Paleocene to the Eocene (Goillot et al., 2011), and the more derived Astrapotheriidae, which originated in the middle Eocene and became extinct during the middle Miocene. Within the latter, two subfamilies are recognized: Astrapotheriinae, which includes the southern genera *Astrapotherium* and *Astrapothericulus*, and Uruguaytheriinae, which includes the genera *Uruguaytherium*, *Xenastrapotherium*, and *Granastrapotherium*

(Carbajal et al., 1977; Cifelli, 1993; Johnson and Madden, 1997; Kramarz and Bond, 2009).

The Uruguaytheriinae shows a successive radiation with one southern South American taxa (*Uruguaytherium*) and two northern South American genera (*Granastrapotherium* and *Xenastrapotherium*). *Uruguaytherium* is recorded in Uruguay, the precise location and age of the deposits is unknown but assumed to be Oligocene or Miocene (Kraglievich, 1928). *Xenastrapotherium* is known from late Oligocene to middle Miocene of Colombia (Gualanday Group, Oligocene; Honda Group, middle Miocene, Laventan SALMA), Venezuela (Chaguaramas Formation, Oligocene to early Miocene), Peruvian Amazonia (Ipururo Formation, late middle Miocene, 13 Ma), Ecuador (Biblian Formation, early Miocene), and Brazil (middle or early late Miocene deposits of Rio Juruá–Rio Breu area) (Johnson and Madden, 1997; Goillot et al., 2011). *Granastrapotherium* is known from the middle Miocene of La Venta, Colombia (Honda Group; Johnson and Madden, 1997), and the Fiztcarrald Arch of the Peruvian Amazonia (late middle Miocene, 13 Ma; Goillot et al., 2011). There are also reports of indeterminate Uruguaytheriinae fragments from Quebrada Honda, Bolivia (middle Miocene, Laventan SALMA; Goillot et al., 2011), and postcranial remains from Venezuela (Castillo Formation, early Miocene) that cannot be unequivocally assigned to Uruguaytheriinae but are different from Patagonian taxa (Weston et al., 2004).

Here we describe a new astrapothere recovered from middle Miocene deposits of the Honda Group, exposed in Malnombre Creek, Vereda Hilarco, south of Purificación Town (Tolima Department, Upper Magdalena Valley, Colombia). The dental formula and other morphological features readily differentiate

*Corresponding author.

this specimen from previously known astrapotheres (Cabrera, 1929; Scott, 1937; Johnson, 1984; Johnson and Madden, 1997; Kramarz, 2009; Kramarz and Bond, 2009, 2011). We compare this new material with collection specimens and published description of astrapotherid taxa. In addition, we used the characters listed in previous publications to analyze the phylogenetic relationships among the Astrapotheriidae.

Institutional Abbreviations—**FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **IGM**, Museo Geológico Nacional Jose Royo y Gómez, Servicio Geológico Colombiano (formerly INGEOMINAS, Instituto Colombiano de Geología y Minería), Bogotá, Colombia; **MLP**, Museo de La Plata, La Plata, Argentina; **NMB**, Naturhistorisches Museum Basel, Basel, Switzerland; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.

Stratigraphic Provenance

The astrapothere remains were found in the Malnombre Creek (3°46′41.91″N, 74°58′37.23″W, municipality of Purificación, Tolima, Colombia), at 348 m above sea level (a.s.l.) and 10 m downstream from the bridge over Malnombre Creek. The deposits are lithologically equivalent to those of the middle Miocene La Victoria Formation, as described by Guerrero (1997) in La Venta area, Upper Magdalena Valley, 69 km southeast of the discovery site (Fig. 1A). The Malnombre Creek stratigraphic section (Fig. 1B) is characterized by interbedded thin layers of claystone, siltstones, sandy limes, and occasional sand lenses. The specimen was found within well-consolidated gray claystones, covered by a layer of quaternary deposits of about 20 cm width. In the Upper Magdalena Valley, some localities of the Honda Group, north of La Venta area, have been assigned to the Laventan SALMA on the basis of fossil mammals (Madden et al., 1997). However, the referral of the Malnombre Creek deposits to the Laventan SALMA is still uncertain, given the lack of index fossils or other geochronological evidence.

Referred Material

Astrapotherium? ruderarium (FMNH 13426); *Astrapotherium magnum* (FMNH P14251, P13173); *Granastrapotherium snorki* (UCMP 40017, 40187, 40188, 40358, 40408); *Parastrapotherium holmbergi* (FMNH 13329); *Parastrapotherium* sp. (FMNH 13569); *Xenastrapotherium kraglievichi* (MLP 12–96, UCMP 38115); *Xenastrapotherium christi* (NMB Aa 21).

SYSTEMATIC PALEONTOLOGY

ASTRAPOTHERIA Lydekker, 1894
ASTRAPOTHERIIDAE Ameghino, 1887
HILARCOTHERIUM, gen. nov.

Type and Only Species—*Hilarcotherium castanedaii*, sp. nov.
Diagnosis—As for type and only species.
Etymology—From the Vereda Hilarco (Tolima Department, Colombia), where the type specimen was found.
Occurrence—Middle Miocene, Tolima Department, Colombia.

HILARCOTHERIUM CASTANEDAII, gen. et sp. nov.
(Figs. 2–5)

Holotype Type—IGM p881231. Partial skull and mandible, a complete left humerus, a vertebral ramus of a dorsal rib, and an incisor associated. The skull includes most of the rostrum, palate with P4–M3, partial left zygomatic arch, and partial basicranium. The mandible lacks incisors, the crown of the right p4, and a portion of the left ramus. The roots of right p4, and right m1–m3 are preserved.

Stratigraphic and Geographic Provenance—Honda Group, La Victoria Formation, Purificación, Tolima, Colombia. Close to Malnombre Creek, Vereda Hilarco, 18 km southwest from the town of Purificación, Tolima Department, Upper Magdalena Valley, Colombia.

Etymology—In honor of Mr. José Alfredo Castañeda who found the holotype specimen.

Diagnosis—Apomorphies: unique dental formula, with 0/3i, 1/1c, 1/1p, and 3/3m; lower canines with subtriangular transversal section at the base. Differs from *Granastrapotherium* and *Xenastrapotherium* in having three lower incisors, diagonal implantation of lower canines, lower molars with lingual cingulid, anterolingual pocket in fourth upper premolar (P4), and hypocone in third upper molar (M3).

Description and Comparisons—The skull of *H. castanedaii* preserves a portion of the premaxillae, most of the maxillaries and palatines, a pterygoid fragment, presphenoid, a small portion of the basisphenoid, the anterior portion of the zygomatic arch, a fragment of the left squamosal, and partial basicranium (Fig. 2A). The premaxillae are edentulous, have no incisive foramina, and are rounded on their anterior end. Maxillaries are large, with the palatine process elongated and convexly curved. The canine alveoli are deep, oval, longer than wider, and laterally oriented. The preserved portion of the orbital region of the maxillaries forms the base of the zygomatic process, which starts at the level of the posterior root of the M2. No foramina are preserved or exposed in the maxillaries. The zygomatic arch is long and slender, it has a constant dorsoventral depth, and the suture with the jugal is slightly visible. Towards the squamosal portion, the dorsoventral depth and width of the zygomatic arch slightly increase, with the arch becoming deepest and widest at its distal end. The preserved portion of the palatines extends from the anterior part of M1 to 35 mm behind the posterior end of M3; they are elongated, slightly convex, with a prominent
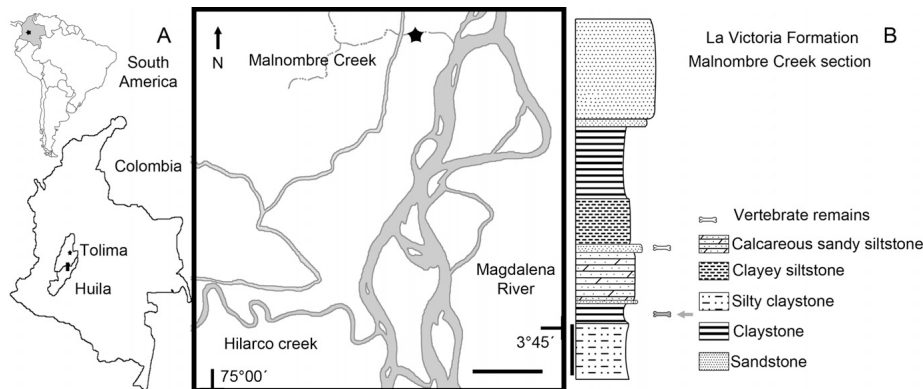

FIGURE 1. Location and stratigraphic provenance of *Hilarcotherium castanedaii*, gen. et sp. nov. **A**, maps of South America, Colombia (inset), and Vereda Hilarco, indicating the place where the fossil was found (black star). Black rectangle in the map of Colombian shows the geographic position of La Venta deposits. Scale bar equals 1 km; **B**, stratigraphic column, Malnombre Creek section, showing the stratigraphic provenience of *Hilarcotherium castanedaii* (gray arrow). Scale bar equals 1 m.
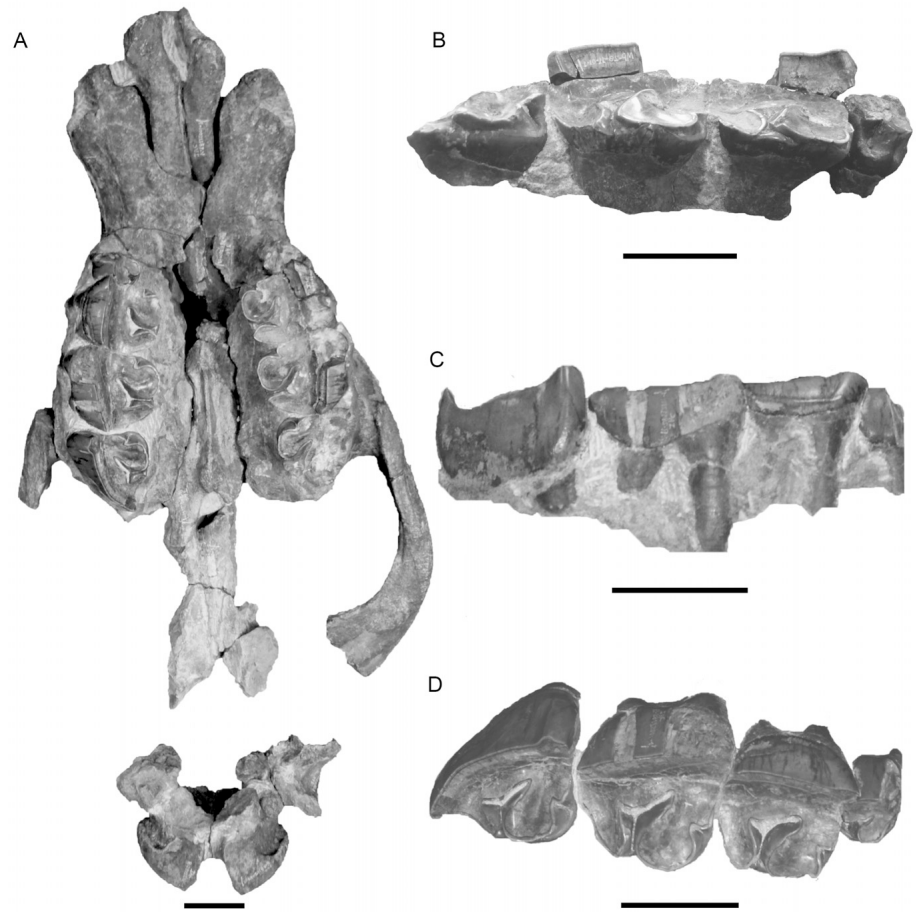
FIGURE 2. *Hilarcotherium castanedaii*, gen. et sp. nov. **A**, cranium with P4–M3, partial left zygomatic arch, and partial basicranium, occlusal view; **B**, right P4–M3, labial view; **C**, left P4–M3, lingual view; **D**, right P4–M3, occlusal view. Scale bars equal 5 cm.

ridge along the suture, as in *Astrapotherium* (Scott, 1937). This ridge becomes a bulge in its posterior end. The presphenoid is medially located, approximately 70 mm long, and with its anterior portion narrower (7.7 mm) than its posterior end (22.5 mm). A small part of the basisphenoid is also preserved. From the pterygoids, only the portion attached to the presphenoids are preserved. The sutures between these two bones are deep and straight. The portion of the basicranium preserves a small portion of the exoccipitals and is better preserved on the left side; the foramen magnum, with 45.3 mm of mediolateral diameter; and a small portion of the basioccipital including the occipital condyles, which are enlarged in the dorsoventral axis.

The dentary is more robust (relationship between depth at the level of m2 and dentary length) than in *Granastrapotherium snorki* and *Xenastrapotherium christi*, although it is similar to *Astrapotherium*? *ruderarium* and *Astrapotherium magnum* (Appendix 1). The width of the mandible at the level of the canines is slightly smaller than in *G. snorki* and *A. magnum*, but larger than in *Astrapotherium*? *ruderarium* and *X. christi* (Appendix 1). The horizontal ramus is narrow and nearly straight in lateral view across the anterior-posterior axis, without ventral inflexion. The angular process does not project posteriorly beyond the level of the condyle. The vertical ramus is high and narrow; the coronoid process is similar to that of *X. christi* and is less prominent than in *G. snorki.* The sigmoid notch of *H. castanedaii* is shorter than in the latter species. The condyles are cylindrical and wide. The symphysis is transversely concave and tilts down posteriorly, making it deeper towards its posterior

end. The relative lower diastema length of *H. castanedaii* (LDL/D in Appendix 1) is higher than in *G. snorki* and *X. christi* and similar to that of *A. magnum*. Three mandibular foramina are observed on both sides of the dentary near the base of the canines.

The dental formula of *Hilarcotherium castanedaii* is 0/3i, 1/1c, 1/1p, 3/3m. The upper canines are not preserved, and the alveoli are oval (Fig. 2A). The upper cheek teeth have unilateral hypsodonty, meaning that their teeth are higher crowned on the labial than on the lingual side. As *Granastrapotherium* and *Comahuetherium*, *H. castanedaii* has only one upper premolar, which is oval and smaller than the molars (Appendix 2), representing the 13% of the total upper cheek tooth series length. However, it is not as small as in *Granastrapotherium*, where the fourth premolar accounts for 10% of the upper cheek tooth row length and is so reduced in height that it fails to come into direct occlusion with the lower teeth (Johnson and Madden, 1997). In contrast with *Granastrapotherium*, in *H. castanedaii* the occlusal surface of the P4 is at the same level of the upper molars, and the wear indicates that it was incorporated in the masticatory function (Fig. 2B–D). The protocone is well developed, the parastylar region is missing in right and left P4s, and, only in the right upper premolar, the posterior portion of the ectoloph is preserved, with no signs of a fold like that of *Astrapothericulus*, *Astrapotherium*, *Parastrapotherium*, *Comahuetherium*, or *Maddenia*. There is a small metaloph extending lingually from the ectoloph. Unlike *Astraponotus*, *Albertogaudrya*, and *Maddenia*, the P4 of *H. castanedaii* does not have a hypocone. As *Granastrapotherium* and

FIGURE 3.   Third upper molar of *Hilarcotherium castanedaii*, gen. et sp. nov. Scale bar equals 1 cm.

Xenastrapotherium, the new taxon lacks the labial cingulum on the P4; however, this structure is present in the lingual side, where it is briefly interrupted towards the mid-length of the tooth and encloses two pockets located in the anterior and posterior portions of the tooth, the anterior one being shallower and smaller than the posterior one, as in *Comahuetherium*. Two slender roots of the P4 can be seen from the labial side, and a thicker one on the lingual side.

The M1 and M2 have a more quadrangular contour than the M3, which is triangular (Fig. 2D). There is a lingual cingulum in all molars, but this structure is absent in the labial side as in all Uruguaytheriinae; however, a remnant of it can be seen as a subtle widening at the base of the M1 (Figs. 2B–D).

The upper molars are characterized by the presence of a 'Y'-shaped central valley opened on the lingual side. This structure is present on the M1 and M2 of all Astrapotheriidae, but only *Comahuetherium*, *Xenastrapotherium*, and this new taxon show this feature on the M3 (Fig. 2D). The internal arms of this 'Y'-shaped valley are formed by the crochet, which is oriented towards the hypocone. All the molars possess a deep anterolingual pocket (Fig. 2B), characteristic shown in *Xenastrapotherium* and *Granastrapotherium* (Johnson and Madden, 1997). The parastylar fold is well developed on the M1, less developed on the M2, and absent in the M3, whereas the labial fold of the paracone is well developed only in the M3, poorly developed on the M2, and absent in the M1. This pattern in which the M2 seems to have a transitional development of the aforementioned features is only seen in *Granastrapotherium*.

The M3 (Fig. 3) has a well-developed hypocone, a feature only seen in *Maddenia* and *Astraponotus*, but unlike these two taxa, the hypocone of *Hilarcotherium* is not closely connected to the posterior slope of the protocone. A lingual cingulum at the base of the hypocone, similar to the one observed in *Granastrapotherium* and *Xenastrapotherium*, connects it with the protocone. The posterior-most portion of the M3, the metastyle, is particularly higher than the rest of the tooth, likely due to differential wear.

The mandibular ramus does not preserve the incisors, but it exhibits six deformed alveoli with irregular dimensions (Fig. 4). The i1 and i3 alveoli have the same diameter but are smaller than i2 (Appendix 2). The associated incisor is bilobed, with a lingual cingulum and a robust root twice the height of the crown; the root is slightly curved toward the mesial side of the tooth (Fig. 4F, G).

Only the basal portion of the lower canine tusks is preserved; they are subtriangular in cross-section and flattened on the lingual side. The implantation of the canine, considered as the orientation of the tooth with respect the horizontal plane of the mandible at the point where the tooth emerges from the bone, is oblique (Fig. 4A). The shape of the alveoli also indicates an oblique implantation of the lower tusk. In the preserved portion of the lower canines, the enamel is not well preserved and only some vertical stripes are visible. A computed tomography (CT) scan of the specimen shows that the tusks are rootless.

The lower cheek tooth series is preserved only in the right side of the mandible (Figs. 4C–E). *H. castanedaii* has one lower premolar, like *Astrapotherium*, *Astrapothericulus*, *Xenastrapotherium*, and *Granastrapotherium*, but only the two roots are preserved. Each one is oval in cross-section, wider than longer, and the posterior root is slightly bigger than the anterior one. Judging from the distance encompassed by the two roots and their positions, p4 crown length should have been somewhat more than half the length of m1.

The lower molars of *Hilarcotherium castanedaii* resemble those of *Uruguaytherium*, *Granastrapotherium*, and *Xenastrapotherium*, lacking the hypoflexid on the buccal side and the labial cingulid (Fig. 4D). In contrast to *Astrapotherium*, *Astrapothericulus*, and *Parastrapotherium*, *H. castanedaii* does not have a pillar in the posterior face of the metalophid in any of their molars. The first lower molar is the smallest one (Appendix 2) and shows a high degree of wear. An entoflexid, enclosed by a lingual cingulid, separates the hypolophid and metalophid (Fig. 4C). Due to dental wear in the anterior region of the molar, the paraflexid is reduced and superficial, characteristic also observed in specimens of *Granastrapotherium* and *Xenastrapotherium* with different stages of wear.

The m2 and m3 are very similar in size and morphology (Appendix 2). They have a paraflexid and an entoflexid. In the occlusal surface, the paraflexid is in between the paralophid and the metalophid, which at the same time is separated from the hypolophid by the entoflexid. The m2 has a discontinuous lingual cingulid that encloses the paraflexid, is interrupted at the metalophid, and is present in the posterior and basal portions of the entoflexid. In the m3, the lingual cingulid is also discontinuous and closes the lingual opening of the paraflexid and the entoflexid, which is less conspicuous than in m2 (Fig. 4D, E).

The holotype of *H. castanedaii* includes a left humerus (Fig. 5A–D), which is 455 mm long (from the greater tuberosity to the mid-trochlea). The head is projecting behind the shaft, has a maximum width of 83.96 mm, and is strongly convex, and only the greater tuberosity can be distinguished, rising above the level of the head. The bicipital groove is broad and deep. The deltoid tuberosity is large and extends through almost the whole length of the shaft (two thirds of the humerus). Its thickness decreases towards the distal portion of the bone as in *A. magnum* (Scott, 1937). The trochlea is pulley-shaped, more symmetrical than in *A. magnum* (Scott, 1937). In contrast to it, the medial and lateral epicondyles are well developed. The coronoid fossa and the olecranon fossa are deep and large, the former being considerably larger.
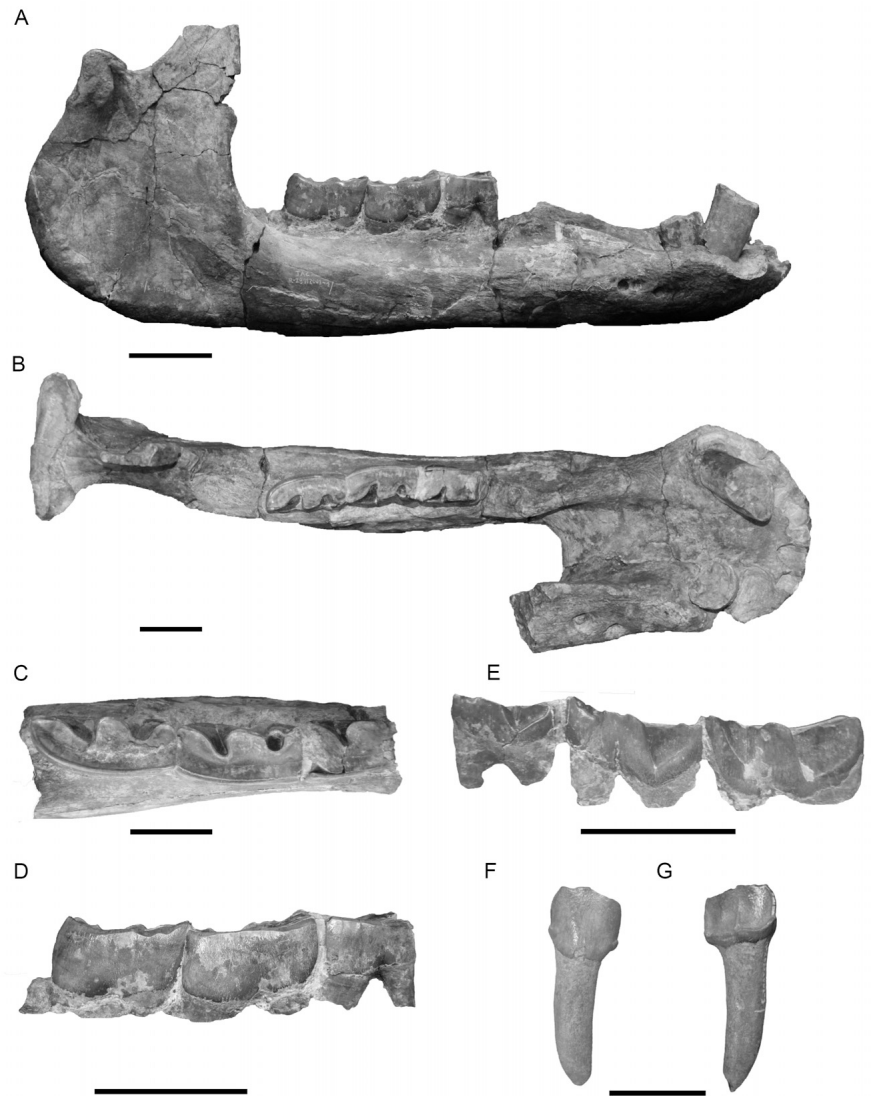
FIGURE 4. *Hilarcotherium castanedaii*, gen. et sp. nov. **A**, **B**, mandible with i1–i3 alveoli, partial c1, p4 roots, and m1–m3 in **A**, lateral and **B**, occlusal views; **C–E**, right m1–m3 in **C**, occlusal; **D**, labial; and **E**, lingual views; **F**, **G**, lower incisor in **F**, labial and **G**, lingual views. **A–E**, scale bars equal 5 cm; **F–G**, scale bar equals 3 cm.

PHYLOGENETIC ANALYSIS

In order to establish the phylogenetic position of *Hilarcotherium* within Astrapotheriidae, we analyzed 64 craniodental characters for 15 taxa within the order Astrapotheria (Supplementary Data 1, 2). The characters are based primarily on Cifelli (1993), Johnson and Madden (1997), and Kramarz and Bond (2009, 2011), with the addition of one new character (20) (Supplementary Data 1, 2). Trigonostylopidae *sensu* Cifelli (1993) were selected as the outgroup including *Eoastrapostylops* Soria and Powell (1981) and Soria (1987, 1988); *Trigonostylops* Simpson (1933) and Soria and Bond (1984); *Tetragonostylops* Soria (1982); *Albertogaudrya* Carbajal et al. (1977); and *Scaglia* Simpson (1957). Besides *Hilarcotherium*, ingroup taxa included *Astraponotus* Kramarz and Bond (2009, 2011) and Kramarz et al. (2011); *Maddenia* Kramarz and Bond (2009); *Comahuetherium* Kramarz and Bond (2011); *Parastrapotherium* Scott (1937) and Kramarz and Bond (2008); *Astrapothericulus* Kramarz (2009); *Astrapotherium* Riggs (1935) and Scott (1937); *Uruguaytherium* Kraglievich (1928) and Kramarz and Bond (2011); *Xenastrapotherium*; and *Granastrapotherium* Johnson (1984) and Johnson and Madden (1997).

We performed a maximum parsimony analysis using heuristic search in PAUP* 4.0 (Swofford, 2003). The options for the analysis included a starting tree obtained via stepwise addition, 'closest' algorithm for sequence addition, and branch-swapping through tree-bisection-reconnection (TBR). Ten uninformative characters (1, 2, 12, 48, 50, 57, 58, 59, 60, and 64) were excluded. Of the remaining 54 characters, 52 were treated as ordered and two as unordered, all characters have equal weights (Supplementary Data 1, 2). Five most parsimonious trees were obtained, with a length of 105 steps, consistency index (CI) of 0.6282, and retention index (RI) of 0.7500. We present the 50% majority rule consensus of the five trees and the tree obtained by reweighting characters by their maximum value of rescaled consistency indices (Fig. 6). For the reweighted tree, of the 54 characters included, 23 had a weight of 1 and 31 had a weight different from 1. The CI was 0.8440 and the RI was 0.9191.

Previous studies on the phylogeny of Astrapotheria have shown that Trigonostylopidae is paraphyletic (Cifelli, 1993; Kramarz, 2009; Kramarz and Bond, 2009, 2011). Within Astrapotheriidae, Johnson and Madden (1997) defined the clade Uruguaytheriinae (*Granastrapotherium* and *Xenastrapotherium*) based on the well-developed anterolingual pocket in M1, loss of
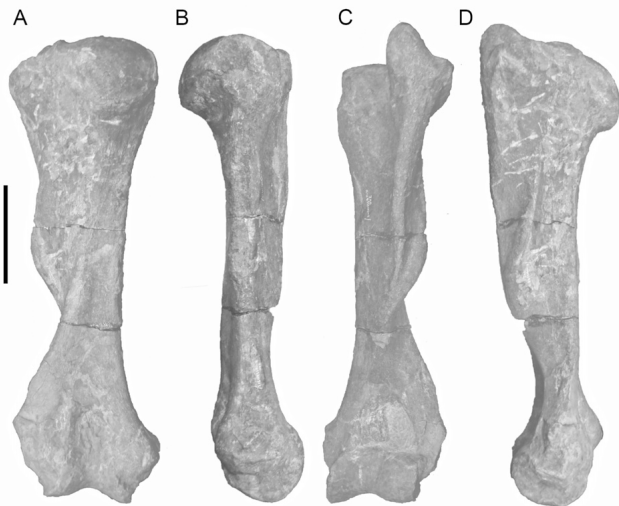
FIGURE 5. *Hilarcotherium castanedaii*, gen. et sp. nov. Left humerus in **A**, posterior; **B**, medial; **C**, anterior; and **D**, lateral views. Scale bar equals 5 cm.

is placed in a polytomy with Uruguaytheriinae and Astrapotheriinae in the 50% majority consensus tree but appears as the sister taxon of the clade Uruguaytheriinae + Astrapotheriinae in the reweighted tree. In agreement with previous analysis of Kramarz and Bond (2009, 2011), we considered *Parastrapotherium* as the sister taxon of the two subfamilies Astrapotheriinae and Uruguaytheriinae.

Here we find support for the monophyly of the two 'subfamilies' within Astrapotheriidae. The Astrapotheriinae clade undoubtedly includes *Astrapotherium* and *Astrapothericulus*, which is supported by the presence of a deep hypoflexid and well-developed lingual cingulid in the lower molars. The Uruguaytheriinae clade includes *Granastrapotherium*, *Xenastrapotherium*, *Hilarcotherium*, and *Uruguaytherium*, which is unambiguously supported by the absence of the hypoflexid in the lower molars, absence of the pillar in the lower molars, and the absence of a labial cingulum in molars. Other cranial and upper dentition characteristics, such as the reduced parastyle in the upper molars; the palatal portion of the palatines narrow, elongated, without lateral palatine notch; and a dorsoventrally shallow zygomatic arch with its maxillary root above M2, are ambiguous synapomorphies of the Uruguaytheriinae.

Within Uruguaytheriinae, only *Uruguaytherium* is found in southern South America, differing from the northern South American genera in having a very penetrating and transversely oriented paraflexid in the lower molars. The neotropical clade includes *Hilarcotherium*, *Xenastrapotherium*, and *Granastrapotherium*. *Hilarcotherium* differs from *Xenastrapotherium* and *Granastrapotherium* by having a diagonal implantation of the lower canines, the presence of three lower incisors, well-developed anterolingual pocket on the P4, lower molars with a lingual cingulid, and the presence of the hypocone in the M3. *Hilarcotherium* shows some primitive traits for the Uruguaytheriinae, such as the aforementioned presence of the i3 and the developed hypocone in the last upper molar, but its relationships within the clade are still unresolved. Nevertheless, our results support the monophyly of an equatorial astrapothere clade.

In summary, our phylogeny supports the monophyly of Astrapotheriinae and Uruguaytheriinae. We confirm the monophyly of the neotropical clade within which *Hilarcotherium* shows some plesiomorphic features.

the lower molar hypoflexid, reduced upper molar parastyle, lower molar metaflexid enclosed by a mesiolingual cingulum, and a lingual valley enclosed by the protoloph ridge in M3. Kramarz and Bond (2009, 2011) latter confirmed monophyly of the Uruguaytheriinae, including *Uruguaytherium*, *Granastrapotherium*, and *Xenastrapotherium*, additionally supported by the absence of labial cingulum on molars and the extreme reduction of the lower molar hypoflexid. Kramarz and Bond (2009, 2011) also confirmed the monophyly of Astrapotheriinae (*Astrapotherium* and *Astrapothericulus*), supported by a deep hypoflexid of the lower molars and the presence of a continuous lingual cingulid. Although Kramarz and Bond (2010) first interpreted *Comahuetherium* as a taxon with Uruguaytheriinae affinities, in the formal description (Kramarz and Bond, 2011), they argued that *Comahuetherium* has no particularly close relationship with Uruguaytheriinae but, on the contrary, is the sister taxon of a clade including *Parastrapotherium*, plus Astrapotheriinae and Uruguaytheriinae.

Our analysis agrees with previous studies in the position of *Astraponotus*, *Maddenia*, and *Comahuetherium*. *Parastrapotherium*

BODY MASS ESTIMATES

We used published regression equations proposed by Damuth (1990) and Janis (1990) to estimate the body mass (BM) of *H.*
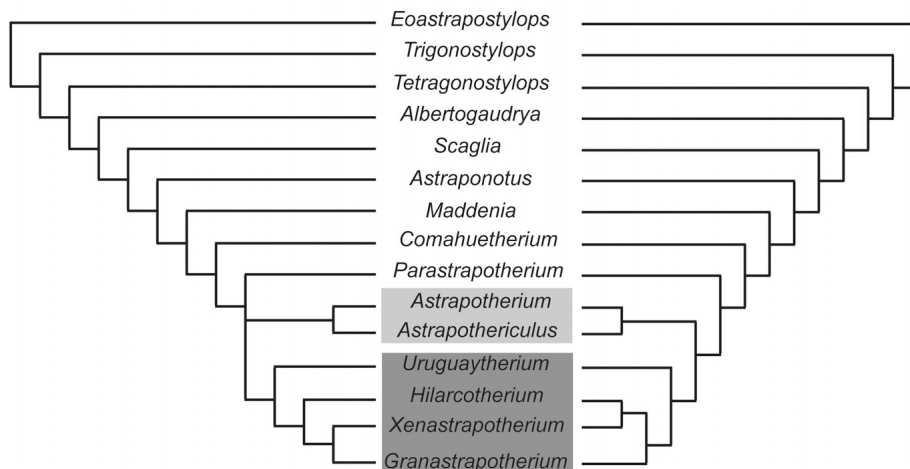

FIGURE 6. Phylogenetic trees. (Left) The 50% majority rule consensus tree of five most parsimonious trees; (right) reweighted tree, with consistency index (CI) = 0.8440 and retention index (RI) = 0.9191. The subfamilies Astrapotheriinae and Uruguaytheriinae are highlighted in light and dark gray rectangles, respectively.

castanedaii and make comparisons with other astrapotheres. Molar row length measurements (Appendices 2, 3) were preferred over other dental parameters because they show a higher correlation with BM and are more independent of changes in the relative proportions of molars (Damuth, 1990; Janis, 1990). Measurements of molar rows were calculated either by measuring along the base of the teeth (Janis, 1990) or adding the individual lengths of teeth following the method of Damuth (1990).

Mammal tooth dimensions are frequently used as a proxy for body size because teeth are taxonomically diagnostic and are preserved in the fossil record more often than other elements. However, tooth size is only indirectly related to body mass, and their dimensions can be affected by morphological differences related to function (Fortelius, 1990; Jungers, 1990). On the other hand, long bones of limbs are weight-bearing elements necessary for locomotion and body support and are considered as a more accurate proxy for estimating body mass (Gingerich, 1990; Jungers, 1990; Scott, 1990). Regression equations proposed by Scott (1983, 1990) were used to calculate body mass estimates from measurements of the associated humerus of *Hilarcotherium* (IGM p881231). The Microsoft QuickBASIC source code given by Gingerich (1990) for the BODYMASS program was adapted for a newer version (0.17b) of BASIC compiler and used to calculate additional body mass estimations from measurements of the associated humerus.

Estimates of body mass from lower molar row length gave values of 1303 and 1369 kg, whereas the estimates from the upper molar row length was approximately 300 kg larger (Appendix 3). The humerus-based body mass estimates range between 1187 and 1306 kg, similar values to those obtained with lower molar row lengths (Appendix 3), suggesting that lower molar row dimensions are a more reliable proxy for body mass. The range of estimated body mass for *H. castanedaii* is comparable to that of some large terrestrial mammals, such as the black rhinoceros (*Diceros bicornis*; 1000–2000 kg) and the giraffe (*Giraffa camelopardalis*; 1180–1930 kg), but still smaller than big specimens of white rhinoceros (*Ceratotherium simum*; 2000–3600 kg) or hippopotamus (*Hippopotamus amphibius*; 2500–3200 kg) (Kingdon, 1997).

Kramarz and Bond (2011:table 3) reported body mass estimates for several astrapothere species, using the lower molar row length regression model provided by Damuth (1990). The body mass for *H. castanedaii*, calculated with the same method (1303 kg), can be used to make comparisons among astrapothere taxa. The calculated body mass of *H. castanedaii* is intermediate among Astrapotheriidae, being bigger than *Comahuetherium coccaorum* (324–504 kg) and *Astrapothericulus iheringi* (956 kg) and more similar to *Xenastrapotherium kraglievichi* (1325 kg) and *Astrapotherium*? *ruderarium* (1060–1214 kg). Estimated body mass for *H. castanedaii* is also lower than in the biggest specimens of *Astrapotherium magnum* (1630–2094 kg), *Astrapotherium giganteum* (3594 kg), *Parastrapotherium holmbergi* (1060–2594 kg), and the gigantic taxa *Granastrapotherium snorki* (3142 kg), *Parastrapotherium martiale* (3484 kg), and *Parastrapotherium herculeum*? (4117 kg). The presence of intermediate (1000–2000 kg) and gigantic (>3000 kg) body sizes in different astrapotheriid lineages indicates that the former was acquired early within Astrapotheriidae, and truly gigantic sizes (>3000 kg) evolved independently at least three different times within the linage: once in the basal Astrapotheriidae (*Parastrapotherium*), once in the Astrapotheriinae (*Astrapotherium giganteum*), and once within Uruguaytheriinae (*Granastrapotherium*).

ACKNOWLEDGMENTS

SUPPLEMENTAL DATA

Vallejo-Pareja et al Supplemental Data

LITERATURE CITED

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. Boletín Museo de La Plata 1:1–26.

Cabrera, A. 1929. Un Astrapotherido de Colombia. Sociedad Argentina de Ciencias Naturales 9:436–443.

Carbajal, E., R. Pascual, R. Pinedo, J. A. Salfity, and M. Vucetich. 1977. Un nuevo mamífero de la Formación Lumbrera (Grupo Salta) de la comarca Carahuasi (Salta, Argentina): edad y correlaciones. Publicaciones del Museo Municipal de Ciencias Naturales "Lorenzo Scaglia" 2(7):148–163.

Cifelli, R. L. 1985. South American ungulate evolution and extinction; pp. 249–266 *in* S. D. Webb and F. G. Stehli (eds.), The Great American Biotic Interchange, Volume 4. Plenum Press, New York.

Cifelli, R. L. 1993. The phylogeny of the native South American ungulates; pp. 195–214 *in* F. S. Szalay, M. J. Novacek, M. C. Mckenna (eds.), Mammal Phylogeny, Placentals. Springer, New York.

Damuth, J. 1990. Problems in estimating body masses of archaic ungulates using dental measurements; pp. 229–253 *in* J. Damuth and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, U.K.

Fortelius, M. 1990. Problems with using fossil teeth to estimate body sizes of extinct mammals; pp. 207–228 *in* J. Damuth and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology:Estimation and Biological Implications. Cambridge University Press, Cambridge, U.K.

Gingerich, P. D. 1990. Prediction of body mass in mammalian species from long bone lengths and diameters. Contributions from the Museum of Paleontology, University of Michigan 28:79–92.

Goillot, C., P. O. Antoine, J. Tejada, F. Pujos, and R. Salas Gismondi. 2011. Middle Miocene Uruguaytheriinae (Mammalia, Astrapotheria) from Peruvian Amazonia and a review of the astrapotheriid fossil record in northern South America. Geodiversitas 33:331–345.

Guerrero, J. 1997. Stratigraphy, sedimentary environments, and the Miocene uplift of the Colombian Andes; pp. 15–43 *in* R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate Paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C.

Janis, C. 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids; pp. 255–299 *in* J. Damuth and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, U.K.

Johnson, S. C. 1984. Astrapotheres from the Miocene of Colombia, South America. Ph.D. dissertation, University of California, Berkeley, California, 182 pp.

Johnson, S. C., and R. H. Madden. 1997. Uruguaytheriinae Astrapotheres of tropical South America; pp. 355–381 *in* R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C.

Jungers, W. L. 1990. Problems and methods in reconstructing body size in fossil primates; pp. 103–118 *in* J. Damuth and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, U.K.

Kingdon, J. S. 1997. The Kingdon Field Guide to African Mammals. Academic Press, London.

Kraglievich, L. 1928. Sobre El Supuesto *Astrapotherium christi*, Stehlin, descubierto en Venezuela, (*Xenastrapotherium* N. gen.) y sus relaciones con *Astrapotherium magnum* y *Uruguaytherium beaulieui*. La Editorial Franco, Buenos, 16 pp.

Kramarz, A. G. 2009. Adiciones al conocimiento de *Astrapothericulus* (Mammalia, Astrapotheria): anatomía cráneo-dentaria, diversidad y distribución. Revista Brasilera de Paleontologia 12(1):55–66.

Kramarz, A. G., and M. Bond. 2008. Revision of *Parastrapotherium* (Mammlia, Astrapotheria) and other deseadanastrapotheres of Patagonia. Ameghiniana 45:537–551.

Kramarz, A. G., and M. Bond. 2009. A new Oligocene astrapothere (Mammalia, Meridungulata) from Patagonia and a new appraisal of astrapothere phylogeny. Journal of Systematic Palaeontology 7:117–128.

Kramarz, A. G., and M. Bond. 2010. Colhuehuapian Astrapotheriidae (Mammalia) from Gran Barranca south of Lake Colhue-Huapi; pp 182–192 *in* R. H. Madden, A. A. Carlini, M. G. Vucetich, and R. F. Kay (eds.), The Paleontology of Gran Barranca. Cambridge University Press, Cambridge, U.K.

Kramarz, A. G., and M. Bond. 2011. A new early Miocene astrapotheriid (Mammalia, Astrapotheria) from Northern Patagonia, Argentina. NeuesJahrbuch fur Geologie und Palaontologie-Abhandlungen 260:277–287.

Kramarz, A. G., M. Bond, and A. M. Forasiepi. 2011. New remains of *Astraponotus* (Mammalia, Astrapotheria) and considerations on astrapothere cranial evolution. Paläontologische Zeitschrift 85:185–200.

Lydekker, R. 1894. Contribution to the knowledge of the fossil vertebrates of Argentina: a study of extinct Argentine ungulates. Anales del Museo de La Plata, Paleontología Argentina 2:1–32.

Madden, R. H, J. Guerrero, R. F. Kay, J. J. Flynn, C. C. Swisher III, and A. H. Walton. 1997. The Laventan Stage and age; pp. 499–519 *in* R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C.

Oliveira, É. V., and F. J. Goin. 2011. A reassessment of bunodont metatherians from the Paleogene of Itaboraí (Brazil): systematics and age of the Itaboraian SALMA. Revista Brasileira de Paleontologia 14:105–136.

Paula Couto, C. 1952. Fossil mammals from the beginning of the Cenozoic in Brazil. Condylarthra, Litopterna, Xenungulata and Astrapotheria. Bulletin of the American Museum of Natural History 99:359–394

Riggs, E. S. 1935. A skeleton of *Astrapotherium*. Geological Series of Field Museum of Natural History 6:167–177.

Scott, K. M. 1983. Prediction of body weight of fossil Artiodactyla. Zoological Journal of the Linnean Society 77:199–215.

Scott, K. M. 1990. Postcranial dimensions of ungulates as predictors of body mass; pp. 301–335 in J. Damuth and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, U.K.

Scott, W. B. 1937. The Astrapotheria. Proceedings of the American Philosophical Society 77:309–393.

Simpson, G. G. 1933. Structure and affinities of *Trigonostylops*. American Museum Novitates 608:1–28.

Simpson, G. G. 1957. A new Casamayoran astrapothere. Revista Del Museo Municipal De Ciencias Naturales y Tradicional De Mar Del Plata 1:11–18.

Simpson, G. G. 1967. The beginning of the Age of mammals in South America: part 2. Bulletin of the American Museum of Natural History 137:12–59.

Soria, M. F. 1982. *Tetragonostylops apthomasi* (Price y Paula Couto, 1950): su asignación a Astrapotheriidae (Mammalia: Astrapotheria). Ameghiniana 19:234–238.

Soria, M. F. 1987. Estudios sobre los Astrapotheria (Mammalia) del Paleoceno y Eoceno. Parte I: descripción de *Eoastrapostylops riolorense* Soria Powell 1982. Ameghiniana 24:21–34.

Soria, M. F. 1988. Estudios sobre los Astrapotheria (Mammalia) del Paleogeno y Eoceno. Parte II: filogenia, origen y relaciones. Ameghiniana 25:47–59.

Soria, M. F., and M. Bond. 1984. Adiciones al conocimiento de *Trigonostylops* (Ameghino, 1897) (Mammalia, Astrapotheria, Trigonostylopidae). Ameghiniana 23:43–51.

Soria, M. F., and J. E. Powell. 1981. Un primitivo Astrapotheria (Mammalia) y la edad de la Formación Rio Loro, Provincia de Tucuman, Republica Argentina. Ameghiniana 18:155–168.

Swofford, D. A. 2003. PAUP* 4.0. Sinauer Associates, Sunderland, Massachusetts.

Vizcaíno, S., G. Cassini, N. Toledo, and M. Bargo. 2012. On the evolution of large size in mammalian herbivores of Cenozoic faunas of Southern South America; pp. 76–101 *in* B. D. Patterson and L. P. Costa (eds.), Bones, Clones, and Biomes: The History and Geography of Recent Neotropical Mammals. University of Chicago Press, Chicago and London.

Weston, E. M., R. H. Madden, and M. R. Sánchez-Villagra 2004. Early Miocene astrapotheres (Mammalia) from northern South America. Special Papers in Paleontology 71:81–97.

APPENDIX 1. Comparative measurements of Astrapotheriinaes and northern Uruguaytheriinaes. **Abbreviations: D**, dentary maximum length (in mm); **Dd**, dentary depth at m2 (in mm); **FMI1**, lower molar length (in mm); **LDL**, lower diastema length (in mm); **Mw**, mandible width, which is the maximum mediolateral width between the lateral margin of lower canines (in mm); **RD**, dentary robustness, i.e., the dentary depth at m2 (Dd)/dentary maximum length (D).

Taxon	Catalog number	D	Dd	RD	Mw
Parastrapotherium sp.	FMNH 13569	—	—	—	—
Astrapotherium? *ruderarium*	FMNH 13426	409.87	74.85	0.183	74.71
Astrapotherium magnum	FMNH P14251	533.02	85.95	0.161	137.99
Xenastrapotherium kraglievichi	UCMP 38115	—	62.64	—	—
Xenastrapotherium kraglievichi	MLP 12–96	—	—	—	—
Xenastrapotherium christi	NMB Aa 21	550	68.7	0.125	107.5
Granastrapotherium snorki	UCMP 40017	584.36	70.73	0.121	126.05
Hilarcotherium castanedaii	IGM p881231	482.81	83.69	0.173	120.9
Taxon	Catalog number	m1/m2	m2/m3	m1/m3	
Parastrapotherium sp.	FMNH 13569	0.928	—	—	
Astrapotherium? ruderarium	FMNH 13426	0.705	0.764	0.538	
Astrapotherium magnum	FMNH P14251	0.627	0.943	0.591	
Xenastrapotherium kraglievichi	UCMP 38115	1.138	2.000	2.277	
Xenastrapotherium kraglievichi	MLP 12–96	—	0.914	—	
Xenastrapotherium christi	NMB Aa 21	0.699	0.939	0.657	
Granastrapotherium snorki	UCMP 40017	0.683	0.984	0.672	
Hilarcotherium castanedaii	IGM p881231	0.691	0.944	0.653	
Taxon	Catalog number	LDL	LDL/D	FMI1	LDL/FMI1
Parastrapotherium sp.	FMNH 13569	—	—	—	—
Astrapotherium? *ruderarium*	FMNH 13426	149.55	0.365	143.94	1.039
Astrapotherium magnum	FMNH P14251	162.76	0.305	211.02	0.771
Xenastrapotherium kraglievichi	UCMP 38115	—	—	—	—
Xenastrapotherium kraglievichi	MLP 12–96	—	—	—	—
Xenastrapotherium christi	NMB Aa 21	127.3	0.231	167.00	0.762
Granastrapotherium snorki	UCMP 40017	129.84	0.222	184.23	0.705
Hilarcotherium castanedaii	IGM p881231	143	0.296	139.85	1.023
Taxon	Catalog number	M1/M2	M2/M3	M1/M3	
Parastrapotherium sp.	FMNH 13329	0.793	1.013	0.803	
Astrapotherium? *ruderarium*	FMNH 13426	—	—	—	
Astrapotherium magnum	FMNH P14251	—	—	—	
Xenastrapotherium kraglievichi	UCMP 38115	—	—	—	
Xenastrapotherium kraglievichi	MLP 12–96	—	—	—	
Xenastrapotherium christi	NMB Aa 21	—	—	—	
Granastrapotherium snorki	UCMP 40358	0.712	0.967	0.688	
Hilarcotherium castanedaii	IGM p881231	0.919	1.073	0.986	

APPENDIX 2. Dental measurements (in mm) of Hilarcotherium castanedaii, gen. et sp. nov. **Abbreviations**: **APL**, anterior-posterior length; **TL**, transverse length. *Measurement taken in the alveoli, tooth not preserved. **Measurement taken at the base of the tooth, due to damage of the crown.

Tooth	Left side		Right side	
	APL	TL	APL	TL
i1	17.7*	13.7*	16.4*	14.4*
i2	20.4*	17.3*	21.4*	13.2*
i3	13.4*	13.2*	11.3*	12.6*
c1	33.36**	25.97**	36.27**	26.9**
p4	—	—	23.6**	13.9**
m1	—	—	36.11	24.24
m2	—	—	48.77	26.05
m3	—	—	55.34	24.23
C1	39.93*	29.11*	41.23*	33.0*
P4	20.32**	28.6**	19**	28.3**
M1	42.47	51.3	44.2	45.72
M2	48.75	51.1	53.61	52.1
M3	54.82**	52.3**	55.34	47.8

APPENDIX 3. Body mass estimates for Hilarcotherium castanedaii, gen. et sp. nov. (IGM p881231). **Abbreviations**: **BM**, body mass. *Measured along the base of teeth (Janis, 1990). **Calculated from dimensions of individual teeth (Damuth, 1990).

Source	Measurement	Value (mm)	log$_{10}$(value)	log BM	BM
Gingerich (1990)	Humerus: parasagittal diameter	76.15			1246
Scott (1983, 1990)	Humerus length	455.00	1.66	3.12	1307
Scott (1983, 1990)	Humerus: parasagittal diameter	76.15	0.88	3.07	1187
Janis (1990)	Lower molar row length*	132.60	1.12	3.13	1346
Damuth (1990)	Upper molar row length**	153.15	2.19	6.21	1607
Damuth (1990)	Lower molar row length**	140.22	2.15	6.11	1303