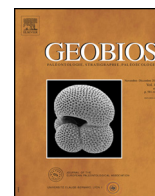




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Original article

# Systematic revision of *Antepithecus brachystephanus* Ameghino, 1901, and dental eruption sequence in Eocene “notopithecines” (Notoungulata) from Patagonia<sup>☆</sup>



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## ABSTRACT

In this contribution, a detailed systematic study of all species previously placed into the genus *Antepithecus*, a Barrancan (middle Eocene) “notopithecine” from Patagonia, is performed. In addition, other species described by Ameghino were studied and are also included in this taxon. The comparative morphological description allows corroborating and introducing new synonyms, and recognizing one valid species, *Antepithecus brachystephanus*. Its diagnosis is expanded and the number of specimens referred to this species is significantly increased. Morphological ontogenetic variations in dentition are recognized and compared with other “notopithecines”. A particular eruption sequence of permanent premolars is ascertained for the Patagonian taxa *Notopithecus*, *Antepithecus*, and *Transpithecus*. These three Casamayoran “notopithecines” have their upper and lower milk molars replaced by permanent premolars in a posterior-anterior direction, P/p4, P/p3, P/p2, contrasting with other notoungulates, including the Mustersan “notopithecine” *Guilielmoscottia*. This peculiar eruption sequence in Casamayoran “notopithecines” and its heterogeneity within the group could reflect a relevant phylogenetic character to clarify inter-specific relationships.

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## 1. Introduction

The “notopithecines” constitute a group of mammals within the endemic South American Order Notoungulata. Ameghino (1897) created the Family Notopithecidae gathering *Notopithecus Ameghino, 1897*, *Transpithecus Ameghino, 1901*, and *Antepithecus Ameghino, 1901*, together with other genera the names of which were later synonymized, typical from the middle Eocene Barrancan subage (Cifelli, 1985; Ré et al., 2010) of the Casamayoran South American Land Mammal Age (SALMA). Afterward, Riggs and Patterson (1935) and Simpson (1945, 1967) considered it as the Subfamily Notopithecinae within the Family Interatheriidae, also including the genus *Guilielmoscottia Ameghino, 1901*, from the Middle-Late Eocene Mustersan SALMA (Ré et al., 2010). Currently, the Family Interatheriidae is a group classified within the Suborder Typotheria, Notoungulata (Simpson, 1967; Reguero and Prevosti, 2010). Under the denomination of Notopithecinae, López and Bond (1995) added the taxon *Punapithecus minor*, the first extra-

Patagonian “notopithecine” from the Geste Formation (Catamarca and Salta provinces, Puna, Argentina), considered Mustersan in age (Alonso et al., 1988; López, 1997). Moreover, Hitz et al. (2006) described *Ignigena minisculus* and *Johnbell hatcheri* from the older strata of the Abanico Formation, estimated to be Casamayoran in age, of central Chile, and performed a phylogenetic analysis of the Interatheriidae, including the mentioned species from Chile and Puna, and the Notopithecinae sensu Simpson (1945). According to Hitz et al. (2000, 2006), “notopithecines” are a paraphyletic assemblage which, together with the Chilean taxa and *Punapithecus*, are considered as “basal interatheriids or non-interatheriine interatheriids”. Nevertheless, a new phylogenetic analysis, which forms part of a comprehensive study of the group (Vera, 2013) and includes relevant characters and more taxa, reveals a different phylogenetic status for “notopithecines”.

Among “notopithecines”, *Antepithecus* was poorly known, ambiguously defined, and often confused with *Notopithecus*. Actually, Simpson (1967: p. 81) included *Antepithecus* in his description of *Notopithecus* and mentioned the difficulty to differentiate them morphologically. However, Simpson (1967) recognized some deciduous teeth (AMNH 28695, AMNH 28701, and AMNH 28821), in some cases doubtfully, as *Antepithecus brachystephanus*, and compared them to the permanent dentition

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of *Notopithecus*. Data presented in this paper deal with the systematic revision of the genus *Antepithecus*, solving some taxonomic misunderstandings, emending its diagnosis, proposing synonyms and revealing some peculiar features with respect to other “notopithecines”.

## 2. Systematic and taxonomic background

*Antepithecus brachystephanus* (original spelling in the French version; *A. brachystephanos* [sic.] in the simultaneous Spanish version) was established by Ameghino (1901). Afterward, Ameghino (1902) described a second species, *A. plexostephanos*, distinguished from *A. brachystephanus* by its larger size, and one year later, Ameghino (1903) defined three other species: *A. innexus*, *A. interrassus*, and *A. gradatus*. Simpson (1967) considered *Antepithecus plexostephanos*, the holotype of which is catalogued as MACN-A 10840, as a synonym of *Maxschlosseria minima* (Ameghino, 1897), and recently López (2008) synonymized it with *Ultrapithecus rutilans*, a Casamayoran Oldfieldthomasiidae. MACN-A 10840 presents characteristics attributable to this group such as the much greater size (MDD = 7.46 mm; LLD = 10.89 mm) and the central fossette transversely oriented and connected with the mesial fossette.

Ameghino (1903: p. 195) described *Antepithecus innexus* as “a little larger than *A. brachystephanus*”, providing the dimensions of a M1 (MDD = 6.5 mm; LLD = 7 mm). The holotype of *A. innexus*, catalogued as MACN-A 10839, consists of a left M1? (Fig. 1(O)); it is the only specimen assigned to this species in the Ameghino collection (MACN). Simpson (1967: p. 99) maintained with doubts the species ?*A. innexus* and pointed out that the type specimen (MACN-A 10839) is structurally similar to, but slightly longer and more transverse than, the M1 of *A. brachystephanus*. Actually, MACN-A 10839 is much larger than any other molar identified as *Antepithecus*; it almost doubles their transverse diameter (Table 1) and it presents a mesostyle and a central fossette oriented mesiodistally, which are diagnostic characteristics of *Oldfieldthomasia* Ameghino, 1901, an oldfieldthomasiid notoungulate from Casamayoran SALMA. In contrast, *Antepithecus* has no mesostyle and the central fossette is more labiolingually oriented. According to this evidence, MACN-A 10839 is ruled out as pertaining to *Antepithecus*, belonging instead to *Oldfieldthomasia*.

Comparing it to the type species, *A. interrassus* was characterized by having upper molars with a basal cingulum on the labial face, more separated hypocone and protocone (Ameghino, 1903), and a more undulating ectoloph (Simpson, 1967). The holotype of *A. interrassus*, catalogued as MACN-A 10859, is composed of a maxillary fragment with right P2-M2 and the beginning of the zygomatic arch (herein designated as MACN-A 10859a; Fig. 1(F), Table 1), although Ameghino (1903) did not figure it and only gave the dimensions of M1 (5 mm × 5.5 mm). Additionally, with the same catalogue number, there is a right M3 that is here identified as MACN-A 10859b (Fig. 1(H), Table 1), which was not mentioned either by Ameghino (1903) or Simpson (1967). There is another set catalogued as *A. interrassus*, MACN-A 10842 (Fig. 1(K), Table 1), which includes isolated left P3?, P4?, M3, and a right M2?. Nevertheless, Simpson (1967) based the synonymy between *A. interrassus* and *A. brachystephanus* only on the specimen MACN-A 10859a. We agree with this proposed synonymy, also including in *A. brachystephanus* the specimens MACN-A 10859b and MACN-A 10842.

The species *Antepithecus gradatus* was differentiated from *A. brachystephanus* by its smaller size, the lack of sulcus between hypocone and protocone, and a softly undulating ectoloph (Ameghino, 1903). The holotype of *A. gradatus*, MACN-A 10828, is a maxillary fragment with left M1-2? artificially joined as

belonging to the same individual (Fig. 1(J)). In addition, with the same number MACN-A 10828, there is a left maxillary fragment too badly preserved to be described or illustrated. The absence of a well-developed sulcus separating hypocone from protocone clearly distinguishes *A. gradatus* from *A. brachystephanus*, the former being closer to *Notopithecus adapinus*. Simpson (1967) indicated that *A. gradatus* is a synonym of *N. adapinus*, an opinion that is shared in this contribution based on the morphological similarities between the holotype of *A. gradatus* and *N. adapinus* (Simpson, 1967; Vera, 2013).

Other species included by Simpson (1967) as junior synonyms of *A. brachystephanus* are *Infrapithecus cinctus* Ameghino, 1901, *Pseudadiantus secans* Ameghino, 1901, *Pseudadiantus imperfectus* Ameghino, 1901, and *Patriarchippus annectens* Ameghino, 1904. The revision of the type materials permits us to corroborate that the holotypes of *Infrapithecus cinctus* (MACN-A 10826; Fig. 2(H), Table 3), *Pseudadiantus secans* (MACN-A 10669a; Fig. 2(C), Table 3), and *P. imperfectus* (MACN-Pv 12677; Fig. 2(D), Table 3) are much similar to specimens referred to as *Antepithecus brachystephanus* and we agree with the proposed synonymies. In contrast, the lectotype of *Patriarchippus annectens* (MACN-A 10691a) was recently recognized as a synonym of *Transpithecus obtentus* by one of us (Vera, 2012a), in disagreement with Simpson's (1967) opinion.

The set catalogued as type of *Adpithecus reduncus*, MACN-A 10858, is composed of two right mandibular fragments: MACN-A 10858a, with m1-2 (Fig. 2(E)), and MACN-A 10858b, with m2-3 (Fig. 2(F)). Simpson (1967) designated MACN-A 10858b (m2-3) as the lectotype and, based on this specimen, proposed a subspecies of *Notopithecus adapinus*, *N. a. reduncus*. Nevertheless, we consider that Simpson's nomenclatural act is an invalid designation because:

- the original description (Ameghino, 1902) mentions m1-2, measuring 9 mm, which coincides with MACN-A 10858a, whereas MACN-A 10858b bears m2-3 and is smaller (Table 3);
- there is no accurate evidence about its condition of syntype. If it is not a syntype, it cannot be chosen as a lectotype (ICZN, 2000: 74.2); however, it is not evident enough that Ameghino only based its description on MACN-A 10858a (if so, it would become the holotype of *A. reduncus*; ICZN, 2000: 73.1); assuming that both specimens are syntypes, the few precise data provided by Ameghino points to MACN-A 10858a, and this is the reason to propose MACN-A 10858a as new lectotype of *Adapinus reduncus* (ICZN, 2000: 74.4).

As MACN-A 10858a is comparable to specimens of *Antepithecus* such as AMNH 28786 and AMNH 28687, we consider *Adpithecus reduncus* a synonym of *Antepithecus brachystephanus*. In contrast, MACN-A 10858b is considered to be *Notopithecus adapinus* due to strong similarities with specimens of this species such as MLP 83-III-1-11 (Vera, 2013).

In regard to *Gonopithecus trigonodontoides*, its type material, catalogued as MACN-A 10827, consists of a set of three molars and one premolar. Simpson (1967: p. 92, pl. 14, fig. 6) recognized the molars as three not associated M3, in contrast to Ameghino's (1903) original interpretation, and assigned them to *Notopithecus adapinus*. Vera (2013) agreed with this identification for the M3 MACN-A 10827a (Fig. 1(A), Table 1) and MACN-A 10827b (Fig. 1(B), Table 1), whereas the third M3, MACN-A 10827d (Fig. 1(D), Table 1), is much more similar to MACN-A 10822c (Fig. 1(I)) and MACN-A 10859b (Fig. 1(H)), herein determined as *Antepithecus brachystephanus*. Based on these identifications of the syntypes, *Gonopithecus trigonodontoides* is synonymous *partim* with *Notopithecus adapinus* and *Antepithecus brachystephanus*. According to the ICZN (2000: 61, 72), every species must have a name-bearing type and,

therefore, we propose the molar MACN 10827b as lectotype of *Gonopithecus trigonodontoides*; we chose this molar because it is the one that Ameghino (1903) originally recognized as M3. The fourth tooth in the set, a right P3? MACN-A 10827c (Fig. 1(C); Table 1), was not mentioned by Ameghino (1903) and therefore we do not consider it as part of the type series of *G. trigonodontoides*; we recognize it as *Antepithecus brachystephanus* by comparison with MACN-A 10859a (Fig. 1(F)).

In summary, *Antepithecus brachystephanus* is recognized as the unique valid species of the genus. Ameghino (1901: pp. 356–357) described *A. brachystephanus* based on upper molars, but only figured (Ameghino, 1904: fig. 234) and gave the dimensions of M1 (MDD = 6.3 mm; LLD = 6.0 mm). The material catalogued as type of *A. brachystephanus* has the number MACN-A 10841 and consists of a set of different pieces: a left maxillary fragment with a broken M2? (MACN-A 10841a; Fig. 1(E), Table 1), a right M1? (MACN-A 10841b; Fig. 1(G), Table 1), a left mandible fragment with m1-2 (MACN-A 10841c; Fig. 2(B)), and a left mandible fragment with m1-3 (MACN-A 10841d; Fig. 2(A), Table 3). The mandibular fragments were not described by Ameghino (1901) and would have been added later in the set or could have not been taken into account by Ameghino; therefore, we exclude them from the type series because the author did not base on them in any way to define the new nominal species (ICZN, 2000: 73.2.1).

Conversely, Simpson (1967) mentioned that the type material of *A. brachystephanus* (MACN-A 10841) consists of seven isolated upper teeth, a maxillary fragment, and two mandibular fragments, not all associated, from the south of Colhué Huapi Lake (Chubut Province). Simpson (1967: p. 96, pl. 16) arbitrarily designated a right M2 as lectotype of the species, which was figured and measured (MDD = 5.7 mm; LLD = 5.7 mm). Unfortunately, this molar is not present among the specimens of the set MACN-A 10841. Keeping in mind the number of specimens to which Simpson (1967) alluded, it is evident that at least six isolated teeth are missing, including the M2 he designed as lectotype and the molar figured by Ameghino (1904: fig. 234).

According to Simpson's (1967: pl. 16) illustration, the selected M2 is morphologically and metrically different from the M1 figured by Ameghino (1904: fig. 234). This M2 has no mesial cingulum, the presence of which is a characteristic of *Antepithecus brachystephanus*. Bearing in mind Ameghino's illustration, we consider that Simpson's designation of the lectotype is not valid, because it does not reflect the original definition of the species, and subsequently it does not provide the objective standard of reference for the application of the name it bears (ICZN, 2000: 61.1). Even though the M1 figured by Ameghino (1904) is lost, it is proposed as new lectotype (ICZN, 2000: 74.4 and recommendation 74B). On the other hand, the absence of mesial cingulum in the M2 is shared with the type specimen of *Patriarchippus annectens* Ameghino, 1904 (MACN-A 10691a), which probably led Simpson (1967) to propose *P. annectens* as a junior synonym of *Antepithecus brachystephanus*; however, *P. annectens* was recently considered to be a subjective junior synonym of *Transpithecus obtentus* (Vera, 2012a).

The preserved M2? MACN-A 10841a (Fig. 1(E)) presents the hypocone and the protocone well differentiated and completely separated from each other by a deep lingual valley that reaches the base of the crown; both cusps are equally high, but the hypocone is more lingually projected; the mesial and distal cingula are well-developed and positioned in the middle of each face. The right molar MACN-A 10841b (Fig. 1(G)) could be a M1 because of its similarity to the M1 MACN-A 10859a (Fig. 1(F)) referred to *Antepithecus*. MACN-A 10841a and MACN-A 10841b have morphological characteristics that correspond to *A. brachystephanus*. Although they were not figured by Ameghino (1901), the author described this species based on upper molars, and it is probable that he had a set of syntypes at hand, even though he only figured

one M1. For this reason, MACN-A 10841a and MACN-A 10841b are herein considered to be part of the type series of *Antepithecus brachystephanus*.

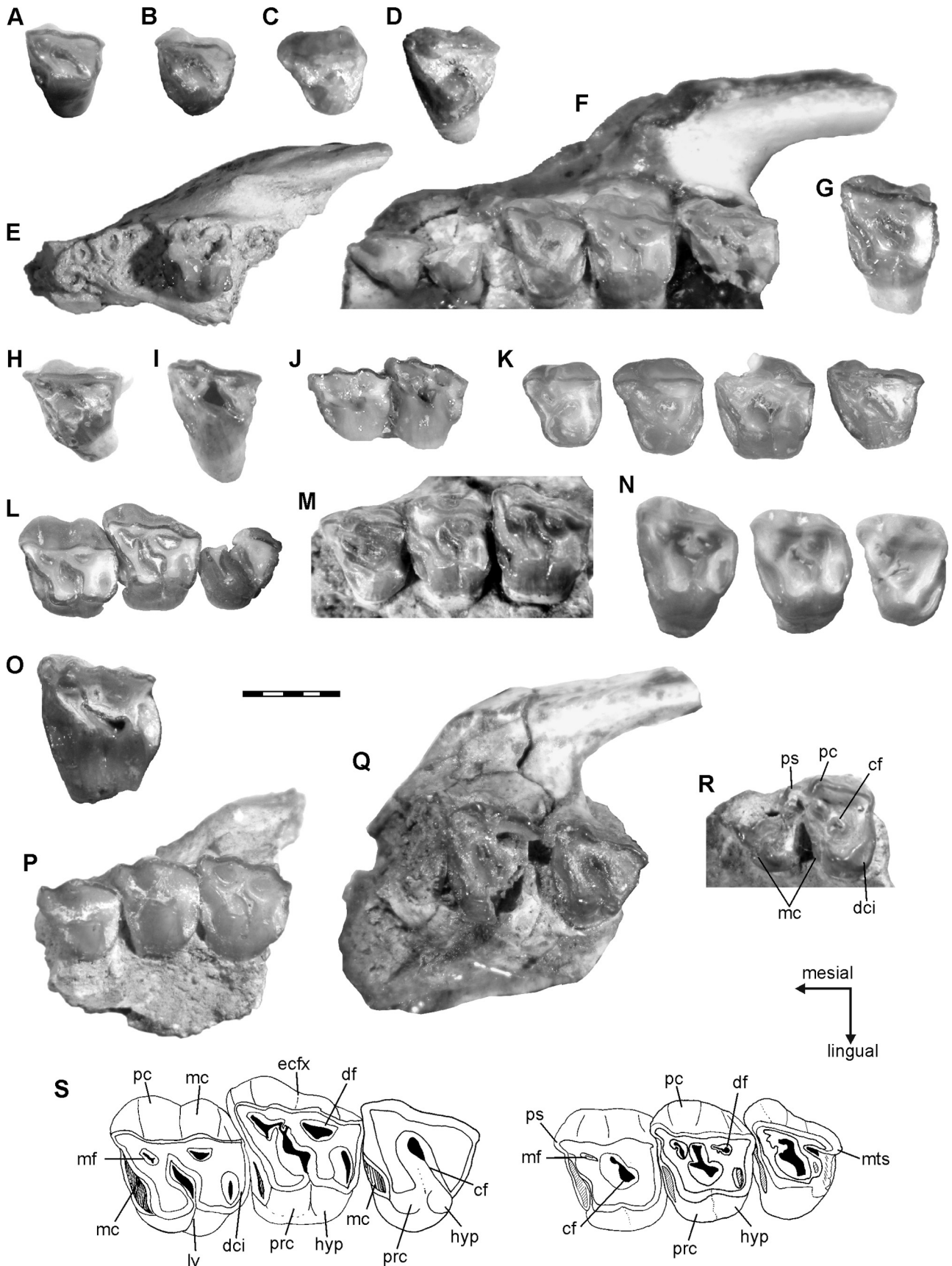
Regarding the mandibular fragments, MACN-A 10841d (Fig. 2(A)) is similar to other specimens referred to *Antepithecus* and is therefore included in this taxon. Instead, MACN-A 10841c (Fig. 2(B)) is not considered to belong to *Antepithecus* or any other "notopithecine"; in contrast, it resembles to early diverging archaehyracids (e.g., *Pseudhyrax* in Simpson, 1967) in having higher crowns, a trigonid shorter than the talonid, the labial face of the trigonid markedly inclined lingually, and a deep groove between the entoconid and the hypoconulid. These features are also observed in the specimen AMNH 28782, referred to the archaepithecoid *Acropithecus rigidus* (Simpson, 1967), and only future broader comparisons will allow an accurate determination.

### 3. Material and methods

More than 100 specimens, most of them previously unpublished or incorrectly identified, are herein recognized as *Antepithecus* and detailed in the Systematic paleontology Section and Table S1 (Appendix A). They belong to the paleontological collections in American Museum of Natural History (AMNH), New York, USA; Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Buenos Aires, Argentina; Museo de La Plata (MLP), La Plata, Argentina; Muséum national d'Histoire naturelle, Casamayoran collection (MNHN CAS), Paris, France; Museo Paleontológico Egidio Feruglio, Vertebrate Palaeontology collection (MPEF-PV), Trelew, Argentina; and Instituto Miguel Lillo, Vertebrate Palaeontology collection (PVL), Tucumán, Argentina. Other material used for comparison belongs to the collections of the Field Museum of Natural History (FMNH), Chicago, USA, and Museo Nacional de Historia Natural, Vertebrate Palaeontology collection (SGOP-PV), Santiago, Chile. The numbers of the specimens (e.g., types) in the Ameghino collection (MACN-A) were given by Florentino Ameghino, but the evidence shows that the last number he assigned was MACN-A 10316, while there is no accurate information about who gave the succeeding numbers (like many of the specimens studied here). In addition, strong evidence indicates that, unfortunately, many specimens suffered a mix up over the years and there are specimens incorrectly included in the type sets (Fericola, 2011, and see Section 2). Following the ICZN, we chose to rely on Ameghino's descriptions and illustrations to guarantee as much as possible which the actual type series were.

Morphological and metrical comparisons were chiefly performed with closer genera *Notopithecus*, *Transpithecus* and *Guilielmoscottia*, mainly based on data from Simpson (1967) and Vera (2012a, 2012b, 2013). Other early diverging interatheriids (*Johnbell*, *Ignigena* and *Punapithecus*) are mentioned when appropriate. Measurements (in millimeters) were taken with a digital caliper and a binocular microscope (Olympus SZ61). Photographs were taken with the microscope camera and a Nikon Coolpix L100 camera. X-rays were performed on some specimens in order to check the sequence of dental eruption. Dental terminology follows Vera (2012a).

**Abbreviations:** C/c, upper/lower canine; cf, central fossette; co, cristid obliqua; DC/dc, upper/lower deciduous canine; dcd, distal cingulid; dci, distal cingulum; df, distal fossette; DI/di, upper/lower deciduous incisor; DP/dp, upper/lower deciduous premolar; ecf, ectoflexid; ecfx, ectoflexus; entd, entoconid; for, foramen; hyfd, hypolophid; hyp, hypocone; hypd, hypoconid; hypcd, hypoconulid; I/i, upper/lower permanent incisor; LLD, labiolingual diameter; lv, lingual valley; M/m, upper/lower molar; mc, mesial cingulum;



**Fig. 1.** Occusal view of upper dentition of *Notopithecus adapinus* (A, B, J) and *Antepithecus brachystephanus* (C–I, K–N, P–R). A, MACN-A 10827a: right M3 (reversed); B, MACN-A 10827b (lectotype of *Gonopithecus trigonodontoides*): right M3 (reversed); C, MACN-A 10827c: right P3? (reversed); D, MACN-A 10827d: right M3 (reversed); E, MACN-A 10841a (paralectotype): left maxillary fragment with M2?; F, MACN-A 10859a (holotype of *Antepithecus interrasus*): right maxillary fragment (reversed) with P2–M2 and anterior root of zygomatic arch; G, MACN-A 10841b (paralectotype): right M1? (reversed); H, MACN-A 10859b: right M3 (reversed); I, MACN-A 10822c: left M3; J, MACN-A 10828 (holotype of

MDD, mesiodistal diameter; metd, metaconid; mf, mesial fossette; mts, metastyle; P/p, upper/lower premolar; pc, paracone; pcd, paraconid; pfd, paralophid; pmcd, postmetacristid; pr, process; prc, protocone; ps, parastyle; ptcd, protoconid.

#### 4. Systematic paleontology

Order NOTOUNGULATA Roth, 1903

Suborder TYPOTHERIA Zittel, 1893

Family INTERATHERIIDAE Ameghino, 1897

Genus *Antepithecus* Ameghino, 1901

1901. *Infrapithecus* nov. gen. – Ameghino, p. 357

1901. *Pseudadiantus* nov. gen. – Ameghino, pp. 372–373.

1949. *Pseudadiantus* Ameghino – Simpson and Minoprio, p. 7.

1967. *Infrapithecus* Ameghino – Simpson, p. 95.

1967. *Pseudadiantus* Ameghino – Simpson, p. 95.

**Type species:** *Antepithecus brachystephanus* Ameghino, 1901.

**Diagnosis:** As for the type and only species.

*Antepithecus brachystephanus* Ameghino, 1901

Figs. 1–4

1901. *Infrapithecus cinctus* nov. sp. – Ameghino, p. 357.

1901. *Pseudadiantus imperfectus* nov. sp. – Ameghino, p. 373.

1901. *Pseudadiantus secans* nov. sp. – Ameghino, pp. 372–373.

1902. *Adpithecus reduncus* nov. sp. – Ameghino, pp. 8–9. New synonym and lectotype here designated.

1903. *Antepithecus interratus* nov. sp. – Ameghino, pp. 195–196.

1903. *Gonopithecus trigonodontoides* nov. sp. – Ameghino, pp. 196–197. Lectotype here designated.

1904. *Gonopithecus trigonodontoides* Ameghino – Ameghino, fig. 234.

1967. *Antepithecus interratus* Ameghino – Simpson, p. 96.

1967. *Gonopithecus trigonodontoides* Ameghino – Simpson, 1967, p. 75, 92, pl. 14, fig. 6. [*partim*, M3 MACN-A 10827d (Fig. 1(D)); incorrect designation].

1967. *Infrapithecus cinctus* Ameghino – Simpson, p. 96.

1967. *Pseudadiantus imperfectus* Ameghino – Simpson, p. 96.

1967. *Pseudadiantus secans* Ameghino – Simpson, p. 96.

**Lectotype:** M1 figured by Ameghino (1904: fig. 234), presently lost. The lectotype proposed by Simpson (1967) was incorrectly defined (see discussion in Section 2).

**Paralectotypes:** MACN-A 10841a, a left maxillary fragment with M2? (Fig. 1(E)), and MACN-A 10841b, a right M1? (Fig. 1(G)). The set MACN-A 10841, labeled as type of *A. brachystephanus*, also includes two left mandibular fragments, MACN-A 10841c (Fig. 2(B)) and MACN-A 10841d (Fig. 2(A)). Neither of these two specimens was mentioned by Ameghino (1901) in his original description of *A. brachystephanus* and therefore both are excluded from the type series of *A. brachystephanus* (see discussion in Section 2).

**Included material:** MACN-A 10669a (holotype of *Pseudadiantus secans*): right mandibular fragment with p2-3; MACN-A 10826 (holotype of *Infrapithecus cinctus*): left mandibular fragment with p2-m3; MACN-A 10858a (lectotype of *Adpithecus reduncus*): right mandibular fragment with m1-2; MACN-A 10859a (holotype of *Antepithecus interratus*): right maxillary fragment with P2-M2 and anterior root of zygomatic arch; MACN-Pv 12677 (holotype of *Pseudadiantus imperfectus*): left mandibular fragment with p1-2. Other referred specimens are detailed in Table S1 (Appendix A).

**Occurrence:** MACN-A 10669a, MACN-A 10826, and MACN-Pv 12677 come from the south of Colhué Huapi lake (Gran Barranca

locality), Chubut Province, Argentina; MACN-A 10858a comes from “Mina de yeso-3-barranca sur del lago Colhué Huapi” locality, Chubut Province, Argentina; MACN-A 10859a has no locality information. All of them were recovered from the Sarmiento Formation, Casamayoran SALMA, Barrancan subage, middle Eocene (Cifelli, 1985; Bellosi, 2010; Ré et al., 2010). Other localities are detailed in Table S1 (Appendix A).

**Measurements:** see Tables 1–4.

**Emended diagnosis:** *Antepithecus* is morphologically very comparable to *Notopithecus*, with larger size (approximately 20% larger than *N. adapinus*, based on dental measurements) and the following combination of characters:

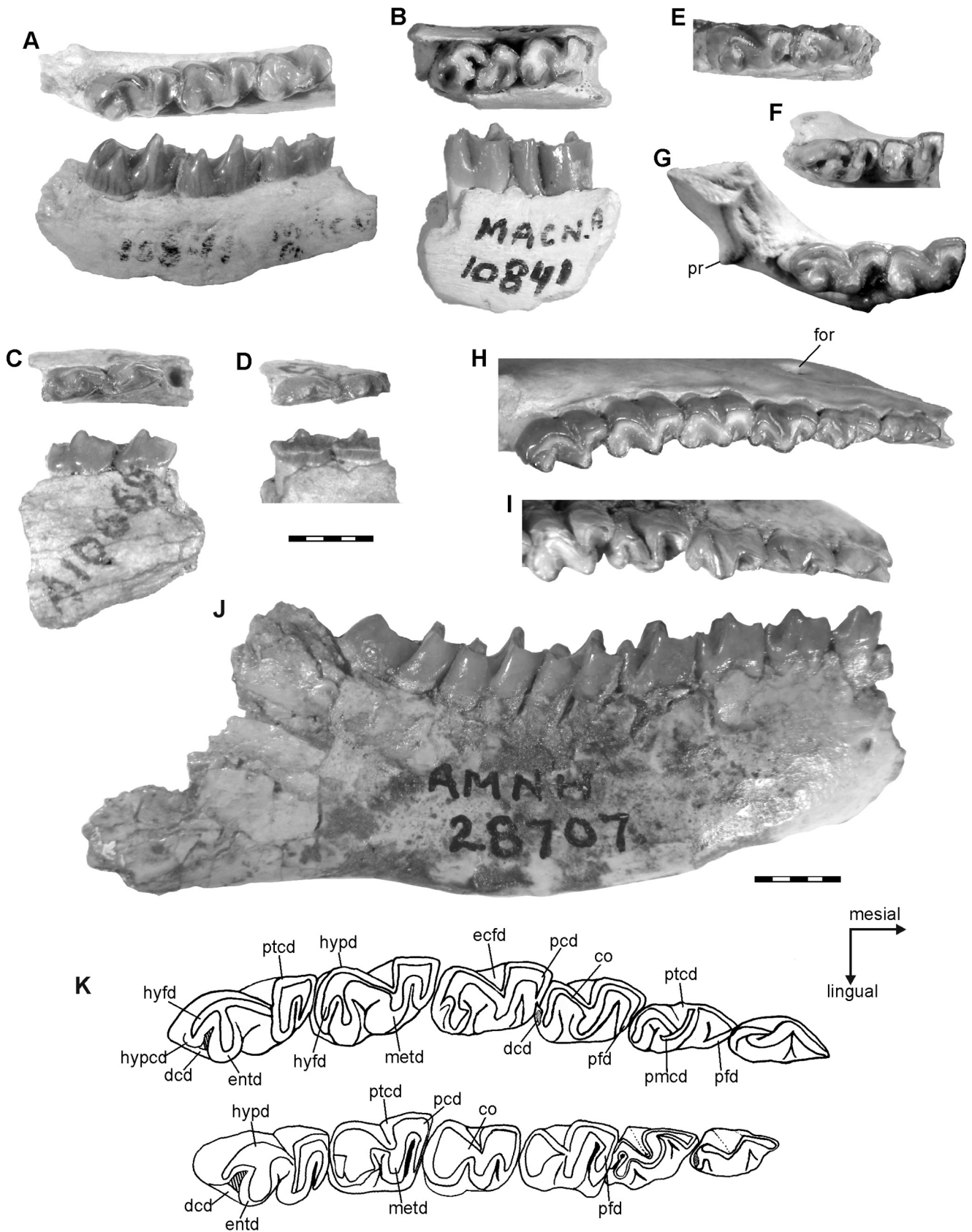
- corpus mandibulae lower than in *Notopithecus*;
- sequence of eruption: M/m1, M/m2, P/p4, M/m3, P/p3, P/p2;
- P3-4 with central fossette joined to the mesial cingulum;
- P4 with strong constriction mesial to the protoloph;
- P2-M2 with distal cingulum;
- mesial cingulum present in P2 and externally more developed in P3-M3 than in *Notopithecus*, while absent in *Transpithecus*;
- M1-2 with deep lingual valley and entoloph forms with advanced wear; protocone more lingually projected than hypocone; ectoloph less undulating than in *Notopithecus*; M1 quadrangular and M2 trapezoidal, very prolonged mesiolabially; labial fossettes obliterate in very old individuals;
- M3 with a narrow and elongated central fossette behind the protocone, a small hypocone and a well-developed protoloph;
- p2-3 with lingual constriction of protolophid, more evident in younger individuals;
- p4 with distal cingulid;
- talonid of m1-2 larger than trigonid, both labially sharp;
- hypolophid of lower molars more developed and trigonid-talonid more separated than in *Notopithecus*.

#### Remarks:

**Skull.** Complete skulls have not been yet ascribed to *Antepithecus brachystephanus*. In the adult specimen AMNH 28673 (Fig. 1(Q)), the descending process of the maxilla is moderately developed at the level of M2. In lateral view, a prominent keel rises from the descending process, drawing an arc and extending forward, as it occurs in *Notopithecus* and *Transpithecus* (Vera, 2012a, 2012b). In the juvenile specimen AMNH 28701 (Fig. 3(A,B)), the descending process of the maxilla is at the level of DP4, and a rounded, large antorbital foramen is at the level of DP2-3.

**Mandible.** The corpus mandibulae is lower than in *Notopithecus* (Table 4) and its height is relatively constant to the level of m2, increasing posteriorly (Fig. 3(C)). In lateral view, the ventral border is undulating between p3 and m2; there is an inflection at the level of m3, as in *Notopithecus*, and it becomes convex posteriorly (Figs. 2(J), 3(C), 4(B–D)). The posterior border of the symphysis reaches the level of c-p1 (Figs. 2(I), 4(A)) or dp1-2 in juvenile individuals (Figs. 3(C), 4(C, D, F, G)). The specimen AMNH 15902a presents four rounded mental foramina: below i2, i3-c, p3, and p4-m1 (Fig. 4(B)), respectively. The presence of a foramen below p3 and p4 is almost constant among the studied specimens. In the juvenile specimen AMNH 28701 (Fig. 3(C)), there is a circular foramen at the level of dc-dp1 and another one below dp3 (visible on the left side). The ascending ramus of the mandible forms an approximately right angle with the horizontal ramus such as in *Notopithecus*. AMNH 28714 (Fig. 2(G)) presents a small process

*Adpithecus gradatus*): maxillary fragment with left M1-2? artificially joined; K, MACN-A 10842: left P3?, P4? and M3, and right M2? (reversed); L, MLP 74-IV-27-15: left maxillary fragment with M1-3; M, AMNH 28498: right maxillary fragment (reversed) with P4-M2; N, MACN-Pv 12694a: right P4, M1 and M2 (reversed); O, MACN-A 10839 (holotype of *Antepithecus inxenus*): left M1?; P, MNHN CAS 944: right maxillary fragment with P3-M1; Q, R, AMNH 28673: maxillary fragment with left M2-3 and right P3-4 (reversed). S. Schematic drawings comparing upper dentition of *Antepithecus* (left, combined M1-2 MLP 74-IV-27-15 and M3 AMNH 28673) vs. *Notopithecus* (right, reversed right M1-3 MLP 82-V-1-50, more aged individual), indicating main dental structures described in the text. Scale bar: 5 mm, except for S (without scale).



**Fig. 2.** Lower dentition of *Antepithecus brachystephanus* (A, C–E, G–J), Archaeopithecidae (B), and *Notopithecus adapinus* (F). A, MACN-A 10841d: left mandible with m1–3, occlusal and lingual views; B, MACN-A 10841c (Archaeopithecidae): left mandible with m1–27, occlusal and labial views; C, MACN-A 10669a (holotype of *Pseudadiantus secans*): right mandible (reversed) with p2–3, occlusal and labial views; D, MACN-Pv 12677 (holotype of *Pseudadiantus imperfectus*): left mandible with p1–2, occlusal and lingual views; E, MACN-A 10858a (lectotype of *Adpithecus redundus*): right mandible (reversed) with m1–2; F, MACN-A 10858b (*N. adapinus*), right mandible with m2–3; G, AMNH 28714: right mandible (reversed) with m2–3; H, MACN-A 10826 (holotype of *Infrapithecus cinctus*): left mandible with p2–m3, occlusal view; I, J, AMNH 28707: right

lingually placed on the alveolar edge, behind m3, which is lacking both in *Notopithecus* and *Transpithecus* (Vera, 2012a, 2012b, 2013).

**P1-DP1/p1-dp1 controversy.** Concerning the first premolar of notoungulates, it is assumed that this tooth is rarely replaced (Shockey et al., 2012: p. 20), and it is interpreted as P1/p1 (Billet et al., 2009) or DP1 (Hitz et al., 2006), being usually a heavily worn tooth. However, authors such as Hitz et al. (2008: table 2) listed a dp1 (without description) and p1 for the interatheriid interatheriine *Brucemacfaddenia* at the same time as they maintained the lack of replacement of P1 in the interatheriine *Federicoanaya*, also based on the extreme wear of the specimens. Within “notopithecines”, the studied sample, though rather scarce and incompletely preserved, seems to reveal a different situation. In the following description and discussion, we refer to the first tooth in the cheek-tooth row as a first premolar without assuming *a priori* its deciduous or permanent condition.

For upper dentition of *Antepithecus*, only the specimen AMNH 28701 preserves a first tooth followed by DP2-4 and M1 (Simpson, 1967, and see below). We interpret it as a moderately-worn DP1 (see description below).

The specimens of *Antepithecus* with a first lower premolar are AMNH 28701 and AMNH 28707, which have been compared to some *Notopithecus* specimens (Table S1). They present a first premolar very convex labially, with an inflection that delimits trigonid from talonid, the latter very small and formed by a unique crest. The trigonid is V-shaped in occlusal view and has the mesial branch longer than the distal one. In both cases, the tooth is practically unworn, but AMNH 28701 (Fig. 3(C, D)) is a young individual with dp2-4 in place together with m1 and m2, whereas AMNH 28707 is an adult with complete permanent cheek-tooth series (Fig. 2(I, J)). The different ontogenetic stage prevents a conclusive interpretation: the lack of wear in the first tooth of the adult specimen may support the correspondence to the p1 that has replaced the dp1, but this is not the same for the young specimen; in this case, it can be interpreted as a dp1 with a wear degree according with the following deciduous teeth (dp2 also unworn, and dp3 barely worn).

In *Notopithecus*, the first lower premolar differs morphologically from that of *Antepithecus* by the presence of a bifurcation in the mesial branch (Fig. 5(G)). In AMNH 28857 (Fig. 5(F)), the first tooth is much worn together with an extremely worn dp2 (i3-c and p3 in place); MACN-A 10860 shows a moderately-worn tooth together with i3-c (Fig. 5(J)) and p3-m2; a similar wear of the first premolar is shown by MLP 83-III-1-69, that is a younger individual with i3-c erupting, and dp2 in place (Fig. 5(G-I)). In turn, AMNH 28792 and MNHN CAS 1038 (Fig. 5(K)) are adult individuals without wear on the first premolar, while AMNH 28951, FMNH P 14718, and MLP 83-III-1-84 are also adults but with the first premolar more worn than p2. These cases are not conclusive, but they seem to support a replacement of the first tooth; in AMNH 28857 and even MLP 83-III-1-69 it can be interpreted as a worn dp1 that would be replaced later, whereas in AMNH 28792 and MNHN CAS 1038 it could be a late erupted p1. The precedent paragraphs evidence that *Antepithecus* and *Notopithecus* specimens do not show a homogeneous pattern of wear to support a lack of replacement of p1, as it is the case of archaehyracids (Billet et al., 2009). This may reflect a variable character within the group concerned, but also a different timing of eruption and wear among individuals; only larger samples of lower and upper complete dentitions of different ontogenetic stages will allow a better understanding of the first cheek-tooth behavior. The following

descriptions allude to these first teeth as we interpret them, without further description or discussion.

**Upper Permanent Teeth.** In spite of sharing some morphological characteristics such as the presence of mesial cingulum, absent in *Transpithecus*, *Antepithecus* clearly differentiates from *Notopithecus* in having larger premolars and molars (Fig. 1(S), 7; Table 4), in addition to the morphological differences detailed below.

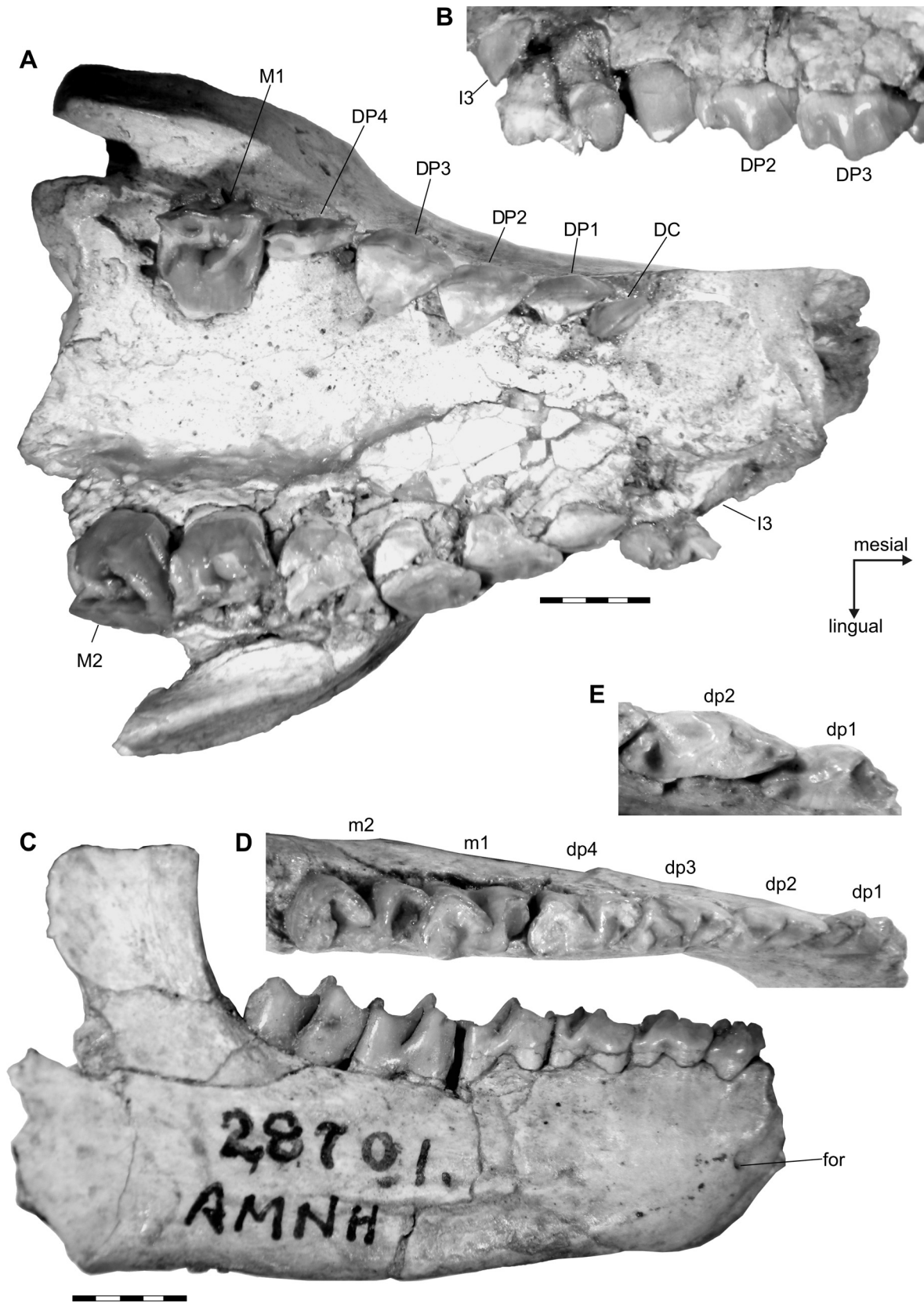
The most anterior tooth in the specimen AMNH 28701 (Fig. 3(A); Table 1) was interpreted by Simpson (1967: p. 97, fig. 26) as a DI3; however, we consider it an I3 because it is still an erupting, unworn tooth compared to the other already worn teeth of the row (DP1-4) and, at the same time, M1-2 are present. It inserts in a mesiolingual-distolabial direction, has a projecting cusp mesially placed, and the mesial end of the tooth is wide and rounded, whereas the distal end is narrower and pointed. Next to the I3, there are two lower incisors incorrectly placed in the locus of the right DC (Fig. 3(A, B)).

P2 is present in MACN-A 10859a (Fig. 1(F); Table 1). It is asymmetrically triangular; the protocone is wide and distally placed; no distal or central fossettes are present, but there is a mesial fossette; there are distal and mesial cingula, whereas the latter is not present in *Notopithecus*; the parastyle is mesially developed; the paracone is convex and the labial wall is lingually inclined behind it.

P3 presents a low and lingually well-developed mesial cingulum and a higher and larger distal cingulum; the metaloph is very inclined mesially; the central fossette opens into the mesial cingulum (Fig. 1(C, K, P, R)).

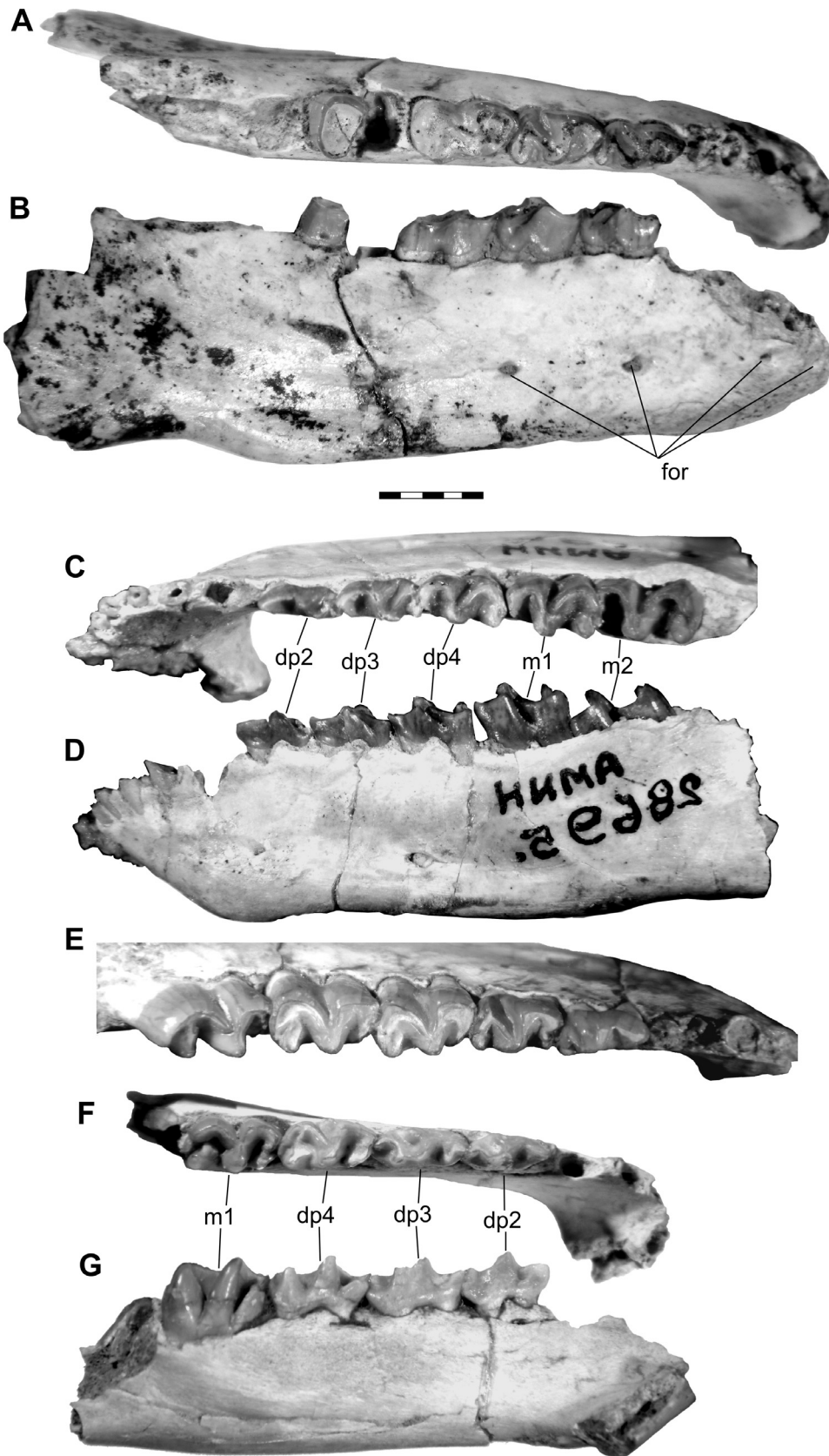
P4 is subtriangular to subquadrangular; the mesial cingulum is low and moderately developed; the distal cingulum is high and notably developed all along the wall (Fig. 2(K, N)), and would fuse with the metaloph with advanced wear; the mesial fossette is narrow and distolingually lengthened; the central fossette is irregular; the parastyle is more prominent than the paracone and the sulcus between them is well marked; the metacone fold is softly convex and wide; the protocone is high and wide, distally placed. A strong constriction is present on the protoloph, mesial to the protocone, generating a notable undulation on the mesial face; the constriction narrows the protoloph so that the central fossette would connect with the mesial cingulum with slight wear. This condition is also observed in the specimens MACN-Pv 12694a (Fig. 1(N)) and MACN-A 10842 (Fig. 1(K)). Comparatively, *Notopithecus* has a barely developed distal cingulum and the central fossette does not connect with the mesial cingulum.

M1 and M2 present a low and well-expanded mesial cingulum on the lingual half, contrasting with the more reduced cingulum in *Notopithecus*; the distal cingulum is moderately high and joins the metaloph with wear, such as it occurs in P4; this gradual process forms a narrow fossette between the metaloph and the cingulum (Fig. 1(L)), which becomes closed with advanced wear, as in *Notopithecus* and *Transpithecus*. The parastyle is not as developed as in P4, and the metacone is as convex as the protocone and more evident than in P4 (Fig. 1(P)). M1 has a small cingulum at the base of the ectoflexus; the metaloph is almost perpendicular to the ectoloph, whereas the protoloph is distally-oriented, being more inclined in M2. The M1-2 of *Antepithecus brachystephanus* have an ectoloph less undulating than in *Notopithecus*; the protocone is lingually projected with respect to the hypocone; both cusps are independent and, consequently, the lingual valley remains open until an advanced stage of wear (e.g., AMNH 28498; Fig. 1(M)); instead, it is the hypocone which projects in *Transpithecus* (Vera, 2012a) and both cusps are roughly equally projected in



**Fig. 3.** *Antepithecus brachystephanus*, AMNH 28701. **A, B.** Partial palate with erupting right I3, DP1-4, and M1-2; left DC?, DP1-3, ectoloph of D4, and M1, occlusal and reversed labial views; **B.** detail of left I3-DP3. **C-E.** Associated mandible with right and left dp1-4 and m1-2, labial (**C**) and occlusal (**D**) views; **E.** detail of left dp1-2. Scale bars: 5 mm (**A, C**); **B, D** and **E** without scale.





**Fig. 4.** Lower dentition of *Antepithecus brachystephanus*. **A, B.** AMNH 15902a: left mandible with p3–m1 and talonid of m2, occlusal and labial (reversed) views. **C, D.** AMNH 28695: right mandible with dp2–4 and m1–2, occlusal and labial (reversed) views. **E.** AMNH 28849: left mandible with p3–m3, roots of p2, and alveolus of i3–c, occlusal view. **F, G.** AMNH 28821: left mandible with dp2–4 and m1, occlusal and lingual views. Scale bar: 5 mm.

**Table 1**  
MD/LL measurements (in mm) of upper permanent teeth of *Antepithecus brachystephanus*, except <sup>Na</sup>: *N. adapinus*.

	I3	P2	P3	P4	M1	M2	M3
AMNH 28498				4.3/4.8	4.5/5.0	5.2/5.5	
AMNH 28673			(3.8)–	4.0/4.7		(4.5)–	4.7/4.5
AMNH 28701	3.3/–				5.0/5.0	5.2/5.2	
AMNH 28748				4.9/5.0	5.4/5.8	(5.7)/6.3	
A 10822c							4.5/4.9
A 10827a <sup>Na</sup>							4.3/3.7
A 10827b <sup>Na</sup>							4.3/4.0
A 10827c			4.6/5.0				
A 10827d							4.7/4.2
A 10839					5.8/7.5		
A 10841a						(4.3)/(3.3)	
A 10841b					5.0/5.6		
A 10842			4.4/4.9	4.9/4.9		5.6/(5.9)	5.5/(5.2)
A 10852a					5.5/5.3	5.6/5.5	
A 10859a		4.1/3.1	–/(4.4)	4.2/5.1	4.9/5.4	5.1/(3.9)	
A 10859b							5.1/4.5
Pv 12694a				4.5/5.5	4.9/5.5	5.2/5.9	
MNHN CAS 944			3.9/3.9	4.1/4.8	4.9/5.0		
MLP 74-IV-27-15					5.0/5.5	5.1/5.9	

Approximate values in parentheses. A and Pv-specimens belong to the MACN collection.

*Notopithecus* (Fig. 1(S); Vera, 2013), in which the entoloph forms immediately with wear. M2 noticeably overlaps M1, a characteristic not so evident in *Notopithecus* (Fig. 1(S)) and shared with *Punapithecus*; the labial face is distolingually more inclined with regard to the sagittal axis, which confers a trapezoid shape that contrasts with the quadrangular shape of M1 (Fig. 1(G, L, S)).

The most striking feature of M3 is the narrow and distally-oriented central fossette, which forms a diagonal and ends behind the protocone (Fig. 1(L, Q)). The mesial cingulum is low, narrow, and labially less developed than in M2 (Fig. 1(D, I, L)); the distal cingulum was not observed in the studied specimens. Unlike *Notopithecus*, the M3 of *Antepithecus* has a small and bunoid hypocone, lower than the protocone, from which it separates by a distinct sulcus (Fig. 1(Q)); the protoloph is more developed and distally projected (Fig. 1(L)); and the mesial cingulum is less extended.

**Lower Permanent Teeth.** The lower molars of *Antepithecus* are larger than in *Notopithecus* (Fig. 1(S); Table 4), with a more developed hypolophid; the talonid is wider than the trigonid and both are more separated. Both p2 and p3 present a deep constriction in the protolophid, just anterior to the protoconid, especially remarkable in young specimens (Fig. 2(H)). Premolars have the protolophid oriented mesiolingually-distolabially, in contrast to molars where this lophid is almost parallel to the sagittal axis and forms a right angle with the metalophid (Fig. 2(K)). The length of the premolar series almost doubles that of the molar series (AMNH 28707:  $L_{p1-4} = 28.71$  mm;  $L_{m1-3} = 15.01$  mm), while they are rather equivalent in *Notopithecus* (Table 4).

**Table 2**  
MD/LL measurements (in mm) of upper and lower deciduous teeth of *Antepithecus brachystephanus*. <sup>Ab</sup>: assigned to *A. brachystephanus* by Hitz et al. (2006), but removed in this paper.

	DC	DP1	DP2	DP3	DP4
AMNH 28701	2.8/1.3	4.0/1.9	4.4/3.0	4.4/3.6	(4.0)–
SGO-PV 3604 <sup>Ab</sup>		4.0/2.0	4.2/3.1	4.4/3.7	4.0/–
		3.0/2.6	3.0/3.5	3.4/3.6	3.8/4.3
	dp1	dp2	dp3	dp4	
AMNH 28695		4.1/1.5	4.0/1.8	4.3/2.2	
AMNH 28701	3.5/1.7	4.4/1.7	3.9/2.0	4.2/2.5	
	3.5/1.7	4.4/1.7	4.3/2.1	4.3/2.6	
AMNH 28821		4.0/1.8	4.7/2.2	4.9/2.6	
MNHN CAS 957				4.1/2.2	

Approximate values in parentheses.

The p2 has differentiated trigonid and talonid; the trigonid is V-shaped, lingually more open than in p1, with the mesial branch larger than the distal one; the talonid, lower and more reduced than the trigonid, is a semicircular crest with a small distal cingulid (Fig. 2(H, I, K)). In comparison with *Notopithecus*, the p2 of *Antepithecus* has a wider and shallower ectoflexid, a less developed talonid, and the mesial branch of the trigonid lingually oriented (nearly parallel to the sagittal axis in *Notopithecus*).

A significant morphological difference exists between p2 and p3 (Fig. 2(K)). In p3, the trigonid is much better defined, with a short paralophid that continues basally as a crest, whereas p2 has no paralophid, although the crest around the trigonid basin is present (Fig. 2(H)). The p3 has a distally-oriented, slightly concave metalophid; the postmetacristid is well-developed and lingually projected; the cristid obliqua contacts the internal face of the postmetacristid; the talonid is wider than the trigonid and has a small distal cingulid. Compared to *Notopithecus* (Fig. 5(K) and MLP 82-V-1-15), the p3 of *Antepithecus* is longer (Table 4), with a deep lingual valley in the talonid and the characteristic constriction of the protolophid. The protoconid is labially as well-developed as in *Transpithecus*, but differs from this taxon in having a larger and V-shaped talonid. Some variations in the shape of p3 were observed among the studied specimens. For example, in AMNH 28687, the cristid obliqua connects to the metalophid, whereas in others the union between cristid obliqua and metalophid is lingual (Figs. 2(C, H), 4(A, E)). This variation was also observed in the p4 of *Notopithecus* (Vera, 2013).

The p4 is wider than p3 (Table 3), with a developed paralophid and a shorter protolophid; it has a distal cingulid (Figs. 2(K), 4(E)) as in *Notopithecus*, although it differs from this taxon in having a deeper lingual valley, which would close with more advanced wear. In contrast, in *Notopithecus* the valley closes earlier and the trigonid becomes rhomboidal (Fig. 5(K)). In most of the specimens of *Antepithecus*, the metaconid turns lingually, but in others it forms a parallel crest (postmetacristid) to the sagittal axis and a sharp angle with the metalophid; the cristid obliqua joins just at the angle between the metaconid and postmetacristid (Fig. 4(E)). In *Notopithecus*, the metalophid can have just the metaconid at the lingual end, as in the molars, or present a postmetacristid. In *Antepithecus*, the talonid of p4 is triangular with two well-defined crests, whereas *Guillielmoscottia* has a p4 molariform, with a greater talonid and entoconid differentiated from hypolophid (Fig. 6(A)).

The m1 and m2 mainly differ from those of *Notopithecus* in being larger (Fig. 7; Table 4), having the hypoconid with an angular

**Table 3**MD/LL measurements (in mm) of lower permanent teeth of *Antepithecus brachystephanus*, except <sup>Na</sup>: *N. adapius*.

	p1	p2	p3	p4	m1	m2	m3
AMNH 15902a			3.7/2.2	4.0/2.6	4.5/2.8	–/2.9	
AMNH 28687		3.8/1.8 3.7/1.7	4.1/1.9	4.2/2.5	4.5/2.8	4.6/3.0 4.4/3.0	5.4/2.9 5.4/2.8
AMNH 28701					4.2/3.0	4.6/3.2	
AMNH 28707	3.0/1.7	3.9/2.0	4.1/2.2	4.1/2.9	4.2/3.3	4.6/3.3	6.0/3.4
AMNH 28715							
AMNH 28815		4.0/1.8	4.5/2.1	4.7/2.6	4.6/3.3		
AMNH 28821					4.0/2.9	4.5/3.0	5.3/2.7
AMNH 28849			4.0/2.1	4.0/2.5	4.6/3.0	5.0/3.2	5.5/3.0
A 10669a		4.0/1.8	4.2/2.1				
A 10826		3.5/1.8	3.8/2.2	3.8/2.6	4.4/2.7	4.7/2.8	6.8/2.8
A 10841d					4.2/3.0	4.3/3.1	5.5/3.0
A 10858a					4.2/(2.3)	4.5/3.0	
A 10858b <sup>Na</sup>						4.0/2.3	5.0/2.5
Pv 12677	(3.2)/1.5	4.1/1.7					

Approximate values in parentheses. A and Pv-specimens belong to the MACN collection.

labial face, and a deeper distal valley in the talonid that remains open with advanced wear (Figs. 2(K), 4(E)). The paraconid and the protoconid form an approximately right angle and the talonid is wider than the trigonid; in *Notopithecus*, the protoconid is more rounded and the talonid and trigonid are quite similar in size. In the m2 of a less worn specimen such as AMNH 28724, the entostylid is conic and mesially connected to the entolophid; another characteristic is that the lingual end of the hypolophid turns mesially, reaching the base of the entoconid, and partially closing the distal valley of the talonid; the paralophid is distolingually well-developed.

The m3 shows a semicircular labial face of the talonid and a more open hypolophid than m1–2; with the presence of an entostylid. In most of the specimens, a cingulid joins the hypolophid with the entolophid and forms a fossettid (Fig. 2(H, K)). The presence of this cingulid is variable as in *Notopithecus*.

**Upper Deciduous Teeth.** The deciduous dentition is described based on the juvenile specimen AMNH 28701 (Fig. 3(A, B)). In this specimen, the anterior border of the orbit is at the level of DP4.

**Table 4**Main univariate statistics of the measurements of upper and lower dentition and mandible, comparing *Antepithecus brachystephanus* and *Notopithecus adapius* (data from Vera, 2013).

		<i>A. brachystephanus</i>			<i>N. adapius</i>		
		n	Mean	s.d.	n	Mean	s.d.
P2	MD	1	4.1	–	45	3.28	0.31
	LL	1	3.1	–	44	2.81	0.24
P3	MD	3	4.05	0.32	55	3.47	0.27
	MD	3	4.39	0.52	54	3.87	0.34
M3	LL	9	4.43	0.32	70	3.72	0.28
	MD	9	4.97	0.23	67	4.58	0.39
p2	LL	14	4.92	0.33	62	4.02	0.42
	MD	12	5.25	0.30	59	4.53	0.33
p3	LL	16	5.10	0.45	71	4.29	0.37
	MD	15	5.26	0.84	67	4.66	0.30
p4	LL	7	4.92	0.35	55	4.17	0.27
	MD	7	4.69	0.34	53	4.21	0.38
m1	LL	14	3.74	0.48	46	3.33	0.43
	MD	14	1.78	0.12	44	1.80	0.29
m2	LL	24	4.19	0.40	58	3.51	0.36
	MD		2.17	0.27	55	2.16	0.25
m3	LL		4.25	0.48	84	3.79	0.36
	MD	34	5.61	0.45	65	5.08	0.47
	LL	34	3.00	0.23	64	2.72	0.26
p1–4		1	28.71	–	11	12.92	0.60
m1–3		8	14.66	0.62	22	12.97	0.87
m1		16	9.45	0.69	38	11.19	1.78

Comparatively, deciduous teeth have a much shorter crown and thinner layer of enamel than permanent teeth.

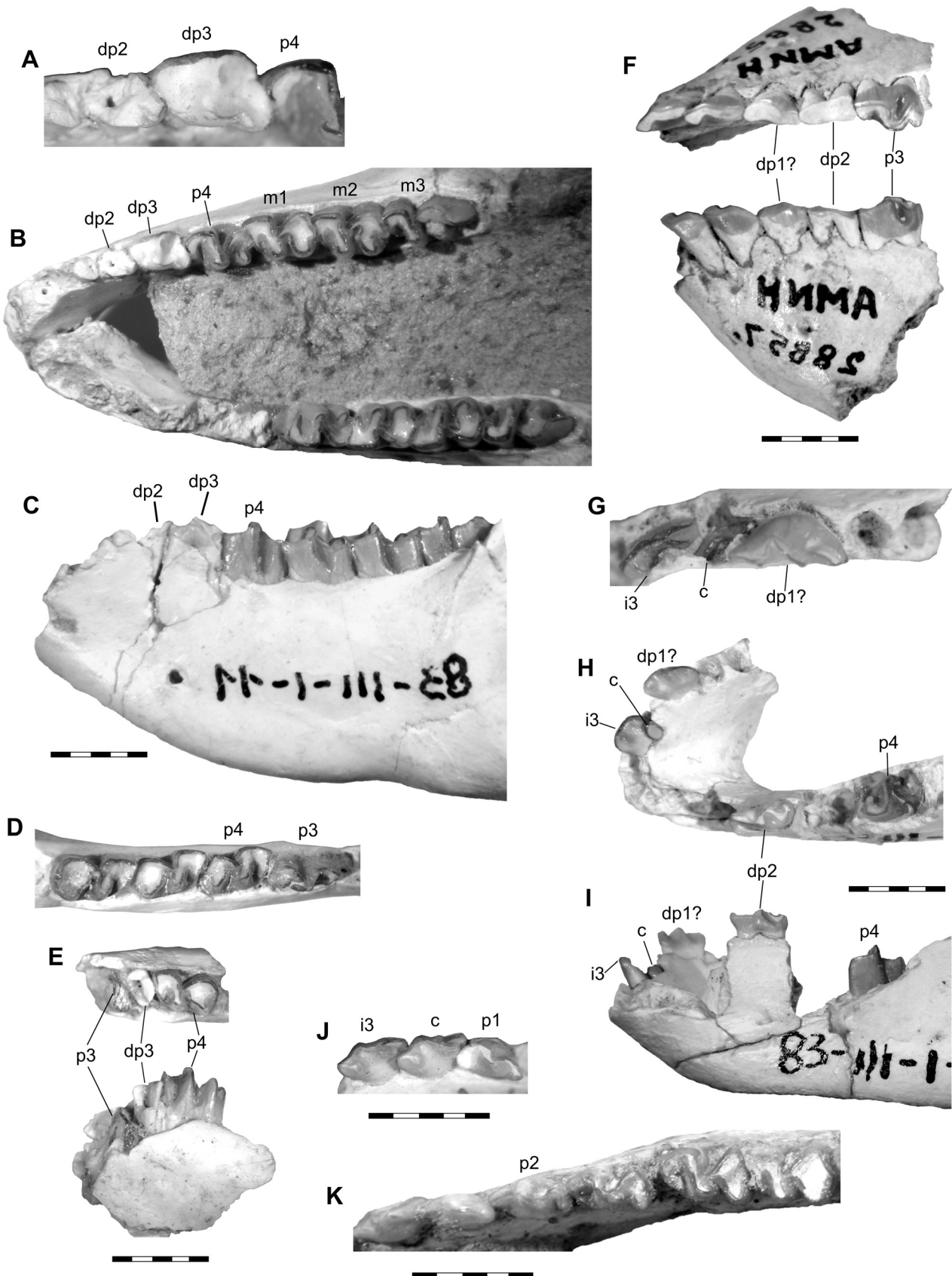
DC is short, narrow, labially convex and with a rounded distal end. It is distally overlapped by DP1 and inserted very inclined with respect to the other teeth.

According to the previous comments, we interpret the first premolar as a DP1 after its degree of wear and the accompanying deciduous teeth (DP2–4). This DP1 is asymmetrically triangular and, in contrast to DC, has a lingually expanded distal talon; the ectoloph is mildly convex and a shallow inflection separates paracone from the little-developed parastyle; a narrow distal cingulum is present. The DP1 of SGO-PV 3604 from the Abanico Formation of central Chile, determined as *Antepithecus brachystephanus* by Hitz et al. (2006), differs from AMNH 28701 in being shorter and wider (Table 2), having a mesial cingulum and a conspicuous parastyle, and being labially and lingually more convex.

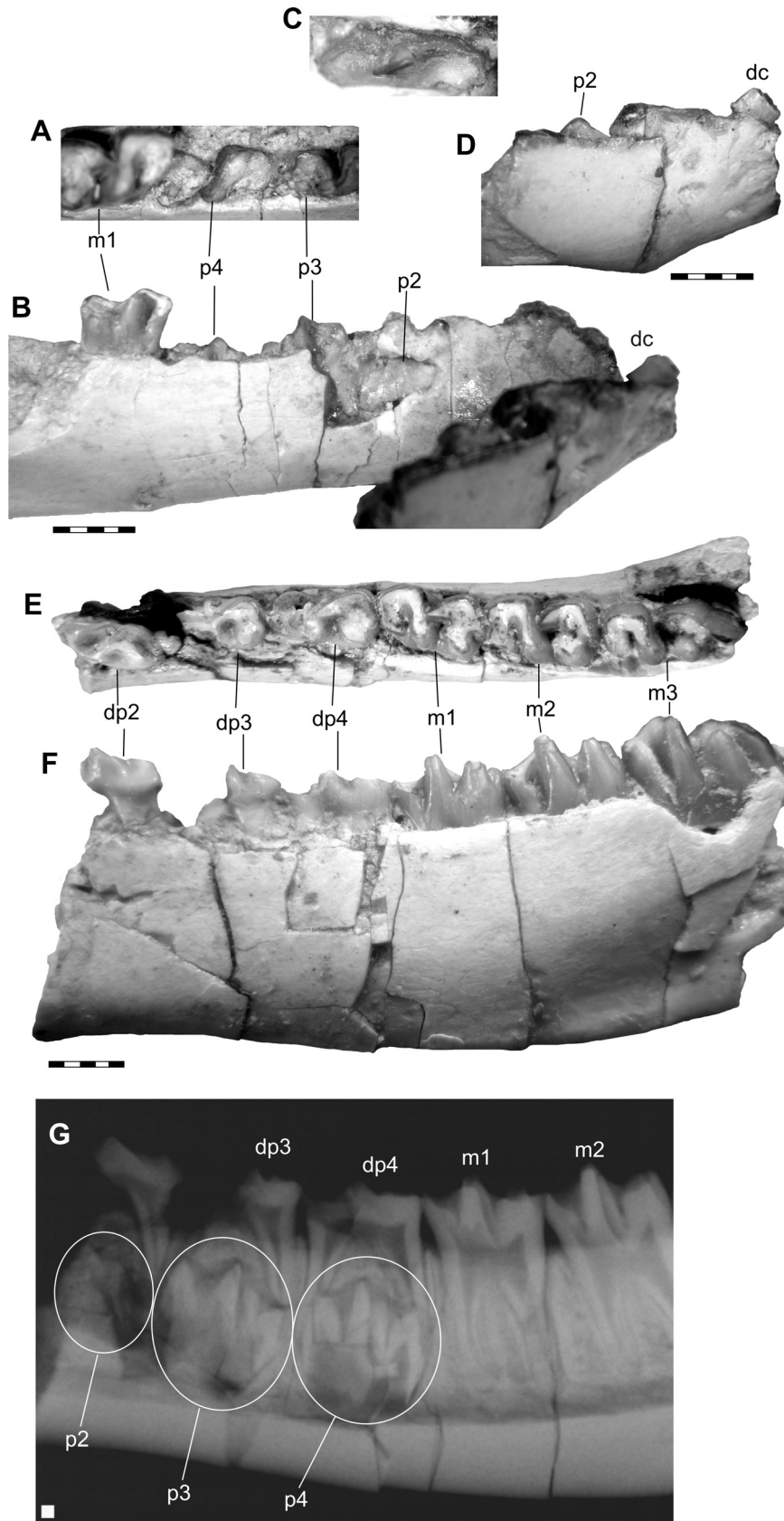
DP2 is asymmetrically triangular, wider than DP1 (Table 2), and has a developed protocone; the distal face is straight and mesiolingually directed; the parastyle prolongs mesially, overlaps DP1 and is separated from the paracone by a wide inflection; the paracone is less evident than in DP1 and, posterior to it, the ectoloph is gently convex and no flexus or metacone fold is defined; the protocone is detached by a deep mesial inflection, a feature that resembles the sulcus present in *Transpithecus* (Vera, 2012a). The DP2 of SGO-PV 3604 (Hitz et al., 2006) is wider than long, but narrower than the homologous tooth of AMNH 28701 (Table 2); the ectoloph is more undulating, especially at the parastyle and paracone folds; the mesial cingulum is rather distinctive.

DP3 is subquadrangular, has a more developed distal cingulum, and its protocone is centrally positioned; the mesial cingulum is high, narrow and covers all the face; the ectoloph is undulating with well-defined paracone and metacone folds; the ectoflexus is shallow and the parastyle is more prominent than the paracone and metacone. Distally to the metacone, the face inclines lingually and is convex, whereas it is straight in DP2. DP3 of SGO-PV 3604 is wider than long (Table 2) and has a more undulating ectoloph than the DP3 of AMNH 28701.

DP4 is quadrangular, molariform, and shows more wear than DP2–3; it has a more undulating ectoloph than DP3. In the specimen AMNH 28701 (Fig. 3(A, B)), DP4 has mesial and distal cingula, but both are already incorporated to the occlusal surface. The distal fossette is elongated and distolabially-mesiolingually oriented; the central fossette is narrow and labiolingually enlarged; there is no defined lingual groove, but an inflection insinuates two lobes despite the advanced wear. DP4 SGO-PV 3604



**Fig. 5.** Lower dentition of *Notopithecus adapinus*. **A-C.** MLP 83-III-1-11: mandible with right dp2 (broken), dp3 and p4-m3, and left p4-m3, occlusal (B) and labial (C, reversed) views; A, detail of left dp2, dp3 and p4. **D.** MLP 83-III-1-72: left mandible with p3-m2, occlusal view. **E.** MLP 83-III-1-101: right mandible with dp3 (broken), erupting p3, and p4, occlusal and lingual views. **F.** AMNH 28857: right mandible with di3?, dc?, dp1?, dp2, p3, occlusal and labial (reversed) views. **G-I.** MLP 83-III-1-69, mandible with left d2, p4 (inside the bone), right erupting i3-c and dp1?, occlusal (H) and labial (I) views; G, detail i3, c and dp1?. **J.** MACN-A 10860, detail of right i3-p1, occlusal view. **K.** MNHN CAS 1038, detail of right c-m1, occlusal view. Scale bars: 5 mm, except for A and G (without scale).



**Fig. 6.** Lower dentition of *Guiliemoscottia plicifera*. **A–D.** MLP 67-VIII-3-15: A, B, left mandible with erupting p2–4 and m1, occlusal and lingual views; C, D, right mandible with p2 (inside the bone) and dc, occlusal and labial views. **E–G.** MLP 67-II-28-8: right mandible with dp2 (broken), dp3, talonid of dp4, and m1–3, occlusal (E) and lingual (F) views; G, X-ray image of MLP 67-II-28-8 showing germs of p2–4. Scale bars: 5 mm, except for A, C and G (without scale).

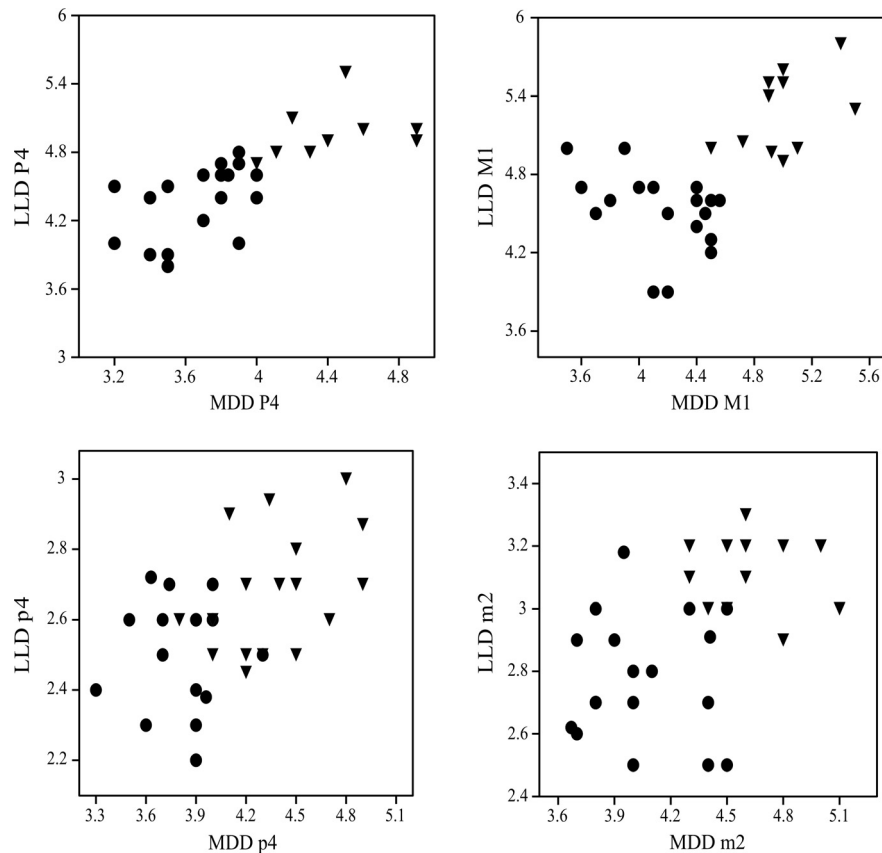


Fig. 7. Bivariate plots of P4, M1, p4 and m2 dimensions (in mm) for *Antepithecus brachystephanus* (inverted triangle) and *Notopithecus adapinus* (dot). Data from Vera (2013).

has a more undulating ectoloph than AMNH 28701. Although Hitz et al. (2006) recognized that SGO-PV 3604 and AMNH 28701 are quite similar, they emphasized some differences such as a more pronounced protocone on the DP1–4 of SGO-PV 3604, resulting in teeth with longer lingual margins, and less triangular in outline than in *A. brachystephanus*.

**Lower Deciduous Teeth.** The morphological variation from dp1 to dp4 is significant (e.g., AMNH 28701). In dp1–2 (see above for identification and description of dp1/p1), the trigonid-talonid junction is lingual between the metalophid and the cristid oblique, whereas in dp3–4 this contact is variable along the metalophid, such as occurs in molars. Another peculiarity is the presence of a deep inflection in dp1–3, mesial to the protoconid, interrupting its occlusal contact with the protolophid (Figs. 2(H), 3(D), 4(C, E)) as observed in the slightly worn permanent premolars (p2–3). The protoconid is well-developed and distally-oriented, more evident in dp2 and dp3.

Contrasting with the first premolar, dp2 has a trigonid more open lingually and a talonid better developed with two crests and a deep lingual valley; the protolophid is lingually oriented (Fig. 4(C)). In comparison to p2, dp2 is relatively larger and narrower (Tables 2 and 3), with a much reduced talonid and a large trigonid, without paralophid (Fig. 4(F)). In turn, the dp2 of *Notopithecus* shows a bifurcation in the mesial branch, the talonid is rounded and as developed as the trigonid, and lacks the incision in the protolophid described for *Antepithecus*.

The dp3 differs from dp2 in having the talonid wider than the trigonid; the latter is larger, with short paralophid and the protolophid more inclined lingually. It is slightly similar to p3–4, presents a small and low distal cingulid, and a deep and wide ectoflexid. The metaconid is joined to the postmetacristid, a crest

parallel to the mesiodistal axis and distally extended that reaches the centre of the talonid basin; the cristid obliqua joins the distal end of the postmetacristid (Figs. 3(D), 4(C)). The dp3 MACN-A 10845 of *Notopithecus* has a straight and angular labial face, not as inclined as in *Antepithecus*.

The dp4 (Figs. 3(D), 4(C, F)) is clearly more molariform than p4 as it presents the talonid larger than the trigonid, a characteristic of the molars, contrary to the reduced talonid of the permanent premolars. However, dp4 resembles dp3 in its distolingually-oriented postmetacristid, but it differs from the latter in having a more labial junction between the cristid obliqua and the metalophid.

## 5. Dental Eruption Sequence

### 5.1. “Notopithecines”

As discussed above, the existence of replacement of the first premolar in “notopithecines” remains debatable, and this section refers to P/p2–P/p4. Although juvenile specimens of “notopithecines” are very few, it has been possible to reconstruct and analyze tooth eruption sequence and replacement in these Patagonian Eocene notoungulates. The described specimen of *Antepithecus brachystephanus*, AMNH 28701 (Fig. 3(A–D)), is an excellent model to interpret the sequence of tooth eruption based on the degree of wear of the preserved deciduous and permanent teeth. In this specimen, DP4 is more worn than DP3, which in turn shows a greater degree of wear than DP2 (Fig. 3(A, B)). This gradual wear pattern indicates that DP4 was the first milk molar to erupt, then DP3, and finally DP2. With the milk molars in place, M1 is the first

**Table 5**

Eruption sequence of the dentition, comparing “notopithecines” and other notoungulates discussed in Section 5.

Taxon	Dentition eruption sequence	Reference
<i>Antepithecus brachystephanus</i>	M/m1, M/m2, P/p4, M/m3, P/p3, P/p2	This paper
<i>Notopithecus adapinus</i>	M/m1, M/m2, P/p4, M/m3, P/p3, P/p2	This paper
<i>Transpithecus obtentus</i>	P4, P3, P2	This paper
<i>Guilielmoscottia plicifera</i>	M/m1, M/m2, M/m3, P/p3, P/p4, P/p2	This paper
<i>Adinotherium ovinum</i>	M/m1, (P/p1), M/m2, P/p2–3, M/m3, P/p4	Scott (1912)
<i>Nesodon imbricatus</i>	M/m1, (P/p1), M/m2, P/p2–3, M/m3, P/p4	Scott (1912)
<i>Trachytherus alloxus</i>	P1, M1, M2, [P2, P3, P4], M3	Billet et al. (2008); Billet and Martin (2011)
“ <i>Plesiotypotherium</i> ” minus	M/m1, M/m2, M/m3, P/p3, P/p4	Townsend and Croft (2010)
<i>Archaeohyrax suniensis</i>	P/p1, M/m1, M/m2, P/p2, P/p3, P/p4, M/m3	Billet et al. (2009)

to erupt, followed by M2; later, P4 would be the first permanent premolar to erupt, followed by P3 and P2. This eruption pattern is the same in the associated mandible AMNH 28701 (Fig. 3(C, D)), which presents a higher degree of wear in dp4, lower in dp3 and the lowest in dp2. This individual allows us to recognize a similar timing of replacement in upper and lower teeth (P/p2–P/p4). The specimens AMNH 28695 (Fig. 4(C, D)) and AMNH 28821 (Fig. 4(F, G)) also show a gradual increasing wear from dp2 to dp4, such as in AMNH 28701. Besides, AMNH 28695 shows the m2 erupting just at the same time as dp2–4 are present.

Conversely, in the specimen SGO-PV 3604 (right and left DP1–4, right and left M1 and erupting right M2) identified as *A. brachystephanus* by Hitz et al. (2006), the authors observed that “the anterior tooth is less worn than the succeeding three”, but also stated that DP4 is “less worn than the first three” (Hitz et al., 2006: p. 15). This statement is incongruent, but we assume they meant DP4 is less worn than DP2–3. They stated that this is the expected pattern of wear for an eruption sequence DP2, DP3, DP4, DP1, M1, M2, M3, P2, P3, and P4, as it is usual in notoungulates. However, it contrasts with our observations on *Antepithecus brachystephanus*. One could argue for an intraspecific variation of this character, but the studied sample does not show any variation (first premolar excluded); instead, this different eruption pattern adds to the morphological features of SGO-PV 3604 commented above and supports its removal from *A. brachystephanus*.

In *Notopithecus adapinus*, the tooth eruption sequence is inferred to be the same as that of *Antepithecus brachystephanus* mainly based on lower dentition (upper deciduous molars are unknown). In MLP 83-III-1-72 (Fig. 5(D)), p3 is just erupted, with practically no wear, in contrast to the markedly worn p4; this shows that p4 erupted before p3. Similarly, in the mandible MLP 83-III-1-101 (Fig. 5(E)), it is possible to observe that p3 appears below dp3 and p4 is already erupted. MLP 83-III-1-11 (Fig. 5(A–C)) preserves dp2 (broken) and dp3, but dp4 has already been replaced by p4; in addition, this specimen shows that p4 is replaced after m2 is in place, and slightly earlier than m3 is fully erupted. The specimen MLP 83-III-1-69 preserves the left dp2 with slight wear, whereas p4 is well-developed inside the mandible (the bone was removed and permits observing it); the right first premolar is also present and slightly worn as well as i3-c just erupting (Fig. 5(G–I)). X-rays performed on MLP 83-III-1-11 and MLP 83-III-1-69 did not reveal any tooth germ below the deciduous teeth, indicating that p2 would erupt clearly later than p4 (dp3/p3 area broken). AMNH 28857 (Fig. 5(F)) shows a moderately-worn p3 together with an extremely worn dp2; this directly suggests that p3 erupts before p2, and indirectly it also suggests that dp3 had erupted before dp2. The same pattern is also observed for upper dentition of *Notopithecus* (e.g., MLP 83-III-1-28; Vera, 2013).

Regarding *Transpithecus obtentus*, its deciduous dentition is not known, but Vera (2012a) recognized six ontogenetic stages in upper and lower jaws based on the occlusal features of permanent

teeth that vary with wear. According to her data, and particularly based on the specimens MLP 82-V-1-49, MPEF-PV 1114, and MLP 83-III-1-91, which show a decreasing degree of wear from P/p4 to P/p2, the inferred eruption pattern for *Transpithecus* is the same as that in *Antepithecus* and *Notopithecus*, that is from back to front: P/p4, P/p3, P/p2.

In contrast to this pattern, the Mustersan “notopithecine” *Guilielmoscottia* presents a different sequence of eruption. In the specimen MLP 61-VIII-3-15 (Fig. 6(A–D)), part of the mandibular bone was removed and the left p2–4 and the right p2 are exposed inside the mandible; at the same time, dc and m1 are completely erupted; probably this individual had dp2–4 in place, but they have not been preserved. Observing the position of p2–4, p3 is closer to the alveolar border than p4, and p2 is below the level of p4, nearer to the ventral mandibular border, which reveals that p3 would erupt first, p4 a little later, and finally p2. The specimen MLP 67-II-28-8 (Fig. 6(E, F)), which presents dp2–4 and m1–3 (m3 is not fully erupted, but its trigonid has slight wear), indicates that the molars erupt before the replacement of deciduous teeth, such as occurs in other groups among Notoungulata (e.g., Santacrucian Pachyrukiinae or Oligocene Interatheriidae from Salla; B.V., pers. obs.). The X-rays of MLP 67-II-28-8 (Fig. 6(G)) show that p3 would erupt before p4, but p2 is almost at the same level than p3. The pattern P3, P4, P2 is also inferred for other specimens of *Guilielmoscottia*, such as MLP 61-VIII-3-17 and MLP 67-II-28-6, with the P3 being more worn than P4.

The observations described above for *Antepithecus* and *Notopithecus*, based on a combination of partial sequences observed from different specimens, show that P/p4 erupt before M/m3 and after M/m2 and M/m1 (Table 5), and present a posterior–anterior direction of replacement of the premolars (P/p1 excluded). The complete sequence of eruption of permanent teeth in these taxa is as follows: M/m1, M/m2, P/p4, M/m3, P/p3, and P/p2 (for the posterior–anterior sequence of premolars also in *Transpithecus*, see above). In turn, in *Guilielmoscottia* dp4 is maintained until m3 is erupted and the sequence is: M/m1, M/m2, M/m3, P/p3, P/p4, and P/p2.

## 5.2. Other interatheriids and notoungulates

The known specimens of *Ignigena* and *Johnbell* from Chile (Hitz et al., 2006) and *Punapithecus* from Mustersan of Puna, Argentina (López and Bond, 1995) are very scarce and, until now, it is not possible to determine the eruption sequence in these basal interatheriids.

Knowledge of deciduous teeth for South American notoungulates is limited: most of them have not ever been described and still fewer illustrated, particularly those of Paleogene notoungulates. Scott (1912) established the eruption sequence M1, (P1), M2, P2–3, M3, and P4 for the early Miocene Toxodontidae *Adinotherium ovinum* and *Nesodon imbricatus*. More recently, Billet et al. (2008)

and Billet and Martin (2011) studied dental replacement in the Oligocene Mesotheriidae *Trachytherus alloxus*, interpreting the following eruption sequence: P1, M1, M2, [P2, P3, P4], and M3. However, for the Miocene mesotheriid “*Plesiotypotherium*” minus, Townsend and Croft (2010) established that dp4 is maintained throughout the eruption of m3. This pattern of full eruption of molars before the replacement of deciduous teeth is noted by Smith (2000) for ungulates with rapid growth rates, such as *Antidorcas* (gazelle). In turn, Billet et al. (2009) inferred the eruption pattern of premolars in Oligocene Archaeohyracidae from Salla (Bolivia) as P/p1, P/p2, P/p3, P/p4; in addition, M1–2 are present at the same time as dp3–4. According to Billet and Martin (2011), in the early diverging mesotheriid *Trachytherus alloxus* and many other notoungulates, M3 erupts after P2–4, contrary to that observed in “notopithecines” (Table 5).

An eruption pattern apparently similar to that of “notopithecines” is present in the Eocene notoungulate *Coquenia bondi* Deraco, Powell and López, 2008, a Leontiniidae from the Lumbra Formation (Salta, Argentina). This is based on the advanced juvenile specimen PVL S-VI-2a, showing the anterior deciduous premolars present together with posterior premolars and M1–2 (Deraco and García López, 2011).

Among other mammal groups, an analogous sequence to that observed in the Casamayoran “notopithecines” is also present in some primates, such as lemuriforms, ceboids and adapoids (Gingerich and Smith, 2010), and talpid insectivores (Luo et al., 2004). According to Smith (2000), the variability in the emergence sequences in each mammal group evidences that tooth eruption is a highly functional adaptive system and its use in phylogenetic studies must be done carefully. However, a preliminary phylogenetic analysis of “notopithecines” (Vera, 2013) seems to reveal that the sequence of tooth eruption might be a relevant phylogenetic character. A further complete analysis is in progress, including more basal notoungulate groups such as the Archaeopithecidae, which may shed light on the importance of this character.

## 6. Conclusions

The present systematic review of the genus *Antepithecus* and other taxa described by Ameghino leads us to recognize a unique valid species, *A. brachystephanus*, to expand its diagnosis, and to increase the number of specimens referred to this taxon. The previously proposed synonymies (Simpson, 1967) of *Antepithecus interrassus*, *Infrapithecus cinctus*, *Pseudadiantus secans*, and *P. imperfectus* with *Antepithecus brachystephanus*, and between *Antepithecus gradatus* and *Notopithecus adapinus* are confirmed. The species *Antepithecus innexus* is removed from *Antepithecus* and placed in the genus *Oldfieldthomasia*. *Antepithecus plexostephanus* is herein related to *Oldfieldthomasiidae*, agreeing with López (2008). In turn, *Patriarchippus annectens*, also synonymized by Simpson (1967) with *Antepithecus brachystephanus*, has been recently recognized as *Transpithecus obtentus* (Vera, 2012a).

*Adpithecus reduncus* is a synonym of *Antepithecus brachystephanus* based on the specimen MACN-A 10858a, which is herein recognized as the lectotype of *A. reduncus*. The designation of the specimen MACN-A 10858b as lectotype of *A. reduncus* by Simpson (1967) is herein considered an invalid nomenclatural act, and MACN-A 10858b is determined as *Notopithecus adapinus*.

The specimen MACN-A 10827b is chosen as the lectotype of *Gonopithecus trigonodontoides* and the synonymy between *G. trigonodontoides* and *Notopithecus adapinus* proposed by Simpson (1967) is maintained. The M3 MACN-A 10827a is also regarded as *N. adapinus*, whereas the M3 MACN-A 10827d and P3 MACN-A 10827c are identified as *Antepithecus brachystephanus*. Likewise,

*Gonopithecus trigonodontoides* is synonymized (*partim*) with *Antepithecus brachystephanus*.

The lectotype designated by Simpson (1967) for *Antepithecus brachystephanus* is an M2, presently lost, which does not present the diagnostic features of *A. brachystephanus* established from Ameghino's (1901, 1904) data and the present revision. The new lectotype here designated is the M1 figured by Ameghino (1904), also presently lost. The specimens MACN-A 10841a and MACN-A 10841b are recognized as paralectotypes.

The two mandibular fragments MACN-A 10841c and MACN-A 10841d that are presently included in the set MACN-A 10841, labeled as type of *A. brachystephanus*, were not mentioned by Ameghino (1901) in his original description of the species, and therefore they are excluded from the type series of *A. brachystephanus*. MACN-A 10841d is similar to other specimens determined as *Antepithecus*, but MACN-A 10841c is close to the morphotype of Archaeopithecidae.

Concerning P/p1, the available *Antepithecus* and *Notopithecus* material does not allow discarding the dental replacement for the first premolar in these taxa, contrary to what has been established for other notoungulate groups.

New data on deciduous dentition and the comparison of juvenile, subadult and adult specimens of *Antepithecus* and *Notopithecus* allow establishing a peculiar dental replacement sequence in these Casamayoran “notopithecines”. This sequence is characterized by the eruption of permanent premolars in a posterior-anterior direction P/p4, P/p3, P/p2, establishing the complete permanent tooth eruption sequence as: M/m1, M/m2, P/p4, M/m3, P/p3, and P/p2. The same sequence of premolars is hypothesized for *Transpithecus* based on the wear pattern of the permanent premolars. The posterior-anterior sequence is also present in some primates, but it is an uncommon pattern in notoungulates. These include the Mustersan “notopithecine” *Guilielmoscottia*, the eruption pattern of which is P/p3, P/p4, P/p2; besides, dp4 is maintained until m3 is erupted and the sequence is: M/m1, M/m2, M/m3, P/p3, P/p4, and P/p2. This variation in the eruption sequence reflects variability within “notopithecines”, a group currently considered a paraphyletic assemblage among Interatheriidae (Hitz et al., 2000, 2006). The phylogenetic signal of this character remains to be tested through further analyses.

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## Appendix A. Supplementary data

Supplementary information (Table S1) associated with this article can be found, in the online version, at: <http://dx.doi.org/10.1016/j.geobios.2014.02.001>.



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