

UNIVERSITY OF CALIFORNIA

Santa Barbara

Two New Oligocene “Notohippids” (Mammalia, Notoungulata, Toxodontia) from the
Central Chilean Andes: Taxonomy and Phylogenetics

A Thesis submitted in partial satisfaction of the
requirements for the degree Master of Science
in Earth Science

by

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March 2019

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ACKNOWLEDGEMENTS

I am extraordinarily grateful for the academic and personal guidance I received while at UC Santa Barbara. This project would not be possible or completed without the seemingly endless knowledge of my primary advisor, Dr. André Wyss. My work benefitted from advice on writing style, content, and proper figure display by Dr. Wyss, Dr. Susannah Porter, Dr. Bruce Tiffney, Andrew McGrath, Chris Everett, Tina Woltz, Dr. Dan Luna, Dr. John Moore, and Dr. Heda Agić.

I credit my enthusiasm for teaching to having served as a teaching assistant for Dr. Luna, Dr. Wyss, Dr. Porter, and Dr. Tiffney. They conducted the most engaging lectures and labs I have been part of.

Finally, thank you to my friends and family for their continued support and interest in my research.

ABSTRACT

Two New Oligocene “Notohippids” (Mammalia, Notoungulata, Toxodontia) from the
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Two new Oligocene “notohippids” from the Abanico Formation, a geographically widespread volcanic and volcanoclastic lithostratigraphic unit in the Andean Main Range of central Chile, are described and subjected to phylogenetic analysis. “Notohippidae” is a paraphyletic assemblage of medium-sized South American native ungulates from the Casamayoran (middle Eocene) to Santacrucian (early Miocene) SALMAs (South American Land Mammal Age). This group belongs to Notoungulata, the most diverse clade of native South American ungulates.

The two new taxa are represented by SGOPV 3750, consisting of a cranium and partial upper dentition recovered near Upeo, Chile (~200 km south of Santiago), which represents a new genus, and SGOPV 3221, a nearly complete upper dentition collected from the Las Leñas drainage basin (100 km SSE of Santiago), representing a new species of *Rhynchippus*. Specimens from the Salla Beds, Bolivia, originally assigned to *Rhynchippus brasiliensis* are here referred to the same new species of *Rhynchippus* as proposed for SGOPV 3221. A phylogenetic analysis resolves a sister group relationship between *Eurygenium* and *Argyrohippus* for the first time, but “Notohippidae” remains paraphyletic. The taxa described here nest within a polytomy including the pairing of *Eurygenium* and *Argyrohippus*, *Rhynchippus equinus*, *R. pumilus*, and a clade comprising *Pascualihippus boliviensis* plus Toxodontidae.

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I. Introduction

OVERVIEW

I describe two new “notohippids” (Mammalia, Notoungulata, Toxodontia) from volcaniclastic deposits of the Andean Main Range of central Chile. This is accompanied by a phylogenetic analysis of the group, and a consideration of its history. The first new taxon, recognized from a partial cranium bearing at least one representative of most upper cheek-tooth positions (SGOPV 3750), represents a new genus. SGOPV 3750 originates from an essentially undescribed fauna from Estero Upeo, ~200 kilometers SSE of Santiago. The Upeo Fauna likely pertains to the Tinguirirican (early Oligocene) or Deseadan (late Oligocene) SALMAs (South American Land Mammal Age), based on the hypsodonty of SGOPV 3750 and other aspects of the fauna. The second taxon, a new species of *Rhynchippus* Ameghino, 1897, is based on a rostrum bearing a largely complete upper dentition (SGOPV 3221), which likely derives from a Deseadan SALMA level in the Las Leñas drainage, ~100 kilometers SSE of Santiago. Specimens from the Deseadan Salla Beds, Bolivia (Shockey, 1997 a, b), are also referred *Rhynchippus*, sp. nov. here.

“Notohippids,” medium-sized notoungulates spanning the Casamayoran (middle Eocene) to Santacrucian (early Miocene) SALMAs, peaked in diversity during the Deseadan (Simpson, 1967; Madden, 1990; López et al., 2010), attaining hypsodonty (high-crowned molars), and lophodonty (ridged occlusal surfaces) early in the group’s history, around 35 Ma (Simpson, 1967; Shockey, 1997a, b; López et al., 2010).

“Notohippids” retain three incisors, a closed dentition, molariform premolars, and lophate, vertically curved (toxodontoid) upper molars bearing a central fossette (Simpson, 1967; López et al., 2010).

Notions of “notohippid” relationships have changed vastly since the group was first recognized, and recent phylogenetic analyses present conflicting views about its internal relationships (Shockey, 1997a, b; Cerdeño and Vera, 2010; Billet, 2011; Dozo and Martínez, 2015; Deraco and García-López, 2016). Notoungulata, of which “notohippids,” are members, are currently considered most closely related to perissodactyls among extant mammals (Welker et al., 2015). Notohippids were initially considered related to equids (Ameghino 1894, 1902), as their name implies. The group’s notoungulate affinities were soon recognized, however, as was a subdivision into “Rhynchippidae” and “Notohippidae” within Toxodontia, a sub-order of Notoungulata (Loomis, 1914). This split was subsequently formalized as “Rhynchippinae” and “Notohippinae,” within “Notohippidae” (Simpson, 1945). Recent cladistic analyses recover “Notohippidae” as paraphyletic (Shockey, 1997a, b; Billet, 2011; Deraco and García-López, 2016). “Notohippidae” is thus placed in quotes, reflecting its status as a toxodontian evolutionary grade, inasmuch as some “notohippids” are more closely related to Toxodontidae than to other “notohippids.” Despite uncertainty about intra-“notohippid” relationships, leontiniids are consistently identified as the nearest outgroup to the clade including “notohippids” and toxodontids (Shockey, 1997a, b; Billet, 2011; Deraco and García-López, 2016).

CENTRAL CHILEAN ANDEAN STRATIGRAPHY AND MAMMALIAN PALEONTOLOGY

The cover rocks of the Andean Main Range in central Chile range from Jurassic (~170 Ma) to Recent in age, consisting of a roughly 10-km-thick sequence of continental and marine sedimentary rocks, volcanics, volcanoclastics, and alluvium (Klohn, 1960; González and Vergara, 1962). The Abanico Formation, from which the fossils described

herein are derived, consists of Late Cretaceous to middle Miocene volcanic and volcanoclastic deposits (Charrier et al., 1996; Godoy et al., 1999; Charrier et al., 2002; Farias et al., 2005; Mosolf et al., 2018). Additionally, the Abanico Formation stratigraphy has been extensively studied on the Tinguiririca Valley, latitudinally between Upeo and Las Leñas, the source areas of the specimens described here. Recently Muñoz et al. (2018) proposed reassigning the lower, evidently non-fossiliferous part of the Abanico Formation in the Tinguiririca Valley to the Plan de los Yeuques Formation. The Abanico Formation, reaches ~1.5-3.6 km in thickness in the Tinguiririca Valley (depending on to the disputed assignment of basal strata to the Plan de los Yeuques Formation). The main Tinguirirican SALMA fossil localities in the valley lie ~40 km NNE of Upeo and ~65 km SSE of Las Leñas. The Abanico Formation, which makes up the volumetrically most important lithostratigraphic unit in the central Chilean Andes (Mosolf et al., 2018), was classically considered Late Cretaceous to early Tertiary in age (Klohn, 1960), but the discovery of Eocene through Miocene fossil mammals in the Tinguiririca Valley and several other major drainages in the region (including Las Leñas and Upeo) proved that substantial portions of the unit are far younger (Wyss et al., 1990).

Fossil mammals of the central Chilean Andes were first discovered in the Río Tinguiririca valley near the resort village of Termas del Flaco (Wyss et al., 1990). Of the several fossil mammal faunas now known from central Chile, the Tinguiririca Fauna remains the best studied. This fauna, the type of the Tinguirirican SALMA (Flynn et al., 2003), is early Oligocene in age, an interval otherwise poorly represented in the South American fossil record (Wyss et al., 1993). The Tinguiririca Fauna is the oldest fauna dominated by hypsodont herbivores globally (Flynn et al., 2003), achieving a degree of hypsodonty not seen on other continents until 15 Mya later (Willis and McElwain, 2002).

Fossils from Las Leñas and Upeo have received only limited attention previously. SGOPV 3221 is only the third specimen described from Las Leñas, while SGOPV 3750 is the first from Upeo. *Chilecebus*, a platyrrhine primate dated at 20.09 ± 0.27 Myr (Flynn et al., 1995), and an interatheriine tyotherid (Luna, 2015) have been described from strata of Miocene age at Las Leñas. Thus, at least two direct stratigraphically superposed SALMAs occur at Las Leñas (one hosting *Chilecebus*, and the other that produced SGOPV 3221), an uncommon occurrence in the South American fossil record. Although just a single isotopic date is currently available from these localities (Las Leñas), recent work (Mosolf et al., 2018) suggests that the stratigraphic sections at Las Leñas and Upeo are eminently datable. The fossiliferous beds at Upeo were originally assigned to a geographically isolated patch of Colimapu Formation (González and Vergara, 1962), a wholly Mesozoic unit, as, curiously, were those that produced the Tinguirirican Fauna near Termas del Flaco. On biostratigraphic lines alone, SGOPV 3750 greatly refines age estimates of the fossil-bearing strata at Upeo. The occurrence of Cenozoic fossil mammals, as well as lithologic features, indicate that the strata in question at Upeo pertain to the Abanico Formation, and are thus tens of millions of years younger than once assumed.

II. The History of “Notohippid” Paleontology

During his historic expedition aboard the H.M.S. Beagle, Charles Darwin became the first scientist to observe what is now known as a toxodontian, having purchased a skull from a Uruguayan farmer (Darwin, 1845). Richard Owen described Darwin’s specimen, naming it *Toxodon* for its curved molars, establishing it as the genotype for Toxodontidae and Toxodontia (Owen, 1837, 1853). Less than ten years later, British Naval Commander Bartholomew James Sullivan sent Owen mammal fossils from Santa Cruz, Argentina, on the basis of which Owen recognized a second toxodontid, *Nesodon*, and proposed that Toxodontia is allied to perissodactyls and artiodactyls among “Ungulata” (Owen, 1846, 1853).

Argentina has remained the center of South American mammalian paleontology ever since. The Ameghino brothers, Carlos and Florentino, carried out enormous collecting and descriptive efforts from the late 1800s through the early 1900s. Florentino described thousands of taxa based on specimens collected by Carlos from the Santa Cruz Formation along the banks of the Río Santa Cruz (Ameghino, 1887) and elsewhere. Carlos’s discoveries in Patagonia included the first “notohippid,” *Notohippus toxodontoides* (Ameghino, 1891), which Florentino initially placed within Litopterna under the family Protoequidae, reflecting his belief that it was an early equid. He later rechristened Protoequidae as “Notohippidae” within the order “Hippoidea” (Ameghino, 1894, 1902)—continuing to consider them ancestral equids, a notion that was quickly superseded (Scott, 1912; Loomis, 1914; Simpson, 1945). Of the 16 genera and 26 species “notohippids” Ameghino named, 12 genera and 19 species are considered valid.

Burmeister (1891a, b, c), Roth (1895, 1900, 1902), and Mercerat (1891) prolifically diagnosed new “notohippids,” unrestrained by peer-review (Madden, 1990).

Many of these taxa have subsequently been reduced to synonymies, as they were based on different stages of tooth wear, sexual dimorphism, or intraspecific variation (Lydekker, 1894).

Loomis (1914) rejected Ameghino's conception of Notohippidae, instead uniting *Rhynchippus*, *Morphippus* Ameghino, 1897, and *Eurygeniops* Ameghino, 1897, under Rhynchippidae, and *Coresodon* Ameghino, 1894, *Interhippus* Ameghino, 1902, *Stilhippus* Ameghino, 1904, and *Nesohippus* Ameghino, 1904 within the Nesodontidae. The Marshall and Scarritt expeditions to Patagonia, led by Elmer Riggs and George G. Simpson respectively, yielded important "notohippid" material, including two new taxa, *Argyrohippus praecox* and *Eomorphippus obscurus* (Patterson, 1934a, b, 1935, 1936, 1937; Simpson 1932, 1934, 1935, 1945, 1967).

Four new "notohippids" were recognized in the late 20th century, including the first from outside Patagonia, *Rhynchippus brasiliensis* (Soria and Alvarenga, 1989) from the Deseadan Tremembé Formation, Brazil. *Pampahippus arenalesi* (Bond and López, 1993) was recovered from the Mustersan Lumbrera Formation, Argentina. Concurrently, Cifelli's pioneering phylogenetic analysis of notoungulates (Cifelli, 1993) identified "Notohippidae" as paraphyletic. The "Notohippinae" (*Notohippus*, *Argyrohippus* Ameghino, 1902, and *Coresodon*), and "Rhynchippinae" (*Rhynchippus* and *Morphippus*), formed a clade to the exclusion of *Eomorphippus*. Shockey (1997a, b) conducted a cladistic analysis of advanced toxodontians, "isotemnids", leontiniids, "notohippids", and toxodontids. "Notohippidae" *sensu* Bond and López, 1993, was determined to be polyphyletic, while *sensu* Simpson 1967 it was paraphyletic (Shockey, 1997a, b). In addition to naming two taxa, *Eurygenium pacegnum*, and *Pascualihippus boliviensis* from Salla, Bolivia, Shockey (1997a, b) noted that hypsodonty was acquired in

“notohippids” ~15-20 Myr earlier than in equids.

Recent advances in our understanding of “notohippids” include the recognition of three new genera and eight new species, detailed anatomical studies, and comprehensive phylogenetic analyses corroborating the paraphyly of “Notohippidae” (Billet, 2011; Deraco and García-López, 2016). Some genera traditionally considered “notohippids” were reassigned to other toxodontian groups, *Puelia* Roth, 1902 and *Pampahippus* Bond and López, 1993 to “Isotemnidae,” and *Ancylocoelus* Ameghino, 1895 to Leontiniidae (Billet, 2011). *Moqueguahippus glycisma* was described from the Deseadan Moquegua Formation, Peru, ~350 km west of Salla, Bolivia (Shockey et al., 2006). The diagnosis of *Eurygenium latirostris* was revised based on an exquisitely preserved cranium from Argentine Patagonia (Marani and Dozo, 2008). *Mendozahippus fierensis* was founded on a nearly complete cranium from the Deseadan Quebrada Fiera, Argentina (Cerdeño and Vera, 2010), ~200 km SSE of Tinguiririca. The discovery of *Patagonhippus canterensis* and *P. dukei* at Gran Barranca, Argentina, added to the already diverse “notohippid” record in the Deseadan (López et al., 2010). *Pampahippus secundus* was recognized from the Mustersan Lumbrera Formation, Argentina (Deraco and García-López, 2016). *Pampahippus powelli* was described from the Mustersan Quebrada de los Colorados Formation, La Poma, Argentina (García-López et al., 2017). Most recently *Eomorphippus bondi* and *Eomorphippus neilopdykei* were described from the Tinguirirican of the Abanico Formation, Tinguiririca, Chile, as was *Rosendo pascuali*—based on type material from evidently coeval strata at Gran Barranca Argentina (Wyss et al., 2018).

III. “Notohippid” Dental Terminology and Morphology

Mammalian teeth are sufficiently distinctive that even partial dentitions can generally be identified securely. Additionally, tooth morphologies shed light on diet and hence paleoecology.

The descriptions of dental characters below employ terminology developed during the early and mid-20th century (Simpson, 1932; Patterson, 1934a, b), as summarized by Shockey (1997a). Although the names of various structures in notoungulate teeth are the same as those used to describe the teeth of other eutherians, the homology of these structures is not implied (Patterson, 1934a).

Notoungulate molars are generally lophate, reflecting the group’s herbivory. The four primordial upper molar cusps, the paracone (anterolabial), protocone (anterolingual), metacone (posterolabial), and hypocone (posterolingual), are subsumed into lophs soon after tooth eruption. The three dominant lophs on the upper cheek teeth connecting the cusps are the protoloph (labio-lingual paracone-protocone connection), ectoloph (anterior-posterior paracone-metacone connection), and metaloph (labial-lingual metacone-hypocone connection). In advanced wear, the protoloph and metaloph connect lingually, closing the central fossette. An additional loph, the crochet, originates on the metaloph; with wear it moves anterolabially to meet the lingual edge of the ectoloph.

IV. ABBREVIATIONS

Institutional Abbreviations: MNHN-Bov, Museo Nacional de Historia Natural, La Paz; SGOPV, Museo Nacional de Historia Natural, Santiago; UF, Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville.

Dental Abbreviations: L, left; R, right; i/I, lower/upper incisor; C, upper canine; p/P, lower/upper premolar; m/M, lower/upper molar; di, deciduous incisor; dp, deciduous premolar; MD, mesiodistal ; AP, anteroposterior; W, width.

V. SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903

Suborder TOXODONTIA Owen, 1853

“Notohippidae” Ameghino, 1894

Unnamed “Notohippid” Genus

TYPE SPECIES— The species is currently unnamed.

DIAGNOSIS— Large “notohippid.” Palate broadens posteriorly. P3 and P4 molariform with a sharp sulcus separating prominent parastyle and paracone ridges. Posterolingual cingulum of P3 and P4 significantly longer than the anterolingual cingulum. Unworn upper molar occlusal cross-sections triangular, becoming trapezoidal with wear. Upper molars wider anteriorly than posteriorly. The molar parastyles overlap the posterolabial corner of the preceding tooth, such that M1 parastyle overlaps the posterolabial edge of P4, and so on. Differs from *Argyrohippus fraterculus* in lacking molar cementum. Distinct from *Argyrohippus praecox* in having a single premolar posterolingual cingulum, whereas *A. praecox* bears two. Lacks the M1 anterolingual cingulum present in *Pascualhippus boliviensis*. Differs from *Eurygenium pacegnum* by bearing upper anterolingual cingula. *Rhynchippus equinus*, *Eomorphippus obscurus*, and *Eurygenium latirostris* lack the upper premolar paracone ridges present in SGOPV 3750. Less hypsodont than *Rhynchippus pumilus*.

Unnamed “Notohippid” Species

Figure 1, Table 1

PROPOSED HOLOTYPE— SGOPV 3750, partial skull, bearing right C, P2-M1, and M3, and left P3-M3, collected near Estero Upeo, Chile, in the Andean Main Range,

approximately 200 km SSE of Santiago.

TENTATIVE AGE— Oligocene, 33.9-23.03 Ma (Cohen et al., 2018). Based on the hypsodonty index (HI) of specimen SGOPV 3750 (HI = ~1.11) it likely represents an Oligocene taxon. *Eomorphippus obscurus*, a Tinguirirican “notohippid” from Cañadón Blanco, Argentina, has a HI ~0.95 and Deseadan “notohippids” have HIs greater than 1.40 (Shockey, 1997a). SGOPV 3750 is potentially a high-crowned Tinguirirican form or a low-crowned Deseadan taxon.

GEOLOGY— SGOPV 3750 was collected from talus sourced from the Abanico Formation.

DIAGNOSIS—As for genus.

DESCRIPTION

SGOPV 3750 consists of a partial skull, including most of the upper post-canine dentition. LP3-LM3, are fully prepared, beautifully preserved, and minimally worn. Right and left P1, left P2, and the anterior dentition are not preserved except for a fragment of the right canine. Only the labial surfaces of the right tooth row, partial C, P2-M1, and M3, are prepared. The left premaxilla and anterior portion of the left maxilla are not preserved. The right premaxilla is well preserved, concave dorsal to P1, becoming convex anterior of the external nares. Exterior surfaces of the left and right maxilla are poorly preserved, revealing the roots of the posterior dentition. The palate is intact and prepared from P1-P3. Outer surfaces of the right nasal and frontal are preserved. The jugal is partially preserved on the specimen’s left side. Auditory and posterior portions of the orbital region are not preserved. The right squamosal and basicranium are poorly preserved. Posterior cranial elements have not been prepared beyond exposing their posterior surfaces. Mensural information is provided in Table 1.

UPPER DENTITION—SGOPV 3750 is inferred to have had a closed and complete upper dentition, based on the spacing of roots where crowns are not represented. The cheek teeth are moderately hypsodont, M1 having a hypsodonty index (HI, crown height/crown length) of 1.11, although the molars are low-crowned compared to other Oligocene “notohippids.”

INCISORS AND CANINES—The specimen is damaged anteriorly. Too little of the premaxilla remains intact to determine how many incisors were retained. The palate, U-shaped and narrow anteriorly, widens posteriorly. In taxa with transverse incisor arcades the incisor roots are large and the palate generally narrows at the canine. Fragments of the right canine are the only elements of the anterior dentition preserved in SGOPV 3750 and its location indicates that the palate is not constricted anteriorly, suggesting that the incisor battery was U-shaped.

FIRST UPPER PREMOLAR—Although P1 is not preserved, judging by the space between the upper canine and P2, P1 roughly matched its neighboring teeth in size.

SECOND UPPER PREMOLAR—The right P2 is partially preserved. The anterolabial third of the tooth was inadvertently cut by a rock saw during preparation. The roots and the lingual-half of the occlusal surface are preserved, but not prepared.

THIRD UPPER PREMOLAR—P3 is square in occlusal outline. It bears a well-developed parastyle and paracone column, with a sharp sulcus separating the two. The metacone column is subdued. Anterior and posterior cingula are present lingually, the latter being about twice the length of the former. The anterior cingulum occurs nearer the base of the crown than the posterior one. The protocone is connected to the hypocone, which encloses a central fossette. The paracone joins the protocone via a thin protoloph.

FOURTH UPPER PREMOLAR—P4 is trapezoidal in occlusal outline. It bears a

distinct parastyle and paracone column, but the sulcus separating them is shallower than on P3. The posterior half of the labial face is smoothly convex, exhibiting no trace of a metacone column. The anterolingual cingulum is nearly twice as close to the roots as the posterior cingulum. Tooth wear has coalesced the posterior cingulum with the metaloph. A connection of the protocone and hypocone closes the central fossette lingually. The ectoloph is thinner than the metaloph.

FIRST UPPER MOLAR— M1 is trapezoidal in occlusal outline, the anterior leg of which is longer and more steeply canted ($\sim 30^\circ$ from the labiolingual axis) than the posterior one. In labial profile, M1 is rectangular. The parastyle is separated from the paracone column by a shallow sulcus that terminates at approximately mid-crown height. The metacone column is broadly convex. The anterior face of the tooth is essentially smooth, with a small bump about one third of the way from the base of the crown perhaps representing a vestigial cingulum. The posterior face of M1 becomes concave towards the occlusal surface and projects posteriorly. The central fossette, oriented anterolabially to posterolingually, is open lingually through roughly one-half of the crown's height.

SECOND UPPER MOLAR— M2, trapezoidal in occlusal view (the anterior leg is angled at $\sim 35^\circ$ from the labiolingual axis, the posterior leg lies on the labiolingual axis), is narrower than M1, but this proportional difference largely reflects its lesser wear. The labial face of M2 is trapezoidal in profile, widening toward the occlusal surface. The parastyle is separated from the paracone column by a sulcus that persists approximately two-thirds the height of the crown. The metacone column is undeveloped. The anterolabial face of M2 is nearly vertical, becoming concave lingually. Posteriorly, M2 is concave, becoming convex near the base of the crown. No cingula are present. Lingually, the opening of the central fossette begins approximately 2 mm from the roots. With wear,

the occlusal surface of M2 would have become wider than that of M1. The M2 protoloph, although narrower than on M1, would have widened with wear. As on M1, the central fossette is oriented anterolabially to posterolingually.

THIRD UPPER MOLAR—M3 is newly erupted and virtually unworn. Its occlusal outline is trapezoidal; the anterior leg, angled $\sim 30^\circ$ from the labiolingual axis, is approximately twice as long as the posterior one. The labial face of the tooth is triangular in outline, the paracone forming the ventral apex. The poorly defined parastyle is separated from the paracone column by a sulcus that runs the height of the crown. Posterior of the paracone column, the labial surface of M3 inflects from concave to convex above the metacone, then returns to concave, terminating at a distinct metastyle. A deep sulcus on the posterior edge of M3 separates the metastyle and hypocone. The lingual face of the tooth is stepped, with the protocone projecting twice as far ventrally as the hypocone. The anterior face of M3 is concave. The central fossette is damaged.

Rhynchippus Ameghino, 1897

TYPE SPECIES—*Rhynchippus equinus* Ameghino, 1897

DIAGNOSIS— (Emended from Martínez et al., 2016.) *Rhynchippus* is distinguished from other “notohippids” in the following combination of characters: arcuate dental arcade (as in *Mendozahippus fierensis* and *Eurygenium pacegnum*, but narrower than in *Eurygenium latirostris*); triangular palate wider than in *M. fierensis* and lacking the constriction exhibited by *P. boliviensis*; upper molars rhomboidal in occlusal view; central fossette opened lingually in M2-3 but eventually closes by wear in M2; labial face of lower incisors convex; well-marked lingual cingulum in lower incisors, usually erased by wear; incisiform lower canines bearing lingual cingulum; talonid significantly longer than trigonid and separated by a conspicuous enamel fold labially;

meta-entoconid and ento-hypoconid folds on talonid form fossettids and eventually disappear with wear; upper incisors decrease in size posteriorly; C smaller than I3 and P1; upper premolars increase in size posteriorly; high mesiolingual cingulum on upper premolars, similar to *Pascualihippus*; two conspicuous incisive foramina on premaxillae on anterior portion of palate; narrower, more elongate nasals compared to *Eurygenium*, with a slight constriction centrally, similar to *M. fierensis*; robust and posteriorly directed postorbital processes; sagittal crest weaker than in *E. latirostris* and shorter than in *M. fierensis*; nuchal crest projects posteriorly.

Rhynchippus, species novum

Figure 2, Table 1

HOLOTYPE— SGOPV 3221, a nearly complete upper dentition lacking RI2-3, RC (or RP1, RP2-3), from the Las Leñas drainage of the Andean Main Range, Chile, ~100 km SSE of Santiago.

REFERRED SPECIMENS— MNHN-Bol-003456, upper dentition lacking only RM3, both P1s, and LP2; MNHN-Bol-V-003457, cranium with mandible; MNHN-Bol-V-003458, rostrum with right and left I1-P3; MNHN-Bol-V-003647, left P2-M1; UF 149201, left mandible with p2-m3; UF 149202, mandibular symphysis with left ramus and left i1-m3, right i1-p3, and associated distal right humerus; UF 149203, left m2-3; UF 149205, right m1-2; UF 149227, distal left humerus; UF 91927, mandible with left di1-2, dp2-4, m1-2 and right di1-2, dp3, and m2.

AGE— Late Oligocene, Deseadan SALMA. The Bolivian specimens were recovered from the Deseadan aged Salla Beds, Bolivia (Shockey, 1997a, b), dated between 29.4 and 25.8 Ma (Kay et al., 1998). SGOPV 3221 is the first definitively Deseadan “notohippid” reported from the western slope of the central Chilean Andes.

GEOLOGY— SGOPV 3221 was collected from a talus fan within the Río de Las Leñas (a tributary of the Río Cachapoal) drainage below >1000 m of steep relief composed entirely of the Abanico Formation. SGOPV 3221 derives from the same small side canyon that produced the Colhuehuapian (early Miocene) platyrrhine primate *Chilecebus* (Flynn et al., 1995), dated at ~20 Ma. Because the current specimen derives from Oligocene strata as determined through biostratigraphic correlation between the Deseadan Salla specimens and SGOPV 3221, it appears that the ~1.5 km-thick section of the Abanico Formation (Charrier et al., 1996) exposed in the Las Leñas drainage spans at least 10 Myr and two SALMAs.

DIAGNOSIS— Dentition larger than *R. pumilus* and smaller than *R. equinus*. Upper incisors hypsodont. Labial surface of I1 flat. I1 with rectangular wear facet. I2-P1 imbricated, the distolingual portion of each tooth cupping the mesiolabial surface of its posterior neighbor. C and P1 incisiform, strongly resembling I3. P2-P4 square in occlusal outline, bearing a small anterolingual cingulum. Molars hypsodont, becoming anteroposteriorly longer and transversely narrower from M1 to M3. M1 slightly trapezoidal. M3 paracone column occupies roughly one-third the length of the labial surface. Differs from *Rhynchippus equinus* in having incisiform upper canine. Distinct from *Rhynchippus pumilus* in having vertical, un-curved incisors and more anteroposteriorly compressed molars.

DESCRIPTION

UPPER DENTITION— The specimen from Las Leñas, SGOPV 3221, consists of a nearly complete upper dentition. All preserved teeth are prepared, exposing their anterior, posterior, and lingual margins, as well as labial and occlusal surfaces. RP4-M2 are beautifully preserved. RM3 is damaged occlusally. LP2-LM3 partially preserve labial

and occlusal surfaces. The palate widens posteriorly from P1 to M3. Mensural information is provided in Table 1.

INCISORS, CANINES, and FIRST UPPER PREMOLARS: LI2-C, RI1, and a sliver of the medial surface of LI1 are preserved. Post-mortem deformation has displaced the vertical axes of I1-P1, but these teeth were most likely vertically implanted and the anterior dental arcade originally U-shaped based on the Bolivian specimens. LI3, the only incisor fully prepared labially, is hypsodont, suggesting that I1-2 were as well. The three chisel-shaped incisors, each approximately 5 mm wide mesiodistally, preserve no wear facets. C is incisiform and slightly wider (6 mm) than the incisors. The sub-triangular canine wear facet is convex lingually; no internal structures or cingula are present. P1 closely matches the canine in shape and size, being strongly incisiform. A displaced incisiform tooth on specimen's right side represents either C or P1.

SECOND UPPER PREMOLAR: P2, square in outline, measures approximately 8 mm in both dimensions. The anterior portion of the parastyle is all that remains of the labial surface due to damage. P2, although considerably worn, appears to have been brachydont to mesodont. Remnants of an anterolingual cingulum occur near the base of the crown. The central fossette, closed and elongated anteroposteriorly, bears no folds.

THIRD UPPER PREMOLAR: P3 is rectangular in outline, being wider labiolingually (10.0mm) than anteroposteriorly (8.0mm). Labially, a shallow trough separates the paracone and metacone columns. A small anterolingual cingulum occurs near the base of the crown. The crescentic central fossette, closed and lacking folds, bears flat ends, and is convex labially.

FOURTH UPPER PREMOLAR: P4 is rectangular in outline, wider transversely (10.4mm) than long (8.1mm), and mesodont. The paracone and metacone columns are

more pronounced than on P3, creating a deeper depression between these structures. The closed central fossette is oriented anteroposteriorly.

FIRST UPPER MOLAR: The upper molars are trapezoidal in outline, lengthening anteroposteriorly and narrowing labiolingually from M1 to M3. A shallow depression separates the paracone and metacone columns, as on the premolars. The anterior and posterior faces of the tooth are flat, while the lingual face is vertically concave. The anterolabially to posterolingually oriented central fossette is closed and proportionally longer than its counterpart on the premolars, at least partly reflecting more advanced wear.

SECOND UPPER MOLAR: M2 is more complex occlusally and labially than M1. A shallow furrow separates the small parastyle from the paracone column. A broad, shallow depression separates the paracone and metacone columns, occupying roughly one-third of the length of the labial face of the tooth. A metastyle lies posterior of the metacone column; the shallow separation between these structures is largely obscured by matrix. The anterior, posterior, and lingual faces of M2 are flat. The central fossette is open lingually, but since the protoloph and metaloph merge slightly nearer the base of the crown, it soon would have closed with additional wear.

THIRD UPPER MOLAR: The M3s are moderately well preserved. RM3 is nearly complete, missing only a chip of the paracone column near the occlusal surface. The parastyle and paracone column are entirely missing on LM3. M3 is markedly more hypsodont anteriorly than posteriorly (10.4 mm in height versus 6.3 mm, measured labially). The small parastyle overlaps the M2 metastyle anteriorly. A shallow groove separates the parastyle from the paracone column, as on M2. A broad, shallow furrow separates the paracone and metacone columns. Nearly half of the labial face of M3 is

occupied by the broad, low metacone column. A third linear depression on the tooth's labial face separates the metacone column from the metastyle. The tooth's anterior face is broadly convex, while its lingual and posterior faces are flat. The perimeter of the closed central fossette is preserved only lingually.

DISCUSSION

The specimens from Bolivia here referred to *Rhynchippus* n. sp. were originally tentatively referred to *Rhynchippus brasiliensis*, a hesitancy reflecting the limitations of DGM 1092-M (the holotype of *R. brasiliensis*), which consists of a partial m2 and complete m3 (Shockey, 1997a, b). *R. brasiliensis* was recognized primarily on its intermediacy in size between *R. equinus* and *R. pumilus* (Soria and Alvarenga, 1989). Uncertainty about how much intraspecific variation and/or sexual dimorphism occurs in the latter two taxa, calls in question whether the *R. brasiliensis* holotype, DGM 1092-M, is in fact distinct (Marani, 2005). Despite the questionable status of *R. brasiliensis*, SGOPV 3221 and the Bolivian fossils clearly represent a taxon distinct from *R. equinus* and *R. pumilus*. Proposing a new species name for clearly diagnosable material (Bolivian specimens and SGOPV 3221) is a better option than referring this material to a name based on an inadequate holotype (*R. brasiliensis*)—as any future referrals to *R. brasiliensis* may be questioned based on that inadequacy.

Figure 1. Left P3-M3 occlusal view line drawing of SGOPV 3750.

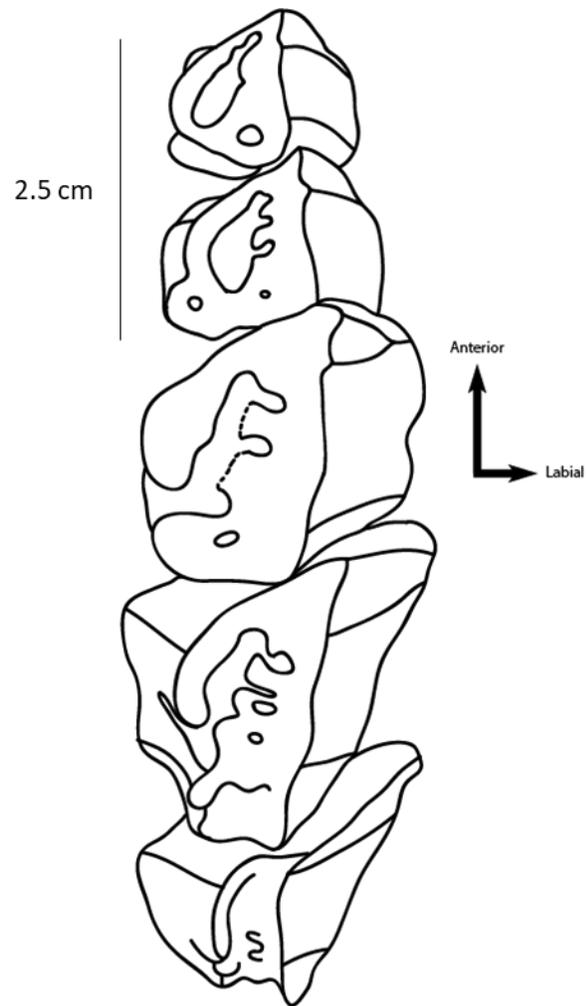


Figure 2. Upper dentition occlusal view line drawing of SGOPV 3221.

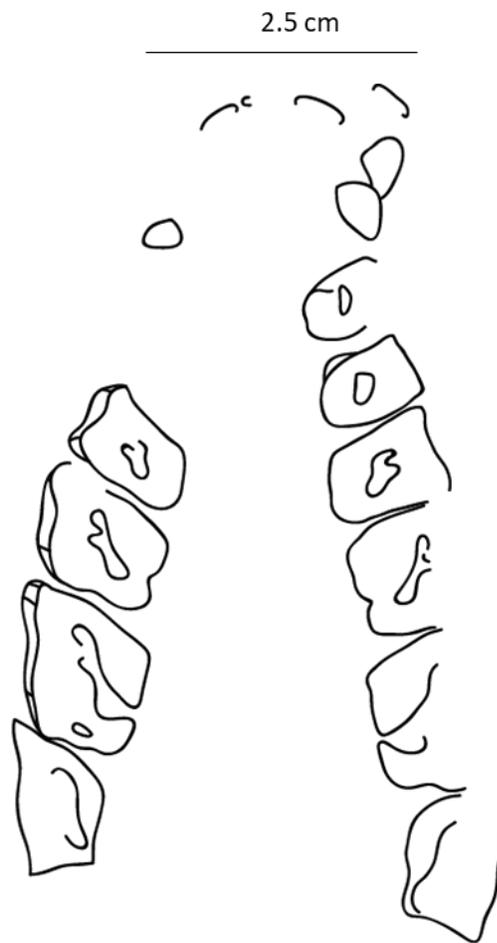


TABLE 1. Dental measurements (mm) of SGOPV 3750 and 3221. L, left; R, right; MD, mesiodistal ; AP, anteroposterior; W, width.

	SGOPV		I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3
Unnamed "notohippid"	3750	L											
		Upper											
		MD/AP								13.1	14.7	22.8	27.1
		W							17.6	20.9	25.1	28.7	28.9
<i>Rhynchippus</i> , species novum	3221	L											
		Upper											
		MD/AP		5.6	4.9	6.4	6.4			8.0			
		W				3.5	3.5	8.1	10.0	10.3			8.9
		R											
		Upper											
		MD/AP	5.3								8.1	12.1	13.8
		W								10.4	13.5	12.9	11.3

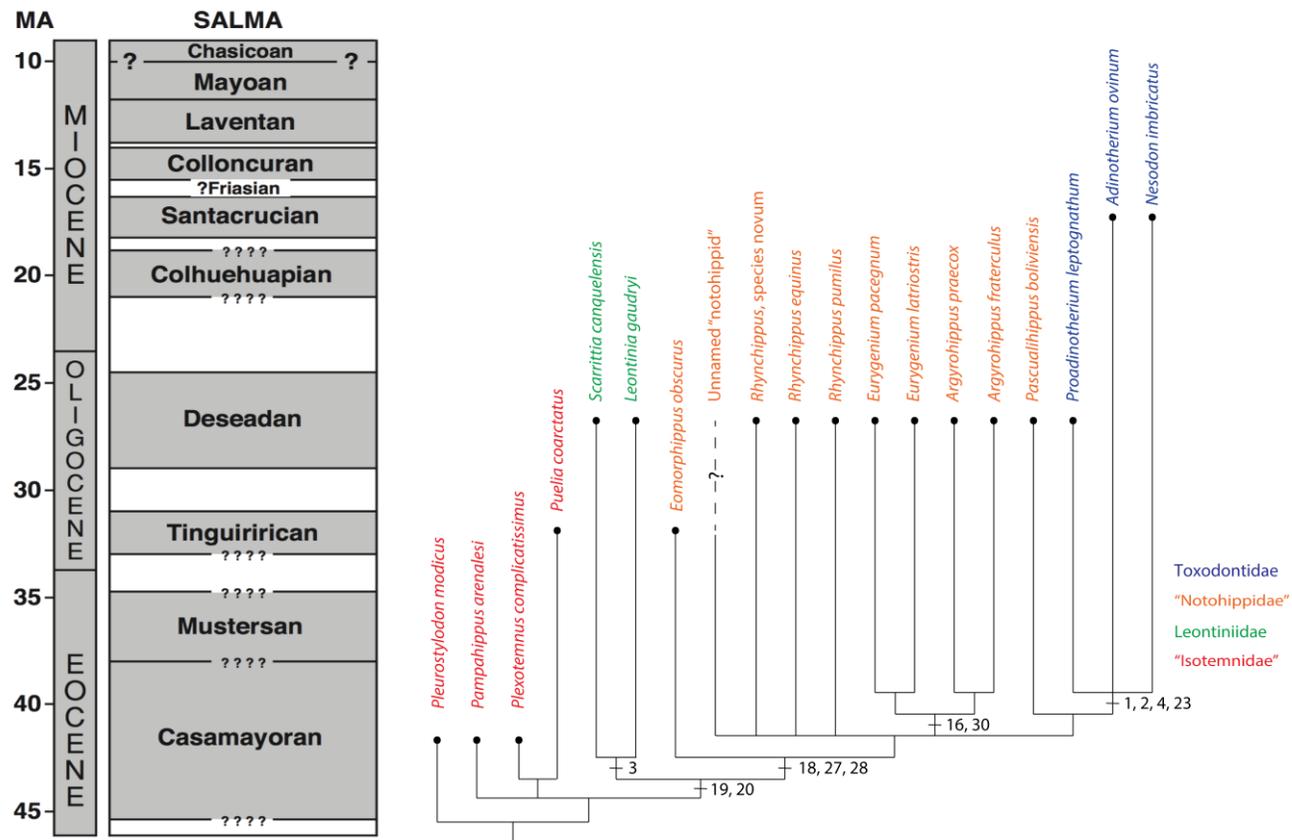
VI. PHYLOGENETIC ANALYSIS

The phylogenetic analysis performed here builds on that of previous researchers (Appendix 1; Cifelli, 1993; Shockey, 1997a, b). A character matrix (Appendix 2) consisting of 30 characters and 19 taxa was analyzed using the implicit enumeration function in the program TNT (Goloboff and Catalano, 2016). Non-“notohippid” toxodontian taxa (“isotemnids”, leontiniids, and toxodontids) were incorporated in the analysis to determine “notohippid” relations to other toxodontian clades (Shockey, 1997a). Advanced-Toxodontia is used to refer collectively to the four clades of Toxodontia evaluated. *Pleurostylodon modicus* is regarded as bearing the plesiomorphic condition with respect to advanced Toxodontia (Cifelli, 1993).

Eight equally parsimonious trees were generated, each 42 steps in length. The 50% majority consensus tree is reported in Figure 3. The synapomorphies identified below are accompanied by their character list number (Appendix 1). “Isotemnidae” (*sensu* Billet, 2011) is a paraphyletic group of basal advanced-toxodontians. Leontiniids, “notohippids”, and toxodontids are diagnosed by their lack of an accessory trigonid cusp (19), and in possessing a talonid that extends far posterior of the entolophid (20). Leontiniidae is monophyletic, characterized by caniniform I1 or I2 (3). “Notohippidae” plus Toxodontidae form a monophyletic group, diagnosed by their lack of an anterolingual cingulum on M1 (18), and I1 and I2 that are wider than I3 (27, 28), the nearest outgroup of which is Leontiniidae. “Notohippids” are paraphyletic, consistent with previous studies (Shockey, 1997a, b; Billet, 2011; Deraco and García-López, 2016). The pairing of *Eurygenium* and *Argyrohippus* is recovered in this analysis based on the absence of an anterolingual cingulum on the upper premolars (16) and molariform P1s (30), a close relationship not identified in earlier analyses. Four synapomorphies unite Toxodontidae:

chisel-like I1 (1), hypselodont anterior dentition (2), I2 triangular in cross-section (4), and the crochets originating lingually on the anterior face of the hypocone (23).

Figure 3. Time-calibrated 50 % majority consensus tree. Branches terminate at the middle of corresponding taxa SALMA. Synapomorphies are indicated by numbers plotted on corresponding branches. 1: I1 chseli-like; 2: Anterior dentition hypselodont; 3: I1-2 caniniform; 4: I2 triangular in cross-section; 16: Upper premolar anterolingual cingulum absent; 18: M1 anterolingual cingulum absent; 19: Accessory trigonid cusp absent; 20: talonid extending well past the entolophid; 23: Crochet originating lingually, at anterior edge of hypocone; 27: I1 broad, greater width than I3; 28: I2 broad, greater width than I3; 30: P1 molariform. SALMA time scale from Flynn et al., 2012.



VII. SUMMARY.

Here, I describe two “notohippid” specimens (SGOPV 3221 and 3750), recognizable as new taxa, from the central Chilean Andes, reclassify previously diagnosed specimens, and conduct a phylogenetic analysis to clarify intra-“notohippid” relations.

Seemingly the older of the two new taxa is the first constituent (SGOPV 3750) of the Upeo Fauna to be formally described. This specimen forms the basis of a new genus. Fossiliferous strata at Upeo are likely Oligocene in age based on the hypsodonty of SGOPV 3750, a dental attribute developed by “notohippids” during the earliest Oligocene (Simpson, 1967; Shockey, 1997a; Billet et al., 2009; López et al., 2010; Madden, 2014). SGOPV 3750 (HI = 1.11) is more hypsodont than the Tinguirirican *Eomorphippus obscurus* (HI = ~0.95), but less hypsodont than all Deseadan “notohippids” (HI > 1.40).

SGOPV 3221, part of the Las Leñas fauna, represents a new species of *Rhynchippus*, a taxon restricted to the Deseadan (late Oligocene). This is the first decisively Deseadan taxon from the western slope of the central Chilean Andes. Specimens from the Deseadan Salla Beds, Bolivia, previously attributed to *Rhynchippus brasiliensis*, are also referred to *Rhynchippus*, sp. nov.

A time-calibrated 50% majority consensus tree of advanced-Toxodontia (“isotemnids”, leontiniids, “notohippids”, and toxodontids) indicates, for the first time, a sister group relationship between *Eurygenium* and *Argyrohippus*. “Notohippidae” is paraphyletic as in previous studies.

The specimens described here emphasize the paleontological importance of the Abanico Formation. The record of *Rhynchippus*, species novum at Las Leñas extends its geographic range from central Chile to west-central Bolivia. Additionally, time periods

unpreserved elsewhere in the South America and superimposed SALMAs at a single locality are recorded within the Abanico Formation.

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APPENDIX

1. CHARACTER LIST (Shockey, 1997b)

* indicates new character.

1. I1 incisiform or caniniform (0); I1 chisel-like (1).
2. Anterior dentition rooted (0); hypselodont (1).
3. I1-2 incisiform (0); I1 or I2 rounded in cross-section, caniniform (1).
4. I2 incisiform (0); I2 triangular in cross-section (1).
5. Upper incisors oriented dorsoventrally (0); incisors procumbent (1).
6. Premaxillary dental arcade U-shaped (0); dental arcade transverse (1).
7. Internal cingulum of upper incisors does not form fossette (0); internal cingulum of upper incisors does form fossettes (1).
8. Canine caniniform (0); canine incisiform (1).
9. Closed tooth row. No diastema (0); diastema between upper canine and incisors (1); diastema between upper canine and incisors, and upper canine and premolars (2).
10. Molars not strongly curved (0); strongly curved, toxodont molars (1).
11. Cheek teeth brachydont [HI of $M1 < 1$] (0); cheek teeth mesodont [HI $M1 \sim 1$] (1); cheek teeth hypsodont [$1 < HI$ $M1 < 2$] (2); cheek teeth euhyppodont [HI $M1 > 2$] (3).
12. Palate not conspicuously broad (0); palate broad (1).
13. No thick layer of cement on cheek teeth (0); cement on cheek teeth pronounced (1).
14. Protoloph on unworn upper premolars complete (0); protocone of upper premolars not attached to ectoloph by a protoloph until significant wear (1).
15. Single posterior cingulum on upper premolars (0); second posterior, cup-shaped cingulum on upper premolars (1).
16. Upper premolars have anterolingual cingulum (0); upper premolar anterolingual

cingulum absent (1).

17. M2 with anterolingual cingulum (0); M2 anterolingual cingulum absent (1).

18. M1 with anterolingual cingulum (0); M1 anterolingual cingulum absent (1).

19. Accessory trigonid cusp on molars (0); accessory trigonid cusp absent (1).

20. Talonid of molars extending a short distance past the entolophid (0); talonid extending well past the entolophid (1).

21. Lower molars lacking an early formed fossettid at the entolophid (0); fossettid forming early along the lateral portion of the entolophid (1).

22. Manus pentadactyl (0); manus tetradactyl (1); manus tridactyl (2).

23. Crochet originating near the midpoint of the metaloph (0); crochet originating lingually, at anterior edge of hypocone (1).

24. Coronal pattern superficial, obscured with wear (0); coronal pattern deep, persisting into advanced wear (1).

25. No more than two well-developed cristae originating from the ectoloph of the upper molars (0); supernumerary cristae present (1).

26. Posterior cingulum of upper premolars or molars not projecting posterolingually (0); posterior cingulum of upper premolars and (to a lesser degree) molars projecting posterolingually, forming a distinct lobe (1).

27. I1 narrow (0); I1 broad, having greater width than I3 (1).

28. I2 narrow (0); I2 broad, having greater width than I3 (1); $I2 > I1 > I3$ (2).

29. Anteroposterior length of P4 subequal to M1 [$P4/M1 > 1/3$] (0); anteroposterior length of P4 diminished relative to M1 [$P4/M1 < 1/3$] (1).

30.* P1 incisiform (0); caniniform (1); molariform (2).

2. TAXON-CHARACTER MATRIX

<i>Pleurostylodon modicus</i>	00000	0?000	00000	00000	0?000	00000
<i>Pampahippus arenalesi</i>	00000	0?100	00010	00000	0?000	00001
<i>Plexotemnus complicatissimus</i>	?????	?????	00010	00000	0?001	1??1?
<i>Puelia coarctatus</i>	?????	?????	00010	00000	0?001	1????
<i>Eomorphippus obscurus</i>	00001	11100	10010	00111	0?000	01100
<i>Pascualihippus boliviensis</i>	00000	11101	20010	01011	1?000	01211
<i>Rhynchippus equinus</i>	00000	01101	20010	01111	12000	01101
<i>Rhynchippus pumilus</i>	00000	01101	20010	01111	1?000	01100
<i>Rhynchippus</i> , sp. nov.	00000	01101	20010	01111	1?000	01101
<i>Eurygenium pacegnum</i>	00000	01101	20010	11111	01000	01112
<i>Eurygenium latirostris</i>	00000	0?101	21010	11111	0?000	01112
<i>Argyrohippus praecox</i>	00000	01111	20111	11111	1?010	0??02
<i>Argyrohippus fraterculus</i>	00000	01121	30111	11111	1?010	0110?
<i>Nesodon imbricatus</i>	11010	1?1?1	20000	01111	12100	01100
<i>Proadinothierium leptognathum</i>	11010	1?1?1	20000	01111	1?100	011??
<i>Adinothierium ovinum</i>	11010	1?1?1	20000	01111	12100	01101
<i>Leontinia gaudryi</i>	00100	00100	00010	0?011	1?000	0001?
<i>Scarrittia canquelensis</i>	00100	00100	00010	0?011	11000	00000
Unnamed “notohippid”, SGOPV 3750	?????	0??01	20010	011??	??000	0??0?