

## Short communication

# Cranial characters associated with the proboscis postnatal-development in *Tapirus* (Perissodactyla: Tapiridae) and comparisons with other extant and fossil hoofed mammals



Silvana Rocio Moyano <sup>a, b, \*</sup>, Norberto Pedro Giannini <sup>c, d, e</sup>

<sup>a</sup> Instituto de Ecorregiones Andinas (INECOA-CONICET), Universidad Nacional de Jujuy, Av. Bolivia 1711, CP. 4600, San Salvador de Jujuy, Jujuy, Argentina

<sup>b</sup> Centro de Estudios Territoriales Ambientales y Sociales (CETAS), Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy, Alberdi 47, CP. 4600, San Salvador de Jujuy, Jujuy, Argentina

<sup>c</sup> Unidad Ejecutora Lillo - Consejo Nacional de Investigaciones Científicas y Técnicas, Miguel Lillo 251, CP. 4000, San Miguel de Tucumán, Tucumán, Argentina

<sup>d</sup> Facultad de Ciencias naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Miguel Lillo 205, CP. 4000, San Miguel de Tucumán, Tucumán, Argentina

<sup>e</sup> American Museum of Natural History, Department of Mammalogy, Central Park West at 79th Street, New York, NY, 10024-5192, USA

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## ABSTRACT

Among extant hoofed mammals, only elephants and tapirs exhibit a true proboscis. We investigated the development of cranial characters potentially associated with the presence of a short proboscis in tapir species, following a comparative framework with a selection of extant and fossil hoofed mammals that exhibit modified narial structures. The core characters present in all taxa (with or without true short proboscis) develop prenatally in tapirs, and other characters that complement the osteological “proboscis syndrome” develop postnatally and are absent or irregularly distributed in other taxa. The taxa examined here showed varying degrees of cranial modification. On the basis of our comparisons, some fossil taxa are indicated as candidates to have possessed a true short proboscis. A terminal addition sequence of character evolution is suggested to explain the development and convergent evolution of the proboscis in hoofed mammals.

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Several mammalian species exhibit a proboscis-like organ. The proboscis is interpreted functionally as a muscular hydrostat (Witmer et al. 1999). According to a recent definition, the term proboscis is restricted to a flexible narial and upper lip extension with food grasping function (Milewski & Dierenfeld 2013). Under this definition, only elephants and tapirs possess a true proboscis among extant mammals. Belonging to two distinct orders, elephants (Proboscidea) and tapirs (Perissodactyla) share to some extent a convergent narial morphology, including a particularly developed narial musculature for food grasping function, and the loss of the skeletal support for the narial structures (Milewski & Dierenfeld 2013 and citations therein). The rigid mammalian structure of bone and nasal cartilage is replaced in tapirs by an

apparatus of connective tissue and specialized muscles, preserving only a septal cartilage forming the roof and rostral portion of the proboscis (Witmer et al. 1999). Tapirs, with their short proboscis, can only use it for grasping in association with its labial surface, not achieving full-opposability as in the case of elephants (Milewski & Dierenfeld 2013 and citations therein).

This contribution is focused on development of selected cranial characters of tapirs, which present a short proboscis serving for a variety of functions, including those related to specific sense organs (Padilla & Dowler 1994; Kemp 2005). Several fossil hoofed mammals from various independent lineages have been proposed to have had a short proboscis, similar to that present in tapirs (see Wall 1980). The accepted definition of a true proboscis is essentially based on the combination of function and soft-anatomy features (Milewski & Dierenfeld 2013), thereby leaving no grounds of applicability for extinct forms for which neither the food grasping function, nor the soft-anatomy evidence, are directly observable. However, the presence of a proboscis has considerable impact on

\* Corresponding author. Centro de Estudios Territoriales Ambientales y Sociales (CETAS), Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy, Alberdi 47, CP. 4600, San Salvador de Jujuy, Jujuy, Argentina.

E-mail address: [s.rociomoyano@gmail.com](mailto:s.rociomoyano@gmail.com) (S.R. Moyano).

the cranial anatomy (see Witmer et al. 1999). Therefore, the fundamental premise here is that the narial morphology of hoofed mammals – that possess a true proboscis – should have a common set of osteological signatures due to the process of proboscis development. Radinsky (1965, 1966, 1969) has argued favoring this association based on the recognition of three cranial evidences: 1. formation of a meatal diverticulum as a caudolateral expansion of the nasal incision; 2. reduction of the premaxilla through loss of its nasal process and its contact with the nasal bone; and 3. length reduction of the nasal bone. Wall (1980) expanded and detailed these relationships between narial osteology and the presence of proboscis by identifying 12 cranial characters putatively related with the evolution of a short proboscis in amynodontid rhinocerotids, notably using extant tapirs as reference in the extant taxa. This set of characters compose a purely osteological “proboscis syndrome” (Fig. 1, Table 1) which we use as independent evidences to unfold the comparative studies here put forwards. We expect that this study allow the identification of taxa with a proboscis in both fossil and extant forms. Previous authors have examined in some detail fossil hoofed mammals as perissodactyls of the early Oligocene, particularly the amynodontid †*Cadurcodon* Kretzoi, 1942; the litoptern †*Macrauchenia* Owen, 1838; and the merycoidodont artiodactyl †*Brachycrus* Matthew, 1901 (Radinsky, 1965; Wall, 1980). In addition, Milewski & Dierenfeld (2013), and other authors previously (e.g., Ameghino 1894; Scott 1937; Kramarz et al. 2011), pointed out osteological features of †Astrapotheria that favor them as strong candidates to have a true short proboscis. In Astrapotheria in particular, reduction of both incisors and premaxilla, presence of an upper jaw distinctly shorter than the mandible, and anterior dentition functionally converted to tusks, makes it “difficult to envisage how food could have been grasped without a proboscis” (Milewski & Dierenfeld 2013; see also Johnson & Madden 1997).

Previously, we have provided a detailed quantitative analysis of postnatal skull development in *Tapirus* (see Moyano & Giannini, 2017). Here we focused on the qualitative analysis of Wall (1980)

“proboscis syndrome” characters that we used to score the South American tapir, *Tapirus terrestris* Linnaeus, 1758, and the Malayan tapir, *Tapirus indicus* Desmarest, 1819. The list of specimens examined is available in the Appendix 1. Among these specimens, AMNH 202838 representing a *T. terrestris* was indicated in the catalog as “embryo”; however, due to its large size and the advanced stage of development the specimen was here interpreted as a near-term fetus. In addition, we scored the same 12 characters (Fig. 1) in selected hoofed mammals, both fossil and extant, with modified cranial structures that presumably indicate the presence of a short proboscis. The following taxa were evaluated based on descriptions and illustration in the literature: †*Cadurcodon* (Panperissodactyla: Perissodactyla: †Amynodontidae; from Wall, 1980); †*Brachycrus* (Artiodactyla: †Merycoidodontidae; from Wall, 1980); †*Astraponotus* Ameghino, 1901 (†Astrapotheria; from Kramarz et al., 2011); †*Pyrotherium* Ameghino, 1888; †*Huayqueriana* Kraglievich, 1934 (Panperissodactyla: †Litopterna: †Macraucheniiidae; from Forasiepi et al., 2016); *Saiga* Gray, 1843 (Artiodactyla: Bovidae: Antilopinae; from Clifford & Witmer, 2004a); *Madoqua guentheri* Thomas, 1894 (Artiodactyla: Bovidae: Antilopinae; from Kingswood & Kumamoto, 1996); and *Alces* Gray, 1821 (Artiodactyla: Cervidae; from Clifford & Witmer, 2004b, Table 1). Pyrotheria in particular has been included in Notoungulata, which in turn has been allied to Perissodactyla; as such, *Pyrotherium* is a member of Panperissodactyla (see Billet 2010; Welker et al. 2015; Buckley 2015).

Following Wall (1980), our selected extant taxa are hoofed mammals with a degree of modification and involvement of narial structures that is greater than just a prehensile upper lip, present in taxa such as the Giraffe *Giraffa camelopardalis* Linnaeus, 1758 (Artiodactyla: Giraffidae) and the Black Rhinoceros *Diceros bicornis* Linnaeus, 1758 (Perissodactyla: Rhinocerotidae). This led us to propose a scheme of transformations (Fig. 2) that matches the definition of proboscis and prorbiscis proposed by Milewski & Dierenfeld (2013). In this scheme, a true proboscis would require the concurrent changes in both upper lip prehensility and the involvement of narial structures. By comparison, prorbiscis is a

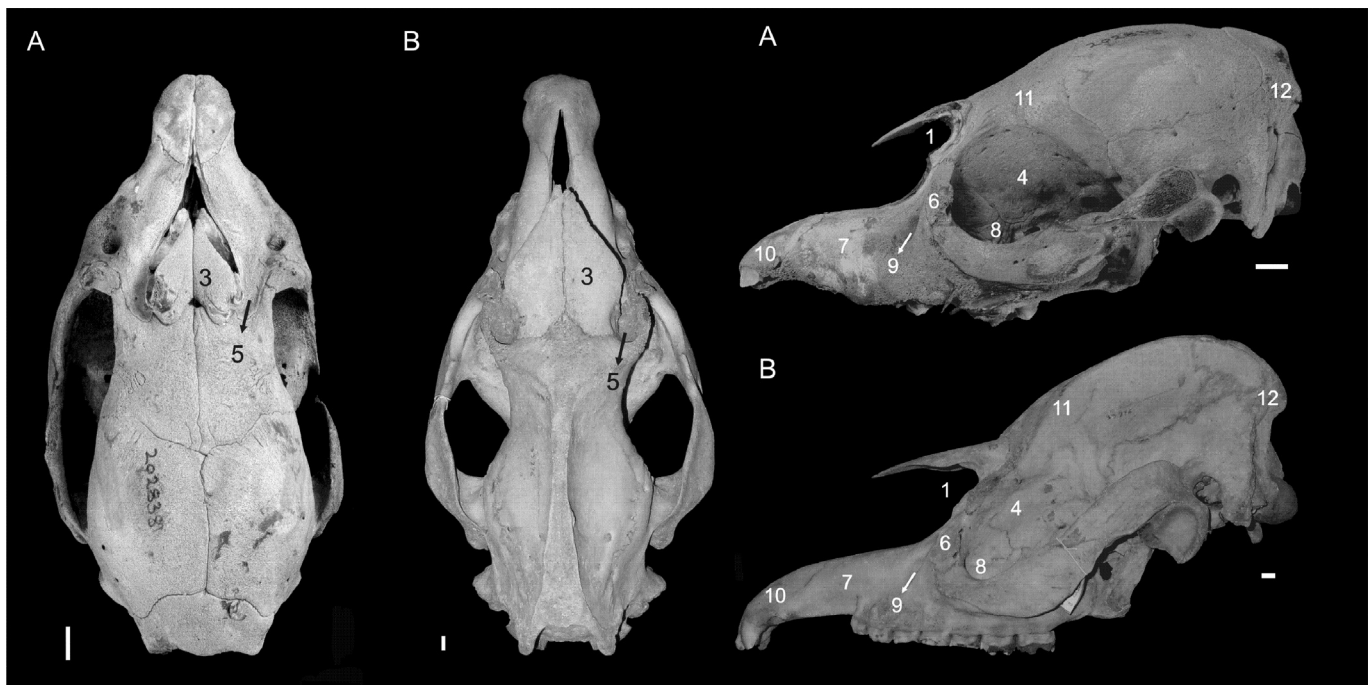


Fig. 1. Skulls of near-term fetus (A, C) and old adult (B, D) specimens of *Tapirus terrestris* in dorsal and lateral views. Wall (1980) characters (see text) are indicated by numbers as in Table 1. Based on Wall (1980: Fig. 1).

**Table 1**  
Characters identified by Wall (1980) as related to proboscis presence and function in the early Oligocene amynodontid.

Characters	Adult <i>Tapirus</i>	near-term fetus <i>Tapirus</i>	† <i>Cadurcodon</i>	† <i>Astraponotus</i>	† <i>Pyrotherium</i>	† <i>Brachycrus</i>	† <i>Huayqueriana</i>	<i>Saiga</i>	<i>Madoqua</i>	<i>Alces</i>
1. Retraction of nasal incision	present	present	present	present	present	present	present	present	present	present
2. Nasal process of premaxilla	absent	absent	absent	absent	present	?	absent	absent	present	present
3. Length reduction of nasal bone	present	present	present	present	?	present	present	present	present	present
4. Posterior displacement of cribriform plate	present	?	present	?	?	?	?	?	?	?
5. Preorbital fossa	present <sup>a</sup>	present <sup>a,d</sup>	present	present	absent	present	present <sup>c</sup>	absent	present <sup>b</sup>	present <sup>b</sup>
6. Bony nobs on lacrimal bone	present	absent small <sup>e</sup>	present	small	?	present	small	small	absent	small
7. Short rostrum	present	present	present	present	present	absent	absent	absent	present	absent
8. Anterior shift of orbit	present	present	present	present	present	absent	absent	absent	present	absent
9. Increased diameter of infraorbital canal	present	absent	present	present	absent	?	present	absent	absent	present
10. Vertical thickening and fusion of premaxilla	present	absent	present	absent	present	present	absent	absent	absent	absent
11. Enlarged frontal sinus	present	absent ? <sup>e</sup>	present	present ?	?	?	present	absent	absent	absent
12. Increased area of attachment of neck musculature	present	absent small <sup>e</sup>	present	present	present	absent	small	absent	absent	absent

†*Cadurcodon* (Perissodactyla, †Amynodontidae) and *Tapirus pinchaque* (Perissodactyla, Tapiridae). Here we report states for †*Cadurcodon* as in Wall, (1980), and code these characters for adult and near-term fetus of *Tapirus* (*T. terrestris* and *T. indicus*) and selected placentals with small proboscis or proboscis-like, the Oligocene–Miocene: †*Astraponotus* (†Astrapotheria; see Kramarz et al., 2011), †*Pyrotherium* (†Pyrotheria; see Billet, 2010), †*Huayqueriana* (†Litopterna: †Macrauchenidae; see Forasiepi et al., 2016), †*Brachycrus* (†Merycoidodontidae; see Wall, 1980), extant: *Saiga* (Artiodactyla: Bovidae; see Clifford & Witmer, 2004a), *Madoqua guentheri* (Artiodactyla: Bovidae; see Kingswood & Kumamoto, 1996), and *Alces* (Artiodactyla: Cervidae; see Clifford & Witmer, 2004b).

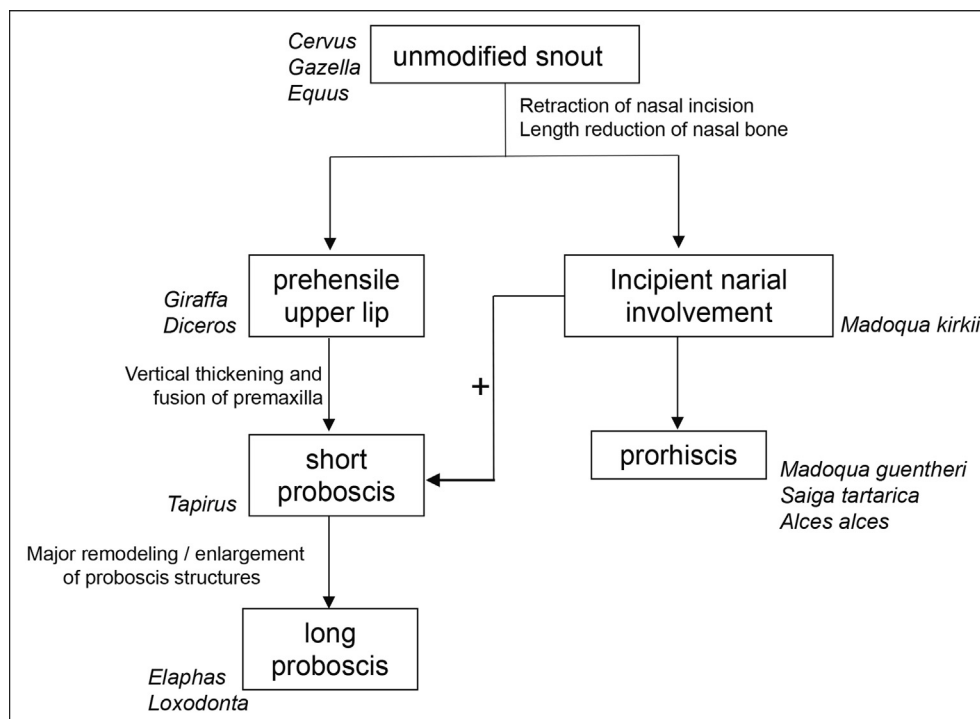
<sup>a</sup> Fossa for the meatal diverticulum.

<sup>b</sup> Fossa for the preorbital gland.

<sup>c</sup> Shallow fossae grouped immediately caudal to the nasal aperture.

<sup>d</sup> Shallow in *Tapirus terrestris*.

<sup>e</sup> In *Tapirus indicus*.



**Fig. 2.** Proposed scheme of transformations (arrows) that produce true proboscis and prorrhiscis in hoofed mammals taxa. Representative genera are named next to each evolutionary stage. See text.

purely narial equivalent of the proboscis lacking the grasping function, and it may evolve the incipient narial modifications into a variety of functions without involvement of the upper lip.

Adult tapirs of both species in our sample (*T. terrestris* and *T. indicus*) exhibited all the character states (either absence or presence) that also characterized *Tapirus pinchaque* in Wall, (1980). There is only two narial attributes shared by all the taxa examined

that is understood as indeed associated to the development of a true proboscis, which are: (i) the retraction of the nasal incision, and (ii) the length reduction of the nasal bone. Hence, together these state conditions may constitute the minimum cranial basis for narial specializations in hoofed mammals that display a proboscis-like adaptation. Notice that certain hoofed mammals exhibit just one of these conditions and, therefore, are not assigned

as candidates for the presence of a proboscis. For example, the extinct horse *Hippidion* Owen, 1869 presents a long nasal incision but the nasal is not reduced in length. A third key character identified by Wall (1980), the nasal process of the premaxilla, is generally absent except in *Madoqua*, *Alces* and *Pyrotherium*. In the latter, the left and right premaxillae form a massive median nasal bulge that may have supported part of the proboscis musculature; (see Billet 2010; Table 1). Notably, the near-term tapir specimen scored identical to the adult in these three fundamental characters. Therefore these states must have been acquired in a prenatal stage, thereby contributing to a functional proboscis right after birth. Two additional characters were also equally scored in newborn and adult tapirs: the short rostrum and the anterior shift of the orbit (Table 1). These character states are shared by the astrapotherian and pyrotherian here examined, but not completely in macraucheniids, merycoidodonts, bovids, or cervids (Table 1). Other potential bearers of a short proboscis studied by Wall (1980) did not share these character states. Interestingly, six characters achieved the derived state of proboscis-bearing hoofed mammals along the postnatal development in tapirs. These character states present in the near-term fetus included a shallow preorbital fossa, absence of bony knobs on the lacrimal, infraorbital canal not enlarged, premaxilla not fused nor thickened, frontal sinus not enlarged, and no enlarged area for neck musculature (nuchal crest inconspicuous). The area for neck musculature might not necessarily be related to the “proboscis syndrome”. Although, side head movements commanded by such muscles indirectly aid in feeding because tapirs may consume the edible part of vegetation by fixing it first with the proboscis and then pulling it away with a strong movement of the entire head (pers. obs.).

In this study, we observed a terminal-addition pattern of development and evolution. This was strongly suggested by the fact that near-term and young tapirs did not exhibit the derived state in these characters as compared with the state of the adult. On the basis of this pattern we propose that the three fundamental characters directly associated with a modified narial structure appeared first, and were present in most taxa examined. Secondary characters states were modified later as refinements of that narial structure. Some of these characters evolved in taxa with a true proboscis and are inferred in fossils, whereas other character states are not present in the derived state in extant taxa with prorrhiscis. Thus, together with †*Cadurcodon*, †*Astrapotonus* and †*Pyrotherium*, tapirs bear more derived character states with respect to *Brachyrus* and more so with respect to *Huayqueriana* among the fossils, and *Saiga*, *Madoqua*, and *Alces* among extant taxa (Table 1). This holds true even when all these taxa are highly derived in other directions (especially macraucheniids; see below). All the latter extant taxa exhibited narial modifications that fall into the category prorrhiscis, this due to the fact that they lack the grasping function used to distinguish the true proboscis (Milewski & Dierenfeld 2013).

The case of macraucheniids (here represented by *Huayqueriana*) is remarkable for its scoring closely matched that of *Alces*, except for one character state (presence of enlarged frontal sinus; Table 1). *Alces* is a taxon strongly associated to water and Milewski & Dierenfeld (2013) assigned a novel function to its prorrhiscis: capturing air that aids in buoyancy. Macraucheniines have been variously associated to water (see Guérin & Faure 2004 and citations therein), and *Huayqueriana* presents a uniquely re-oriented air pathway with the meatus nasi transformed into a large nasal diverticulum without anterior opening (see Forasiepi et al. 2016). This highly modified meatus may act as an air trap for buoyancy, as proposed by Milewski & Dierenfeld (2013) for *Alces*, and may be also for respiration (our speculation), together with the presumed prorrhiscis. Still, macraucheniids are unique in many aspects of the snout anatomy (see details in Forasiepi et al. 2016), so it remains to

be investigated whether macraucheniids, and macraucheniines in particular, such as *Huayqueriana* and *Macrauchenia*, match the proposed narial function of *Alces*.

In conclusion, a true short proboscis must have been present in later representatives amynodontids, astrapotherians, pyrotherians, and possibly some merycoidodonts, among other fossil hoofed mammals. Neither macraucheniids nor any extant hoofed mammals, other than tapirs, can be interpreted as presenting a true short proboscis. In fact, these should be interpreted as cases of prorrhiscis. The core characters present in all taxa examined develop prenatally in tapirs, which are born with a functional proboscis but may start using it for the grasping function only when they first incorporate solid food in the diet. Other characters that refine or complement the osteological “proboscis syndrome” (Table 1) develop postnatally in tapirs and are absent or irregularly distributed in other taxa, suggesting a terminal addition sequence of character evolution in several independent taxa. In addition, we note that modifications of narial structures involved in the prorrhiscis (Milewski & Dierenfeld 2013); offer much interesting variation both in extant and fossil taxa. This invites further comparative research to elucidate hidden functional variation in hoofed mammals.

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## Appendix A. Specimens of *Tapirus terrestris* and *T. indicus* examined in this study.

Tapirus terrestris (n = 31)		Tapirus indicus (n = 14)	
Catalog	CBL (mm)	Catalog	CBL (mm)
AMNH 202838	163.9	USNM 267365	276.3
FMNH 60441	165.5	FMNH 41393	329.9
MACN 4.339	166.2	MACN 12.9	352.8
USNM 143861	193.5	AMNH 167309	359.3
AMNH 100133	234.5	AMNH 167844	392.7
AMNH 23547	243.2	AMNH 130108	412.2
AMNH 173573	314.2	USNM 155410	420.0
MACN 48.330	324.0	MACN 29.926	420.8
MACN 52.77	346.9	USNM 283565	427.7
CML 8139	NA	AMNH 201799	428.1
MACN 11.11	NA	AMNH 54960	432.3
MACN 25.34	NA	AMNH 180030	441.7
MACN 25.35	NA	FMNH 123664	443.9



(continued)

Tapirus terrestris (n = 31)		Tapirus indicus (n = 14)	
MACN 26.70	NA	FMNH 60010	458.8
MACN 36.139	NA		
MACN 48.329	NA		
CML 6347	356.0		
MACN 10.26	358.3		
MACN 4.329	358.8		
CML 9817	377.8		
MNH 703	382.2		
MACN 50.559	384.9		
CML 9819	386.0		
CML 9830	386.6		
MACN 25836	386.8		
CML 6346	390.7		
CML 9829	392.6		
CML 9818	394.2		
FMNH 134499	394.5		
FMNH 60768	397.3		
MACN 33.276	399.8		

Abbreviations of the Institutions: **AMNH**, American Museum of Natural History, New York; **CML**, Colección Mamíferos Lillo, Tucumán, Argentina; **FMNH**, Field Museum of Natural History, Chicago; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MNH**, Museo Nacional de Historia Natural, Montevideo, Uruguay; **USNM**, Smithsonian Institution, Washington, DC. Other abbreviations: **CBL**, condyle-basal length; **NA**, Not Available (specimens with premaxilla or occipital lacking so CBL missing).

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