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Morphological novelties from additional specimens of the Middle Miocene Proteropithecia neuquenensis (Primates, Platyrrhini), and new absolute age of its type locality in Argentine Patagonia

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Morphological novelties from additional specimens of the Middle Miocene *Proteropithecia neuquenensis* (Primates, Platyrrhini), and new absolute age of its type locality in Argentine Patagonia

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Abstract

Proteropithecia neuquenensis, from the Middle Miocene Collón Curá Formation of Cañadón del Tordillo, Neuquén Province, Argentina, represents the youngest known fossil primate from Patagonia, and has been regarded as an early representative of the Pitheciinae. However, its fossil record remained scarce and consisted predominantly of isolated teeth, limiting morphological and evolutionary interpretations. Here we describe seven new primate specimens from Cañadón del Tordillo, including the first mandibular symphysis attributed to *Proteropithecia*, preserving p2–p3 and the roots of the anterior dentition, as well as a complete lower canine and isolated upper and lower teeth, which also include the first upper molars for the genus. The mandibular symphysis provides previously unknown information on the anterior dentition and reveals a combination of features characteristic of pitheciines, including procumbent incisors, a relatively large canine, and an enlarged and projecting p2. Additional dental remains show further similarities with extant pitheciines, including incipient enamel crenulation. We also obtained a new U–Pb zircon age of 15.3 ± 0.5 Ma for the pyroclastic middle member of the Collón Curá Formation at Cañadón del Tordillo, providing a new temporal constraint for the fossil-bearing succession. Together, the new morphological and geochronological evidence improves our knowledge of *Proteropithecia* and strengthens its morphological affinities with crown Pitheciinae, with implications for understanding the early evolutionary history of the clade in South America.

Keywords: Fossil platyrrhines, Collón Curá Formation, *Proteropithecia*, *Soriacebus*, *Mazzonicebus*, pitheciines

1. Introduction

During the Early to Middle Miocene, approximately from 20 to 15.8 Ma, the southernmost region of South America, Patagonia, developed suitable environments that were inhabited by at least eight genera and eleven primates species documented across four geological formations (see Tejedor and Novo 2018, and references therein). This time period is coincident with the environmental trends towards the Miocene Climatic Optimum (Steinthorsdottir et al. 2021, and references therein), when the platyrrhine primates expanded their geographic distribution to the southernmost regions of South America (Silvestro et al. 2019). However, platyrrhines appeared in the fossil record of Patagonia by the Early Miocene in four localities of the Sarmiento Formation (Fm) in the Argentine province of Chubut, where three species have been described: *Tremacebus harringtoni* from Sacanana (Rusconi 1933; Herskovitz 1974), *Dolichocebus gaimanensis* from Gaiman (Bordas 1942; Kraglievich 1951; Kay et al. 2008), and *Mazzonicebus almendrae* from Gran Barranca (~20 Ma; Kay 2010) and La Estrella (Novo et al. 2017). In addition, two isolated teeth from the Cerro Bandera Fm, in Neuquen province, have been referred to an indeterminate taxon that may be somewhat older than the specimens from Chubut (Kramarz et al. 2012).

In addition, other primate discoveries came from Santa Cruz Fm (Early Miocene, ~16.5 Ma, Tejedor et al. 2006; ~16.9 Ma; Trayler et al. 2020) located in the southeastern coastal area of Santa Cruz Province, where the number of fossil taxa remains controversial. Currently, *Killikaike blakei* (Tejedor et al. 2006) as well as two species of *Homunculus, H. patagonicus* and *H. vizcainoi*, have been reported (Ameghino 1891; Tauber 1991; Tejedor and Rosenberger 2008; Perry et al. 2010, 2014; Novo et al. 2018; Kay and Perry 2019). The biggest diversity of species comes from the

Early Miocene Pinturas Fm, in northwestern Santa Cruz Province (~17 Ma for the primate levels of the Fm), representing the second largest assemblage of fossil platyrrhines after La Venta, in Colombia (see Novo et al. 2021). At least two genera and four primate species have been recognized in this unit: *Carlocebus carmenensis*, *Carlocebus intermedius*, *Soriacebus ameghinorum*, and *Soriacebus adrianae* (Fleagle et al. 1987; Fleagle 1990), as well as a third yet unpublished genus (Tejedor et al. Ms).

The youngest known Patagonian primate is *Proteropithecia neuquenensis* from the Middle Miocene Collón Curá Formation at Cañadón del Tordillo, Neuquén Province (Pardiñas 1991; Kay et al. 1998; Novo et al. 2025). This taxon is also among the northernmost Patagonian primate records, except for the older indeterminate specimens from the Cerro Banderas Formation, located slightly farther north in Neuquén Province (Kramarz et al. 2012). Its temporal and geographic position makes *Proteropithecia* particularly relevant for assessing the latest record of primates in Patagonia and their possible biogeographic relationships with younger platyrrhine radiations at lower latitudes. Despite this significance, *Proteropithecia* remained poorly known. Previously described material comprises 18 specimens, predominantly isolated teeth together with a talus (Kay et al. 1998; Novo et al. 2025). Additional primate remains from Middle Miocene deposits at Alto Río Cisnes, Chile, show morphological affinities with *Proteropithecia* and may represent a broadly comparable record from southern South America (Bobe et al. 2022).

The age of the Cañadón del Tordillo primate assemblage has traditionally been constrained by a $^{40}Ar/^{39}Ar$ age of 15.71 ± 0.07 Ma attributed to the underlying Pilcaniyeu Ignimbrite (Kay et al. 1998). However, the provenance and analytical uncertainty of this determination were not documented in the original source cited by Kay et al. (1998).

Here, we describe seven new specimens attributed to *Proteropithecia*, from fossil-bearing beds immediately above the Pilcaniyeu Ignimbrite, and provide a new U-Pb age for the ignimbrite at Cañadón del Tordillo. Together, the new fossil material and geochronological data improve the morphological and temporal framework of the youngest known Patagonian primate.

2. Geological background

The Cañadón del Tordillo site is located in the present-day Limay River drainage basin (-40.384444, -70.202500), approximately 40 km southwest of Piedra del Águila, Neuquén Province, Argentina (Fig. 1a, b). The locality comprises a NW–SE trending canyon, approximately 7 km long and 3 km wide, bounded by basement highs to the northeast, northwest, and southwest. These highs are composed of Paleozoic igneous-metamorphic rocks, including the Mamil Choique Formation and the Yuncón Granite (Fig. 1c). The Collón Curá Formation crops out discontinuously along the axis of the canyon, where at least five fossiliferous sites have been recognized. The exposures are largely surrounded and locally by a regional mantle of modern alluvial sediments (Fig. 1c; Vucetich et al. 1993).

At Cañadón del Tordillo, the Collón Curá Formation (Yrigoyen 1969; Cucchi et al. 1998) was subdivided into three members by Vucetich et al. (1993): the Lower Member, the Pilcaniyeu Ignimbrite (Middle Member), and the Upper Member. The Lower and Upper members consist predominantly of volcaniclastic deposits and contain fossil-bearing levels, whereas the Middle Member corresponds to a primary pyroclastic deposit (Rabassa 1975; Mazzoni and Benvenuto 1990). The Pilcaniyeu Ignimbrite is regionally distributed across northern Patagonia and constitutes an important

129 stratigraphic marker (Mazzoni and Benvenuto 1990; Vucetich et al. 1993; López et al.
130 2019).

131 Available radiometric ages indicate that deposition of the Collón Curá
132 Formation extended through a substantial part of the Middle Miocene. Early K-Ar
133 determinations of the Pilcaniyeu Ignimbrite yielded ages mostly between 15.4 and 14.0
134 Ma (Rabassa 1975; Marshall et al. 1977; Mazzoni and Benvenuto 1990). Flynn and
135 Swisher (1995) later reported at least twenty-five $^{40}Ar/^{39}Ar$ analyses of an ignimbrite
136 from four localities, all stratigraphically bracketed by Colloncuran faunas, with ages
137 tightly clustered around 15.7 Ma. Madden et al. (1997) also referred to a $^{40}Ar/^{39}Ar$ age
138 of 15.7 Ma for the Pilcaniyeu Ignimbrite in establishing the chronology of the
139 Colloncuran fauna. More recent U-Pb geochronology in northwestern Chubut Province
140 yielded maximum depositional ages of 14.7 ± 0.2 Ma and 10.1 ± 0.2 Ma for the lower
141 and upper parts of the Collón Curá Formation, respectively (Butler et al. 2020). Bucher
142 et al. (2019) obtained broadly consistent U-Pb ages from primary ash-fall deposits, with
143 14.45 ± 0.1 Ma from the lower part of the formation and 11.6 ± 0.4 Ma from the upper
144 part. The underlying La Pava Formation is also constrained by U-Pb geochronology,
145 with a maximum depositional age of 14.6 ± 0.4 Ma in northwestern Chubut (Butler et
146 al. 2020) and an age of 14.38 ± 0.19 Ma from a primary pyroclastic deposit in
147 southwestern Río Negro Province (Kramarz et al. 2025).

148 Kay et al. (1998), citing Madden et al. (1997), attributed a $^{40}Ar/^{39}Ar$ age of 15.71
149 ± 0.07 Ma to the Pilcaniyeu Ignimbrite at Cañadón del Tordillo. However, Madden et
150 al. (1997) provided neither the locality nor the analytical uncertainty associated with
151 their reported age of 15.7 Ma. Thus, although the succession at Cañadón del Tordillo
152 can be confidently assigned to the Middle Miocene, direct radiometric constraints on its
153 local stratigraphy remained limited.

3. Materials and Methods

3.1. Fossiliferous sites

At Cañadón del Tordillo locality, Vucetich et al. (1993) recognized five fossiliferous sites (Fig. 1c). Kay et al. (1998) retained this numbering scheme and reported that nearly all specimens of *Proteropithecia* were recovered from Site 4, except one specimen from Site 3. Here, we retain the original numbering of these five fossiliferous sites and recognize an additional one, designated here as Site 6. During our fieldwork, we did not recover fossils from Site 4 as designated by Kay et al. (1998). Based on our field observations and information provided by Ulyses F. J. Pardiñas (personal communication), who was the first to collect several of the specimens subsequently reported by Kay et al. (1998), we tentatively suggest that their Site 4 corresponds to our Site 1. This correlation remains provisional. Within Sites 1 and 6, individual fossil-bearing levels recognized in the measured sections are additionally identified by lowercase letters (Fig. 2). The new primate specimens reported here were recovered from levels 1b and 5a.

FIGURE 1 HERE

3.2. Fossil material

The newly discovered primate specimens include a partial mandibular symphysis (MMCh-PV 350) with right p2-3, a right c_1 (MMCh-PV351), a left P^2

(MMCh-PV 349), a right lower m1or m2, an M1 or M2 (MMCh-PV 347), and an M3 (MMCh-PV 348). The specimens will be housed permanently at the Colección de Paleontología de Vertebrados of the Museo Municipal 'Ernesto Bachman' (MMCh-PV), Villa El Chocón, Neuquén, Argentina.

The partial mandibular symphysis (MMCh-PV 350) and the isolated right canine (MMCh-PV 351) were micro-CT scanned and three-dimensional models were generated from the resulting datasets. The two elements were subsequently digitally articulated to evaluate their anatomical correspondence. The isolated canine precisely fits the preserved portion of the canine root within the mandibular symphysis, allowing the original position and orientation of the tooth to be reconstructed. The three-dimensional models and associated digital data have been deposited in a digital repository x

The new specimens were described qualitatively and quantitatively, and compared with previously described material attributed to *Proteropithecia* (Kay et al. 1998; Novo et al. 2025), as well as with other Patagonian primates, including *Soriacebus* and *Mazzonicebus*. Dental measurements are presented in Table 1.

3.3. Sedimentary sections and sampling

Two sedimentary sections (T1 and T2; Figs. 1c and 2) were measured to establish the stratigraphic position of the fossil-bearing levels and the sample collected for geochronological analysis. Section T1 encompasses the Lower, Middle, and Upper members of the Collón Curá Formation, whereas section T2 exposes only the Upper Member. The sections were correlated based on their stratigraphic and lithological relationships. Descriptive logs record lithology, grain size, sedimentary structures, and

pedogenic features. Volcaniclastic deposits were described following the terminology of Chough and Sohn (1990).

FIGURE 2 HERE

3.4. Geochronology

Sample LIdat, approximately 2.4 kilograms of material, was collected from the base of the Pilcaniyeu Ignimbrite (Middle Member) in section T1 for U-Pb zircon geochronology (Fig. 2).

Sample preparation and U-Pb analyses were performed at the Centro Tecnológico Productivo I+D LA.TE. ANDES (Salta, Argentina) for. The sample was crushed, ground, and sieved, and heavy minerals were concentrated using conventional mechanical, magnetic, and gravimetric techniques. Zircons grains were hand-picked under a binocular microscope and mounted in epoxy resin. U-Pb analyses were performed by LA-ICP-MS (Laser Ablation-Inductively Coupled Plasma-Mass Spectrometry) using a RESOlution 193 nm ablation laser system coupled to an Agilent Technologies 8900 triple-quadrupole ICP-MS. Analyses showing normal or reverse discordance greater than 12% were excluded. Ages are reported with absolute uncertainties of 1σ. The age of the Pilcaniyeu Ignimbrite was estimated using the Minimum Age Model implemented in Iso-plotR (Vermeesch 2018). Complete analytical data are provided in the Supplementary Material.

4. Results

224 *4.1. Sedimentology of the Collón Cura Formation at Cañadón del Tordillo*

225 The Collón Curá Formation at Cañadón del Tordillo reaches a composite
226 thickness of ~33 m thick and rests unconformably on the Paleozoic basement (Figs. 1c,
227 2). Its upper boundary is a sharp erosional surface overlain by modern alluvial deposits.
228 The succession comprises the Lower, Middle, and Upper members recognized by
229 Vucetich et al. (1983). The Lower and Upper members consist of broadly tabular,
230 poorly defined beds, generally 0.4 to 2 m thick (Fig. 2). They are composed of
231 brownish, poorly sorted, matrix-supported, tuffaceous conglomerates and fine- to
232 coarse-grained tuffaceous sandstones. Both lithologies are predominantly massive.
233 Pedogenic features are common and include blocky structure, carbonate nodules,
234 calcareous rhizocretions, rhizohaloes, and insect trace fossils.

235 Fossil remains occur in both the Lower and Upper members and are commonly
236 dispersed within massive tuffaceous sandstones beds (Fig. 2). The new primate
237 specimens were recovered from levels 1b and 5a within the Upper Member,
238 stratigraphically above the Pilcaniyeu Ignimbrite (Middle Member).

239 The Middle Member forms a broadly tabular unit that reaches ~7.5 m in
240 thickness along the axis and thins toward the basement high. It is composed of poorly
241 sorted, massive lapilli tuff containing inversely graded pumice clasts (Fig. 2). Where the
242 ignimbrite wedges out toward the basins margins, distinction between the Lower and
243 Upper members becomes less evident.

244 The tabular geometry, poor sorting, massive character, and volcaniclastic
245 composition of beds within the Lower and Upper members indicate deposition from
246 recurrent, largely unconfined sediment-gravity flows. Similar deposits elsewhere in the
247 Collón Curá Basin have been interpreted as product of non-channelized subaerial

248 volcaniclastic flows (López et al. 2022). The widespread development of pedogenic
249 features indicates that depositional events were separated by intervals of landscape
250 stability and soil formation. Together, these characteristics suggest episodic
251 volcaniclastic sedimentation within an alluvial setting. In contrast, the massive lapilli
252 tuff of the Middle Members records a primary pyroclastic depositional event and is
253 interpreted as a pyroclastic density-current deposit (PDC), consistent with previous
254 interpretations of the Pilcaniyeu Ignimbrite (Rabassa 1975; Mazzoni and Benvenuto
255 1990). Calcareous rhizocretions, becoming more abundant toward the upper part of the
256 composite succession, suggests comparatively drier soil-forming conditions through
257 time, consistent with the regional Middle Miocene climatic trend documented from
258 paleosols in northern Patagonia (Bucher et al. 2020).

259

260 *4.2. U–Pb LA-ICP-MS analyses*

261 A total of 55 zircon grains were analysed. Most grains are euhedral, 150–200 μm
262 long, and display elongate prismatic habits (Fig. 3a). Of the 55 analysed grains, 36
263 yielded concordant distribution (see Supplementary Material). Their age distribution is
264 multimodal, with three main populations of Middle Miocene, Cretaceous, and Permian
265 age (Fig. 3b, c).

266 The youngest population, comprising six zircons grains, yields a Minimum Age
267 Model of 15.3 ± 0.5 Ma (1σ; Fig. 3b), which is interpreted as the best estimate for
268 emplacement of the Pilcaniyeu Ignimbrite at Cañadón del Tordillo. The older
269 Cretaceous and Permian zircon populations are interpreted as inherited or reworked
270 components incorporated into the pyroclastic deposit.

271

FIGURE 3 HERE

4.3 Description and Comparisons of the new specimens

MMCh-PV 350 (Fig. 4a, d) is a right mandibular symphysis with p2-3 with a single root, canine root and procumbent four incisor roots, as well as relatively large alveolus of the right canine. The p2 is tall and projecting, with a predominant trigonid and a restricted talonid that is lingually open. The protoconid exhibits a buccal swelling at its base as is typical in platyrrhines, and is the unique cusp on the trigonid, from which a protocristid descends posterolingually to reach the moderately developed lingual cingulum that resembles that of MLP 1-121 (the only previously recorded p2; the other specimen, MLP 1-122, is lost). In both specimens, a moderately developed anterolabial cingulum is present, also similar to that observed in *Soriacebus*. As in all know platyrrhines, the talonid is small with the hypoconid and the entoconid absent. Although slightly longer anterolabially than MLP 1-122, they are similar in overall size. Morphological comparisons between these two premolars indicate close similarity, although more specific details are limited by the wear in MLP 1-122. Although MMCh-PV 350 is slightly smaller, it closely resembles the p2 of the holotype of *Soriacebus ameghinorum* (MACN Pv SC2) in general morphology, and a series of tiny enamel cuspules are seen on the lingual cingulum mesial to the protocristid, that are also present on p2 of the type of *Soriacebus ameghinorum*. Additionally, the p2 projects above the p3 similar of *Soriacebus*. The mesial side of the symphysis is procumbent as shown also by the incisor roots that are laterally compressed and the relative size of the incisors roots indicate that they were large. In overall morphology, the procumbent symphysis, incisors, and large canine indicate clear affinities with an adaptation as sclerocarpic harvesters, as

297 seen in modern pitheciines, adding that the p2 is further enlarged as in *Soriacebus*
298 *ameghinorum*. Even when the mandibular corpus below p2 is broken, it clearly indicates
299 a deepening posteriorly, as it is seen also in living pitheciines and the extinct
300 *Mazzonicebus*, but even deeper in *Soriacebus*. The p3 represents the first record of that
301 tooth for *Proteropithecia*. It has a single root, as in all know platyrrhines, and exhibits a
302 mesially closed trigonid basin, an incipient metaconid, a protoconid that is much less
303 developed than in p2, and the absence of a paraconid. The talonid has a short cristid
304 obliqua with an incipient hypoconid, whereas the entoconid is more developed. The
305 talonid is distally open, in this case through a postentoconid groove. No labial or lingual
306 cingula are present. Mesiodistally, the trigonid is slightly longer than the talonid.
307 MMCh-PV 351 (Fig. 4c, f) is a right lower c1, the only completely preserved
308 lower canine from Cañadón del Tordillo up to now, since the previously published right
309 lower canine MLP 90-II-20-65 (Kay et al. 1998) had a broken crown and little can be said
310 about its general morphology. This new canine has a long root, approximately two thirds
311 of the total length of the tooth. The crown is mesiodistally compressed, relatively
312 triangular in cross-section, giving two surfaces separated by a sharp entocristid, and has
313 a well-developed lingual cingulum. The overall morphology of the tooth indicates a
314 moderately projecting, and seemingly everted crown. The crown outline and height, as
315 well as the shape and orientation of the entocristid, the mesiolingual groove, and the
316 development of the lingual cingulum resemble the morphology seen in the left lower
317 canine MPEF-PV 5349 of *Mazzonicebus* (Kay 2010, Fig. 15.4a). On the other hand, since
318 the previous canine record from Cañadón del Tordillo (MLP 90-II-20-65) is broken, it is
319 not possible to assign it confidently either to *Proteropithecia* or *Mazzonicebus*.
320
321 FIGURE 4 HERE

MMCh-PV 349 (Fig. 5a) is a left P2 with a single root. The crown outline is subtriangular, and it bears a paracone well-developed, and an incipient protocone, being the hypocone absent. Labially, the pre and post paracrista end in a small parastyle and a broken metastyle, respectively; also, there is a poorly developed buccal cingulum. In comparison with the recently reported upper premolar (MMCh-PV 313; Novo et al. 2025) assigned to *Proteropithecia*, the two specimens exhibit differences particularly in overall width, and it may be due to the position in the dental series. This specimen represents the third upper premolar recovered from Cañadón del Tordillo (MLP 91 IX-1-133; Kay et al., 1998; MMCh-PV 313, Novo et al. 2025; and MMCh-PV 349, present work). As previously noted by Novo et al. (2025), MMCh-PV 313 is more comparable to the P3s in the maxillary fragments MPEF-PV 6282 and MPEF-PV 5344, both assigned to *Mazzonicebus almendrae* (see Kay 2010, figs. 15.8 and 15.9). In addition, MMCh-PV 313 also differs from MLP 91 IX-1-133 (Kay et al. 1998) in the more expanded buccal side with inflated enamel. For these reasons, MMCh-PV 313 has not been confidently referred to *Proteropithecia*, suggesting it may be a different taxon (Novo et al. 2025). The new premolar described here, that also shows differences with respect to MMCh-PV 313, further reinforces this hypothesis of being morphologically closer to *Mazzonicebus*.

MMCh-PV 347 (Fig. 5b) is a left upper molar, most probably M1, heavily worn. It presents three roots: one lingual and a second anterolabial, both broken at their bases, and an additional posterolabial root broken below the crown level. This is the only upper molar recorded from Site 1 of Cañadón del Tordillo. Due to the advanced degree of wear, little morphological information can be obtained; however, it has a trapezoidal outline being the lingual side narrower, and the ectoloph has a sulcus separating postparacrista and premetacrista.

MMCh-PV 348 (Fig. 5c) is a right M3 with a single root and a fractured labial portion. Lingually, the protocone and the hypocone are small and heavily worn. The most developed cusp is the paracone, whereas the metacone is more reduced and strongly worn. The crown has an overall oval outline and, based on its size, it is considerably smaller than the aforementioned MMCh-PV 347 (see Table 1). As a remarkable trait, enamel crenulations are seen in the mesial border on the occlusal surface, which indicates a clear affinity with modern pitheciines.

MMCh-PV 346 (Fig. 5d) is a right lower molar, probably m2, heavily worn, recovered from Cañadón del Tordillo, Site 1**,** from exactly the same pit as the upper molar described above (MMCh-PV 347); based on the degree of wear, and the fact that they match the size and occlusion almost perfectly, both specimens could easily belong to the same individual. It has complete posterior roots, whereas the anterior root is broken near the crown level; however, it is evident that both roots were completely separated. Almost all the occlusal surface is worn, with only a small posterolabial portion preserving enamel. The tooth is nearly quadrate in outline, reminding the shape seen in living pitheciines; a remnant cuspule on the ectoflexid in the labial side is the same as seen in other *Proteropithecia* molars, especially MLP 91-IX-1-131 (Kay et al. 1998, Fig 2), also sharing similar outline and approximate trigonid/talonid mesiodistal and buccolingual proportions. These shared similarities with MLP 91-IX-1-131, and its occlusion with the upper molar MMCh-PV 347 found in the same pit, allow to confirm the *Proteropithecia* status of the upper molar, too (see Table 1).

MMCh-PV 415 (Fig. 5e) is a left lower molar recovered from Site 1, identified as either an m1 or m2. The labial side is entirely absent due to a fracture, and the roots are also broken. The specimen is indistinguishable from the holotype of *Proteropithecia*. It exhibits low cusps and slightly crenulated enamel. The trigonid is short and broad,

resembling the proportions observed in extant pitheciines, although it is not rectangular in outline. This is due to the oblique orientation of the distal wall of the trigonid, resulting from the position of the partially preserved metaconid, which is situated slightly posterolingual to the protoconid. The talonid is posteriorly expanded, lacks a hypoconulid, and does not exhibit a postentoconid sulcus. Because the labial portion of the molar is missing, it is not possible to determine the orientation of the cristid obliqua or the presence of a small labial cingulum, as observed in lower molars referred to *Proteropithecia*.

FIGURE 5 HERE

5. Discussion and conclusions

As the youngest record from Patagonia, *Proteropithecia neuquenensis* deserves careful consideration regarding its dental adaptations for being a precursor, Middle Miocene sclerocarpic harvester, an adaptive acquisition that makes it an almost uncontroversial fossil pitheciine based on different opinions among scholars (Kay et al. 1998; Tejedor 2013; Kay 2015; Tejedor and Novo 2018; Novo et al. 2025). *Proteropithecia* is also a taxon scarcely represented by 24 specimens up to now, mostly isolated teeth and one symphysis. However, the definitive pitheciine traits characterize the taxon as an ancient representative of the living clade formed by *Pithecia*, *Chiropotes* and *Cacajao.* Some of these relevant characters are found in some new specimens here described, thus reinforcing the hypothesis of its pitheciine status. As novelties, the present work describes the first records of a symphysis, a complete lower canine, a p3 (*in situ* in the symphysis), and also the first record of upper molars for *Proteropithecia*.

Some specimens still remain with doubtful attribution, but certainly represent morphological patterns also seen in other Patagonian primates such as *Mazzonicebus* and *Soriacebus*. As described above, the isolated P2 MMCh-PV 349 exhibits similarities with MMCh-PV 313, another P2 from Cañadón del Tordillo described in Novo et al. (2025), and these two premolars resemble *Mazzonicebus* (MPEF-PV 6282 and MPEF-PV 5344; Kay 2010) more than the P2 of *Proteropithecia* (MLP 91 IX-1-133; Kay et al. 1998). The same line of reasoning may be applied to the lower canine MMCh-PV 351 that matches well with size and shape of the canine root of the symphysis, and has overall resemblances with MPEF-PV 5349 of *Mazzonicebus* (Kay 2010); unfortunately, it cannot be morphologically compared to the broken lower canine from Cañadón del Tordillo previously described (Kay et al. 1998).

The symphysis MMCh-PV 350 is the first record of a more complete specimen of *Proteropithecia*, especially because it closely represents the derived conditions seen in living pitheciines, a combination of characters also seen in *Soriacebus* and *Mazzonicebus*, among them some of high taxonomic significance, such as the procumbent, narrow incisors (judging for the narrow roots), relatively projecting canines with developed entocristid, large and projecting p2, and low-crowned molars that also preserve incipient enamel crenulations in *Proteropithecia*.

Due to some morphological resemblances with *Mazzonicebus*, we can infer some phylogenetic significance. A long controversy arose on the position of *Proteropithecia*, on one hand, as the oldest known pitheciine, and *Soriacebus* and *Mazzonicebus*, on the other hand as either the oldest known pitheciines ("the Long Lineages Hypothesis", LLH; Rosenberger 2002; Rosenberger 2010; Tejedor 2013; Tejedor and Novo 2018; Novo et al. 2025) or stem group ("the Stem Hypothesis", SH; Kay et al. 2008; Kay 2015). Based on the characters described in these new representative specimens of *Proteropithecia*, and

morphological similarities with *Mazzonicebus* and, for instance, *Soriacebus*, the hypothesis of the Long Lineages appears as the most closely acceptable based on morphology and evolutionary inferences.

We present here a new dating that is less than 1 million years younger than the records from Santa Cruz Formation. From an evolutionary point of view, a character complex like that exhibited by *Proteropithecia*, *Soriacebus*, and *Mazzonicebus* is exceedingly rare to be shared by unrelated primates, especially because it represents a dietary adaptation ending in an ecologically restricted, derived and unique group of platyrrhines, the living pitheciines. Even though the present work mainly intends to present a more complete morphological knowledge and age for *Proteropithecia*, these phylogenetic inferences become significantly reinforced.

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447

448 **7. References**

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587

588 **Figure captions**

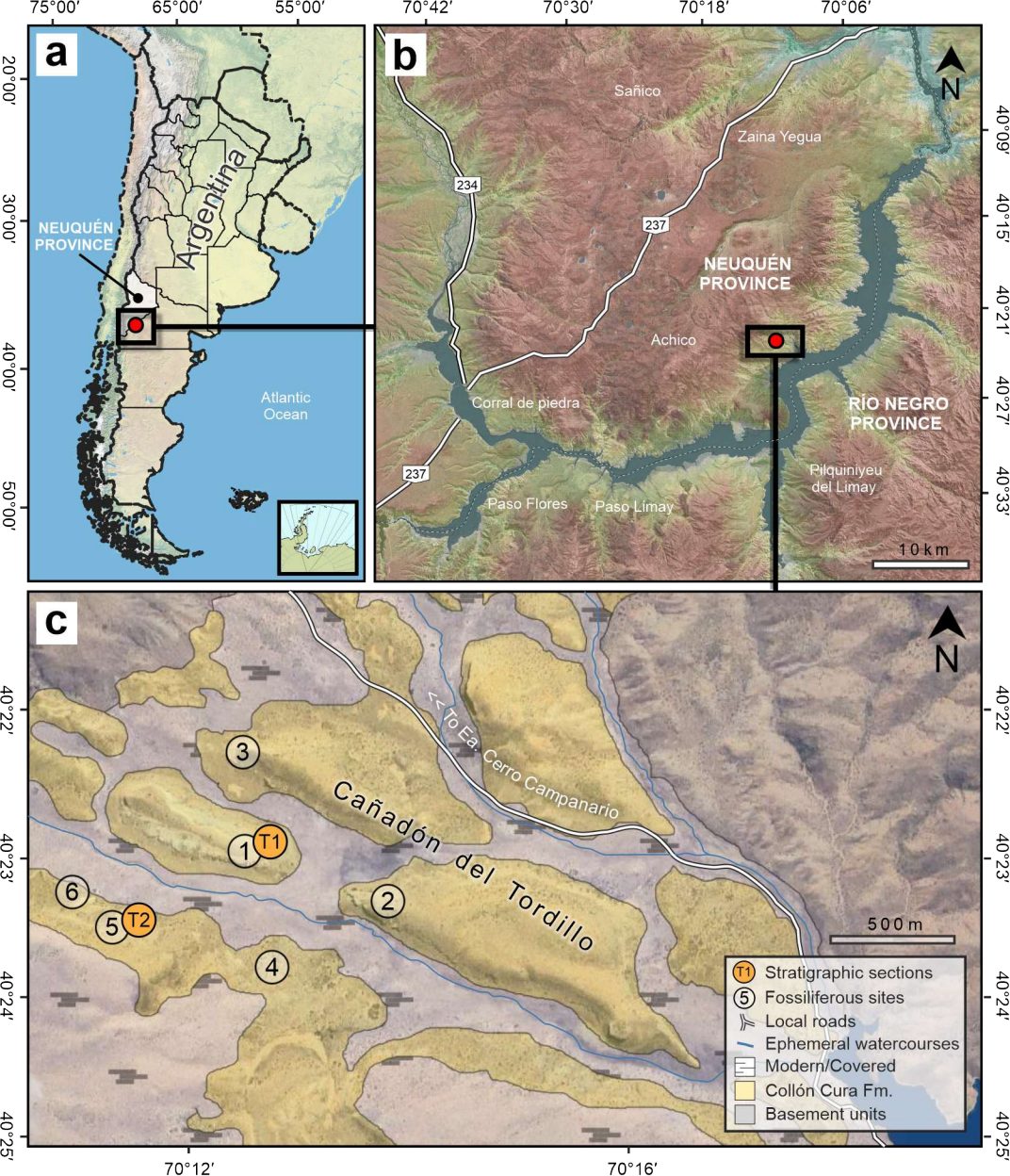
589 **Fig. 1.** Location and geological setting of the study area. (A) Location of Cañadón del
590 Tordillo in Argentina. (B) Regional setting in southern Neuquén and southwestern Río
591 Negro Provinces. Red circle in (A) and (B) indicates the locality of Cañadón del
592 Tordillo. (C) Geological map of Cañadón del Tordillo showing the distribution of the
593 Collón Curá Formation, the fossiliferous sites recognized by Vucetich et al. (1993), and
594 the location of the sedimentary sections measured in this study.

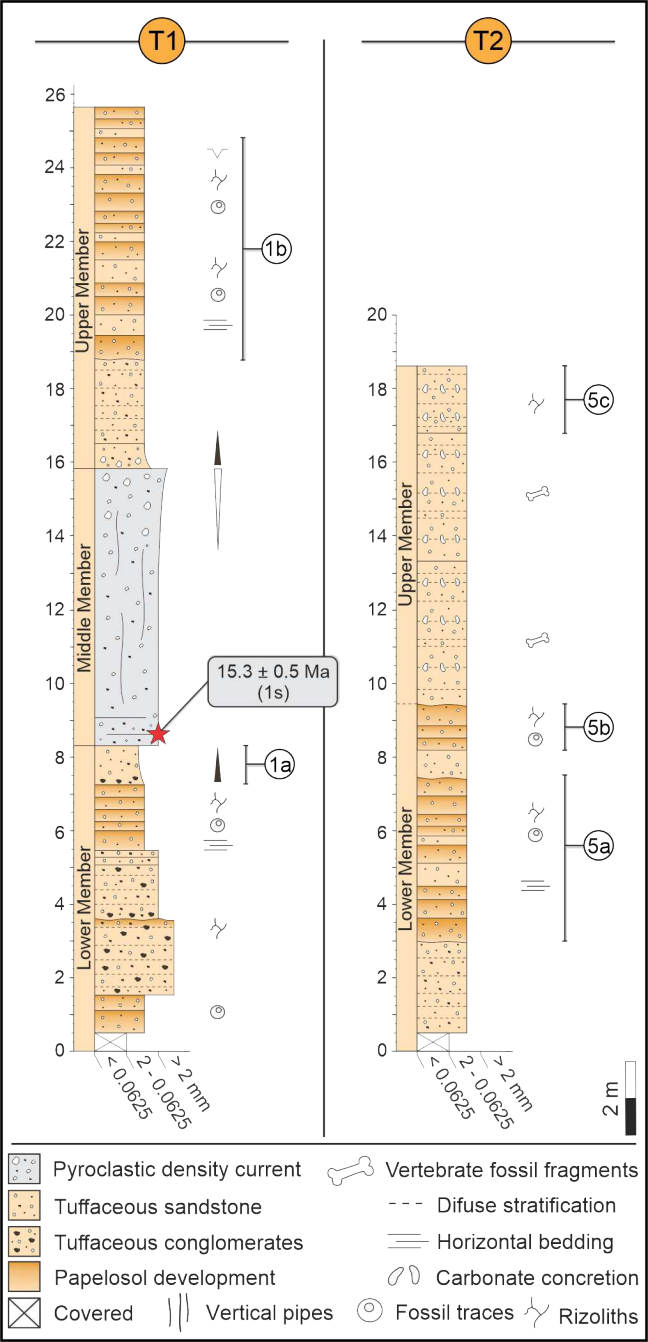
Fig. 2. Sedimentary sections of the Collón Cura Formation at Cañadón del Tordillo (T1 and T2, locations in Figure 1). Numbers refer to the fossiliferous sites originally recognized by Vucetich et al. (1993), whereas lowercase letters identify individual fossil-bearing levels within the measured sections. The new primate specimens were recovered from levels 1b and 5a in the Upper Member. The dashed grey line indicates the correlation between measured sections T1 and T2. The red star marks the stratigraphic position of sample used for U–Pb geochronology.

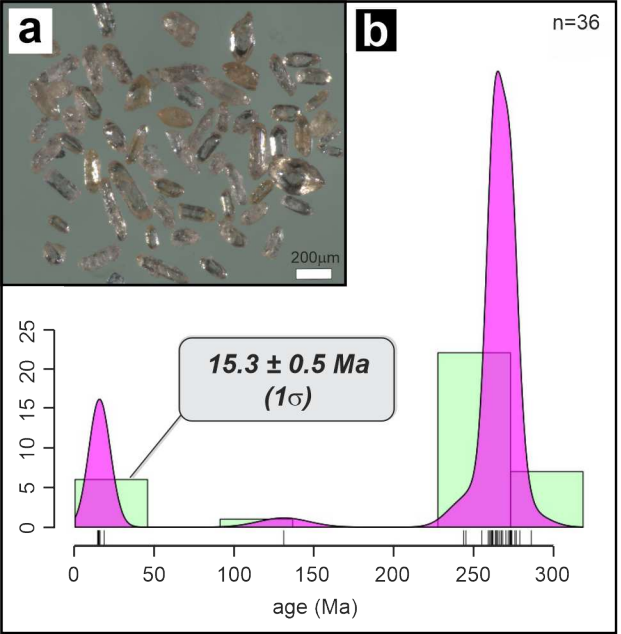
Fig. 3. U–Pb LA-ICP-MS geochronological results for zircon grains from sample LI6dat, collected from the base of the Pilcaniyeu Ignimbrite (Middle Member; Fig. 2). (A) Binocular-microscope image of representative zircon grains. (B) Kernel density estimate (KDE) of concordant zircon ages (n = 36), showing the main Middle Miocene, Cretaceous, and Permian age populations. The youngest zircon population yields a Minimum Age Model of 15.3 ± 0.5 Ma (1σ). (C) Wetherill concordia diagram for all analyzed zircon grains (n = 55); concordant analyses according to the filtering criteria used in this study (100 ± 12%) are highlighted in green.

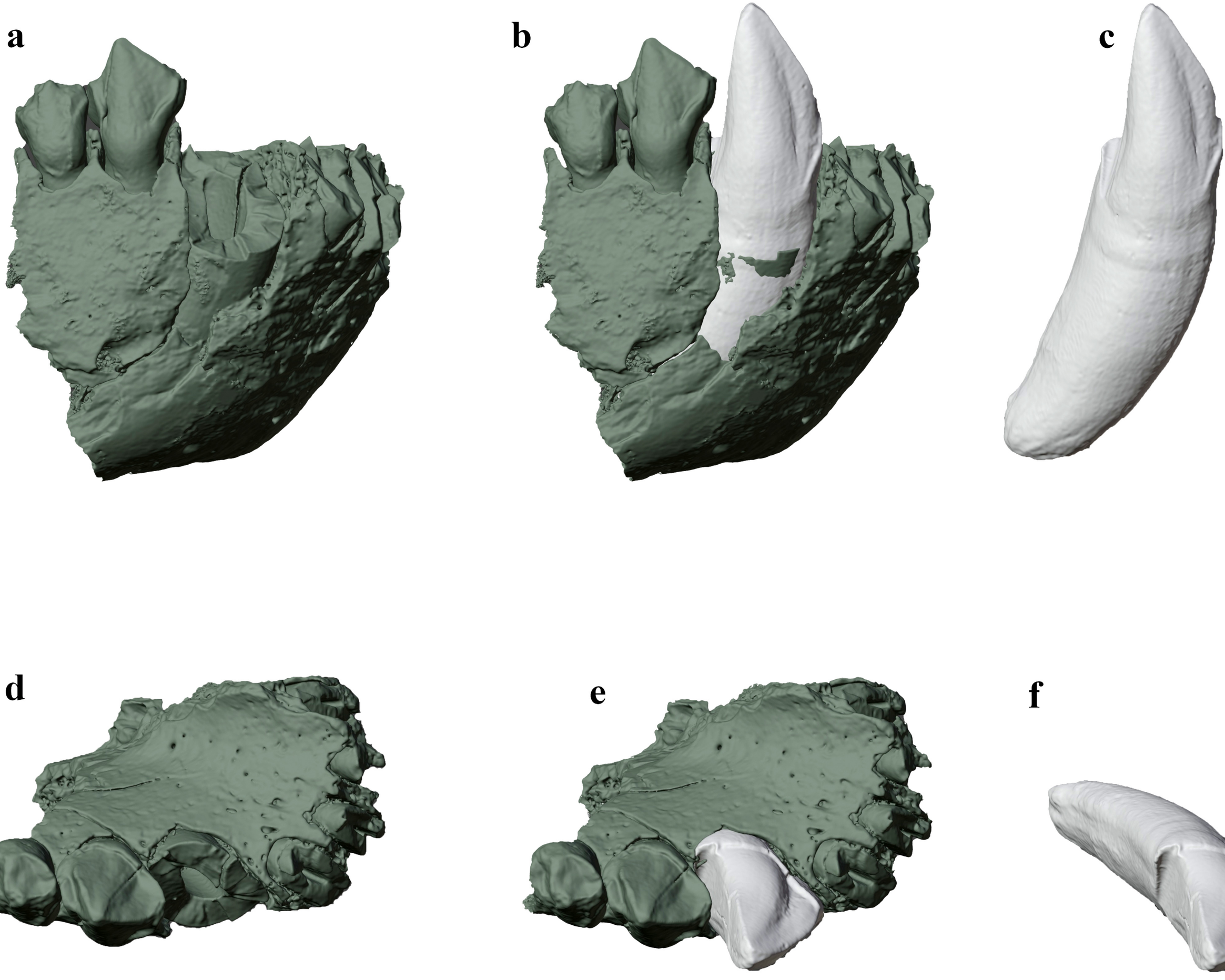
Fig. 4. Three-dimensional reconstruction of the partial mandibular symphysis and right lower canine of *Proteropithecia neuquenensis*. (a, d) Mandibular symphysis MMCh-PV-350. (b, e) Mandibular symphysis MMCh-PV-350 with the right lower canine MMCh-PV-351 digitally placed in the anatomical position to match the broken canine of the symphysis. (c, f) Isolated, right lower canine MMCh-PV-351 in labial (a–c), and occlusal (d–f) views. Scale bar = 5 mm.

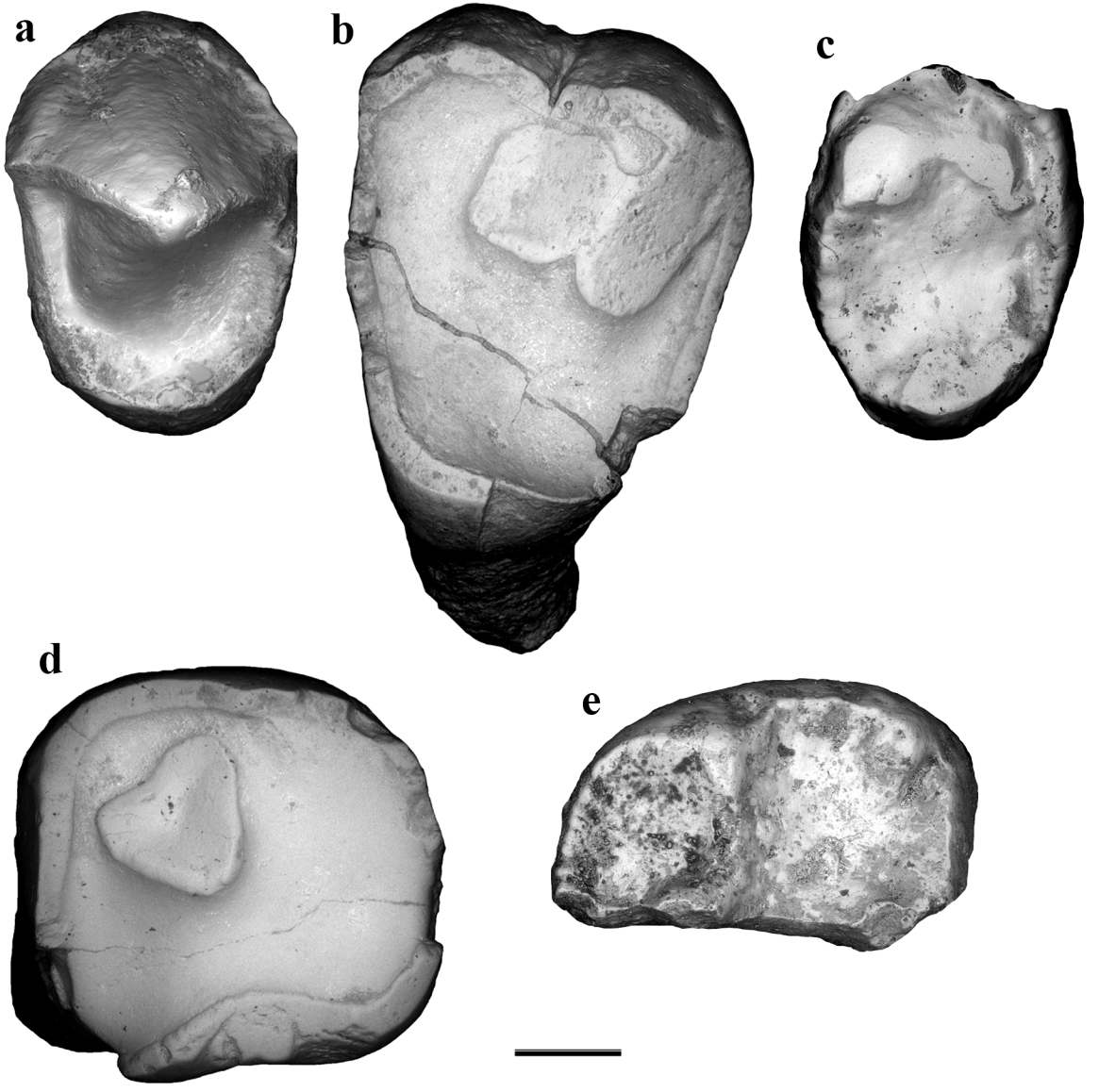
Fig. 5. New dental specimens attributed to *Proteropithecia neuquenensis* from Cañadón del Tordillo in occlusal view. (a) Left P2 (MMCh-PV 349). (b) M1 or M2 (MMCh-PV 347). (c) M3 (MMCh-PV 348). (d) Right lower molar, probably m2 (MMCh-PV 346). (e) Lower molar (MMCh-PV 415).


a
b
c
75°00′
65°00′
55°00′
70°42′
70°30′
70°18′
70°06′
20°00′
30°00′
40°00′
50°00′
40°09′
40°15′
40°21′
40°27′
40°33′
NEUQUÉN PROVINCE
Argentina
Atlantic Ocean
Sañico
Zaina Yegua
234
237
NEUQUÉN PROVINCE
Achico
Corral de piedra
RÍO NEGRO PROVINCE
Pilquiniyeu del Limay
Paso Flores
Paso Limay
10 km
N
40°22′
40°23′
40°24′
40°25′
70°12′
70°16′
Cañadón del Tordillo
Cerro Campanario
1
2
3
4
5
6
T1
T2
500 m
Stratigraphic sections
Fossiliferous sites
Local roads
Ephemeral watercourses
Modern/Covered
Collón Cura Fm.
Basement units


T1
T2
Upper Member
Middle Member
Lower Member
15.3 ± 0.5 Ma
(1s)
1a
1b
5a
5b
5c
< 0.0625
2 - 0.0625
> 2 mm
2 m
Pyroclastic density current
Tuffaceous sandstone
Tuffaceous conglomerates
Papelosol development
Covered
Vertebrate fossil fragments
Difuse stratification
Horizontal bedding
Carbonate concretion
Vertical pipes
Fossil traces
Rizoliths


a
200μm
b
n=36
15.3 ± 0.5 Ma
(1σ)
0
5
10
15
20
25
0
50
100
150
200
250
300
age (Ma)
c
n=55
500
400
300
200
100
0
0.00
0.02
0.04
0.06
0.08
206Pb/238U
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
207Pb/235U


a
b
c
d
e
f


a
b
c
d
e

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- NovoetalTable1.xlsx
- NovoetalMatsup.xlsx