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9 The Notohippidae (Mammalia, Notoungulata) from Gran Barranca: preliminary considerations

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Abstract

The Notohippidae include notoungulates from Casamayoran to the "*Piso Notohippidense*" of the early Santacrucian. The oldest forms have brachydont to mesodont dentitions, while later forms attain hypsodonty and some taxa from the late Oligocene to middle Miocene evolved a thick coating of external cement on their teeth. The greatest diversity of taxa has been found in the Deseadan localities of La Flecha, Cabeza Blanca, and Scarritt Pocket in Argentine Patagonia. New material of Notohippidae has been recovered from several stratigraphic levels of different ages at Gran Barranca. GBV-3 "El Rosado" (Rosado Member) from the Mustersan SALMA has yielded material referred to *Puelia* with some doubt. GBV-4 "La Cancha" (Vera Member) of Tinguiririan SALMA has yielded fragmentary remains that suggest considerable diversity, including material referred to *Puelia plicata, Puelia* sp., *Eomorphippus obscurus*, *Eomorphippus pascuali*, and *Eomorphippus* sp. GBV-19 "La Cantera" (Unit 3, Upper Puesto Almendra Member) of pre-Deseadan aspect has yielded two new notohippids: *Patagonhippus canterensis* n. gen. et sp. and *Patagonhippus dukei* n. gen. et sp. Both species are closely related to well-known taxa from La Flecha and Cabeza Blanca, but are more primitive morphologically. Finally in the Lower Fossil Zone of the Colhue-Huapi Member, of Colhuehuapian SALMA age, occurs *Argyrohippus* cf. *A. boulei*.

Resumen

Los Notoungulata Notohippidae se registran desde niveles referibles a la SALMA Casamayorense hasta el "Piso Notohippidense" de la SALMA Santacrucense. Los Notohippidae basales presentan dentición brachyodonta-mesodonta, mientras que las formas terminales son claramente hypsodonctas y pastadoras. Algunos taxones del Oligoceno tardío-Mioceno desarrollan una gruesa cobertura de cemento en sus dientes. La mayor diversidad ha sido registrada en las localidades deseadenses de La Flecha, Cabeza Blanca y Scarritt Pocket (Patagonia, Argentina). Nuevos materiales de esta familia han sido recuperados de varios niveles estratigráficos de Gran Barranca. En el nivel GBV-3 "EL Rosado" (Miembro Rosado, SALMA Mustersense) se registra *Puelia*?. El GBV-4 "La Cancha" (Miembro Vera, SALMA Tinguiririquense) presenta una considerable diversidad, incluyendo materiales referidos a *Puelia plicata*, *Puelia* sp., *Eomorphippus obscurus*, *Eomorphippus pascuali* y *Eomorphippus* sp. En el nivel GBV-19 "La Cantera" (Unit 3, Miembro Puesto Almendra Superior, Deseadense temprano?) se registran dos nuevos Notohipidae: *Patagonhippus canterensis* n. gen. et sp. y *Patagonhippus dukei* n. gen. et sp. Ambas especies están relacionadas con las registradas en las localidades de La Flecha y Cabeza Blanca, pero morfológicamente son más generalizadas. Finalmente en la Zona Fosilífera Inferior del Miembro Colhue-Huapi (SALMA Colhuehuapense) se registra *Argyrohippus* cf. *A. boulei*.

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Introduction

The Notohippidae are medium-sized notoungulates with a distinctive cheek tooth occlusal morphology of "toxodontoid" pattern (see for example Simpson 1932) but differing from the Toxodontidae in the retention of all upper incisors and without developing "tusk-like" I2 and I3. The notohippids range in age from Casamayoran to the "*Piso Notohippidense*" of the early Santacrucian South American Land Mammal Age (SALMA). The oldest taxa in the family have brachydont dentitions and later forms attain hypsodonty. Also some specialized later taxa display a thick layer of external cementum around the perimeter of the crown. Judging broadly by cheek tooth crown height, some early notohippids may have been browsers but most have been interpreted as open-country grazers based on the hyposodonty and cementum. The best-known notohippids are from the Deseadan SALMA of Patagonia. Recent discoveries at Gran Barranca warrant a review of the taxonomy of the Patagonian members of the family to achieve a better understanding of their phylogenetics and adaptive diversity.

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Eocene notohippids (i.e. *Pampahippus*, *Plexotemnus*, *Puelia, Eomorphippus*, and *Trimerostephanus*) are the least well-known members of the family and generally comprise the smaller Toxodontia in paleofaunas where they occur (Bond and López 1993). The Patagonian *Plexotemnus*, *Puelia*, and *Eomorphippus* have had a long and complex taxonomic history (Simpson 1967). The family attained peak diversity in the Deseadan (i.e. *Morphippus, Rhynchippus, Interhippus, Nesohippus, Eurygenium, Coresodon*, *Pascualippus*, and *Moqueguahippus*) when their range extended from Patagonian Argentina to Bolivia, Brazil, and Peru. The family quickly declined thereafter such that by the middle Miocene Colhuehuapian SALMA only *Argyrohippus* is known. The last surviving representative, the rather poorly known *Notohippus*, was found in the "Notohippidense" fauna at Karaiken in western Patagonia before the turn of the twentieth century (Ameghino 1891; Ribeiro and Bond 1999). In those taxa where the postcranium is known, notohippids were quadrupedal terrestrial herbivores displaying some specializations for cursorial locomotion (Shockey 1997a, 1997b).

Notohippid dental morphology is generally described as being similar to that of the horse, that is, with an arcade of incisors and canines that form a functionally unified homomorphic "cropping" battery set in a smoothly rounded anterior rostrum, and unilaterally hypsodont cheek teeth with a complex pattern of enamel folds and fossettes variably obliterated by wear. In pre-Miocene taxa the dentition is complete and closed, but the anterior teeth become separated from the cheek teeth by a diastema and a thick layer of external cementum envelops the crowns in taxa from the Colhuehuapian SALMA (*Argyrohippus*) and "Piso Notohippidense" (*Notohippus*). A newly described notohippid from the Deseadan SALMA of southern Peru also displays external cementum on the crown (Shockey *et al.* 2006).

Ameghino (1906) included Notohippidae in Hippoidea and recognized 14 genera and many species among the South American branches of the superfamily. Loomis (1914) abandoned the family term Notohippidae and proposed the family Rhynchippidae (suborder Toxodontia, order Notoungulata) for the Deseadan genera *Rhynchippus*, *Morphippus*, and *Eurygenium*. He included in Nesodontidae the Deseadan taxa *Coresodon*, *Interhippus*, and *Nesohippus*.

Simpson (1932) followed Loomis (1914) and recognized the family Rhynchippidae, but differed with Ameghino (1897) on the relationship between *Rhynchippus* and *Notohippus* by including *Argyrohippus* together with *Notohippus* in another family, the Notohippidae. By contrast, Patterson (1934) did not recognize Rhynchippidae, and returned the genera that Loomis (1914) included in Nesodontidae to the Notohippidae.

Simpson (1945) proposed two subfamilies Notohippinae and Rhynchippinae, and included *Interhippus*, *Nesohippus*, *Argyrohippus*, *Stilhippus*, *Perhippidium*, and *Notohippus* in the former and *Pseudostylops*, *Morphippus*, *Rhynchippus*, and *Eurygenium* in the latter.

Patterson simplified the taxonomy of the Deseadan and Colhuehuapian notohippids in his unpublished revision and synonymy of the Ameghino collection (1952). Simpson (1967) and Patterson (in Simpson 1967) further simplified the taxonomy of the oldest members of the family by recognizing *Pseudostylops* to be a synonym of *Eomorphippus*, and *Interhippus* a synonym of *Coresodon*. In the case of *Nesohippus*, Simpson (1967, p. 180) believed it to have been listed by Ameghino (1906) mistakenly "because no Mustersan species was ever described, there are in the Mustersan specimens in the Ameghino Collection labeled as of this genus, and there is no other mention of its occurrence in the Mustersan."

When Bond and López (1993) described *Pampahippus arenalesi* from Lumbrera Formation (Salta Province, northwestern Argentina), the isotemnid-like taxa *Plexotemnus* and *Puelia* were included in Notohippidae. Other Paleogene genera (e.g. *Coelostylodon* and *Trimerostephanus*) were regarded as notohippids. This proposal was discussed by Shockey (1997b).

The record of notohippids outside Argentina is less well known. In Brazil, Soria and Alvarenga (1989) described *Rhynchippus brasiliensis* and a Notohippidae indet. from the Oligocene Tremembé Formation in the Taubaté Basin of São Paulo State. Paula-Couto (1981, 1982) described *Notohippus* sp. and *Purperia cribatidens* from localities 48 and 28, respectively, in the Miocene Solimões Formation along the Juruá River in Acre State. Paula-Couto's specimens are considered Notohippidae indet. and Leontiniidae respectively by Ribeiro and Bond (2000).

Shockey (1997a, 1997b) described *Pascualihippus* from the Deseadan of Salla, Bolivia, whose rostral morphology seems to suggest a close relationship with the origin of the Toxodontidae. Based on a phylogenetic analysis he inserted toxodontids within the paraphyletic Notohippidae. This clade also has a close relationship with the Leontiniidae. *Pampahippus*, *Plexotemnus*, and *Puelia* are considered to be Notohippidae *sensu lato* when Leontinnidae are included. These results differ from Cifelli (1993) who viewed Oligocene to Miocene notohippids as comprising a monophyletic clade. Shockey (1997a, 1997b) described two other taxa from Salla: *Eurygenium pacegnum* and *Rhynchippus brasiliensis*.

Shockey *et al.* (2004) described a very small m1 (or m2) (smaller than *Rhynchippus pumilus*) as cf. Notohippidae. The specimen is from the west bank of the Juruá River near its confluence with the Rio Breu, in Ucayali Department, Peru. Recently, Shockey *et al.* (2006) described *Moqueguahippus glycisma* from southern Peru, thus increasing the geographic distribution of this group during the Deseadan.

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Table 9.1. *Notohippidae species reported at Gran Barranca from the literature before this chapter*

Species	Current status[a]	SALMA[b]
Argyrohippus boulei Ameghino 1901	*Argyrohippus boulei* (Patterson 1952, *in litteris*)	Co
Argyrohippus fraterculus Ameghino 1901	*Argyrohippus boulei* (Patterson 1952, *in litteris*)	Co
Eomorphippus obscurus Ameghino 1901	*Eomorphippus obscurus* (Simpson 1967)	M
?*Eomorphippus pascuali* Simpson 1967	?*Eomorphippus pascuali* (Simpson 1967)	M
Interhippus deflexus Ameghino 1902	*Nomen dubium* (Simpson 1967)	?T
Perhippidion tetragonidens Ameghino 1904	*Argyrohippus boulei* (Patterson 1952, *in litteris*)	Co
Plexotemnus complicatissimus Simpson 1970	*Plexotemnus complicatissimus* (Bond and López 1993)	C
Pseudhippus tournoueri Ameghino 1902	*Argyrohippus boulei* (Patterson 1952, *in litteris*)	Co
Pseudostylops subquadratus Ameghino 1901	*Eomorphippus obscurus* (Simpson 1967)	M
Stilhippus deterioratus Ameghino 1904	*Argyrohippus boulei* (Patterson 1952, *in litteris*)	Co
Trimerostephanus coalitus Ameghino 1901	*Trimerostephanus coalitus* (Bond and López, 1993)	M
	Patagonhippus canterensis n. gen. et sp.	?De
	Patagonhippus dukei n. gen. et sp.	?De

Notes: [a]Bibliographical references in parentheses.
[b]Co, Colhuehuapian; M, Mustersan; T, Tiguiririan.

The greatest diversity of notohippid taxa is found in the Deseadan of Argentine Patagonia at localities such as La Flecha, Cabeza Blanca, Scarritt Pocket, and Gran Barranca (see Table 9.1). Here we describe new material of Notohippidae from the Sarmiento Formation at Gran Barranca. This material was collected at GBV-3 "El Rosado", GBV-4 "La Cancha", GBV-19 "La Cantera", and from levels of the Colhue-Huapi Member.

The Sarmiento Formation (middle Eocene – early Miocene) at Gran Barranca is the most complete continental sequence of middle Cenozoic mammal-bearing sedimentary rocks anywhere in South America, and serves as the standard reference section for this interval. Based on the stratigraphic occurrences of index and guide taxa, at least six different faunal zones can been differentiated (Carlini *et al*. 2005; Bellosi this book).

Three levels at Gran Barranca are of major importance for this work: localities GBV-3 "El Rosado" and GBV-4 "La Cancha," and GBV-19 "La Cantera." GBV-4 lies stratigraphically above GBV-3 and is separated from it by several stratigraphic discontinuities (Bellosi this book). In turn GBV-19 is younger than GVB-4 based on radiometric, paleomagnetic, and stratigraphic evidence (Ré *et al*. Chapter 3, this book; Bellosi this book). Locality GBV-3 is referred to the Mustersan SALMA on the basis of the composition of its native ungulates (Madden *et al*. this book). The locality contains some notoungulate taxa characteristic of the Mustersan SALMA but also has taxa not found in the Mustersan but characteristic of the Tinguiririan SALMA (e.g. *Archaeotypotherium propheticus*, *Protarchaeohyrax gracilis*, and *Proargyrohyrax* sp.) and also includes other toxodontian families of a Deseadan age (López *et al*. 2005). The marsupial fauna of GVB-4 closely resembles that of the Tinguiririan (Goin *et al*. this book) and the absence of rodents is significant (Vucetich *et al*. this book). Overlying the Tinguiririan level is GBV-19. GVB-19 contains a mix of Deseadan and pre-Deseadan elements (Goin *et al*. this book; Carlini *et al*. this book; Vucetich *et al*. this book; see also Bond *et al*. 2004), befitting its intermediate stratigraphic and temporal position in the Gran Barranca sequence.

Abbreviations

Specimens of notohippids were studied in the following collections (given with their abbreviations used in the text): FMNH, Field Museum of Natural History, Chicago, USA; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires; MLP, Museo de La Plata, La Plata; MPEF-PV, Museo Paleontológico "Egidio Feruglio," Trelew. Dental terminology follows the convention of using upper-case letters for the upper incisor, canines, premolars, and molars, lower-case for the lower series.

Systematic paleontology

Order **NOTOUNGULATA** Roth 1903
Suborder **TOXODONTIA** Owen 1853
Family **NOTOHIPPIDAE** Ameghino 1894
Genus Puelia Roth 1902
Puelia plicata Roth 1902
Material MPEF-PV 6215, upper molars, MPEF-PV 6186, M2.
Locality Gran Barranca, GBV-4 "La Cancha" level, Vera Member, Sarmiento Formation.

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***Puelia* sp.**

Material MPEF-PV 6170, right and left upper molars.

Locality Gran Barranca, GBV-4 "La Cancha" level.

Puelia? sp.

Material and localities PEF-PV 6713, jugal and maxilla fragments, MPEF-PV 6853, left upper M1 from Gran Barranca, GBV-3 "El Rosado," Rosado Member, Sarmiento Formation. MPEF-PV 5732, upper molar, MPEF-PV 6180, P4 and M1, MPEF-PV 6200, right lower p3, MPEF-PV 6206, left upper M1 from Gran Barranca, GBV-4 "La Cancha" level.

Comments To date, *Puelia* has been reported from the Mustersan localities of Cerro del Humo, Sierra Talquino, Gran Hondonada, and Laguna del Mate. The materials here presented are the first record of the genus at Gran Barranca, and the discovery of more complete remains may permit recognition of a new species, as well as the extension of the stratigraphic distribution of the genus to the Tinguiririan SALMA. Some even more fragmentary material from GBV-3 El Rosado (MPEF-PV 6713 and MPEF-PV 6853) may be related to *Puelia?* sp.

The problem of the systematic arrangement of *Puelia* is complex. Bond and López (1993) recognize this taxon as a form related to *Pampahippus* and *Plexotemnus*, two Casamayoran genera that they considered basal Notohippidae (as does Shockey 1997b). Simpson (1967) was well acquainted with the similarities that his "*Acoelohyrax*" group (including what we are calling now *Plexotemnus* and *Puelia*) had with the earlier Notohippidae such as *Eomorphippus*. Confronted with the possibility that his "*Acoelohyrax*" group could be either an early offshoot of the Notohippidae or Isotemnidae evolving in parallel, Simpson (1967) thought their many resemblances possibly but unlikely convergent and stated that "the difference between the two interpretations is rather formal and not very important" a somewhat surprising statement given the phylogenetic consequences. Bond and López (1993) evaluating the characters mentioned by Simpson (1967) and other not known to him for *Plexotemnus* (such as the incisor region) concluded that *Pampahippus*, *Plexotemnus*, and *Puelia*, could be clearly segregated from the Isotemnidae and considered early representatives of the Notohippidae.

Bond and López (1993) recognized three valid species within genus *Puelia*, namely *P. plicata* Roth 1902, the larger-sized *P. coarctatus* Ameghino 1901, and *P. sigma* Ameghino 1901. However, the validity of the latter species remains uncertain, and it could be a junior synonym of *P. plicata*. Several specimens at GBV-4 "La Cancha" are referred to *Puelia*. MPEF 6215 is a left M1 or M2 that is referred to *Puelia plicata*, and represents the youngest record for this species, formerly known only from the Mustersan SALMA. The type and other referred specimens come from other Mustersan localities (e.g. Cerro del Humo, in Chubut: Simpson 1967). Some fragmentary upper and lower molars (i.e. MPEF-PV 6170) also from GBV-4 are referred to *Puelia* sp.

Genus ***Eomorphippus*** Ameghino 1901

Eomorphippus obscurus Ameghino 1901

Fig. 9.1A–B.

Material MPEF-PV 6154, isolated upper and lower premolars and molars; MPEF-PV 6188, left lower m3; MPEF-PV 6197, isolated lower incisor; MPEF-PV 6791, isolated upper incisor; MPEF-PV 7945, left dentary fragment with p4–m3.

Locality Gran Barranca, GBV-4 "La Cancha" level.

***Eomorphippus* sp.**

Material MPEF-PV 6217, isolated upper premolars and molars.

Locality Gran Barranca, GBV-4 "La Cancha" level.

Comments The genus *Eomorphippus* presents a suite of characters including mesodonty and the absence of external cementum that place it in an intermediate position phylogenetically between the Casamayoran–Mustersan taxa on the one hand (e.g. *Pampahippus*, *Plexotemnus*, *Puelia*) and those of the Deseadan on the other hand (e.g. *Rhynchippus, Morphippus*). This intermediate phylogenetic position agrees with stratigraphic superposition at Gran Barranca, between the Mustersan levels with *Puelia* and pre-Deseadan (GVB-19) and Deseadan levels with more progressive notohippids. *Eomorphippus* occurs exclusively in Tinguiririan SALMA levels of Patagonia (Gran Barranca and Cañadón Blanco) and Chile. In addition to materials collected by Simpson in Profile M at Gran Barranca and Feruglio from the same bed in Profile K, we identify new materials (e.g. a dentary fragment, upper and lower incisors, as well as isolated molars) from GBV-4 in Profile K at Gran Barranca. The GVB-4 is a manganese-rich locality and the fossils are covered with manganese oxides. Much of the material described by Ameghino from "une partie supérieure" of the *Astraponoteen* (see Reguero *et al*. 2004) is also covered with manganese (e.g. *Pseudopachyrucos foliiformis* Ameghino 1901 and *Interhippus deflexus* Ameghino 1904).

Eomorphippus pascuali Simpson 1967

Material MPEF-PV 6159, right upper M1–2 and left upper M3, MPEF-PV 6243, right m2.

Locality Gran Barranca, GBV-4 "La Cancha" level.

Comments Simpson (1967, plate 41, figures 13–15) described a new species of Notohippidae collected by Coley Williams from the fluvial beds from near the top of his Profile M, and referred with doubt to the

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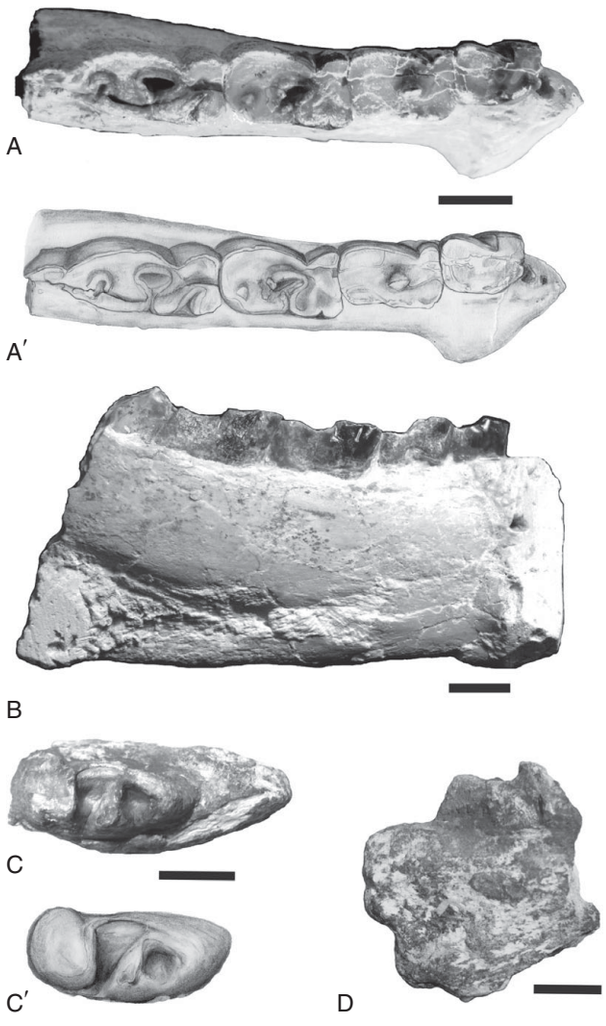

Fig. 9.1. (A, A′, B) *Eomorphippus obscurus* Ameghino 1901; MPEF-PV 7945, left dentary fragment with p4–m3 in occlusal and lingual views. (C, C′, D) *Eomorphippus pascuali* Simpson 1967; MPEF-PV 6243, right m2 isolated in occlusal and labial views. Scale bar 1 cm.

genus *Eomorphippus* as *E.? pascuali*, characterized among other things by its small size when compared to *E. obscurus*. *Eomorphippus pascuali* is clearly different morphologically from *E. obscurus* and as Simpson (1967) opined, it could represent a new genus. Given our state of knowledge of this taxon, we maintain it as *E. pascuali*. *Eomorphippus pascuali* is larger than the two known species of *Puelia*, with higher upper molars crowns and deeper lingual clefts reaching nearly to the bases of the molar crowns. In these characters *E. pascuali* is more progressive than *Puelia*. In this light, the synonymy of *E. pascuali* to *Puelia* (Wyss *et al*. 2005) cannot be accepted. In the new collections made at Gran Barranca there are some upper molars that can be referred to *E. pascuali*, and an m3 (MPEF-PV 6243, Fig. 9.1C–D) very similar in size to the m3 in the lower jaw assigned by Simpson (1967) to *E. pascuali*. These crowns are lower than those of *E. obscurus*. The new material establishes the presence of *E. pascuali* at GBV-4 "La Cancha" level at Profile K. They also serve to show that this taxon represents a notohippid distinct and more progressive than *Puelia* and also distinct, but lower crowned, than *E. obscurus*. Pending revision of all Tinguiririan notohippids we prefer to maintain *E. pascuali* as a distinct taxon until its generic assignment can be fully resolved.

Genus *Patagonhippus* n. gen.

Type species *Patagonhippus canterensis* n. sp.

Referred species *Patagonhippus canterensis* n. sp. and *Patagonhippus dukei* n. sp.

Etymology From Patagonia, the geographic area where this taxon was found, and *hippus*, a suffix commonly used for notohippid genera.

Diagnosis Notohippidae with teeth lacking cement, as in all the Deseadan notohippids with the exception of *Argyrohippus praecox, Eurygenium latirostris*, and *Moqueguahippus glycisma*. Subtriangular upper premolars differ from the molarized premolars of *Pascualihippus, Rhynchippus*, and *Eurygenium*. Premolars and molars with paracone column and parastyle more pronounced than in *Rhynchippus, Coresodon*, and *Eurygenium* and with a straight ectoloph. Mesial cingulum in upper premolars as in *Rhynchippus* but not *Eurygenium*. M1–2 with a groove in the mesiolingual corner of the protocone that originates as a mesial expansion as in *Eurygenium*. M1–2 with first crista in the lingual ectoloph and central valley open lingually as distinct from *Pascualihippus*. M3 with central valley open distally similar to *Eurygenium*. Lower molars with deep groove on the lingual face and without posterior fossettid in the entolophid as in *Eurygenium*, *Morphippus*, and *Moqueguahippus* and different of *Rhynchippus* and *Coresodon*.

Geographic and chronologic distribution Argentina, early? Deseadan SALMA.

Patagonhippus canterensis n. sp.

Fig. 9.2.

Holotype MPEF-PV 7087, maxilla fragments with right P2–M3 and left M2–3.

Referred material MPEF-PV 6264, right dentary with p3–m3 and left dentary with canine, p1 and m3; MPEF-PV 5775, left P2–M1; MPEF-PV 6112, left lower m2–3; MPEF-PV 6120, incisor; MPEF-PV 6136, left lower p4; MPEF-PV 6138, upper right P1 or P2; MPEF-PV 6239, left upper molar; MPEF-PV

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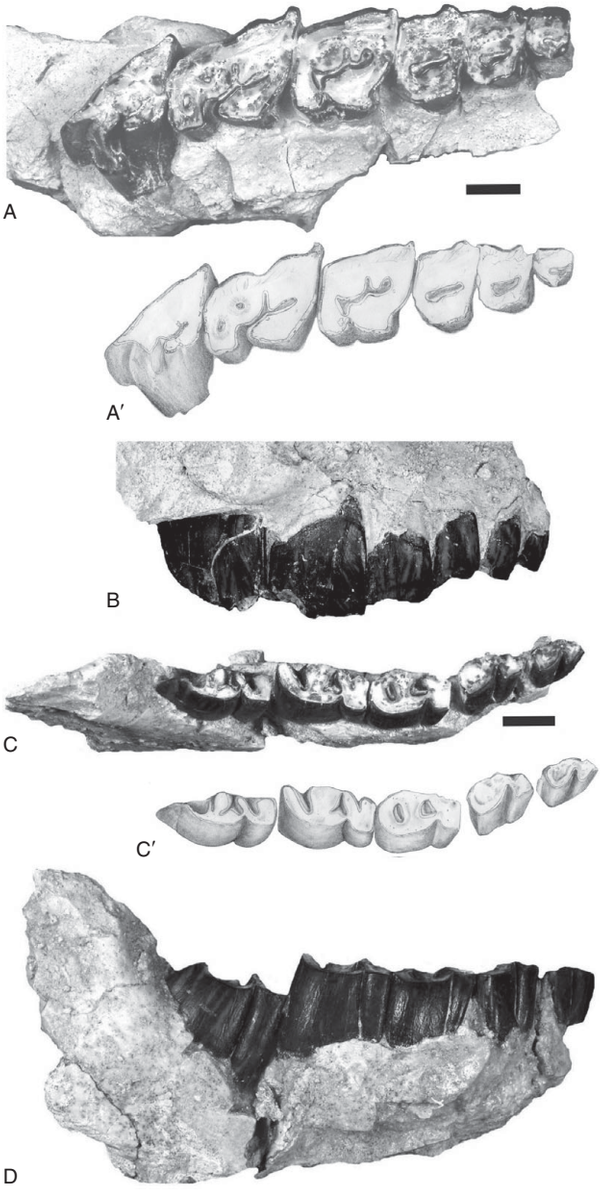

Fig. 9.2. *Patagonhippus canterensis* n. gen. et n. sp. (A–B) MPEF-PV 7087, right maxilla fragment with P2-M3 in occlusal and labial views. (C–D) MPEF-PV 6264, right dentary with p3–m3 in occlusal and labial views. Scale bar 1 cm.

6247, left lower p2; MPEF-PV 6255, dentary fragment with p4–m2; MPEF-PV 6272, right upper M1; MPEF-PV 6617, right dentary fragment with dp4, m1–2 and left dentary fragment with m1; MPEF-PV 6811, premolar; MPEF-PV 7501, P4–M2, MPEF-PV 7698, dentary fragment with m1; MPEF-PV 7720, left dentary with m2–3; MPEF-PV 7721, teeth; MPEF-PV 7729, mandible; MPEF-PV 7740, symphysis with teeth; MPEF-PV 7742, dentary fragment with teeth; MPEF-PV 7743, dentary fragment with teeth; MPEF-PV 7746, mandible; MPEF-PV 7762, teeth; MPEF-PV 7775, right maxilla with M1; MPEF-PV 7776, upper incisor; MPEF-PV 7777, dentary fragment with tooth; MPEF-PV 7834, teeth.

Type locality GBV-19 "La Cantera," Unit 3, Upper Puesto Almendra Member, Sarmiento Formation at Gran Barranca, Chubut Province, Argentina.

Etymology In reference to the La Cantera locality at Gran Barranca.

Diagnosis Similar in size to *Morphippus imbricatus* and 10% smaller than *Rhynchippus equinus*. P2 half the size of P3 (unlike *Rhynchippus equinus*, *Pascualihippus boliviensis*, *Eurygenium latirostris*, and *E. pacegnum*) and with protocone less developed than the hypocone. P3–4 subtriangular in outline; compared with other Deseadan species (*Pascualihippus boliviensis, Eurygenium latirostris*, and *E. pacegnum*), the upper premolars and molars are less hypsodont and have a more persistent mesial cingulum. Upper molars central valley opens lingually and the lingual groove is deep and persists into advanced stages of wear. Lower molars without posterior fossettid in the entolophid, as in *E. pacegnum* and *M. imbricatus* but differs from these species in having a deeper groove between metalophid and entolophid, and entolophid and hypolophid.

***Patagonhippus dukei* n. sp**.

Fig. 9.3.

Holotype MPEF 6127, right dentary fragment with canine, p1–4, m1–3.

Type locality GBV-19 "La Cantera," Unit 3, Upper Puesto Almendra Member, Profile A, Sarmiento Formation at Gran Barranca, Chubut Province, Argentina.

Etymology For Duke University, North Carolina, in recognition of the contributions of its faculty to the knowledge of the Patagonian vertebrate fossils.

Diagnosis Morphologically similar to *Patagonhippus canterensis* n. sp., but 50% smaller in size. Size comparable to *Rhynchippus pumilus*, but differs from this species because lacks a posterior fossettid in the entolophid.

Comments and discussion As commented previously, Deseadan notohippids include *Rhynchippus*, *Eurygenium*, *Morphippus*, *Coresodon, Argyrohippus praecox, Pascualihippus*, and *Moqueguahippus*. The first five taxa are known from the Deseadan of Patagonia and occur in localities with typical Deseadan faunas (e.g. Cabeza Blanca, La Flecha), whereas the latter are from tropical areas (Peru and Bolivia). The type material of *Morphippus imbricatus* (MACN A 52–76), *Coresodon scalpridens* (MACN A 52–1), and *Argyrohippus praecox* (FMNH P13334) comes

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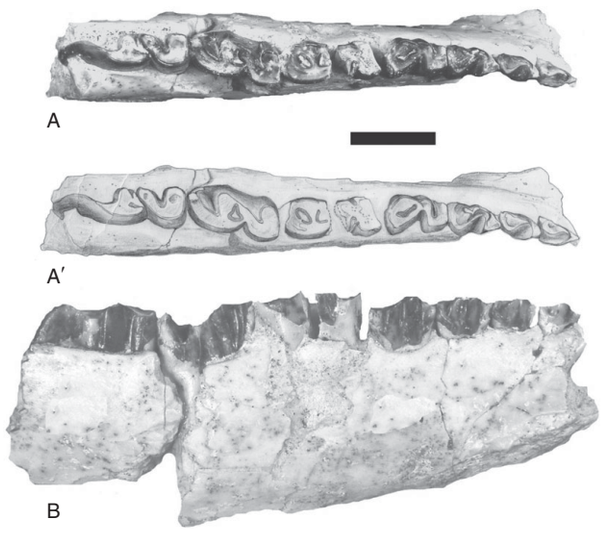

Fig. 9.3. *Patagonhippus dukei* n. gen. et n. sp. (A–B) MPEF-PV 6127, right dentary fragment with canine, p1–m3 in occlusal and lingual (reversed) views. Scale bar 1 cm.

from La Flecha, while the type material of the two species of *Rhynchippus* (i.e. *R. equinus* MACN A 52–31 and *R. pumilus* MACN A 52–61) comes from Cabeza Blanca. The type locality of *Eurygenium latirostris* (MACN A 52–70) is unknown (probably Cabeza Blanca or La Flecha). *Patagonhippus* from the La Cantera level (early? Deseadan) at Gran Barranca represents the first record of a new notohippid genus for Patagonia since the time of Ameghino.

When compared with taxa from the Mustersan and Tinguiririca, *Patagonhippus canterensis* n. gen. et n. sp. and *P. dukei* n. gen. et n. sp. share the absence of a posterior fossettid, but have a more hypsodont dentition.

Patagonhippus canterensis and *P. dukei* differ in many respects from Deseadan taxa *Rhynchippus and Coresodon* (occlusal morphology), and *Argyrohippus* (e.g. absence of cement), and have a closer affinity with *Morphippus* and *Eurygenium*.

Six species were proposed for the genus *Morphippus* (*M. complicatus* Ameghino 1897, *M. hypselodus* Ameghino 1897, *M. fraternus* Ameghino 1901, *M. imbricatus* Ameghino 1897, *M. quadrilobus* Ameghino 1901, and *M. corrugatus* Ameghino 1899). Loomis (1914) considered the first five species as *M. imbricatus*, but Patterson (1952) in his unpublished revision recognized *M. imbricatus* (only the specimen MACN A 52–76) as valid species; he considered *M. quadrilobus* to be a toxodontid; and he placed *M. complicatus, M. hypselodus, M. fraternus*, and *M. imbricatus* (specimen MACN A 52–59) into synonymy with *Rhynchippus equinus* Ameghino 1897; Patterson does not mention *M. corrugatus*. Examination of the type material (MACN A 52–602) of the latter shows it to be a toxodontid.

Patagonhippus canterensis is similar in size to *M. imbricatus* (MACN A 52–76, right dentary with all teeth). The two resemble one another in having lower molars without a posterior fossettid on the entolophid, but differ in the depth of the groove between the entolophid and hypolophid; *Patagonhippus dukei* also differs from *M. imbricatus* by the smaller size (50%).

Also in the Patagonia Deseadan, two species were proposed for the genus *Eurygenium* (*E. latirostris* Ameghino 1894 and *E. normalis* Ameghino 1897). Patterson (1952) recognized *E. latirostris* as valid but he sank *E. normalis*, based on MACN A 52–85, a left maxilla fragment with P4–M3, into *Morphippus imbricatus* but Marani and Dozo (2008) retain *E. normalis* as a smaller species of *Eurygenium* because it possesses premolar characters of that genus. More recently Shockey (1997b) described a new species of *Eurygenium, E. pacegnum*, from the Deseadan of Bolivia.

Patagonhippus canterensis shares with *E. latirostris* (MACN A 52–71 and UNPSJB-PV-60) the first crista on the lingual ectoloph and with *E. pacegnum* (MNHN-Bol-V-003643) the absence of posterior fossettid on the entolophid, but differs from both species in having a mesial premolar cingulum, in lacking cementum on the mesial faces of the cheek teeth and in having deeper grooves between metalophid and entolophid, and entolophid and hypolophid. *Patagonhippus dukei* has the diagnostic *Patagonhippus* characters mentioned above and is 50% smaller than *E. latirostris* and *E. pacegnum.*

Others two species of Deseadan notohippids are recognized outside Patagonia: *Pascualihippus boliviensis* Shockey 1997a from Salla, Bolivia, and *Moqueguahippus glycisma* Shockey *et al*. 2006, from the upper Moquegua Formation, Peru. Both new species differ from *P. boliviensis* in having subtriangular premolars, P2 and P3 having the first crista in the lingual ectoloph and lacking a posterior fossettid on the entolophid. The two new species *P. canterensis* and *P. dukei* share the posterior fossettid in the entolophid with *M. glycisma*, but differ in absence of cementum, present in *M. glycisma*.

Genus *Argyrohippus* Ameghino 1901

Argyrohippus cf. *A. boulei* Ameghino 1901

Material MPEF-PV 5388, mandible with right and left i1–3, c, p2–m3; MPEF-PV 5922, fragment of upper molar and left lower m1; MPEF-PV 7325, left lower molar.

Locality Lower Fossil Zone, Colhue-Huapi Member of the Sarmiento Formation at Gran Barranca, Chubut Province, Argentina. Colhuehuapian SALMA.

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Comments Three species have been described for *Argyrohippus*: *A. boulei* Ameghino 1901 and *A. fraterculus* Ameghino 1901 from the Colhuehuapian levels at Gran Barranca, and *A. praecox* Patterson 1935 from the Deseadan at Cabeza Blanca. Patterson (1952 *in litteris*) considered the two Colhuehuapian species to be conspecific with *A. boulei* the nominal species. These species are based on fragmentary remains, and new material MPEF-PV 5388 contributes a better knowledge of this taxon.

Bioestratigraphy and paleoecology

Some notohippid taxa at Gran Barranca cannot be referred with certainty to any known species. This suggests that either the stratigraphic levels are not equivalent in age with localities in Patagonia yielding previously known taxa, or that the evolutionary radiation of notohippids in this interval was characterized by morphological experimentation and rapid transformation.

As with equids, the major trends observed in the history of notohippids are towards increasing height of the cheek teeth from brachyodont to hypsodont, but notohippids were more conservative in podial morphology, and never attained the extreme reduction in the number of digits seen in horses (Loomis 1914; Shockey 1997b).

An extended, continuous and rich fossiliferous sequence of notohippids at Gran Barranca is an ideal opportunity to follow the evolutionary increase in crown height. In the low levels of this stratigraphic sequence ("El Rosado") the notohippids are represented by remains assigned to *Puelia?*, which has low-crowned cheek teeth. "La Cancha" level has yielded remains that suggest a high diversity of brachyodont notohippid taxa (*Puelia plicata* and *Puelia* sp.) along with others that are somewhat more high-crowned or mesodont: *Eomorphippus obscurus* and *Eomorphippus pascuali*. Mesodont taxa occur further up in the sequence. "La Cantera" level has yielded two new mesodont notohippids (*Patagonhippus canterensis* and *P. dukei*), and the Lower Fossil Zone of the Colhue-Huapi Member, has the mesodont taxon *Argyrohippus* cf. *A. boulei*.

Although *Moqueguahippus glycisma*, a Deseadan notohippid from southern Peru, has a layer of external cementum surrounding the crowns, in the sequence at Gran Barranca this feature does not appears before the Colhuehuapian levels (*Argyrohippus*).

These changes in tooth morphology and limb structure are accompanied by an increase in body size during notohippid evolution. These changes have been proposed as a consequence of the appearance and development of grassland biomes at a time of major environmental change that occurred during the late Eocene through the late Oligocene interval in South America (Pascual and Ortiz Jaureguizar 1990). *Eomorphippus obscurus* was among the earliest notoungulates to developed high-crowned teeth (Patterson and Pascual 1972). Some more advanced forms present external cement, which possibly made these animals more suited to foraging on plants like grasses that contain large amounts of silica phytoliths or to diets containing more grit in general. Notohippidae show a reduction of the lateral digits (loss of digit I and reduction of digit V), having tetradactyl but functionally tridactyl feet (Shockey 1997b). Other modifications in the body and tarsus, indicate that they probably had been animals of cursorial habits, possibly living in more opened areas.

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