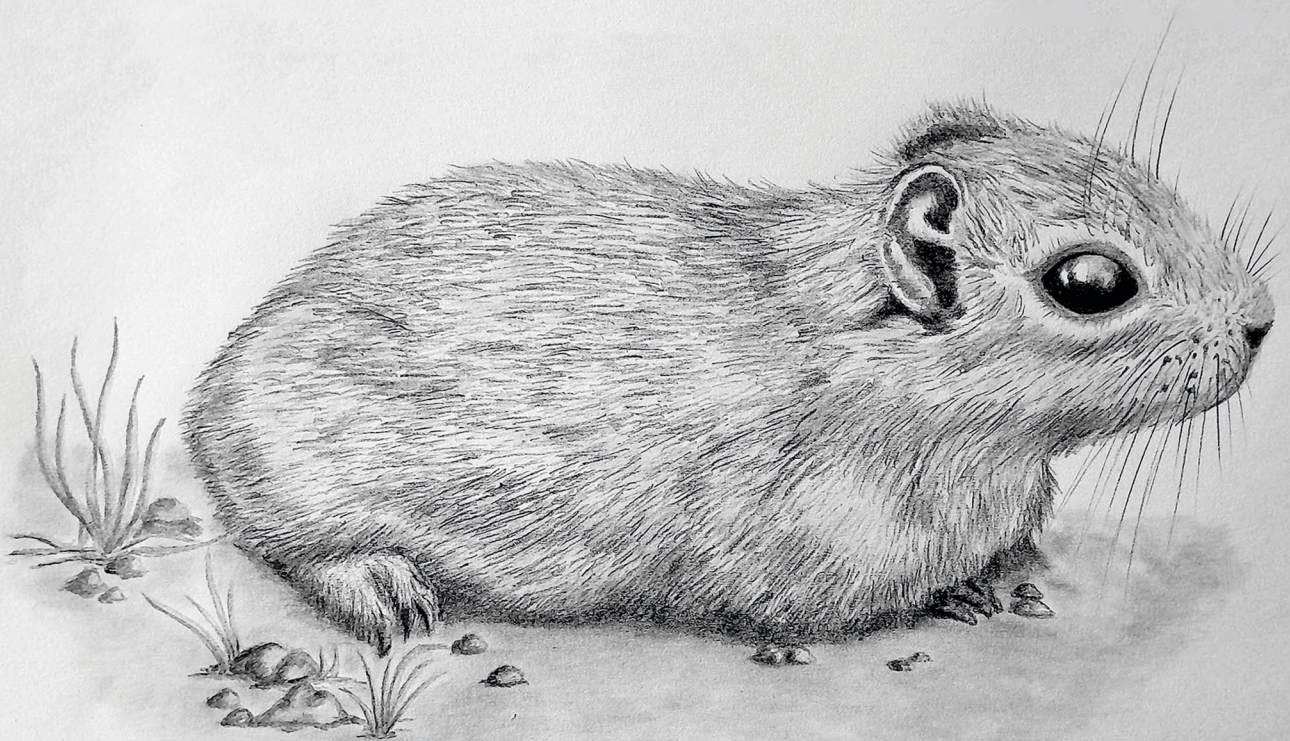


Redescription of a small Caviidae (Rodentia,
Hystricognathi) from the Neogene of northwestern
Argentina and its systematic implications

María Carolina MADOZZO JAÉN & María Encarnación PÉREZ



DIRECTEURS DE LA PUBLICATION / PUBLICATION DIRECTORS :
Gilles Bloch, Président du Muséum national d'Histoire naturelle
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

RÉDACTEURS EN CHEF / EDITORS-IN-CHIEF: Michel Laurin (CNRS), Philippe Taquet (Académie des sciences)

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR: Adenise Lopes (Académie des sciences; cr-palevol@academie-sciences.fr)

MISE EN PAGE / PAGE LAYOUT: Audrina Neveu (Muséum national d'Histoire naturelle; audrina.neveu@mnhn.fr)

RÉVISIONS LINGUISTIQUES DES TEXTES ANGLAIS / ENGLISH LANGUAGE REVISIONS: Kevin Padian (University of California at Berkeley)

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS (*, took charge of the editorial process of the article/a pris en charge le suivi éditorial de l'article):

Micropaléontologie/Micropalaeontology

Lorenzo Consorti (Institute of Marine Sciences, Italian National Research Council, Trieste)

Paléobotanique/Palaeobotany

Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Métazoaires/Metazoa

Annalisa Ferretti (Università di Modena e Reggio Emilia, Modena)

Paléochthyologie/Palaeoichthyology

Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/Mesozoic amniotes

Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/Turtles

Walter Joyce (Universität Freiburg, Switzerland)

Lépidosauromorphes/Lepidosauromorphs

Hussam Zaher (Universidade de São Paulo)

Oiseaux/Birds

Jingmai O'Connor (Field Museum, Chicago)

Paléomammalogie (mammifères de moyenne et grande taille)/Palaeomammalogy (large and mid-sized mammals)

Lorenzo Rook* (Università degli Studi di Firenze, Firenze)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/Palaeomammalogy (small mammals except for Euarchontoglires)

Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/Palaeomammalogy (Euarchontoglires)

K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/Palaeoanthropology

Aurélien Mounier (CNRS/Muséum national d'Histoire naturelle, Paris)

Archéologie préhistorique (Paléolithique et Mésolithique)/Prehistoric archaeology (Palaeolithic and Mesolithic)

Nicolas Teyssandier (CNRS/Université de Toulouse, Toulouse)

Archéologie préhistorique (Néolithique et âge du bronze)/Prehistoric archaeology (Neolithic and Bronze Age)

Marc Vander Linden (Bournemouth University, Bournemouth)

RÉFÉRÉS / REVIEWERS: <https://sciencepress.mnhn.fr/fr/periodiques/comptes-rendus-palevol/referes-du-journal>

COUVERTURE / COVER:

Reconstruction of the extinct species *Orocavia andina*. Credits: Rosa Virginia Palmas.

Comptes Rendus Palevol est indexé dans / *Comptes Rendus Palevol is indexed by:*

- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par /
Articles and nomenclatural novelties published in Comptes Rendus Palevol are registered on:

- ZooBank® (<http://zoobank.org>)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*

Adansonia, Geodiversitas, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections *Algologie, Bryologie, Mycologie*.

L'Académie des sciences publie aussi / *The Académie des sciences also publishes:*

Comptes Rendus Mathématique, Comptes Rendus Physique, Comptes Rendus Mécanique, Comptes Rendus Chimie, Comptes Rendus Géoscience, Comptes Rendus Biologies.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél. : 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>)
ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

Redescription of a small Caviidae (Rodentia: Hystricognathi) from the Neogene of northwestern Argentina and its systematic implications

María Carolina MADOZZO JAÉN

Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET),
Superior de Correlación Geológica (INSUGEO), Facultad de Ciencias Naturales
e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Miguel Lillo 205,
T4000JFE, San Miguel de Tucumán (Argentina)
cmadozzo@csnat.unt.edu.ar (corresponding author)

María Encarnación PÉREZ

Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET),
Museo Paleontológico Egidio Feruglio (MEF), Avenida Fontana 140,
Trelew, U9100GYO Chubut (Argentina)
mperez@mef.org.ar

Submitted on 25 November 2019 | Accepted on 29 April 2024 | Published on 8 August 2024

urn:lsid:zoobank.org:pub:15C1CD83-2D0A-42FE-B630-B322F93E799D

Madozzo Jaén M. C. & Pérez M. E. 2024. — Redescription of a small Caviidae (Rodentia: Hystricognathi) from the Neogene of northwestern Argentina and its systematic implications. *Comptes Rendus Palevol* 23 (20): 269–292. <https://doi.org/10.5852/cr-palevol2024v23a20>

ABSTRACT

The understanding of the taxonomy, diversity, and evolutionary patterns of caviids in northwestern Argentina is still in the process of development. This paper presents new insights into the systematic and evolution of *Orthomyctera andina* (Rovereto, 1914), one of the most abundant species within Caviidae Fischer de Waldheim, 1817, in the fossil record of this region. A comprehensive anatomical description and taxonomic review of *Orthomyctera andina* in a phylogenetic context is provided. Moreover, it includes a redescription of the type specimen of *Orthomyctera rigens* (Ameghino, 1888). The taxonomical results confirm that *O. andina* belongs to a different genus: *Orocavia* (Kraglievich, 1932). The phylogenetic analysis further confirms the placement of both species within Caviinae Fischer de Waldheim, 1817. *Orthomyctera andina* is the sister taxon of the clade that includes *Microcavia* Gervais & Ameghino, 1880, *Dolicavia* Ameghino, 1916, *Neocavia* Kraglievich, 1932, and *Orthomyctera* Ameghino, 1889. It is supported by a combination of plesiomorphic characters (e.g. furrow opposite to hypoflexus/id in molariforms) shared with basal taxa and Dolichotinae Pocock, 1922 and derived characters (such as a terreced palate, external auditory meatus below the occlusal surface, length of p4-m1 shorter than length of m2-m3) shared with Caviinae. This study aims to elucidate the taxonomic status of these poorly known rodents and their relationships within Caviidae. Additionally, it incorporates a biogeographic analysis of caviomorph communities from the late Neogene in Argentina.

KEY WORDS

Caviinae,
taxonomy,
phylogeny,
diversity,
Miocene-Pliocene,
South America,
new combination.

RÉSUMÉ

Redescription d'un petit Caviidae (Rodentia: Hystricognathi) du Néogène du Nord-Ouest de l'Argentine et ses implications systématiques.

La compréhension de la taxonomie, de la diversité et des schémas évolutifs des caviidés du Nord-Ouest de l'Argentine est encore en cours de développement. Dans cet article, nous reportons les avancées sur la taxonomie et l'évolution de l'une des espèces de Caviidae Fischer de Waldheim, 1817 les plus abondantes dans le registre fossile de cette région, *Orthomyctera andina* (Rovereto, 1914). Nous avons réalisé une description anatomique exhaustive, ainsi qu'une révision taxonomique dans un contexte phylogénétique, d'*O. andina* et de l'espèce type *O. rigens* (Ameghino, 1888). Nous concluons ici qu'*Orthomyctera* Ameghino, 1889 est un genre valide, mais *O. andina* appartient à un autre genre. Aussi, nous confirmons l'appartenance des deux espèces aux Caviinae Fischer de Waldheim, 1817, et leur proche relation avec les lignées de *Microcavia* Gervais & Ameghino, 1880, *Dolicavia* Ameghino, 1916, et *Neocavia* Kraglievich, 1932. Le nouveau genre prend une place basale au sein du clade de part la présence d'une mosaïque de caractères plésiomorphiques (partagés avec les formes basales de Dolichotinae Pocock, 1922) et dérivés (partagés avec les Caviinae). Une discussion sur le possible comportement fossilifère d'*O. andina* est incluse. Ce travail contribue à l'interprétation taxonomique, phylogénétique et biogéographique des communautés de caviomorphes de la fin du Néogène en Argentina.

MOTS CLÉS

Caviinae,
taxonomie,
phylogénie,
diversité,
Miocène-Pliocène,
Amérique du Sud,
combinaison nouvelle.

INTRODUCTION

The caviomorph rodents, autochthonous to South America, are currently classified into four main clades: Cavoidea (Fischer de Waldheim, 1817), Chinchilloidea Bennett, 1833, Erethizontoidea Bonaparte, 1845, and Octodontoidea Waterhouse, 1839. They are primarily found along the Andes, throughout much of the Amazonia and the Atlantic Forest, as well as in certain areas of central and northeastern Brazil (Maestri & Patterson 2016). Cavoidea which includes cavies, maras, capybaras, pacas, and agoutis can be found across the lowland forest of the Neotropical, stretching from eastern and southern Mexico to Santa Cruz province in Argentina and southern Chile (Dunnum 2015). They highest species richness is concentrated in the central Andes and the Caatinga in Brazil (Maestri & Patterson 2016). Within Cavoidea, the Caviidae Fischer de Waldheim, 1817 exhibits remarkable diversity comprising 22 species grouped into six genera: *Cavia* Pallas, 1766, *Dolichotis* Desmarest, 1820, *Galea* Meyen, 1832, *Hydrochoerus* Brisson, 1762, *Kerodon* Cuvier, 1825, and *Microcavia* Gervais & Ameghino, 1880 (Dunnum 2015; Madozzo Jaén *et al.* 2021, but see Campo *et al.* 2020; Teta & Campo 2017). This family boasts the widest geographic distribution and the most extensive size range among all living rodents (Dunnum 2015). The three Subfamilies of Caviidae present well-differentiated ecomorphological patterns: Hydrochoerinae Gill, 1872 (capybaras) are the most giant rodents currently known; they exhibit some adaptations to the cursoriality and for a semi-aquatic lifestyle (García-Esponda & Candela 2016); the medium-sized Dolichotinae Pocock, 1922 (mara and conejo de los palos) with cursorial adaptations, and Caviinae Fischer de Waldheim, 1817 (cavies) which are small in size with a locomotor behavior ambulatory (Dunnum 2015). Despite their great diversity, that of the fossil record is more than double that of today (Vucetich *et al.* 2015a). The origin of Caviidae and the diversification of the three main lineages

(Caviinae, Dolichotinae and Hydrochoerinae) are estimated at the Middle Miocene (Pérez & Pol 2012). Over the past decades, efforts to order the taxonomy of the fossil caviid forms have increased (e.g. Quintana 1996; Vucetich *et al.* 2005, 2014a, b, 2015a, b; Deschamps *et al.* 2007, 2009, 2013; Pérez *et al.* 2014, 2018; Cerdeño *et al.* 2019; Madozzo Jaén 2019; Madozzo Jaén *et al.* 2021). However, the status and/or validity of several nominal taxa remains unresolved (e.g. Vucetich *et al.* 2015a). Such is the case, for example, of the genera *Orthomyctera* Ameghino, 1889, *Dolichotis*, or *Prodolichotis* Kraglievich, 1932 from the Late Miocene-Pleistocene. Recently, the taxonomical status of some species included in them has been partially revised (e.g. Madozzo Jaén 2019; Madozzo Jaén *et al.* 2021), but there are still several nominal species that need an exhaustive revision.

Traditionally *Orthomyctera* was related to the subfamily Dolichotinae (Kraglievich 1930; Simpson 1945; Castellanos 1958; McKenna & Bell 1997) or Caviinae (Kraglievich 1932; Quintana 1998; Ubilla & Rinderknecht 2003). The type species of the genus, *O. rigens* (Ameghino, 1888), was designated by Kraglievich (1930; not *O. lata* Ameghino, 1889 in Pascual 1966: see below comments section). It was originally described as *Cavia rigens* (Ameghino, 1888) posteriorly transferred to a new genus *Orthomyctera* (Ameghino 1889). Some fossil species of *Dolichotis* (e.g. *Dolichotis andina* Rovereto, 1914; Appendix 1) and other nominal species (e.g. *O. vaga* Ameghino, 1889; Appendix 1) were referred to *Orthomyctera*. Moreover, some taxa previously assigned to *Orthomyctera* were transferred to *Prodolichotis* (e.g. *O. lacunosa* (Ameghino, 1888) Kraglievich 1932) or *Dolichotis* (e.g. Rovereto 1914, but see: Kraglievich 1932; Cabrera 1953; Madozzo Jaén *et al.* 2021). Except for *O. andina* (Rovereto, 1914), most of these species are known exclusively from the type material (e.g. *O. perfecta* Ameghino, 1908, *O. brocherense* Castellanos, 1936).

Fossil remains assigned to *Orthomyctera* are recorded with certainty from the Late Miocene of Argentina (Rovereto 1914; Kraglievich 1932) and with doubts from the same period in

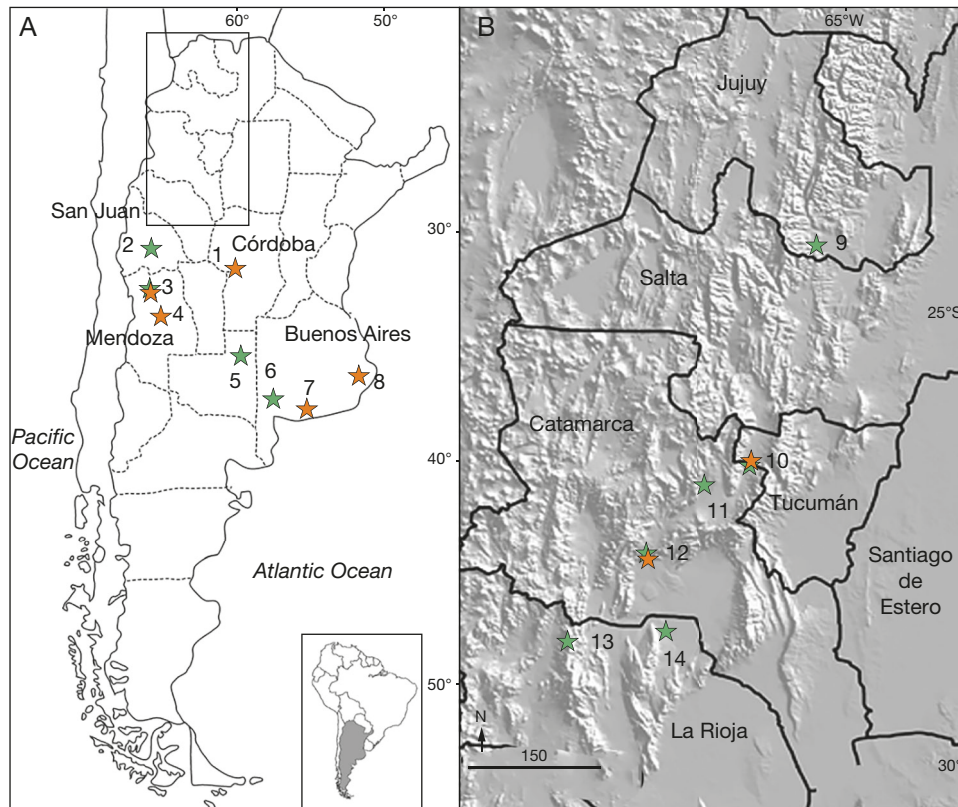


FIG. 1. — Location map indicating the geographic distribution of fossil Caviidae: **A**, fossil record of *Orthomyctera* Ameghino, 1889 in Argentina; **B**, in northwestern Argentina. Colours: **green**, Late Miocene-Early Pliocene; **orange**, Pliocene. Numbers: 1, Los Reartes valley, Córdoba; 2, Loma de las Tapias, San Juan; 3, Huayquerías, 4, Río Atuel, Mendoza; 5, Caleufú, La Pampa; 6, Arroyo Chasicó; 7, Monte Hermoso; 8, Chapadmalal, Buenos Aires; 9, Los Alisos, Jujuy; 10, Encallilla, Tucumán; Entre Ríos, Catamarca; Santa María valley; 11, El Cajón valley; 12, Villavil-Quillay basin; 13, Vinchina; 14, El degolladito, La Rioja.

Bolivia (Villarroel & Marshall 1989). However, their most diversity comes from the Pliocene of Argentina, from Monte Hermoso and Chapadmalal localities Buenos Aires Province, and some mentions from the Pliocene of Córdoba Province (Fig. 1A; Ameghino 1889; Rovereto 1914; Kraglievich 1932; Castellanos 1958; Pascual 1966; Vucetich & Pérez 2011). Other records were reported from the Late Miocene of Arroyo Chasicó, Buenos Aires, Caleufú, La Pampa Province; Huayquerías, Río Atuel; Mendoza Province; Lomas de las Tapias, San Juan Province (Fig. 1A; Verzi & Montalvo 2008; Contreras & Barald 2011; Vucetich & Pérez 2011; Contreras *et al.* 2019; Garrido *et al.* 2014; Pérez *et al.* 2019). In northwestern Argentina (NWA) (Fig. 1B) *Orthomyctera* from the Late Miocene-Early Pliocene (Araucanian fauna) of Catamarca, Jujuy, Tucumán, and La Rioja provinces (Marshall & Patterson 1981; Powell *et al.* 1998; Herbst *et al.* 2000; Brandoni *et al.* 2012; Madozzo Jaén *et al.* 2013; Esteban *et al.* 2014, 2019); Armella *et al.* 2016; Ercoli *et al.* 2019). Most of these records consist of isolated teeth and fragments of the skull and jaws that have not been revised or have not been specifically assigned (Powell *et al.* 1998; Brandoni *et al.* 2012; Madozzo Jaén *et al.* 2013; Bonini 2014; Contreras *et al.* 2019; Ercoli *et al.* 2019; Montalvo *et al.* 2019).

One of the most abundant species of *Orthomyctera* in quantity of specimen remains, is *O. andina* from northwestern Argentina. *Orthomyctera andina* was initially described as *Dolichotis andina*,

from the Santa María valley, Catamarca Province (Araucana Formation, Late Miocene-Early Pliocene). This species was subsequently transferred to *Orthomyctera* (*Orocavia*) (within Caviinae) by Kraglievich (1932, 1934), although it was not explained the creation of the new subgenus.

Further works referred only to the name *Orthomyctera andina*, disregarding the subgenus *Orocavia* Kraglievich, 1932 (e.g. Quintana 1998; Ubilla & Rinderknecht 2003), again without any justification. This species is also reported from the Late Miocene-Pliocene of the Villavil-Quillay basin (Chiquimil Formation [Powell *et al.* 1998; Herbst *et al.* 2000; Madozzo Jaén 2017]); and recently, in Mendoza Province (Huayquerías and Tunuyán Formation [Pérez *et al.* 2019] [Fig. 1A]).

Since the last description of *Orthomyctera andina* (Kraglievich 1932, 1934) numerous fossils remain assigned to it or to *Orthomyctera* sp. and two specimens to *O. rigens* have been collected in northwestern Argentina (Marshall & Patterson 1981; Powell *et al.* 1998; Esteban *et al.* 2014; Madozzo Jaén 2017; Bonini *et al.* 2021). Although *O. andina* is very common in the fossil record, it is very poorly known at a systematic level.

The main goal of this work is to carry out the taxonomic revision of *Orthomyctera andina*. It includes the analysis of materials previously assigned to this species (some skulls and jaws with good preservation), and also those referred to *Orthomyctera rigens*, and *Orthomyctera* sp. coming from NWA.

TABLE 1. — Compared measurements (in mm) of skull and dentary of *Orthomyctera rigens* (Ameghino, 1888) and *Orocavia andina* n. comb. Abbreviations: **Bw**, brain-case width; **DI**, diastema length; **m2l**, dorsoventral length at the level of m2 (excluding molariforms); **MAEw**, external auditory meatus width; **MFI**, dorsoventral length at the level of the mentonian foramen; **p4l**, dorsoventral length at the level of p4 (excluding molariforms); **PI**, palate length (from the P4 level to the apex of the mesoptergoid fossa); **PwM3**, palate width at M3 level (measured in the anterior lobe without including teeth); **PwP4**, palate width at P4 level (measured in the anterior lobe without including teeth); **RI**, rostrum length (to nasal-frontal suture); **Rw**, rostrum width (between nasal-frontal-prmx suture); **Iw**, interorbital width; **Sl**, skull length (from nasal-frontal suture); **Stl**, skull total length (dorsal view). *, average measurements.

Mesures	<i>Orthomyctera rigens</i>	<i>Caviidae</i> indet.	<i>Orocavia andina</i> n. comb.											
	MACN-A 1661 (holotype)	MACN-A 1662	MACN-Pv 8350 (holotype)	FHNM-P 14464	FHNM-P 14370	MACN-Pv 8351	MACN-Pv 8399	MACN-Pv 8401	FHNM-P 1094	MACN-Pv 8300	MACN-Pv 8411	MACN-Pv 8412	MACN-Pv 8414	MACN-Pv 8349
Stl	*55.54	–	*53.73	–	*54.26	–	–	–	–	–	–	–	–	–
SI	–	–	36.06	–	*39.93	36.61	37.23	–	–	–	–	–	–	–
DI	*12.93	–	14.47	–	–	–	–	–	–	–	–	–	–	–
RI	–	–	19.68	–	*14.19	–	–	–	–	–	–	–	–	–
Rw	–	–	8.71	–	*11.58	9.71	9.75	–	–	–	–	–	–	–
Iw	–	–	11.57	–	*10.51	12.89	13.11	–	–	–	–	–	–	–
Bw	–	–	24.80	–	>25.21	25.88	–	24.73	–	–	–	–	–	–
PwP4	1.210	–	1.04	2.08	1.26	1.61	1.39	1.27	–	–	–	–	–	–
PwM3	–	–	6.08	7.77	7.82	7.68	8.96	6.07	–	–	–	–	–	–
MAEw	–	–	19.71	–	–	22.77	–	–	–	–	–	–	–	–
PI	11.00	–	8.17	9.03	9.85	8.64	9.92	8.12	–	–	–	–	–	–
MFI	–	4.51	4.16	–	–	–	–	–	4.50	–	–	3.61	4.49	4.61
p4l	–	8.25	–	–	–	–	–	–	6.85	4.63	–	5.60	7.23	–
m2l	–	–	7.24	–	–	–	–	–	7.63	7.07	–	7.38	7.91	–

A detailed description of *O. andina* and the specimen type of *O. rigens* are performed. The phylogenetic position of *O. andina* within Caviioidea is tested, and the systematic and biogeographic implications are discussed.

MATERIAL AND METHODS

ANATOMICAL NOMENCLATURE AND MEASUREMENTS

The cranial nomenclature follows that of Wahlert (1974), Popesco *et al.* (1992) and Cherem & Ferigolo (2012). The mandibular nomenclature follows that of Woods & Howland (1979) and Pérez (2010). The dental nomenclature follows Mones (1991), Vucetich *et al.* (2005) with modifications according to Cerdeño *et al.* (2019), and Pérez (2010). Measurements were taken with a 0.01 mm resolution digital caliper (Table 1-3).

PHYLOGENETIC ANALYSIS

To test the affinities of *Orocavia andina* n. comb. within Caviidae, a cladistic analysis using a modified version of the datasets of Urrea-Barreto *et al.* (2023). The combined matrix (Appendix 2) for this analysis resulted in 80 taxa, 164 morphological characters (Appendix 3), and 4178 characters from DNA sequences gathered from GenBank (Pérez & Pol 2012). The equally weighted parsimony analysis was conducted using TNT 1.1 (Goloboff & Catalano 2016). The search was performed with the implemented tree fusing and sectorial searches (new technology searches), and it was set to stop after reaching the minimum length 1000 times. We performed constrained searches with TNT to evaluate

the suboptimality of the groupings not found in the most parsimonious trees. In addition, the support values, bootstrap, and Jackknife were calculated with TNT.

ABBREVIATIONS

Institutional abbreviations

The fossil specimens described below are housed in the following paleontological collections:

FMNH-P	Paleontological Collection, Field Museum of Natural History, Chicago;
MACN-A	Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ameghino Collection, Buenos Aires;
MACN-Pv	Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Colección Paleontología de Vertebrados, Ciudad Autónoma de Buenos Aires;
MCH-P	Museo Arqueológico Provincial Condor Huasi Sección Paleontología, Catamarca;
PVL	Colección Paleontología de Vertebrados Lillo, San Miguel de Tucumán, Tucumán Province.

Anatomical abbreviations

APL	anteroposterior length;
Chin	mental process
HPE	external primary flexus;
HSE	external secondary flexus;
HFI/hse	hypoflexus/id;
hpi	primary internal flexid;
M1/m1	upper/lower first molar;
M2/m2	upper/lower second molar;
M3/m3	upper/lower third molar;
Mae	external auditory meatus
MPTs	most parsimonious trees;
nMpi	notch for <i>masseter medialis pars infraorbitalis</i> muscle;
NWA	Northwest Argentina;

TABLE 2. — Compared measurements (in mm) of the upper molariforms of *Orthomyctera rigens* (Ameghino, 1888) and *Orocavia andina* n. comb. Abbreviations: APL, anteroposterior length; LLA, anteroposterior length of anterior lobe; LPL, anteroposterior length of posterior lobe. Abbreviations: L, left; R, right.

		<i>Orthomyctera rigens</i>					<i>Orocavia andina</i> n. comb.								
Mesures	Side	MACN-A 1661 (holotype)	MACN 8350 (holotype)	FNMH-P 14370	FNMH-P 14464	MACN-Pv 8351	MACN -Pv 8399	MACN-Pv 8401	MACN-Pv 8402	MACN-Pv 8403	MACN-Pv 8404	MACN-Pv 8409	MCH-P 90	MCH-P 91	PVL 4892
APL dental series	R	–	12.44	13.73*	–	13.24	11.63	10.60	10.78	–	–	–	11.265	–	–
	L	14.54	–	13.84	11.99	12.93	12.33	10.68	–	14.052	11.65	–	–	–	11.86
APL P4	R	3.28	–	3.35*	–	3.13	2.65	2.22	2.18	3.24	–	–	2.33	–	–
	L	3.24	2.64	2.58*	2.64	2.81	2.83	2.11	2.20	3.12	1.97	–	–	–	2.86
LLA	R	1.59	1.39	1.75*	–	1.68	1.33	1.09	1.06	1.67	–	–	1.08	–	–
	L	1.58	1.20	1.25	1.22	1.51	1.53	1.00	1.20	1.51	–	–	–	–	1.51
LPL	R	1.42	–	1.38*	–	1.28	1.14	1.00	0.95*	1.33	–	–	1.07	–	–
	L	1.47	1.17	1.273	1.22	1.14	1.17	1.00	0.94*	1.38	–	–	–	–	1.27
APL M1	R	3.03	2.53	2.98	–	2.74	2.47	2.45	2.18	3.20	2.99	–	2.53	2.86	–
	L	3.02	2.64	–	2.70	2.71	2.57	2.38	2.28	3.01	2.61	2.23	–	–	2.49
LLA	R	1.55	1.12	–	–	1.37	1.25	1.19	1.08	1.55	1.48	–	1.19	1.34	–
	L	1.45	1.18	1.34	1.29	1.30	1.24	1.19	1.02	1.45	1.15	1.02	–	–	1.13
LPL	R	1.66	1.20	1.35	–	1.23	1.23	1.16	–	1.44	1.18	1.15	1.25	1.15	–
	L	1.54	1.19	1.47	1.25	1.37	1.19	1.05	1.14	1.33	1.24	1.17	–	–	1.18
APL M2	R	3.44	2.66	2.98	–	2.89	2.54	–	–	3.17	–	2.64	2.77	3.11	–
	L	3.40	2.77	2.93	2.81	2.86	2.74	2.60	2.20	3.11	2.85	2.62	–	–	2.77
LLA	R	1.65	1.21	1.39	–	1.36	1.28	–	1.22	1.49	–	1.25	1.31	1.29	–
	L	1.96	1.20	1.42	1.28	1.33	1.23	1.23	0.95*	1.51	1.33	1.26	–	–	1.30
LPL	R	–	1.26	1.33	–	1.40	1.24	–	–	1.51	–	1.25	1.33	1.55	–
	L	1.70	1.34	1.33	1.39	1.36	1.32	1.24	0.99*	1.49	1.08	1.18	–	–	1.27
APL M3	R	–	3.69	4.09	–	4.35	4.15	3.70	3.54	–	–	3.18*	3.70	–	–
	L	5.18	3.92	4.42	3.85	4.12	4.35	3.53	2.71*	4.48	4.22	3.38	–	–	3.70
LLA	R	–	1.10	1.20	–	1.28	1.35	1.21	1.07	–	–	1.14	–	–	–
	L	1.79	1.11	1.21	1.26	1.30	1.31	1.19	–	1.41	1.35	1.17	–	–	1.23
LPL	R	–	2.42	2.66*	–	2.95	2.77	2.35	2.35	–	–	1.91*	–	–	–
	L	3.30	2.54	3.04	2.37	2.66	2.95	2.31	–	2.89	2.80	2.03	–	–	2.24
angle of the M3	–	–	87.46°	–	–	107.47°	74.41°	123.25°	102.23°	108.34°	111.46°	–	–	–	–

pet epitympanic sinus;
 pmp mastoid portion of petrosal;
 rMx lateral ridge of infraorbital groove (ridge of maxillary *in* Madozzo Jaén *et al.* 2018);
 P4/p4 upper/lower fourth premolar.

TYPE MATERIAL. — **Lectotype.** Argentina. MACN-A 1661, incomplete skull, with left P4-M3 and right P4-M2.

TYPE LOCALITY. — Argentina, Buenos Aires Province, 60 km east from Bahía Blanca locality, Monte Hermoso locality, (Ameghino 1889) (Fig. 1A).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
 Infraorder HYSTRICOGNATHI Tullberg, 1899
 Superfamily CAVIOIDEA (Fischer de Waldheim, 1817)
 Family CAVIIDAE Fischer de Waldheim, 1817
 Sub-family CAVIINAE Fischer de Waldheim, 1817

Genus *Orthomyctera* Ameghino, 1889

TYPE SPECIES. — *Cavia rigens* (Ameghino, 1888) by original designation.

Orthomyctera rigens (Ameghino, 1888)
 (Figs 2; 3; Tables 1; 2)

Cavia rigens Ameghino, 1888: 12.

Orthomyctera Ameghino, 1889: 372.

GEOGRAPHICAL AND STRATIGRAPHIC PROVENANCE. — Argentina, Buenos Aires, Monte Hermoso locality, Monte Hermoso Formation, Early Pliocene (Deschamps *et al.* 2012; Tomassini *et al.* 2013; Prevosti *et al.* 2021).

DESCRIPTION AND COMPARISON

Cranium

The skull and only known specimen of *Orthomyctera rigens* is poorly preserved (Fig. 2A-D), missing most of the rostrum, the zygomatic process, and the braincase. The anteroposterior length of the skull is incomplete because it is broken, but larger than in *Microcavia australis*, and it seems smaller than of *Dolicavia* Ameghino, 1916 (Table 1; Appendices 4; 5).

Premaxilla. The premaxilla (Table 1) is poorly preserved in the ventral view (Fig. 2D), the incisive foramina seem triangular-shaped, as in *M. australis* and *D. minuscula*.

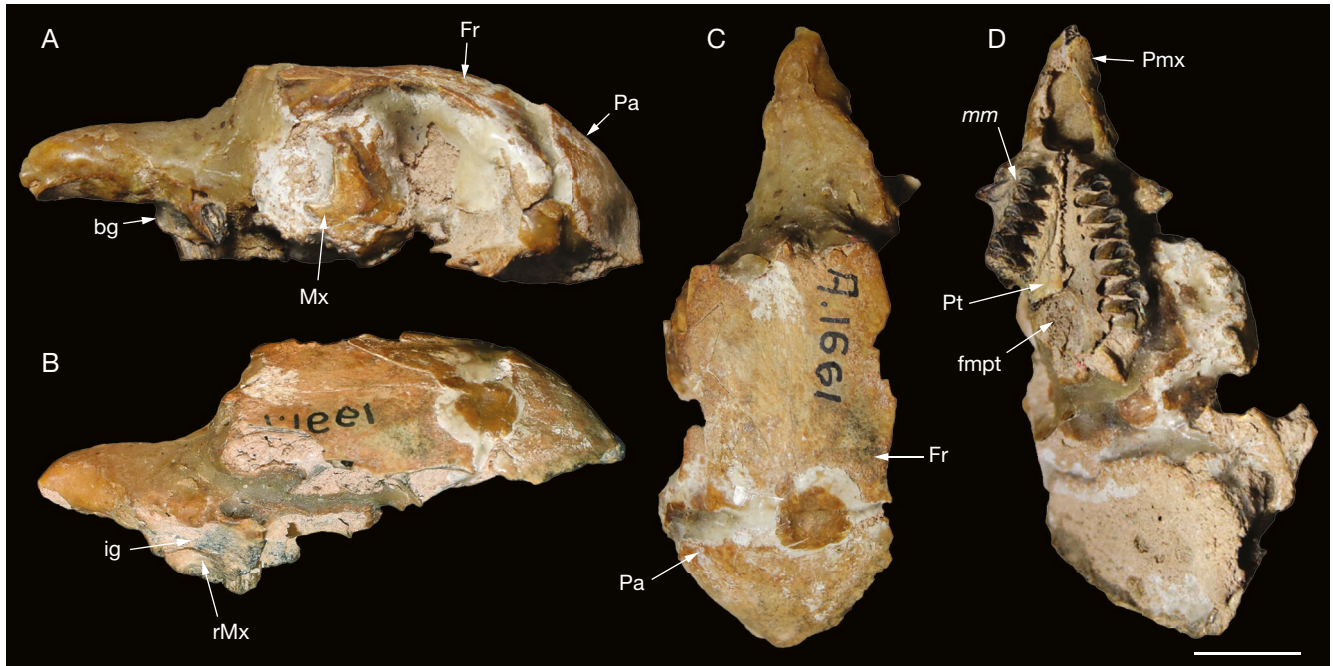


FIG. 2. — *Orthomyctera rigens* (Ameghino, 1888) MACN-A 1661 (holotype): **A**, lateral view; **B**, detail of lateral view; **C**, dorsal view; **D**, ventral view. Abbreviations: **bg**, bulge; **fmpt**, mesopterygoid fossa; **Fr**, frontal; **ig**, infraorbital groove; **mm**, notch for the tendon of medial part of masseter muscle; **Mx**, Maxilla; **Pa**, parietal; **Pmx**, premaxilla, **Pt**, palatine; **rMx**, lateral ridge of infraorbital groove. Scale bar: 10 mm.

Maxilla. The lateral ridge of the infraorbital groove (rMx; Fig. 2B) is similar than *Neocavia lozanoi* and some specimens of *Dolicavia* (e.g. MMP 536-S), while dorsoventrally is lower than in *M. australis* and other specimens of *Dolicavia* (e.g. MACN-Pv 10617). In lateral view, the posterior border of the diastema is vertical, and the suture between both maxillae forms a small bulge (Fig. 2A), as in *M. australis* and in *D. minuscula*. A small portion of the maxillary zygomatic process is preserved on the left side at the level of P4-M1. In ventral view, the notch for the tendon of the medial part of the masseter muscle in the origin of the zygomatic arch is an elliptical concavity with well-defined edges (Fig. 2D) as *D. minuscula*. The palate is terraced (maxillopalatal portion of the palate more dorsal than the lateral maxillary portion; Fig. 2D). This terracing is similar to the condition of “*Orthomyctera andina* and *N. lozanoi* and is shallower than in *Dolicavia* and *M. australis*.”

Frontal. In dorsal view, the anterior portion of the frontal are flat (Fig. 2B, C), at the level of the orbital region. Other characteristics (e.g. ledge or the dorsal hole or orbital constriction) described by Ameghino (1889) cannot be confirmed due to poor preservation of the remains.

Parietal. The parietal is displaced from its original position and broken in the posterior portion. The conserved portion is convex as in *M. australis*, *D. minuscula*, and *N. lozanoi*; the left temporal fossa seems as shallow as in other caviines (e.g. *M. australis*) the right portion is not preserved.

Palatine. The palatine bone occupies 25% of the anteroposterior length (APL) of the palate (Fig. 2D). The medial suture between both maxillary counterparts and between maxilla and palatine are not completely fused, indicating that it could be a still young individual. The anterior border of the mesopterygoid fossa is U-shaped, extending up to the anterior lobe of M3, as in other Caviinae (e.g. *Dolicavia*, *G. musteloides*, *M. australis*). However, it differs from *Cavia*, which presents a palatal process; it also differs from Dolichotinae in which the mesopterygoid fossa extends up to M2 and has a V-shape (see Ameghino 1889).

Cheek teeth

In the publication of 1889, Ameghino wrote: “*todas las muelas del lado derecho y las tres primeras del izquierdo*”, that means “all the molars on the right side and the first three on the left”. However, this is a simple confusion that needs to be clarified, since the specimen MACN-A 1661 preserves the left P4-M3 and right P4-M2 (Fig. 3A).

The cheek teeth are euhyposodont and double heart-shaped, with a constriction in the lingual apex of the lobes, and a transverse dentine crest in the middle of the occlusal surface of each lobe (Fig. 3A), as in other Caviinae and Dolichotinae. The hypoflexus is funnel-shaped with cement; enamel is interrupted at the labial wall, except along the external secondary flexus (HSE). The HSE of molariforms of *O. rigens* is similar to *Dolicavia* and shallower than in other caviines (e.g. *Cavia*, *Neocavia*) and, differs from the flexus of *Dolichotis* and “*O.*” *andina* in that these taxa have the flexus as a labial furrow opposite to the hypoflexus (Madozzo Jaén *et al.* 2021; but see Ameghino 1888, 1889; see below).

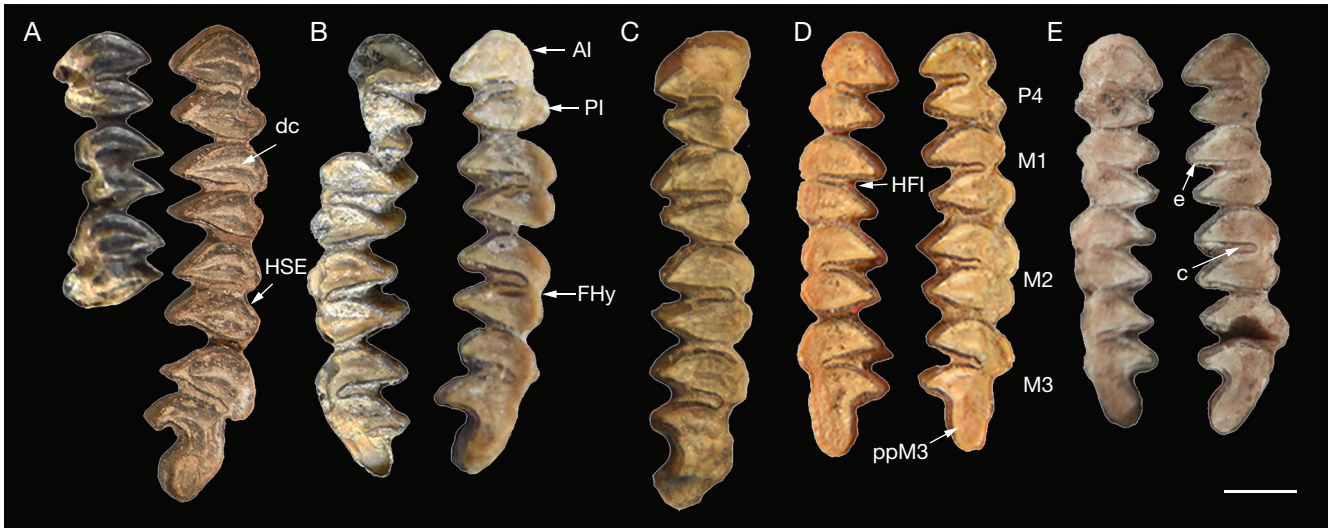


FIG. 3. — Upper dental series of *Orthomyctera rigens* (Ameghino, 1888) and *Orocavia andina* n. comb.: **A**, *O. rigens*, MACN-A 1661 (holotype); **B-E**, *Orocavia andina* n. comb.: **B**, MACN-Pv 8350 (holotype); **C**, MACN-Pv 8351; **D**, MACN-Pv 8399; **E**, MACN-Pv 8401. Abbreviations: **Al**, anterior lobe; **c**, cement; **dc**, dentine crest; **e**, enamel; **FHly**, furrow opposite to hypoflexus; **HFI**, hypoflexus; **HSE**, external secondary flexus; **M1**, upper first molar; **M2**, upper second molar; **M3**, upper third molar; **Pl**, posterior lobe; **ppM3**, posterior projection of M3; **P4**, upper fourth premolar. Scale bar: 2 mm.

The APL of M1 is the shortest of the cheek teeth, while the APL of P4 is shorter than that of M2, and M2 is shorter than that of M3 (Table 2). It differs from *M. australis* in which the APL of M1 is similar to that of M2. The M3 has a developed posterior projection of the posterior lobe, shorter than in *Neocavia*, *Dolicavia*, and “*O.*” *andina*; and differs from *M. australis*, in which the posterior projection is an incipient lobe.

REMARKS

The type species of Orthomyctera

Orthomyctera rigens was designated the type species of the genus *Orthomyctera* by Kraglievich (1930: 71). Posteriorly, Pascual (1966) considered *Orthomyctera lata* as the type species of the genus, without any kind of justification. According to the nomenclature code (International Code of Zoological Nomenclature: art. 69.1) if no type species was designated in the original publication, the first designation is valid.

The type material of Orthomyctera rigens

Ameghino (1888) established *Cavia rigens* based on characters of the upper and lower teeth without specifying on which specimens the determination was made. Posteriorly, Ameghino (1889) erected the genus *Orthomyctera*, which includes the species *Cavia rigens*, among others (*Orthomyctera vaga*, *O. lata*, and *Dolichotis lacunosa* Ameghino, 1888). In that work he figured a skull (MACN-A 1661 see Lam. XI, 6-7), and a jaw (MACN-A 1662) as *Orthomyctera rigens*. Subsequently, both specimens have been considered the type material of this species (e.g. Croft *et al.* 2011). From the morphological analysis here, it is inferred that the skull and the mandible do not correspond to the same individual and even correspond to different taxonomic entities because of the follow morphological differences: 1) lower m1 of MACN-A 1662 smaller than the upper molars of MACN-A 1661

(see Table 2) lower m1 of MACN-A 1662 with an opposite furrow to the hypoflexid, contrasting with that condition of the upper molars of MACN-A 1661 in which the HSE is present. Since Ameghino (1889) focused the description of this species on the skull MACN-A 1661, we designated this specimen as the lectotype of *O. rigens*.

Referred material to Orthomyctera rigens

Appendices 6-8 provides a revision of the fossil specimens previously referred to as *O. rigens* in the literature. However, here is necessary to clarify that the mention of *O. rigens* in Pardiñas *et al.* (2017) (that was taken in turn of Frenguelli (1928)), from the Quequén Salado River, “Irenense” Fauna (Buenos Aires Province), could not be corroborated because the authors did not provide details of the material or the corresponding collection number.

Orocavia Kraglievich, 1932

Orthomyctera (*Orocavia*) Kraglievich, 1932: 25.

TYPE SPECIES. — *Dolichotis andina* Rovereto, 1914 by original designation.

GENERIC DIAGNOSIS. — As for the type and only known species.

Orocavia andina (Rovereto, 1914) n. comb. (Figs 3-7; Tables 1-3)

Dolichotis andina Rovereto, 1914: 58, fig. 25.

Orthomyctera (*Orocavia*) *andina* Kraglievich, 1932: 163.

TYPE MATERIAL. — **Holotype**, **Argentina**, MACN-Pv 8350, skull with articulated atlas, complete upper dental series, and left mandibular fragment with i, p4-m3.

TABLE 3. — Compared measurements (in mm) of the lower molariforms *Orocavia andina* n. comb. and Caviidae indet. Abbreviations: **APL**, anteroposterior length; **LLA**, anteroposterior length of anterior lobe; **LPL**, anteroposterior length of posterior lobe.

Measures	Side	<i>Orocavia andina</i> n. comb.											Caviidae indet.
		MACN 8350 (holotype)	FMNH-P 1094	MACN-Pv 8300	MACN-Pv 8349	MACN-Pv 8411	MACN-Pv 8412	MACN -Pv8414	MCH-P 94	MCH-P 360	MCH-P 361	PVL 3293	MACN -A 1662
APL dental series	R	-	-	11.01	-	-	10.96	-	-	-	-	-	-
	L	-	-	-	-	-	-	13.32	-	-	-	11.84	-
LAP p4	R	-	-	2.16	-	-	2.29	-	-	-	-	-	-
	L	-	-	-	-	-	-	2.70	2.51*	-	-	2.61	-
LLA	R	-	-	1.08	-	-	1.10	-	-	-	-	-	-
	L	-	-	-	-	-	-	1.36	-	-	-	1.32	-
LPL	R	-	-	1.06	-	-	1.00	-	-	-	-	-	-
	L	-	1.21	-	1.34	-	-	1.31	-	-	-	1.17	-
APL m1	R	-	-	2.70	-	3.28	2.63	-	-	-	-	-	-
	L	2.79	3.10	-	3.03	-	-	3.04	2.61	2.62	3.26	2.88	2.73
LLA	R	-	-	1.10	-	1.61	1.17	-	-	-	-	-	-
	L	1.26	1.51	-	1.22	-	-	1.43	1.05	1.17	1.44	1.33	1.22
LPL	R	-	-	1.34	-	1.66	1.26	-	-	-	-	-	-
	L	1.42	1.48	-	1.67	-	-	1.53	1.35	1.33	1.63	1.40	1.36
APL m2	R	-	-	2.85	-	3.43	2.94	-	-	2.54	-	-	-
	L	3.14	3.13	-	3.54	-	-	3.14	2.97	-	3.62	2.98	-
LLA	R	-	-	1.25	-	1.59	1.41	-	-	-	-	-	-
	L	1.39	1.50	-	1.69	-	-	1.57	1.29	1.11	1.62	1.48	-
LPL	R	-	-	1.39	-	1.62	1.33	-	-	-	-	-	-
	L	1.57	1.53	-	1.72	-	-	1.51	1.36	1.23	1.75	1.42	-
APL m3	R	-	-	3.10	-	3.73	3.10	-	-	-	-	-	-
	L	3.63	-	-	3.99	-	-	3.52	-	-	-	3.25	-
LLA	R	-	-	1.28	-	1.64	1.34	-	-	-	-	-	-
	L	1.53	-	-	1.69	-	-	1.41	-	-	-	1.50	-
LPL	R	-	-	1.55	-	1.94	1.48	-	-	-	-	-	-
	L	1.94	-	-	2.14	-	-	1.82	-	-	-	1.63	-

REFERRED MATERIAL. — MACN-Pv 8300, right mandible fragment with p4-m3; MACN-Pv 8347, palatal fragment with right P4-M2 and fragment of M3 and left P4-M1; MACN-Pv 8349, left mandible fragment with p4-m2; MACN-Pv 8351, fragment of skull with complete dental series; MACN-Pv 8399, fragment of skull with complete dental series; MACN-Pv 8401, fragment of skull with complete dental series; MACN-Pv 8402, palatal fragment with complete dental series; MACN-Pv 8403, palatal fragment with left P4-M3 and right P4-M2; MACN-Pv 8404, palatal fragment with left M1-M3 and right P4-M1; MACN-Pv 8409, palatal fragment with left M1-M3; MACN-Pv 8411, right mandible fragment with m1-m3; MACN-Pv 8412, right mandible fragment with p4-m3; MACN-Pv 8414, left mandible fragment with p4-m3; PVL 3293, left mandible fragment with p4-m3; FMNH P 14464, fragment of skull with complete dental series; FMNH PM 1094, fragment right mandible p4-m2; FMNH P 14370, fragment of skull with complete dental series and atlas; PVL 4892, fragment of skull with complete dental series; MCH-P 90, fragment of skull with right complete dental series and left P4-M2 and anterior lobe of M3; MCH-P 91, fragment of skull with left M1 and right M1-M2; MCH-P 94, left mandible fragment with p4-m2; MCH-P 345 right mandible fragment with p4-m2; MCH-P 346 left mandible fragment with m1-m2; MCH-P 360 left mandible fragment with m1-m2; MCH-P 361 left mandible fragment with m1-m2; MCH-P 366 maxilla fragment with right P4-M2 and fragment of M3 and left P4-M1 and left mandible fragment with m1; MCH-P 367 left mandible fragment with p4. The provenance of each referred material is detailed in Appendix 9.

MODIFIED DIAGNOSIS. — Caviinae diagnosed by the following unique combination of characters (apomorphies marked with an asterisk): cheek teeth euhyposodont, bilobed, and each heart-shaped; constriction in the apex of each lobe present; hypoflexus/id funnel-shaped; dentine crest in the middle of occlusal surface in each lobe; cement in the hypoflexus/id present; *furrow opposite to hypoflexus/ids present as in Dolichotinae, differing from the other Caviinae (*Galea*, *Cavia*, *Microcavia*, *Palaeocavia*, *Neocavia*, *Dolicavia*, and *Orthomyctera*); enamel interrupted on the labial side in upper cheek teeth, and on the medial side in lower ones, except on the furrow opposite to hypoflexus/id; M1 shorter and M3 longer than the other cheek teeth as in *O. rigens*; posterior projection of M3 anteroposteriorly long, shorter than in *Dolicavia*; anterior projection of p4 anteriorly well-developed differing from *Palaeocavia* and *Cavia*. Lateral ridge of the infraorbital groove absent; posterior portion of diastema oblique and shorter than in *Cavia aperea* Erxleben, 1777 and *Galea leucoblephara*, differing from *O. rigens*, *Microcavia* and *Dolicavia*. Terraced palate shallower than in *Neocavia*, *O. rigens*, *Dolicavia*, and *M. australis*. Tympanic bullae with respect to skull length are large as *Dolicavia*, *M. australis*, and *Neocavia*, but smaller than in *N. lozanoi*. External auditory meatus more ventral respect to the occlusal dental series, as in *Dolicavia*, *M. australis*, and *N. lozanoi*. Notch for insertion of the tendon of the masseter medialis pars infraorbitalis muscle is deeper depth than dorsal fossa of horizontal crest.

TYPE LOCALITY. — Argentina, Andalhuala locality, Catamarca Province, Santa María Valley. Late Miocene-early Pliocene ("Araucanian").

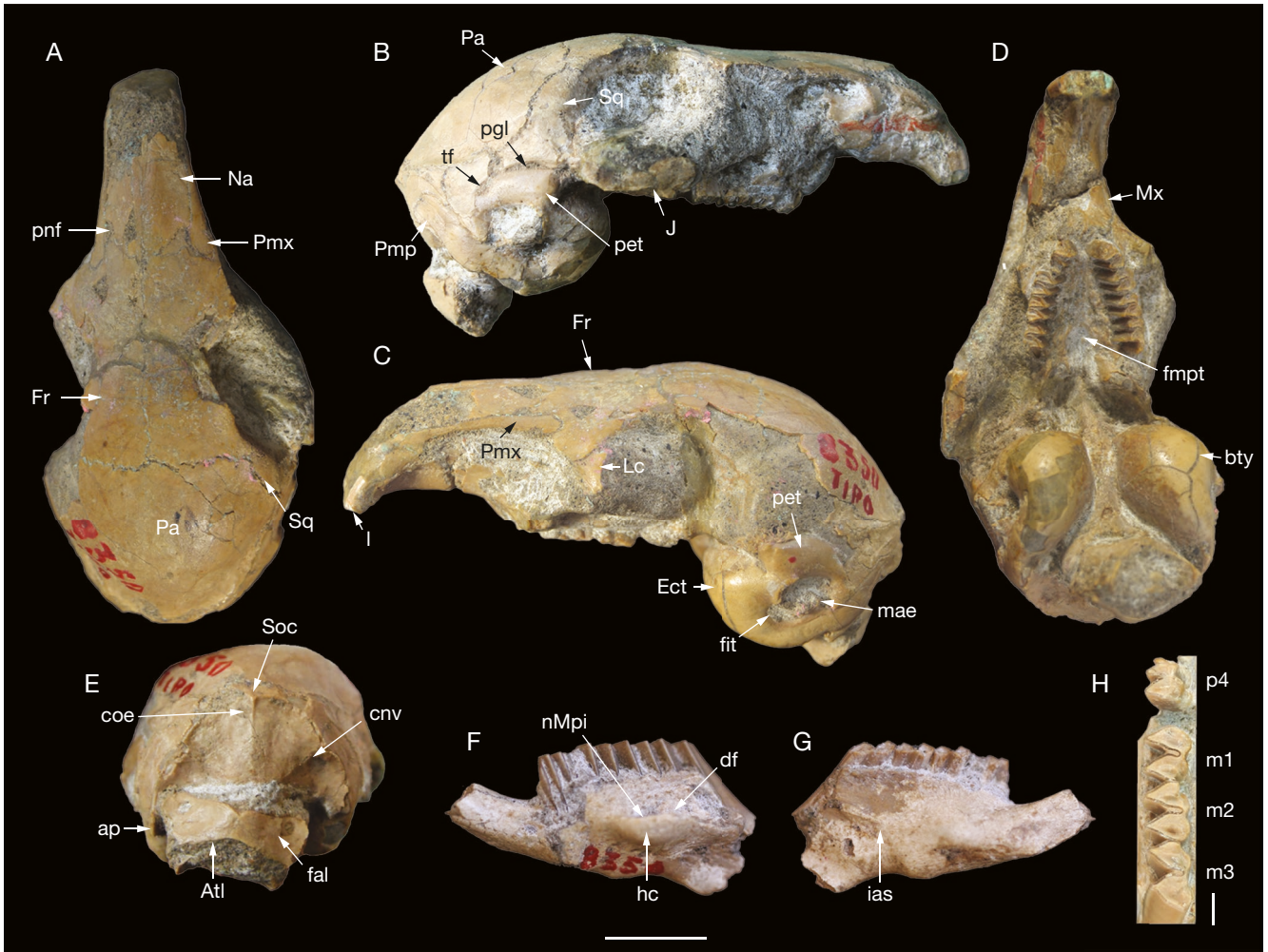


FIG. 4. — Skull and mandible of *Orocavia andina* n. comb. MACN-Pv 8350 (holotype): **A-E**, skull; **F-H**, mandible. **A**, dorsal view; **B**, **C**, lateral view; **D**, ventral view; **E**, posterior view; **F**, labial view; **G**, medial view; **H**, lower dental series. Abbreviations: **ap**, paraoccipital apophysis; **Atl**, atlas; **bty**, tympanic bulla; **cnv**, ventral nuchal crest; **coe**, occipital external crest; **df**, dorsal fossa; **Ect**, ectotympanic; **fal**, alar foramen of the atlas; **fit**, infratympanic fenestra; **fmpt**, mesoptergoid fossa; **Fr**, frontal; **hc**, horizontal crest; **I**, incisive; **ias**, incisive alveolar sheath; **Lc**, lacrimal; **mae**, external auditory meatus; **Mx**, maxillary; **m1**, first molar; **m2**, second molar; **m3**, third molar; **Na**, nasal; **nMpi**, *masseter medialis* pars infraorbitalis muscle; **Pa**, parietal; **pet**, petrous or epitympanic sinus; **Pmp**, mastoid portion of petrous; **Pmx**, premaxilla; **pnf**, nasal process of frontal; **Soc**, supraoccipital; **Sq**, squamosal; **tf**, foramen for ramus temporalis. Scale bars: A-G, 10 mm; H, 2 mm.

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCE. — Santa María Valley, Catamarca Province: in Andalhuala and “Al sureste de ex Chiquimil”, [Southeast from ex Chiquimil] Entre Ríos localities, without precise stratigraphic data (Late Miocene-Early Pliocene, and “Araucanense”; Marshall & Patterson 1981); Entre Ríos (ex Chiquimil) locality, Andalhuala Formation, in levels XVIIIa and XVIIIb; Loma Rica locality in level XVII (Late Miocene, Marshall & Patterson 1981). Villavil-Quillay basin, Catamarca Province in Villavil locality, Chiquimil Formation, El Jarillal Member, (Late Miocene, Powell *et al.* 1998; Esteban *et al.* 2014); Western Slope of Cerro Pampa (San Fernando Sur locality), Andalhuala Formation (Late Miocene-Early Pliocene; Bonini *et al.* 2021).

DESCRIPTION AND COMPARISON

Cranium

The anteroposterior length of *Orocavia andina* n. comb. is approximately similar to that of *Orthomyctera rigens* (Fig. 2), larger than in *M. australis* and smaller than *Dolicavia* (Appendices 4; 5). The APL of the rostrum in relation to APL of the skull is larger than in *M. australis* (approxima-

tively 7.5% longer) and *Dolicavia* (approx. 4% longer). The width of the braincase is smaller than in *Dolicavia* (approximately 20% less) and somewhat larger than in *M. australis* and *Neocavia lozanoi* (approximately 10% longer) Table 1; Appendices 4; 5).

Nasal. The nasals are better preserved in the holotype, but the anterior portion is missing (Fig. 4A). In dorsal view, this bone is relatively wider than in *M. australis*, and narrower than that of *Dolicavia*. The nasofrontal suture is anteriorly concave (Fig. 4A-C) as in *Dolicavia* or slightly concave (Fig. 5A) as in *M. australis*. In lateral view, the nasal is dorsally convex in the medial portion (Fig. 6A, B; Appendices 4; 5).

Premaxilla. In dorsal view (Figs 4A; 5A), the dorsal process of the premaxilla is narrow along the contact with the nasal, widening posteriorly. In lateral view, the alveoli of the upper incisors are broken in all the specimens that preserve this por-

tion (Figs 4B, C; 6A). The premaxillary portion of the rostral masseteric fossa is shallow as in *Dolicavia*. The premaxilla-maxilla suture in the lateral wall of the rostrum is unclear in the holotype because this region is deteriorated (Fig. 4B, C).

In ventral view, the suture is located on the posterior half portion of the diastema, as in *Dolicavia* and *M. australis*. Approximately 75% of the margins of the incisive foramen are formed by the premaxilla. This foramen (Figs 4D; 5D) is similar in size and shape to those of *Dolicavia*, *Microcavia* (Appendices 4; 5).

Maxilla. In lateral view, the maxillary portion of the rostral masseteric fossa is in the middle of the rostrum (Figs 4B, C; 6A), this fossa is less developed than in *M. australis*. At the P4 level, a lateral vacuity of the nasolacrimal duct (nasolacrimal foramen *sensu* Ubilla *et al.* 1999; maxillary lacrimal canal *sensu* Cherem & Ferigolo 2012) is present (Fig. 6C). This vacuity is present in Caviinae and Hydrochoerinae (e.g. *Hydrochoerus*), but absent in Dolichotinae (e.g. *Dolichotis*). In the posterior portion of the diastema, the maxilla is obliquely oriented respect to alveolar line (Figs 4B, C; 6G), and this condition differs from *M. australis*, *Dolicavia*, and *N. lozanoi* (see above). The lateral ridge of the infraorbital groove is absent. It differs from *O. rigens*, *N. lozanoi*, *Dolicavia*, and *M. australis*, in which it is present. The sphenopalatine foramen is between groove infraorbital and alveolar protuberances of P4 and M1 (Cherem & Ferigolo 2012; Fig. 6D, E). Dorsally to the alveolar protuberance of M2 (Fig. 6C-E), the lacrimomaxillary fissure (*sensu* Cherem & Ferigolo 2012) extends posteriorly. The maxillary process of the zygomatic arch originates at the level of P4, anteriorly is elongated and dorsoventrally low (Fig. 6A-F). In ventral view, the origin of the zygomatic arch presents a shallow notch of the tendon of the medial part of masseter muscle (Fig. 5D). This notch is an elliptical concavity with well-defined edges in *O. rigens* (Fig. 2D) and *Dolicavia* (Appendices 4; 5). The palate is triangular and terraced; the central portion is more dorsal than the alveolar border but this difference is less marked than *Neocavia*, *O. rigens*, *Dolicavia*, and *M. australis* (Figs 2D; 4D; Appendices 4; 5).

Palatine. The notch for the minor palatine nerve and vessels (*sensu* Wible *et al.* 2005) is medial to the posterior projection of M3 (Fig. 5C). Some specimens (Fig. 5D, F) have preserved a palatine crest on the middle line that extends up to the M1-M2 level. The anterior apex of the mesopterygoid fossa is U-shaped and anteriorly extended up to the level of the anterior lobe of M3 (Figs 4D; 5D), as in *M. australis*. The anterior margin of sphenopalatine vacuity (*sensu* Cherem & Ferigolo 2012); is limited by palatine and medially by the presphenoid; the posterior margin is not preserved (Fig. 5C).

Frontal. In dorsal view, the nasal process of the frontal (*sensu* Cherem & Ferigolo 2012; i.e., the anterior projection of the frontal, between the nasal and the premaxilla) is triangular-shaped and conspicuously extended anteriorly in the holotype (Fig. 4A); whereas in MACN-Pv 8351 (Fig. 5A) is not anteriorly projected. The interorbital width

is similar to that of *M. australis* and smaller than in *Dolicavia* (Appendices 4; 5). The contacts with parietals are straight as *M. australis*, *D. minuscula*.

Parietal. The parietal is dorsolaterally convex (Fig. 4A), as in *O. rigens* *Dolicavia*, *M. australis* (Appendices 4; 5), and *N. lozanoi*, but differs from *D. patagonum* which have anterior portion slightly convex (see Rovereto 1914). The temporal fossae are shallow and do not developed a sagittal crest; there is a differentiated plane area named the “interposed flat zone” by Quintana (1998) Fig. 4A), as in *Dolicavia* and *M. australis*. The specimens of *Or. andina* n. comb. consists of adult individuals in which the interparietal is not recognized; this condition differs from *Dolicavia* in which the interparietal is not fused with the parietal in adult specimens. This region is deformed in other skulls of *Or. andina* (e.g. MACN-Pv 8351, MACN-Pv 8401; Figs 5A; 6E).

Lacrimal. In lateral view, the anterodorsal portion of the zygomatic arch of the holotype (Fig. 4C) has a fragmentary bone interpreted here as a portion of the lacrimal with the moderately developed facial process. In other specimens, the lacrimal is very fragmentary (Fig. 6E).

Jugal. In lateral view, in the holotype (Fig. 4B) only preserved the jugal-squamosal suture, which is posterior to M3. The maxilla-jugal suture of FMNH-P 14370 (Fig. 6A) is indistinct for bad preservation. In contrast, the contact with the squamosal is anteriorly convex and ventrally straight. The maximum height (2.5 mm) of jugal is at the level of the M3. The insertion of the deep part of the masseter muscle is ventral in the anterior portion and lateroventral in the posterior portion (Fig. 5D), as in *Dolicavia*. This condition differs from that of *M. australis* in which in the anterior portion the insertion is lateral (Appendices 4; 5).

Squamosal. The exposed dorsal surface of the squamosal is larger than in *Dolicavia* and *M. australis* (Figs 4A; 5A). In lateral view, the zygomatic process of the squamosal is narrow (Figs 4B; 6A). The caudal process of the squamosal is antero-posteriorly straight, and the posterior portion is ventrally projected penetrating between the bulla and the occipital complex (Figs 4B; 6D, E). It differs from *Dolicavia* and *M. australis* in that the posterior projection is less ventrally extended. We interpreted as postglenoid (or retroarticular) foramen, an oval-shaped fissure between the caudal process of the squamosal and epitympanic region of the tympanic bulla (Fig. 4B, C). A posterior and smaller circular-shaped fissure could correspond to the foramen for ramus temporalis (Wahlert 1974; Wible *et al.* 2005; Wible 2011).

Tympanic bulla. In lateral view, the tympanic bullae are prominent (Figs 4B, C; 6A, D-G), proportionally smaller than in *N. lozanoi* but larger than in the other caviies (Table 1; and see Madozzo Jaén *et al.* 2018; and reference there). Dorsal and posterior to the external auditory meatus, the epitympanic sinus (pet) is laterally inflated (Fig. 4B, C), differing from

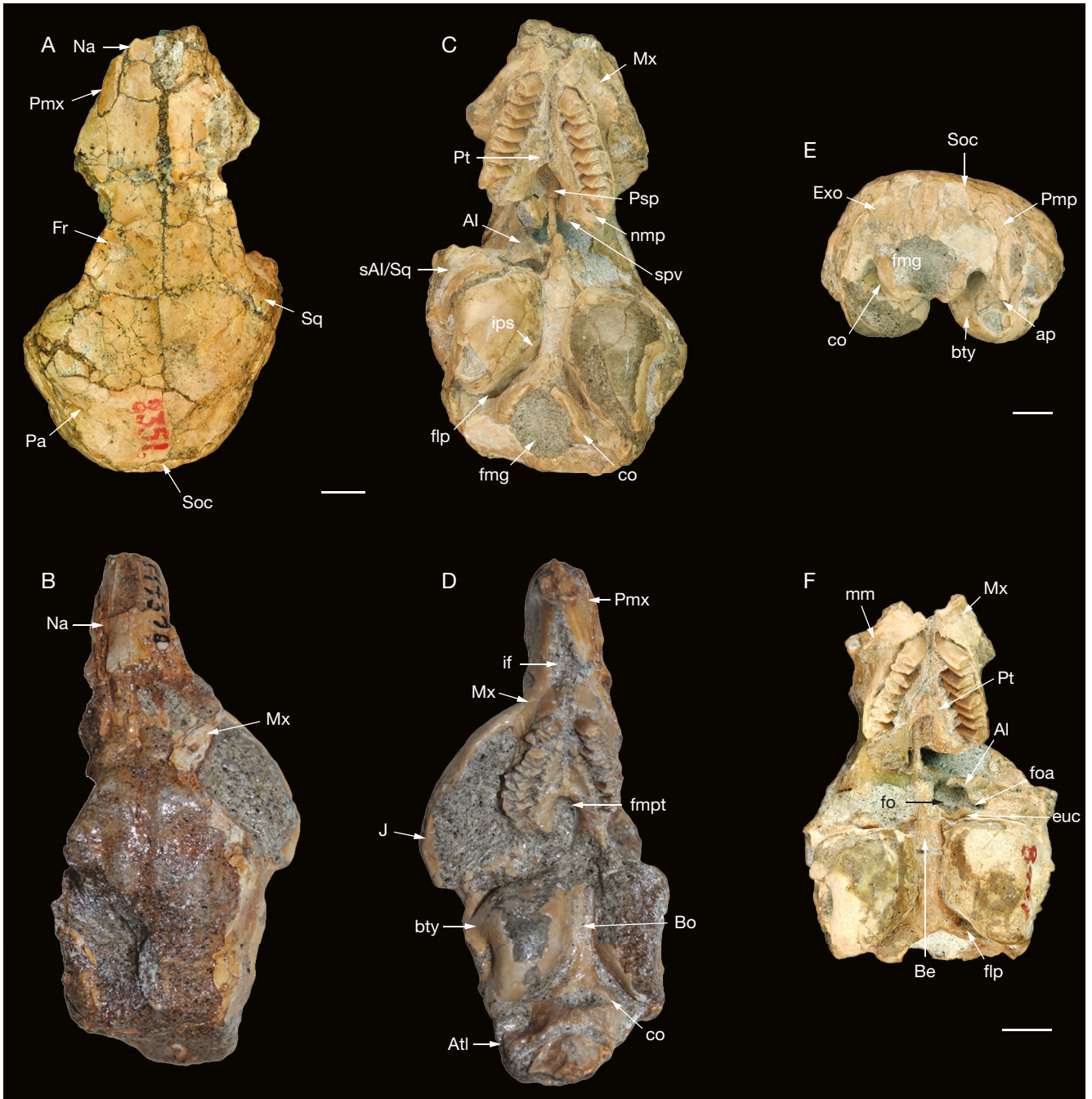


FIG. 5. — Skull fragments of specimens referred to *Orocavia andina* n. comb.: **A, C, E**, MACN-Pv 8351; **B, D**, FMNH-P 14370; **F**, MACN-Pv 8401: **A, B**, dorsal view; **C, D, F**, ventral view; **E**, posterior view. Abbreviations: **Al**, alisphenoid; **ap**, paraoccipital apophysis; **Atl**, atlas; **Be**, basisphenoid; **Bo**, basioccipital; **bty**, tympanic bulla; **co**, occipital condyle; **euc**, eustachian canal; **Exo**, exoccipital; **flp**, posterior lacerated foramen; **fmg**, foramen magnum; **fmpt**, mesopterigoid fossa; **fo**, ovale foramen ovale; **foa**, foramen accessory ovale; **Fr**, frontal; **if**, incisive foramen; **ips**, inferior petrosal sinus; **J**, jugal; **mm**, notch for the tendon of medial part of masseter muscle; **Mx**, maxilla; **Na**, nasal; **nmp**, notch for the minor palatine nerve and vessels; **Pa**, parietal; **Pmp**, mastoid portion of petrous; **Pmx**, premaxilla; **Psp**, presphenoid; **Pt**, palatine; **sAl-Sq**, alisphenoid-squamosal suture; **Soc**, supraoccipital; **spv**, sphenopalatine vacuity; **Sq**, squamosal. Scale bar: 5 mm.

Dolicavia and *M. australis* in which the pet is less bloated. The mastoid portion of the petrosal (pmp) is flat in the dorsal half and convex in the ventral half, whereas in *Dolicavia* and *M. australis*, the pmp is convex in all extensions. The external auditory meatus (mae) is broad and rounded, central in the tympanic bulla; it is located below the level of the dental series (Figs 4B, C; 6A, D, E) as in *Dolicavia*, *M. australis*, and *N. lozanoi*. In some specimens, a rim surrounds the meatus,

it is incomplete on the dorsal edge (Figs 4B, C; 6D-G). The circular infratympanic fenestra is small and ventral to mae, in MACN 8401 it is isolated to mae, the other specimens are connected, possibly due to poor preservation and the stylomastoid foramen is posterior to mae (Fig. 6F, G). It is remarkable the marked skull flexion (the angle that the palate forms with the basicranium, and the foramen magnum opening posteroventrally), as in *Microcavia*, *Dolicavia* and *Neocavia*.

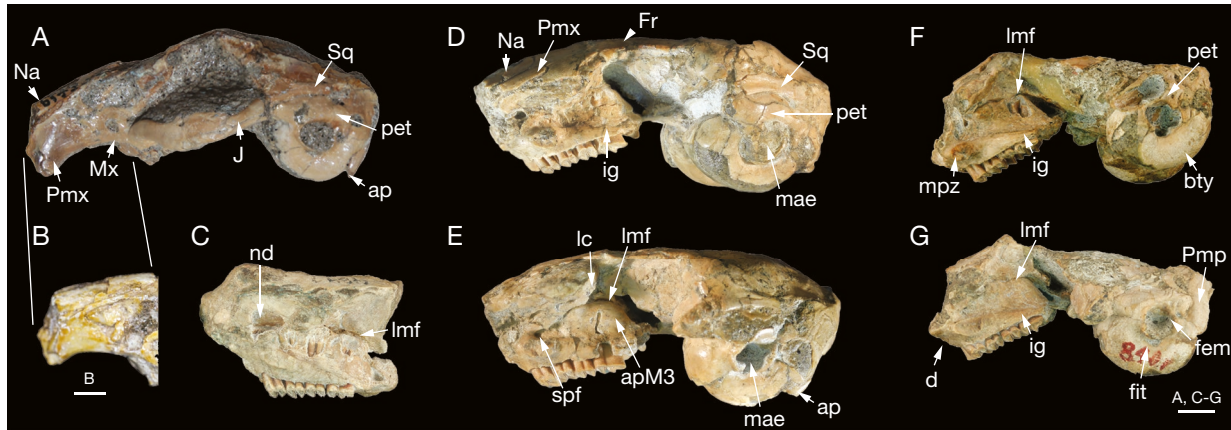


FIG. 6. — Skull fragments of specimens referred to *Orocavia andina* n. comb in lateral view: **A, B**, FMNH-P14370; **C**, PVL 4298; **D, E**, MACN-Pv 8351; **F, G**, MACN-Pv 8401. Abbreviations: **ap**, paraoccipital apophysis; **apM3**, alveolar protuberance of M3; **bty**, tympanic bullae; **d**, posterior border of diastema; **fem**, stylomastoid foramen; **fit**, infratympanic fenestra; **Fr**, frontal; **ig**, infraorbital groove; **J**, jugal; **lc**, lacrimal; **lmf**, lacrimomaxillary fissure; **mae**, external auditory meatus; **mpz**, maxillary process of the zygomatic arch; **Mx**, maxilla; **Na**, nasal; **nd**, nasolacrimal duct; **pet**, epitympanic sinus; **Pmp**, mastoid of petrous; **Pmx**, premaxilla; **spf**, shenopalatine foramen; **Sq**, squamosal. Scale bars: 5 mm.

In ventral view (Figs 4D; 5C-E), the major axis of the tympanic bulla is approximately 45% of the APL of the skull (Madozzo Jaén *et al.* 2018; table 1). This proportion is smaller than in *N. lozanoi* (50%) and larger than in *M. australis* [40%] and *C. aperea* [28,5%] (see Madozzo Jaén *et al.* 2018). The posterior lacerate foramen (*sensu* Cherem & Ferigolo 2012) is a fissure between the tympanic bullae and the occipital condyle (Fig. 5C-F). Other structures, such as the apertures for the passage of vessels and nerves, are concealed by sediment.

Presphenoid and basisphenoid. In both bones, the anterior half is narrower than the posterior portion. The basisphenoid has a ridge in the midline at the anterior two-thirds of its length (Fig. 5C-E).

Alisphenoids. In ventral view, the alisphenoid (Fig. 5C, F) is thicker than in *M. australis* and *Dolicavia*, in which it is a thin lamina (Appendices 4; 5; see Quintana 1997). The foramen ovale opens in the alisphenoid, the medial and ventral margins of this bone are concave and form the margin of the foramen, the medial margin of the foramen ovale is not preserved. The accessory ovale foramen is smaller and more lateral than the foramen ovale (Fig. 5F; Wahlert 1974). Posteriorly, between the alisphenoid and tympanic bullae, a small foramen (Fig. 5F) could correspond to the exit of the eustachian canal (Wahlert 1974). Cherem & Ferigolo (2012) named, in *Cavia*, this foramen as carotid foramen, but this one should be located adjacent to the central stem, medial to the foramen ovale, and directly lateral to the position of the hypophysis (De Beer 1937).

Occipital complex. In ventral view, the basioccipital is rectangular, widening posteriorly, following the medial outline of the tympanic bulla (Figs 4D; 5C, D, F). The aperture for the inferior petrosal sinus (Fig. 5C) is between basioccipital and the tympanic bulla, which does not present a marked notch for the foramen, as in *Dolicavia* (e.g. PVL 3745; PVL 3765,

Appendices 4; 5). The paraoccipital apophysis is broken in all specimens, but in lateral view, it extends at least below the level of the external auditory meatus (Figs 4B, C, E; 5E).

In posterior view, the holotype (other specimens are deformed; e.g. Fig. 5E) has a rounded outline dorsally and laterally with the foramen magnum opening posteroventrally somewhat smaller than in *Dolicavia*. The external occipital crest of the exoccipital is a low ridge (Figs 4E; 5E); it is similar to *M. australis* but differs from *Dolicavia*, in which it has a well-defined ridge (Appendices 4; 5). The ventral nuchal crest is slightly developed (Figs 4E; 5E). The occipital articulates with the atlas in the holotype and FMNH-P 14370 (Figs 4E; 5D see below). In dorsal view, a small portion of the supraoccipital (Figs 4A; 5A) is exposed as in the other caviids. The occipital condyles have a medial-ventral orientation-laterodorsal orientation, with a thickening in the central part.

Mandible

The dentary is more robust than in *M. australis* and *N. lozanoi*, and smaller than in *Dolicavia* (Quintana 1996, 1997; Madozzo Jaén *et al.* 2018). In lateral view (Figs 4F; 7B, C), the orientation of the anterior portion of the diastema is oblique with respect to the dental series. The mental foramen is anterior to p4, at the dorsoventral middle point of the mandible, more dorsal than in *M. australis* and *Dolicavia*. The mental process (chin) is moderately developed as in *Microcavia*. The lateral crest is almost straight, and the notch for the insertion of the tendon of the *masseter medialis pars infraorbitalis* muscle (nMpi) is located between m1-m2, similar to *Dolicavia*, *M. australis*, and *N. lozanoi*. The horizontal crest is well-developed, forming a laterally projected shelf that connects to the nMpi as in the other caviids (Fig. 7B, C; see Rovereto 1914). The depth of the dorsal fossa for masseter medialis insertion is less than that of the nMpi. (Fig. 7H). In the ventral margin, the alveolar protuberance of m1 is well-developed (Figs 4F; 7C).

In medial view, the incisor extends posteriorly to the level of the posterior lobe of m1, differing from *Dolichotis* in which the incisor is extended more posteriorly (Kraglievich

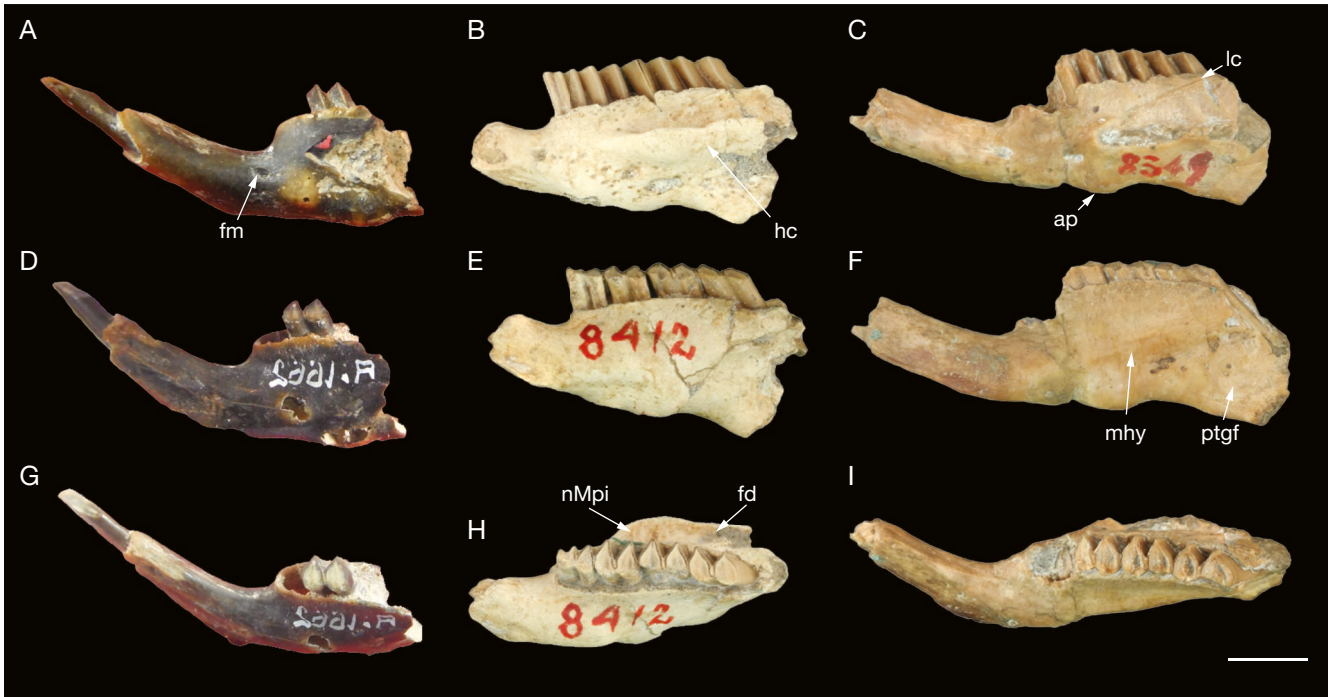


FIG. 7. — Mandible of Caviidae indet. (MACN-A 1662 [A, D, G]) and *Orocavia andina* n. comb. (MACN-Pv 8412 [B, E, H]; MACN-Pv 8349 [C, F, I]): A-C, labial view; D-F, medial view; G-I, occlusal view. Abbreviations: ap, alveolar protuberance; fd, dorsal fossa; fm, mental foramen; hc, horizontal crest; lc, lateral crest; mhy, mylohyoid crest; nMpi, notch for the insertion of the tendon of the *masseter medialis pars infraorbitalis* muscle; ptgf, pterygoid fossa. Scale bar: 5 mm.

1932). The mylohyoid crest is present as in *Dolicavia* and the pterygoid fossa is shallow, only preserved in MACN 8349 (Fig. 7E, F). The mandibular foramen is at the level of m3. The coronoid and angular process and the condyle are not preserved in any specimens.

Cheek teeth

The cheek teeth are anteriorly convergent into the palate, these are euhyposodont and double heart-shaped, with a constriction in the apex of the lobes, and with a transverse dentine crest in the middle of the occlusal surface of each lobe, as in other Caviinae and Dolichotinae (Figs 3B-F; 7H, I). The molariforms have a furrow opposite the hypoflexus/id, as in *Dolichotis* and *Prodolichotis* (Dolichotinae). This condition differs from that of *Cavia*, *Dolicavia*, *Neocavia*, *Microcavia*, *Palaeocavia*, and *O. rigens* in which are external secondary flexus (HSE) and primary internal flexid (hpi), and from *Galea* that has HSE and primary external fissure (HPE) in and hpi. In *Or. andina* n. comb. the hypoflexus/id (HFI/hse) are funnel-shaped with cement; the enamel is interrupted on the labial wall of the upper molariforms and on the lingual wall of the lower ones, except in the furrow opposite the hypoflexus/id, which resembles the condition of Caviinae and Dolichotinae.

The upper incisors have an orthodont position (Figs 4B; 6A), differing from the condition of *Dolicavia*, in which the position of the upper incisors are proodont (Appendices 4; 5). The APL of P4 is subtly larger than M1; M2 is larger than M1, and M3 is larger than the other molariforms (Table 2). The third molar has a well-developed projection in the posterior lobe, which is posteriorly oriented. The angle between the

posterior lobe and the posterior projection is slightly variable between specimens (Figs 3B-F; Table 2). The configuration of M3 of *Or. andina* n. comb. is similar to *Dolicavia*, differing from *Dolichotis* (Rovereto 1914) and *M. australis*, in which the posterior projection is developed as an incipient third lobe with cement in the flexus formed with the posterior lobe (Appendices 4; 5). The APL of p4 is smaller than m1, m1 is smaller than m2, and m2 is smaller than m3 (Table 3; Figs 4H; 6F-H; 7H, I). The projection of the anterior lobe of p4 is somewhat variable in size; the m1 and m2 are similar, more similar to each other than to the other molars, and the posterior lobe of the m3 has the larger APL.

Atlas

The atlas is preserved articulated with the occipital in the holotype and FMNH-P14370 (Figs 4D, E; 5D). In caudal view, the anterior margin is roughly straight with the spinous process broken, and the posterior margin is posteriorly concave. In the holotype, the alar foramen is anterolateral, on the transverse process (Figs 4D, E). In addition, the ventral tubercle, ventral arch, and caudal articular fovea are broken in ventral view.

REMARKS

In the original description of *Dolichotis andina*, Rovereto (1914) figured upper and lower right cheek teeth (Rovereto 1914: fig. 25). About the mandible he clarified “La serie dentaria es derecha” (the dental series is right). Kraglievich (1932) assigned that species to *Orthomyctera* (*Orocavia*) and redescribed it based on a skull and mandible. He considered the skull MACN-Pv 8350 as the type. Posteriorly, Kraglievich

(1934) briefly redescribed the type MACN-Pv 8350, including the skull and the mandible. In none of the publications Kraglievich (1932, 1934) clarified whether the jaw is right or left.

Currently, the collection number MACN-Pv 8530 includes a skull and a left mandible (not right as published Rovereto) and is considered as the type of *Orthomyctera* (*Orocavia*) *andina* (synonym of *Dolichotis andina*). The left mandible was missing for a while but was recently relocated, and the size and morphological characters match with those of the skull. Here, it is considered that the holotype MACN-Pv 8350 is composed by the skull and the left mandible.

PHYLOGENETIC ANALYSIS

The combined cladistic analysis resulted in a total of 1774 most parsimonious trees (MPTs) of 3438 steps, a strict consensus of all trees was calculated (see Fig. 8A; Appendix 10). *Orthomyctera rigens* and *Orocavia andina* n. comb. are included within Caviinae (Fig. 8). *Orocavia andina* n. comb. is placed as the sister taxon to the clade encompassing the species of *Microcavia*, *Dolicavia*, *Neocavia*, and *Orthomyctera* (Fig. 8, node A). It is supported by six unambiguous synapomorphies: flat area between temporal fossae (character [c.] 45, state [s.] 0); external auditory meatus below the occlusal surface (c. 54, s. 1); anterior-posterior length of posterior border of the upper diastema up to 10% of maxilla (c. 56, s. 0); posterior margin of the incisive foramina wide (c. 58, s. 1); terraced palatal surface (c. 59, s. 3); length of p4-m1 shorter than the length of m2-m3 (c. 125, s. 0). *Orocavia andina* n. comb. has three unambiguous apomorphies: furrow opposite to hypoflexus/id in p4 [c. 86, s. 0]; m1-m2 [c. 117, s. 0] and M1- M2 [c. 142, s. 0]. The *Microcavia*, *Dolicavia*, *Neocavia*, and *Orthomyctera rigens* clade (Fig. 8, node B) is supported by three synapomorphies: anteroposterior length of the upper diastema shorter than the molariform series (c. 47, s. 1); posterior border of superior diastema vertical (c. 55, s. 1) and labial projection on the anterior lobe is present in M1-M2 [c. 138, s. 1).

Dolicavia is the sister group of the clade formed by *O. rigens* and *Neocavia lozanoi*, *N. pampeana* and *Neocavia* sp. (Fig. 8, node C). The clade that includes *O. rigens* and *Neocavia* (Fig. 8A, node D) collapses in a polytomy generated by the instability of *Orthomyctera* (see the alternative resolutions in Fig. 8B). This node is supported by three unambiguous synapomorphies: the root of the lower incisors extended up to the level of the anterior lobe of m1 (c. 20, s. 4); developed lateral ridge of the infraorbital groove (c. 51, s. 1); anterior projection on the pr1 of p4 absent (c.82, s.0).

DISCUSSION

The anatomical reassessment of the holotype of *Orthomyctera* (*Orocavia*) *andina* along with several specimens from northwestern Argentina (previously assigned to *Orthomyctera andina*, *Orthomyctera rigens*, and *Orthomyctera* sp.), facilitated an analysis of the taxonomic status of this species. Additionally, to conduct a thorough anatomical comparison of *O. andina*,

a re-description of the type specimen *Orthomyctera rigens*, was undertaken. The taxonomic evaluation of *Orthomyctera* (*Orocavia*) *andina* (*sensu* Kraglievich 1932), based on dental, mandibular, maxillary, and cranial materials, allowed us to establish the validity of the species. However, differences from the type species *Orthomyctera rigens*, and other caviids, justified its classification into a separate genus: *Orocavia*. It is confirmed that *Or. andina* n. comb. was not previously designated as the type species of another genus or subgenus of Caviidae, thus elevating *Orocavia* to the genus level.

Phylogenetic analysis confirmed the placement of *Orthomyctera rigens* (see Madozzo Jaén *et al.* 2021) and *Orocavia andina* n. comb. within the subfamily Caviinae. Forcing *O. rigens* and *Or. andina* n. comb. within the Dolichotinae clade necessitates a minimum of 21 additional steps, indicating strong support for their inclusion within the Caviinae node (but see Boivin *et al.* 2022). Previous proposals by Kraglievich (1932); Quintana (1998) and, Ubilla & Rinderknecht (2003), advocated for the inclusion in Caviinae primarily due to their the small size of the specimens, presence of lateral vacuity of the nasolacrimal duct (nasolacrimal foramen), and posterior projection of M3, among other characteristics. Both species are nested within the clade comprising *Microcavia*, *Dolicavia*, and *Neocavia*. While *O. rigens* is closely related to *Neocavia* (Fig. 8) but its position within the node is unstable due to skull damaged, preventing evaluation of certain characters. *Or. andina* n. comb. is the sister taxon of the clade consisting of *Microcavia* + (*Dolicavia* + (*Neocavia* + *Orthomyctera*)).

Orocavia exhibits a combination of plesiomorphic and derived characters. *Orocavia* is the only Caviinae that retaining the plesiomorphic condition observed in species of the stem group of Cavoioidea *sensu stricto* (e.g. *Schistomys erro*, *Eocardia excavata*, or *Guiomys unica*; Pérez 2010), the presence of a furrow opposite to the hypoflexus/ id (HFI/hse) in upper and lower cheek teeth. Within Caviidae the presence of a furrow opposite to the hypoflexus/id is also noted in Dolichotinae, while other caviines and in Hydrochoerinae exhibit the derived condition for Cavoioidea, which is the presence of an hpi and HSE (Vucetich *et al.* 2005, 2014a, b; Pérez *et al.* 2014, 2018; Cerdeño *et al.* 2019).

Orocavia shares several derived characters with the clade of *Microcavia*, *Dolicavia*, *Neocavia*, and *Orthomyctera* including a terraced palate, shorter length of the posterior border of upper diastema; flat surface between temporal fossae, without forming a sagittal crest; the position of the external auditory meatus below the occlusal surface, associated with the hypertrophied tympanic bullae present in the clade (see below). The length of p4-m1 shorter than length of m2-m3 is recovered as a synapomorphy for this clade, but confirmation in *O. rigens* is not feasible.

The *Orocavia* clade also shares the presence of hypertrophied tympanic bullae, which have been linked to living in arid and cold environments, or possessing fossorial habits or specialized locomotor habits or, although these associations remain inconclusive in rodent (e.g. Álvarez *et al.* 2015; Argyle & Mason 2008; Mason 2015, 2016; Mason *et al.* 2016; Arnaudo *et al.* 2020; Scarpitti & Calede 2022).

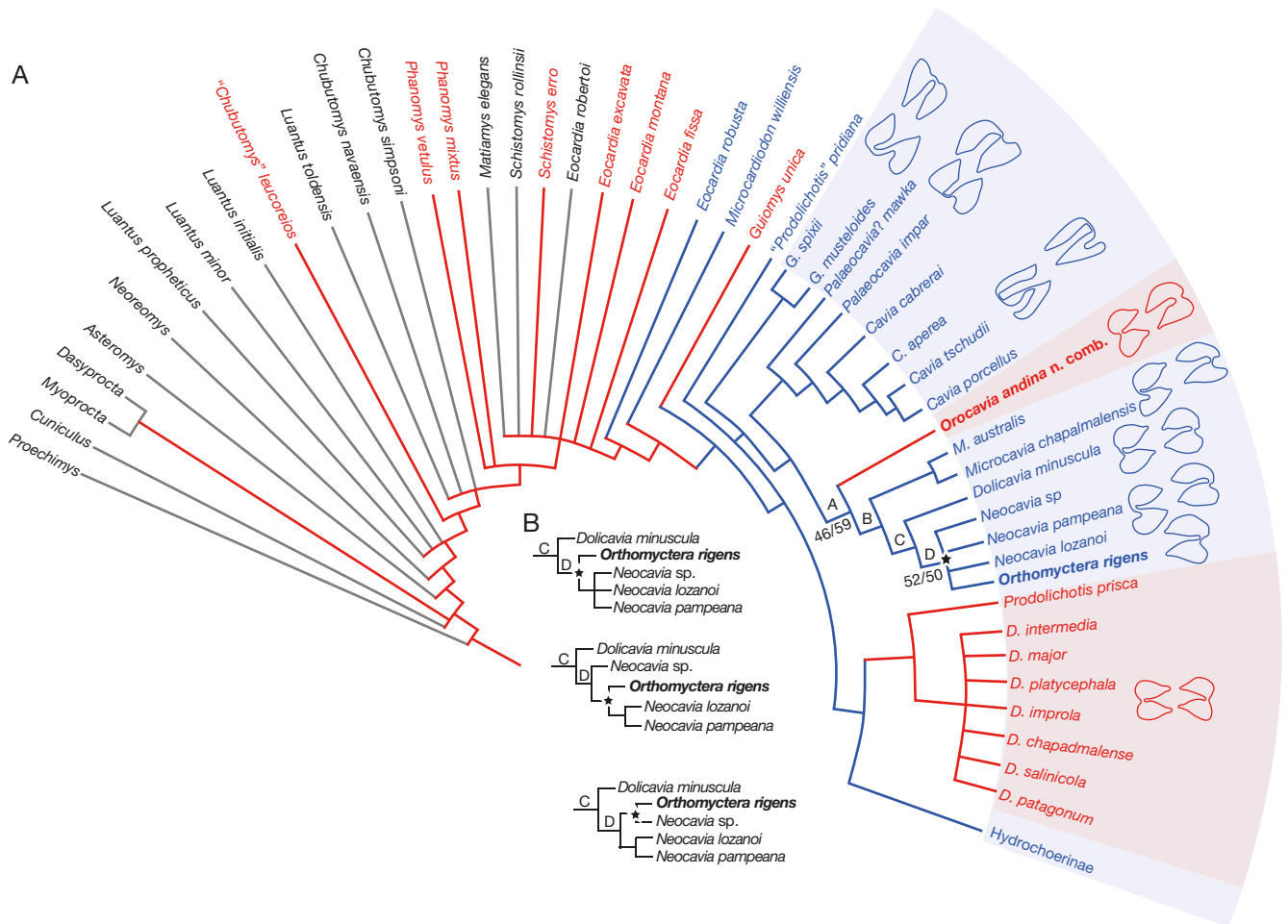


FIG. 8. — **A**, Reduced consensus from the 1774 most parsimonious phylogenetic trees; **B**, the alternative resolutions of node B. The color indicate the state of character 117 and 142: longitudinal furrow opposite to hypoflexid in m1-m2/M1-M2 (red); hpi/HSE in M1-M2/ m1-m2 (blue).

The fossorial habits of *Neocavia*, inferred from its close relationship with *Dolicavia* and *Microcavia* (Madozzo Jaén *et al.* 2018). Paleocave records from the Chapadmalense Formation (Pliocene) suggest a likely coexistence between *Dolicavia* and *Actenomys* (Octodontidae). The presence of *Dolicavia* in these records may indicate either peripheral utilization or opportunistic occupancy of pre-existing caves (Elissamburu *et al.* 2011). *Microcavia* exhibits both cursorial and semi-fossil behaviors, along with a high degree of flexibility in habitat requirements, allowing it to inhabit a wide range of environments and maintain a broad distribution (Taraborelli *et al.* 2019). Research has demonstrated that *Microcavia* constructs both main and satellite burrows with varying dimensions, entrance numbers, and purposes (Taraborelli 2009; Andino *et al.* 2011, 2016; Taraborelli *et al.* 2019). These burrows are communal and serve as refuge for extended periods, accommodating multiple generations (Taraborelli 2009; Elissamburu *et al.* 2011). Due to its close relationship with these genera, it could be inferred that *Orocavia* may have fossorial or semi-fossorial habits. This could increase the probability of preservation and be associated with the relative abundance of this species.

BIOSTRATIGRAPHIC

Orocavia andina n. comb. was described from sediments in the Santa María Valley with an unclear stratigraphic location. The holotype and multiple remains of this species (refer to Appendix 9) were obtained from the “Araucana” Formation in the Santa María Valley (Rovereto 1914), collected through various campaigns and acquired through purchases or donations (see Bonini 2014). Unfortunately, the lack of lithostratigraphic positioning makes it impossible to accurately place these findings. Nonetheless, remains from more recent excavation campaigns do have a precise stratigraphic location. In the Entre Ríos (Chiquimil) and Loma Rica localities in the Catamarca Province to Andalhuala Formation (Santa María Valley), dating between 6.88-6.02 Ma (Marshall & Patterson 1981; Bonini *et al.* 2017; Georgieff *et al.* 2017). In the Villavil-Quillay Basin, the Chiquimil Formation contains the oldest known records of the species, with an absolute age between 9 to 7 Ma (Latorre *et al.* 1997; Sasso 1997; Esteban *et al.* 2014). Other records from this basin are found in the sediments of the Andalhuala Formation on the western slope of Cerro Pampa (San Fernando Sur locality), Catamarca, with an age of c. 7-4.79 Ma (Bonini *et al.* 2017; 2021).

From the newly discovered records, it is estimated that *Orocavia* in NWA was present during 9-5 Ma approximately (Late Miocene-Early Pliocene). During the Late Miocene, *Orocavia* coexisted with the remains of older NWA caviids such as *Palaeocavia*, *Prodolichotis*, *Cardiomys* and *Cardiatherium*. (Marshall & Patterson 1981; Esteban *et al.* 2014; Madozzo Jaén & Pérez 2017; Madozzo Jaén *et al.* 2018; Pérez *et al.* 2018). In the Pliocene, the record is complemented by *Neocavia* (Madozzo Jaén *et al.* 2018) as well as the earliest evidence of modern caviids in NWA (c.f. *Microcavia* from Santa María Valley; Armella *et al.* 2016; *Cavia* from Villavil-Quillay Basin Candela & Bonini 2018). To contribute to the study of the interaction between fossils and the current genus of Caviidae in the NWA is needed to adjust the provenance and age of some remains, conduct new survey campaigns, construct lithological profiles, and their date.

CONCLUSIONS

The taxonomic and phylogenetic relationships of one of the most common and numerous South American genera of Mio-Pliocene caviomorphs, *Orocavia*, are becoming apparent. *Orocavia* is a distinct genus of *Orthomyctera*. *Orthomyctera* (*O. rigens*) and *Orocavia* belong to the Caviinae subfamily and they are closely related to *Microcavia*, *Dolicavia*, and *Neocavia*. *Orocavia andina* n. comb. shared a mosaic of plesiomorphic characters, the furrow opposite to the hypoflexus/id shared with basal taxa and Dolichotinae clade and derived characters as the flat surface between temporal fossa, a terraced palate, and the disposition of the external auditory meatus below the occlusal surface, shared with *Microcavia*, *Dolicavia*, *Neocavia*, and *Orthomyctera*. From the comparison of the habits of *Microcavia* and those inferred for *Dolicavia* and *Neocavia*, we could surmise that fossorial or semi-fossorial habit for *Orocavia*. The fossil record of *Orocavia* in the NWA in Andalhuala and Chiquimil formations from Santa María Valley and Villavil-Quillay basin extends at least between c. 9-7 and 5 Ma. The present studies postulate that due to the phylogenetic position of *Orocavia*, a minimum time of acquisition of hypertrophied tympanic bullae can be estimated between 9 and 7 Ma. It is confirmed that no remains of *Orthomyctera* have been recorded in the NWA, at the moment. This genus is abundantly present in Argentina's faunal lists of the Mio-Pliocene period. Its first occurrences are documented in early correlations, such as Kraglievich (1934), and recent studies, like Brandoni *et al.* (2012), Contreras & Barald (2011), Contreras *et al.* (2019), Ercoli *et al.* (2019), Montalvo *et al.* (2019), and related literature. The absence of a review of the specimens – including some since their original descriptions – and their taxonomy hinders their capacity to serve as biostratigraphic tools. Furthermore, their mentioning presents confused biostratigraphic correlations. Solving these aspects through studies is fundamental and enhances the biostratigraphic value of these taxa, which is abundant in the fossil record. This study illuminates the diversity of

caviids and enlarges the taxonomic, phylogenetic, and biogeographic comprehension of the caviomorph communities from the late Neogene in Argentina.

Acknowledgements

The authors thank Adenise Lopes (Editorial Office/Redaction of *Comptes Rendus Palevol*), the associated editor, Lorenzo Rook, Audrina Neveu the desk editor, one anonymous reviewer and A. Kramarz (Museo Argentino de Ciencias Naturales Bernardino Rivadavia [MACN], Argentina) for their contributions with valuable comments that greatly improved the final version of the manuscript. The authors thank the curators L. Chornogubsky, S. M. Alvarez, P. Teta, and S. Lucero (MACN); M. Reguero (Museo de Ciencias Naturales de La Plata [MLP]), M. Díaz, R. Barquez, and F. Lopez Berrisbeistía (Colección Mamíferos Lillo [CML], Argentina), and †J. E. Powell, P. E. Ortiz and R. F. González (Colección Paleontología de Vertebrados Lillo [PVL], Universidad Nacional de Tucumán [UNT], Argentina) for the access to the material under their care; E. Ruigomez (Museo Paleontológico Egidio Feruglio [MEF], Argentina) and the technical staff of MEF for material preparation. N. Nasif and P. E. Ortiz (Instituto Superior de Correlación Geológica [INSUGEO-UNT], Argentina), K. Angielczyk and W. Simpson (Paleontological Collection, Field Museum of Natural History, Chicago, USA [FMNH]) and R. Bonini (Investigaciones arqueológicas y paleontológicas del Cuaternario Pampeano - [INCUAPA]-CONICET) for providing the fossil material and biostratigraphy discussion; A. Mones and E. Vlachos (MEF) for nomenclature issues; C. Deschamps (Museo de La Plata [MLP], Argentina) and C. Ronez for revisions of the texts in English and French. D. García-López (INSUGEO-UNT) for anatomical revisions; M. Armella (INSUGEO-UNT) for the assistance with photographs, R. V. Palmas for the cover, and C. Deschamps (MLP) for valuable comments that improved the manuscript. This work was supported by the Consejo de Investigaciones de la Universidad Nacional de Tucumán (G513), the Agencia Nacional de Promoción Científica y Tecnológica (PICT-2016-0566, PICT-2018- 3798), and a grant for graduate students of the Asociación Paleontológica Argentina (APA).

REFERENCES

- ÁLVAREZ A., PÉREZ S. I. & VERZI D. H. 2015. — The role of evolutionary integration in the morphological evolution of the skull of caviomorph rodents (Rodentia: Hystricomorpha). *Evolutionary Biology* 42: 312-327. <https://doi.org/10.1007/s11692-015-9326-7>
- AMEGHINO F. 1888. — *Lista de especies de mamíferos fósiles del Mioceno superior de Monte Hermoso hasta ahora conocidas*. Coni PE e hijos, Buenos Aires: 1-21.
- AMEGHINO F. 1889. — Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional Ciencias* 6: 1-1027. <https://doi.org/10.5962/bhl.title.121288>
- AMEGHINO F. 1908. — Las formaciones sedimentarias de la región litoral de Mar del Plata y Chapadmalán. *Museo de Historia Natural de Buenos Aires* 3: 343-428.

- ANDINO N., REUS L., CAPPÀ F., CAMPOS V. & GIANNONI S. M. 2011. — Social environment and agonistic interactions: strategies in a small social mammal. *Ethology* 117 (11): 992-1002. <https://doi.org/10.1111/j.1439-0310.2011.01956.x>
- ANDINO N., BORCHI C. E. & GIANNONI S. M. 2016. — Characterization and selection of microhabitat of *Microcavia australis* (Rodentia: Caviidae): first data in a rocky habitat in the hyperarid Monte Desert of Argentina. *Mammalia* 80 (1): 71-81. <https://doi.org/10.1515/mammalia-2014-0081>
- ARGYLE E. C. & MASON M. J. 2008. — Middle ear structures of *Octodon degus* (Rodentia, Octodontidae), in comparison with those of subterranean caviomorphs. *Journal of Mammalogy* 89:1447-1455. <https://doi.org/10.1644/07-MAMM-A-401.1>
- ARMELLA M. A., MADOZZO JAÉN M. C., NASIF N. L., GARCÍA-LÓPEZ D. A., ESTEBAN G., ORTIZ P. E., GONZÁLEZ R., BABOT M. J. & GEORGIEFF S. 2016. — Vertebrados de la Formación Andalhuala en la Localidad de Encalilla, Tucumán, Argentina. III Simposio del Mio-Pleistoceno del Centro y Norte de Argentina. *Ameghiniana Suplemento Resúmenes. Ameghiniana* 53 (2): 142-159. <https://doi.org/10.5710/AMGH.16.11.2015.2933>
- ARNAUDO M. E., ARNAL M. & EKDALE E. G. 2020. — The auditory region of a caviomorph rodent (Hystricognathi) from the early Miocene of Patagonia (South America) and evolutionary considerations. *Journal of Vertebrate Paleontology* 40 (2): e1777557. <https://doi.org/10.1080/02724634.2020.1777557>
- BRANDONI D., SCHMIDT G. I., CANDELA A. M., NORIEGA J. I., BRUNETTO E. & FIORELLI L. E. 2012. — Mammals from the Salicas Formation (Late Miocene), La Rioja Province, northwestern Argentina: paleobiogeography, age, and paleoenvironment. *Ameghiniana* 49 (3): 375-388. [https://doi.org/10.5710/AMGH.v49i3\(467\)](https://doi.org/10.5710/AMGH.v49i3(467))
- BOIVIN M., ÁLVAREZ A. & ERCOLI M. D. 2022. — Integration patterns of cheek teeth and ecomorphological evolution in grinding herbivores: the case of caviine rodents (Caviomorpha: Caviidae). *Zoological Journal of the Linnean Society* 196 (3): 1094-1116. <https://doi.org/10.1093/zoolinnean/zlac005>
- BONINI R. A. 2014. — *Bioestratigrafía y Diversidad de los Mamíferos del Neógeno de San Fernando y Puerta de Corral Quemado (Catamarca, Argentina)*. Unpublished PhD thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires, 334 p.
- BONINI R. A., GEORGIEFF S. M. & CANDELA A. M. 2017. — Stratigraphy, geochronology, and paleoenvironments of Miocene-Pliocene boundary of San Fernando, Belén (Catamarca, northwest of Argentina). *Journal of South American Earth Sciences* 79: 459-471. <https://doi.org/10.1016/j.jsames.2017.08.020>
- BONINI R. A., PREVOSTI F. J., ROMANO C. O., RAFUSE D. J., NÚÑEZ BLASCO A., ARMELLA M. A., MADOZZO JAÉN M. C. & GEORGIEFF S. M. 2021. — *Análisis preliminar de las dinámicas de diversidad de los mamíferos del Mioceno Tardío - Plioceno de la Cuenca Villavil Quillay y del Valle de Santa María (Catamarca, Argentina)*. XII Congreso de la Asociación Paleontológica Argentina (CAPA), 51 R.
- CABRERA 1953. — *Los roedores argentinos de la familia Caviidae*. Publicaciones de la Escuela Veterinaria, Universidad de Buenos Aires 6: 1-93.
- CAMPO D. H., CARABALLO D. A., CASSINI G. H., LUCERO S. O. & TETA P. 2020. — Integrative taxonomy of extant maras supports the recognition of the genera *Pediolagus* and *Dolichotis* within the *Dolichotinae* (Rodentia, Caviidae). *Journal of Mammalogy* 101 (3): 817-834. <https://doi.org/10.1093/jmammal/gyaa038>
- CANDELA A. M. & BONINI R. A. 2018. — A new guinea pig (Rodentia, Caviomorpha) from northwestern Argentina: implications for the origin of the genus *Cavia*. *Journal of Vertebrate Paleontology* 37 (4): e1352591-2. <https://doi.org/10.1080/02724634.2017.1352591>
- CASTELLANOS A. 1958. — *Nota preliminar sobre nuevos restos de mamíferos fósiles en el Brocherense del Valle de Los Reartes (provincia de Córdoba, Argentina)*. Congreso Geológico Internacional, Mexico: 217-233.
- CERDEÑO E., PÉREZ M. E., DESCHAMPS C. M. & CONTRERAS V. H. 2019. — A new capybara from the late Miocene of San Juan Province, Argentina, and its phylogenetic implications. *Acta Palaeontologica Polonica* 64: 199-212. <https://doi.org/10.4202/app.00544.2018>
- CHEREM J. J. & FERIGOLO J. 2012. — Descrição do sincrônio de *Cavia aperea* (Rodentia, Caviidae) e comparação com as demais espécies do gênero no Brasil. *Papéis Avulsos de Zoologia* 52 (3): 21-50. <https://doi.org/10.1590/S0031-10492012000300001>
- CONTRERAS V. H. & BARALD J. A. 2011. — Calibration of the Chasicooan-Huayquerian stages boundary (Neogene), San Juan, western Argentina. *Cenozoic geology of the Central Andes of Argentina* 111: 111-121.
- CONTRERAS V. H., BRACCO A. I. & BARALDO J. A. 2019. — Estratigrafía, bioestratigrafía y cronología del Mioceno superior de la provincia de San Juan (Argentina). Mioceno al Pleistoceno del Centro y Norte de Argentina. *Opera Lilloana* 52: 177-206.
- CROFT D. A., CHICK J. M. & ANAYA F. 2011. — New middle miocene caviomorph rodents from Quebrada Honda, Bolivia. *Journal of Mammalian Evolution* 18 (4): 245-268. <https://doi.org/10.1007/s10914-011-9164-z>
- DE BEER G. 1937. — *The Development of Vertebrate Skull*. University Press, Oxford, 554 p.
- DESCHAMPS C. M., OLIVARES A. I., VIEYTES E. C. & VUCETICH M. G. 2007. — Ontogeny and diversity of the oldest capybaras (Rodentia: Hydrochoeridae; late Miocene of Argentina). *Journal of Vertebrate Paleontology* 27 (3): 683-692. [https://doi.org/10.1671/0272-4634\(2007\)27\[683:OADOTO\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27[683:OADOTO]2.0.CO;2)
- DESCHAMPS C. M., VIEYTES E. C., OLIVARES A. I. & VUCETICH M. G. 2009. — Primer registro de *Cardiatherium chasicooense* (Rodentia, Hydrochoeridae) fuera del área pampeana (Argentina) y su valor bioestratigráfico. *Journal of South American Earth Sciences* 46: 295-305. <http://hdl.handle.net/11336/45172>
- DESCHAMPS C. M., VUCETICH M. G., VERZI D. H. & OLIVARES A. I. 2012. — Biostratigraphy and correlation of the Monte Hermoso Formation (early Pliocene, Argentina): the evidence from caviomorph rodents. *Journal of South American Earth Sciences* 35:1-9. <https://doi.org/10.1016/j.jsames.2011.10.006>
- DESCHAMPS C. M., VUCETICH M. G., MONTALVO C. I. & ZÁRATE M. A. 2013. — Capybaras (Rodentia, Hydrochoeridae, Hydrochoerinae) and their bearing in the calibration of the Late Miocene-Pliocene sequences of South America. *Journal of South American Earth Sciences* 48: 145-158. <https://doi.org/10.1016/j.jsames.2013.09.007>
- DUNNUM J. L. 2015. — Family Caviidae, in PATTON J. L., PARDIÑAS U. F. J. & D'ELIA G. (eds), *Mammals of South America: Volume 2 Rodents*. The University of Chicago Press, Chicago, IL: 690-726.
- ELISSAMBURU A., DONDAS A. & DE SANTIS L. 2011. — Morfometría de las paleocuevas de la Formación Chapadmalal y su asignación a *Actenomys* (Rodentia), *Paedotherium* (Notoungulata) y otros mamíferos fósiles hospedantes. *Mastozoología neotropical* 18: 227-238.
- ERCOLI M. D., ÁLVAREZ A., SANTAMANS C., PATAGUA S. A. G., ULBERICH J. P. V. & CONSTANTINI O. E. 2019. — Los Alisos, a new fossiliferous locality for Guanaco Formation (Late Miocene) in Jujuy (Argentina), and a first approach of its paleoecological and biochronology implications. *Journal of South American Earth Sciences* 93: 203-213. <https://doi.org/10.1016/j.jsames.2019.04.024>
- ESTEBAN G., NASIF N. & GEORGIEFF S. M. 2014. — Cronobioestratigrafía del Mioceno tardío-Plioceno temprano, Puerta de Corral Quemado y Villavil, Catamarca, Argentina. *Acta Geológica Lilloana* 26: 165-192.
- ESTEBAN G., GEORGIEFF S., NASIF N., IBÁÑEZ L. & BONINI R. 2019. — Marco estratigráfico, paleontología de vertebrados y paleoambientes del Plioceno de Catamarca, Tucumán y Santiago del Estero, Argentina. *Opera Lilloana* 52: 348-367.

- FRENGUELLI J. 1928. — *Observaciones geológicas en la región costanera sur de la Provincia de Buenos Aires*. Universidad Nacional del Litoral, Facultad de Ciencias de la Educación, Anales 2, Santa Fe, 145 p.
- GARCÍA-ESPONDA C. M. & CANDELA A. M. 2016. — Hindlimb musculature of the largest living rodent *Hydrochoerus hydrochaeris* (Caviomorpha): Adaptations to semiaquatic and terrestrial styles of life. *Journal of morphology* 277 (3): 286-305. <https://doi.org/10.1002/jmor.20495>
- GARRIDO A. C., TURAZZINI G. F., BOND M., AGUIRREZABALA G. & FORASIEPI A. M. 2014. — Estratigrafía, vertebrados fósiles y evolución tectosedimentaria de los depósitos neógenos del Bloque de San Rafael (Mioceno-Plioceno), Mendoza, Argentina. *Acta geológica lilloana* 26 (2): 133-164.
- GEORGIJEFF S. M., MURUAGA C. M., IBAÑEZ L. M., SPAGNUOLO C., BONINI R., ESTEBAN G., NASIF N. & DEL PERO M. A. 2017. — Estilos de deformación, cronoestratigrafía y evolución paleoambiental de las unidades neógenas de las Sierras Pampeanas Noroccidentales de Catamarca y Tucumán, Argentina, in MURUAGA C. M. & GROSSE P. (eds), *Ciencias de la Tierra y Recursos Naturales del NOA*. Relatorio del XX Congreso Geológico Argentino, San Miguel de Tucumán: 254-268.
- GOLOBOFF P. A. & CATALANO S. A. 2016. — TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32 (3): 221-238. <https://doi.org/10.1111/cla.12160>
- HERBST R., ANZÓTEGUI L. M., ESTEBAN G., MAUTINO L. R., MORTON S. & NASIF N. 2000. — Síntesis paleontológica del Mioceno de los valles Calchaquíes, noroeste argentino. El Neógeno de Argentina. INSUGEO, *Serie de Correlación Geológica* 14: 263-288.
- INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE. — KRAGLIEVICH L. 1930. — Diagnosis osteológico-dentaria de los géneros vivientes de la subfamilia Caviinae. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 36: 59-95.
- KRAGLIEVICH L. 1932. — Diagnosis de nuevos géneros y especies de roedores cávidos y eumegámidos fósiles de la Argentina. *Anales de la Sociedad Científica Argentina* CXIV: 155-237.
- KRAGLIEVICH L. 1934. — La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron. *Imprenta El Siglo Ilustrado*, Buenos Aires, 136 p.
- LATORRE C., QUADE J. & MCINTOSH W. C. 1997. — The expansion of C4 grasses and global change in the late Miocene: stable isotope evidence from the Americas. *Earth and Planetary Science Letters* 146 (1-2): 83-96. [https://doi.org/10.1016/S0012-821X\(96\)00231-2](https://doi.org/10.1016/S0012-821X(96)00231-2)
- MCKENNA M. C. & BELL S. K. 1997. — *Classification of mammals: above the species level*. Columbia University Press, New York, 631 p.
- MADOZZO JAÉN M. C. 2017. — *Los Caviinae (Mammalia, Rodentia, Caviidae) del Cenozoico Tardío del Noroeste de Argentina: Evolución y Relaciones Filogenéticas*. Unpublished PhD thesis, Facultad de Ciencias Naturales, Universidad Nacional De Tucumán, 240 p.
- MADOZZO JAÉN M. C. 2019. — Systematic and phylogeny of *Prodolichotis prisca* (Caviidae, Dolichotinae) from the Northwest of Argentina (Late Miocene-Early Pliocene): advances in the knowledge of the evolutionary history of maras. *Comptes Rendus Palevol* 18 (1): 33-50. <https://doi.org/10.1016/j.crpv.2018.07.003>
- MADOZZO JAÉN M. C. & PÉREZ M. E. 2017. — The most ancient caviine rodent (Hystricognathi, Cavoioidea) comes from the Late Miocene of Northwest Argentina (South America). *Historical Biology* 29 (3): 376-383. <https://doi.org/10.1080/08912963.2016.1166360>
- MADOZZO JAÉN M. C., ORTIZ P. E. & NASIF N. 2013. — Diversidad de la Familia Caviidae en el noroeste de Argentina. Interpretaciones evolutivas. II Simposio del Mioceno-Pleistoceno del Centro y Norte de Argentina. *Ameghiniana* 49: 5R.
- MADOZZO JAÉN M. C., PÉREZ M. E., MONTALVO C. I. & TOMASSINI R. L. 2018. — Systematic review of *Neocavia* (Rodentia, Caviidae) from the Neogene of Argentina: phylogenetic and evolutionary implications. *Acta Palaeontologica Polonica* 63 (2): 241-260. <https://doi.org/10.4202/app.00464.2018>
- MADOZZO JAÉN M. C., PÉREZ M. E. & DESCHAMPS C. M. 2021. — The oldest species of *Dolichotis* (Rodentia, Hystricognathi) from the Pliocene of Argentina: redescription and taxonomic status of “Orthomyctera” chapalmalense. *Journal of Mammalian Evolution* 28: 995-1013. <https://doi.org/10.1007/s10914-021-09559-4>
- MAESTRI R. & PATTERSON B. D. 2016. — Patterns of species richness and turnover for the South American rodent fauna. *PLoS ONE* 11: 0151895. <https://doi.org/10.1371/journal.pone.0151895>
- MARSHALL L. G. & PATTERSON B. 1981. — Geology and geochronology of the mammal-bearing Tertiary of the Valle de Santa María and Río Corral Quemado, Catamarca Province, Argentina. *Fieldiana Geology* 9: 1-80. <https://doi.org/10.5962/bhl.title.3461>
- MASON M. J. 2015. — Functional morphology of rodent middle ears, in COX P. G. & HAUTIER L. (eds), *Evolution of the Rodents: Advances in Phylogeny, Functional Morphology and Development*. Cambridge University Press, Cambridge: 373-404. <https://doi.org/10.1017/CBO9781107360150.015>
- MASON M. J. 2016. — Structure and function of the mammalian middle ear. I: Large middle ears in small desert mammals. *Journal of Anatomy* 228 (2): 284-299. <https://doi.org/10.1111/joa.12313>
- MASON M. J., CORNWALL H. L. & SMITH E. S. J. 2016. — Ear structures of the naked mole-rat, *Heterocephalus glaber*, and its relatives (Rodentia, Bathyergidae). *PLoS ONE* 11: e0167079. <https://doi.org/10.1371/journal.pone.0167079>
- MONES A. 1991. — Monografía de la Familia Hydrochoeridae (Mammalia, Rodentia): Sistemática – Paleontología – Bibliografía. *Courier Forschungsinstitut Senckenberg* 134: 1-235
- MONTALVO C. I., TOMASSINI R. L., SOSTILLO R., CERDEÑO E., VERZI D., VISCONTI G. ... & SCHMIDT G. I. 2019. — A Chasicóan (Late Miocene) vertebrate assemblage from Cerro Azul Formation, central Argentina. Geomorphological and biochronological considerations. *Journal of South American Earth Sciences* 95: 102218. <https://doi.org/10.1016/j.jsames.2019.102218>
- NASIF N., ESTEBAN G. & HERBST R. 2006. — Nuevos registros de vertebrados en el Grupo Payogastilla (Terciario tardío), provincia de Salta, Argentina. *Ameghiniana* 43 (4) Suplemento: 47R.
- PARDIÑAS U. F., PREVOSTI F. J., VOGLINO D. & CENIZO M. 2017. — A controversial unit within the argentine neogene: the “Irenean” fauna. *Ameghiniana* 54 (6): 655-680. <https://doi.org/10.5710/AMGH.24.04.2017.3080>
- PASCUAL R. 1966. — Caviidae, in BORRELLO A. V. & PASCUAL R. (eds), *Paleontografía Bonaerense*. Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, Buenos Aires: 103-113.
- PÉREZ M. E. 2010. — A new Rodent (Cavoioidea, Hystricognathi) from the middle Miocene of Patagonia, mandibular homologies, and the origin of the crown group Cavoioidea *sensu stricto*. *Journal of vertebrate Paleontology* 30 (6): 1848-1859. <https://doi.org/10.1080/02724634.2010.522432>
- PÉREZ M. E. & POL D. 2012. — Major radiations in the evolution of Caviid rodents: reconciling fossils, ghost lineages, and relaxed molecular clocks. *PLoS ONE* 7: 1-21. <https://doi.org/10.1371/journal.pone.0048380>
- PÉREZ M. E., VUCETICH M. G. & DESCHAMPS C. M. 2014. — Mandibular remains of *Procardiomys martinoi* Pascual, 1961 (Hystricognathi, Cavoioidea) from the Arroyo Chasicó Formation (early Late Miocene) of Argentina: anatomy the phylogenetic position of the genus within Caviidae. *Historical Biology* 26 (1): 16-25. <https://doi.org/10.1080/08912963.2012.751383>
- PÉREZ M. E., DESCHAMPS C. M. & VUCETICH M. G. 2018. — Diversity, phylogeny and biogeography of the South American “cardiomyine” rodents (Hystricognathi, Cavoioidea) with a description of two new species. *Paper in Palaeontology* 4 (1): 1-19. <https://doi.org/10.1002/spp2.1095>

- PÉREZ M. E., MADOZZO JAÉN M. C., FORASIEPI A., PREVOSTI F. & GARRIDO A. 2019. — Los Roedores Caviidae de las Huayquerías del Este (Mioceno Tardío-Plioceno?) de la Provincia de Mendoza (Argentina). *Avances en el estudio taxonómico y filogenético de Dolichotinae (Rodentia, Caviidae) del Mioceno tardío-Plioceno. PRE-APA* 19: 70R.
- PREVOSTI F. J., ROMANO C. O., FORASIEPI A. M., HEMMING S., BONINI R., CANDELA A. M., CERDEÑO E., MADOZZO JAÉN M. C., ORTIZ P. E., PUJOS F., RASIA L., SCHMIDT G. I., TAGLIORETTI M., MACPHEE R. D. E. & PARDIÑAS U. F. J. 2021. New radiometric ^{40}Ar - ^{39}Ar dates and faunistic analyses refine evolutionary dynamics of Neogene vertebrate assemblages in southern South America. *Scientific Reports* 11 (1): 9830. <https://doi.org/10.1038/s41598-021-89135-1>
- POPEŠKO P., RAJTOVÁ V. & HORÁK J. 1992. — Colour atlas of the anatomy of small laboratory animals. *Wolfe Pub. Ltd.* 240 p.
- POWELL J. E., MULÉ P., DUARTE R., ORTÍZ P. E., SANAGUA J. & MURUAGA C. 1998. — Mamíferos de la Formación Chiquimil (Mioceno superior) de la vertiente occidental de la Sierra de Hualfín, Provincia de Catamarca. *Acta Geológica Lilloana* 18: 178R.
- QUINTANA C. 1996. — Diversidad del roedor *Microcavia* (Caviomorpha, Caviidae) de América del sur. *Mastozoología Neotropical* 3: 63-86.
- QUINTANA C. 1997. — El roedor *Dolicavia minuscula* (Caviomorpha, Caviidae) del Plioceno superior de la provincia de Buenos Aires, Argentina. *Historia Animalium* 3: 55-71.
- QUINTANA C. 1998. — Relaciones filogenéticas de roedores Caviinae (Caviomorpha, Caviidae), de América del Sur. *Boletín de la Sociedad Española de Historia Natural (Sección Biológica)* 94: 125-134.
- ROVERETO C. 1914. — Los estratos araucanos y sus fósiles. *Anales del Museo de Historia Natural de Buenos Aires* 25: 1-247.
- SASSO A. 1997. — *Geological evolution and tecthallogenic relationships of the Farallón Negro Volcanic Complex, NW Argentina*. Thesis Doctoral, Queens University (inédito), Kingston, Ontario, 268 p.
- SCARPITTI E. A. & CALEDE J. J. 2022. — Ecological correlates of the morphology of the auditory bulla in rodents: application to the fossil record. *Journal of Anatomy* 240 (4): 647-668. <https://doi.org/10.1111/joa.13579>
- SIMPSON G. G. 1945. — The principles of classification and a classification of mammals. *Bulletin of American Museum of Natural History* 85 (1), 350 p. <https://doi.org/10.1002/ajpa.1330040218>
- TARABORELLI P. 2009. — Is communal burrowing or burrow sharing a benefit of group living in the lesser cavy *Microcavia australis*?. *Acta Theriologica* 54: 249-258. <https://doi.org/10.4098/jat.0001-7051.043.2008>
- TARABORELLI P., TETA P., D'HIRIART S., TARQUINO-CARBONELL A. P., OJEDA R. A. 2019. — *Microcavia australis*. Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción. Lista Roja de los mamíferos de Argentina. Available at: <http://cma.sarem.org.ar>
- TAUBER A. A. 2005. — Mamíferos fósiles y edad de la Formación Salicas (Mioceno tardío) de la sierra de Velasco, La Rioja, Argentina. *Ameghiniana* 42 (2): 443-460. <https://www.ameghiniana.org.ar/index.php/ameghiniana/article/view/902>
- TETA P. V. & CAMPO D. H. 2017. — Is *Galea tixiensis* Quintana, 2001 a synonym of *G. leucoblephara* Burmeister, 1861? *Therya* 8 (3): 209-216. <https://doi.org/10.12933/therya-17-497>
- TOMASSINI R. L., MONTALVO C. I., DESCHAMPS C. M. & MANERA T. 2013. — Biostratigraphy and biochronology of the Monte Hermoso Formation (early Pliocene) at its type locality, Buenos Aires Province, Argentina. *Journal of South American Earth Sciences* 48: 31-42. <https://doi.org/10.1016/j.jsames.2013.08.002>
- UBILLA M. & RINDERKNECHT A. 2003. — A Late Miocene Dolichotinae (Mammalia, Rodentia, Caviidae) from Uruguay, with comments about the relationships of some related fossil species. *Mastozoología Neotropical* 10: 293-302.
- UBILLA M., PIÑEIRO G. & QUINTANA C. A. 1999. — A new extinct species of the genus *Microcavia* (Rodentia, Caviidae) from the Upper Pleistocene of the northern basin of Uruguay, with paleobiogeographic and paleoenvironmental comments. *Studies on Neotropical Fauna and Environment* 34: 141-149.
- URREA-BARRETO F. J., LINK, ANDRÉS, CARRILLO J. D., VANEGAS A., PERDOMO C. A., COOKE S. B., TALLMAN M. & PÉREZ M. E. 2023. — Systematic revision of *Neoreomys huilensis* Fields (Rodentia, Hystricognathi) from the Middle Miocene of La Venta (Vilavieja, Huila, Colombia), in CARRILLO J. D. (ed.), Neotropical palaeontology: the Miocene La Venta biome. *Geodiversitas* 45 (25): 721-737. <https://doi.org/10.5252/geodiversitas2023v45a25>. <http://geodiversitas.com/45/25>
- VERZI D. H. & MONTALVO C. I. 2008. — The oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora): Late Miocene faunal turnover in central Argentina and the Great American Biotic Interchange. *Palaeogeography, Palaeoclimatology, Palaeoecology* 267 (3-4): 284-291. <https://doi.org/10.1016/j.palaeo.2008.07.003>
- VILLARROEL C. & MARSHALL L. G. 1989. — A new fossil land mammal locality of late Miocene (Huayquerian) age from Muylu Huasi, southcentral Bolivia. *Boletín del Servicio Geológico de Bolivia* 4: 27-40.
- VUCETICH M. G. & PÉREZ M. E. 2011. — The putative cardiomyines (Rodentia, Cavioidae) of the middle Miocene of Patagonia (Argentina) and the differentiation of the Family Hydrochoeridae. *Journal of Vertebrate Paleontology* 31 (6): 1382-1386. <https://doi.org/10.1080/02724634.2011.618194>
- VUCETICH M. G., DESCHAMPS C. M., OLIVARES A. I. & DOZO M. T. 2005. — Capybaras, size, shape, and time: a model kit. *Acta Palaeontologica Polonica* 50: 259-272.
- VUCETICH M. G., DESCHAMPS C. M., PÉREZ M. E. & MONTALVO C. I. 2014a. — The taxonomic status of the Pliocene capybaras (Rodentia) *Phugatherium* Ameghino and *Chapalmatherium* Ameghino. *Ameghiniana* 51 (3): 173-183. <https://doi.org/10.5710/AMGH.05.02.2014.2074>
- VUCETICH M. G., DESCHAMPS C. M., VIEYTES E. C. & MONTALVO C. I. 2014b. — Late Miocene capybaras from Argentina: skull anatomy, taxonomy, evolution, and biochronology. *Acta Palaeontologica Polonica* 59: 517-535.
- VUCETICH M. G., ARNAL M., DESCHAMPS C. M., PÉREZ M. E. & VIEYTES E. C. 2015a. — A brief history of caviomorph rodents as told by the fossil record, in VASSALLO Á. & ANTONUCCI D. (eds), *Biology of caviomorph rodents diversity and evolution*. SAREM, Buenos Aires: 11-62.
- VUCETICH M. G., DESCHAMPS C. M. & PÉREZ M. E. 2015b. — The first capybaras (Rodentia, Caviidae, Hydrochoerinae) involved in the Great American Biotic Interchange. *Ameghiniana* 52 (3): 324-333. <https://doi.org/10.5710/AMGH.05.02.2015.2874>
- WAHLERT J. H. 1974. — The cranial foramina of protrogomorphous rodents: an anatomical and phylogenetic study. *Bulletin of the Museum of Comparative Zoology* 146: 363-400.
- WIBLE J. R., WANG Y., LI C. & DAWSON M. R. 2005. — Cranial anatomy and relationships of a new Ctenodactyloid (Mammalia, Rodentia) from the early Eocene of Hubei Province, China. *Annals of Carnegie Museum* 74 (2): 91-151. [https://doi.org/10.2992/0097-4463\(2005\)74\[91:CAAROA\]2.0.CO;2](https://doi.org/10.2992/0097-4463(2005)74[91:CAAROA]2.0.CO;2)
- WIBLE J. R. 2011. — On the treeshrew skull (Mammalia, Placentalia, Scandentia). *Annals of Carnegie Museum* 79 (3): 149-230. <https://doi.org/10.2992/007.079.0301>
- WOODS C. A. & HOWLAND E. B. 1979. — Adaptive radiation of Caviomyid rodents: anatomy of the masticatory apparatus. *Journal of Mammalogy* 60 (1): 95-116. <https://doi.org/10.2307/1379762>

Submitted on 25 November 2019;
accepted on 29 April 2024;
published on 8 August 2024.

APPENDICES

APPENDIX 1. — Taxonomic history of *Orthomyctera* Ameghino, 1889.

– *Orthomyctera rigens* Ameghino, 1889

Cavia rigens Ameghino, 1888: 12.

Orthomyctera rigens Ameghino, 1889: 372.

TYPE LOCALITY. — Monte Hermoso, Buenos Aires (Fig. 1).

– *Orthomyctera vaga* Ameghino 1889

TYPE LOCALITY. — Monte Hermoso, Buenos Aires (Fig. 1).

– *Orthomyctera perfecta* Ameghino, 1908

Prodolichotis perfecta Kraglievich, 1932: 158.

TYPE LOCALITY. — Chapadmalal, Buenos Aires Province (Fig. 1).

– *Orocavia andina* n. comb. (this paper)

Dolichotis andina Rovereto, 1914: 58.

Orthomyctera (Orocavia) andina Kraglievich, 1932: 163.

TYPE LOCALITY. — Andalhuala, Catamarca (Fig. 1).

– *Prodolichotis lacunosa* Kraglievich, 1932

Dolichotis lacunosa Ameghino, 1888: 12.

Orthomyctera lacunosa Ameghino, 1889: 220.

TYPE LOCALITY. — Monte Hermoso, Buenos Aires (Fig. 1).

– *Orthomyctera brocherense* Castellanos, 1956

TYPE LOCALITY. — Valle de Los Reartes; Córdoba (Fig. 1)

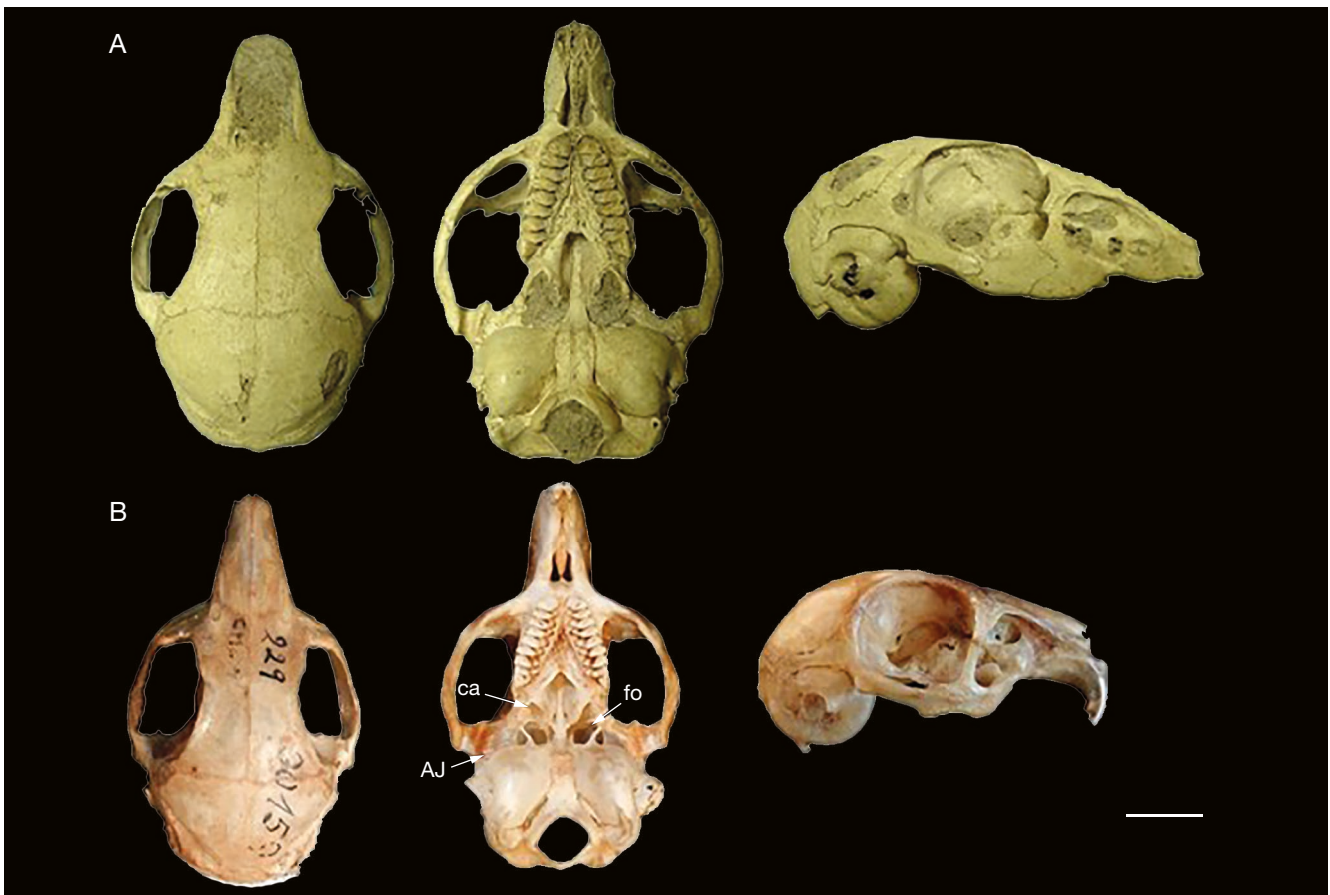
APPENDIX 2. — Combined matrix. Available at: https://doi.org/10.5852/cr-palevol2024v23a20_s1

APPENDIX 3. — Morphological character list, GenBank accession numbers. Characters with an asterisk (*) are considered “ordered”. Available at: https://doi.org/10.5852/cr-palevol2024v23a20_s2

APPENDIX 4. — Cranial measurements (in mm) of *Microcavia australis* (l. Geoffroy Saint-Hilaire & d'Orbigny, 1833) and *Dolicavia minuscula* (Ameghino, 1908). Compared measurements (in mm) of skull and dentary of *M. australis* (CML 841; CML 8410; CML 1010; CML 1012; CML 7239) and *D. minuscula* (MLP 91-VI-5333; MACN 10617; MMP 210-S; MMP 500-M; MMP 846-M). *, average measurements.

Measures	<i>Microcavia australis</i> *	<i>Dolicavia minuscula</i> *
skull total length (dorsal view)	49.85	59.10
skull length (from nasal-frontal suture)	33.82	40.22
length of diastema	12.07	13.94
rostrum length (from nasal-frontal suture)	16.36	19.24
rostrum width (between nasal-frontal-prmx suture)	7.45	8.99
orbital constriction width	12.08	16.53
braincase width	23.14	29.47
palate width at P4 level (measured in the anterior lobe without including teeth)	0.92	1.14
palate width at M3 level (measured in the anterior lobe without including teeth)	5.94	7.16
width at mae level	20.28	24.75
palate length (from the P4 level to the apex of the mesopterigoid fossa)	9.68	12.81

APPENDIX 5. — **A**, *Dolicavia minuscula* (Ameghino, 1908) MLP 91-VI-5.333; **B**, *Microcavia australis* Geoffroy Saint-Hilaire & d'Orbigny, 1833 CML 8410. Abbreviations: **Al**, alisphenoid; **ca**, canal alar; **fo**, foramen ovale. Scale bar: 10 mm.



SPECIMENS PREVIOUSLY REFERRED
TO AS *ORTHOMYCTERA RIGENS*

The MACN-Pv 7319 from Monte Hermoso, Buenos Aires, Argentina, is a skull with complete molariforms series, was referred in *scheldula* to *Orthomyctera rigens* and in Quintana (1997), Ubilla & Rinderknecht (2003). In the MACN-Pv 7319, the posterior border of the diastema is oblique, and the length of this is longer than in the type of *O. rigens*; the anterior border of the mesopterygoid fossa is V-shaped and is extended up to the posterior lobe of M2, unlike *O. rigens*. The specimen MACN-Pv 7319 is not a *O. rigens*, could be a new morphotype of caviine.

FMNH P 15250 (table from Puerta de Corral Quemado, Catamarca, without precise stratigraphic location; Marshall & Patterson 1981; Appendices 7; 8). It is a fragment of a skull with molariforms, which differs from the type of *O. rigens* because lacks the molars HSE and differs from this and *Or. andina* n. comb. because has a V-shaped mesopterygoid fossa. This specimen would correspond to another taxonomic entity.

FMNH P 15300 from Puerta de Corral Quemado, Catamarca, without precise stratigraphic location (Marshall & Patterson 1981; Appendices 7; 8) is a fragment of maxilla with P4-M3 that have a shallow HSE and the anterior lobe of M1 has a posterolabial extension, which differentiates it from *O. rigens* and *Or. andina* n. comb. This specimen is a Caviinae, more studies are needed for a precise designation.

SPECIMENS REFERRED TO AS *ORTHOMYCTERA ANDINA*

CRILAR Pv 39 is a maxillary fragment P4-M1 from the Salica Formation (late Miocene; Tauber 2005), the molariforms have an APL and the posterior portion of the diastema is larger than *O. rigens*, *Or. andina* n. comb. In this work, we refer to it as Dolichotinae.

CRILAR Pv 41 is a right mandibular fragment p4-m2 and CRILAR Pv 50 is a right mandibular fragment with p4-m3 from the Salica Formation (Late Miocene; Tauber 2005). The molariforms are larger and more rounded than *O. andina*, in this work, we refer to them as Dolichotinae.

Specimens from Entre Rios (ex Chiquimil; Marshall & Patterson 1981, see below), in level XVII: FMNH P 14337 (Appendix 8) is a maxilla with right P4-M3 and left P4, the FMNH P 14343 (Appendices 7; 8) is a mandible with

p4-m3 but poor conservation cannot be ruled out that it belongs to the species.

FMNH 14534 (Appendix 8) is a fragment of the skull with both fragmented M3 and large tympanic bulla from Entre Rios (ex Chiquimil; Marshall & Patterson 1981) in level VIIIb. Due to poor conservation, it is difficult to assign it to a genus or species, but due to the relationship between bullae and skull length, it could refer to as *Neocavia*.

FMNH 14463 is a fragment of the skull with M1-M3 left and M2-M3 right from Entre Rios (ex Chiquimil) in level XVII (Marshall & Patterson 1981; Appendix 8). The molariforms are some larger than *O. andina* the anterior lobe of M2 is more elongated and the posterior projection of M3 is short and more rounded than *O. andina*. Because of these differences, we prefer a doubtful assignment to a species assignment.

SPECIMENS REFERRED TO AS *ORTHOMYCTERA* SP.

In El Morterito Formation, El Cajón valley (late Miocene-early Pliocene) *Orthomyctera* sp. was cited by Herbst *et al.* (2000) but the authors do not refer to citations or the number of materials; the belonging to the genus is not possible to corroborate.

The fragment of the palate with molariforms from Angastaco Formation, Salta (MAS-P 006; Nasif *et al.* 2006; Appendices 7; 8) and the skull (PVL 4891, Chiquimil Formation, Catamarca (Powell *et al.* 1998; Madozzo-Jaén *et al.* 2013; Appendices 7; 8) have the posterior portion of the diastema oblique which differ than *O. rigens* and its portion is anterodorsal-posteroventrally larger than in *Orocavia andina* n. comb. (see below). The molariforms are larger labio-lingually than in *Orthomyctera rigens* and maxillary portion of the palate does not have the ridge parallel to the alveolus of the molariforms. Due to these characteristics, the material corresponds to a different genus than *Orthomyctera* and *Orocavia*.

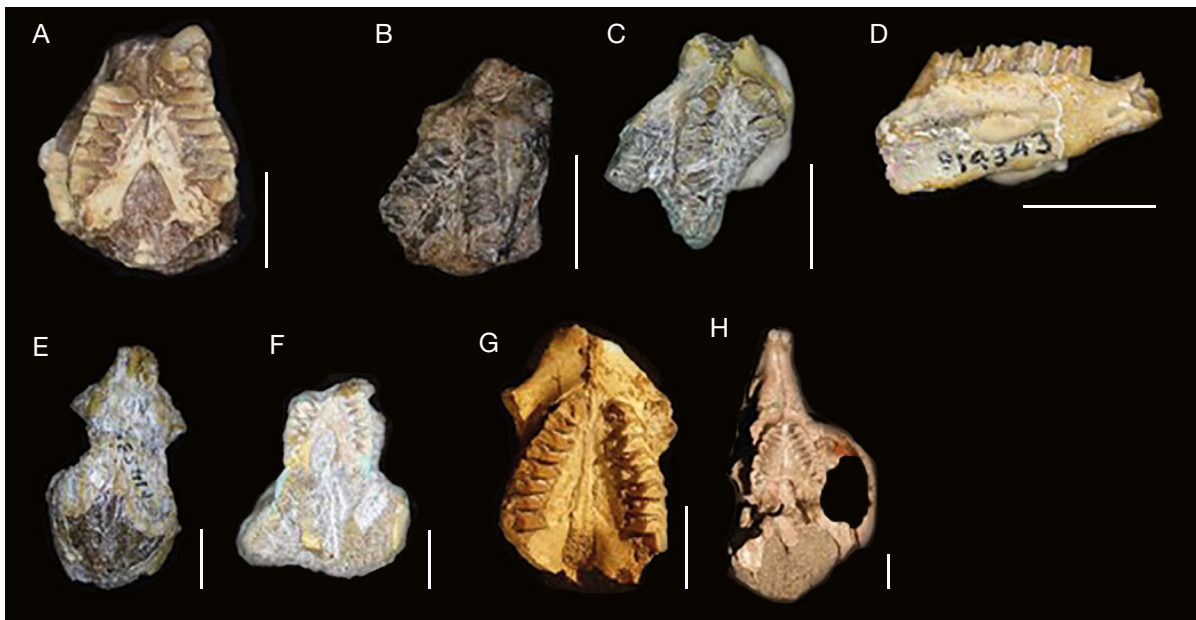
The CRILAR Pv 423 is a left mandible with the p4-m3 series from the Salica Formation (Brandoni *et al.* 2012). The molariforms are larger and less rounded than in *O. andina*, in this work, we refer to them as Dolichotinae.

The insolated molars (JUY-P-146) from the Guanaco Formation (late Miocene; Ercoli *et al.* 2019), differ from *O. rigens* to have opposite furrow and are smaller (for measurements Ercoli *et al.* 2019) than the holotype of *O. rigens* (MACN-A 1661).

APPENDIX 7. — Compared measurements (in mm) of the molariforms of remains misassigned or described as *Orthomyctera rigens* (Ameghino, 1888), “*Orthomyctera andina*” (Rovereto, 1914) or *Orthomyctera* sp. Abbreviations: **LAP**, anteroposterior length; **LLA**, anteroposterior length of anterior lobe; **LPL**, anteroposterior length of posterior lobe.

Measures	Orientation	FNMH-P 15300	FNMH-P 15250	FNMH-P 14343	FNMH-P 14463	MAS-P006	PVL 4891
LAP dental series	right	–	–	12.21	–	16.39	18.77
	left	–	16.05	–	–	–	–
LAP P4	right	2.71	–	–	–	4.41	4.19
	left	2.80	–	–	–	–	–
LLA	right	1.23	–	1.36	–	2.25	2.03
	left	1.28	–	–	–	–	–
LPL	right	1.37	–	–	–	1.77	1.97
	left	1.31	2.12	–	–	–	–
LAP M1	right	2.92	3.16	2.77	–	4.02	3.84
	left	2.98	3.31	–	2.90	–	–
LLA	right	1.21	1.45	1.23	–	1.87	1.81
	left	1.13	1.58	–	1.30	–	–
LPL	right	1.55	1.49	1.51	–	1.92	2.04
	left	1.37	1.53	–	1.28	–	–
LAP M2	right	–	3.35	3.26	2.00	4.23	4.40
	left	2.80	3.54	–	2.93	–	–
LLA	right	1.43	1.52	1.61	0.97	2.05	1.86
	left	1.28	1.50	–	1.28	–	–
LPL	right	–	1.68	1.50	1.19	1.96	2.30
	left	1.37	1.80	–	1.47	–	–
LAP M3	right	–	4.95	2.90	3.00	6.13	6.13
	left	–	4.89	–	4.08	–	–
LLA	right	–	1.66	1.12	1.00	1.93	1.96
	left	1.22	1.57	–	1.25	–	–
LPL	right	–	3.12	1.64	2.00	3.76	3.71
	left	–	3.19	–	2.63	–	–

APPENDIX 8. — **A, B**, Specimen referred to as *Orthomyctera rigens* (Ameghino 1888). FMNH P 15250 **B**. FMNH P 15300; **C-F**, specimens referred to as *Orthomyctera andina* (Rovereto, 1914); **C**, FMNH P 14337; **D**, FMNH P 14343; **E**, FMNH 14534; **F**, FMNH 14463; **G, H**, specimens referred to as *Orthomyctera* Ameghino, 1889: **G**, MAS-P 006; **H**, PVL 4891. Scale bars, 10 mm.



APPENDIX 9. — Assigned material with their geographical and stratigraphic provenance of *Orocavia andina* n. comb.

Andalhuala locality, Catamarca Province, Santa María Valley. Late Miocene-early Pliocene.

MACN-Pv 8300, right mandible fragment with p4-m3

MACN-Pv 8347, palatal fragment with right P4-M2 and fragment of M3 and left P4-M1.

MACN-Pv 8349, left mandible fragment with p4-m2

MACN-Pv 8350, fragment of skull and mandible with complete dental series (holotype)

MACN-Pv 8351, fragment of skull with complete dental series

MACN-Pv 8399, fragment of skull with complete dental series

MACN-Pv 8401, fragment of skull with complete dental series

MACN-Pv 8402, palatal fragment with complete dental series

MACN-Pv 8403, palatal fragment with left P4-M3 and right P4-M2

MACN-Pv 8404, palatal fragment with left M1-M3 and right P4-M1

MACN-Pv 8409, palatal fragment with left M1-M3.

MACN-Pv 8411, right mandible fragment with m1-m3

MACN-Pv 8412, right mandible fragment with p4-m3

MACN-Pv 8414, left mandible fragment with p4-m3

“Al sureste de ex Chiquimil”, [Southeast from ex Chiquimil],

Entre Ríos locality, Catamarca Province, Santa María Valley.

Late Miocene-Early Pliocene.

PVL 3293, left mandible fragment with p4-m3

Entre Ríos (Chiquimil) locality, Catamarca Province, Santa María Valley, Andalhuala Formation, level XVIIIa (Marshall & Patterson 1981). Late Miocene.

FMNH PM 1094, fragment of right mandible with p4-m2

Entre Ríos (Chiquimil) locality, Catamarca Province, Santa María Valley, Andalhuala Formation, level XVIIIb (Marshall & Patterson 1981). Late Miocene.

FMNH P 14370, fragment of skull with complete dental series and atlas

Loma Rica, locality, Catamarca Province, Santa María Valley, Andalhuala Formation, level XVII (Marshall & Patterson 1981). Late Miocene.

FMNH P 14464, fragment of skull with complete dental series.

Villavil locality, Catamarca, Villavil-Quillay basin, Chiquimil Formation, El Jarillal Member, Late Miocene (Powell *et al.* 1998; Esteban *et al.* 2014)

MCH-P 90, fragment of skull with right complete dental series and left P4-M2 and anterior lobe of M3

MCH-P 91, fragment of skull with left M1 and right M1-M2

MCH-P 94, left mandible fragment with p4-m2

MCH-P 345 right mandible fragment with p4-m2

MCH-P 346 left mandible fragment with m1-m2

MCH-P 360 left mandible fragment with m1-m2

MCH-P 361 left mandible fragment with m1-m2

PVL 4892, fragment of skull with complete dental series

Western Slope of Cerro Pampa (San Fernando Sur locality), Catamarca, Villavil-Quillay basin, Andalhuala Formation, Late Miocene-Early Pliocene (Bonini *et al.* 2021)

MCH-P 366 maxilla fragment with right P4-M2 and fragment of M3 and left P4-M1 and left mandible fragment with m1 (1688 m; 5.59-4.79 Ma).

MCH-P 367 left mandible fragment with p4 (*c.* 7-5.59 Ma).

APPENDIX 10. — Reduced consensus from the 1774 most parsimonious phylogenetic trees. Available at: https://doi.org/10.5852/cr-palevol2024v23a20_s3