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Systematic revision of *Neoreomys huilensis* Fields, 1957 (Rodentia, Hystricognathi) from the Middle Miocene of La Venta (Villavieja, Colombia)

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ABSTRACT

Neoreomys Ameghino, 1887 is among the most representative genera of South American Miocene rodents. The systematics of this taxon have been unclear, but currently, the most accepted hypothesis places it within Cavioidea, with ambiguous relationships inside the clade. *Neoreomys* is abundant and well-represented at high latitudes, with two species from the Early Miocene of Patagonia: *N. australis* Ameghino, 1887 and *N. pinturensis* Kramarz, 2006. A third species, *N. huilensis* Fields, 1957, is recognized from the Mid-Miocene of La Venta, Colombia, in low latitudes of South America. *Neoreomys huilensis* has been known from a few fragmentary specimens from which Fields (1957) described its holotype. Based on additional collections, Walton (1997) concluded that this species was probably not part of the genus. This study aims to reevaluate the taxonomy, phylogenetic relationships, and paleobiogeography of *N.huilensis* based on previously and recently collected materials. We present a detailed description of *Neoreomys huilensis*, corroborating the validity of this species as part of the genera. Our phylogenetic analysis is the first to include the three *Neoreomys* species, it supports the monophyly of the genus and suggests that it is not directly related to Dasyproctidae, instead corresponds to a plesiomorphic form within Cavioidea *sensu stricto*. Finally, we propose that the origin of the most recent common ancestor of the *Neoreomys* species could have occurred in the Andean region or some geographical location in mid-latitudes along the South American Transition Zone. A subsequent northward dispersal along the eastern flank of the Andes Mountain range would have given place to the appearance of *N. huilensis* in lower latitudes.

RÉSUMÉ

Révision systématique de Neoreomys huilensis *Fields, 1957 (Rodentia, Hystricognathi) du Miocène moyen de La Venta (Villavieja, Huila, Colombie).*

Le genre *Neoreomys* Ameghino, 1887 est emblématique des rongeurs du Miocène en Amérique du Sud. Sa systématique n'est pas claire, mais l'hypothèse la plus acceptée le place dans la super-famille Cavioidea, avec des relations ambigües au sein du clade. *Neoreomys* est abondant et bien représenté dans les latitudes élevées, avec deux espèces au Miocène inférieur en Patagonie : *N. australis* Ameghino, 1887 et *N. pinturensis* Kramarz, 2006. Une troisième espèce, *N. huilensis* Fields, 1957, a été décrite dans les latitudes basses du continent, au Miocène moyen de La Venta, en Colombie. *Neoreomys huilensis* a été décrit par Fields (1957) à partir de spécimens fragmentaires. Walton (1997) a conclu que sa classification au sein du genre devait être réévaluée. Le but de ce travail est de réanalyser la taxonomie de *Neoreomys huilensis*, ses relations phylogénétiques et ses implications paléobiogéographiques à partir d'anciens et de nouveaux matériel. Notre présentation décriptée et détaillée de *N. huilensis* confirme la validité de cette espèce en tant que partie du genre. Nous effectuons la première analyse phylogénétique incluant les trois espèces et soutenons la monophylie du genre, révélant qu'il n'est pas directement lié aux Dasyproctidae, mais qu'il correspond à une forme plésiomorphique au sein des Cavioidea *sensu stricto*. Enfin, nous proposons que l'ancêtre commun le plus récent des espèces de *Neoreomys* ait pu avoir son origine dans la région andine ou dans les latitudes moyennes, dans la zone de transition sud-américaine. Une dispersion vers le nord à travers la cordillère des Andes aurait conduit à l'apparition de *N. huilensis* dans des latitudes plus basses.

RESUMEN

Revisión sistemática de Neoreomys huilensis *Fields, 1957 (Rodentia, Hystricognathi) del Mioceno Medio de La Venta (Villavieja, Huila, Colombia).*

Neoreomys Ameghino, 1887 es uno de los géneros de roedores más representativos del Mioceno de Suramérica. Su sistemática ha sido confusa, pero actualmente la hipótesis más aceptada sitúa al género en Cavioidea, con relaciones ambiguas dentro del clado. *Neoreomys* es abundante y bien representado en latitudes altas, con dos especies del Mioceno Temprano en la Patagonia: *N. australis* Ameghino, 1887 y *N. pinturensis* Kramarz, 2006. Una tercera especie, *Neoreomys huilensis* Fields, 1957, fue descrita para latitudes bajas del continente, en el Mioceno Medio de La Venta, Colombia. *N. huilensis* fue descrita por Fields (1957) a partir de unos pocos especímenes fragmentarios. Posteriormente, Walton (1997) concluyó que su clasificación dentro del género debía ser reevaluada. El objetivo de este trabajo es reanalizar la taxonomía de *Neoreomys huilensis*, sus relaciones filogenéticas y sus implicaciones paleobiogeográficas a la luz del material previamente descrito y del nuevo material recolectado. Presentamos una descripción detallada de *N. huilensis* y corroboramos la validez de esta especie como parte del género. Además, realizamos el primer análisis filogenético que incluye a las tres especies y soporta la monofilia del género, revelando que no está directamente relacionado con Dasyproctidae, sino que corresponde a una forma plesiomórfica dentro de Cavioidea *sensu stricto*. Finalmente, proponemos que el ancestro común más reciente de las especies de *Neoreomys* podría haberse originado en la región Andina o en latitudes medias, en la zona de transición suramericana. Una dispersión hacia el norte a través de la cordillera de los Andes habría dado lugar a la aparición de *N. huilensis* en latitudes más bajas.

INTRODUCTION

The Caviomorpha clade includes the New World hystricognath rodents, which radiated into one of the most abundant and diverse groups of South American mammals by the end of the Paleogene (Landry 1957; Wood & Patterson 1959; Antoine *et al.* 2012; Boivin *et al.* 2017; Campbell *et al.* 2021; Arnal *et al.* 2022). During the beginning of the global cooling starting in the Oligocene (Zachos *et al.* 2001, 2008), caviomorph rodents were already highly diversified, had achieved a great eco-morphological diversity, and were distributed throughout the South American continent (Pérez & Pol 2012; Arnal & Vucetich 2015; Vucetich *et al.* 2015a; Rasia *et al.* 2021).

The caviomorphs from the Andean region (*sensu* Morrone 2004a, 2006) have been traditionally better known, mainly due to the good fossil record and excellent quality of the Cenozoic outcrops (Pérez & Pol 2012; Vucetich *et al.* 2015a). However, the exploration efforts in the Tropical region of the Americas (*sensu* Morrone 2014) during the last decades yielded significant contributions to the understanding of the evolutionary history of these rodents (Walton 1997; Frailey & Campbell 2004; Horovitz *et al.* 2010; Sánchez-Villagra *et al.* 2010; Croft *et al.* 2011a, 2016; Antoine *et al.* 2012, 2016; Vucetich *et al.* 2015b; Tejada-Lara *et al.* 2015; Kerber *et al.* 2017; Pérez *et al.* 2017; Assemat *et al.* 2019; Arnal *et al.* 2020, 2022; Campbell *et al.* 2021).

The La Venta fossil site (Fig. 1) in the upper Magdalena River valley (Colombia) has one of the most remarkable fossil faunas known from the Miocene of low latitudes of South America (e.g., Sánchez-Villagra *et al.* 2010; Carrillo *et al.* 2015; Antoine *et al.* 2016; Croft & Simeonovski 2016; Defler 2019). This vertebrate assemblage includes freshwater fishes, squamates, amphibians, crocodilians, turtles, birds, and at least 72 species of mammals (Kay *et al.* 1997). Its rich fossil record was the basis for defining the Laventan South American Land Mammal Age (SALMA) (Madden *et al.* 1997).

Among the extinct mammals collected at La Venta, about a quarter of the described taxa are caviomorph rodents (Fields 1957; Walton 1997). The rodent fauna from La Venta includes at least 20 species, with taxa representing the four main clades of Caviomorpha (i.e., Cavioidea, Chinchilloidea, Erethizontoidea, and Octodontoidea). Despite their importance and abundance, research on these rodents has been limited to a few studies conducted in the last century (Stehlin 1940; Fields 1957; Walton 1997) and more recently by Boivin *et al.* (2021). Other studies have only referred to the rodent material collected at La Venta or have established taxonomic comparisons with Laventan caviomorphs (e.g., Pérez 2010; Croft *et al.* 2011b; Tejada-Lara *et al.* 2015; Arnal *et al.* 2017).

One of the most representative taxa of the Miocene South American rodent fauna is *Neoreomys* Ameghino, 1887 (Ameghino 1887, 1889; Scott 1905; Fields 1957; Vucetich 1984; Kramarz 2006a; Vucetich *et al.* 2015a; Solórzano *et al.* 2020; McGrath *et al.* 2022; Vizcaíno *et al.* 2022). The phylogenetic relationships of this genus are unclear, and it has been suggested they may be related to Myocastorinae (e.g., Ameghino 1887, 1889), Capromyidae (e.g., Scott 1905; Fields 1957), or Dasyproctidae (e.g., Wood & Patterson 1959; Pat-

terson & Wood 1982; Vucetich 1984; Walton 1997; Kramarz 2006a). Patterson & Wood (1982) suggested the inclusion of *Neoreomys* in Cavioidea and this was recently supported by phylogenetic analyses (Boivin *et al.* 2019).

Neoreomys is highly abundant at high latitudes, mainly in Santa Cruz Formation in Argentina, with some specimens represented by skulls, teeth, and articulated skeletons (e.g., Scott 1905; Arnal *et al.* 2019). This genus has also been recorded at the Pinturas, Sarmiento, Collón Curá, and Cerro Boleadoras Formations in Argentina (Vucetich 1984; Vucetich *et al.* 1993; Kramarz 2006a; Kramarz *et al.* 2010; Vizcaíno *et al.* 2022), and at the Alto Río Cisnes, Curá Mallín, Trapa Trapa, and Galera Formations in Chile (Flynn *et al.* 2008; Bostelmann *et al.* 2012; Solórzano *et al.* 2020; McGrath *et al.* 2022). For the Santacrucian SALMA (Early – Middle Miocene; Cuitiño *et al.* 2016). Ameghino (1887) described up to nine species within the genus *Neoreomys* and subgenus *Pseudoneoreomys* for the Santa Cruz Formation. Later, Scott (1905) reduced this diversity to three species, while Fields (1957) proposed *Neoreomys australis* Ameghino, 1887 as the only valid species in the Santa Cruz Formation with a wide morphological and ontogenetic variation at the intraspecific level. This hypothesis was followed by Kramarz (2006a) and accepted in subsequent studies (Vucetich *et al.* 2015b; Arnal *et al.* 2019; McGrath *et al.* 2022; Vizcaíno *et al.* 2022). Kramarz (2006a) described *Neoreomys pinturensis* Kramarz, 2006 for the Early Miocene of Pinturas Formation, and with some specimens recorded in the Early Miocene of Sarmiento Formation, a few isolated teeth represent it. Additionally, López *et al.* (2011) mentioned a *Neoreomys* cf. *Neoreomys australis* for the Chinches Formation (Early Miocene, San Juan Province). Several specimens from the Early to Middle Miocene at high latitudes have been assigned to *Neoreomys* sp. (e.g., Vucetich 1984; Vucetich *et al.* 1993; Solórzano *et al.* 2020).

The only species of *Neoreomys* recorded from lower latitudes is *N. huilensis* Fields, 1957 from La Venta. Walton (1997) questioned the assignment of this species to the genus *Neoreomys*, so she included quotation marks on the generic name: "*Neoreomys*" *huilensis*. This taxon is recorded throughout La Victoria Formation and at the base of the Villavieja Formation, specifically in the Monkey Beds (Fields 1957; Walton 1997). This study aims to reanalyze the taxonomy and phylogenetic relations of *N. huilensis* (the only protohypsodont cavioid of La Venta) based on old and new collected materials from a taxonomic, phylogenetic, and biogeographic perspective.

GEOLOGICAL SETTING

All specimens come from the fossiliferous outcrops of La Venta, located in the Tatacoa Desert, on the upper valley of the Magdalena River at the northeast of the village of Villavieja, Huila Department in Colombia (Figs 1; 2). The fossiliferous sediments of La Venta span from *c.* 16 Ma to 10.5 Ma (Flynn *et al.* 1997; Montes *et al.* 2021; Mora-Rojas *et al.* 2023), with most of the sediment accumulation occurring between 13.8 and 11.8 Ma (Middle Miocene, Laventan SALMA; Madden
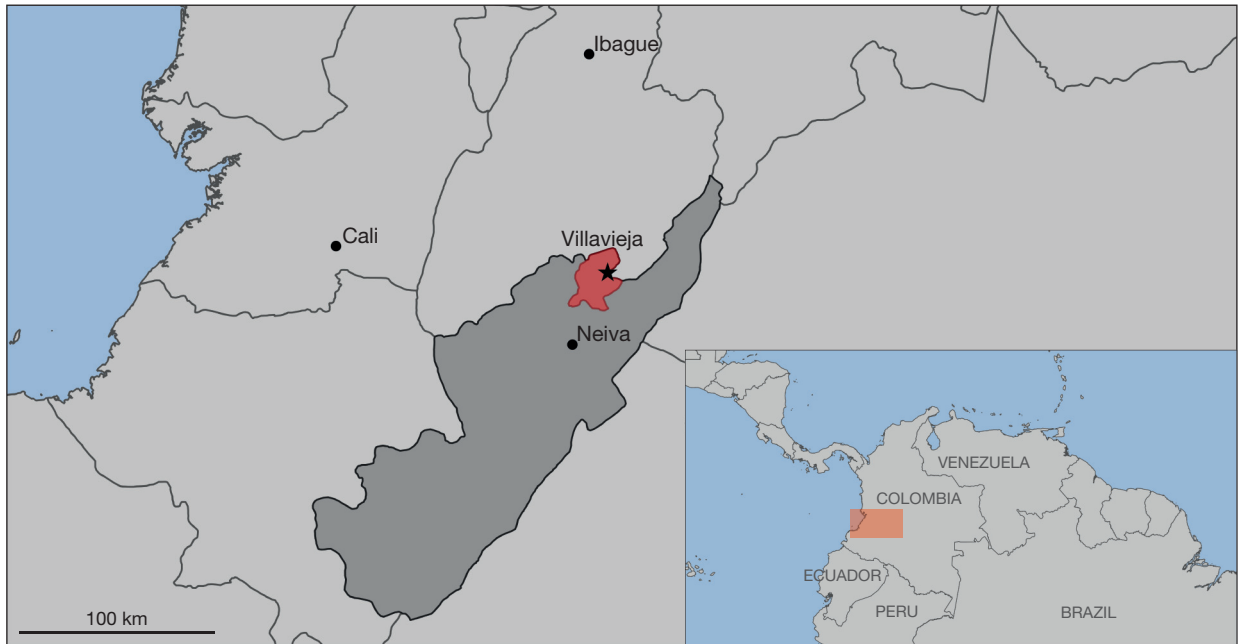
Fɪɢ. 1. — Geographic location of the Tatacoa Desert in Colombia, and bordering countries of South America.

et al. 1997). The Honda Group has been divided formally into two main units: the lower La Victoria Formation and the upper Villavieja Formation (Guerrero 1997; Montes *et al.* 2021; Mora-Rojas *et al.* 2023). The stratigraphic scheme of Montes *et al.* (2021) recognized the following units for the Honda Group. For the La Victoria Formation from the bottom to the top, the sequence is: "San Alfonso Beds", "Cerro Gordo beds", "Chunchullo Beds", "Tatacoa Beds", and "Cerbatana conglomerate beds". For The Villavieja Formation, the sequence from bottom to top is: "Cerbatana beds" (which includes the "Monkey beds", "Fish beds" and "Ferruginous beds" of Guerrero 1997), "La Venta Red Beds", and "El Cardón Red Beds" (Flynn *et al.* 1997; Guerrero 1997; Montes *et al.* 2021; Mora-Rojas *et al.* 2023). To see the provenance of the *Neoreomys huilensis* material herein mentioned, see Systematic Paleontology.

MATERIAL AND METHODS

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AMNH DPV — Department of Vertebrate Paleontology, American Museum of Natural History;

FMNH PM — Paleomammalogy, Field Museum of Natural History, Chicago, United States;

IGM (INGEOMINAS) — housed in Museo Geológico Nacional José Royó y Gómez (Servicio Geológico Colombiano), Bogotá, Colombia;

KU — (Kyoto University), housed in Museo Geológico Nacional José Royó y Gómez (Servicio Geológico Colombiano), Bogotá, Colombia;

MPEF-PV — Colección de Paleovertebrados, Museo Paleontológico Egidio Feruglio;

MPM-PV — Colección de Paleovertebrados, Museo Regional Padre Jesús Molina;

LA — Colección Paleontológica de la Universidad de Los Andes, Bogotá, Colombia;

UCMP — University of California Museum of Paleontology, Berkeley, California, United States;

VPPLT — Vigías del Patrimonio Paleontológico de La Tatacoa (Museo de Historia Natural La Tatacoa), Villavieja, Colombia;

YMS — (Field number), housed in Museo Geológico Nacional José Royó y Gómez (Servicio Geológico Colombiano), Bogotá, Colombia.

Aɴᴀᴛᴏᴍɪᴄᴀʟ ɴᴏᴍᴇɴᴄʟᴀᴛᴜʀᴇ

The dental terminology is based on Arnal & Vucetich (2015) and Boivin & Marivaux (2018) following modifications by (Arnal *et al.* 2019). The occlusal morphology of dp4 is here interpreted following Candela (2002). Lower cheek teeth are designated with lowercase letters, and upper cheek teeth with uppercase letters. Mandibular morphology and related nomenclature follow Woods & Howland (1979).

Pʜʏʟᴏɢᴇɴᴇᴛɪᴄ ᴀɴᴀʟʏsɪs

The affinities of *Neoreomys huilensis* within Cavioidea are tested using a modified version of the combined dataset from Pérez & Pol (2012) and Madozzo-Jaén *et al.* (2021). The modifications consist of the inclusion of two taxa: *Neoreomys pinturensis* and *Neoreomys huilensis*. The new dataset includes 79 taxa (i.e., 14 extant and 65 extinct) scored for 164 morphological characters (i.e., cranial, mandibular, dental, postcranial, and tegumentary) and 4014 mitochondrial and nuclear DNA sequences (i.e.,
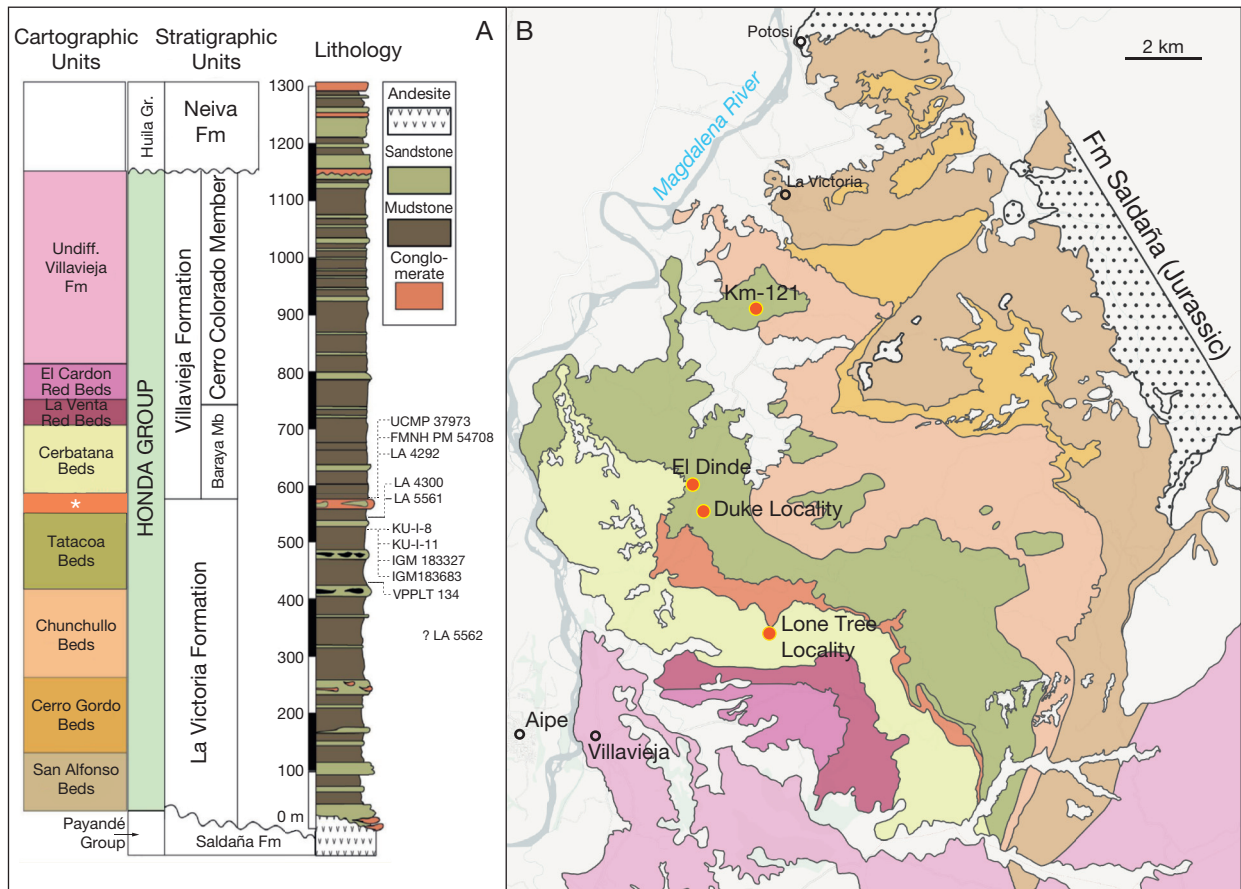
Fig. 2. — Geographic and stratigraphic occurrences of specimens of *Neoreomys huilensis*. **A,** Stratigraphic scheme of the Honda Group, La Venta (modified from Montes *et al.* 2021); and stratigraphic provenance of the fossil material. **B,** Map showing the localities where fossils were recovered on the geologic map of the Tatacoa desert (modified from Montes *et al.* 2021). The asterisk (*) denotes the Cerbatana conglomerate. LA 5562 comes from an unknown locality in the La Victoria Fm.

12s, Cyb, Tth and Ghr) taken from GenBank for ten extant cavioids (see Appendices 1; 2). The morphological data were mainly scored from the specimens directly, while in other cases, they were obtained from photographs and literature. The molecular data were aligned using CLUSTAL X (Thompson *et al.* 1997) using the default values of gap opening (10/100) and gap extension (0.1). In cases where the molecular data only indicated the generic name, they were kept the same so that parsimony analysis could be implemented in TNT. However, the species in the morphological dataset are *Proechimys poliopus*, *Cuniculus paca*, and *Dasyprocta azarae*. Thirty-nine multistate morphological partition characters were considered additive based on increasing degrees of similarity between the character states or in cases of nested homologies. The combined matrix was analyzed using TNT 1.5 (Goloboff & Catalano 2016), treating gaps as missing data for the DNA sequences. Equally weighted parsimony was used to minimize the number of postulated evolutionary transformations. 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. Support values were calculated using Bremer indices (Bremer 1994), as well as Bootstrap (Felsenstein 1985) and Jackknife (Lanyon

1985; Farris *et al.* 1996) resampling techniques. The modified Stratigraphic Manhattan Measure (Pol & Norell 2005) was used to calibrate the most parsimonious phylogenetic trees and the chronostratigraphic information for fossil taxa using TNT.

TAXONOMIC BACKGROUND

Fields (1957) described the species *Neoreomys huilensis* based on a left mandibular fragment preserving the incisor and p4-m3 (UCMP 37973; Fig. 3A-C; Fields 1957: fig. 28). Although the author mentioned a second specimen at the beginning of the discussion, he did not give specific details about the specimen or include it in the description. Fields only clarified that both specimens came from the same locality (Lone Tree in Monkey Unit; Fields 1957: 379). This author included *N. huilensis* in the genus *Neoreomys* given its similarity with the type species *Neoreomys australis* in the lower dental pattern, cheek teeth subhypsodont (relatively high dental crown with the formation of roots), broad hypoflexid, increasing size from m1 to m3, p4, and m3 equal in the anteroposterior diameter, relatively shallow and broad mandible, enlarged coronoid process, and a narrow alveolar border posterior to the m3.

Also, he differentiated *N. huilensis* from *N. australis* based on the size, some morphological characters of the mandible (e.g., more elevated alveolar border), and the anteroposterior extension of the incisor (Fields 1957:378-379).

Vucetich (1984:73) published some specimens assigned to *Neoreomys* cf. *Neoreomys australis* from the Middle Miocene of Patagonia (Río Frías Formation). The author explained that *N. australis* and *N. huilensis* are indistinguishable in dental morphology but that the Colombian species is smaller than Patagonia's. In addition, Vucetich (1984) considered that the fundamental differences between both species are in the skull; however, the fact that no known cranial remains are available for *N. huilensis*, prevents this hypothesis from being tested.

Analyzing specimens from the UCMP and new collections made by Duke University/INGEOMINAS, Walton (1997) reviewed the caviomorph fauna of La Venta, considering all materials available at the time. Regarding *Neoreomys huilensis*, Walton only provides the collection number and illustrations of three specimens: FMNH PM 54708 (Fig. 3G-I; Walton 1997: fig. 24.3A), IGM 183327 (Walton 1997: fig. 24.3B) and IGM 183683 (Walton 1997: fig. 24.3C). However, Walton (1997: fig. 24.9) also shows the minimum number of individuals of "*N.*" *huilensis* per stratigraphic level, indicating ten specimens from La Victoria Formation, and seven from Monkey Beds level in Villavieja Formation. Therefore, Walton (1997) had at least 17 specimens of "*N.*" *huilensis*. Walton regarded "*N.*" *huilensis* to be similar to the type species of *Neoreomys* but not close enough to be considered the same genus because "*N.*" *huilensis* has a slenderer incisor than *N. australis* and a pentalophodont dp4 that is tetralophodont in the type species (Walton 1997: 396). Moreover, with a more extensive specimen sampling, Walton also recognized a greater size range in "*N.*" *huilensis* than that previously recognized by Fields (1957). Madden *et al.* (1997: 513) explained that the assignment of "*N.*" *huilensis* to *Neoreomys* (Fields 1957) was possibly incorrect and that further taxonomic revision was needed; quotation marks were added to the generic name. Kay & Madden (1997: 547-550) listed the faunal assemblage of the vertebrate fauna from the Miocene Honda Group in appendix 30.1. They included "*N.*" *huilensis* and "*Neoreomys*" sp. nov. (large) [sic] without further explanation. However, this is likely because of the greater size range among "*Neoreomys*" specimens previously indicated by Walton (1997: 396).

Kramarz (2006a) established the species *Neoreomys pinturensis* from the Early Miocene of Patagonia. He indicated that the short ectolophid and the long mesolophid (= metalophulid II; see anatomical nomenclature above) on the cheek teeth of *N. pinturensis* are shared with *N. huilensis*, while in *N. australis*, these characters vary within the same dental series. In that study, Kramarz considered *N. huilensis* following Fields (1957), disregarding Walton's (1997) revision.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Parvorder CAVIOMORPHA Wood, 1955
Superfamily CAVIOIDEA (Fischer de Waldheim, 1817)

Genus *Neoreomys* Ameghino, 1887

TYPE SPECIES. — *Neoreomys australis* Ameghino, 1887 by original designation.

REFERRED SPECIES. — *Neoreomys australis* (type species), *Neoreomys huilensis* Fields, 1957, and *Neoreomys pinturensis* Kramarz, 2006.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION. — Pinturas and Santa Cruz formations (Early-Middle Miocene) in Chubut and Santa Cruz provinces (Bordas 1939; Kramarz 2006a; Kramarz *et al.* 2010; Arnal *et al.* 2019; Montalvo *et al.* 2019); Chinches Formation (late Early Miocene) in San Juan Province (López *et al.* 2011); Collón Curá Formation (Middle Miocene) in Chubut, Río Negro and Neuquén provinces (Bondesio *et al.* 1980; Vucetich *et al.* 1993); Río Frías Formation (Vucetich 1984), and Río Zeballos Formation (Pérez & Gonzáles Ruiz 2022) Chubut province; La Tiza Formation (Early Miocene), Neuquén Province, Argentina (Garrido *et al.* 2012). Cura-Mallín Formation (late Early-Middle Miocene) in Biobío Region, Pampa Castillo and Galera formations in Chile (Flynn *et al.* 2008; Solórzano *et al.* 2020; McGrath *et al.* 2022). La Victoria and Villavieja formations (Middle Miocene), in Huila Department, Colombia (Fields 1957; Walton 1997).

REMARKS
Neoreomys differs from *Dasyprocta*, *Myoprocta*, and *Cuniculus* in several characters of the skull and mandible (e.g., development and configuration of the masseteric crest, horizontal crest, notch for the insertion of the tendon of the *masseter medialis pars infraorbitalis* muscle; development of the bones that conform the zygomatic arch; convergence of the molar series; development of the maxillary and palatine bones in the palate). The crown of the cheek teeth of *Dasyprocta* and *Myoprocta* are much lower, and the occlusal surface is more complex than in *Neoreomys* (e.g., presence and development of lophs/ids; retention of fossettes/ids). Concerning *Cuniculus* and *Capromys*, the morphology of the occlusal surface differs from *Neoreomys* in terms of the depth of the flexi/flexids and the extension of the lophs/ids. The differences between *Alloiomys* and *Neoreomys* are detailed in Vucetich (1977). Still, they can be highlighted: cheek teeth higher than in *Neoreomys*, a solid tendency to lamination, abundant cement, and dental series more convergent than in *Neoreomys*. The cheek teeth in *Mesoprocta* (Croft *et al.* 2011a) are higher than in *Neoreomys* and do not form roots. The flexus/ids and fossetes/ids disappear more quickly with wear and present a significant quantity of cement. *Chubutomys* and *Phanomys* differ from *Neoreomys* in the higher degree of hypsodonty, more ephimerous flexus/ids and fossetes/ids, and less thick enamel layer (see Pérez & Vucetich 2012; Pérez *et al.* 2012).

FIG. 3. — *Neoreomys huilensis* Fields, 1957 from La Venta, Colombia: **A-C**, UCMP 37973 (holotype) left mandibular fragment with p4-m3; **A**, occlusal view; **B**, buccal view (reversed); **C**, lingual view; **D-F**, LA 4300 right mandibular fragment with dp4-m1; **D**, occlusal view (reversed); **E**, buccal view; **F**, lingual view (reversed); **G-I**, FMNH 54708 left mandibular fragment with dp4-m3; **G**, occlusal view; **H**, buccal view (reversed); **I**, lingual view; **J, K**, LA 5561 left mandibular fragment with p4-m3; **J**, occlusal view; **K**, buccal view (reversed); **L**, IGM 183327 right m2-m3 occlusal view (reversed); **M**, YMS-Y3 left m1-m3 occlusal view (reversed); **N**, KU-I-11 right m2 and m3 occlusal view (reversed); **O**, KU-I-18 left m1 occlusal view (reversed); **P**, LA5562 left m1 occlusal view (reversed); **Q**, VPPLT 134 left m3 occlusal view;
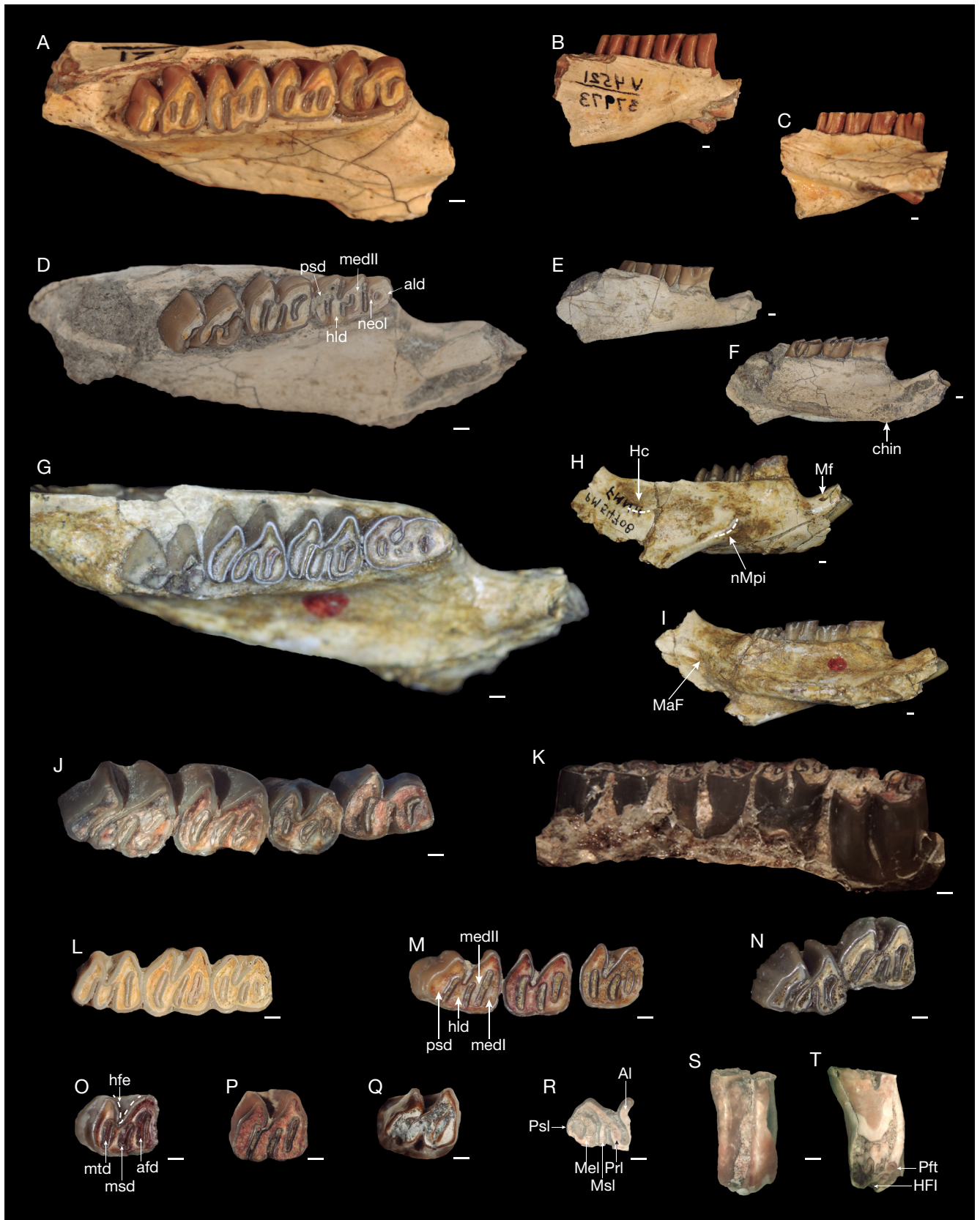
R-T, LA 4292 fragmentary left M3?; **R**, occlusal view; **S**, buccal view (reversed); **T**, lingual view. Mandibular nomenclature abbreviations: **Hc**, horizontal crest; **Mf**, mental foramen; **MaF**, mandibular foramen; **nMpi**, notch for the insertion of the tendon of the *masseter medialis pars infraorbitalis* muscle. Upper tooth abbreviations: **Al**, Anteroloph; **Mel**, Mesoloph; **Msl**, Metaloph; **Psl**, Posteroloph. Lower tooth abbreviations: **ald**, anterolophid; **afd**, anterofossetid; **hfld**, hypoflexid; **hld**, hypolophid; **medI**, metalophulid I; **medII**, metalophulid II;**msd**, mesofossettid; **mtf**, metafossettid; **neol**, neolophid; **psd**, posterolophid. Upper tooth abbreviations: **Al**, Anteroloph; **Hflx**, Hypofelxus; **Mel**, Metaloph; **Msl**, mesoloph; **Pft**, Parafossette; **Prl**, Protoloph. Scale bars: 1 mm.

TABLE 1. — Dental measurements of *Neoreomys huilensis* Fields, 1957 in milimeters. Abbreviations: **APL**, anteroposterior length; **AW**, anterior width; **PW**, posterior width.

Specimen	Tooth	APL	AW	PW
UCMP 37937	p4	4.28	2.82	3.32
	m1	4.27	3.66	–
	m2	4.16	3.87	3.87
	m3	4.54	3.81	2.98
FMNH 54708	dp4	5.48	2.71	3.21
	m1	4.55	3.86	3.81
	m2	4.76	3.77	3.44
	m3	4.52	3.28	2.59
KU-I-11	m2	5	4.27	4.13
	m3	5.32	4	3.36
KU-I-18	m2	4.32	3.93	3.8
LA 4292	M3	*c.* 3.938	3.116	*c.* 3.449
LA 4300	dp4	5.72	3.31	3.45
	m1	4.75	3.49	3.72
	m2	4.73	3.42	3.63
LA 5561	p4	4.99	2.9	3.81
	m1	4.1	3.68	3.39
	m2	5.06	3.86	3.98
	m3	5.85	3.84	3.6
LA 5562	m1	*c.* 4.87	4.36	3.89
IGM 183327	m1	4.39	4.25	4.37
	m2	5.05	4.86	4.89
	m3	5.13	4.46	3.8
IGM 183683	p4	6.12	4.15	5.1
	m1	5.51	4.63	5.19
	m2	6.09	5.05	5.16
VPPLT 134	m3	4.78	4.04	2.73
YMS-Y-3	m1	4.34	4.15	4.35
	m2	4.62	4.49	4.54
	m3	5.03	4.35	3.45

On the other hand, *Eocardia*, *Schistomys* and *Matiamys* presents euhypsodonts cheek teeth (continuous growth without root formation) (see Pérez 2010).

Neoreomys huilensis Fields, 1957

Neoreomys huilensis Fields, 1957: 376-380.

"*Neoreomys*" *huilensis* – Walton 1997: 396.

HOLOTYPE. — UCMP 37973, incomplete left dentary bone with p4 to m3 and the base of the incisor.

REFERRED SPECIMENS. — FMNH PM 54708, left mandibular fragment with dp4 to recently erupted m3 and the base of the incisor. — IGM 183327, rigth mandibular fragment with m1-m3. — IGM 183683, rigth mandibular fragment with p4 to m2 (although Walton considered it as m1-m3). — KU-I-11, right mandibular fragment with m2 and m3. — KU-I-18, right mandibular fragment with m1. — LA 4292, fragmentary M3?. — LA 4300, right mandibular fragment with dp4, m1, recently erupted m2 and base of the incisor. — LA 5561, left mandibular fragment with p4 to m3. — LA 5562, mandibular fragment bearing m1 with negligible wear. — VPPLT 134, isolated left m3. — YMS-Y3, left mandibular fragment with m1 to m3.

STRATIGRAPHIC AND GEOGRAPHIC PROVENANCE. — The holotype (UCMP 37973) comes from the Lone Tree Locality, at the Monkey Beds, in the Cerbatana Beds, Villavieja Formation. — FMNH PM 54708 comes from the Monkey Beds, Villavieja Formation. — KU-I-8 and KU-I-11 come from the El Dinde Locality (3°16'48"N, 75°11'52"W), Tatacoa Beds, La Victoria Formation. — IGM 183327 and IGM 183683 come from the Tatacoa Beds, La Victoria Formation. — LA 4292 comes from the Monkey Beds, Villavieja Formation. — LA 4300 and LA 5561 come from "Duke Locality" (3°16'48"N, 75°11'45"W), Tatacoa Beds, La Victoria Formation. — LA 5562 comes from an unknown locality in the La Victoria Formation. — VPPLT 134 comes from the Km 121 Locality (3°19'29"N, 75°10'55"W), Tatacoa Beds, La Victoria Formation. — YMS-Y3, La Venta, unknown provenance.

REVISED DIAGNOSIS. — Cavioid rodent diagnosed by the following unique combination of characters: nearly 50% smaller than *Neoreomys australis* and *N. pinturensis*; cheek teeth high-crowned with the formation of roots, similar to *N. pinturensis* but lower than *N. australis*; mesial flexid on the anterior wall of the lower molars more persistent than in *N. australis* and *Luantus*, but less persistent than in *Asteromys*.

REMARKS
In addition to the holotype (UCMP 37973, Fig. 3A-C), the three specimens illustrated in Walton (1997: fig. 24.1.G and 24.3.A-C; FMANH PM 54708, IGM 183327 and IGM 183683) had an associated provenance in her work, but there was no data on each specimen's anatomy. IGM 183683 (a right mandibular fragment with p4-m2) is the largest specimen among the material assigned to "*Neoreomys*" *huilensis* by Walton (1997). Unfortunately, we were unable to locate this specimen for this review, and the collection number is currently assigned to a sloth *Pseudoprepotherium* (pers. comm. R. Kay 2021). Thus, it can only be compared and measured from Walton's publication (Walton 1997: fig. 24.3.C). We assigned IGM 183683 (as described by Walton 1997) to *N. huilensis*, given that its occlusal morphology resembles that of the other specimens here described. Nonetheless, size variation within our sample is not high enough to consider two taxa within it (even including IGM 183683; see Table 1), bearing in mind the wide variability in size observed in other species of the genus (see Table 2).

DESCRIPTION AND COMPARISONS
The sample consists mainly of dentary bones and lower cheek teeth; an isolated upper molar (LA 4292), was recently found and here referred to as *Neoreomys huilensis* by its size and morphological pattern (similar to the other *Neoreomys* species; see description below).

Dentary
The dentary bones are fragmentary; most of the sample consists of pieces of the corpus, and even in the most complete ones (e.g., Fig. 3A-I), most anterior and posterior portions were lost. The lateral wall, anteriorly to the p4, has a mental foramen close to the dorsal margin of the diastema that opens dorsolaterally (Fig. 3E, H) as in *N. australis* and *Dasyprocta* (the dentary of *Mesoprocta*, UF 26915 is deteriorated so the presence of a mental foramen cannot be confirmed; Croft *et al.* 2011a: fig. 4). The notch for the insertion of

TABLE 2. — Mean, number of specimens (**n**), standard deviation (**SD**), range, and variation coefficient (**VC**) for dental measurements, in millimeters, of three species of *Neoreomys*: *N. huilensis* Fields, 1957, *N. pinturensis* Kramarz, 2006, and *N. australis* Ameghino, 1887. The measurements for *Neoreomys australis* were taken from specimens housed at AMNH DPV, MPEF-PV, and MPM-PV, while the measurements for *Neoreomys pinturensis* were extracted from Kramarz 2006a. Abbreviations: **APL,** anteroposterior length; **AW**, anterior width; **PW**, posterior width, **TW**, Transversal Width.

Species	Locus	n	Measurement	Mean	SD	Range	VC
Neoreomys huilensis	p4	3	APL	5.13	0.93	1.84	18.13
			AW	3.29	0.75	1.33	22.80
			PW	4.08	0.92	1.78	22.55
	m1	8	APL	4.60	0.45	1.41	9.78
			AW	4.01	0.40	1.14	9.98
			PW	4.10	0.59	1.80	14.39
	m2	9	APL	4.87	0.56	1.93	11.50
			AW	4.17	0.54	1.63	12.95
			PW	4.16	0.58	1.72	13.94
	m1 or m2	17	APL	4.74	0.51	1.99	10.76
			AW	4.09	0.47	1.63	11.49
			PW	4.14	0.55	1.75	13.30
	m3	8	APL	4.89	0.58	1.91	11.86
			AW	3.86	0.47	1.34	12.18
			PW	3.24	0.43	1.21	13.27
Neoreomys pinturensis	p4	3	APL	7.47	0.84	1.50	11.24
			AW	5.50	0.80	0.44	14.55
	m1 or m2	7	APL	6.00	0.45	1.30	7.50
			AW	5.63	0.29	0.80	5.15
	m3	3	APL	6.13	0.55	1.00	8.97
			TW	5.83	0.21	0.30	3.60
Neoreomys australis	p4	10	APL	6.92	0.52	1.89	7.56
			AW	4.40	0.48	1.66	10.91
			PW	5.44	0.67	2.28	12.32
	m1	16	APL	6.34	0.84	2.83	13.25
			AW	5.46	0.53	1.54	9.71
			PW	5.56	0.57	2.22	10.25
	m2	14	APL	6.74	0.63	2.21	9.35
			AW	5.80	0.79	2.52	13.62
			PW	5.63	0.88	3.05	15.63
	m1 or m2	30	APL	6.53	0.76	2.85	11.64
			AW	5.62	0.68	2.52	12.10
			PW	5.59	0.72	3.05	12.88
	m3	9	APL	6.97	0.86	3.10	12.34
			AW	5.50	1.00	3.36	18.18
			PW	4.81	0.89	2.97	18.50

the tendon of the *masseter medialis pars infraorbitalis* muscle (nMpi) is below m1 and develops without forming a shelf around the notch (Fig. 3B, E, H). The nMpi is connected to the masseteric crest, which arises below the m1-m2. The horizontal crest is better observed in FMNH PM 54708 (Fig. 3H) as a low and broad ridge, similar to *N. australis*. On the medial side, the incisor is posteriorly extended at the level of the m3 (Fig. 3C, F, I). The incisor is slender, and the enamel face is less flattened than in *N. australis*. On LA 4300 (Fig. 3F), the chin seems to be at the level of the dp4/p4 and is not exposed on its lateral side, probably because it is broken. The mandibular foramen (MaF) is only observed in the most complete specimen (Fig. 3I) and is ventrally placed to the retromolar fossa, as in *N. australis*. The pterygoid fossa is shallow, like that of *N. australis*. The only dentary bone fragment assigned to *N. pinturensis* is broken and significantly deteriorated, so its morphology cannot be evaluated.

Lower cheek teeth
Almost all cheek teeth except for dp4 are tetralophodont with transverse and wide crests (Fig. 3A, D, G, J, L-Q). They are high-crowned with the formation of roots (i.e., protohypsodont sensu Mones 1982; hypsodont *sensu* Janis & Fortelius 1988), similar to *N. pinturensis*, but lower-crowned compared to *N. australis* at the same stage of wear (*sensu* Kramarz 2006a). The mesial and distal walls are convex, while the lingual margin is straight. The enamel layer is continuous and thick around the entire crown, so it is the one that delimits flexids and fossetids. The hypoflexid has the shape of a narrow "V" (as in the other species of *Neoreomys*), with straight borders, and reaches up to the transverse midpoint of the crown in occlusal view. Molars lack cementum in juvenile and adult ontogenetic stages (no known specimens in senile stages) as in *N. pinturensis*, while in *N. australis* it presents cementum only in senile ontogenetic stages. The lingual flexids become transversely elongated fossetids, more persistent than in *N. australis*, *Mesoprocta*, and *Dasyprocta*.

Deciduous premolar (dp4)
The dp4 is pentalofodont, mesiodistally longer (Fig. 3D, G), and lower-crowned than the other teeth (Fig. 3E, F, H, I). It has two big roots (mesial and distal) as in the dp4 of *N. australis* (e.g., MPEF-PV 1636), and other cavioids such as *Asteromys*, *Luantus*, *Phanomys*, or *Eocardia* (Kramarz 2006b; Pérez 2010; Pérez *et al.* 2012). The anterolophid is labiolingually short with a rounded mesial border, and the neolophid is long and straight. Between them is a small and round fossetid. From the protoconid area, lingually arises the metalophulid II and distally an oblique ectolophid. Between the neolophid and metalophulid II is a straight and labio-lingually very long labial flexid. A lingual spur of the ectolophid and a labial widening lingual portion of the metalophulid II could represent a mesolophid's lingual and labial portions. A central S-shaped fossetid separates these two structures. The hypoconid area is a little more lingual with respect to the protoconid area. The hypolophid is straight, and the posterolophid is long and distally convex. The hypoflexid is similar to that of other lower teeth, with the shape of a narrow "V", and its apex faces the hypolophid. The posteroflexid is thin, slightly convex, and still lingually open on LA 4300. This general morphology is similar to the dp4 of some specimens of *Dasyprocta* (e.g., FMNH 69559, FMNH 95792). In FMNH PM 54708 (Fig. 3G-I), the crown is more worn, the enamel layer is narrower than in the dp4 of LA 4300 specimen (Fig. 3D-F) and is entirely absent on the mesiolingual border. The hypoflexid closes and forms an hypofossetid. The lingual flexids are closed, and there are four small lingual fossetids that were about to disappear with wear; among them, the mesial and distal fossetids are transversally elongated, and the two central ones are subcircular (Fig. 3G). Among the reviewed specimens of *N. australis* with dp4, the specimen MPM-PV 19179 shows a similar (or even younger) ontogenetic stage to that of LA 4300 but with a higher degree of wear (Vizcaíno *et al.* 2022: fig. 9A). So far, no dp4 has been recognized for *N. pinturensis* (Kramarz 2006a) and *Mesoprocta* (Croft *et al.* 2011a).

Premolar (p4)
Only two sample specimens preserve their p4 (UCMP 37973 and LA 5561; Fig. 3A-C, J-K). The mesial and lingual margins of the crown are straight, whereas the distal border is slightly convex. On the mesial wall of both specimens is a straight metalophulid I. This lophid comprises a lingual and a labial portion, nearly joined in the holotype (UCMP 37973; Fig. 3A) and recently connected in the other specimen (LA 5561; Fig. 3J), forming a fossetid. This could result from merging a mesial flexid with the lingual anteroflexid that probably closes in the early stages of wear as occurs in *N. australis* (e.g., AMNH DPV 97727). The second crest in position (metalophulid II) converges with the metalophulid I in the metaconid area. The protoconid area and an oblique ectolophid form a labially convex region that is continuous with the hypolophid. The hypoconid area and the posterolophid form the transversally longest lophid that is as wide as the hypolophid. The mesoflexid is

still lingually open, very narrow, and much deeper in the lingual wall than the metaflexid, which is almost closed. In the holotype (Fig. 3A), the metaflexid and the hypoflexid are merged, splitting the occlusal surface completely. The meta- and hypoflexid separate at a slightly advanced wear stage (LA5561; Fig. 3J).

Lower molars
In the most juvenile specimens (Fig. 3D-I), the molars present a mesial flexid (flexid or notch between the protoconid and metalophulid I that disappears with wear) that has merged to the anteroflexid/anterofossetid, as in the p4 of the holotype (Fig. 3A). The mesial flexid is more persistent in *N. huilensis* than in *N. australis* and *Luantus propheticus* (e.g., Kramarz 2006b: fig. 3G), but more ephemeral than in *Asteromys punctus*. In the youngest individual (LA 4300; Fig. 3D), this mesial flexid has closed at the m1, forming part of the anterofossetid; but in the m2, it remains mesially open. Likewise, in the other juvenile specimen (FMNH PM 54708; Fig. 3G), the mesial flexid is closed in m1 and m2 but remains mesially open in m3. The protoconid + ectolophid area and the hypolophid form an oblique and wide lophid (e.g., m2 in Fig. 3D). From the metaconid area arises a wide lingual portion of the second lophid in position (m2 in Fig. 3D). At early stages of wear the hypoflexid and metaflexid merge as an extended flexid that splits the occlusal surface (m1 or m2 in Fig. 3D, G, P; m3 in Fig. 3A, D, G, J, N, Q), and the meso- and metaflexid are lingually open (Fig. 3D, G). The posterolophid is oblique and linguolabially short (m2 in Fig. 3D; m3 in Fig. 3A, G, J, Q).

At more advanced stages of wear (Fig. 3A, J, L, M, O), the metaflexid becomes wholly separated from the hypoflexid. Generally, the metaflexid closes lingually before the meso-flexid; however, this is variable, like the condition observed in *N. australis* or *Luantus*. Thus, three elongated and narrow fossetids are formed. Some molars (m 2-3, Fig. 3J) have an anterofossetid that splits into two smaller ones (labial and lingual). This variable condition is also observed in some specimens of *N. australis*, *Luantus propheticus,* and *Asteromys*. The hypoflexid is extended to less than half of the transverse occlusal area, and its apex is opposite to the hypolophid. The second crest in position (metalophulid II) is transversely long (Fig. 3D, G), as in *N. pinturensis*. The extension of the ectolophid and the second crest in position is variable in the cheek teeth of *N. australis*, both in the same dental series and among different specimens (see Kramarz 2006a). In the m3, the metaflexid remains lingually open and shows a noticeable reduction in the length of the posterolophid (Fig. 3A, J, N, Q).

Upper cheek teeth
The tooth described here is the first upper molar described for *Neoreomys huilensis*. A left upper molar, probably an M3, LA 4292 (Fig. 3R-T), displays a pentalophodont pattern as in *N. australis* and *N. pinturensis*. Although the mesial and labial walls of the tooth are broken, the enamel appears to be continuous around the crown, and lacks cement. The
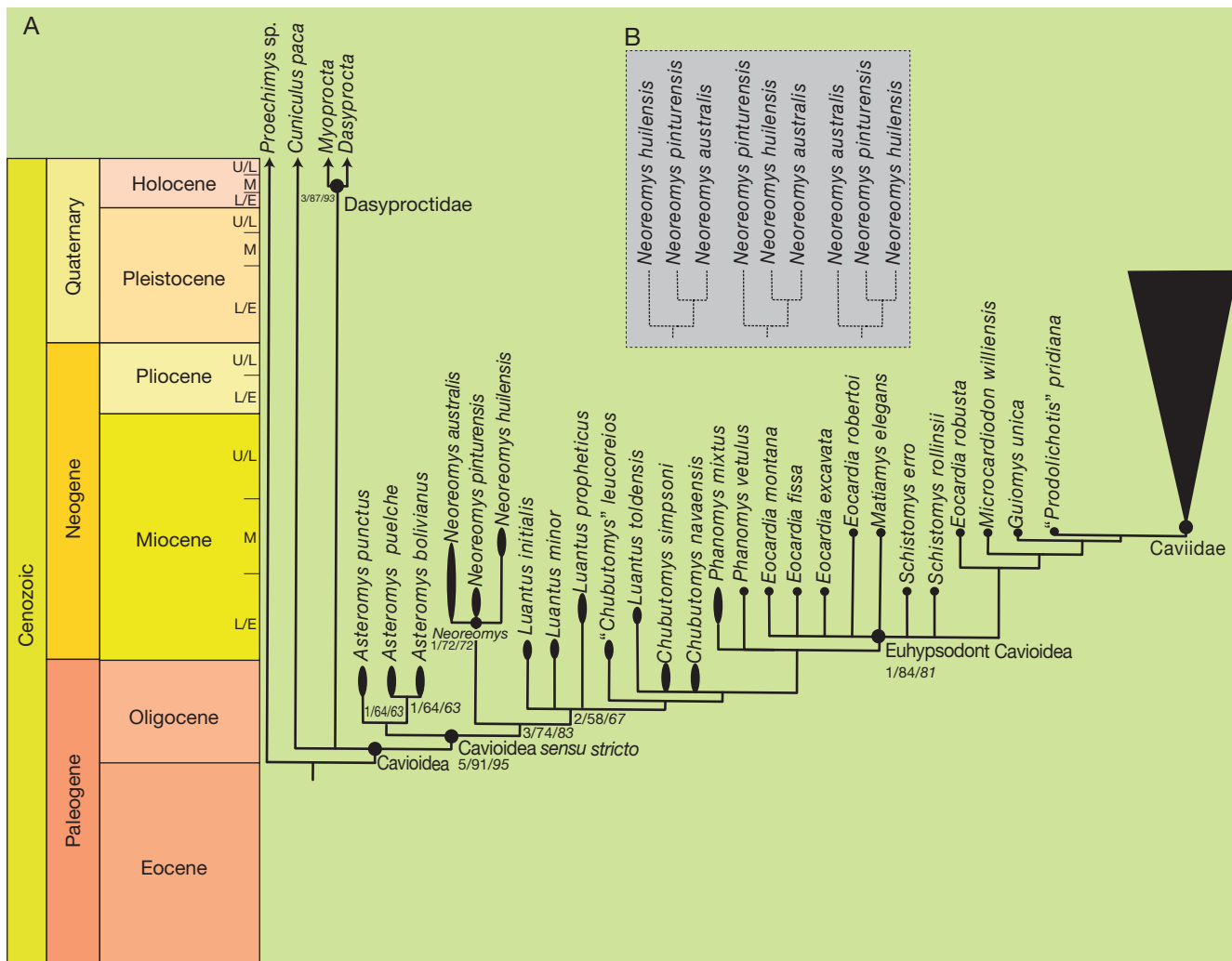
FIG. 4. — Reduced strict consensus of 1834 most parsimonious trees (MPTs) of 3433 steps of phylogenetic analysis showing *Neoreomys* Ameghino, 1887 clade nested within Cavioidea *sensu stricto*, and the polytomy among *N. huilensis* Fields, 1957, *N. australis* Ameghino, 1887, and *N. pinturensis* Kramarz, 2006. The strict consensus is calibrated against geological time. Regular numbers indicate Bremer support values; Bold numbers indicate Bootstrap values; Italicized numbers indicate Jackknife values at the main nodes. **B**, Different possible topological resolutions of the relationships among the three *Neoreomys* species.

tooth is high-crowned, and the hypoflexus is still open, but the base of the root is broken. At this stage of wear, the labial flexi/fossettes persist. In occlusal view, the hypoflexus is continuous with the parafossette (as in *N. australis* and *N. pinturensis*), the mesoflexus and metaflexus are labially open, and this latter is extended and narrow. The posterofossette is rounded, broad, and shallower than the others (Fig. 3R). The labial flexi is closed at the tooth base, the hypoflexus and parafossette are separated, and the para, meso, and meta fossettes are small and rounded (Fig. 3T). The mesio-distal length (even though the mesial border is broken) is greater than the transverse width (Table 1). Compared to other *Neoreomys* species in similar wear stages, the tooth is smaller, and the crests are relatively wider. The anteroloph is mesially broken. The protoloph is long and widens on the labial side. The third crest in position (mesoloph?) is long and straight. The metaloph is wide and relatively long and is attached to the posterloph. This posterloph is shorter and narrower than the others.

PHYLOGENETIC ANALYSIS

The phylogenetic analysis resulted in 1834 most parsimo-nious trees (MPTs) with tree lengths of 3433 steps. The reduced strict consensus of the MPTs is shown in Fig. 3A. *N. australis*, *N. huilensis,* and *N. pinturensis* form a poly-tomy (Fig. 4A) and share one unambiguous synapomorphy: hypoflexus/id of M1/m1-M2/m2 with the shape of a narrow V (124[1], in all MPTs). The possible resolutions of this node are shown in Fig. 4B. This polytomy happens due to the lack of a complete character set for *N. pinturensis* and *N. huilensis*, which are known by fragmentary specimens (only isolated teeth and broken mandibles). However, the available information from the fossil record is sufficient to support the close relationship between the three species and the monophyly of *Neoreomys*. This analysis also reveals that *Neoreomys* is nested within Cavioidea *sensu stricto* (Pérez 2010), being most closely related to *Luantus* and more derived cavioids than with the living Dasyproctidae

(*Dasyprocta* and *Myoprocta*, node Dasyproctidae). The following unambiguous synapomorphies support the most derived position of *Neoreomys* with respect to *Asteromys*: location of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* (nMpi) with respect to the tooth row below m1 (21[1]); anterior origin of the masseteric crest with respect to the tooth row between m1 and m2 (27[1]); the presence of cement in late ontogenetic stages (67[1]); transverse extension of the hfi/hfe (fundamental internal fissure [hypoflexus] / fundamental external fissure [hypoflexid], respectively) in M1/m1-M2/m2 of adult stage from the margin up to the transverse midpoint of the crown (122[1]); presence of a posterior projection of the posterior lobe in M3, when the pattern is not laminar (148[1]); and in some MPTs: protohypsodont, having the root and the anteroposterior length of the occlusal surface less than half the height of the crown (66[2]). Supporting analyses (Fig. 4A) yielded low Bremer values and relatively weak Bootstrap and Jackknife values for the *Neoreomys* clade due to lack of resolution.

DISCUSSION

TAXONOMIC STATUS AND SYSTEMATIC AFFINITIES OF *NEOREOMYS HUILENSIS*

The morphological characters that support the validity of *N. huilensis* are: tetralophodont pattern in lower molars and pentalophodont in upper ones, a lower degree of hypsodonty than in *N. australis*, smaller size than in the other species of *the* genus (Fields 1957; Walton 1997; Kramarz 2006a), mesial flexid in the anterior wall of lower p4-m3 more persistent than in *N. australis* and *Luantus* (e.g., Kramarz 2006b: 3F-G), but less persistent than in *Asteromys punctus* (e.g., Pérez & Vucetich 2012: fig. 2.3-2.4[longitudinal furrow]). Kramarz (2006a) proposed that *N. huilensis* shares with *N. pinturensis* more penetrating lingual flexids than in *N. australis*. However, the variability of the type species is too wide to confirm this hypotesis.

Our study comprises the first phylogenetic analysis that includes the three species of *Neoreomys* and supports the monophyly of the genus. The three species of *Neoreomys* form a polytomy, a clade with low support (Bremmer support = 1), in which they share one unambiguous synapomorphy (see Phylogenetic Analysis Section). The low resolution within the clade is due to the impossibility of scoring several characters in specimens of *N. pinturensis* and *N. huilensis,* which are mainly fragmentary remains. The cladistic analysis shows the position of *Neoreomys* as part of the stem group of Cavioidea *sensu stricto* (*sensu* Pérez 2010). This hypothesis was previously suggested by Vucetich *et al.* (2015a) and is corroborated now in this study. A more extensive taxonomic sampling of outgroups, such as cephalomyids, and representatives of other clades of caviomorphs, should be included to obtain a greater robustness of this hypothesis. According to support analyses (Bremmer, Jackknife, and Bootstrap), *Luantus* has closer affinities than *Asteromys*.

According to the latest phylogenetic analyses, including morphological and/or molecular data, Cavioidea includes three families: Cuniculidae, Caviidae, and Dasyproctidae (Dunnum 2015). The latter consists of the two extant genera, *Dasyprocta* and *Myoprocta* (e.g., Upham & Patterson 2015; Candela *et al.* 2021). However, phylogenetic relationships within Cavioidea of several fossil taxa are still unresolved. Although several taxa since the early Neogene have been considered members of the Dasyproctidae (e.g., *Australoprocta*, *Neoreomys*), recent phylogenetic analyses do not support this proposal (e.g., Boivin *et al.* 2019; Candela *et al.* 2021; this study). Furthermore, most of the fossil species assigned to Dasyproctidae have not yet been included in phylogenetic analyses within the Cavioidea (for example, *Andemys* [pan-Dasyproctidae *sensu* Bertrand *et al.* 2012], *Mesoprocta*, *Plesiaguti*). It is likely that those taxa that share a combination of character states, at least during certain ontogenetic stages, between living dasyproctids and cavids (e.g., high-crowned teeth with root formation, continuous enamel distribution, absence/presence of cementum, retention of fossettes/ids), form part of the stem-group of Cavioidea *s.s.* and are not directly related to Dasyproctidae. That is the case of *Neoreomys* in the present study, which is not directly related to *Dasyprocta* or *Myoprocta*.

Our phylogenetic results adjusted in a stratigraphic context (Fig. 4A) suggests that the lineage leading to the clade *Neoreomys* would have originated during the Oligocene, given the phylogenetic position of *Chubutomys simpsoni* and *C. navaensis*. The evolutionary novelties would have been acquired at least during the Deseadan SALMA (early - late Oligocene). This aligns with the pulse of diversification for Cavioidea, previously proposed by Pérez & Pol (2012) for the Oligocene, and coincides with the beginning of the "icehouse" worldwide and significant climatic-environmental changes that took place in South America (Zachos *et al.* 2001; Kohn *et al.* 2015; Selkin *et al.* 2015; Westerhold *et al.* 2020).

BIOGEOGRAPHIC IMPLICATIONS

As mentioned above, the phylogenetic analysis performed in this study would benefit from a broader taxonomic sampling. This would also help to establish more robust biogeographic patterns in some taxa of the stem-group of Cavioidea *s.s.* (e.g., *Asteromys*, *Neoreomys*). However, based on our review and the analysis presented here, we propose two alternative hypotheses about the origin of *Neoreomys* and a possible dispersion route that could have led to the speciation event that gave rise to *N. huilensis*.

Since many lineages of the stem Cavioidea *s.s.,* including the Paleogene indisputable cavioids, *Asteromys* and *Chubutomys,* share a Patagonian origin according to the available evidence (e.g., *Luantus*, *Phanomys*); proposing an Andean (*sensu* Morrone 2014) origin for the clade seems reasonable. If this is the case, the most recent common ancestor (MRCA) of the *Neoreomys* species would have originated in the southern part of the continent during the early-late Oligocene (Deseadan SALMA). Nevertheless, it is worth noting that as with *Neoreomys*, other related genera have representatives both in Patagonia and west-central Argentina as well as other

adjacent countries, as follows: Manantiales Basin (*Eocardia* and *Neoreomys*, López *et al.* 2011), and Quebrada Fiera (*Asteromys,* Candela *et al.* 2021) in Argentina; the Salla-Luribay Basin (*Asteromys*, Pérez *et al.* 2019) in Bolivia; and Alto Río Cisnes (*Neoreomys*, Bostelmann *et al.* 2012), Laguna del Laja (*Phanomys*, *Luantus*, *Neoreomys*, Solórzano *et al.* 2020), and Pampa Castillo (*Eocardia*, *Luantus*, *Neoreomys*, McGrath *et al.* 2022) in Chile. Given this, we propose that it is also probable that the event that gave origin to the clade that led to the *Neoreomys* species could have taken place in mid-latitudes of the continent, in some geographical location along the South American Transition Zone (*sensu* Morrone, 2004a, 2004b, 2006, 2014), an area where multiple ecological and historical processes took place (Morrone 2004b, 2014; Goin *et al.* 2016; Morrone *et al.* 2022).

Whether the MRCA of *Neoreomys* originated in the Andean region or the South American Transition Zone, the presence of *N. huilensis* in the Middle Miocene sediments of Colombia suggests a dispersal of the genera towards low latitudes at some point between the Early and Middle Miocene. We propose as a possible dispersal route a migration northward, through the South American Transition Zone, along the eastern flank of the Andes, similar to movements seen in other caviomorphs and other mammal taxa (Pascual *et al.* 1996; Candela & Morrone 2003; Ortiz-Jaureguizar & Cladera 2006; Croft & Simeonovski 2016; Arnal *et al.* 2017).

Predominant climatic-environmental conditions at the beginning of the Neogene must have favored the proliferation of this taxon at the south of the continent since it is one of the most abundant caviomorphs in the Early Miocene deposits of Patagonia (represented by *N. australis* and *N. pinturensis*; Kramarz 2006a; Arnal *et al.* 2019), even being quite common in Middle Miocene Patagonian sites (represented by *Neoreomys* sp. [e.g., Vucetich *et al.* 1993], probably *N. australis* pers. obs. MEP). From Patagonia, the drastic climatic changes that started in the late Oligocene in this region could have promoted the dispersion (Ortiz-Jaureguizar & Cladera 2006). Migration to lower latitudes could have been favored by suitable habitats occurring along subandean environments. It would have been delimited by two barriers: the Andes Mountain range and the Arid Diagonal (a belt of arid and semi-arid climates that divides the Neotropical and the Andean Region and worked like a faunistic corridor; Goin *et al.* 2016).

According to the available data, the dispersal would have reached low latitudes, where the records of *N. huilensis* are found during the Middle Miocene at La Venta. However, the lack of evidence of *Neoreomys* individuals in other areas towards low latitudes, particularly in the northern Andes, presents a challenge in pinpointing a potential area in which *N. huilensis* diverged from other species within the genus. Moreover, despite intensive sampling efforts, the scarcity of *N. huilensis* at La Venta sets it apart from its southern relatives (particularly with *N. australis*), which may be attributed to multiple factors that remain unknown (e.g., evolutionary or ecological traits). To shed light on these matters, a thorough examination and analysis of these possibilities should be conducted in future studies.

CONCLUSIONS

We present a detailed description of the morphology of *Neoreomys huilensis* based on prevoisly described and recently collected material, from which we were able to corroborate the validity of the genus and the species. This study comprises the first phylogenetic analysis that groups the three *Neoreomys* species as a monophyletic group inside Cavioidea *s.s.*, and shows that this clade would have diverged from other cavioid during the Oligocene, but only diversified until the Miocene. Its position in the phylogenetic tree also reveals that these taxa are not directly related to Dasyproctidae, as it was previously proposed, but instead, it would correspond to an early diverging lineage form within the clade Cavioidea *sensu stricto* that includes the crown Caviidae. Finally, we propose that the origin of the MRCA of the *Neoreomys* species could have taken place in the Andean region or in some geographical location, in mid-latitudes along the South American Transition Zone, with a subsequent northward dispersal along the eastern flank of the Andes Mountain range, until reaching lower latitudes.

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Appendix 1. — Integrated Morphological and Molecular Data Matrix. This text file, generated by the TNT program, presents a combined matrix encompassing morphological and molecular data. https://doi.org/10.5852/geodiversitas2023v45a25_s1

Appendix 2. — Morphological Character List and GenBank Accessions. This Word file provides a comprehensive compilation of morphological characters used and the character states, accompanied by the GenBank accession numbers for molecular data. https://doi.org/10.5852/geodiversitas2023v45a25_s2