Middle Miocene Uruguaytheriinae (Mammalia, Astrapotheria) from Peruvian Amazonia and a review of the astrapotheriid fossil record in northern South America

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ABSTRACT

Five mandibular and dental specimens referred to the extinct South American ungulate clade Astrapotheria are described. They originate from late middle Miocene deposits of the Ipururo Formation in the Río Inuya-Río

Mapuya area, Peruvian Amazonia. The first Peruvian astrapothere remains unearthed in a controlled stratigraphical context reveal the co-occurrence of the uruguaytheriine astrapotheriids *Xenastrapotherium* sp. and *Granastrapotherium* cf. *snorki*. Bispecific uruguaytheriine assemblages were so far restricted to the early Miocene of Venezuela and the late middle Miocene of Colombia. The Fitzcarrald local fauna, including the uruguaytheriines described here, recalls unequivocally the *Xenastrapotherium kraglievichi* Cabrera, 1929-*Granastrapotherium snorki* assemblage, which characterizes the 13.6-12.76 Ma interval in the Honda Group of La Venta area, Colombia. The spatio-temporal distribution of low-latitude astrapotheriids (< 30°S) is then reviewed, illustrated, and further detailed in both stratigraphical and taxonomic points of view. The group appears in the fossil record during the Oligocene or the earliest Miocene (*Uruguaytherium* Kraglievich, 1928 and *Xenastrapotherium* Kraglievich, 1928 in Uruguay and Venezuela, respectively). Uruguaytheriinae are conspicuous elements of middle Miocene mammal assemblages of northern South America (Colombia, Brazil, Bolivia, and now Peru). Astrapotheria probably become extinct during the late Miocene (Huayquerian South American Land Mammal Age), but the youngest specimens are of uncertain taxonomic affinities and/or might be reworked (Astrapotheriidae indet. in Urumaco Formation of Venezuela; ?Astrapotheria in Rio Acre local fauna of Brazil).

KEY WORDS
Mammalia,
Astrapotheria,
Astrapotheriidae,
Uruguaytheriinae,
Xenastrapotherium,
Granastrapotherium,
Fitzcarrald Arch,
Río Inuya,
Río Mapuya,
neotropics.

RÉSUMÉ

Les Uruguaytheriinae (Mammalia, Astrapotheria) du Miocène moyen d'Amazonie péruvienne et une revue du registre fossile des Astrapotheriidae dans le nord de l'Amérique du Sud.

Cinq restes mandibulaires et dentaires attribués à des astrapothères, clade éteint de grands ongulés sud-américains, sont décrits. Ils proviennent du Miocène moyen tardif de la Formation Ipururo dans la région du Río Inuya et du Río Mapuya, en Amazonie péruvienne. Les premiers restes d'astrapothères découverts au Pérou dans un contexte stratigraphique contrôlé révèlent la co-existence des Astrapotheriidae Uruguaytheriinae *Xenastrapotherium* sp. et *Granastrapotherium* cf. *snorki*. De tels assemblages bispécifiques d'Uruguaytheriinae étaient jusqu'alors restreints au Miocène inférieur du Venezuela et au Miocène moyen de Colombie. La faune locale de Fitzcarrald, qui inclut les Uruguaytheriinae ici décrits, rappelle sans équivoque l'association *Xenastrapotherium kraglievichi* Cabrera, 1929-*Granastrapotherium snorki*, qui caractérise l'intervalle 13.6-12.76 Ma dans le Groupe Honda de La Venta, en Colombie. La distribution spatio-temporelle des Astrapotheriidae de basse latitude (< 30°S) est ensuite révisée, illustrée et détaillée à la fois des points de vue stratigraphique et taxinomique. Le groupe apparaît dans le registre fossile pendant l'Oligocène ou au Miocène basal (avec *Uruguaytherium* Kraglievich, 1928 et *Xenastrapotherium* Kraglievich, 1928, respectivement en Uruguay et au Venezuela). Les Uruguaytheriinae apparaissent comme des éléments habituels des faunes de mammifères du Miocène moyen d'Amérique du Sud septentrionale (Colombie, Brésil, Bolivie et dorénavant Pérou), avant de se raréfier ensuite. Les Astrapotheria ont probablement disparu au cours du Miocène supérieur (étage mammalien Huayquérien), mais les spécimens les plus récents sont d'affinités incertaines et/ou pourraient être remaniés (Astrapotheriidae indet. dans la Formation Urumaco au Venezuela; ?Astrapotheria dans la faune locale du Rio Acre au Brésil).

MOTS CLÉS
Mammalia,
Astrapotheria,
Astrapotheriidae,
Uruguaytheriinae,
Xenastrapotherium,
Granastrapotherium,
Arche de Fitzcarrald,
Río Inuya,
Río Mapuya,
néotropiques.

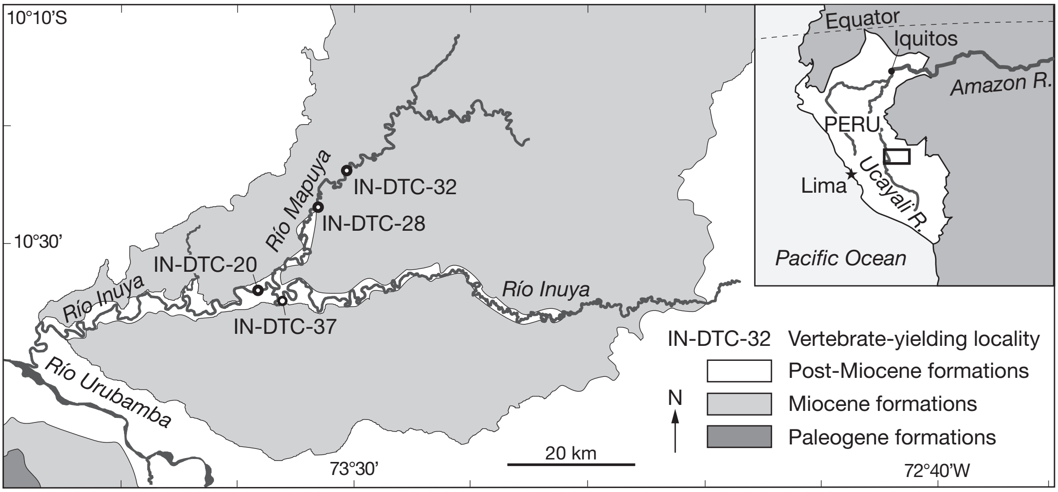

Fig. 1. — Location map of the late middle Miocene astrapotheriid-yielding vertebrate localities in the Río Inuya and Río Mapuya area ("Fitzcarrald local fauna", Ipururo Formation), Ucayali Department, eastern Peru.

INTRODUCTION

Astrapotheres are an extinct clade of large herbivorous ungulates endemic of South America, grouped into the order Astrapotheria. Their cranial and dental morphology is particularly puzzling, being superficially reminiscent of both rhinoceroses (upper and lower cheek teeth) and elephants (enlarged tusk-like canines and putative proboscis; Ameghino 1894; Scott 1928, 1937; Kramarz & Bond 2008). The group spans the Paleocene-Miocene period and it ranges from northernmost South America (Venezuela and Colombia; Kraglievich 1928; Cabrera 1929) to West Antarctica (Bond *et al.* 1990; Hooker 1992). The astrapotheres are usually split into two families, the Palaeocene-Eocene Trigonostylopidae Ameghino, 1901 (Simpson 1967; Cifelli 1993; McKenna & Bell 1997) and the Eocene-Miocene Astrapotheriidae Ameghino, 1887 (Scott 1937; Johnson & Madden 1997). Based on the phylogenetic analysis proposed by Kramarz & Bond (2009), the Astrapotheriidae include *Astraponotus* Ameghino, 1901 (middle Eocene), *Maddenia* Kramarz & Bond, 2009 (early Oligocene), and *Parastrapotherium* Ameghino, 1895 (late Oligocene-early Miocene) as early offshoots (i.e. Astrapotheriidae *incertae sedis*), as well as the clades Astrapotheriinae and Uruguaytheriinae. The Astrapotheriinae consist of *Astrapothericulus* Ameghino, 1901 (early Miocene) and *Astrapotherium* Burmeister, 1870 (early to early middle Mocene). All these genera are restricted to Patagonia and adjacent areas in Argentina and Chile (e.g., Kramarz & Bond 2008). By contrast, the uruguaytheriine clade traditionally includes post-Eocene astrapotheriids originating from elsewhere in South America: *Xenastrapotherium* Kraglievich, 1928 (late Oligocene-middle Miocene of northern South America; Johnson & Madden 1997), *Granastrapotherium* Johnson & Madden, 1997 (middle Miocene of Colombia; Johnson & Madden 1997), and *Uruguaytherium* Kraglievich, 1928 from Uruguay (Kraglievich 1928; Simpson 1940). In other words, and with the notable exception of *Uruguaytherium* – the age of which is not well constrained –, Uruguaytheriinae are restricted to Northern South America, ranging from Colombia and Venezuela to the North to southern Bolivia to the South (Kraglievich 1928; Cabrera 1929; Hoffstetter 1977; Frailey 1987; Johnson & Madden 1997; Croft 2007).

In August 2005, a French-Peruvian team explored the Ríos Inuya and Mapuya (Fig. 1), focusing on geological data (Espurt *et al.* 2006, 2007, 2010) and palaeontological evidence (Antoine *et al.* 2007; Salas-Gismondi *et al.* 2007). Among hundreds of vertebrate remains unearthed in the Inuya-Mapuya area in 2005, five mandibular and dental specimens can be referred to Astrapotheria. With the exception of a lower molar and a left edentulous maxilla collected floating on a bank along the Río Inuya – "Locality VF56, Playa Mapuya" according to Willard (1966) – and subsequently referred to the uruguaytheriine astrapotheriid cf. *Granastrapotherium* (Johnson & Madden 1997), this order was unknown in Peru to date. This work is aimed to describe and identify the first Peruvian astrapothere assemblage unearthed in a controlled stratigraphical context.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Fitzcarrald Arch shows widespread dissected relieves of Miocene sediments coeval to the more northern Pebas deposits (Espurt *et al.* 2007, 2010). The Inuya localities are located in a slightly deformed part of the Fitzcarrald Arch (Fig. 1; Regard *et al.* 2009). They correspond to middle Miocene outcrops of the Amazon foreland strata, with tidal facies attesting the presence of giant estuaries alimented by Andean rivers (Espurt *et al.* 2007, 2010).

Vertebrate remains accumulate mainly in Miocene conglomerates from the Ipururo Formation, interpreted as storm deposits channelized in nearshore environment (Espurt *et al.* 2007, 2010). These conglomerates are topped by tidal deposits yielding some scattered vertebrates and fossil wood. Pliocene conglomerates and sandstones of the Juanjui Formation, with fossil wood but no vertebrate, unconformably overlay these tidal Miocene sandy clays. Pleistocene units correspond to terrace deposits of the Ucayali Formation, placed 50 m above the Río Mapuya (Regard *et al.* 2009; Espurt *et al.* 2010).

MATERIAL AND METHODS

The described material is stored in the Paleontology Department of the MUSM.

Comparison with other representatives of Astrapotheria was performed thanks to the collections stored in the MACN, the MLP, the MUSM, the UCMP, the Field Museum of Natural History (Chicago), the American Museum of Natural History (New York), the Yale Peabody Museum (New Haven), the Museo Nacional de Historia Natural (La Paz), the Universidad Nacional de Colombia (Bogotá), the Museo Geológico Nacional del Instituto Colombiano de Geología y Minería (Bogotá), and the Muséum national d'Histoire naturelle (Paris).

ABBREVIATIONS

Upper case letters are used for upper dentition (I, C, P, and M) and lower case letters for lower dentition (i, c, p, and m).

Institutions

MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina;
MLP	Museo de Ciencias Naturales, La Plata, Argentina;
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru;
UCMP	University of California Museum of Paleontology, Berkeley, USA.

Other abbreviations

APD	anteroposterior diameter;
H	height;
LLL	labio-lingual length;
max	maximal;
MDL	mesio-distal length;
SALMA	south american land mammal age.

SYSTEMATICS

The systematic arrangement hereunder follows that proposed by McKenna & Bell (1997) and Johnson & Madden (1997), refined by Kramarz & Bond (2009).

Two other fragmentary specimens unearthed in the field in 2005 were doubtfully referable to Astrapotheria (MUSM F-2005-58: partial edentulous mandible symphysis from IN-DTC-32, mentioned by Antoine *et al.* (2007); MUSM F-2005-005: small fragment of a canine, from IN-007). We chose not to include them in the following description, as they would not provide further morphological or taxonomic information on the current astrapotheriid assemblage.

Class MAMMALIA Linnaeus, 1758
Order ASTRAPOTHERIA Lydekker, 1894
Family ASTRAPOTHERIIDAE Ameghino, 1887
Subfamily URUGUAYTHERIINAE Kraglievich, 1928

Genus *Xenastrapotherium* Kraglievich, 1928

TYPE SPECIES. — *Astrapotherium christi* Stehlin, 1928 from the ?late Oligocene-early Miocene of Venezuela, by original designation (Kraglievich 1928).

OTHER REFERRED SPECIES. — *Xenastrapotherium kraglievichi* Cabrera, 1929, middle Miocene of Colombia; *X. amazonense* Paula Couto, 1976, middle Miocene of Brazil; *X. aequatorialis* Johnson & Madden, 1997, early Miocene of Ecuador; *X. chaparralensis* Johnson & Madden, 1997, early Miocene of Colombia.

***Xenastrapotherium* sp.**
(Fig. 2)

?*Xenastrapotherium* sp. – Antoine *et al.* 2007: 21.

Granastrapotherium snorki (partim) – Antoine *et al.* 2007: 21.

Xenastrapotherium sp. – Negri *et al.* 2010: 247.

MATERIAL EXAMINED. — Edentulous symphysis with canine alveoli (MUSM 1468) and left i1 (MUSM 1466), IN-DTC 20 locality; left P3 without ectoloph (MUSM 1467), IN-DTC 37 locality.

LOCALITY AND DISTRIBUTION. — Río Inuya, *c.* 2 km downstream the confluence with Río Mapuya (IN-DTC 20) and *c.* 500 m upstream the confluence with Río Mapuya (IN-DTC 37), Atalaya Department, Ucayali, Peru (Fig. 1).

FORMATION AND AGE. — Ipururo Formation, *c.* 500 m above the base of the formation, late middle Miocene, *c.* 13 Ma (Antoine *et al.* 2007; Espurt *et al.* 2010).

DESCRIPTION

MUSM 1468 is a much damaged fragment of an edentulous mandibular symphysis (Fig. 2A-F). In dorsal view, the symphysis is sagittally elongate (preserved APD = 117 mm), with a shallow sagittal gutter between canine alveoli; only the lingual part of them is preserved, on each side of the symphysis; the preserved part of the concerned alveolus has a circular transverse section; the canines were hypsodont to hypselodont; they were converging frontward in the posterior half of the symphysis, parallel, then diverging in the anterior half; there is neither obligate alveoli for front teeth (incisors) nor for cheek teeth in the preserved part; the posterior border of the symphysis is regularly concave; the intermandibular space was very wide and reached *c.* 50 mm. In rostral view, the ventral border of the symphysis is slightly convex; the dorsal border, corresponding to the shallow sagittal gutter described before, is regularly concave between the canine alveoli; three shallow circular pits are observed on the rostral tip of the symphysis ; two are located on the left side while a single one is preserved on the right side; they are not perfectly symmetrical with respect to the median axis, and as such, cast a doubt on their meaning; nevertheless, the most probable hypothesis is that they could represent vestigial incisor alveoli. In lateral view, both ventral and dorsal borders are parallel and sub-horizontal; canine alveoli are also horizontal in their central part and slightly oriented upward in their rostral and caudal parts. In ventral view, four mental foramina open forming a small irregular semicircle in the rostral part of the symphysis; two larger foramina, more remote than the latter, are visible close to the caudal border of the symphysis; this caudal border is large and regularly concave.

MUSM 1467 is a worn and broken biradiculate tooth (max preserved MDL = 21.6 mm; max preserved LLL = 22.1 mm; est LLL ≈ 25 mm). The labial and lingual roots are totally fused distally and separate by a deep longitudinal groove on the mesiolingual side (Fig. 2I, J). Except where worn or broken, the crown is surrounded by finely wrinkled enamel. The ectoloph is badly broken and enamel is completely lacking on it. In occlusal view, the crown is triangular, wider distally than mesially, and with a slightly convex lingual edge (Fig. 2G, H); the single lingual cusp (?protocone) is conical and anteriorly connected to the ectoloph by a thin and low crest interpreted as a protoloph; a short, low and oblique cingulum is visible on the mesiolingual side of the tooth; the preserved part of the ectoloph is slightly higher than the protocone; distally, the ectoloph and the protocone are connected by a thick and worn crest, thus forming a metaloph at late stages of wear; the mesiolingual pocket forms a circular pit; the weak distal cingulum is low and smooth, thicker labially, and defining a low distal pocket.

MUSM 1466 is a worn incisiform tooth, with a low crown and a long and single root (*c.* 40 mm long; Fig. 2K-M). Except where worn, the crown is entirely surrounded by finely wrinkled enamel. In occlusal view, the crown is sub-oval (MDL = 17.4 mm; LLL = 12.4 mm), with two convex and elongate opposite sides (i.e. lingual/labial), slightly converging on the right side; there is a low horizontal cingulid, located just above the neck on both sides, but no vertical groove. The root is flattened transversely and elongate sagittally.

COMPARISON

MUSM 1468 was first mentioned by Antoine *et al.* (2007) as documenting *Granastrapotherium snorki*, but further observation revealed the putative presence of three incisor alveoli, which precludes its referral to *G. snorki* (devoid of incisors; Johnson & Madden 1997). At the same time, similar alveoli occur in early ontogenetic stages of *X. kraglievichi* from La Venta (UCMP 45069). Orientation of the canines (nearly horizontal) is similar to that observed in *X. kraglievichi* (UCMP 45069), and at a lesser degree to *G. snorki* (UCMP 40017), in which they are perfectly horizontal. On the other hand, their orientation is pretty distinct from what is observed in the holotypes of *Parastrapotherium martiale* Ameghino, 1901 (MACN A52-604) and of *Astrapotherium giganteum* Ameghino, 1898 (MACN A3274-3278), as well as in the mandible MACN 3207 (*A. magnum* Burmeister, 1879), i.e. upraised.

The triangular occlusal outline and distal widening of MUSM 1467 do not match the P4s referred to *G. snorki* (rounded) and to *X. kraglievichi* (quadrangular), while such features are observable on the P3 UCMP 38847 from La Venta, belonging to the hypodigm of *X. kraglievichi*, as illustrated by Johnson & Madden (1997: figs 22.1; 22.3). Besides, the estimated dimensions of MUSM 1467 (*c.* 22 × 25 mm) are similar to those of UCMP 38847 (MDL = 20.5 mm; LLL = 23.4 mm; Johnson & Madden 1997: table 22.1). *Granastrapotherium* does not retain P3 and P4 is much larger (range = 26.7-38.4 mm; mean = 33.2 mm; Johnson & Madden 1997: table 22.4).

The presence of enamel all around the crown of MUSM 1466 impedes referring it to a toxodont notoungulate, the only associated astrapothere-sized taxon. When compared to astrapothere teeth, this unicuspid, single-rooted, and brachydont tooth can be identified as a lower incisor. The crown is low, which points either to an i1 or i3, rather than to an i2 (high-crowned). Furthermore, its bilateral symmetry implies it was located axially on the symphysis. As a consequence, it is tentatively interpreted as an i1, which tends to be confirmed by its strong sagittal development and by the strong wear of the crown. Moreover, Astrapotheriidae generally display deep median longitudinal grooves on both labial and lingual sides of the incisors (i1-i3), and their absence is only observed in i1s of a few astrapotheriid taxa. MUSM 1466 differs from those referred to *Astrapotherium* (Santacrucian SALMA, Argentina: MACN 3207; Colhuehuapian SALMA, Argentina: A52-513 and A52-525; Kramarz & Bond 2010), *Astrapothericulus* Ameghino, 1901 (Santacrucian, Argentina: MACN A52-405; Kramarz 2009) and *Parastrapotherium* (Deseadan SALMA, Argentina: MACN A52-506), but is similar to i1s of the early astrapotheriid *Astraponotus* (Mustersan/Deseadan SALMA, Argentina; MLP 52-XI-4-151-160). *Granastrapotherium* is devoid of any incisor (Johnson & Madden 1997). The incisors referred to *Xenastrapotherium* from the Honda Group, Colombia, have shallow median grooves restricted to the distal half of the crown, which disappear before late stages of wear (direct observation by C.G., UCMP, Bogotá). Given the stratigraphical context of IN-DTC 20, MUSM 1466 cannot be referred to *Astraponotus*; its morphology would be consistent with that of *Xenastrapotherium*.

Following Johnson & Madden (1997), two species are referred to *Xenastrapotherium* in the middle Miocene of northern South America, but *X. amazonense* Paula Couto, 1976 (Brazil) might be a junior synonym of *X. kraglievichi* Cabrera, 1929 (Colombia). However, given the present sample and pending a taxonomic revision of the genus, we refer to the corresponding remains as *Xenastrapotherium* sp.

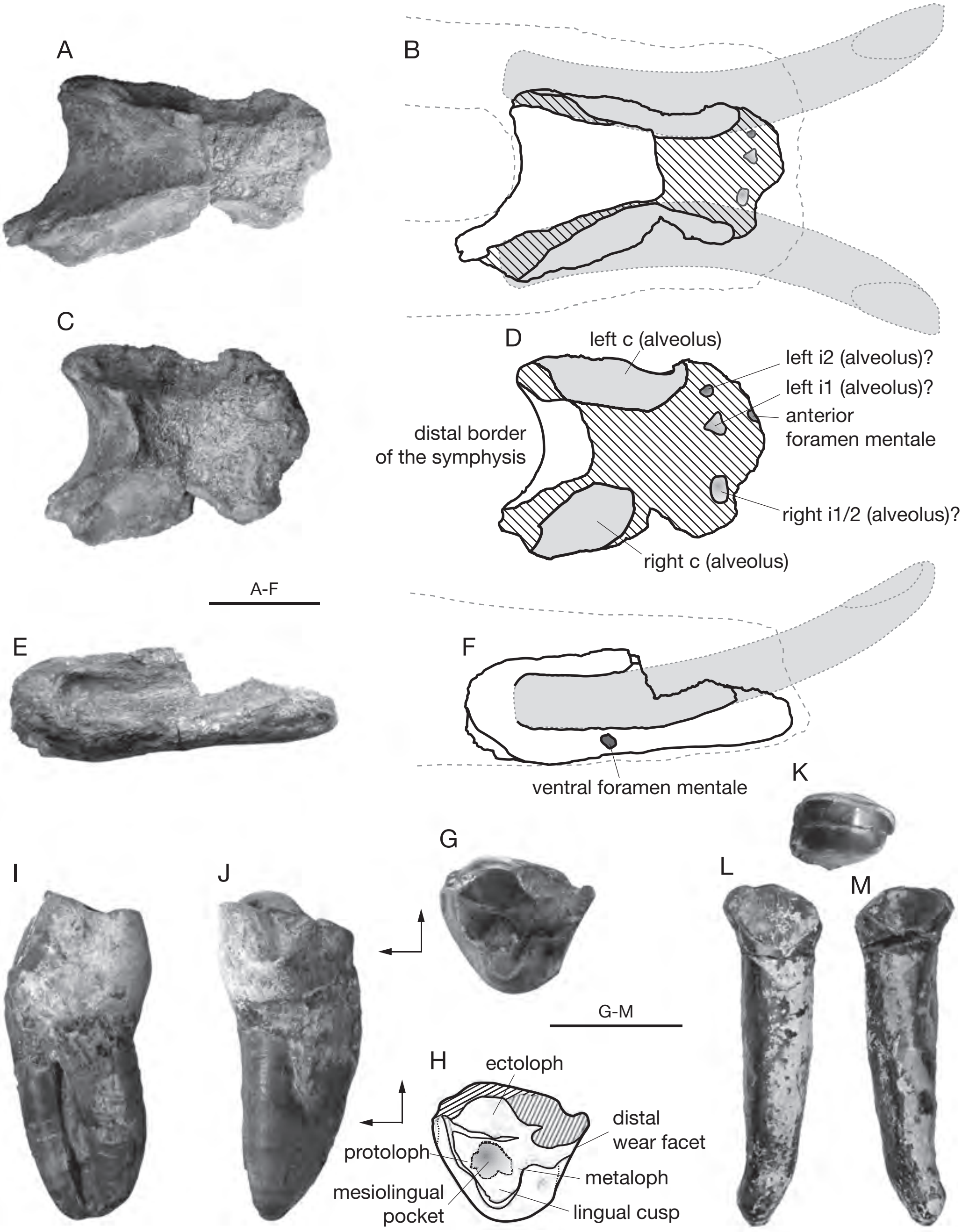

FIG. 2. — *Xenastrapotherium* sp. from the late middle Miocene Fitzcarrald local fauna, Peruvian Amazonia: **A**-**F**, edentulous symphysis with canine alveoli (MUSM 1468), IN-DTC 20 locality; **A**, dorsal view; **B**, interpretative reconstruction with canines, same view; **C**, rostro-dorsal view; **D**, interpretative reconstruction with alveoli of anterior teeth, same view; **E**, right lateral view; **F**, interpretative reconstruction with canines, same view; **G**-**J**, left P3 without ectoloph (MUSM 1467), IN-DTC 37 locality; **G**, occlusal view; **H**, interpretative sketch of the occlusal view, with main observed features; **I**, mesiolingual view; **J**, distal view; **K**-**M**, left i1 (MUSM 1466), IN-DTC 20 locality; **K**, occlusal view; **L**, labial view; **M**, lingual view. Leftward and upward arrows show mesial and labial sides, respectively. Scale bars: A-F, 50 mm; G-M, 20 mm.

Genus *Granastrapotherium*
Johnson & Madden, 1997

TYPE AND ONLY SPECIES. — *Granastrapotherium snorki* Johnson & Madden, 1997 from the middle Miocene of Colombia, by original designation.

Granastrapotherium* cf. *snorki
(Fig. 3)

Granastrapotherium snorki (partim) – Antoine *et al.* 2007: 21.

Granastrapotherium snorki – Negri *et al.* 2010: 247.

MATERIAL EXAMINED. — Left broken M2, without ectoloph (MUSM 994), IN-DTC 28 locality (float); fragmentary ectometaloph of a left M3 (MUSM 1477), IN-DTC-32 locality.

LOCALITY AND DISTRIBUTION. — Río Mapuya, 14 km upstream the confluence with Río Inuya (IN-DTC 28) and 7 km upstream the latter locality (IN-DTC-32), Atalaya Department, Ucayali, Peru, and Río Inuya.

FORMATION AND AGE. — Ipururo Formation, late middle Miocene, *c.* 13 Ma (Antoine *et al.* 2007; Espurt *et al.* 2010).

DESCRIPTION

MUSM 994 is a worn and broken tooth, lacking its labial part and its roots. The crown as a whole, except where worn or broken, is surrounded by finely wrinkled enamel (Fig. 3A). The complete crown is elongate sagittally. In occlusal view, the labial third of the crown is broken; the protoloph is nearly parallel to the preserved part of the ectoloph; the anterior and posterior sides make an angle of *c.* 45° converging lingually; the protocone and the labial part of the protoloph are very large at this advanced wear stage; the protocone is constricted anteriorly by a large valley and it shows a lingual groove (Fig. 3B); a bulge is observed on the lingual side of the ectoloph; a large median valley opens lingually; a thick hypocone joins the ectoloph, thus forming a metaloph, separate from the ectoloph by a sharp groove; no lingual cingulum can be observed; thickness of the enamel varies from 0.5 mm on the lingual side of the ectoloph to 1.7 mm on the anterior side of the protocone. The tooth is 60 mm long and its estimated dimensions once reconstructed (Fig. 3C) are 70 mm (ectoloph MDL), 60 mm (anterior LLL), and 38 mm (posterior LLL).

MUSM 1477 is the posterior part of the ectoloph of an M3, with a sharp and oblique occlusal edge. The enamel is finely striated vertically. The preserved height reaches 73 mm.

COMPARISON

MUSM 994 is "∏-shaped" (two transverse lophs and an ectoloph) and brachydont, and it displays a mesial valley (anterior constriction of the protocone), which allows us to interpret it as an upper molar of an astrapothere, rather than a toxodont tooth (Fig. 3). The protocone is large and conical and the lingual valley is deep; despite the advanced stage of wear, its sagittal elongation tends to indicate MUSM 994 is not an M1, while the presence of a conspicuous metaloph-hypocone crest impedes identifying it as a M3 either. On the other hand, the general shape of the tooth fits perfectly M2s of uruguaytheriine astrapotheres (Johnson & Madden 1997). There is no lingual cingulum, contrarily to what is observed in all astrapotheriids, including *Xenastrapotherium* (Johnson & Madden 1997; Kramarz & Bond 2009). Together with the large size of the tooth (*c.* 70 × 60 mm, i.e. exceeding by 10% the largest M2 referred to *X. kraglievichi*, but coinciding with the mean value for *G. snorki*; Johnson & Madden 1997: tables 22.1; 22.4), the absence of lingual cingulum strongly supports the assignation of MUSM 994 to *Granastrapotherium*. Accordingly, due to its very large dimensions (*c.* 30% larger than M3s of *X. kraglievichi*; Johnson & Madden 1997; pers. obs. CG 2008), the fragmentary ectometaloph MUSM 1477 is likely to document the same large-sized taxon, tentatively referred to as *Granastrapotherium* cf. *snorki*.

DISCUSSION

AGE OF THE FITZCARRALD LOCAL FAUNA, EASTERN PERU

The specimens described in the present work substantiate the uruguaytheriine astrapotheriid record in Amazonian Peru, primarily based on float specimens from the Río Inuya/Mapuya area mentioned by Willard (1966) and subsequently referred to "cf. *Granastrapotherium*" by Johnson & Madden (1997). The new remains document two uruguaytheriine taxa: *Xenastrapotherium* sp. and *Granastrapotherium* cf. *snorki*. In northern South America, bispecific astrapotheriid assemblages were so far restricted to the early Miocene of Venezuela (Castillo Formation; Sánchez-Villagra *et al.* 2004), and the late middle Miocene of Colombia (Honda Group; Johnson & Madden 1997).

Such co-occurrence recalls unequivocally the *Xenastrapotherium kraglievichi-Granastrapotherium snorki* assemblage, which characterizes the late middle Miocene "*Miocochilius* Assemblage Zone" of La Venta, Colombia (Johnson & Madden 1997; Madden *et al.* 1997). By the way, the Fitzcarrald local fauna also includes other biostratigraphical markers of the Laventan SALMA (13.5-11.8 Ma), such as the small interatheriid notoungulate *Miocochilius anomopodus* Stirton, 1953, the large toxodontid notoungulate *Pericotoxodon platignathus* Madden, 1997, and the dinomyid rodents "'*Olenopsis*' sp., large" *sensu* Walton 1997 and "*Scleromys*" *schurmanni sensu* Walton 1997 (Antoine *et al.* 2007). This assemblage as a whole further points to the 13.6-12.76 Ma interval in the Honda Group of Colombia (C5ABn-C5Ar.2r chrons; Madden *et al.* 1997: fig. 29.6; Gradstein *et al.* 2005: 68, table 5.2). To a lesser extent, the Fitzcarrald local fauna resembles the Quebrada Honda assemblage of southern Bolivia, which notably yields another species of *Miocochilius*, *M. federicoi* Croft, 2007, and a large uruguaytheriine astrapotheriid (Antoine *et al.* 2007; Croft 2007).

THE ASTRAPOTHERIID FOSSIL RECORD IN NORTHERN SOUTH AMERICA

The spatio-temporal distribution of uruguaytheriine astrapotheres is illustrated in the Figure 4 and further detailed in the section below. In high- and middle-latitudes (> 30°S; mostly from Argentina and Chile), the last astrapotheriids are reported during the "Friasian" stage (e.g., Pascual & Odreman Rivas 1971). This informal stage represents a short interval intercalated between the late early Miocene Santacrucian SALMA and the early middle Miocene Colloncuran SALMA (Flynn *et al.* 2002, 2008; Croft 2007; Forasiepi *et al.* 2009; Kramarz & Bond 2009). Therefore, uruguaytheriines as conspicuous

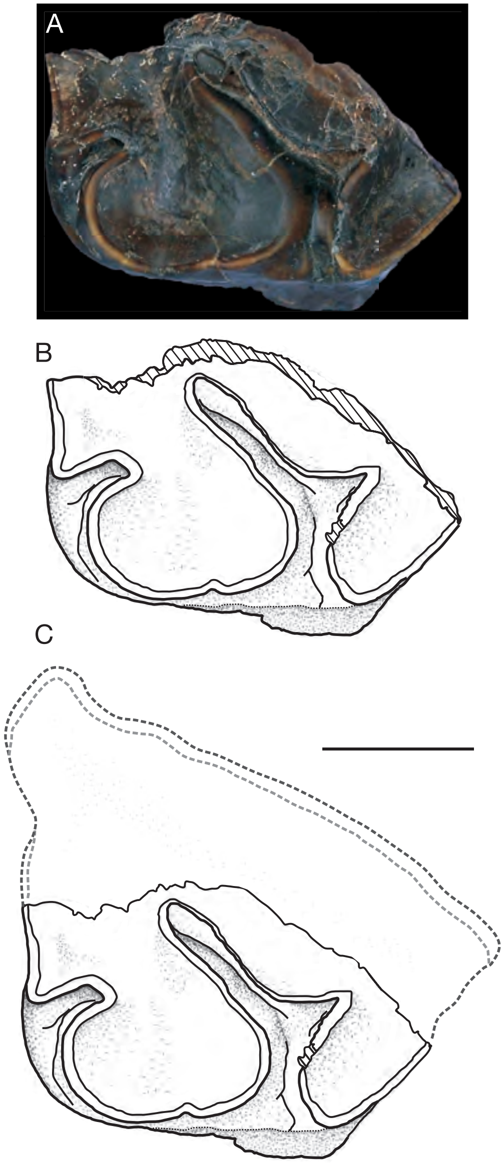

FIG. 3. — *Granastrapotherium* cf. *snorki* from the late middle Miocene Fitzcarrald local fauna, Peruvian Amazonia. Left broken M2 without ectoloph (MUSM 994), IN-DTC 28 locality (float): **A**, occlusal view; **B**, interpretative sketch of the occlusal view; **C**, tentative reconstruction of the whole tooth. Scale bar: 20 mm.

elements of the mammalian faunas are the last well-documented representatives of Astrapotheria, throughout the late middle Miocene (Laventan SALMA; Johnson & Madden 1997). They might persist until middle late Miocene times (Huayquerian SALMA) in Venezuela and Amazonian Brazil, with fragmentary remains only identified at family level and likely to be reworked or misidentified (Frailey 1986; Linares 2004; Carlos Jaramillo pers. com. 2008).

Xenastrapotherium is widely distributed, both stratigraphically (ranging at least from the early Miocene to the late middle Miocene) and geographically (Venezuela, Colombia, Ecuador, Brazil, and Peru; Fig. 4). *Xenastrapotherium chaparralensis*, from the Chaparral local fauna of Colombia (Tuné Formation, Tolima Department), was formerly considered as the earliest uruguaytheriine, dating back from the Deseadan (Stirton 1953). The associated mammalian assemblage suggests this fauna is rather Colhuehuapian or early Santacrucian in age (early Miocene; Johnson & Madden 1997: 365).

A single mandible described by Stehlin (1928) documents *X. christi*. It originates from the "Cucharo Formation", near Zaraza, northeastern Guárico State, Venezuela (Stehlin 1928; Simpson 1940). This formation was later synonymized with the Chaguaramas Formation, which spans the late Oligocene-early Miocene interval (Isea 1987). As such, *X. christi* might be the earliest uruguaytheriine with *Uruguaytherium*, for which an Oligocene age cannot be discarded either (see hereafter; Simpson 1940).

Xenastrapotherium aequatorialis is also known only by a partial right mandible with m1-m2, "reported to have been collected along the banks of the Río Burgay [...] 1 km south of Biblián, Province of Cañar, Ecuador" (Johnson & Madden 1997: 362). Several K-Ar datings on andesitic lavas at the top of the Biblián Formation, which crops out in that area, constrain an early Miocene age for this mandible (>19.7 ± 0.5 Ma; for review see Lavenu *et al.* 1995).

By contrast, the mandibular and dental morphology of *X. kraglievichi* is well documented, with about three dozens referred specimens from various localities of the Villavieja Formation, La Venta area, Colombia (Johnson & Madden 1997). Following the same authors and Madden *et al.* (1997: 508, fig. 29.5), a right M3 originating from the uppermost vertebrate locality of the underlying La Victoria Formation, in the same area, is also referable to *X. kraglievichi*. The corresponding stratigraphical interval is magnetostratigraphically constrained, and ranging from 13.183 up to 12.73 Ma (Madden *et al.* 1997; Gradstein *et al.* 2005).

Xenastrapotherium amazonense is known by a maxillary fragment with M3 from Pedra Pintada locality (Paula Couto 1976) and several teeth from Cachoeira locality (= Torre Da Lua; Rancy 1981) found on banks of the Alto Río Juruá, in Amazonian Brazil (Paula Couto 1976, 1982; Johnson & Madden 1997; Negri *et al.* 2010). Several fragmentary teeth originating from surrounding localities were either referred to as "?*Synastrapotherium amazonense*" by Paula Couto (1976), "Astrapotheriinae indet." (*sensu* Simpson 1945, i.e. corresponding to Astrapotheriidae *sensu* McKenna & Bell 1997) by Rancy (1981), or Astrapotheriidae *incertae sedis* by Paula Couto (1982). All these remains originate from middle or early late Miocene deposits of the Rio Juruá-Río Breu confluence area, at the Peruvian border (Paula Couto 1976, 1982; Negri *et al.* 2010).

At last, the present work extends the geographical range to Amazonian Peru, with *Xenastrapotherium* sp. reported here from the Fitzcarrald local fauna (late middle Miocene, eastern Peru), in deposits roughly coeval to the Alto Juruá fossiliferous levels (Fig. 4; Negri *et al.* 2010).

Granastrapotherium s.s. was so far restricted to the middle Miocene Honda Group of Colombia, with *c.* 30 cranio-dental and postcranial remains referred to *G. snorki*, ranging from the base of La Victoria Formation (near Coima, Tolima Department) up to the Polonia Red Beds of the upper Villavieja Formation in La Venta area, 50 km more to the South (Johnson & Madden 1997; Madden *et al.* 1997). From a chronostratigraphical point of view, the corresponding interval ranges from 13.734 Ma up to 12.82 Ma (Madden *et al.* 1997; Gradstein *et al.* 2005). *Granastrapotherium* is the only uruguaytheriine for which appendicular skeleton is somewhat available (Johnson & Madden 1997). In addition, two craniodental specimens collected

FIG. 4. — Location map and fossil record of northern South American Astrapotheriidae Ameghino, 1887, based on data from Kraglievich (1928), Stehlin (1928), Scott (1937), Simpson (1940), Paula Couto (1976, 1982), Rancy (1981), Frailey (1986, 1987), Isea (1987), Johnson & Madden (1997), Flynn *et al*. (2002, 2008), Sánchez-Villagra *et al*. (2004), Weston *et al*. (2004), Antoine *et al*. (2007), Croft (2007), and Negri *et al*. (2010). Abbreviations: **LO**, late Oligocene; **EM**, early Miocene; **MM**, middle Miocene; **LM**, late Miocene.

by Willard (1966) in the Río Inuya/Mapuya area of eastern Peru – without stratigraphical control neither opportunity for comparing the present specimens – document a close ally, referred to as cf. *Granastrapotherium* by Johnson & Madden (1997). The remains described in the present work originate unambiguously from the same levels and might document the same taxon (*Granastrapotherium* cf. *snorki*).

Uruguaytherium beaulieui Kraglievich, 1928 is the type and only species referred to *Uruguaytherium*. It is based on a single specimen, a left mandible with m2-m3 originating from an unknown locality of western Uruguay ("Río Negro Dept."), assumed to be either Oligocene or Miocene in age (Kraglievich 1928; McKenna & Bell 1997).

Other astrapotheriid remains with uncertain taxonomic affinities were reported from several Miocene localities of northern South America in the last decades (Fig. 4): a bispecific assemblage based on five postcranials from the early Miocene Castillo Formation is described at Cerro La Cruz, western Venezuela ("Astrapotheriidae indet. A" and "Astrapotheriidae indet. B"; Sánchez-Villagra *et al.* 2004; Weston *et al.* 2004).

A large uruguaytheriine occurs in the middle Miocene of Quebrada Honda, South Bolivia: Hoffstetter (1977) first referred several isolated teeth to the "*Uruguaytherium-Xenastrapotherium* group". Then, a badly preserved neurocranium, larger than those of *Astrapotherium*, was described as belonging to "?*Xenastrapotherium*" by Frailey (1987). Given the large dimensions of the corresponding remains, notably its bizygomatic width, referral to the latter genus was discarded for the benefit of "Uruguaytheriinae, gen. et sp. incertae sedis" (Johnson & Madden 1997: 377). The age of the concerned deposits is extrapolated at *c.* 12.7-13.0 Ma (K/Ar and magnetostratigraphy; MacFadden *et al.* 1990), which coincides with the middle part of the late middle Miocene Laventan SALMA (Croft 2007).

To our knowledge, only two late Miocene astrapotheriid mentions are reported in the literature. "Astrapotheriidae indet. A" and "Astrapotheriidae indet. B" – distinct from the unidentified astrapotheriids found in association in the early Miocene of western Venezuela (Fig. 4), as reported by Weston *et al.* (2004) and discussed above – occur in the middle and the upper member of the Urumaco Formation of Northern Venezuela, respectively (Linares 2004). The nature and number of the corresponding remains (grouped as "Astrapotheriidae indet." in Figure 4) are not detailed, except that they are badly preserved and/or fragmentary, which might indicate they are reworked from underlying formations of the same area, such as the Laventan Socorro Formation, as it often occurs (Linares 2004; Carlos Jaramillo pers. com. 2008). Owing to mammalian and foraminiferan biochronology, the concerned deposits are assumed to be middle late Miocene in age (Chasicoan-Huayquerian SALMAs; Linares 2004).

At last, an upper canine originating from the late Miocene Río Acre local fauna of Amazonian Brazil (Huayquerian SALMA; Cozzuol 2006), originally identified as "*Xenastrapotherium amazonense*" by Frailey (1986, fig. 26D), was subsequently "referred only questionably to Astrapotheria" (Johnson & Madden 1997: 366).

To sum up, the late Miocene astrapotheriid record is far from being well constrained, and a late middle Miocene – Laventan – age for the Last Appearance Datum of Astrapotheria cannot be discarded to date.

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