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ARTICLE

NEW DATA ON DIVERSITY OF NOTOHIPPIDAE FROM THE OLIGOCENE OF MENDOZA, ARGENTINA

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ABSTRACT—Notohippidae (Notoungulata) specimens from the late Oligocene Quebrada Fiera locality (Mendoza, Argentina) were previously identified as a new taxon, *Mendozahippus fierensis* Cerdeño and Vera. New cranial, mandibular, and postcranial remains allow enhanced description of this species and its ontogenetic variation. The ectocuneiform corresponding to the holotype (MCNAM-PV 4004) of *M. fierensis* was discovered when reexamining a block belonging to the sediment surrounding the holotype. It corresponds with the metatarsal III that was associated with the holotype skull. On the other hand, MCNAM-PV 3851, a poorly preserved maxillary fragment, is recognized as a second notohippid taxon, which differs from *M. fierensis* in the different position and relative size of I3–C. The canine is placed labially to P1 and its section shows a similar size to that of the latter; ahead of the canine, the preserved root of I3 is also labially placed, and its section is clearly larger than that of the canine. This condition differs from other Deseadan notohippids. Enlargement of the muzzle at the level of I3–C and a developed paracone on premolars are present in *Eurygenium* and *Pascualihippus*; the convergence of the premaxillae anterior to I3 in MCNAM-PV 3851 is closer to the condition in *Eurygenium*. The incompleteness of this specimen, however, prevents its proper definition and it is considered as Notohippidae indet.

INTRODUCTION

Deseadan mammals (late Oligocene) from Quebrada Fiera, Mendoza Province (Argentina), have provided interesting novelties over the last years (Cerdeño, 2011, and references therein; Forasiepi et al., in press). Native ungulate remains are the most abundant within the faunal association; some groups have already been studied in detail (Cerdeño and Vera, 2010; Cerdeño et al., 2010; Cerdeño and Reguero, in press), whereas others are currently under study (Leontiniidae). Within notoungulates, a new taxon of Notohippidae, *Mendozahippus fierensis* Cerdeño and Vera, 2010, was defined, including the description of a skull with two associated metatarsals, a maxilla of another individual, and several isolated teeth. Since publication of that paper, new dental and postcranial remains were found, which allows us to increase the knowledge of this species as well as to propose the coexistence of a second notohippid taxon at Quebrada Fiera.

Geographic and geological characteristics of the Quebrada Fiera site, located in the South of Mendoza Province, near the border with Neuquén Province, are detailed in previous works (Gorroño et al., 1979; Cerdeño and Vera, 2010; Cerdeño et al., 2010). Most remains come from the same area, at 36°33′13.3″S, 69°42′3.5″W, 1406 m of altitude, but during the field season in 2010, some fossils were recovered from the south side of the ravine, at 36°33′26″S, 69°41′35″W, 1316 m; sedimentary level and faunal association at this locality are the same. The fossils found there include part of the material herein described (mandible and associated bones of notohippid), teeth and bones of *Pyrotherium*, dental remains of interatheriids, and a fragment of tarsometatarsus of a phorusrhacid bird.

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MATERIALS AND METHODS

Fossil remains recovered during recent field works at the Quebrada Fiera locality are in the vertebrate paleontology collection of the Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano' in the city of Mendoza.

The material assigned to Notohippidae includes up to now 24 specimens that are detailed in Systematic Paleontology; they range from a nearly complete skull to maxillary and mandibular fragments or isolated teeth, as well as some postcranial bones (see Description sections). Among the new specimens, two can be highlighted: MCNAM-PV 4368, composed of a mandibular fragment and several associated bones, and the ectocuneiform found while examining some small blocks of sediment corresponding to MCNAM-PV 4004 (skull and metatarsals), the holotype of *M. fierensis*; this tarsal bone corresponds perfectly with the right Mt III previously described (Cerdeño and Vera, 2010); therefore, it adds to the holotype of *M. fierensis*.

The new material has been described, and compared with previous data of *M. fierensis*, as well as with other South American notohippids.

Institutional Abbreviations—FMNH-P, Field Museum of Natural History, Paleontological Collection, Chicago, U.S.A.; **MCNAM-PV**, Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano'—Vertebrate Paleontology Collection, Mendoza, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN-Bol-V**, Museo Nacional de Historia Natural, La Paz, Bolivia; **MUSM**, Museo de Historia Natural, Lima, Peru.

Anatomical Abbreviations—ant., anterior; **APD**, anteroposterior diameter; **C**, canine; **for**, foramen; **H**, height; **I**, incisor; **L**, length; **M/m**, upper/lower molar; **max.**, maximum; **min.**, minimum; **Mt**, metatarsal; **P/p**, upper/lower premolar; **post.**, posterior; **prox.**, proximal; **TD**, transversal diameter; **W**, width.

SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903
Family NOTOHIPPIDAE Ameghino, 1894
Genus *MENDOZAHIPPUS* Cerdeño and Vera, 2010
MENDOZAHIPPUS FIERENSIS Cerdeño and Vera, 2010
(Figs. 1–3)

Holotype—MCNAM-PV 4004, nearly complete skull with some teeth, right Mt III, proximal end of right Mt IV, and right ectocuneiform of an aged individual.

Included Material—MCNAM-PV 3846, right and left maxillary fragments (Cerdeño and Vera, 2010); MCNAM-PV 3853, upper and lower molar fragments; MCNAM-PV 3956, right mandibular fragment with m2; MCNAM-PV 4049, left maxillary fragment with M2–M3; MCNAM-PV 4050, left maxillary fragment with M1? remains; MCNAM-PV 4051, left P3?; MCNAM-PV 4052, right lower premolar (p3?); MCNAM-PV 4056, left mandibular fragment with m3; MCNAM-PV 4209, upper molar fragments; MCNAM-PV 4213, left isolated p2; MCNAM-PV 4237, right maxillary fragment with M2–M3; MCNAM-PV 4240, right upper molar; MCNAM-PV 4285, right mandibular fragment with m3 and talonid of m2; MCNAM-PV 4306, PV 4309, and PV 4310, upper molar fragments; MCNAM-PV 4368, left mandibular fragment with m1 (broken)–m3 and associated bones (fragments of right and left femora, tibiae, and fibulae); MCNAM-PV 4370, palatal fragment with right P4–M3, left M2–M3, and the beginning of the zygomatic arches; MCNAM-PV 4371, left maxillary fragment with P2–P3 and M1–M3 (the fragment was broken at the level of the P4 alveolus); MCNAM-PV 4380, right mandibular fragment with m2 (incomplete) and m3; MCNAM-PV 4393, left mandibular fragment with m1? and the isolated trigonid of left m3 apparently of the same individual; MLP 96-XI-20-14, isolated upper teeth (Cerdeño and Vera, 2010, as cf. *M. fierensis*).

Expanded Diagnosis—Medium-sized notohippid, with complete, brachydont dentition, and the following features: (1) skull long and narrow, similar to but lower than *Rhynchippus equinus*, differing from the notably wider, shorter, and more robust skull of *Eurygenium* and *Pascualihippus*; (2) sagittal crest well developed, longer than that of *R. equinus* and *R. pumilus*; (3) pterygoid processes short, slender; (4) palate narrower than in *R. equinus* and *R. pumilus*, with jugal nearly parallel; (5) dentition without diastemata or cement; (6) jugal teeth without postfossette; (7) M3 with very short metaloph and protocone projected lingually; (8) upper incisors and canine subequal in size and morphology, with a lingual median vertical crest, in contrast to *Eomorphippus*, *Rhynchippus*, *Eurygenium*, and *Pascualihippus*; (9) upper premolars and molars with or without low anterolingual cingulum; (10) horizontal ramus of the mandible lower and more flattened lingually than that of *Rhynchippus*; (11) p2 with an individualized entoconid and a marked protoconid fold; (12) lower teeth with entolophid fossettid, in contrast to *Eurygenium*, *Patagonhippus*, and *Moqueguahippus*; (13) lower molars with shorter and more convex trigonid than those of *Rhynchippus* and *Moqueguahippus*.

As originally remarked (Cerdeño and Vera, 2010), incisor morphology (8) and presence of anterolingual cingulum (9) are observed only for MCNAM-PV 3846.

Description

The new remains herein described add new data on upper and lower dentition and postcranial bones of *M. fierensis*.

Upper Dentition—The most complete maxillary fragments are MCNAM-PV 4370 and MCNAM-4371, representing two individuals from a different ontogenetic stage. MCNAM-PV 4371 (Fig. 1B; Table 1) corresponds to a very old individual, with teeth that are even more worn than those of the holotype MCNAM-PV 4004, hardly preserving lingual and labial enamel on M2 (the only complete molar). As in the skull, premolars are short and wide, with lingual border projected. M3 shows an anomalous occlusal wear on its posterolingual area, which appears as an extremely worn concave surface that reaches the level of the maxillary bone. All teeth preserve a central fossette. In turn, MCNAM-PV 4370 (Fig. 1A) presents moderate wear and still has high labial walls. This specimen allows visibility of the anterior face of P4, and the considerable difference in crown height between the lingual and labial walls, according to the curvature of the tooth. Such teeth are comparable to those included by Koenigswald (2011) in the category 'partial hypsodonty,' although this author referred to rodents and lagomorphs whose higher enamel wall is lingual instead of labial; at the same time, he mentioned most notoungulates within the category 'sidewall hypsodonty,' whereas this one does not show such a difference in height between tooth walls. That 'partial hypsodonty' condition implies a wear process that explains the later appearance of premolars as wider teeth with apparently projected lingual borders. Cheek teeth of MCNAM-PV 4370 are very similar to the isolated molars (MLP 96-XI-20-14) described by Cerdeño and Vera (2010) as cf. *M. fierensis*. As expected, the new material (see more data below) suggests that the observed variations in size and occlusal outline among the studied specimens is due to ontogenetic differences within *M. fierensis*. Proceeding from lower to higher degrees of wear, specimens are as follows: MCNAM-PV 3846 $\leq$ PV 4049 $<$ PV 4237$<$ PV 4370 $\leq$ PV 4051$<$ PV 4004 $<$ PV 4371. The difference between MCNAM-PV 3846 and PV 4049 is hard to discern because of the poor preservation of molars in the former. In general, the two former specimens represent young adults, the following three are full adults, and the last two are very old individuals.

MCNAM-PV 4370 (Fig. 1A) preserves on the right side a large, rounded antorbital foramen at the level of the paracone of M2, which was not mentioned for the skull MCNAM-PV 4004, but we have now realized that it exists, although it is filled with cemented sediment. This foramen in MCNAM-PV 4370 opens posteriorly upon a large, slightly concave zygomatic plate, whose posterior edge lies behind M3. This plate is inclined and seems to be more elevated with respect to the zygomatic arch than in the type skull (Cerdeño and Vera, 2010); the holotype does not show a good preservation of the plate, because sediment has penetrated the bone and its complete removal is not possible without altering the plate. The maximum diameters of the plate in MCNAM-PV 4370 are 39 and 42 mm; the bizygomatic transverse diameter would be greater than 95.2 mm (106.7 mm in MCNAM-PV 4004) for part of the palate is compressed.

MCNAM-PV 4237 (Fig. 1C; Table 1) preserves M2 and M3 that are identical to those just described. Thin remains of cement are observable on several areas of these molars, close to the roots and irregularly distributed. This cement, however, does not seem to be comparable to the thick layer around the crown described for other notohippid taxa (see López et al., 2010:143–144), such as *Argyrohippus*, *Notohippus*, and *Moqueguahippus*, because most of the crown shows no trace of cement. The case of MCNAM-PV 4237 appears by now to be individual variation. According to the higher crown and lower wear, this is a younger individual than MCNAM-PV 4370.

With the same morphology but clearly smaller (Table 1), the specimen MCNAM-PV 4049 preserves M2 (incomplete) and M3, and shows less wear than all other specimens, because it has protoloph and metaloph in contact but not fused, indicating a younger condition (Fig. 1D). It is closer in size to the M3 of MLP 96-XI-20-14 (Cerdeño and Vera, 2010).

MCNAM-PV 4051 is an isolated upper premolar, interpreted as a P3 (Fig. 1E), morphologically similar to, but smaller than, the P4 of MCNAM-PV 4370, with different proportions than the P3 of MCNAM-PV 4371 due to less wear (Table 1), and a large difference in height between lingual and labial walls. Both MCNAM-PV 4051 and the P4 of MCNAM-PV 4370 do

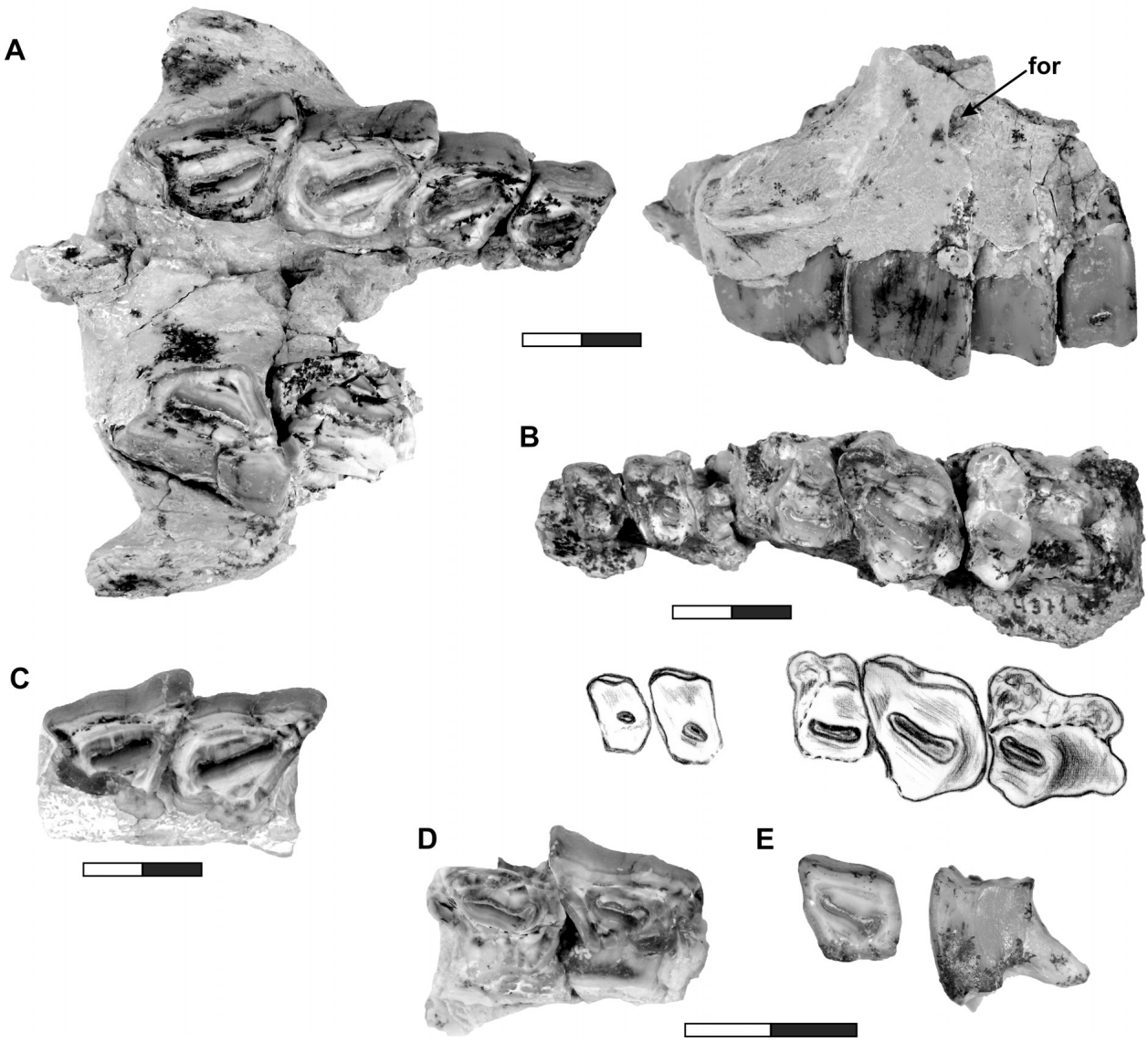

FIGURE 1. Upper dentition of *Mendozahippus fierensis*. **A**, MCNAM-PV 4370, palatal fragment with right P4–M3, left M2 and M3, and beginning of the zygomatic arches, occlusal and labial views; **B**, MCNAM-PV 4371, left maxillary fragment with P2, P3, M1, and M3, occlusal view (original and drawing); **C**, MCNAM-PV 4237, right maxillary fragment with M2 and M3, occlusal view; **D**, MCNAM-PV 4049, left maxillary fragment with M2 and M3, occlusal view; **E**, MCNAM-PV 4051, left P3?, occlusal and mesial views. Scale bars equal 10 mm.

not present the slight basal cingulum that occurs in MCNAM-PV 3846 (Cerdeño and Vera, 2010); as commented in that paper, MCNAM-PV 3846 showed some characters not observable in the skull MCNAM-PV 4004, but we maintain that both specimens pertain to the same taxon (Cerdeño and Vera, 2010:1812). The lack of cingulum in moderate worn premolars such as MCNAM-PV 4370 or PV 4051 allows the interpretation of a specific difference, but available material is still insufficient to support this view.

The other listed upper dental specimens are too fragmentary to be described.

Mandible and Lower Dentition—In the previous paper on notohippids from Quebrada Fiera, no lower dentition had been attributed with certainty to this group of notoungulates. Now, a partial left mandible with m1–m3, MCNAM-PV 4368, is herein assigned to *M. fierensis*, thus enhancing the knowledge of this species. Ascribing this specimen to this species instead of to the second taxon herein recognized is tentative, but justified because most notohippid remains are assigned to *M. fierensis*, its size fits well with the skull MCNAM-PV 4004, and it shows differences with Patagonian and Bolivian taxa (e.g., *Eurygenium*) to which the second taxon could be more related (see below).

The horizontal ramus is low, lingually flattened, and markedly convex labially (Fig. 2A). Dimensions of the ramus, at the level of m2 and m3, are as follows: TD, 16.6 and 18.5 mm, respectively; labial H, 33.0 and 38.1 mm, respectively. Remains of the vertical ramus show that it is only slightly inclined anteriorly. There is a small labial foramen below the trigonid-talonid groove of m3, closer to the ventral border. The m1 is incomplete and badly preserved. The m2, although fragmented, exhibits a short trigonid, somewhat wider than the talonid, which presents three small fossettids. The m3 is better preserved (Fig. 2A; Table 1); it also has three fossettids, hardly larger than the anterior one; the talonid is long and posteriorly pointed, with no distinguishable lingual

TABLE 1. Dental measurements (in mm) of *M. fierensis* and (*) Notohippidae indet. from Quebrada Fiera, Mendoza.

Specimen	I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3
PV 3846											
L	6.9/7.1	6.9/7.1	6.4/—	6.6/—	6.1/—	7.8/8.4	9.3/9.3	11.2/—			
W	5.0/4.1	3.7/3.5	4.4/—	4.6/—	7.7/—	9.2/10.0	10.1/10.0	12.0/—			
W basal					8.0/—	11.5/11.9	13.5/13.6	16.0/—			
PV 4004			(root)	(root)							
L			(4.6)	(5.4)	(5)/—	(7)/(7.5)	9.4/(9)	11.0/(12.3)	14.1/<16	22.1/(20)	28.3/27.2
W			(3.4)	(4.3)	(7.7)/—	10.6/(10.7)	13.8/13.6	17.0/17.7	20.0/<23	22.9/21.5	24.4/24.0
PV 4371											
L						7.2	9.9	—	(12.4)	19.3	(23.2)
W						13.8	15.6	—	(17)	23.3	(23.1)
PV 4370											
L								13.3	17.9/—	22.0/(20.5)	25.0/25.3
W								15.2	18.3/—	19.6/(19.8)	17.4/20.2
PV 4051											
L							11.4				
W							11.3				
PV 4237											
L										22.4	24.4
W										22.0	17.9
PV 4049											
L										(13.3)	18.0
W										—	12.0
MLP 96-XI-20-14											
L										14.2	17.4/>17
W										>13.5	11.0/—
PV 3851*			(base)	(base)							
L			9.4	6.9	6.5	9.8	10.5	14.1	24.6		
W basal			9.3	7.8	9.3	13.6	15.0	—	—		

	L I1—P4	L I1—C	L P1—P4	L P1—M3	L M1—M3
PV 3846	58.5	23.8	36.0		
PV 4004	—	—	(35)	(93.1)/(91)	62.3/60.7
PV 4371					57.6
PV 4370			42.3		59.6
PV 3851*					

m1	PV 4368	PV 4285	PV 4393	PV 3956	PV 4056
L	18.6		16.4		
W ant.	(12)		6.8		
W post.			8.3		
m2					
L	20.3			19.0	
W ant.	(12.8)			7.2	
W post.	10.9			6.7	
m3					
L	27.4	29.6	—		19.0
W ant.	10.3	(8.1)	6.9		5.9
W post.	9.0	9.1	—		5.4

The slash (/) separates right and left teeth of a same individual. Approximate values in parentheses.

groove. Both molars have a well-marked labial groove between trigonid and talonid, and a smooth undulation on the talonid wall.

The same morphology as in MCNAM-PV 4368 is observed in specimens MCNAM-PV 4285, PV 3956, PV 4393, and PV 4056, which are also similar in size (Table 1). MCNAM-PV 4285 (Fig. 2B) has a small labial foramen at the same level as MCNAM-PV 4368; its dimensions are also very similar (TD, 16.9 and 20.6 mm at the level of m2 and m3, respectively; H, 33.5 and 38 mm, respectively). The m3 has slightly larger fossettids and a slightly longer talonid, more markedly undulated lingually. MCNAM-PV 4393 is composed of m1? with a fragment of the lingual bone and part of the m3 (Fig. 2C) of a younger and smaller individual (Table 1); in m1?, the posterior fossettid is not formed yet, and in m3 trigonid and talonid remain unfused lingually. In lingual view, both molars show grooves fading out distally, replaced by corresponding fossettids. In labial view, they show a marked difference in height as noted for MCNAM-PV 4368 (Fig. 2A). MCNAM-PV 3956 (Fig. 2D) represents the youngest individual among lower dentitions; its fossettids are not totally developed, just the second one on the talonid is well defined. In occlusal view, the talonid is narrow and elongated posteriorly, with a marked lingual groove, which disappears about 9 mm below; at this level, the posterior edge of the molar becomes more rounded (the mandibular bone would reach this level, but it is broken). MCNAM-PV 4056 is a much smaller specimen (Fig. 2G; Table 1); its posterior groove is still open and the fossettid would form about 4 mm below the occlusal surface. Its diameter would increase with age, although it seems probable that it would be a smaller individual than MCNAM-PV 4368 or MCNAM-PV 4285, maybe reflecting sexual dimorphism in size or simply intraspecific variation.

In addition to these molars, MCNAM-PV 4213 is an isolated, little worn p2 that presents a strong, wide labial groove (Fig. 2E). On the talonid, there is a separate entoconid that becomes fused to the hypoconulid with little wear. The trigonid has a marked protoconid fold; the paraconid is curved anterolingually and connected to the cingulid, which reaches the metaconid and partially closes the anterior valley at its base. A 'V'-shaped lingual cingulid is also present at the base of the talonid, from the posterior edge of the metaconid to the end of the hypoconulid (Fig. 2E). The size of this premolar, whose maximum dimensions

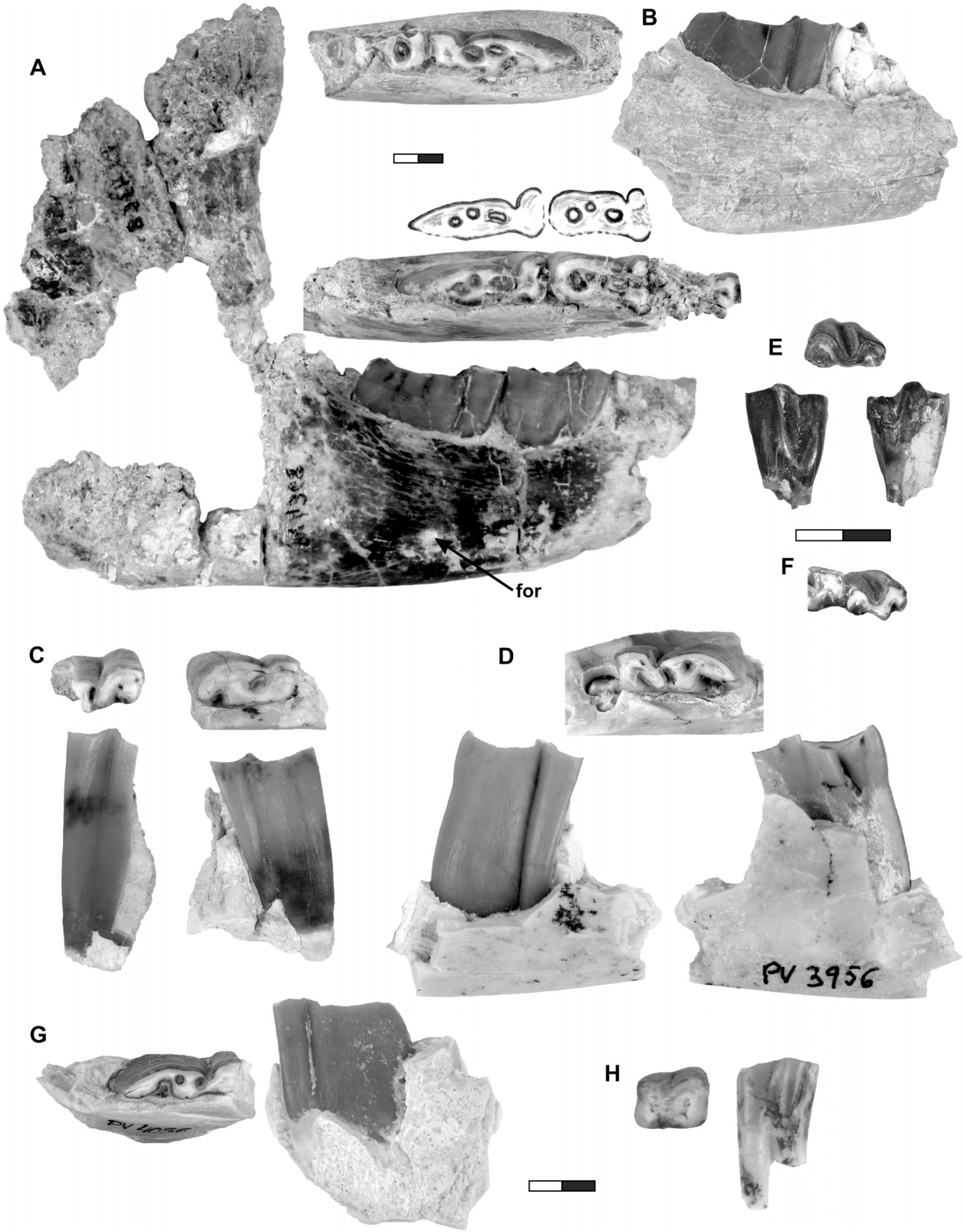

FIGURE 2. **A**–**E**, **G**–**H**, lower dentition of *Mendozahippus fierensis*. **A**, MCNAM-PV 4368, left mandibular fragment with m1 (broken)–m3, occlusal (original and drawing) and labial (reversed) views; **B**, MCNAM-PV 4285, right mandibular fragment with m3 and talonid of m2, occlusal and labial views; **C**, MCNAM-PV 4393, left mandibular fragment with m1? and the isolated trigonid of left m3, occlusal and labial views; **D**, MCNAM-PV 3956, right mandibular fragment with m2, occlusal, labial, and lingual views; **E**, MCNAM-PV 4213, left isolated p2, occlusal, labial, and lingual views; **G**, MCNAM-PV 4056, left mandibular fragment with m3, occlusal and labial views; **H**, MCNAM-PV 4052, right lower premolar (p3?), occlusal and labial views. **F**, *Rhynchippus pumilus*, FMNH-P 14691, detail of left p2 in occlusal view. Scale bars equal 10 mm.

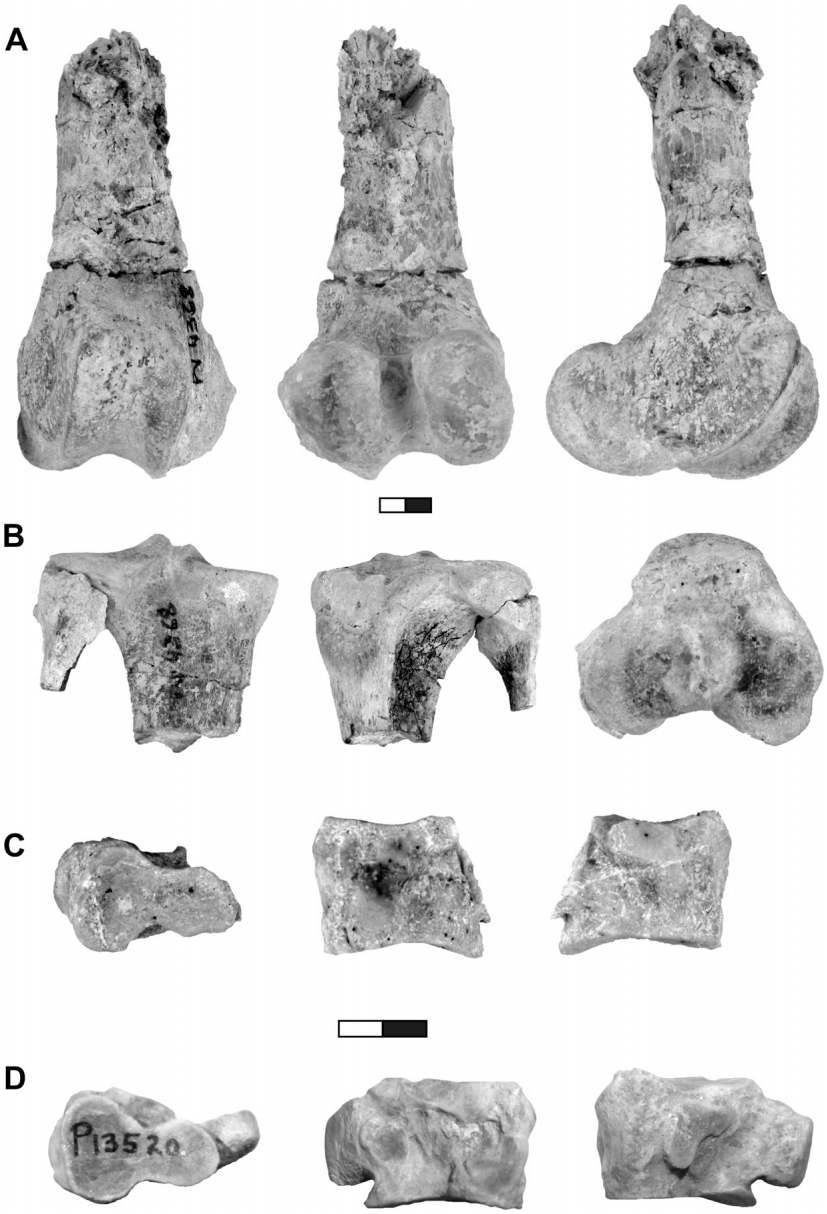

FIGURE 3. **A–C**, Postcranium of *Mendozahippus fierensis*. **A**, **B**, MCNAM-PV 4368: **A**, distal epiphysis of left femur, anterior, posterior, and medial views; **B**, proximal epiphysis of left tibia-fibula, anterior, posterior, and proximal views; **C**, MCNAM-PV 4004 (holotype): right ectocuneiform, distal, medial, and lateral views. **D**, cf. *Rhynchippus equinus*, FMNH-P 13520, left ectocuneiform, distal, medial, and lateral views. Scale bars equal 10 mm.

are L = 8.5 mm and W = 4.8 mm, seems too small compared with the mandible MCNAM-PV 4368, but not with respect to the small molars such as MCNAM-PV 4056 (Table 1); additionally, its slight wear reflects a young individual.

MCNAM-PV 4052 is a worn lower premolar, likely a p3 or p4 (Fig. 2H), rectangular in general outline, although it preserves a still marked labial groove between trigonid and talonid; this groove fades out toward the base of the crown. Its dimensions are L = 10.0 mm, W = 8.1 mm. It has parallel, straight anterior and posterior roots.

Postcranial Bones—Incomplete hind-limb bones were found associated with the mandible MCNAM-PV 4368. The best-preserved fragments are the distal part of the left femur and the proximal part of the left tibia-fibula. Epiphyses are not especially enlarged and the preserved diaphysis of the femur is also narrow (Fig. 3A); a small semispherical femur head (20.5 × 22.3 mm) is also preserved with part of the short neck. All these fragments reveal slender bones. The trochlea of the femur is narrow and rather symmetric (Fig. 3A; Table 2), with little difference between lateral and medial edges; its dorsal edge continues smoothly to the diaphysis in a shallow depressed area; above this, the bone is damaged and broken. The lateral epicondyle is little expanded. In posterior view, the condyles are equally developed in height but the lateral one is a little wider, with a smooth median crest. The diaphysis of the right femur (minimum diameters: TD = 21.3 mm, APD = 18.0 mm) is distorted and does not connect with the preserved right epiphysis.

The tibia (Fig. 3B; Table 2) has the tibial tuberosity anteriorly flattened, its lateral border is acute, but it does not detach from the epiphysis. The proximal facets form a slightly elevated intercondylar eminence; the medial facet is smoothly concave, whereas the wider lateral facet is slightly convex anteroposteriorly. Lateral and posterior sides of the tibial epiphysis form an acute border between them; the transverse section of the fragment is an irregular triangle with a concave lateral side and a longer, straight anteromedial side. The fibula starts just below

TABLE 2. Comparative measurements (in mm) of postcranial bones of *Mendozahippus fierensis*, Quebrada Fiera, Mendoza, and *Rhynchippus equinus*, Cabeza Blanca, Chubut.

Element	Specimen	APD	Distal APD	TD	H
Ectocuneiform	MCNAM-PV 4004	(>21)	18.3	13.1	15.7
	FMNH P 13520†	24.8	18.0	*	15.2
			Trochlea		
		Distal TD	TD	H	Distal APD (medial side)
Femur	MCNAM-PV 4368	43.6	22.3	32.9	47.4
		> 42.7	22.6	32.4	—
				Proximal articulation	
		Proximal TD	Proximal APD	TD	APD
Tibia	MCNAM-PV 4368	45.3	36.1	43.7	29.2

Approximate values in parentheses.
†*Rhynchippus equinus*, Cabeza Blanca, Chubut.
*Not measured; other dimensions after the photograph.

the lateral proximal facet of the tibia, as a fused bone only at this level, and immediately narrows distally.

As previously mentioned, we found the right ectocuneiform of the holotype MCNAM-PV 4004; it is a narrow, high, and deep small bone (Fig. 3C; Table 2), lacking a fragment of the posterior apophysis and the posterior end of the proximal facet for the navicular. This facet is pear-shaped and slightly concave. The distal facet is longer, with its anterior half wider than the posterior one, and with a strong narrowing in between, more marked laterally than medially. On the medial face, there are three differentiated articular areas. One along the proximal border, for the mesocuneiform, with its posterior end markedly projected medially, which makes it concave at this point, and its anterodistal border convex and directed to the second facet. A second one, anterodistally placed and convex, would articulate with Mt II, as well as a third facet placed posteriorly, which is incomplete and poorly defined. On the lateral face, there is an 'L'-shaped, flattened facet for the cuboid. On both sides, the bone presents depressions under the articular surfaces, becoming a very narrow bone at its posterior half.

Comparison

The morphology of most of the new upper dental remains of notohippid from Quebrada Fiera can be added to the previous material described as *Mendozahippus fierensis*, as stated above. Consequently, affinities and differences with other taxa of this group are the same as noted by Cerdeño and Vera (2010); *M. fierensis* presents cranial and dental features closer to *Rhynchippus* than to *Eurygenium* or *Pascualihippus*, although the cladistic analysis did not reflect a close relationship between them (Cerdeño and Vera, 2010:fig.7).

Regarding the mandible, the horizontal rami of MCNAM-PV 4368 and MCNAM-PV 4285 are lower and more flattened lingually than in FMNH-P 14691, labeled as *Rhynchippus pumilus* from Cabeza Blanca (Chubut, Argentina). The ventral border of the Patagonian specimen shows a marked inflection at the level of m1; the mandible MCNAM-PV 4368 is broken at this level, but the preserved border is less convex anteroposteriorly and it would likely not have had such inflection anteriorly. Molars of FMNH-P 14691 have a labially flattened and longer trigonid than our specimens; they present a rather low degree of wear, and consequently fossettids in m2 and m3 are not completely formed. Judging from the available photograph, this specimen is smaller (length of m2 around 12 mm) than MCNAM-PV 4368 and PV 3956 (Table 1). On the other hand, FMNH-P 14691 preserves the p2 (Fig. 2F), similar to that of MCNAM-PV 4213 (Fig. 2E), but with some differences: there is no separate entoconid (the tooth is more worn, but the outline of the talonid does not coincide with what MCNAM-PV 4213 would present with a more advanced degree of wear); the protoconid fold is less acute; and the trigonid valley is deeper with respect to the talonid valley. A lingual cingulid on the talonid is also present in this specimen.

Among the notohippids from Salla, lower teeth of *Eurygenium pacegnum* differ from most Deseadan notohippids in the lack of entolophid fossettid (Shockey, 1997), which is present in our specimens. This author did not refer any lower dentition to *Pascualihippus boliviensis.* The entolophid fossettid is also absent in *Patagonhippus* from early? Deseadan levels of La Cantera locality at Gran Barranca, Chubut (López et al., 2010).

Moqueguahippus glycisma Shockey et al., 2006 (see also Shockey et al., 2009), a notohippid from the Deseadan of Peru, also lacks persistent entolophid fossettid. This species is one of the notohippids characterized by the presence of cement covering the teeth, but, as explained above, the irregular cement in MCNAM-PV 4237 is not comparable to this condition. The size of the m2 of *M. glycisma* (20.1 × 11.9 mm after Shockey et al., 2006) is similar to that of the specimen MCNAM-PV 4368 and a little larger than in the other specimens of *Mendozahippus fierensis* (Table 1), but the m2 MUSM 348 of *M. glycisma* has maximum width at the talonid (Shockey et al., 2006 :fig. 3), whereas the trigonid is wider than the talonid in MCNAM-PV 4368 (Fig. 2A).

Concerning postcranial bones, the ectocuneiform is very similar in size (Table 2) and morphology to the specimen FMNH-P 13520 (Fig. 3D) labeled as cf. *Rhynchippus equinus* Ameghino, 1895, from the Deseadan Cabeza Blanca locality (Chubut); this specimen has better defined facets, with the anterodistal lateral facet being kidney-shaped. Shockey (1997) and Shockey and Anaya (2008) described a nearly complete skeleton of *Eurygenium pacegnum* and a partial pes of cf. *Pascualihippus*, respectively, but without details on the ectocuneiform. Shockey (1997:table 3) provided the total length of the femur and tibia of *E. pacegnum*, which cannot be accurately compared with our remains; from the schematic drawing of the femur, the trochlea has an approximate TD of 20.5 mm, and a maximal distal TD of around 30.7 mm, both dimensions smaller than those of MCNAM-PV 4368 (Table 2). This author stated that the cross-section of the diaphysis is teardrop-shaped, pointing medially, whereas in our diaphysis fragment it points laterally. Furthermore, Loomis (1914:102) indicated for *Rhynchippus equinus* a femur shaft that becomes circular in section distally; with respect to the tibia, he provided a maximum proximal diameter of 51 mm, which is greater than for MCNAM-PV 4368 (Table 2).

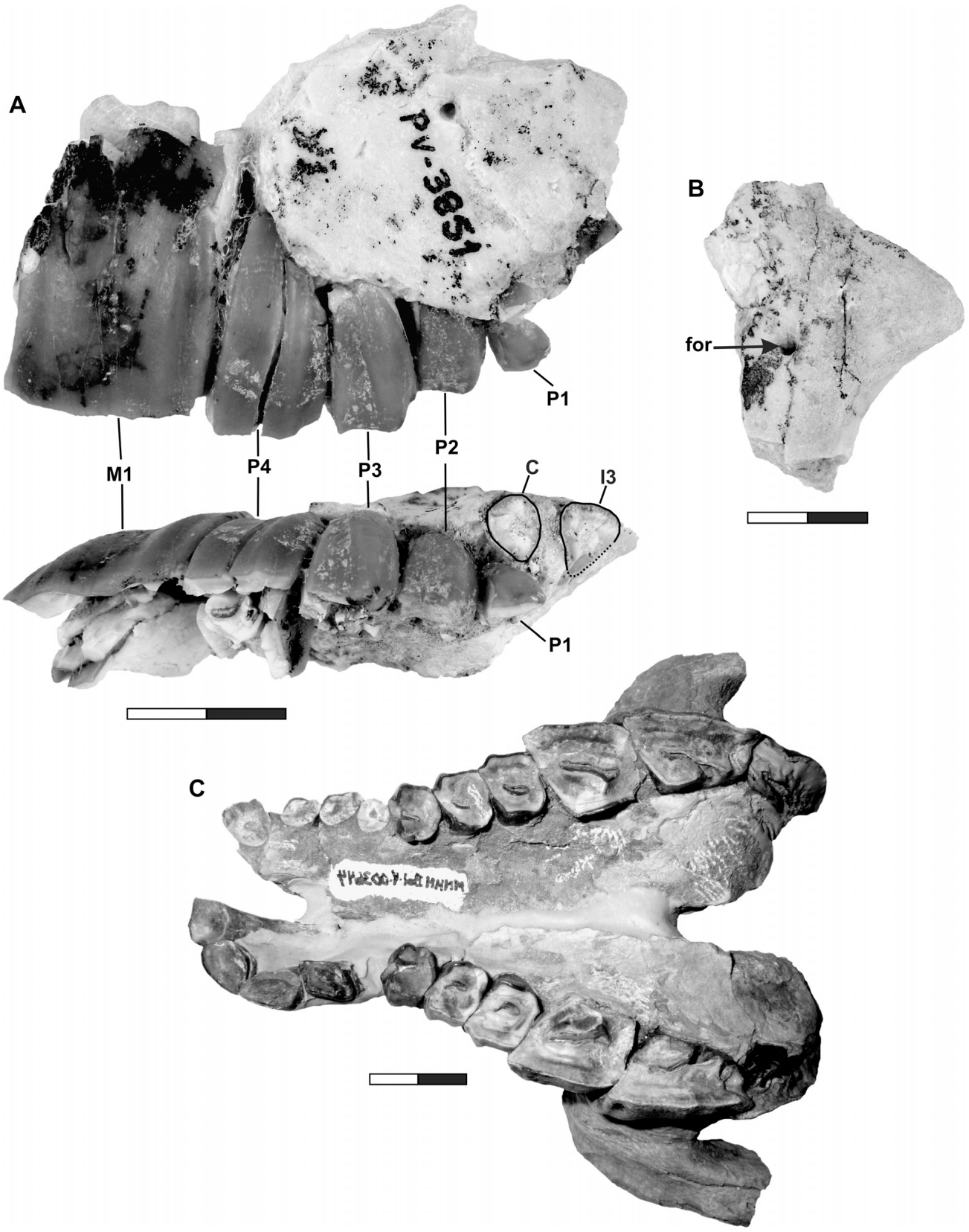

FIGURE 4. Notohippidae indet. **A**, **B**, MCNAM-PV 3851: **A**, right maxillary fragment preserving the base of I3–C (outlined) and remains of P1–M1, labial and occlusal views; **B**, cranial fragment, ventral view; **C**, MNHN-Bol-V-003644, cranial fragment of *Eurygenium pacegnum* from Salla, palatal view (reversed). Scale bars equal 10 mm.

Notohippidae indet.
(Fig. 4A, B)

Included Material—MCNAM-PV 3851, right maxillary fragment preserving the base of I3–C inside the bone, and remains of P1–M1 (basically just their ectolophs are preserved). MCNAM-PV 3842, ectoloph of right upper molar (M2?).

Description

MCNAM-PV 3851 (Table 1) is very incomplete, but some observable features allow its separation from the material identified as *Mendozahippus fierensis*.

The main difference between MCNAM-PV 3851 and MCNAM-PV 3846 lies in the position and relative size of I3 and C. In MCNAM-PV 3846 of *M. fierensis* (Cerdeño and Vera, 2010), I3 and the canine are small and subequal teeth, very similar relative to I1 and I2, and all of them are aligned (there is a slight deviation on the left side of MCNAM-PV 3846, but it is due to poor preservation of the bone at the base of the incisors). Conversely, in MCNAM-PV 3851 (Fig. 4A), the canine is placed labially to P1 and the preserved section shows a similar size to that of P1 (Table 1); it is larger than that of the canine in MCNAM-PV 3846 and with more posteriorly directed anterolingual wall. Besides, anterior to the C, the root of I3 is preserved, also labially placed with respect to the premolar series, with a subtriangular section clearly larger than that of the C; it is relatively greater than the canine of *M. fierensis*.

In addition to these features, there are two other characters that support the taxonomic separation of MCNAM-PV 3851: the greater development of the paracone fold on P2–P4, which appears as a strong convexity along most of the crown height, and the ectoloph of M1 relatively much longer than that of P4, compared with that observed between P4 and M1 on MCNAM-PV 3846.

Although the anterior part of the muzzle is lacking, the preserved bone of MCNAM-PV 3851 (Fig. 4A) allows concluding that the premaxillae converge anteriorly to the I3, so the maximum width of the muzzle would be at the level of I3–C.

Concerning general size, MCNAM-PV 3851 (Table 1) shows larger dimensions than the specimens assigned to *M. fierensis*. In turn, MCNAM-PV 3842 possesses an ectoloph very similar to that of the M1 MCNAM-PV 3851, but a little longer (L = 28.5 mm) and higher, perhaps corresponding to a M2.

Together with the maxillary fragment, there are some small cranial fragments assumed to be from the same individual, but only one provides some information. It is the area corresponding to the right postorbital process (Fig. 4B), which is short, well developed, and nearly perpendicular to the sagittal axis. There is a small supraorbital foramen and a ventral one, not connected between them but both directed posteriorly; neither of them opens into the inner concavity that occurs medially to the postorbital process. In dorsal view, a fine ridge can be observed along the posterior border of the postorbital process. This small fragment displays several differences with the skull of *M. fierensis* (Cerdeño and Vera, 2010): (1) the postorbital process is not so posteriorly directed as in MCNAM-PV 4004, and has its posterior border less concave; (2) the mentioned ridge is different, as in MCNAM-PV 4004, this area appears as a dorsal depression limited by a ridge that becomes posteriorly a frontoparietal crest; and (3) the postorbital process is larger and more robust.

Comparison

Once we had defined the differences with the other notohippid present in Quebrada Fiera, we attempted to discern the affinities of MCNAM-PV 3851 with other members of the family. The labial position of I3–C indicates taxa characterized at this level by a wide muzzle, such as the late Oligocene genera *Eurygenium* Ameghino, 1895, and *Pascualihippus* Shockey, 1997, whereas the coeval *Rhynchippus* Ameghino, 1895, has a longer and narrower muzzle.

Regarding *Pascualihippus bolivianus* (Shockey, 1997), the C of MCNAM-PV 3851 is more labially placed, almost parallel to P1, whereas in *P. bolivianus* it is situated anterolabially to P1, and more compressed. In addition, the I3 of this species is not very different in size from the C, contrary to that observed in MCNAM-PV 3851 (Table 1). In *P. bolivianus*, I2 is the largest anterior tooth, which is placed at the same transverse plane as I1, resulting in a maximum width of the muzzle at the I1–I2 level.

In contrast with *Pascualihippus*, *Eurygenium* has a more convex arcade and I2 is not so enlarged; I3–C are also more labially placed than P1, but not so much as in MCNAM-PV 3851, and both teeth are rather subequal in size. Both *E. latirostris* Ameghino, 1895 (see Marani and Dozo, 2008), and *E. pacegnum* Shockey, 1997 (see also MNHN-Bol-V-003644 in Fig. 4C), show a slightly larger canine than P1, different to that observed in MCNAM-PV 3851. The inferred convergence of the premaxillae anterior to I3 in MCNAM-PV 3851 would be closer to the condition in *Eurygenium* (Shockey, 1997:fig. 2).

The development of the paracone fold on premolars is present both in *Pascualihippus* and *Eurygenium*, as well as in other notohippid taxa of different age. The condition of MCNAM-PV 3851 is rather similar to that of the mentioned specimen MNHN-Bol-V-003644 of *E. pacegnum* (Fig. 4C) from Salla, Bolivia.

In summary, the described differences allow a taxonomic separation of MCNAM-PV 3851 from the other Deseadan notohippids. However, the incompleteness of this specimen prevents a full comparison and an adequate definition, which is the reason to refer it to an undetermined Notohippidae, keeping in mind the possibility that it might represent a new taxon. For now, it can be stated that it resembles the Bolivian taxa from Salla, *Pascualihippus* and *Eurygenium*, by the wide muzzle at the level of I3–C (closer to *Eurygenium*) and the developed paracone of premolars, and it might be a related form. If this relationship is confirmed, it would be another mammal from Quebrada Fiera that suggested a biogeographic relationship between these two South American areas during Deseadan times, such as the archaeohyracid *Archaeohyrax suniensis* (Cerdeño et al., 2010). At the same time, specific or generic relationships have been also established between Quebrada Fiera and Patagonia, which, together with exclusive taxa, provides a paleobiogeographic significance to the faunal association from Mendoza (Cerdeño, 2011; Forasiepi et al., in press).

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