

New Eocene South American native ungulates from the Quebrada de los Colorados Formation at Los Cardones National Park, Argentina

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In the last few years, the Quebrada de Los Colorados Formation has become an important middle Eocene fossiliferous unit in Northwestern Argentina. In this unit, the South American native ungulates were until now only represented by the order Notoungulata, including one family of Typotheria and three of Toxodontia. In this contribution, we present a new faunistic assemblage of South American native ungulates, collected from outcrops of the Quebrada de Los Colorados Formation at Los Cardones National Park, Calchaquí Valleys, Salta Province (Argentina). This new assemblage is constituted by the following taxa: lioptern Didolodontidae cf. *Ernestokokenia* sp., Astrapotheria indet., and notoungulate Notostylipidae *Homalostylops* sp., a ?*Homalostylops* sp., typothere “Oldfieldthomasiidae” *Colbertia falui* sp. nov., *Colbertia lumbrerense*, and *Colbertia* sp. and toxodont “Notohippidae” *Pampahippus secundus*. *Colbertia falui* sp. nov. differs from the other species of *Colbertia* by the following features: lower cheek teeth with both more labially angular and oblique trigonid; lower premolars more labio-lingually compressed; with proportionally larger trigonid, and shorter talonid; ectoflexid transversally deeper; lower molars with a more developed paralophid, and more expanded metalophid and entoconid; the latter is located in a more mesial position, being closer to the metaconid; deep and lingually narrower talonid basin; disto-lingual sulcus transversally shallower; more developed cingulids; and m3 with less lingually projected hypoconulid. This new fauna markedly increases the taxonomic richness known for this formation since it includes the first mention of notostylipids, “oldfieldthomasiids”, lioptern didolodontids, and astrapotheres. With the current evidence, we postulate an ungulate migration from Patagonia to Northwestern Argentina during the Eocene. We also hypothesize that the observed taxonomic differences among the Quebrada de Los Colorados, Geste, and Lumbrera formations are more probably associated to orogenic factors that have regulated the faunal dynamic in Northwestern Argentina during the Paleogene than to a differential sampling effort or taphonomic biases.

Key words: Mammalia, South American native ungulates, Casamayoran SALMA, Paleogene, Quebrada de Los Colorados Formation, Argentina.

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Introduction

South America was separated from North America and the remaining continents during most of the Cenozoic. Throughout this time, several mammalian groups evolved in absolute isolation. Among them, the South American native ungulates (SANUs) stand out due to their morphological, taxonomical, and ecological diversity. The SANUs are extinct lineages, widely distributed in the fossil record of South America. This group is traditionally divided into five orders: Astrapotheria, Litopterna, Notoungulata, Pyrotheria, and Xenungulata (Patterson and Pascual 1968; Simpson 1980; Cifelli 1993; Bond et al. 1995; Croft et al. 2020), and many less diverse taxa whose phylogenetic relationships are not completely clear (Croft et al. 2020), such as Didolodontidae. Nevertheless, this latter family is tentatively considered a primitive Litopterna group with some dental similarities with North American archaic ungulates (e.g., Scott 1913; Soria 2001; Gelfo 2006; Armella et al. 2016; Gelfo et al. 2016, 2020).

In recent decades, Northwestern Argentina has become an important SANUs fossil reservoir, providing major remains allowing the increase of our knowledge of the Paleogene representatives of this group. In this region, a remarkable and singular ungulate fauna, constituted by notoungulates (e.g., Vucetich 1980; Bond 1981; Vucetich and Bond 1982; Bond et al. 1984; Bond and López 1993; López 1995, 1997; López and Bond 1995; Hongn et al. 2007; Deraco et al. 2008; García-López and Powell 2009, 2011; Payrola-Bosio et al. 2009; García-López 2015; García-López and Babot 2015; Deraco and García-López 2016; García-López et al. 2018, 2019, 2020), astrapotheres (e.g., Carbajal et al. 1977; López 1997), litopterns (e.g., Bond and Vucetich 1983; López 1997; Gelfo et al. 2016, 2020), and pyrotheres (e.g., López 1997), comes from the Eocene deposits exposed in the formations: Casa Grande (Jujuy Province); Lumbrera (Salta Province); Geste (Catamarca and Salta provinces); and Quebrada de Los Colorados (Salta Province) (see Pascual et al. 1981; López 1997; Del Papa et al. 2010; Powell et al. 2011; Babot et al. 2017, 2018, and references therein). This fauna displays a restricted geographic distribution, given it only shares a few taxa with other regions (e.g., Patagonia), but it is also, in many cases, temporally restricted, since only a few taxa have been recorded in more than one of the stratigraphic units cropping out in the region.

In the last few years, the Quebrada de Los Colorados Formation became an important source of new information of notoungulates, mainly due to the preservations of cranial bones. Until this contribution, litopterns (including didolodontids), pyrotheres, astrapotheres, notoungulate notostylopids, “campanorcid”, “oldfieldthomasiids”, and interatheriids were not identified in the Quebrada de Los Colorados Fm. (Pascual et al. 1981; Del Papa et al. 2010; Powell et al. 2011; Babot et al. 2017, 2018). In this context, Hongn et al. (2007) mentioned the presence in the Quebrada de Los Colorados Fm. of two toxodonts

at Cerro Bayo, La Poma locality (Salta), which the authors referred as “Notohippidae” indet. (currently known as *Pampahippus powelli* García-López, Deraco, and del Papa, 2018) and Leontinidae indet. Then, Payrola-Bosio et al. (2009) mentioned a toxodont “Isotemnidae” indet. from Luracatao Valley (Salta), and García-López et al. (2017) described a well-preserved Toxodontia indet. collected at Valle del Tonco (Salta). More recently, García-López et al. (2020) described the first typothere “Archaeohyracidae” from this unit, which were referred as “aff. *Eohyrax* sp. indet.” and “Archaeohyracidae” gen. et sp. indet. 1 and 2. When comparing this formation to the other units, “Archaeohyracidae”, “Isotemnidae”, and “Notohippidae” have also been identified in the Geste Fm. (see López 1995, 1997; Reguero et al. 2008; García-López and Babot 2015; García-López et al. 2020), the last two families plus Leontiniidae in Lumbrera Fm. (see Vucetich and Bond 1982; Bond and López 1993; Deraco et al. 2008; Powell et al. 2011; Deraco and García-López 2016; García-López et al. 2020), and “Isotemnidae” and Leontinidae in Casa Grande Fm. (see Bond and López 1995). In contrast to the Quebrada de Los Colorados Fm., Didolodontidae, astrapotheres Astrapotheriidae, basal notoungulate Noto-stylopidae, and typothere “Oldfieldthomasiidae” have been recorded in Lumbrera and Geste formations (see Carbajal et al. 1977; Vucetich 1980; Bond 1981; López 1995, 1997; García-López and Powell 2009; García-López and Babot 2015; Gelfo et al. 2016, 2020). In addition, litopterns (except for didolodontids) and typothere “Campanorcidae” (informal family) have been recognized in the Lumbrera Fm. (see Bond and Vucetich 1983; Bond et al. 1984; Powell et al. 2011), whereas pyrothere Pyrotheriidae and typothere Interatheriidae were recovered in the Geste Fm. (see López and Bond 1995; López 1997; García-López and Babot 2015; Armella et al. 2016).

In this contribution, we present a new assemblage of SANUs, collected from the Quebrada de Los Colorados Fm. at Los Cardones National Park, Salta Province (Argentina). We also study the main systematic and evolutionary implications of these findings, and contextualize this new fauna within the framework of the South American native ungulates record of Northwestern Argentina. In addition, we discuss the different hypotheses that could explain the taxonomic differences recognized among the Quebrada de Los Colorados, Geste, and Lumbrera formations.

Institutional abbreviations.—IBIGEO-P, Paleontological Collection at the Instituto de Bio y Geociencias del Noroeste Argentino, Salta Province, Argentina; PVL, Colección Paleontología de Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán Province, Argentina.

Other abbreviations.—Fm., Formation; i, lower incisor; M/m, upper/lower molar; P/p, upper/lower premolar; SALMA, South American Land Mammal Age; SANU, South American native ungulate.

Material and methods

Studied material.—The new specimens studied here were collected during field trips in November 2016–2017, from the lower levels of the Quebrada de Los Colorados Formation exposed along the Camino de los Colorados road, mostly at the Quebrada Grande locality (see SOM 1–3, Supplementary Online Information available at http://app.pan.pl/SOM/app66-Fernandez_et_al_SOM.pdf, for the geological setting). These materials are stored in the Paleontological Collection at the Instituto de Bio y Geociencias del Noroeste Argentino, Rosario de Lerma (Salta Province, Argentina).

Taxonomic analysis.—The new materials were identified through comparison with the type and referred specimens housed at different institutions. When there is a lack of consensus concerning the monophyly of a certain suprageneric taxon, its name is written between quotation marks.

All the nomenclatural acts follow the regulations established by the ICZN (2000). The dental terminology mainly follows Bown and Kraus (1979), Hooker (1986), and Smith and Dodson (2003). The measurements indicated in this contribution were taken with a Vernier digital calliper (± 0.001 mm). The photographs were taken with Nikon Micrometrics 318CU 3.2MP CMOS and Nikon Coolpix L110 cameras.

Definition of the Lumbrera Formation.—The Lumbrera Fm. was defined by Moreno (1970), and informally divided into three sections (Gómez Omil et al. 1989; Marquillas et al. 2005) or two sections (Del Papa 2006; Del Papa et al. 2010). Some authors consider the lower section of the Lumbrera Fm. and the upper section of the Lumbrera Fm. as individual units (e.g., Del Papa et al. 2017; Chornogubsky et al. 2018; García-López et al. 2019); however, there is a lack of consensus in its usage because some authors alternatively treated the Lumbrera Fm. as a single stratigraphic unit (e.g., Andrews et al. 2018; Payrola-Bossio et al. 2020). Due to the lack of a formal (and applicable) definition for the whole northwestern region, in this contribution we follow Del Papa et al. (2010), who maintain the concept of the Lumbrera Fm. as a single unit composed of two sections.

Systematic palaeontology

Class Mammalia Linnaeus, 1758

Panperissodactyla Welker, Collins et al., 2015

Order Litopterna Ameghino, 1889

Family Didolodontidae Scott, 1913

Genus *Ernestokokenia* Ameghino, 1901

Type species: *Ernestokokenia nitida* Ameghino, 190; Gran Barranca, Chubut Province, Argentina; Casamayoran SALMA, Eocene.

cf. *Ernestokokenia* sp.

Fig. 1A.

Material.—IBIGEO-P 65, fragmented left upper cheek tooth from Quebrada Grande, Los Cardones National Park, Casamayoran SALMA, Eocene.

Description.—Despite the fact that IBIGEO-P 65 is a very fragmented material, what is preserved shows some morphological features in the occlusal surface that resembles closely *Ernestokokenia*. There is a bunoid protocone that is connected to the metaconule by a well-defined crest, and which is separated from a well-developed and bunoid hypocone by a lingual sulcus; a broken distal cingulum can be identified.

Remarks.—In Northwestern Argentina, these archaic ungulates are unusual and are represented until now by scarce and incomplete material. López (1997) described an isolated lower molar as cf. *Ernestokokenia* for the Geste Fm. (late Eocene) at Antofagasta de la Sierra (Catamarca). Based on an astragalus collected in the same unit, Armella et al. (2016) mentioned the presence of *Ernestokokenia* cf. *E. yirunhor*. More recently, Gelfo et al. (2020) mentioned a new bunodont Didolodontidae, based on a mandibular fragment with associated dentition, from the Lumbrera Fm., near San Antonio de Los Cobres (Salta).

Order Astrapotheria Lydekker, 1894

Astrapotheria indet.

Fig. 1B.

Material.—IBIGEO-P 66, left maxillary fragment with three broken molariforms, Quebrada Grande, Los Cardones National Park, Casamayoran SALMA, Eocene.

Description.—The three molariforms of IBIGEO-P 66 exhibit long roots that can be easily identified due to the breakage of the maxilla (Fig. 1B₁), and are subrectangular in outline (Fig. 1B₃). Their occlusal surfaces are poorly preserved. Nevertheless, it is possible to recognize the dental enamel distributed in vertically oriented Hunter-Schreger bands (Fig. 1B₄), which is a remarkable feature in all astrapotheres, which is particularly evident on the slightly undulated fragmented ectoloph of the last tooth. These three molariforms show a closer size to *Albertogaudrya* (see Carbajal et al. 1977), but the poor preservation of the occlusal surface of the specimen does not allow achieving a more specific taxonomic identification, which is the reason why it is identified as Astrapotheria indet.

Remarks.—During the Eocene, the astrapotheres are represented in Northwestern Argentina by *Albertogaudrya carahuasensis* Carbajal, Pascual, Pinedo, Salfity, and Vucetich, 1977, which has been collected in levels of the lower section of Lumbrera Fm. at La Comarca de Carahuasi, Salta (Carbajal et al. 1977), and an Astrapotheriidae indet. from the Geste Fm. at Antofagasta de la Sierra (López 1997).

Order Notoungulata Roth, 1903

Family Notostylopidae Ameghino, 1897

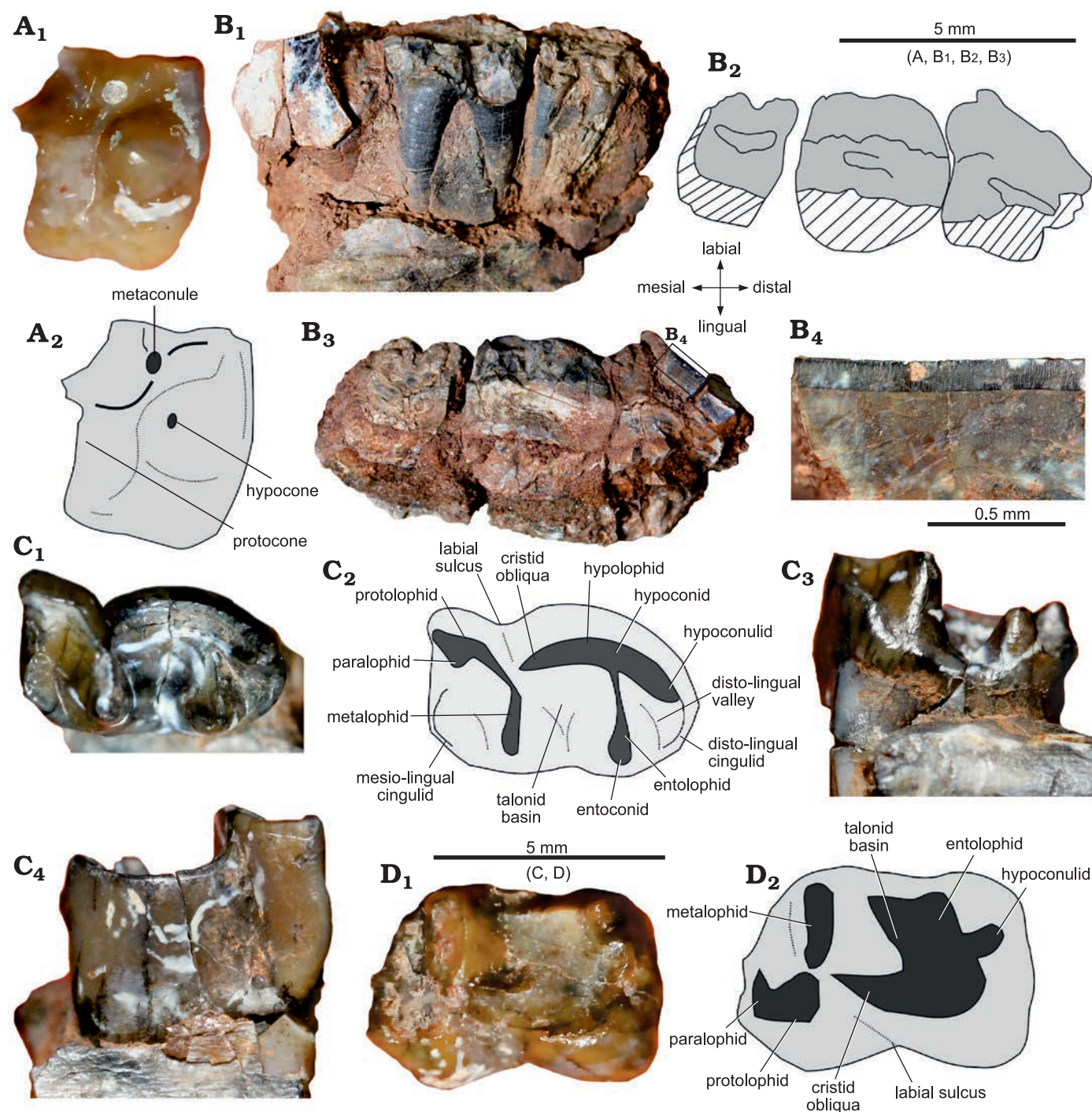


Fig. 1. New fossil materials of Litopterna, Astrapotheria, and Notostylopidae from the Quebrada de Los Colorados Formation exposed at Quebrada Grande locality, Los Cardones National Park (Salta Province), Casamayoran SALMA, Eocene. **A.** cf. *Ernestokokenia* sp. (IBIGEO-P 65), fragmented left upper cheek tooth in occlusal view. **B.** Astrapotheria indet. (IBIGEO-P 66), left maxillary fragment with three broken molariforms in lingual (B₁) and occlusal (B₃) views, and detail showing Hunter-Schreger bands (B₄); dashed area in B₂ indicates broken or missing dental areas. **C.** *Homalostylops* sp. (IBIGEO-P 57b), right m2? in occlusal (C₁), lingual (C₃), and labial (C₄) views. **D.** ?*Homalostylops* sp. (IBIGEO-P 57a), left m1? in occlusal view. Photographs (A₁, B₁, B₃, B₄, C₁, C₃, C₄, D₁), explanatory drawings (A₂, B₂, C₂, D₂).

Genus *Homalostylops* Ameghino, 1901

Type species: *Homalostylops rigeo* Ameghino, 1901; Gran Barranca, Chubut Province, Argentina; Casamayoran SALMA, Eocene.

Homalostylops sp.

Fig. 1C.

Material.—IBIGEO-P 57b, right m2?, Quebrada Grande, Los Cardones National Park, Casamayoran SALMA, Eocene.

Description.—IBIGEO-P 57b is a low-crowned tooth, more brachyodont than in species of *Boreostylops*, and subrectangular in outline, being more mesio-distally expanded (i.e.,

longer) than labio-lingually expanded (i.e., wide); the trigonid is simple, high and subrectangular in contour, being wider than long; the protolophid is slightly mesio-labially directed, and its labial wall is straight; the paralophid is conspicuous and directs linguallly; a lower mesio-lingual cingulid can be identified, which will eventually merge with the paralophid with wear; the metalophid is simple, well developed, and disto-lingually directed, but much less disto-lingually directed and narrower than in species of *Boreastylops*, and it is higher than the paralophid; there is no trace of a paraconid or any accessory cuspid in the mesial wall of the metalophid; the cristid obliqua is connected to the labial half of the metalophid, more labially than in species of *Boreastylops*; the labial sulcus is both transversally and longitudinally deep; the talonid is well developed, subquadrangular in outline, being longer than wide, and labially convex; it is longer, lower, and slightly narrower than the trigonid; the talonid basin is deep and wide; the lophoid entoconid is transversally expanded and connected to the hypoconid region, and its distal face is located mesial to the hypoconulid; the latter is well separated from the entoconid region by a deep valley; the hypolophid is well developed and linguallly curved; and a low disto-lingual cingulid connected to the hypoconulid can be recognized.

Remarks.—Due to the combination of features described above, IBIGEO-P 57b can be discarded as a specimen assignable to *Boreastylops*, which was, up to this contribution, the only Notostylopidae genus recorded in Northwestern Argentina (Vucetich 1980). Nevertheless, characteristics such as the presence of a lower crown and a narrower talonid are similar to those observed in Paleogene forms from Patagonia such as *Notostylops* and *Homalostylops*. Both of these genera exhibit an important morphological resemblance (see Simpson 1948); as a result, and primarily due to the size of IBIGEO-P 57b (see Table 1) that falls within the range of *Homalostylops* (see Simpson 1948 for comparative measurements of *Notostylops* and *Homalostylops*), we identify the specimen as *Homalostylops* sp. This undoubtedly represents the first record in Northwestern Argentina of this genus, previously known only from Patagonia.

?*Homalostylops* sp.

Fig. 1D.

Material.—IBIGEO-P 57a, left m1?, Quebrada Grande, Los Cardones National Park, Casamayoran SALMA, Eocene.

Description.—IBIGEO-P 57a is a worn cheek tooth, probably the m1. It is a low-crowned tooth, subrectangular in outline; the trigonid is simple and presents a subrectangular contour, being wider than long; the protolophid is short and mesio-lingually directed; the paralophid is more developed than the protolophid, and has already been fused to the mesial cingulid, deriving in an slightly disto-lingually directed lophid; the metalophid is almost transversal and well developed, protruding more linguallly than the paralophid, and there is no trace of a paraconid or any accessory cuspid. The

Table 1. Measurements (in mm) of the dental specimens. Abbreviations: *, approximate measurements due to the breakage of the specimen; LLL, labio-lingual length; MDL, mesio-distal length.

Taxon	Specimen	Locus	MDL	LLL
<i>Astrapotheria</i> indet.	IBIGEO-P 66	M1	>22.62	>30.00
		M2	>30.22	>35.42
		M3	>35.35	—
<i>Colbertia lumbrense</i>	IBIGEO-P 45	P4	>4.58	>4.44
		M3	5.62	7.24
	IBIGEO-P 56	M1 or M2	5.43*	5.17*
<i>Colbertia</i> sp.	IBIGEO-P 58a	M2	7.28*	—
		M3	7.52*	—
	IBIGEO-P 58b	P4	5.25*	7.95
		M1	5.43*	8.40
		M2	5.45*	8.32*
		M3	6.00*	8.00*
? <i>Homalostylops</i> sp.	IBIGEO-P 57a	m1?	5.85	4.15
<i>Homalostylops</i> sp.	IBIGEO-P 57b	m2?	7.15	4.43
<i>Pampahippus secundus</i>	IBIGEO-P 62	m1	>5.77	4.39*
	IBIGEO-P 63	p3 or p4	>7.70	5.44*
	IBIGEO-P 64	m1	>7.90	5.00
<i>Colbertia falui</i>	IBIGEO-P 55	p3	4.70	3.91
		p4	5.38	4.38
	IBIGEO-P 59	m2	6.85	5.00*
		m3	7.83	4.53
	IBIGEO-P 61	m2	7.73	5.40
		m3	9.70	4.78
	IBIGEO-P 67	m2	>5.48	4.57*
		m3	7.91	4.30

talonid is well developed and subquadrangular in outline, it is much longer than the trigonid, but both present a similar width; the cristid obliqua is conspicuous, and it is connected to the labial portion of the metalophid; the labial sulcus is transversally deep; there are traces of the disto-lingual sulcus that separates the hypoconulid from the distal face of the entoconid.

Remarks.—As mentioned above, the specimen IBIGEO-P 57a is very worn cheek tooth, but its morphology and size (see Table 1) fit well within the general characteristics and size recorded for the m1 in other species of *Homalostylops* (see Simpson 1948 for comparative measurements). Nevertheless, and mainly due to the heavy state of wear, we refer this specimen with doubts to the genus *Homalostylops*.

Suborder Typotheria Zittel, 1893

Family “Oldfieldthomasiidae” Simpson, 1945

Genus *Colbertia* Paula Couto, 1952

Type species: *Colbertia magellanica* Paula Couto, 1952; São José de Itaboraí, Brazil; Itaboraian SALMA, Eocene.

Colbertia lumbrense Bond, 1981

Fig. 2A, B.

Holotype: PVL 4607, incomplete skull with right C, P1–P4, and left M1–M3; and mandible with left i2–m3, and right p2–m3.

Type locality: Estancia Pampa Grande, Salta Province, Argentina.

Type horizon: Lower sections of the Lumbrera Formation, middle Eocene.

Material.—IBIGEO-P 45 (Fig. 2A), right maxillary fragment with P4 and M3 from the same individual (both teeth were erroneously glued together, but due to their state of preservation they cannot be separated without breaking the material); and IBIGEO-P 56 (Fig. 2B), broken right M1 or M2. Quebrada Grande, Los Cardones National Park, Casamayoran SALMA, Eocene.

Description.—IBIGEO-P 45 and IBIGEO-P 56 were not found associated; nevertheless, according to their similar structures and size, both are considered here as belonging to the same species. IBIGEO-P 45 presents poorly preserved P4 and M3; both teeth are brachydont and subquadrangular in outline. Unfortunately, not much can be mentioned from the former tooth since only its labial portion, including a broken ectoloph, is preserved. The M3 is less worn than the P4, and preserves its lingual portion; the protoloph is well developed and runs disto-lingually; there is a low mesial cingulum, which is lingually interrupted, whereas the distal cingulum continues more lingually; a reduced hypocone is identified in the metaloph. IBIGEO-P 56 is a low-crowned M1 or M2, subquadrangular in outline; it is also broken and lacks its ectoloph, but it is little worn and the remaining structures are well preserved; the mesio-lingual cingulum is located lower on the crown and well developed, and it is lingually interrupted; there is a reduced, but continuous lingual cingulum that surrounds the lingual region of the protoloph; both protoloph and metaloph are well developed, but the former is wider and more oblique than the latter; the protoloph is curved and runs disto-lingually, whereas the metaloph runs mesio-lingually; the lingual end of the metaloph (hypocone region) unites with the lingual end of the protoloph (protocone region), isolating a central fossette; the central fossette is narrow and oblique, disto-lingually directed; a vestigial lingual sulcus persists to the connection of the protoloph and metaloph; the crochet is short and runs mesio-labially from the metaloph to the ectoloph, isolating the disto-labial fossette, which is shallow in this specimen; the disto-lingual cingulum is higher than the mesio-lingual cingulum, and it is also lingually interrupted. All of these characteristics plus their size (see Table 1) allow us to identify IBIGEO-P 45 and IBIGEO-P 56 as *Colbertia lumbrerense*.

Remarks.—*Colbertia lumbrerense* was previously known only for the lower Lumbrera Fm. at Pampa Grande, Salta (Bond 1981). In addition, *Colbertia* sp. has also been recognized in Geste Fm., Antofagasta de la Sierra (López 1997), and in the early Eocene of Brazil (Itaboraia SALMA; Paula Couto 1952).

Stratigraphic and geographic range.—Upper section of the Lumbrera and Quebrada de Los Colorados formations, middle Eocene; Salta Province, Argentina.

Colbertia falui sp. nov.

Fig. 2C–F.

Etymology: In honor of Eduardo Falú (1923–2013), an Argentinian folk music composer and guitarist, strongly influenced by the folk traditions of Salta Province.

Holotype: IBIGEO-P 67 (Fig. 2C), left mandibular fragment with m2–m3.

Type locality: Los Cardones National Park, Salta Province, Argentina.

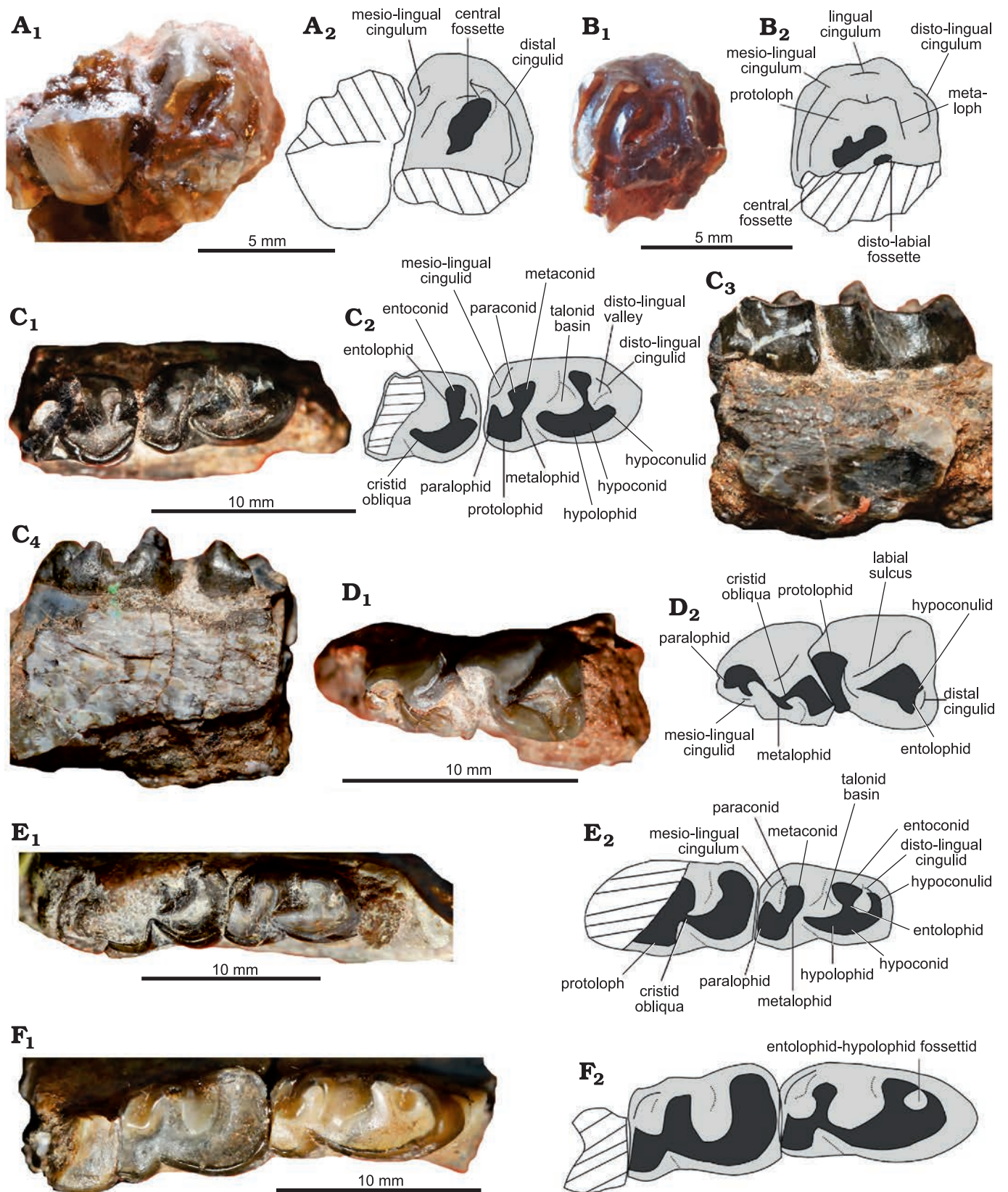
Type horizon: Quebrada de Los Colorados Fm., Casamayoran SALMA, Eocene.

Material.—IBIGEO-P 55 (Fig. 2D), right mandibular fragment with p3–p4; IBIGEO-P 59 (Fig. 2E), left mandibular fragment with m2–m3; IBIGEO-P 61 (Fig. 2F), left mandibular fragment with the talonid of m1, and m2–m3. Quebrada Grande, Los Cardones National Park, Casamayoran SALMA, Eocene.

Diagnosis.—Small notoungulate with brachydont dentition. *Colbertia falui* exhibits a similar size to the larger specimens of *C. magellanica* and *C. lumbrerense*. *C. falui* matches *C. lumbrerense*, and differs from *C. magellanica*, in the presence of a proportionally less elongated talonid of m3. *C. falui* differs from both *C. magellanica* and *C. lumbrerense* in the presence of lower cheek teeth with both more labially angular and oblique trigonid; lower premolars more labio-lingually compressed; with proportionally larger trigonid, and shorter talonid; ectoflexid transversally deeper; lower molars with more complex occlusal surfaces due to the presence of a more developed paralophid and more expanded metalophid and entoconid; the latter is located in a more mesial position, being closer to the region of the metaconid; deep talonid basin that is lingually narrower; disto-lingual sulcus transversally shallower; more developed cingulids; and the m3 with less lingually projected hypoconulid.

Description.—All the materials assigned to this species are well preserved. In IBIGEO-P 55, the p3 is longer than wide; the trigonid is subtriangular in outline, and slightly higher than the talonid; both protoconid and metaconid are well defined, the latter being slightly lower than the former; the protoconid is located in a more labial position than the paralophid and exhibits a mesial crest; the paralophid is low and lingually curved; the protoconid is connected to the metaconid by a short crest (= metalophid); the metaconid extends disto-lingually by a descendent crest; there is no trace of a paraconid; the talonid is short, subtriangular in outline, and lingually curved, and it is slightly narrower and markedly shorter than the trigonid; the cristid obliqua is connected to the disto-lingual region of the metalophid; the mesio-lingual sulcus of the trigonid is wide and opens lingually, whereas the disto-lingual sulcus in the talonid is short and narrow; the labial sulcus is deep and narrow; there

Fig. 2. New fossil specimens of Typotheria from the Quebrada de Los Colorados Fm. exposed at Quebrada Grande locality, Los Cardones National Park (Salta Province), Casamayoran SALMA, Eocene. **A, B.** *Colbertia lumbrerense* Bond, 1981. **A.** IBIGEO-P 45, right maxillary fragment with →



P4 and M3 in occlusal view. **B.** IBIGEO-P 56, broken right M1 or M2 in occlusal view. **C–F.** *Colbertia falui* sp. nov. **C.** IBIGEO-P 67, left mandibular fragment with m2–m3 (holotype) in occlusal (C₁), labial (C₃), and lingual (C₄) views. **D.** IBIGEO-P 55, right mandibular fragment with p3–p4 in occlusal view. **E.** IBIGEO-P 59, left mandibular fragment with m2–m3 in occlusal view. **F.** IBIGEO-P 61, left mandibular fragment with m1 (talonid)–m3 in occlusal view. Photographs (A₁, B₁, C₁, C₃, C₄, D₁, E₁, F₁), explanatory drawings (A₂–F₂). Dashed area indicates broken or missing dental areas.

are no traces of labial and lingual cingulids; a reduced mesio-lingual cingulid is identified. The p4 is larger and more molariform than the p3, but not completely molariform; it shows the same general features as described above for p3, but it is distinguished from it by the presence of a more developed talonid, which is also more lingually curved; the metaconid is higher than the protoconid and the paralophid; the entoconid is differentiated and lophoid, separated from the metaconid region; the hypoconulid is markedly reduced (unidentified in p3), and connected to a distal cingulid that does not extend lingually. The m1 is only represented by a broken talonid (IBIGEO-P 61) that exhibits the same general characteristics as the m2, except that it is more subquadrangular in outline. In IBIGEO-P 59, 61, and 67, the trigonid of m2 is wider than long, and slightly higher than the talonid; the paralophid is well developed, and directs lingually; a lower mesio-lingual cingulid is connected to the lingual edge of the paralophid that will eventually merge with it with wear; the metalophid is mesio-distally expanded and there is a small extension in the mesial wall of the metaconid, which suggests a fused paraconid; the metaconid is the highest cuspid; the metalophid is well developed, almost straight and slightly disto-lingually directed; the cristid obliqua is connected to the middle portion of the metalophid; the labial sulcus is both transversally and longitudinally deep; the talonid is well developed, and it is wider and much larger than the trigonid, and subrectangular in outline; the talonid basin is wide and deep; the lophoid entoconid is well developed, and mesially and transversally expanded, connected to the hypoconid; the distal face of the entoconid is located mesio-lingually to the hypoconulid; the latter is separated from the former by a deep valley, which is limited by a low disto-lingual cingulid that connects the entoconid and the hypoconulid; the hypolophid is reduced and slightly lingually curved. The m3 is larger than the m2 and shows the same general features, but it can be distinguished from its predecessor by the following characteristics: presence of an enlarged talonid due to a larger and more lingually curved hypolophid; talonid slightly narrower than the trigonid; presence of a deeper distal valley; and more conspicuous disto-lingual cingulid that connects the hypoconulid and the disto-lingual wall of the entoconid; with wear, these structures merge and isolate a small fossettid as observed in IBIGEO-P 61, which is the most worn specimen assignable to *C. falui*.

Stratigraphic and geographic range.—Quebrada de Los Colorados Formation, middle Eocene; Salta Province, Argentina

Colbertia sp.

Fig. 3A, B.

Material.—IBIGEO-P 58a (Fig. 3A), left maxillary fragment with M2–M3, and IBIGEO-P 58b (Fig. 3B), left maxillary fragment with P4–M3. Quebrada Grande, Los Cardones National Park, Casamayoran SALMA.

Description.—IBIGEO-P 58a and 58b are poorly preserved, completely razed and heavily worn; only the M3 of IBIGEO-P 58a and the P4–M2 of IBIGEO-P 58b are better preserved, as their labial and lingual faces, respectively, are present. All cheek teeth are low-crowned and subquadrangular in outline; the well-developed protoloph and the metaloph are curved and united by their lingual ends, isolating a central fossette that runs disto-lingually.

Remarks.—According to the combination of characteristics described above, IBIGEO-P 58a and 58b are identified as belonging to the genus *Colbertia*. Unfortunately, and due to the bad preservation of the specimens and the general resemblance of the dental features of *Colbertia lumbrerense* and *C. magellanica*, it is not possible to establish if they belong to a given species within the genus, particularly because *Colbertia falui* is known only by its lower dentition. Due to all of this, IBIGEO-P 58a and 58b are considered here as *Colbertia* sp.

Suborder Toxodontia Owen, 1853

Family “Notohippidae” Ameghino, 1895

Genus *Pampahippus* Bond and López, 1993

Type species: *Pampahippus arenalesi* Bond and López, 1993; Guachipas, Salta Province, Argentina; Vacan sub-age, Casamayoran SALMA, Eocene.

Pampahippus secundus Deraco and García-López, 2016

Fig. 3C–E.

Holotype: PVL 6426, right maxillary fragment with P2–M3.

Type locality: El Simbolar, Guachipas Department, Salta Province, Argentina.

Type horizon: Upper section of the Lumbrera Formation, middle Eocene.

Material.—IBIGEO-P 62, right trigonid and incomplete talonid of a lower molar (Fig. 3C), and an upper fragmented cheek tooth; IBIGEO-P 63 (Fig. 3D), fragmented left p3 or p4; IBIGEO-P 64 (Fig. 3E), left m1?. Quebrada Grande, Los Cardones National Park, Casamayoran SALMA.

Description.—IBIGEO-P 62–64 are brachydont cheek teeth, subrectangular in outline. Although IBIGEO-P 63 is broken, it is probable that this cheek tooth is a p3 or p4 due to the following characteristics; the trigonid and talonid are separated by a deep labial sulcus; the cristid obliqua is connected to the distal wall of the metalophid; the metalophid is straight and disto-lingually directed; the talonid is short and shows a conspicuous bunoid and isolated entoconid; the hypoconulid is located distal to the distal wall of the entoconid. IBIGEO-P 62 is a molariform cheek tooth; due to its breakage it is not possible to determine which tooth it is, but some recognizable features and the absence of others allow us to infer that it could be a lower molar; the trigonid is subrectangular in outline, being wider than long; the protolophid is almost straight; the paralophid is short, narrow, and

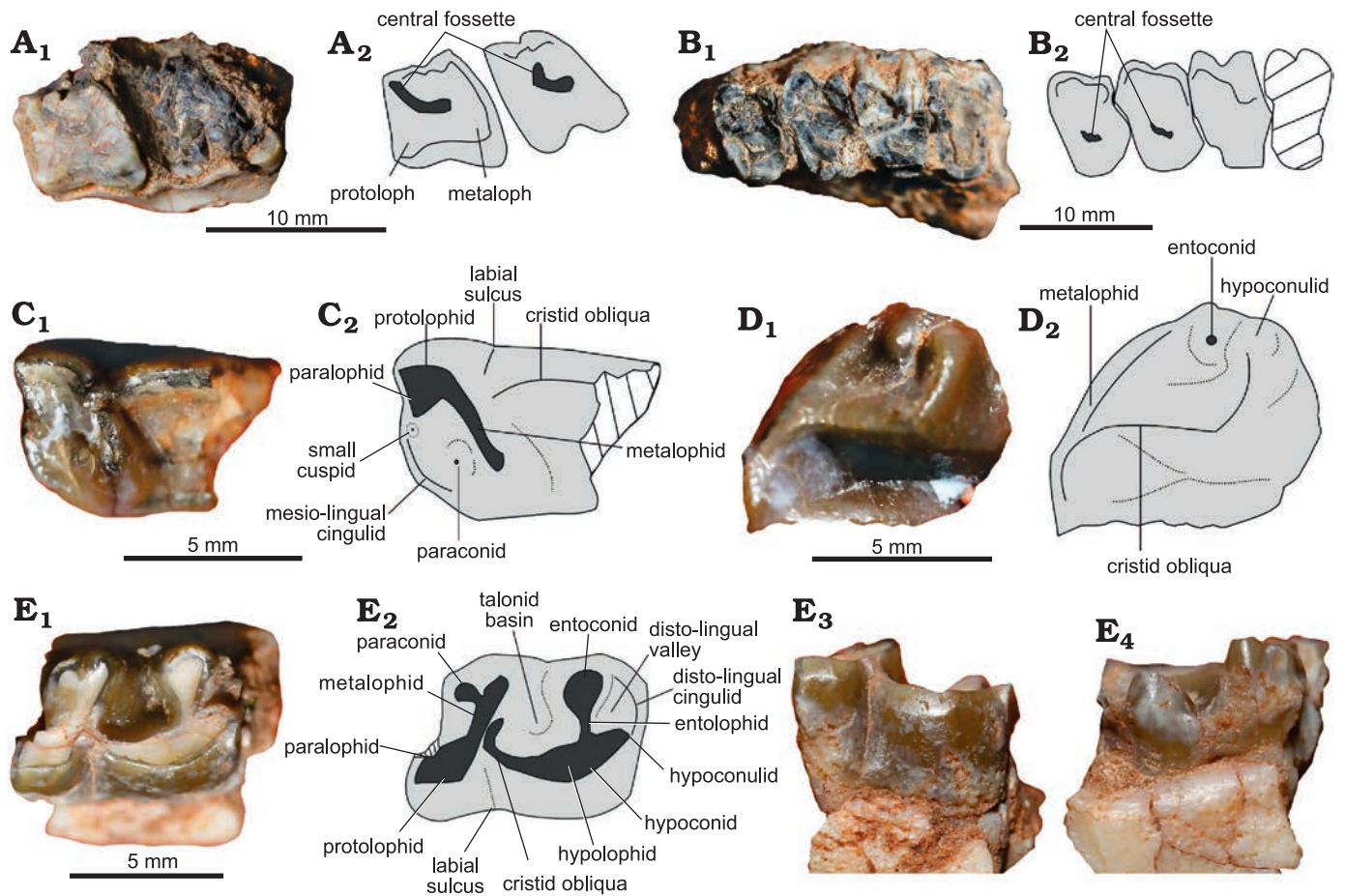


Fig. 3. New fossil specimens of *Typotheria* and *Toxodontia* from the Quebrada de Los Colorados Formation exposed at Quebrada Grande locality, Los Cardones National Park (Salta Province), Casamayoran SALMA. **A, B.** *Colbertia* sp. **A.** IBIGEO-P 58a, left maxillary fragment with M2–M3 in occlusal view. **B.** IBIGEO-P 58b, left maxillary fragment with P4–M3 in occlusal view. **C–E.** *Pampahippus secundus* Deraco and García-López, 2016. **C.** IBIGEO-P 62, right trigonid and incomplete talonid of a lower right molar in occlusal view. **D.** IBIGEO-P 63, fragmented left p3 or p4 in occlusal view. **E.** IBIGEO-P 64, left m1? in occlusal (**E₁**), labial (**E₂**), and lingual (**E₃**) views. Photographs (**A₁–E₁**, **E₃**, **E₄**), explanatory drawings (**A₂–E₂**). Dashed area indicates broken or missing dental areas.

lingually directed; the mesio-lingual cingulid is reduced and separated from the lingual region of the paralophid, but, based on the height of the cingulid on the crown, its location on the trigonid, and its proximity to the paralophid, with wear, the mesio-lingual cingulid fuses to the paralophid; a small cusp is identified between these structures; the trigonid presents a conspicuous paraconid mesial to the mesio-labial wall of the metalophid; the metalophid is straight, conspicuous, and disto-lingually directed; the cristid obliqua is united to the labial portion of the metalophid; the labial sulcus is transversally and longitudinally deep; the talonid is larger and lower than the trigonid, and subquadrangular in outline; there are no traces of labial and lingual cingulids. In IBIGEO-P 64, the protolophid is almost straight and mesio-labially directed; despite the breakage of the paralophid, it seems to be disto-lingually directed; the metalophid is straight and disto-lingually directed; the paraconid is conspicuous and connected to the mesio-labial face of the metalophid; the cristid obliqua is connected to the labial portion of the metalophid; the labial sulcus is transversally and longitudinally deep; the talonid is labially convex, and

larger and slightly lower than the trigonid, but both present almost the same width; the talonid basin is shallow and wide; the lophoid entoconid is well developed and transversally expanded, connected to the hypoconid region, and separated from the hypoconulid by the a small disto-lingual valley, which is limited by a disto-lingual cingulid that connects the hypoconulid and the entoconid; the hypolophid is moderately short and curved as it slightly protrudes from the distal face of the entoconid; there are no traces of labial or lingual cingulids. To sum up, IBIGEO-P 62–64 present a combination of characteristics, including their size, the mesio-distal expansion of lower cheek tooth, the identification of a small paraconid mesial to the metaconid, the presence of a well-developed entoconid being bunoid in premolars and lophoid in molars, and the absence of lingual and labial cingulids on molars, all of which allowing their identification as *Pampahippus secundus*.

Stratigraphic and geographic range.—Lower and upper sections of the Lumbrera and Quebrada de Los Colorados Formations, middle Eocene; Salta Province, Argentina.

Remarks.—*Pampahippus secundus* has been identified in the lower (Deraco and García-López 2016) and upper levels (García-López et al. 2019) of the Lumbrera Fm., at El Simbolar (Salta). In addition, *Pampahippus* has also been recognized in the lower section of the Lumbrera Fm. at Pampa Grande, Salta (Bond and López 1993), Quebrada de Los Colorados Fm. at La Poma, Salta (García-López et al. 2018), and Geste Fm. at Antofagasta de la Sierra, Catamarca (López 1997).

Discussion and conclusions

SANU richness in the Quebrada de Los Colorados Formation.—In the last few years, the Quebrada de Los Colorados Fm. has become an important Eocene vertebrate-bearing unit in Northwestern Argentina (García-López et al. 2017, 2018, 2020). Up to this contribution, the taxonomic richness of the SANU in this unit has been restricted to the order Notoungulata, or more precisely, to the toxodont Leontiniidae, “Isotemnidae”, and “Notohippidae”, and the typother “Archaeohyracidae”. The new specimens presented here considerably increase the known taxonomic richness of the unit. In the framework of the SANUs, and in addition to notoungulates, the orders Astrapotheria and Litopterna, the latter being represented by the family Didolodontidae, are recorded for the first time in the Quebrada de Los Colorados Fm. Among Notoungulata, the families Notostylopidae and “Oldfieldthomasiidae” are also part of this unit.

Middle Eocene SANUs of Northwestern Argentina.—The SANUs are well represented in all middle Eocene units in Northwestern Argentina. As explained in the following paragraphs, the most abundant records correspond to notoungulates, followed by litopterns (including didolodontids), astrapotheres, and pyrotheres. These records, at generic and specific level, are summarized in SOM 4.

Notoungulata: A Notoungulata indet. was reported by García-López and Babot (2015), based on a broken lower molar, from the Geste Fm. Among basal notoungulates, Notostylopidae are represented in the middle Eocene of Northwestern Argentina by *Boreastylops lumbrerensis* Vucetich, 1980, collected from the lower section of the Lumbrera Fm. (Vucetich 1980; Powell et al. 2011); a Notostylopidae indet. from the Geste Fm. (López 1997); and the *Homalostylops* sp. and the ?*Homalostylops* sp. described in this contribution for the Quebrada de Los Colorados Fm. The new reports of *Homalostylops* sp. and ?*Homalostylops* sp. are particularly interesting because they correspond to the first mention of the genus in Northwestern Argentina, since the genus had been known from the middle Eocene of Argentinean Patagonia (Barrancan, Casamayoran).

Concerning the suborder Toxodontia, two Toxodontia indet. have been recognized in the Quebrada de Los Colorados (García-López et al. 2018) and Geste (Armella et al. 2016) formations. Among the four traditional families included

in this suborder, the “Notohippidae”, “Isotemnidae”, and Leontiniidae are represented in the middle Eocene of Northwestern Argentina. In this context, the following seven “isotemnids” have been identified: *Pampatemnus infernalis* and *P. deuterus*, recorded in the lower section of Lumbrera Fm. (Vucetich and Bond 1982); and five “Isotemnidae” indet., two from Casa Grande Fm. (Bond and López 1995), two from the Geste Fm. (López 1997; García-López and Babot 2015), and the last one, interpreted as closely related to *Pleurostylodon* and *Pampatemnus*, from the Quebrada de Los Colorados Fm. (Payrola-Bossio et al. 2009). Five “notohippids” have also been mentioned: *Pampahippus arenalesi*, recovered from the lower Lumbrera Fm. (Bond and López 1993); *P. secundus* from the lower (Deraco and García-López 2016) and upper sections of the Lumbrera Fm. (García-López et al. 2019); and *P. powelli* (García-López et al. 2018), erected from the holotype previously presented as a new unnamed genus and species by Hongn et al. (2007), from the Quebrada de Los Colorados Fm.; and a cf. *Pampahippus* (López 1997) and a “Notohippidae” indet. (García-López and Babot 2015) from the Geste Fm. It is worth mentioning that *Pampahippus* presents the greatest species richness among the notoungulates from Northwestern Argentina since the three known species of the genus have been recognized in this region, and the new record in the Quebrada de Los Colorados Fm. reinforces it as a conspicuous element of the Eocene Northwestern Argentinean faunas, being recorded from the lower section of Lumbrera Fm. to the Geste Fm. faunas. Regarding the third toxodont family, the following four leontinids have been recognized in the region during the middle Eocene: *Martinmiguelia fernandezi*, collected in Casa Grande Fm. (Bond and López 1995); a Leontiniidae indet. (Hongn et al. 2007; García-López et al. 2018) from the Quebrada de Los Colorados Fm.; and *Coquenia bondi* (Deraco et al. 2008) and cf. *Coquenia* (Powell et al. 2011) from the upper section of the Lumbrera Fm.

In the suborder Typotheria, two Typotheria indet. (A and B) have been recognized in the Geste Fm. (García-López and Babot 2015), and a Typotheria incertae sedis known as *Griphotherion peiranoi* García-López and Powell, 2011, based on an incomplete skeleton, has been reported in the lower section of the Lumbrera Fm. (García-López and Powell 2011). Among the seven traditional families within Typotheria, the “Oldfieldthomasiidae”, “Archaeohyracidae”, Interatheriidae, and the informal family “Campanorciidae” are represented in the middle Eocene of Northwestern Argentina (Fig. 6). Within “Campanorciidae”, Bond et al. (1984) presented “*Campanorco inauguralis*” (an invalid name that is commonly used in the literature), and Powell et al. (2011) mentioned “*Campanorco*” sp. nov., both coming from the upper section of the Lumbrera Fm. “Oldfieldthomasiidae” are represented in Northwestern Argentina by the following taxa: *Suniodon catamarcensis* (López 1995, 1997), *Suniodon* sp. nov. (García-López and Babot 2015), and two “Oldfieldthomasiidae” indet. (López 1995, 1997), all coming from the Geste Fm.; *Dolichostylodon salten-*

sis was recovered from the upper section of the Lumbrera (García-López and Powell 2009); *Colbertia lumbrerense* has been recognized in the lower section of the Lumbrera Fm. (Bond 1981) and, according to the results shown here, in the Quebrada de Los Colorados Fm.; *Colbertia falui* presented in this contribution as a new species is recovered from the last unit; and two *Colbertia* sp. have been recorded, one of them presented here for the Quebrada de Los Colorados Fm., and the other mentioned by López (1997) for the exposures of the Geste Fm. It is worth mentioning that due to the new species of *Colbertia* presented here, this genus equals *Pampahippus* in terms of the specific richness, but, in contrast to *Pampahippus*, only two species among the three known species of *Colbertia* (*C. lumbrerense* and *C. falui*) have been identified in the Eocene Northwestern Argentina. However, *Colbertia* has also become another conspicuous element of the region in where it is recorded from the lower section of Lumbrera Fm. to the Geste Fm. faunas. Among the “Archaeohyracidae”, nine taxa have been mentioned for the middle Eocene of the area: *Punahyrax bondesioi* (Reguero et al. 2008; García-López et al. 2020), “*Punahyrax* sp. nov.”, *Pseudhyrax eutrachytheroides*, and “*Pseudhyrax* sp. nov.” (García-López et al. 2020), all of them from the Geste Fm.; and an “aff. *Eohyrax* sp. indet.” and two “Archaeohyracidae” indet. from the Quebrada de Los Colorados Fm. (García-López et al. 2020). The last identified tyotheriidae family is Interatheriidae, which is restricted to the Geste Fm., and is represented by the following taxa in the middle Eocene of Northwestern Argentina: two non-interatheriine interatheriids, *Punapithecus minor* (López and Bond 1995; García-López and Babot 2015), the smallest known notoungulate, and *Antofagasta turneri* (García-López and Babot 2015); and three Interatheriidae indet. (A, B, and C), based on postcranial remains that exhibit features more consistent with the morphology of early diverging Interatheriidae (Armella et al. 2016).

Litopterna: This order is represented in the middle Eocene of Northwestern Argentina by two families, Indaleciidae and Didolodontidae. Regarding the former family, *Indalecia grandensis* has been mentioned based on a well-preserved skull from the lower section of the Lumbrera Fm. (Bond and Vucetich 1983). The first didolodontids came from the Geste Fm., and have been referred as cf. *Ernestokokenia* (López 1997) and *Ernestokokenia* cf. *E. yirunhor* (Armella et al. 2016). Recently, Gelfo et al. (2020) found *Saltaodus sirolli* Gelfo, Madden, Alonso, and Carlini, 2020, from undifferentiated levels of the Lumbrera Fm. at the Puna Plateau.

Astrapotheria: This order is represented by the following three taxa: the first astrapotherid was mentioned as *Albertogaudrya? carahuasensis* from the lower levels of the Lower Lumbrera Fm. (Carbajal et al. 1977). Although this taxon has been referred to a genus present in Patagonia, the morphological features of *A. carahuasensis* are quite different from those of the Patagonian species referred to the genus; for that reason it was dubiously referred to the Patagonian genus *Albertogaudrya*, and it was recog-

nized that perhaps it could pertain to a different genus. The remaining two astrapotheres have been identified as Astrapotheriidae indet.; one of them has been mentioned by López (1997) for the Geste Fm., based on a lower premolar that presented some resemblances with *Albertogaudrya*, and the other is the Astrapotheria indet. presented in this contribution from the Quebrada de Los Colorados Fm. This new record reaffirms the group as a conspicuous element in the regional context.

Pyrotheria: In the middle Eocene of Northwestern Argentina, this order is only represented by a distal portion of a lower tusk, collected in the Geste Fm. (López 1997), which was referred to *Propyrotherium* sp.

For a long time, the absence of shared ungulate genera between Northwestern Argentinean faunas and the remaining South American faunas, especially the Patagonian ones, was considered as evidence of a biogeographical isolation of the area (see as review Powell et al. 2011). However, in the last few years the Eocene ungulate diversity substantially increased (Babot et al. 2017), and several genera already recorded in other regions of South America (in this context mentioned from now on as “foreign” taxa) were identified in the Eocene faunas of Northwestern Argentina. The first chronological record of non-endemic genera corresponds to the Brazilian oldfieldthomasiid *Colbertia*, recovered from the lower section of the Lumbrera Fm. According to the current record, the number of foreign genera notably increased during the late middle Eocene (see SOM 5), when the pyrotheriid *Propyrotherium*, the didolodontid *Ernestokokenia*, the notostyloid *Homalostylops*, and the archaeohyracids *Eohyrax* and *Pseudhyrax* were added to *Colbertia*. In this context, *Eohyrax*, *Propyrotherium*, *Homalostylops*, *Ernestokokenia*, and *Pseudhyrax* have been also identified in the Eocene of Patagonia (Marshall et al. 1983), *Eohyrax* and *Ernestokokenia* in the Eocene of Chile (Hitz et al. 2006; Croft et al. 2008), and *Pseudhyrax* (Croft et al. 2003; García-López et al. 2020) in the Oligocene of Chile. Moreover, it is striking that most of the foreign ungulates have been recovered from the Quebrada de los Colorados and Geste formations, whereas the upper section of Lumbrera Fm. has only yielded endemic taxa (see SOM 5). Thus, the concept of the strong regional endemism of the Eocene Northwestern Argentinean fauna as mentioned by Powell et al. (2011) is not supported by the current evidence; nevertheless, it is evident the existence of a local endemism in the east. All of this suggests that the Northwestern Argentinean faunas are not homogeneous across a longitudinal transect, a fact that could be the result of underlying landscape evolution.

In summary, the above context reinforces the importance of palaeontological prospection in the Paleogene levels of Northwestern Argentina, particularly in the Calchaquí Valleys (upper levels of the Quebrada de los Colorados Fm., and lower levels of the Lumbrera Fm.), which appear as a hiatus in the regional palaeontological record (see SOM 5–7 for the discussion of the Northwestern faunas along the topographical gradient).

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