THE MIDDLE MIOCENE (LAVENTAN) QUEBRADA HONDA FAUNA, SOUTHERN BOLIVIA AND A DESCRIPTION OF ITS NOTOUNGULATES

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Abstract: The Laventan Quebrada Honda Fauna of southern Bolivia is one of the best sampled middle Miocene South American faunas. The present study describes the toxodontid, interatheriid and mesotheriid notoungulates from Quebrada Honda and summarizes the present state of knowledge of the fauna. Toxodontid specimens from Quebrada Honda include two isolated molars, one upper and one lower. The upper molar compares favourably with *Paratrigodon* and may represent a new species, but too little material is known to make an adequate diagnosis. The lower molar may pertain to the same taxon, or to a distinct species that is even more poorly represented. A new species of the interatheriid *Miocochilius* is described, *M. federicoi*, on the basis of a partial skull. It differs from *M. anomopodus* in its significantly smaller size (at least 20 per cent smaller based on linear upper molar dimensions); relatively wider P4 with deeper lingual sulcus; more prominent middle lobes on upper molars; and M3 with deeper lingual sulcus and more prominent metastyle (distal lobe). The generic allocation of this new species is considered tentative, pending a better understanding of the phylogenetic relationships among currently recognized species of *Miocochilius* and *Protypotherium*. Mesotheriids are represented at Quebrada Honda by a pair of poorly preserved mandibles that are referred to *Plesiotypotherium minor*, a species previously recorded from slightly older

deposits near Cerdas, Bolivia. A newly revised faunal list for Quebrada Honda is compiled that includes 30 species of non-volant mammals, 27 of which have been identified to at least genus level. This revised faunal list is used to compare Quebrada Honda to other well-sampled middle–late Miocene faunas (including La Venta, Columbia; Collón-Curá, Argentina; and Arroyo Chasicó, Argentina) using the Simpson Index of faunal similarity. In order to compensate for inadequately identified specimens (i.e. those not identified to genus level), minimum and maximum values of faunal similarly were estimated using two different sets of assumptions. The analysis indicates that the middle-latitude Quebrada Honda Fauna is more similar to the slightly older high-latitude fauna of Collón-Curá than to the contemporaneous low-latitude fauna of La Venta, suggesting that isolating mechanisms between the low and middle latitudes were in place during the early and/or middle Miocene. The relative paucity of taxa shared between Quebrada Honda and La Venta, despite their contemporaneity, suggests that the system of South American Land Mammal 'Ages' (SALMAs) may not be useful for biocorrelation between low-latitude faunas and those from elsewhere in South America.

Key words: biogeography, Bolivia, endemism, Laventan, Miocene, Notoungulata, SALMA.

SOUTH AMERICA is well known for its outstanding fossil mammal record (Simpson 1940, 1980; Patterson and Pascual 1968; Flynn and Wyss 1998). The vast majority of these fossils have come from Argentina, but efforts to broaden geographical sampling during the past several decades have yielded many important new specimens from Bolivia (e.g. Hoffstetter 1969; Villarroel 1974; Mac-Fadden and Wolff 1981; Patterson and Wood 1982; Muizon *et al.* 1983; Villarroel and Marshall 1983; MacFadden *et al.* 1985; Engelmann 1987; Muizon and Marshall 1992; Shockey 1997; Muizon 1999; Muizon and Cifelli 2001; Saint-André and de Iuliis 2001; Shockey and Anaya 2004), Brazil (e.g. Paula Couto 1981, 1982, 1983*a*, *b*; Frai-

ley 1986; Czaplewski 1996; Bergqvist *et al.* 1998, 2004; Oliveira and Bergqvist 1998; Negri and Ferigolo 1999), Chile (e.g. Wyss *et al.* 1993, 1994, 2003, 2004; Flynn *et al.* 1995, 2002*a*, *b*, 2003; Flynn and Wyss 1998, 2004; Croft *et al.* 2003*a*, 2004), Colombia (e.g. Kay *et al.* 1997 and references therein), Ecuador (e.g. Madden *et al.* 1989, 1993, 1994), Perú (e.g. Muizon and McDonald 1995; McDonald and Muizon 2002; Muizon *et al.* 2003, 2004*a*, *b*; Shockey *et al.* 2003; Campbell 2004 and references therein; Pujos and Salas 2004), Uruguay (e.g. Ubilla *et al.* 1994, 1999; Reguero *et al.* 1995, 2003) and Venezuela (e.g. Sánchez-Villagra *et al.* 2000*a*, 2003, 2004; Linares 2004). Despite these endeavours, low- and middle-latitude

South American faunas are unknown for many time intervals and those that are known have generally been sparsely sampled and/or studied only preliminarily. The most conspicuous exception to this pattern is the extraordinary middle Miocene fauna of La Venta, Colombia, which has been the focus of a comprehensive edited volume (Kay *et al.* 1997). It potentially represents 'the best known tropical mammal fauna in the world' (Flynn and Wyss 1998, p. 453) and sets a standard for synthetic taxonomic, geological and palaeoecological studies. Based on radioisotopic and palaeomagnetic constraints, the La Venta Fauna is middle Miocene in age (13·5–11·8 Ma; Madden *et al.* 1997), and fills what was previously a temporal hiatus in the sequence of Miocene South American Land Mammal 'Ages' (SALMAs).

Faunas slightly older or slightly younger than La Venta have long been known from Argentina, but only one other South American assemblage is definitely known to pertain to the Laventan Stage (i.e. the particular period of time during which the La Venta Fauna was deposited): the Quebrada Honda Fauna of southern Bolivia. Given the great distance between La Venta (*c.* 5° N) and classic middle Miocene faunas from Argentina (*c.* 40° S), 'the geographical position of [Quebrada Honda] at a latitude intermediate between Colombia and Patagonia makes its study of compelling interest' (Madden *et al.* 1997, p. 518). Preliminary faunal lists for Quebrada Honda have been published previously (MacFadden and Wolff 1981; Marshall and Sempere 1991), and a few taxa from the site have been studied in detail (e.g. Sánchez-Villagra *et al.* 2000*b*; Goin *et al.* 2003; Croft and Anaya 2004, 2006), but no published study has compared the fauna of Quebrada Honda to contemporaneous or near-contemporaneous faunas from elsewhere in South America.

The purpose of the present study is threefold: to describe the non-hegetotheriid notoungulates from Quebrada Honda; to produce a revised taxonomic list for the assemblage that incorporates new data from studies published subsequent to Marshall and Sempere's (1991) review; and to compare the Quebrada Honda Fauna to other well-sampled middle–late Miocene South American faunas, including La Venta.

Quebrada Honda is located in southern Bolivia (Text-fig. 1) at *c.* 21°57′ S, 65°25′ W (MacFadden and Wolff 1981). The area was first collected by both Hoffstetter and Villarroel in 1976, and the first report on the fauna was published by Hoffstetter the following year (Hoffstetter 1977). A team from the University of Florida visited the locality in 1978, and published a preliminary report on the fauna several years later (MacFadden and Wolff 1981). This report also included a description of the geology of the area, and indicated the presence of a second site, Río Rosario, *c.* 5 km distant from the original locality (MacFadden and Wolff 1981). A team from the Research Institute of
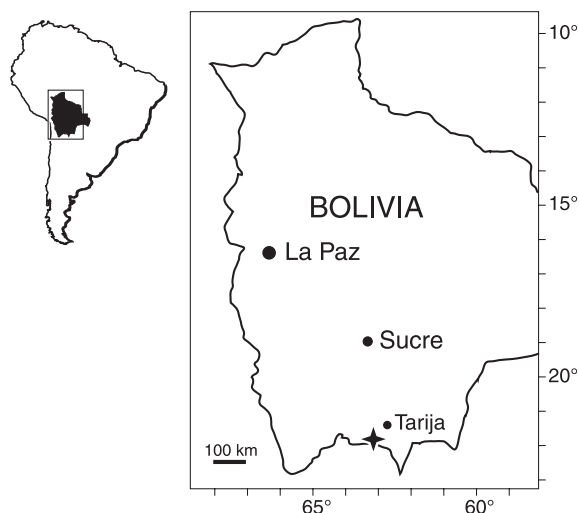
TEXT-FIG. 1. Map showing location of Quebrada Honda (star) south-west of Tarija, Bolivia (Croft and Anaya 2006). Boxed area in map of South America (left) is represented by inset map (right).

Evolutionary Biology (Tokyo) made a small collection from Quebrada Honda in 1982 and published preliminary descriptions of the specimens two years later (Takai *et al.* 1984). More detailed treatments of the astrapotheres (Frailey 1987) and the xenarthrans (Frailey 1988) from the University of Florida collections followed. Palaeomagnetic and radioisotopic data for Quebrada Honda were reported in 1990 (MacFadden 1990), providing an extrapolated age for the fauna of 12·7–13·0 Ma, contemporaneous with La Venta (Text-fig. 2). This report also indicated that the original Quebrada Honda site and Río Rosario were probably of equivalent age, though the two could not be definitively correlated stratigraphically; since no faunal differences between the two sites have been reported, they are considered a single fauna for the purposes of the present study. A slightly revised faunal list for Quebrada Honda was included in Marshall and Sempere's (1991) review of Tertiary vertebrate localities in Bolivia, and this is the most recent account of the taxa known from the area. Several publications since 1991 have examined specific Quebrada Honda marsupials (Sánchez-Villagra *et al.* 2000*b*; Goin *et al.* 2003), xenarthrans (Scillato-Yané and Carlini 1999) and notoungulates (Croft and Anaya 2004), and unpublished identifications have been made of other marsupials (A. Forasiepi, pers. comm. 2005) and of the rodents.

MATERIAL AND METHODS

Middle Miocene faunas in South America have traditionally been grouped together in a single informal biochronologic unit, the Friasian SALMA. The Friasian

('étage friaséen') was first used by Ameghino (1906) in reference to a fauna discovered by Santiago Roth (1899, 1908) at the headwaters of the 'Río Frias' (more properly known as the Río Cisnes; Marshall 1990) in southern Chile. Kraglievich (1930) reviewed Roth's fauna and other similarly aged assemblages from Patagonian Argentina (e.g. Río Collón-Curá, Río Fénix, Río Mayo) and grouped them together as the Formación (Ciclo Faunístico) Friaseana; within this formation he distinguished several horizons including the Colloncurense, Friasense and Mayoense. Simpson (1940) recognized the Friasian in his review of the mammal-bearing Tertiary of South America, and only tentatively recognized the Colloncuran and 'Mayan' stages. By the publication of Patterson and Pascual's (1968) landmark review of South American mammal evolution, the Friasian had come to encompass all faunas appearing (based on the 'stage of evolution' of the mammals) to be younger than the Santacrucian SALMA but older than the Chasicoan SALMA, including the Colloncurense and the Mayoense. Most subsequent publications (e.g. Pascual and Odreman Rivas 1971; Marshall *et al.* 1983; MacFadden 1990; Marshall 1990; Pascual and Ortiz Jaureguizar 1990) essentially followed this same scheme. A series of more recent efforts to clarify the chronology of Miocene SALMAs (Flynn and Swisher 1995; Madden *et al.* 1997) have once again recognized the distinctiveness of Kraglievich's (1930) horizons and have suggested that the Friasian *sensu lato* be subdivided into more restricted units including a Friasian *sensu stricto* (i.e. the period of time represented by the type locality in Chile) and several units based on other middle Miocene faunas (Text-fig. 2). It is this arrangement of SALMAs that is followed in the present study.

The fossil specimens described below are housed in the vertebrate palaeontology collections of the Museo Nacional de Historia Natural in La Paz, Bolivia. Measurements of these and other specimens were made to the nearest 0·1 mm using a digital caliper, unless otherwise noted. Comparative data were gathered from original specimens housed in various North and South American museums (see 'Institutional abbreviations' and 'Acknowledgements') and from the scientific literature.

In the following descriptions, upper tooth loci are indicated by upper-case letters (e.g. I1, P2, M1) and lower tooth loci by lower-case letters (e.g. i1, p2, m1). The terminology for toxodontid molar morphology follows Madden (1990). Diagnoses list the character states used to refer specimens to the cited clades and are generally abbreviated (relative to the complete diagnosis of the taxon) owing to the incomplete nature of the specimens. Following Croft *et al.* (2004), the distribution cited for each taxon is based on firsthand observations and published sources.
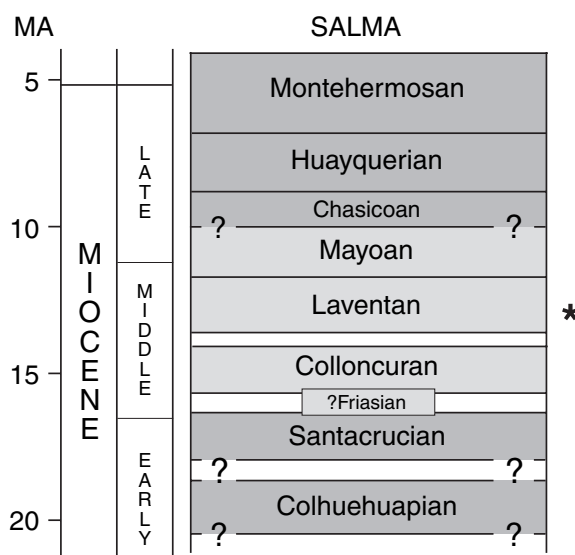
TEXT-FIG. 2. Chronology of Miocene South American Land Mammal 'Ages' (SALMAs) followed in this study, with the extrapolated age of the Quebrada Honda Fauna indicated by an asterisk (*). The SALMA chronology and approximate dates follow Flynn and Swisher (1995), although the Santacrucian SALMA has been extended to earlier than 17·5 Ma based on revised mammal identifications and new radioisotopic dates associated with the Santacrucian Chucal Fauna of northern Chile (Bond and García 2002; Croft *et al.* 2004). The lightly shaded SALMAs (Friasian *sensu stricto*, Colloncuran, Laventan and Mayoan) are those that have previously been subsumed within the Friasian *sensu lato*.

Institutional abbreviations. FLMNH, Florida Museum of Natural History, Gainesville; FMNH, Field Museum of Natural History, Chicago; GB, Servicio Geológico de Bolivia (housed at the Museo Nacional de Historia Natural, La Paz); MLP, Museo de La Plata, Argentina; MNHN, Museo Nacional de Historia Natural, La Paz; MNHN-P, Muséum National d'Histoire Naturelle, Paris; PU, Princeton University Collection (now housed at Yale University, New Haven, Connecticut).

SYSTEMATIC PALAEONTOLOGY

NOTOUNGULATA Roth, 1903
TOXODONTIA Owen, 1853
TOXODONTIDAE Gervais, 1847
TOXODONTINAE Owen, 1845

Diagnosis (molar characters only). Toxodontines differ from nesodontines (*sensu* Nasif *et al.* 2000) and more basal toxodontids (e.g. *Proadinotherium*) in presence of persistently rootless (i.e. ever-growing) molars; presence of simple ectolophs; absence of fossettes and fossettids; and absence of protocone and metacone confluence with wear.

Remarks. Toxodontids comprise a diverse family of not-oungulates that ranged throughout South America during the Miocene, Pliocene and early Pleistocene (Patterson and Pascual 1968; Cifelli 1985; Madden 1997; Croft 1999). Because of their generally large size, fossil remains of toxodontids are relatively common (Croft *et al.* 2003*a*). Many of these remains are fragmentary and have formed the basis for a variety of poorly founded taxa (Madden 1990). The combination of high species diversity within the group and poorly characterized species has obscured the interrelationships among toxodontid taxa and the status of many traditionally recognized subclades (e.g. subfamilies). Madden (1990) provided a thorough review of the history of the family and included taxa, but a brief summary is included below.

Over the past century or so, the group presently recognized as Toxodontidae has been subdivided into as many as five subgroups (subfamilies): Nesodontinae, Xotodontinae, Toxodontinae, Haplodontheriinae and Dinotoxodontinae. These five clades were supported in Madden's (1990, 1997) cladistic analysis of toxodontid relationships, but subsequent authors (e.g. Saint-André 1993; McKenna and Bell 1997; Nasif *et al.* 2000) have questioned the validity and/or composition of nearly all of these. Most recently, Nasif *et al.* (2000) performed a cladistic analysis of 20 toxodontid genera and proposed that only two toxodontid subfamilies should be recognized: Nesodontinae (*Nesodon* and *Adinotherium*) and Toxodontinae (including 17 of the remaining 18 genera). Although three minor clades were supported within this more broadly conceived Toxodontinae (Nasif *et al.* 2000), none closely conformed to any of the subfamilial grouping outlined by Madden (1990, 1997). Pending further clarification of toxodontid subfamilial membership, the present study follows Nasif *et al.* (2000) in recognizing a Toxodontinae clade that also includes taxa previously referred to Xotodontinae, Haplodontheriinae and Dinotoxodontinae.

Genus PARATRIGODON Cabrera and Kraglievich, 1931

Type species. *Paratrigodon euguii* Cabrera and Kraglievich, 1931, from the Arroyo Chasicó Formation, Arroyo Chasicó, Argentina.

Included species. The type only.

Age and distribution. Vivero (Lower) Member, Arroyo Chasicó Formation, Buenos Aires, Argentina, late Miocene age, Chasicoan SALMA (Cabrera and Kraglievich 1931; Pascual 1965; Bondesio *et al.* 1980*a*); unnamed formation (Quebrada Honda Fauna), southern Bolivia, middle Miocene age, Laventan SALMA (present study).

Diagnosis (M1/M2 characters only). Differs from all other toxodontines except *Ocnerotherium*, *Pisanodon* (= *Palaeotoxodon*), *Xotodon* and *Gyrinodon* in having upper molars with a single simple (i.e. non-bifurcating) lingual primary enamel fold and a smooth distolingual sulcus (i.e. no enamel plication as in *Toxodon* and *Hoffstetterius*). Differs from *Ocnerotherium*, *Pisanodon* and *Xotodon* in presence of lingual pillar on protoloph (Madden 1990; Nasif *et al.* 2000). Differs from *Gyrinodon* in presence of distolingual pillar on metaloph (Madden 1990).

Remarks. Cabrera and Kraglievich (1931) named *Paratrigodon* based on a partial skull (MLP 12-1664) from the Vivero (Lower) Member of the late Miocene Arroyo Chasicó locality (Buenos Aires province, Argentina). The name was in reference to the late Miocene–early Pliocene horned toxodontid *Trigodon*, a taxon with which *Paratrigodon* shared several characteristics, including the possible presence of a median horn (Cabrera and Kraglievich 1931; Kraglievich 1934). Only a brief description of the taxon was provided in the original publication, but a much more complete treatment was provided by Pascual (1965) in his analysis of the toxodontids from Arroyo Chasicó. The occurrence of *Paratrigodon* in the middle Miocene of Bolivia would represent a slight temporal increase in the range of this taxon (*c.* 2–3 Ma; Text-fig. 2) and would also extend its geographical range into the middle latitudes.

cf. *Paratrigodon* sp.
Text-figure 3A–B

Referred material. MNHN 6542, right M1 or M2.

Locality and horizon. Level 3, Quebrada Honda.

Description. MNHN 6542 is a well-preserved complete M1 or M2. It measures 48·3 × 27·0 mm (length × width). The ectoloph is nearly straight, as is the mesial face of the protoloph. The protoloph is separated from the remainder of the tooth by a simple, straight primary enamel fold, and is closely appressed to the metaloph. A lingual pillar is present. A slight inflection (concavity) exists on the lingual surface of the tooth just distal to the primary enamel fold. Distal to this concavity is a weakly developed posterior lingual pillar. The distal face of the tooth is straight and joins the ectoloph at an angle of *c.* 110 degrees. Enamel extends from the occlusal surface to the base of the tooth (which is rootless) but is restricted to the ectoloph, the mesial face and the distolingual face.

Remarks. The accurate identification of isolated notoungulate teeth, especially those from hypsodont or hypselodont taxa, can be quite difficult (Madden 1990; Croft

et al. 2003b). Thus, such identifications inspire only limited confidence. That being said, MNHN 6542 appears to most closely resemble *Paratrigodon* among well-characterized toxodontines. The presence of a non-bifurcate primary lingual fold distinguishes this specimen from a variety of other toxodontines including contemporaneous *Pericotoxodon* (La Venta, Colombia; Madden 1997) and nearly contemporaneous *Palyeidodon* (Patagonia, Chile and Argentina; Madden 1990). This specimen is further distinguished from *Pericotoxodon* by its relatively small protoloph pillar and its relatively large metaloph pillar. MNHN 6542 is broadly similar to *Ocnerotherium* (central Argentina) but has a broader metaloph and a much less pronounced distolingual sulcus. The specimen could potentially pertain to *Gyrinodon* (Venezuela) but is broader distally and has a less developed protoloph pillar. Additional material of *Gyrinodon* would certainly aid comparisons; it is only known from a few isolated teeth, an undescribed partial mandible and some postcranial elements.

Although MNHN 6542 appears to be most similar to *Paratrigodon* among toxodontines, it does exhibit some differences compared with the only described species, *P. euguii*. In size, MNHN 6542 is *c.* 20–30 per cent larger than the corresponding tooth of the holotype specimen, MLP 12-1664. This is outside the expected range of variation for *P. euguii*, but the relatively small number of specimens precludes a rigorous comparison. MNHN 6542 also differs from *P. euguii* in shape; the ectoloph meets the distal face at a slightly more acute angle in the former than in the latter. The taxonomic relevance of this character is unknown, however. Taken together, these differences suggest that this specimen may pertain to a species distinct from, but closely related to, *P. euguii*. Given the temporal and geographical differences between Quebrada Honda and Arroyo Chasicó, this would not be unexpected.

Gen. et sp. indet.
Text-figure 3C

Referred material. MNHN 6543, left mandibular fragment bearing a mostly complete left m1 or m2.

Locality. Río Rosario.

Diagnosis. Differs from all toxodontines represented by lower dentitions except *Palyeidodon* and *Pericotoxodon* in having a buccal talonid face that is smoothly tapered mesially and forms a slightly rounded right angle distally (Madden 1990). Differs from *Palyeidodon* and *Pericotoxodon* in absence of a sharply angled distobuccal trigonid and presence of an enlarged metaconid.
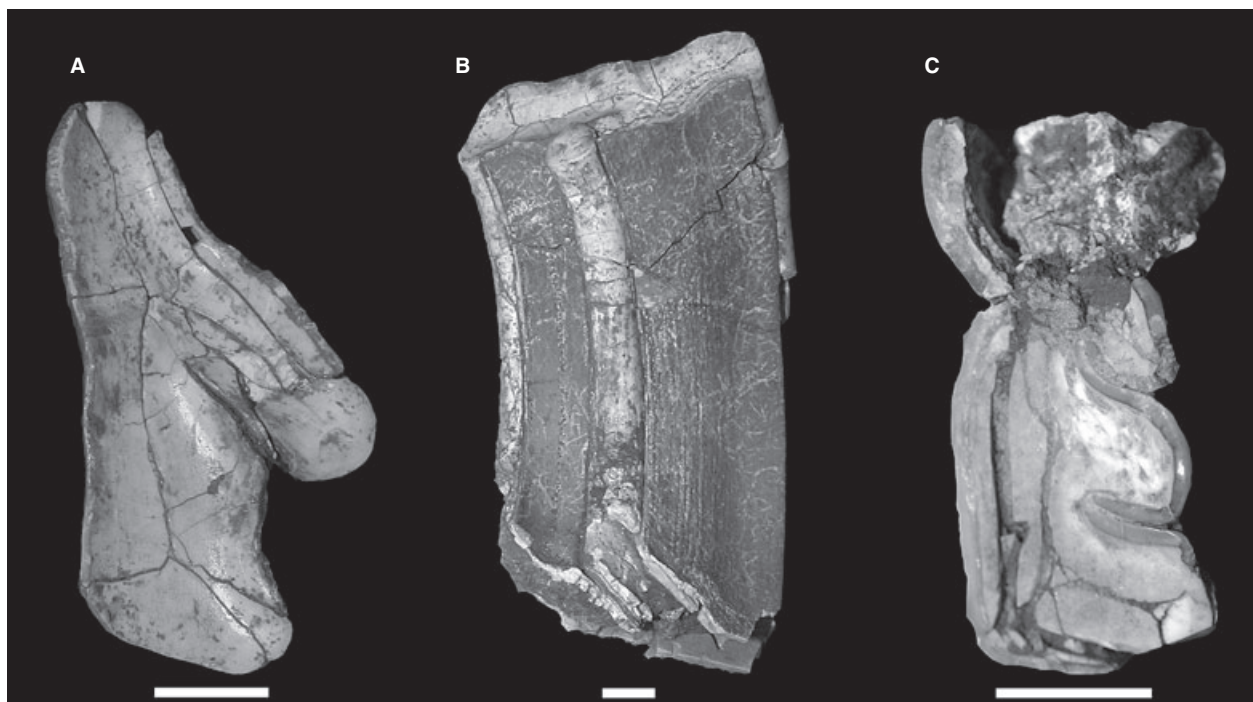
TEXT-FIG. 3. Toxodontid teeth from Quebrada Honda, Bolivia. A, occlusal view of MNHN 6542, a right upper M1 or M2 referred to cf. *Paratrigodon* sp. B, lingual view of MNHN 6542. C, occlusal view MNHN 6543, a left m1 or m2 of an indeterminate toxodontid. All scale bars represent 1 cm.

Description. MNHN 6543 is a left mandibular fragment bearing a mostly complete left m1 or m2; the mesiolingual portion of the trigonid is damaged and the buccal face has separated slightly from the remainder of the trigonid. It measures *c.* 32 × 15 mm (length × width). The buccal face is generally straight and flat except for a broad, deep, smoothly contoured, symmetrical groove separating the trigonid and the talonid. The buccal face of the trigonid itself is gently convex. Owing to damage and incomplete preparation, the remaining morphology of the trigonid cannot be ascertained with confidence. The meta-entoconid fold is well developed and is directed both buccally and mesially; it delineates the distal face of a robust metaconid. The ento-hypoconid fold is also well developed and is primarily directed buccally. The entolophid is nearly square, with its mesiodistal breadth approximately equal to its buccolingual breadth. The distal face of the tooth is roughly perpendicular to the ectoloph and the angle formed by the two is only slightly rounded. Enamel covers the entire buccal face of the tooth and extends approximately half-way along the buccal side of the distal face. Lingually, enamel extends from at least the mesial end of the metaconid to just distal to the ento-hypoconid fold (comprising *c.* 52 per cent of total tooth length).

Remarks. The combination of character states present in MNHN 6543 appears to be unique among known Toxodontidae. However, not all toxodontines are known from mandibular specimens (e.g. *Paratrigodon*) and it is therefore possible that MNHN 6543 pertains to such a species. It is also possible that the smoothly tapering distobuccal corner of the trigonid is an artefact of preservation (or lack thereof) and that its morphology is not as distinct as it might appear. Even so, the shape of the distobuccal corner differentiates this specimen from most other toxodontids with the exception of *Palyeidodon* and *Pericotoxodon*. MNHN 6543 clearly differs from *Palyeidodon* in the presence of lingual enamel folds that extend to the base of the tooth (as opposed to forming fossettes) and from *Pericotoxodon* in its expanded metaconid. In overall structure it is perhaps most similar to the recently described *Calchaquitherium* from Catamarca, Argentina (Nasif *et al.* 2000). *Calchaquitherium* and MNHN 6543 share a relatively large metaconid and entolophid but differ in size (*Calchaquitherium* is 25–30 per cent larger mesiodistally) and in buccal morphology (*Calchaquitherium* has a more acute angle separating the buccal trigonid and talonid faces, and the distobuccal corner forms a rounded, obtuse angle). It also appears that the anterior lingual fold would have been positioned slightly further mesially in MNHN 6543 than in *Calchaquitherium*, had this area been completely preserved.

MNHN 6543 may pertain to the same taxon as MNHN 6542, but as the two specimens were collected from different localities, no evidence other than their presence in the same fauna suggests a common specific identity. The size difference between MNHN 6542 and MNHN 6543 is comparable with that present in single-species samples of *Pericotoxodon platignathus* (Madden 1997) and, thus, it is metrically possible that these two specimens are conspecific. Pending recovery of more material, the taxonomic identity of MNHN 6543 is left as indeterminate.

TYPOTHERIA Zittel, 1893
INTERATHERIIDAE Ameghino, 1887
INTERATHERIINAE Ameghino, 1887

Diagnosis. Interatheriines are distinguished from other interatheriids by the following synapomorphies: very shallow parastyle/paracone groove on M1-3; smooth distal ectoloph on M1-3; very high-crowned cheek teeth; distinctly bilobed p3-m3 with persistent buccal and lingual sulci; maxilla excluded from the superior orbital border by an anteriorly projecting sliver of frontal (Hitz 1997; Hitz *et al.* 2000; Reguero *et al.* 2003).

Remarks. Interatheriids have traditionally been divided into two subfamilies (as is true of most groups of typothere notoungulates): Notopithecinae and Interatheriinae. Phylogenetic analyses of the family indicate that the former is probably paraphyletic whereas the latter is probably monophyletic (Cifelli 1993; Hitz 1997; Hitz *et al.* 2000; Reguero *et al.* 2003). Interatheriines range from the Tinguirirican SALMA (earliest Oligocene; Flynn *et al.* 2003) to the Chasicoan SALMA (late Miocene; Bondesio *et al.* 1980*a*) and potentially to the Huayquerian SALMA (late Miocene; Tauber 2005); most taxa are represented by excellent craniodental specimens. Interatheriines are generally abundant in the faunas in which they occur and are among the most abundant mammals in Patagonia Santacrucian SALMA faunas (Sinclair 1909; Tauber 1996; Flynn *et al.* 2002*b*) and in the La Venta Fauna of Colombia (Stirton 1953; Kay and Madden 1997). Following Reguero *et al.* (2003) ten genera are recognized.

MIOCOCHILIUS Stirton, 1953

Type species. *Miocochilius anomopodus* Stirton, 1953, from the Honda Formation of La Venta, Colombia.

Included species. The type, *M. federicoi.*

Age and distribution. Honda Formation, central Colombia and an unnamed formation (Quebrada Honda Fauna), southern Bolivia, both of middle Miocene age, Laventan SALMA.

Diagnosis (skull and upper cheek tooth characters only, primarily from Reguero *et al.* 2003). Differs from

Eopachyrucos, *Santiagorothia*, *Proargyrohyrax*, *Archaeophylus* and *Progaleopithecus* in having extremely high crowned teeth (hypsodonty index > 1·0); presence of thick cement; and absence of enamel on much of mesial and distal faces of upper cheek teeth. Differs from *Cochilius* and *Interatherium* in presence of long, low skull; anterior displacement of lingual sulcus on P3-4; absence of prominently developed descending process of the maxilla; and variable presence of prominent metastyle on M3. Differs from *Protypotherium* in more open lingual enamel folds on P3-M3; variable presence of small/tiny median lobe on upper molars; and molars with more rounded distal lobes. Differs from *Plagiarthrus* in absence of fossettes on upper molars (also differentiates *Miocochilius* from *Eopachyrucos*, *Santiagorothia* and *Proargyrohyrax*) and absence of proportionately large and molariform P3-4 (also differentiates *Miocochilius* from *Cochilius*).

Remarks. *Miocochilius* is one of the latest-occurring members of the Interatheriidae (Patterson and Pascual 1968; Cifelli 1985; Croft 1999) and prior to this report, the taxon had only been reported from the middle Miocene of La Venta, Colombia (Stirton 1953; Madden *et al.* 1997). It is the most abundant mammal at La Venta, and is known from excellent material including nearly complete skeletons (Stirton 1953). Although the occurrence of *Miocochilius* at Quebrada Honda does not extend the temporal range of this taxon (it is still only known from the Laventan SALMA), it does extend the geographical range of the genus south approximately 25 degrees. Two other interatheriid genera have been reported from the middle Miocene: *Interatherium* (Colloncuran SALMA; Bondesio *et al.* 1980*b*) and *Protypotherium* (Colloncuran and Chasicoan SALMAs; Bondesio *et al.* 1980*a*, *b*) but these are both restricted to localities south of Bolivia.

Miocochilius federicoi sp. nov.
Text-figure 4, Table 1

Holotype. MNHN 8626, palate and zygomatic arches bearing left C, left and right P1-M3.

Hypodigm. The type only.

Derivation of name. After Federico Anaya, a scientist and field collector who has been instrumental in advancing vertebrate palaeontology in Bolivia.

Type locality. Quebrada Honda (unspecified level).

Age and distribution. Unnamed formation (Quebrada Honda Fauna), southern Bolivia, middle Miocene age, Laventan SALMA.

Diagnosis (upper dentition characteristics only). Differs from *M. anomopodus* in significantly smaller size (at least 20 per cent smaller based on linear upper molar dimensions); relatively wider P4 with deeper lingual sulcus; more prominent middle lobes on upper molars; and M3 with deeper lingual sulcus and more prominent metastyle (distal lobe).

Description. MNHN 8626 is a palate and zygomatic arches bearing left and right P1-M3. Dental measurements are provided in Table 1. Although the descending processes of the maxillae are only partly preserved, they do not appear to be developed to the degree exhibited by *Interatherium* and *Cochilius*. The palate is relatively long and narrow. The suture between the palatines and maxillae is mostly obliterated and extends anteriorly as far as the distal part of M1. P1 is simple in form, somewhat oval in occlusal view, and longer than P2. Its buccal surface bears a single well-pronounced groove that separates the paracone and metacone. In buccal view, the paracone exhibits much higher occlusal relief than the more distal metacone. P2 more closely resembles the other premolars; it approximates a right triangle with the hypotenuse directed lingually and a single, shallow lingual sulcus is located in approximately the middle of the lingual face. Unlike P3 and P4, it does not exhibit well-demarcated paracone and parastyle folds. P3 is only partly preserved on both sides but appears to be similar to P2 in both size and morphology, with the exception of the mesiobuccal folds that are present. P4 bears a deep lingual sulcus and is roughly equidimensional; this contrasts with the P4 of *M. anomopodus*, which bears a shallower sulcus and is mesiodistally elongate. All four premolars are closely positioned to each other with no significant intervening diastemata. M1 exhibits few distinguishing characteristics save for its deep, wide lingual sulcus. The enamel on the buccal end of the sulcus is not preserved in left M1 but in right M1 a small middle lobe is present. This is reminiscent of the condition seen in *Plagiarthrus* (and more basal interatheriines) and is probably an ancestral character state for interatheriines (Hitz 1997; Reguero *et al.* 2003). Although *M. anomopodus* has not been described previously as possessing a similar middle lobe on the upper molars, the molars do bear the same wide lingual sulcus as *M. federicoi* and some specimens (e.g. FMNH PM 54761; Text-fig. 5) exhibit a very slight evagination on the distal side of the sulcus, approximating a tiny lobe. In both *M. federicoi* and *M. anomopodus*, the M1 lobes are rounded lingually, contrasting with the more angular condition commonly seen in specimens of *Protypotherium*. M2 of *M. federicoi* is narrower than M1, and also bears a middle lobe. This lobe is directed more mesiolingually than that of M1. M3 has a morphology unique among interatheriines, though it does resemble the M3 of some specimens of *M. anomopodus* in certain respects. In addition to the deep lingual sulcus (which is deeper than that of *M. anomopodus*) M3 exhibits a pronounced distolingual sulcus that demarcates a large, distally directed metastyle. This metastyle is broad (approximately half as wide as M3) and roughly rectangular in shape. A similar condition is present in the M3 of some specimens of *M. anomopodus* (e.g. FMNH PM 54761) but in such cases the metastyle is bounded by a shallower distolingual sulcus.
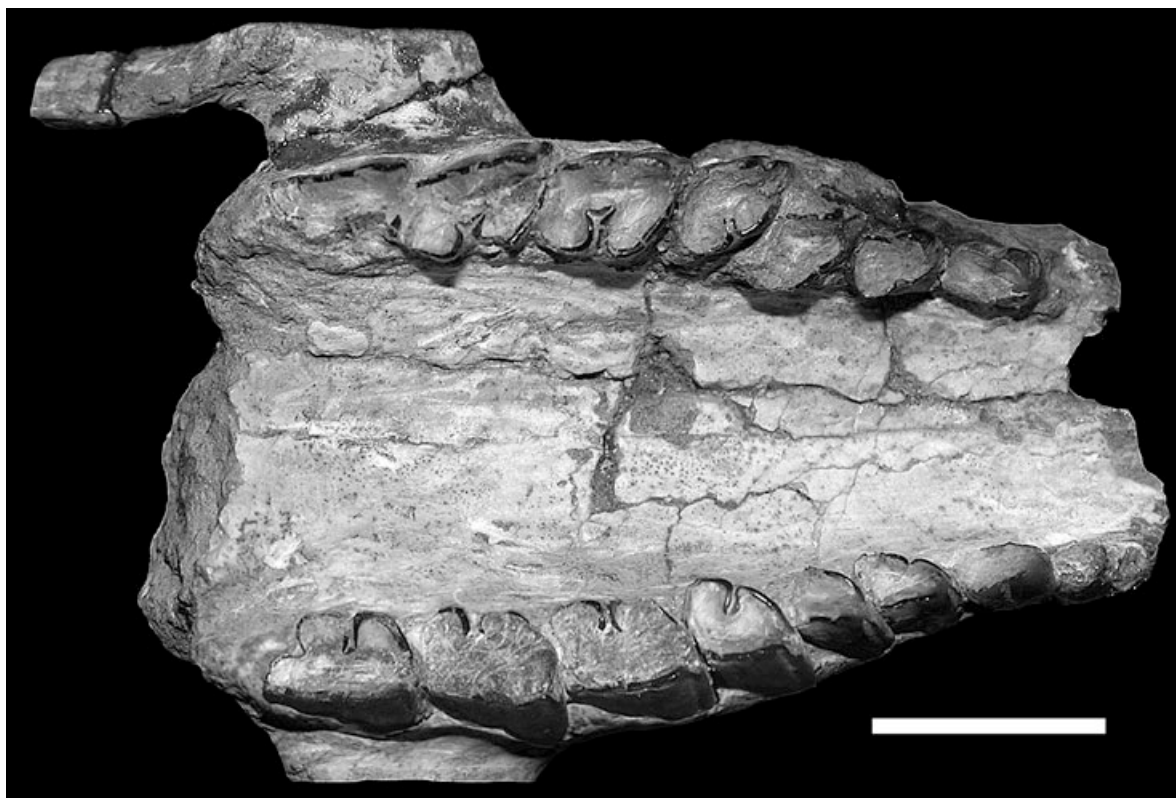
TEXT-FIG. 4. Occlusal view of MNHN 8626, holotype of *Miocochilius federicoi* sp. nov. (Interatheriidae), a palate and partial zygomatic arches preserving left C and left and right P1-M3. Anterior is to the right. Scale bar represents 1 cm.

TEXT-FIG. 5. Right maxilla of *Miocochilius anomopodus* (Interatheriidae) bearing P2-M3 from La Venta, Colombia (part of FMNH PM 54761). Scale bar represents 1 cm.

Remarks. There is little doubt that the single interatheriine specimen from Quebrada Honda represents a new species. Although it is similar in overall form to both *Protypotherium* and *M. anomopodus*, the metric and morphological differences described above clearly distinguish this specimen from those two taxa. What is less clear is the proper generic designation of this taxon. Given the differences noted above, one might be inclined to name a new genus rather than refer it to *Miocochilius*. I prefer the chosen option for several reasons. First, South American palaeomammalogy is already plagued by a veritable cornucopia of poorly founded names. All other things being equal, I would rather conservatively allocate a new species to a pre-existing genus and later have it elevated to generic status than to name a new genus only to have it fall into synonymy later when additional specimens are discovered. Second, although MNHN 8626 is an excellent specimen, it is still only a single specimen and therefore cannot speak to variation within the species. It is unclear if any of the distinguishing characteristics noted above represent individual variation; if significant variation is present, this new species could be less distinct from *M. anomopodus* than it currently appears (thus diminishing the evidence for erecting a new genus.) Third, although it has never been suggested that *Miocochilius* and *Protypotherium* be synonymized (despite near universal agreement on their close relationship; Cifelli 1985, 1993; Madden 1995; Hitz 1997; Reguero *et al.* 2003), only one character out of 30 in the most recent analysis of interatheriine relationships was coded differently in the two taxa (Reguero *et al.* 2003). This might imply that the traits distinguishing the two genera are not reliable and/or phylogenetically useful, but I prefer to interpret this observation as indicating that further analyses are needed to clarify this portion of the interatheriine phylogenetic tree. Until such investigations have taken place, I

Table 1. Dental measurements of MNHN 8626 (holotype skull of *Miocochilius federicoi*) and other selected interatheriine specimens.

Taxon	Specimen	Source	P1		P2		P3		P4		M1		M2		M3	
			L	W	L	W	L	W	L	W	L	W	L	W	L	W
Miocochilius federicoi	MNHN 8626* (R)	primary observation	4·0	2·5	3·2	3·0	–	–	4·0	4·0	6·0	4·8	5·8	4·4	6·5	4·0
Miocochilius federicoi	MNHN 8626* (L)	primary observation	3·9	2·9	3·1	3·3	4·1	4·9	4·1	4·0	6·0	4·8	6·4	4·1	–	–
Miocochilius anomopodus	38409*	Stirton (1953)	5·2	4·1	7·5	5·0	8·0	5·0	8·5	5·0	–	–	–	–	–	–
Miocochilius sp.	FMNH PM 54761	primary observation			5·0	5·3	5·6	5·4	6·1	5·4	7·3	5·8	7·0	5·0	7·9	4·5
Miocochilius sp.	FMNH PM 54524	primary observation			5·0	4·8	5·5	5·2	6·0	4·9	7·5	5·1	7·2	4·8		
Protypotherium australe	PU 15828	Sinclair (1909)	5·0	3·0	5·8	4·0	6·5	4·5	6·0	5·0	8·8	5·8	8·5	5·0	8·0	4·5
Protypotherium australe	PU 9565	Sinclair (1909)	5·0	2·7	5·5	3·7	6·0	4·5	6·0	4·5	8·0	5·0	7·3	5·0	7·5	4·5
Protypotherium australe	PU 15598	Sinclair (1909)	5·0	2·8	5·3	3·5	6·0	4·0	5·5	4·5	8·0	5·4	7·3	4·5	6·6	4·0
Protypotherium australe	PU 9149	Sinclair (1909)	4·0	2·5	4·5	3·5	5·5	4·0	4·8	4·5	7·5	5·2	6·5	4·8	6·5	4·0
Protypotherium attenuatum	PU 9187	Sinclair (1909)	3·0	2·3	3·5	2·6	4·0	3·0	4·0	3·2	6·0	4·0	5·8	3·5	5·7	3·0
Protypotherium attenuatum	PU 15665	Sinclair (1909)	2·7	2·0	3·5	2·7	4·5	3·5	4·4	4·0	6·5	4·6	6·0	4·0	5·5	3·3
Interatherium robustum	PU 15100	Sinclair (1909)	–	–	3·5	2·5	3·6	3·2	4·2	3·5	4·6	3·5	4·3	3·5	5·0	3·0
Interatherium robustum	PU 15401	Sinclair (1909)	–	–	3·5	2·5	4·0	3·8	4·6	4·0	5·0	4·0	4·6	3·6	4·5	3·4

* Holotype.

feel there is insufficient evidence to judge a new taxon related to *Miocochilius* and *Protypotherium* as 'generically distinct'. Finally, I prefer to allocate the new Quebrada Honda species to *Miocochilius* rather than to *Protypotherium* because the characters distinguishing the new species, although relative, are more similar to the states present in the former than in the latter.

More than one species of *Miocochilius* may be present at La Venta (Madden 1995; Kay and Madden 1997; Madden *et al.* 1997), but only a single species has been described thus far. *M. federicoi* therefore represents the second recognized member of the genus.

MESOTHERIIDAE Alston, 1876
MESOTHERIINAE Simpson, 1945

Diagnosis (lower cheek tooth characters only). Differs from 'trachytheriines' in absence of i3-p3 and absence of fossettids in the adult (Reguero and Castro 2004).

Remarks. The family Mesotheriidae includes the 'Trachytheriinae' (generally regarded as paraphyletic) and the monophyletic Mesotheriinae (Simpson 1945; Francis 1965; Cifelli 1985; Reguero and Castro 2002, 2004). Mesotheriines are readily distinguished from other notoungulates by their hypselodont (rootless) dentition, their enlarged I1, the presence of a large diastema between the incisors and the cheek teeth, and characteristically trilobed upper molars (Francis 1965; Cerdeño and Montalvo 2001). The earliest mesotheriines occur in late early Miocene deposits in Chile (Flynn *et al.* 2002*a*; Croft *et al.* 2004) and the group persists into the lower Pleistocene, primarily in Argentina (Francis 1965). Mesotheriines are diverse and common in the lower and middle Miocene of Chile and Bolivia, and it has been suggested that the middle latitudes of South America represent the region of diversification of the group (Croft *et al.* 2003*c*, 2004).

PLESIOTYPOTHERIUM Villarroel, 1974

Type species. Plesiotypotherium achirense Villarroel, 1974, from the Mauri Formation of Achiri, Bolivia.

Included species. The type, *P. majus*, *P. minus*.

Age and distribution. 'Estratos de Cerdas', southern Bolivia, early middle Miocene age, Friasian (*s.s.*) SALMA (Villarroel 1978; MacFadden *et al.* 1995); Nazareno Formation, southern Bolivia, ?middle Miocene age (Oiso 1991); Mauri Formation, western Bolivia, late Miocene age, Mayoan SALMA (Villarroel 1974; Marshall *et al.* 1992); unnamed formation (Quebrada Honda Fauna), southern Bolivia, middle Miocene age, Laventan SALMA (present study); Quehua Formation, south-west Bolivia, middle–late Miocene age (Villarroel 1978; MacFadden *et al.* 1995); Casira (Kasira) Formation, southern Bolivia, age unknown (Anaya *et al.* 1989).

Diagnosis (lower cheek tooth characters only). Differs from *Pseudotypotherium*, *Mesotherium* and *Microtypotherium* in m2 proportions (length/width between 1·60 and 2·30 in *Plesiotypotherium*, > 2·30 in *Pseudotypotherium* and *Mesotherium*, < 1·60 in *Microtypotherium*; Croft *et al.* 2004). Differs from *Caraguatypotherium* in absence of two lingual sulci on m3 talonid (Flynn *et al.* 2005). Differs from *Altitypotherium* and *Eotypotherium* in larger size (at least 10 per cent larger than *Altitypotherium* and 20 per cent larger than *Eotypotherium* based on linear dental measurements) (Croft *et al.* 2004).

Remarks. Mesotheriines are better distinguished by upper dental characters than lower dental characters (Cerdeño and Montalvo 2001; Croft *et al.* 2004) and, unfortunately, no characters are preserved in MNHN 6510 that suggest referral to *Plesiotypotherium* rather than *Eutypotherium* or *Typotheriopsis*. However, as detailed below, the size of MNHN 6510 is outside the range exhibited by *Eutypotherium* and *Typotheriopsis* and closely corresponds to the smallest species of *Plesiotypotherium*, *P. minus*. This, combined with the fact that neither *Eutypotherium* nor *Typotheriopsis* has previously been recorded in Bolivia (Marshall and Sempere 1991), suggests that the specimen under consideration most likely pertains to *Plesiotypotherium*.

Plesiotypotherium minus Villarroel, 1978
Text-figure 6, Table 2

Referred material. MNHN 6510, pair of mandibles bearing p4-m3 in varying states of completeness.

Locality. Río Rosario.

Age and distribution. Quehua Formation ('Estratos de Cerdas'), southern Bolivia, early middle Miocene age, Friasian (*s.s.*) SALMA; unnamed formation (Quebrada Honda Fauna), southern Bolivia, middle Miocene age, Laventan SALMA.

Diagnosis. Differs from *P. achirense* and *P. majus* in its smaller size (*c.* 20–25 per cent smaller than *P. achirense*

and *c.* 40 per cent smaller than *P. majus*, based on linear molar measurements.).

Description. MNHN 6510 consists of a pair of poorly preserved mandibles with portions of p4-m3 on both sides. Direct measurements for p4-m1 and estimates for m2–3 are provided in Table 2. The teeth are typically mesotheriine in form with the trigonid and talonid of each tooth separated by a deep buccal sulcus that extends nearly to the lingual side of the tooth. No fossettes are present save for that formed by the lingual sulcus. P4 is small and triangular with a talonid that is much larger than the trigonid. M1 and M2 both roughly approximate a figure eight in occlusal view. In both teeth the trigonid is much larger than the talonid and is wider buccolingually than mesiodistally. The talonid of m1 is more circular in shape while that of m2 is mesiodistally elongate and bears a slight lingual sulcus. The trigonid of m3 resembles that of the other molars, but the talonid is much longer (mesiodistally) and narrower (buccolingually), and comes to a point distally. As in m2, it bears a slight lingual sulcus.

Remarks. MNHN 6510 is typically mesotheriine in form and closely resembles that of other middle–late Miocene mesotheriines (e.g. *Eutypotherium*, *Typotheriopsis*). As noted above, however, the lower dentition of mesotheriines bears relatively few characters that permit discrimination among genera. The most noteworthy aspect of MNHN 6510 is its very close correspondence in size to the holotype of *P. minus* described by Villarroel (1978), which comes from a slightly older locality about 150 km to the north-west of Quebrada Honda (MacFadden *et al.* 1995). No other species of mesotheriine this size has been

TEXT-FIG. 6. MNHN 6510, a pair of mandibles referred to *Plesiotypotherium minus* (Mesotheriidae) bearing p4-m3. Scale bar represents 1 cm.

Table 2. Dental measurements of selected specimens of *Plesiotypotherium*. Holotypes are indicated by an asterisk (*). Measurements in parentheses are estimates to the nearest 0·5 mm.

Taxon	Specimen	Source	P4		M1		M2		M3	
			L	W	L	W	L	W	L	W
Plesiotypotherium minus	MNHN 6510 (R)	primary observation	8·0	5·6	–	–	–	–	–	–
Plesiotypotherium minus	MNHN 6510 (L)	primary observation	–	–	11·4	6·9	(11·5)	(6·5)	(16·0)	(5·5)
Plesiotypotherium minus	MNHN GB-227*	Villarroel (1978)	7·9	5·5	11·8	7·2	12·9	6·6	19·0	6·0
Plesiotypotherium achirense	MNHN-P ACH26*	Villarroel (1974)	11·8	8·2	15·0	9·7	16·0	9·2	22·5	8·5

described previously, suggesting that the specimen from Quebrada Honda can be confidently referred to *P. minus*.

FAUNAL COMPARISONS

With the addition of the taxa described above, the revised faunal list for Quebrada Honda includes 30 mammal species, 27 of which are identified to at least genus level (Table 3). The most recent faunal summary of Quebrada Honda (Marshall and Sempere 1991) included generic designations for only six taxa, and two of these designations (*Hegetotherium* and *Hapalops*) are no longer applicable. Mammals from Quebrada Honda represent 19 families and are evenly distributed among marsupials (six spp.), xenarthrans (eight spp.), rodents (nine spp.) and endemic ungulates (seven spp.). Although some of these species have received detailed treatment in recent years (e.g. *Acdestis*, *Hondalagus*) many others (e.g. the rodents) are preliminarily identified and no doubt in need of further study. Nevertheless, the fauna of Quebrada Honda is well sampled and reasonably well described, making it suitable for comparisons with other similarly aged faunas in South America.

Using a common measure of faunal similarity, the Simpson Coefficient (SC; Simpson 1960), the revised fauna of Quebrada Honda was compared with four other well-sampled middle–late Miocene faunas (see Appendix). In general terms, the Simpson Coefficient measures the number of taxa (at any taxonomic level) shared between two faunas, expressed as a percentage of the number of taxa in the smaller fauna. Faunas that have no taxa in common have a faunal resemblance of zero; if all taxa in the smaller fauna also occur in the larger fauna, the similarity is 100. The Simpson Coefficient is particularly amenable to comparisons among fossil faunas (Flynn 1986) and has been used recently at the generic level to examine temporal and geographical trends among South American Miocene mammal faunas (e.g. Madden *et al.* 1997; Croft and Anaya 2004; Croft *et al.* 2004). The four faunas to which Quebrada Honda was compared were chosen because: they are reasonably well sampled (i.e. have been collected over several field seasons and include both large- and small-bodied taxa); they are temporally

and geographically constrained; and faunal lists and modifications to those lists have been published within the past 50 years. They include Collón-Curá (CC; Río Negro, Argentina), La Venta (LV; central Colombia), and the lower and upper levels of Arroyo Chasicó (LAC and UAC, respectively; Buenos Aires, Argentina).

One impediment to the calculation of faunal similarity among fossil faunas is the presence of specimens that have not been (or cannot be) identified to the taxonomic level of interest. For example, mammal postcranial specimens are generally identifiable to the familial level, but recognizing the generic or specific affinities of such remains is often not possible (e.g. if generic differences are based solely on craniodental characters). Excluding such specimens from a generic analysis of faunal similarity is not an attractive option because it ignores potentially important faunal data, especially in cases where such remains indicate the presence of a family or other taxon unrepresented by more diagnostic material.

In order to deal with the issue of inadequately identified specimens, minimum and maximum values of faunal similarity (SCmin and SCmax, respectively) were calculated for each pair of localities (Table 4). In calculating minimum similarity, it was assumed that suprageneric taxa present in one fauna (i.e. specimens not identifiable to genus level) were distinct from related genera recorded in other faunas (e.g. Echimyidae gen. et sp. indet. from LV was considered to be distinct from the various echimyid genera recorded at CC, QH and LAC; see Appendix). Maximum similarity was calculated assuming that such taxa were referable to genera recorded in other faunas, where applicable (i.e. as Echimyidae gen. et sp. indet. from LV could pertain to any one of the echimyid genera present at CC, QH or LAC, it was treated as a shared genus between LV and each of these three other faunas). Given the geographical and temporal ranges of the faunas considered in the present study, neither of these calculations should be considered the more 'conservative' option; the minimum value is likely to be more accurate for pairs of faunas that vary significantly in age or location whereas the maximum value is probably more applicable to faunas that are close in age and/or location. In reality, as both assumptions apply to

Table 3. Revised taxonomic list for Quebrada Honda (including Río Rosario) based on published sources (included below), specimen labels at Florida Museum of Natural History (FLMNH), and identifications provided in the present publication.

Marsupialia
  Didelphimorphia
    Sparassocynidae
      Sparassocynus sp. (FLMNH)
  Paucituberculata
    Palaeothentidae
      Acdestis maddeni (Goin *et al.* 2003)
      Palaeothentes lemoinei (FLMNH)
      Palaeothentes minutus (FLMNH)
    Argyrolagidae
      Hondalagus altiplanensis (Villarroel and Marshall 1988;
        Sánchez-Villagra *et al.* 2000*b*)
  Sparassodonta
    Borhyaenidae (Marshall and Sempere 1990)
      Acyon sp. nov. (A. Forasiepi, pers. comm. 2005)
Xenarthra
  Cingulata
    Dasypodidae
      Prozaedyus sp. (Hoffstetter 1977; Scillato-Yané and Carlini 1999)
      Neophractus sp. nov. (Scillato-Yané and Carlini 1999;
        ≈ *Paraeuphractus/Euphractus* of Hoffstetter 1977)
    Glyptodontidae
      cf. *Asterostemma* sp. (Scillato-Yané and Carlini 1999)
      Propalaehoplophorus andinus (Frailey 1988)
      Sclerocalyptinae sp. nov. 1 (Scillato-Yané and Carlini 1999;
        ≈ *Hoplophorus* of Takai *et al.* 1984)
      Sclerocalyptinae sp. nov. 2 (Scillato-Yané and Carlini 1999)
  Pilosa
    Nothrotheriini
      Xyophorus villarroeli (Scillato-Yané and Carlini 1999;
        = *Hapalops angustipalatus* of Frailey 1988)
    Mylodontidae
      gen. et sp. indet. (Takai *et al.* 1984)

Rodentia
  Dasyproctidae
    Cephalomys sp. (FLMNH)
    Neoreomys sp. (FLMNH)
  Eocardiidae
    Eocardia montana (FLMNH)
    Schistomys sp. (FLMNH)
  Octodontidae
    Acaremyinae sp. indet. (FLMNH)
  Echimyidae
    Spaniomys sp. (FLMNH)
  Chinchillidae
    Prolagostomus divisus (FLMNH)
    Prolagostomus imperialis (FLMNH)
    Prolagostomus profluens (FLMNH)
Litopterna
  Proterotheriidae
    Diadiaphorus sp. (Takai *et al.* 1984)
  Macraucheniidae
    gen. et sp. indet. (Hoffstetter 1977)
Notoungulata
  Toxodontidae
    cf. *Paratrigodon* sp. (present study)
  Interatheriidae
    Miocochilius federicoi (present study)
  Mesotheriidae
    Plesiotypotherium minor (present study)
  Hegetotheriidae
    Hemihegetotherium trilobus (Croft and Anaya 2004, 2006)
Astrapotheria
  Astrapotheriidae
    Uruguaytheriinae gen. et sp. *incertae sedis* (Johnson and
      Madden 1997; = ?*Xenastrapotherium* of Frailey 1987)

pairs of faunas to different degrees, neither the minimum nor the maximum similarity probably represents the 'true' similarity; the 'true' similarity should be bracketed by the two statistics.

Among the assemblages compared with Quebrada Honda, Collón-Curá has the highest SC values; QH-CC SCmin is 23·1 and SCmax is 38·5 (Table 4). These values are potentially the highest for any pair of faunas, exceeded only by SCmin of the superimposed Lower and Upper Arroyo Chasicó faunas (LAC-UAC SCmin is 31·6, SCmax is 36·8). La Venta is second most similar to Quebrada Honda (SCmin of 10·5, SCmax of 26·7), though the overlap of the upper part of this range with that of the QH-CC SC values suggests that more precise taxonomic identifications could theoretically result in greater faunal resemblance between QH-LV than QH-CC. There is presently no reason to suspect this might be the case, however. The SC range of LV-CC is similar to that of LV-QH. The SC values for most Arroyo Chasicó comparisons are low, though LAC-CC is only slightly lower than LV-CC.

Taken as a whole, SC values suggest the five faunas can be divided into two groups: middle Miocene faunas (CC, QH, LV) and late Miocene faunas (LAC, UAC). Both

Table 4. Range (minimum and maximum) of faunal resemblance indices (Simpson Coefficients) among selected pairs of well-sampled middle–late Miocene South American faunas. Simpson Coefficients are calculated as (number of shared genera/number of genera in the smaller fauna) × 100. See text for explanation of minimum and maximum values and Appendix for complete faunal lists.

	Collón-Curá	Quebrada Honda	La Venta	Lower Arroyo Chasicó
Quebrada Honda	23·1–38·5	–	11·5–30·8	9·1–17·4
La Venta	10·5–23·7	10·0–26·7	–	9·1–26·1
Lower Arroyo Chasicó	8·7–13·0	9·1–17·4	9·1–26·1	–
Upper Arroyo Chasicó	5·3–15·8	5·3–26·3	0·0–10·5	31·6–36·8

groups have relatively high intra-group SC values and relatively low inter-group SC values. The closest overlap between the two groups is between Collón-Curá and Lower Arroyo Chasicó, the geographically closest pair of middle and late Miocene faunas. Among middle Miocene faunas, presently available evidence suggests that Quebrada Honda is much more similar to the slightly older Collón-Curá fauna than to the contemporaneous La Venta fauna (see below).

DISCUSSION

The Quebrada Honda Fauna

Although the fauna of Quebrada Honda is still incompletely known, it is presently the best sampled Miocene fauna from Bolivia and one of the best sampled from the middle latitudes of South America. All major groups of mammals present in South America at that time have been recorded at Quebrada Honda, with the exception of primates (Table 3). Given the general rarity of primates in the South American fossil record, it cannot be determined with confidence if they were absent from the area at the time of deposition or whether this is a taphonomic effect.

The marsupials from Quebrada Honda include several small argyrolagids and palaeothentids, a sparassocynid didelphimorphian, and a borhyaenid. The preservation of most of these taxa is exceptional: the palaeothentid *Acdestis maddeni* is represented by the most complete skull known for the family (Goin *et al.* 2003); specimens attributed to the argyrolagid *Hondalagus altiplanensis* include a nearly complete skull and mandibles (Sánchez-Villagra *et al.* 2000*b*); and a new borhyaenid is represented by an equally impressive skull and associated mandibles (A. Forasiepi, pers. comm. 2005). Quebrada Honda may eventually prove to be one of the richest localities for Neogene marsupial specimens.

Quebrada Honda xenarthrans include two dasypodids, several glyptodontids and probably two pilosans. Although only the glyptodontid *Propalaehoplophorus andinus* and the nothrothere pilosan *Xyophorus villarroeli* have been described in detail (Frailey 1986; Saint-André 1996), it appears that the majority of the eight xenarthran species are endemic to Bolivia (Scillato-Yané and Carlini 1999). Takai *et al.* (1984) provisionally identified two isolated osteoderms from Quebrada Honda as belonging to *Hoplophorus*, a genus of glyptodonts otherwise restricted to the Pleistocene of Patagonia (McKenna and Bell 1997). Based on the photographs of these specimens provided by Takai *et al.* (1984), these specimens could pertain equally well to one of the other glyptodontids recorded from Quebrada Honda. As the presence of *Hoplophorus* in the

middle Miocene of Bolivia would represent a significant temporal range extension of the taxon, it is excluded from the faunal list pending the recovery of more diagnostic material.

None of the rodents from Quebrada Honda has been described in detail, and therefore all identifications should be considered preliminary. They are presently assigned to five families: Dasyproctidae, Eocardiidae, Octodontidae, Echimyidae and Chinchillidae. Rodents were apparently abundant at Quebrada Honda during the time the fossils were deposited, especially chinchillids (MacFadden and Wolff 1981). All chinchillids that have been collected from Quebrada Honda are lagostomines, as is the case for Patagonian Miocene localities; this contrasts sharply with the presence of only chinchilline chinchillids in the slightly older Chucal Fauna of northern Chile (Flynn *et al.* 2002*a*). Two families of rodents included in the preliminary report of MacFadden and Wolff (1981) do not appear to be present at Quebrada Honda: Caviidae and Capromyidae. As noted by MacPhee (2005) the presence of capromyids in the middle Miocene of Bolivia would be especially notable given that their distribution is otherwise restricted to the Greater Antilles. Based on the taxa now known to be present at Quebrada Honda, these apparent 'misidentifications' appear more likely to be attributable to changes in taxonomy; *Eocardia* (Eocardiidae) was once considered a caviid and *Neoreomys* (Dasyproctidae) was once considered a capromyid (e.g. Scott 1905).

At least seven species of endemic ungulates are present at Quebrada Honda and all are referable to distinct families. Takai *et al.* (1984) identified the proterotheriid litoptern *Diadiaphorus* based on excellent mandibular dental material, but did not refer the specimens to a particular species. The presence of a macraucheniid litoptern was noted by Hoffstetter (1977) based on an isolated lateral metapodial; no additional material has been noted in the literature. Astrapotheres were also first identified at Quebrada Honda by Hoffstetter (1977); the species appears to be a member of the Uruguaytheriinae, but its generic allocation has yet to be determined (see further discussion below).

As detailed previously, the notoungulates of Quebrada Honda include an hegetotheriid, a toxodontid (possibly two), an interatheriid and a mesotheriid. Among these, the hegetotheriid and interatheriid are endemic to Quebrada Honda; the toxodontid is potentially endemic to Quebrada Honda but is not represented by sufficiently diagnostic material; and the mesotheriid occurs in at least one other Bolivian locality but appears to be endemic to the region (Croft and Anaya 2004, 2006, present study). Given the age and geographical position of Quebrada Honda, the presence of many endemic ungulate species is not unexpected. What is unexpected is the abundance of the hegetotheriid *Hemihegetotherium* and

Table 5. General taxonomic composition of Miocene faunas examined in this study. The raw number indicates the number of species in each ordinal or supraordinal group. The percentage in parentheses indicates the proportion of the non-primate terrestrial mammal fauna represented by each group in each assemblage. The total number of species for each fauna is listed in the bottom row

	Collón-Curá	Quebrada Honda	La Venta	Lower Arroyo Chasicó	Upper Arroyo Chasicó
Marsupials	2 (5%)	6 (20%)	12 (20%)	2 (8%)	–
Xenarthrans	12 (32·5%)	8 (27%)	16 (27%)	5 (21%)	7 (35%)
Rodents	12 (32·5%)	9 (30%)	18 (31%)	9 (38%)	4 (20%)
Primates	1	–	9	–	–
Ungulates	11 (30%)	7 (23%)	13 (22%)	8 (33%)	9 (45%)
TOTAL	38	30	68	24	20

the rarity of the other three taxa. As discussed by Croft *et al.* (2004) and Croft and Anaya (2004, 2006), mesotheriids are typically the most abundant notoungulates in early–middle Miocene localities of northern Chile and Bolivia, whereas hegetotheriids are much less so. In the collections from Quebrada Honda housed at the MNHN, *Hemihegetotherium* is represented by some three dozen specimens (Croft and Anaya 2006) but only a single specimen of the mesotheriid *Plesiotypotherium* has been recovered. Similarly, interatheriids and toxodontids are generally abundant in the faunas in which they occur (e.g. La Venta, Santa Cruz), but only one specimen of *Miocochilius* and two toxodontid teeth have been collected from Quebrada Honda. The composition of the notoungulate community at Quebrada Honda appears to be unique among middle Miocene faunas and further study may help clarify environmental or ecological factors that might have contributed to this condition.

One other noteworthy aspect of the Quebrada Honda Fauna is the nearly even distribution of species among the main groups of South American mammals (namely marsupials, xenarthrans, rodents and ungulates); each comprises 20–30 per cent of the total faunal species richness. Compared with the other Miocene faunas analysed above, this corresponds most closely (almost exactly) to the distribution of species at La Venta, excluding primates (Table 5). Given that the total species richness of La Venta is twice as great as that of Quebrada Honda, it seems unlikely that this even distribution of species is indicative of a similar habitat at the two localities. Rather, it seems more likely that this pattern results from less complete sampling of rodents and marsupials in the other faunas, especially as these groups tend to be uncommon and/or of small body size in most faunas. A testable hypothesis is that additional sampling of these Argentine faunas would disproportionately increase the number of marsupial and rodent species, creating a distribution more similar to that of Quebrada Honda and La Venta. This relatively even distribution among major groups may therefore be typical for middle–late Miocene faunas.

Palaeogeography

The analysis of faunal resemblance presented above suggests that the fauna of Quebrada Honda is more similar to that of the slightly asynchronous Patagonian locality of Collón-Curá than to the synchronous low-latitude La Venta Fauna. This does not appear to result from geographical proximity, however, as Quebrada Honda is positioned roughly half-way between Collón-Curá and La Venta. Rather, it appears that this middle-latitude locality bears a greater resemblance to Patagonian localities than to low-latitude localities, despite slight age differences; one would expect that a Laventan fauna from Patagonia would demonstrate even greater faunal resemblance to Quebrada Honda than a Colloncuran one, thus lending increased support for a biogeographical tie between the middle and upper latitudes during the middle Miocene. A more robust test of this hypothesis would involve a greater number of localities of this age from all latitudes, but this must await discovery and description of additional faunas.

It would have been enlightening to include a Mayoan SALMA fauna (late middle–early late Miocene; Textfig. 2) in the analysis of faunal resemblance to see whether Quebrada is more similar to slightly older or slightly younger Patagonian localities. Kay and Madden (1997) demonstrated that the fauna of La Venta more closely resembled the former (e.g. Santacrucian and Colloncuran faunas) than the latter (e.g. Mayoan and Chasicoan faunas) and, therefore, Quebrada Honda might be expected to show the same pattern. The lack of available faunal data for the Mayoan precludes such an analysis. The lack of inclusion of a temporally intermediate Mayoan fauna probably accounts for the separation of the five faunas into two temporal groups (i.e. middle Miocene and late Miocene) as noted above.

Kay and Madden (1997, fig. 30.1) reconstructed La Venta as sitting on a peninsula or island during the middle Miocene and suggested that this palaeogeographical isolation might have partially contributed to that fauna's high level of endemism. This was supported by faunal resemblance indices for La Venta ranging from 13 to 19 among comparisons with older faunas, and 2 to 10 among comparisons with younger faunas (Kay and Madden 1997, table 30.9). These values differ only slightly from those obtained in the present study (Table 4). The fact that the La Venta Fauna shares approximately the same proportion of taxa with Quebrada Honda as with the Patagonian Collón-Curá Fauna, despite the much closer geographical position of Quebrada Honda, lends support to the idea of a geographical or environmental barrier isolating the northern portion of South American during the middle Miocene.

South American Land Mammal 'Ages'

A fundamental question in South American palaeomammalogy is whether the informal system of Land Mammal 'Ages' is applicable on a continent-wide scale (Flynn and Swisher 1995; Madden et al. 1997; Flynn and Wyss 1998). In contrast to the northern continents, this is an issue in South America for several reasons: South America spans a large range of latitude (approximately 65°); its system of land mammal ages is based on localities in a very limited geographical area (Patagonia) relative to the size of the continent; and the SALMA sequence lacks directly superimposed faunas (and therefore has gaps) in many sections (Flynn and Swisher 1995; Madden et al. 1997). Madden et al. (1997) examined the question of the continent-wide applicability of SALMAs by comparing the fauna of La Venta with other Miocene faunas and noted (p. 505) that 'As presently defined and characterized, the Miocene SALMAs do not appear to be very powerful tools for refined temporal correlation across the latitudinal extremes of the continent.'

One acknowledged shortcoming of the aforementioned analysis, however, was the lack of contemporaneous pairs of faunas spanning the latitudinal range of South America; with La Venta being the only well-represented low-latitude fauna, it could only be compared with slightly older and slightly younger faunas from Patagonia (Madden et al. 1997). New middle-latitude faunas from localities such as Chucal (c. 18° S; Flynn et al. 2002a; Croft et al. 2004) and Quebrada Honda (c. 22° S) are approximately contemporaneous with high-latitude Patagonian faunas (Santa Cruz and Pampa Castillo in the case of Chucal; Flynn et al. 2002b; Croft et al. 2004) or low-latitude tropical faunas (La Venta in the case of Quebrada Honda) and, therefore, should provide more robust tests

of the continent-wide utility of SALMAs. Can a fauna such as Chucal or Quebrada Honda confidently be referred to a particular SALMA in the absence of radio-isotopic dates? If not, then such designations may be superfluous for discussions of faunas spanning more than a regional scale, at least in certain areas and during certain intervals of time.

Comparisons of the ungulates of Chucal with those of more southerly Santacrucian faunas have not only highlighted significant late early Miocene provinciality in South America but also permitted confident referral of the Chucal Fauna to the Santacrucian SALMA (Croft et al. 2004). Thus, SALMAs appear to be useful for intracontinental correlation on a limited scale (i.e. not necessarily for the entire length of the continent), at least during the early Miocene. More detailed comparisons between Chucal and other faunas must await description of the non-ungulate components of the fauna.

In the case of Quebrada Honda, the applicability of SALMAs is less clear. Although Madden et al. (1997, p. 519) were 'equivocal about the proposition of a formal "Laventan LMA"', they did define a Laventan Stage and corresponding Laventan Age. The boundaries of the Laventan Stage (and Age) were based on the coincident stratigraphic first and last occurrences of a variety of characteristic La Venta taxa, collectively referred to as the 'Miocochilius Assemblage Zone' (Madden et al. 1997; see Appendix). This assemblage zone was named after the interatheriid notoungulate Miocochilius, the most abundant and characteristic taxon of La Venta. A single-taxon range zone based on the stratigraphic occurrence of this genus was proposed informally, but the authors preferred the assemblage zone definition in the 'belief that it will eventually prove to be more stable and more useful for biocorrelation' (Madden et al. 1997, p. 509). The Laventan SALMA, though never formally proposed, subsequently has been considered part of the standard SALMA sequence (e.g. Flynn and Wyss 1998).

Of the mammals present in the Miocochilius Assemblage Zone, only a single taxon definitively is present at Quebrada Honda: Miocochilius (Table 3; Appendix). The presence of this genus at both localities despite the great distance between them supports its informal designation as the 'indicator taxon' for the Laventan SALMA. It should be taken in account, however, that M. federicoi does not itself occur at La Venta and that the precise generic designation of the species (presently referred to Miocochilius) is not obvious (see 'Systematic palaeontology', above). If subsequent phylogenetic analyses of the Interatheriinae were to indicate that M. federicoi and M. anomopodus do not share a common ancestor exclusive of other interatheriines (e.g. Protypotherium spp.), then Miocochilius would no longer appear to be useful for biostratigraphic correlation. For the present, the genus

appears to be the most useful biochronologic indicator of this time interval.

A second endemic ungulate from the *Miocochilius* Assemblage Zone of La Venta might be present at Quebrada Honda: a 'large, advanced astrapothere … represented by a highly fragmented skull that consists of the cranium and pieces of the palate and upper teeth' (Frailey 1987, p. 5). This specimen was referred by Frailey (1987) to ?*Xenastrapotherium*, a taxon otherwise known from Venezuela and Colombia. Hoffstetter (1977) had earlier referred isolated dental specimens from Quebrada Honda to 'le groupe *Uruguaytherium-Xenastrapotherium*' and Johnson and Madden (1997) chose to refer these and the specimen described by Frailey (1987) to Uruguaytheriinae gen. et sp. *incertae sedis*, pending more detailed analyses of the Quebrada Honda astrapothere material. Johnson and Madden (1997, p. 377) did observe that 'Among the Astrapotheriidae for which this portion of the cranium is known, the general shape and configuration of the base of the neurocranium in UF 26679 [the Quebrada Honda specimen described by Frailey 1987] is most similar to *Granastrapotherium snorki*', a species known only from La Venta. If the Quebrada Honda material does, indeed, pertain to *Granastrapotherium* (presently a monospecific taxon), the genus could represent a useful biochronologic indicator for the Laventan SALMA. Similarly, referral of the Quebrada Honda taxon to Laventan *Xenastrapotherium kraglievichi* (another uruguaytheriine astrapothere) would suggest that this species (but not the genus) is a useful biochronologic indicator; the genus as a whole spans a broader range of ages, based on occurrences in Brazil, Colombia, Ecuador and Venezuela (Johnson and Madden 1997). An undescribed juvenile astrapothere skull from Quebrada Honda (MNHN 3672) will undoubtedly provide important new data for determining the precise affinities of the taxon and should clarify the biochronologic utility of middle Miocene uruguaytheriine astrapotheres.

Of the non-ungulate taxa from Quebrada Honda, only a single characteristic taxon of the Laventan is potentially present: *Neoreomys* sp. (Table 3; Appendix). *Neoreomys huilensis* from La Venta was originally described by Fields (1957), but later work by Walton (1990, 1997) recommended that the species be referred to a distinct (as yet unnamed) genus. Preliminary identification of the species from Quebrada Honda suggests that it is more closely allied to Patagonian *Neoreomys* than to '*Neoreomys*' *huilensis* from La Venta, but this must be confirmed by more detailed study and collection of additional material. The glyptodontid *Asterostemma* has been recorded at both La Venta and Quebrada Honda, but this is not a characteristic taxon of the Laventan, and the species from La Venta may be generically distinct from Patagonian *Asterostemma* (Carlini *et al.* 1997).

Overall, the Quebrada Honda Fauna provides weak support, at best, for the continent-wide applicability of SALMAs. Of the 15 defining and characteristic non-primate mammals of the *Miocochilius* Assemblage Zone (Madden *et al.* 1997, fig. 29.6), only three are potentially present at Quebrada Honda, and one of these is doubtful. Three genera are potentially shared by the two faunas (two of them characteristic of the assemblage zone), representing 11·5 per cent of currently recorded Quebrada Honda genera; this is approximately half the proportion shared by Quebrada Honda and Collón-Curá and only slightly more than the proportion shared between Quebrada Honda and the Lower Arroyo Chasicó (Table 4).

By contrast, 100 per cent of the genera recorded from the Santacrucian Pampa Castillo locality of southern Chile also occur at the type locality for the Santacrucian SALMA (Flynn *et al.* 2002b); similarly, 57 per cent of the ungulates from the Santacrucian Chucal locality of northern Chile are also known from Santa Cruz (Croft *et al.* 2004) despite the significant difference in latitude. Combined with the data presented here, these early and middle Miocene faunas suggest that SALMAs are likely to be useful for biocorrelation among high- and mid-latitude faunas, but that low-latitude faunas should rely on a distinct system of LMAs for temporal correlation. Although the proportion of taxa shared among these faunas will certainly be modified with better sampling and further taxonomic studies, it appears unlikely that the overall pattern of faunal similarity will change significantly enough to alter these broad patterns.

SUMMARY AND CONCLUSIONS

To understand the complex history of mammals in South America it is necessary to have well-sampled faunas not only from throughout the Cenozoic but also from throughout the continent. We are just now in the early stages of having enough representative faunas to begin to look at patterns of intracontinental endemism. Low- and middle-latitude faunas are critical for these sorts of analyses, and continued study of the Quebrada Honda Fauna will no doubt provide new insights into Miocene mammalian palaeobiogeography.

The present paper describes three notoungulates from Quebrada Honda and reviews the current state of knowledge of the fauna as a whole. These notoungulates include: a toxodontid comparing favourably with *Paratrigodon* that might represent a new species; a new species of the interatheriid *Miocochilius*, *M. federicoi*; and the diminutive mesotheriine *Plesiotypotherium minor*. Together with a recently described new hegetotheriid from Quebrada Honda (Croft and Anaya 2004, 2006), the

notoungulates of this locality demonstrate a high level of endemism typical of early middle Miocene faunas from this region of the continent. The fauna is atypical, however, in that hegetotheriid remains dramatically outnumber those of the other three notoungulates combined.

The Quebrada Honda Fauna presently includes at least 30 species of mammals, making it one of the better sampled middle–late Miocene South American faunas. The fauna as a whole is more similar to asynchronous high-latitude faunas in Patagonia than to the contemporary La Venta fauna of Colombia, lending support to the presence of isolating mechanisms between low- and middle-latitude faunas in the early–middle Miocene. Owing to these isolating mechanisms, the system of South American Land Mammal 'Ages' (SALMAs) that have been based on southern (especially Patagonian) faunas does not appear to be useful for biocorrelation between low-latitude faunas such as La Venta and those positioned in more southerly regions of the continent, at least for the middle Miocene. Additional low- and middle-latitude faunas should be sought out and carefully studied to test this assertion more robustly and to see if such a pattern also typifies other temporal intervals.

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APPENDIX

Non-volant mammals recorded at selected well-sampled middle–late Miocene South American localities. Genera and higher taxa are indicated in the left-hand column. Species present in each fauna are indicated to the right of the corresponding genus (or higher taxon, if generic identification is unknown) in the column corresponding to that fauna. A question mark (?) next to the species name indicates a questionable occurrence. The Collón-Curá faunal list is taken primarily from Bondesio *et al.* (1980*b*) with modifications by Scillato-Yané (1976), Vucetich (1984), Pardiñas (1991), Vucetich *et al.* (1993), Kay *et al.* (1998) and Vucetich and Kramarz (2003). The La Venta faunal list is primarily from Madden *et al.* (1997) with modifications from Goin (1997), Meldrum and Kay (1997) and

Villarroel (2000). 'Defining and characteristic taxa' of the Laventan Age (Madden *et al.* 1997, p. 510) are denoted by an asterisk (*). The sources for the Quebrada Honda faunal list are given in Table 3. The faunal lists for Arroyo Chasicó are based on the analysis of Bondesio *et al.* (1980*a*) with modifications from Vucetich (1984), Scillato-Yané *et al.* (1987), Vucetich *et al.* (1993), Bond and López (1995), Bond (1996), Cerdeño and Bond (1998), Cerdeño (2000, 2003) and Forasiepi *et al.* (2003). Lower Arroyo Chasicó corresponds to the Vivero Member and Upper Arroyo Chasicó corresponds to the Las Barrancas Member of the Arroyo Chasicó Formation (Bondesio *et al.* 1980a).

Taxon	Fm Collón-Curá	La Venta	Q. Honda	Lower A. Chasicó	Upper A. Chasicó
Microbiotheria					
Microbiotheriidae					
Pachybiotherium		*minor*			
Didelphimorphia					
Didelphidae				(9)	(9)
Micoureus		*laventicus*			
Thylamys		*colombianus*			
		minutus			
Didelphinae		gen. and sp. indet.			
Sparassocynidae					
Sparassocynus			sp. indet.		
Paucituberculata				(9)	(9)
Palaeothentidae					
Acdestis			*maddeni*		
Palaeothentes			*lemoinei*		
			minutus		
gen. indet.	sp. indet.				
Abderitidae					
Hondathentes		*cazador*			
Pithiculites		*chenche*			
Argyrolagidae					
Hondalagus			*altiplanensis*		
Sparassodonta					
Hondadelphidae					
Hondadelphys		*fieldsi*			
Borhyaenidae				(9)	(9)
Arctodictis	sp. indet.	(4)			
Acyon			sp. nov.		
Pseudolycopsis				*cabrerai*	
Lycopsis		*longirostrus*		*viverensis*	
Dukecynus		*magnus*			
Thylacosmilidae					
Anachlysictis		*gracilis*			
gen. indet.		sp. indet.			
Xenarthra					
Dasypodidae					
Prozaedyus	not listed		sp. indet.		
Neophractus			sp. nov.		
Kraglievichia					sp. indet.
Proeuphractus					*limpidus*
Vetelia	not listed			*perforata*	*perforata*
Chasicotatus					*ameghinoi*
Stenotatus	not listed				
Proeutatus	not listed				
Anadasypus		*hondanus*			
Pedrolypeutes		*praecursor**			
Nanoastegotherium		*prostatum*			
Stegotheriini	gen. and sp. indet.				
Peltephilinae				gen. and sp. indet.	

Appendix. Continued

Taxon	Fm Collón-Curá	La Venta	Q. Honda	Lower A. Chasicó	Upper A. Chasicó
Pampatheriidae					
Scirrotherium		*hondaensis**			
Glyptodontidae					
cf. *Asterostemma*		*gigantea*	sp. indet.		
		cf. *acostae*			
Propalaehoplophorus	not listed (?)		*andinus*		
Eucinepeltus	not listed				
Neoglyptatelus		*originalis*			
Palaehoplophorini					gen. and sp. indet.
Plohophorini					gen. and sp. indet.
Sclerocalyptini			sp. nov. 1		gen. and sp. indet.
			sp. nov. 2		
Myrmecophagidae					
Neotamandua		*borealis*			
Mylodontidae					
Octomylodon				*robertoscagliai*	
Brievabradys		*laventensis* (5)*			
Pseudoprepotherium		*confusum*			
gen. indet.			sp. indet.		
Megatheriidae					
Plesiomegatherium				*halmyronomum*	
Eucholoeops	not listed (?)				
Megathericulus	not listed				
Prepotherium	not listed (?)				
Diellipsodon	not listed				
Chasicobradys				*intermedius*	
Xyophorus			*villarroeli*		
cf. *Hapalops*	not listed (1)	large sp. indet.			
Nothrotheriinae		gen. and sp. indet.			
Megatheriinae		gen. and sp. indet.			
Megalonychidae					
Neonematherium		*flabellatum*			
gen. indet.		small sp.			
		large sp.			
Rodentia					
Erethizontidae					
Microsteiromys		*jacobsi*			
?*Steiromys*		small sp.			
		large sp.			
?*Neosteiromys*	*tordillense*				
Dasyproctidae					
Cephalomys			sp. indet.		
Neoreomys	sp. indet.		sp. indet.		
'Neoreomys'		*huilensis* (6)*			
Microscleromys		*paradoxalis*			
		cribiphilus			
Alloiomys	sp. indet.				
gen. indet.	sp. indet.				
Eocardiidae					
Eocardia	*robertoi*		*montata*		
Schistomys			sp. indet.		
Megastus	*elongatus*				
Matiamys	*elegans*				

Appendix. Continued

Taxon	Fm Collón-Curá	La Venta	Q. Honda	Lower A. Chasicó	Upper A. Chasicó
Dinomyidae					
Carlesia				cf. *pendolai*	
Tetrastylus				?sp. indet.	
'Olenopsis'		small sp. indet.*			
		large sp. indet.*			
'Scleromys'		*colombianus**			
		*schurmanni**			
gen. indet.		large sp. indet.			
Caviidae					
Cardiomys					sp. indet.
Parodimys				sp. indet. (?)	
Orthomyctera				sp. indet.	sp. indet.
Prodolichotis		*pridiana**			
Dolichotinae		small sp. indet.			
		large sp. indet.			
Hydrochoeridae					
Procardiatherium					sp. indet.
Octodontidae					
Chasicomys				octodontiformes	
Acaremyidae					
?*Galileomys*	*colloncurense*				
gen. indet.			sp. indet.		
Echimyidae					
Spaniomys			sp. indet.		
Chasichimys				bonaerense	
Cercomys				primitiva	
Pattersomys				scagliai	
Maruchito	trilofodonte				
Acarechimys	sp. indet.	cf. *minutissimus*			
Ricardomys		longidens			
Protacaremys	denisae				
General indet.		sp. indet.			
?Echimyidae		gen. and sp. indet.			
Chinchillidae					
Prolagostomus	sp. indet		*divisus*		
			imperialis		
			sp. nov.		
Lagostominae				gen. and sp. indet.	gen. and sp. indet.
Primates					
Callitrichidae					
Patasola		magdalenae			
Lagonimico		conclucatus			
Cebidae					
Neosaimiri		annectens			
		fieldsi			
Cebupithecia		sarmientoi			
Mohanamico		hershkovitzi			
Stirtonia		tatacoensis*			
		victoriae*			
Propithecia	neuquenensis				
Nuciruptor		rubricae			

Appendix. Continued

Taxon	Fm Collón-Curá	La Venta	Q. Honda	Lower A. Chasicó	Upper A. Chasicó
Litopterna					
Macraucheniidae					
Cullinia				*levis*	
Theosodon	not listed	sp. indet.			
gen. indet.			sp. indet.		
Macraucheniinae					*hystatus* (10)
Proterotheriidae					
Diadiaphorus	not listed		sp. indet.		
Prolicaphrium		*sanalfolsensis*			
Prothoatherium		*colombianus*			
Megadolodus		*molariformis*			
Villarroelia		*totoyoi*			
Neobrachytherium					*ullumense* (11)
gen. indet.		sp. indet.			
Notoungulata					
Homalodotheriidae					
Chasicotherium				*rothi*	
Homalodotherium	not listed				
Leontiniidae					
Huilatherium		*pluriplicatum**			
Toxodontidae					
Nesodon	(2)				
Palyeidodon	not listed				
Pisanodon					*nazari*
Prototrigodon	not listed				
Paratrigodon			sp. indet.	*euguii*	
Nesodonopsis	not listed				
Hyperoxotodon	not listed				
Pericotoxodon		*platignathus**			
Interatheriidae					
Protypotherium	not listed			*distinctum*	
				minutum	
Interatherium	not listed				
Epipatriarchus	(3)				
Miocochilius		*anomopodus**	sp. nov.		
		sp. nov. 1*			
		sp. nov. 2			
Mesotheriidae					
Plesiotypotherium			*minus*		
Typotheriopsis				sp. indet.	*chasicoensis*
Hegetotheriidae					
Hegetotherium	not listed				
Hemihegetotherium			*trilobus*		*torresi* (12)
					sp. indet.
Hegetotheriinae					gen. and sp. indet.
Paedotherium				*minor*	*minor*
Pachyrukhos	not listed				
Tremacyllus				sp. indet. (?)	sp. indet.
Astrapotheria					
Astrapotheriidae					
Xenastrapotherium		*kraglievichi**			
Granastrapotherium		*snorki**			
gen. indet.			sp. indet. (8)		

Appendix. Continued

Taxon	Fm Collón-Curá	La Venta	Q. Honda	Lower A. Chasicó	Upper A. Chasicó
Sirenia					
Trichechidae					
Potamosiren		*magdalenensis* (7)			

(1) following McKenna and Bell (1997), *Pseudhapalops* from Collón-Curá is treated as a junior synonym of *Hapalops*.

(2) the Collón-Curá '*Nesodon*' is probably *Palyeidodon* (Madden 1997; Croft *et al.* 2003*a*).

(3) following Hitz (1997) and Reguero *et al.* (2003), *Epipatriarchus* is not recognized as a distinct genus.

(4) although Madden *et al.* (1997) listed *Arctodictis* as occurring in the Monkey Beds (fig. 29·5), it is excluded from the present list owing to its absence from Goin's (1997, table 11.3) tabulation of La Venta marsupials.

(5) this species includes the material referred by McDonald (1997) to *Glossotheriopsis pascuali*, a species listed as a 'characteristic taxon' of the Laventan Age.

(6) this species is listed as '*Neoreomys*' (Walton 1997) because it does not appear to pertain to this genus but has not been referred to another.

(7) the sirenian from La Venta is included here for the sake of completeness, but is not included in calculations of faunal resemblance.

(8) the Quebrada Honda astrapothere was referred to ?*Xenastrapotherium* by Frailey (1987) but Johnson and Madden (1997) noted its resemblance to *Granastrapotherium snorki*. Although its generic identity is unclear, based on these authors' assessments, it is assumed to represent one of the two genera present in the La Venta Fauna.

(9) several Arroyo Chasicó marsupials were not included in the list of Bondesio *et al.* (1980*a*) owing to the lack of precise stratigraphic data associated with the specimens. They include: an indeterminate didelphid, probably a didelphine (Reig 1957; Marshall 1976); the borhyaenid *Chasicostylus castroi* (Reig 1957); and the caenolestid *Pliolestes tripotamicus* (Pascual and Herrera 1973). As these taxa could not be confidently referred to the upper or lower part of the formation, it was not possible to include them in the present faunal list; the marsupial components of these faunas are therefore somewhat depauperate.

(10) Bond and López (1995) recognized '*Theosodon*' *hystatus* as a valid species, but disputed its referral to *Theosodon* and instead suggested it pertains to an indeterminate genus of Macraucheniinae.

(11) this is assumed to be the same as Proterotheriinae gen. et sp. indet. listed by Bondesio *et al.* (1980*a*) for the Las Barrancas Member.

(12) following Bond (1997) and Cerdeño and Contreras (2000), the hegetotheriine from Arroyo Chasicó is recognized as pertaining to *Hemihegetotherium* rather than a distinct genus, *Pseudohegetotherium*.

NOTE ADDED IN PROOF

A formal description of the new species of *Acyon* referred to in the text and in Table 3 was published while the present paper was in press. The citation is:

FORASIEPI, A. M., SÁNCHEZ-VILLAGRA, M. R., GOIN, F. J., TAKAI, M., SHIGEHARA, N. and KAY, R. F. 2006. A new species of Hathliacynidae (Metatheria, Sparassodonta) from the middle Miocene of Quebrada Honda, Bolivia. *Journal of Vertebrate Paleontology* **26**, 670–684.