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## GRIPHOTHERION PEIRANOI, GEN. ET SP. NOV., A NEW EOCENE NOTOUNGULATA (MAMMALIA, MERIDIUNGULATA) FROM NORTHWESTERN ARGENTINA

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**ABSTRACT**—*Griphotherion peiranoi*, a new genus and species of notoungulate from northwestern Argentina, is presented here. The material studied consists of a nearly complete skull and part of the postcranial skeleton, recovered in the Lumbrera Formation (Eocene) at the locality of El Simbolar (Salta Province, northwestern Argentina). The specimen was evaluated in terms of a matrix of 28 craniodental characters and compared with 11 typotherian genera. Additionally, characters of the new taxon were compared to those included in a previously published data matrix that includes several native South American ungulates. The particular features present in the specimen indicate unequivocally that this is a new notoungulate taxon; nevertheless, due to its distinctiveness, we opted not to place the novel taxon in any of the known families of Notoungulata. The results of the analyses performed indicate that *G. peiranoi* is closely related to Mesotheriidae, Hegetotheriidae, and Archaeohyracidae. These families represent the 'rodent-like' notoungulates that evolved during the Late Paleogene and the Neogene. This new record contributes to our knowledge of the Eocene notoungulate fauna of northwestern Argentina. It also supports the broader perspective that this region played an important role as an area of origin and diversification for several lineages of this remarkable order of endemic South American ungulates.

**RESUMEN**—Se presenta un nuevo género y especie de notoungulado del noroeste argentino, *Griphotherion peiranoi*. El material estudiado consiste en un cráneo casi completo y la parte anterior del esqueleto postcranial y fue colectado en niveles de la Formación Lumbrera (Eoceno) en la localidad de El Simbolar (provincia de Salta, noroeste argentino). El espécimen fue incluido en una matriz de 28 caracteres craneodentales y 11 géneros de tipoterios. Adicionalmente, el nuevo taxón fue incluido en una matriz de datos con varios ungulados nativos sudamericanos previamente publicada. Las características particulares presentes en el espécimen indican que se trata indudablemente de un nuevo taxón de notoungulado. Por lo tanto, se eligió una hipótesis taxonómica abierta y el taxón no fue incluido en ninguna de las familias conocidas para el orden. Los resultados de los análisis realizados indican que *G. peiranoi* está cercanamente relacionado a Mesotheriidae, Hegetotheriidae y Archaeohyracidae. Estas familias representan los notoungulados 'roentiformes' que evolucionaron durante la última parte del Paleógeno y el Neógeno. Este nuevo registro mejora el conocimiento de las faunas de notoungulados en el noroeste argentino y apoya la idea de que esta región jugó un papel importante como área de origen y diversificación para varios linajes de este importante orden de ungulados nativos sudamericanos.

### INTRODUCTION

The order Notoungulata is the most diverse of those containing the extinct endemic South American ungulates (Bond, 1986, 1999; Cifelli, 1993; Bond et al., 1995; Cerdeño and Bond, 1998; Miño Boilini et al., 2006). Notoungulates have been recorded from the Paleocene to the Quaternary and are conspicuously represented in almost all of the Paleogene and Neogene South American fossil faunas. The Paleogene was a period of major importance for the evolution and diversification of this order (Bond, 1986; Croft et al., 2008; Reguero and Prevosti, 2010). Most of these fossils have been recovered in Argentina, and the presence of several Paleogene families is well established from a variety of localities, particularly in Patagonia and the central and northwestern regions of the country. These discoveries have resulted in a substantial amount of published information (e.g., Ameghino, 1897, 1901; Scott, 1912; Patterson, 1936; Simpson, 1936, 1948, 1967; Simpson et al., 1962; Pascual et al., 1978, 1981; Bond, 1986; Bond and López, 1993; López and Bond, 1995; López, 1997; Montalvo and Bond, 1998). In addition, other important records have been reported from Brazil, Uruguay, Bolivia, Chile, and Perú (Paula Couto, 1952, 1954, 1983; Cifelli,

1983; Soria and Ferraz de Alvarenga, 1989; Shockey, 1997; Bond et al., 1998; Ubilla et al., 1999; Flynn et al., 2002a, 2002b, 2003; Croft et al., 2003; Hitz et al., 2006; Billet et al., 2008, 2009).

The phylogenetic relationships among many representatives of this order remain unresolved, and this is particularly true for Paleogene taxa. Few attempts have been made in the past to elucidate the early evolution of notoungulates, whereas most of the studies that do exist have been focused on representatives of particular families or genera (Shockey, 1997; Cerdeño and Bond, 1998; Hitz et al., 2000; Croft et al., 2003; Reguero and Castro, 2004; Croft and Anaya, 2006). Only a few analyses have been sufficiently extensive in terms of their taxonomic scope to contribute to the resolution of inter-family relationships within the order (e.g., Cifelli, 1993; Billet, 2010, 2011; Reguero and Prevosti, 2010). Previously, the monophyly of the order has been accepted by most authors (Cifelli, 1993). However, Billet's (2010) recent phylogenetic proposal has challenged this perspective, reigniting the debate regarding the inclusion of Pyrotheria within Notoungulata, a viewpoint previously considered by other researchers (e.g., Patterson and Pascual, 1968; Patterson, 1977).

In northwestern Argentina, the Eocene Lumbrera Formation has been an important source of notoungulate fossils (Pascual et al., 1981). This formation represents the upper unit of the Santa Bárbara Subgroup and is made up of reddish to red claystones and siltstones, either massive or at times showing bioturbation

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and development of paleosols. Green and gray claystones, yellowish limestones, and fine sandstones are also present in the sequence (del Papa and Salfity, 1999). The formation also includes two green mudstone strata associated with lacustrine events known as 'Faja Verde I' and 'Faja Verde II,' with 'Faja Verde II' the most widespread in the region (Bond, 1981; Salfity and del Papa, 1999; Malabarba et al., 2006). Recently, the formation was divided into two major sedimentary events or subunits: lower Lumbrera, which includes all of the levels below 'Faja Verde I' and 'Faja Verde II,' and upper Lumbrera, which includes the levels above 'Faja Verde II' (del Papa, 2006). In a recent contribution, del Papa et al. (2010) reported an absolute U-Pb zircon age of 39.9 Ma for upper Lumbrera. They correlated these levels with the middle to late Eocene Barrancan Subage of the Casamayoran South American Land Mammal Age (SALMA), and correlated lower Lumbrera levels with the middle Eocene Vacan Subage of the SALMA.

The fossil vertebrate assemblages from lower Lumbrera are the best studied to date, and include Crocodylia, Squamata, and mammalian taxa including metatherians, xenarthrans, litopterns, astrapotherians, and notoungulates (Pascual et al., 1981; del Papa and Salfity, 1999; del Papa et al., 2010). Notoungulate fossils from multiple families have been described from those levels (Vucetich, 1980; Bond, 1981; Vucetich and Bond, 1982; Bond and López, 1993), and include representatives of the families Notostylopidae, Oldfieldthomasiidae, Notohippidae, and Isotemnidae.

In the present contribution, a new notoungulate is reported from lower Lumbrera, recovered from the sediments located below 'Faja Verde II' and above 'Faja Verde I' at the locality of El Simbolar (Salta Province, northwestern Argentina). In addition to providing a description of the cranial and dental features of this new taxon, a phylogenetic analysis is performed in terms of comparison with several representatives of Typotheria. Additionally, this new taxon and other Eocene genera from northwestern Argentina are incorporated into the character-taxon matrix presented by Billet (2010), with the purpose of comparing the results reported here with those of other recent comparative studies.

## MATERIALS AND METHODS

The material studied includes a complete skull and mandibles with full dentition, and part of the postcranial skeleton that includes ribs, cervical and thoracic vertebrae, and the right forelimb. The specimen is now curated in the Colección Paleontología Vertebrados Lillo (Instituto Miguel Lillo, Tucumán, Argentina).

This study was primarily focused on the craniodental features of the specimen, which are most commonly used to assess the affinities of Paleogene forms of Notoungulata. The terminology used in the description of the skull follows the Nomina Anatomica Veterinaria and Evans and Christensen (1979). In certain cases, terms commonly used in the literature that focused on Notoungulata were applied. For dental features, the terminology mainly follows the nomenclature proposed by Bown and Kraus (1979), with some variation when referring to terms such as lophs and lophids (e.g., paracrist = paraloph). This is related to the lophodont nature of notoungulate cheek teeth.

To assess the relationships of the new taxon, a phylogenetic analysis of several typotherian taxa was performed. The matrix was based on 28 craniodental characters and included 11 typotherian genera (Appendix 1 and Matrix 1 in Supplementary Data, available online at [www.vertpaleo.org/jvp/JVPcontents.html](http://www.vertpaleo.org/jvp/JVPcontents.html)). Furthermore, the Paleogene genus *Simpsonotus* Pascual et al., 1978, was included. Most characters were taken from the study described in García López (2009). However, other characters

were based on the previous work of other authors (Cifelli, 1993; Croft et al., 2003; López, 2008; Billet, 2010). The data matrix was analyzed using TNT (Tree Analysis Using New Technology) (Goloboff et al., 2003) with all characters set as non-additive and using the tree bisection-reconnection (TBR) swapping algorithm. Support indices were calculated with the same program using Jackknife and Bremer supports.

In addition to this analysis, the new taxon, along with the genus *Boreastylops* Vucetich, 1980, were incorporated into the data matrix of Billet (2010). Furthermore, several characters of the olfieldthomasiid *Colbertia* Paula Couto, 1952, coded as missing entries in the cited study, could be incorporated here on the basis of recently studied material (García López, 2011), specifically the Lumbrera species *C. lumbrerense* Bond, 1981 (see Matrix 2 in Supplementary Data). The pyrothere genus *Proticia* Patterson, 1977, was excluded from the analysis because of the large number of missing entries (see Billet, 2010) and, in contrast to the analysis performed by the latter author, the matrix was analyzed with all characters set as non-additive.

**Institutional Abbreviation**—PVL, Colección Paleontología Vertebrados Lillo, Tucumán, Argentina.

**Anatomical Abbreviations**—**I**, upper incisor; **i**, lower incisor; **M**, upper molar; **m**, lower molar; **P**, upper premolar; **p**, lower premolar.

## SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903

Suborder TYPOTHERIA Zittel, 1893

Family indet.

*GRIPHOTHERION*, gen. nov.

(Fig. 1)

**Type Species**—*Griphotherion peiranoi*.

**Diagnosis**—As for type and only species.

**Etymology**—'Griphos,' Greek term for puzzling, intricate, in reference to the set of different characters present in the species and the difficulty of assigning it to any of the known notoungulate families; and 'therion,' Greek term for beast.

*GRIPHOTHERION PEIRANOI*, sp. nov.

(Fig. 1)

**Holotype**—PVL 5903; complete skull and mandibles with complete dentition and part of the postcranial skeleton, including ribs, cervical, and thoracic vertebrae, and the right forelimb.

**Etymology**—The species epithet honors Dr. Abel Peirano and his valuable contributions to the field of geology in northwestern Argentina and to the advancement of the Universidad Nacional de Tucumán.

**Locality and Stratigraphic Context**—El Simbolar, Guachipas Department, Salta Province, Argentina (Fig. 2). Lumbrera Formation (lower Lumbrera; del Papa, 2006; del Papa et al., 2010), middle Eocene.

**Diagnosis**—This new taxon differs from all other notoungulates by a poorly developed or virtually absent nasal process, a virtually absent meatal crest, and the presence of a maxillary constriction at the level of the P1. *Griphotherion peiranoi* is a member of Typotheria because it presents a rodent-like I1, somewhat enlarged, and the characteristic 'face pattern' of this group (Cifelli, 1993; Billet et al., 2009); however, it lacks the postpalatal platform present in the group. It differs from early diverging typotherians (except archaehyracids) by the presence of a small but lingually closed fossettid on m2–3 talonid, the reduction of the jugal bone (although it reaches the lacrimal), and the presence of a cup-like structure formed by the fusion of the retroarticular process and the external auditory meatus (a character shared with *Campanorco* Bond et al., 1984); differs from *Campanorco* by the presence of a well-developed, flat area for the origin of the deep masseter muscle, the presence of a

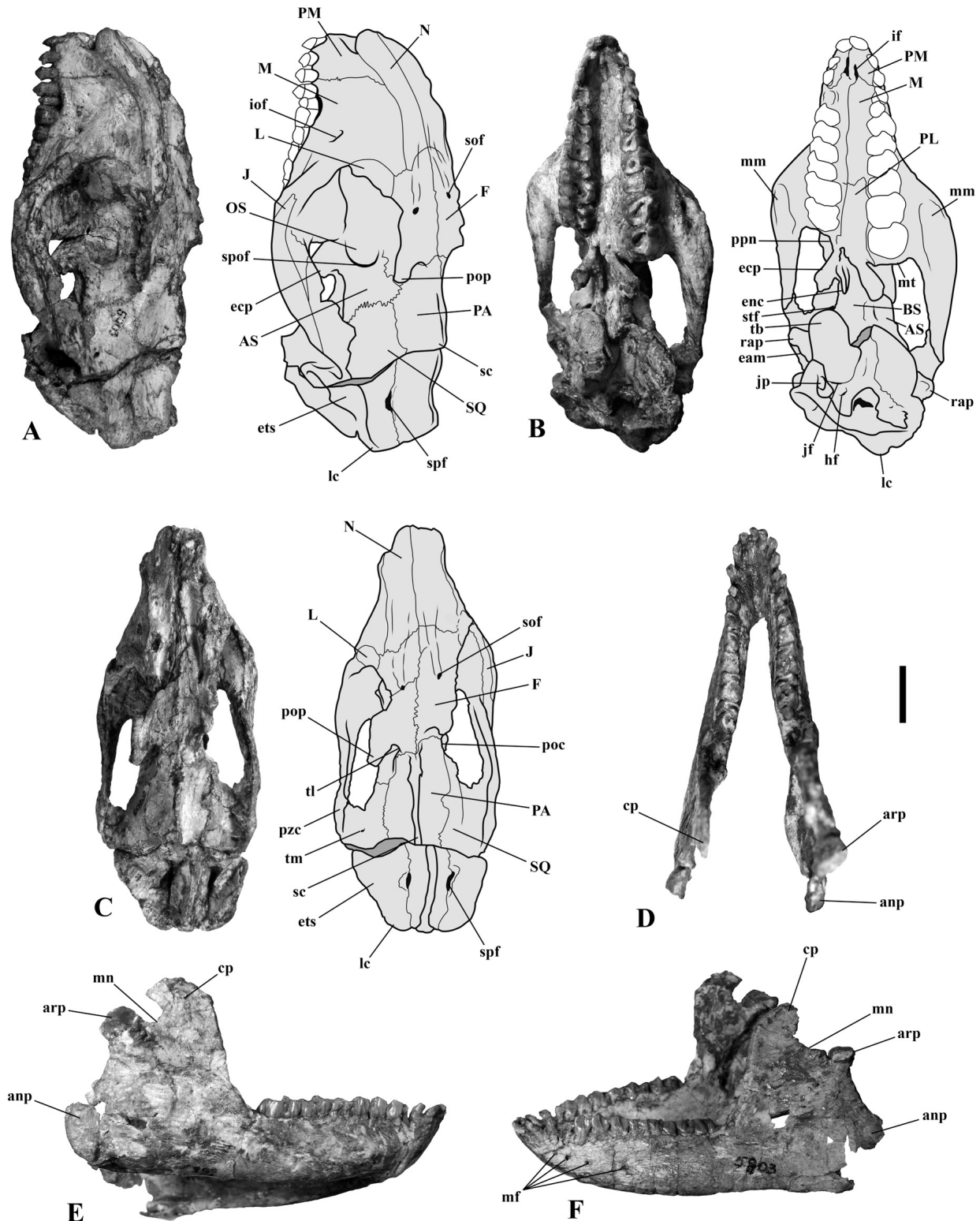


FIGURE 1. *Griphotherion peiranoi*, PVL 5903, holotype. **A**, skull in left dorsolateral view; **B**, skull in ventral view; **C**, skull in dorsal view; **D**, mandibles in dorsal view; **E**, mandibles in right view; **F**, mandibles in left lateral view. **Abbreviations:** anp, angular process; arp, articular process; AS, alisphenoid; BS, basisphenoid; cp, coronoid process; ecp, ectopterygoid crest; enc, entopterygoid crest; ets, (area of) epitympanic sinus; F, frontal; hf, hypoglossal foramen; if, incisive foramen; iof, infraorbital foramen; J, jugal (incomplete on the left side of the skull); jf, jugular foramen; jp, jugular process; L, lacrimal; lc, lambdoid crest; M, maxilla; mf, mental foramen; mm, origin of deep masseter muscle; mn, mandibular notch; mt, maxillar tuberosity; N, nasal; OS, orbitosphenoid; PA, parietal; PL, palatine; PM, premaxilla; poc, postorbital constriction; pop, postorbital process; ppn, postpalatine notch; pzc, postzygomatic crest; rap, retroarticular process; sc, sagittal crest; sof, supraorbital foramen; spf, squamosal-parietal fenestration; spof, sphenorbital fissure; stf, sphenotympanic fissure; tb, tympanic bulla; tl, temporal line; tm, temporal meatus. Scale bar equals 1 cm.

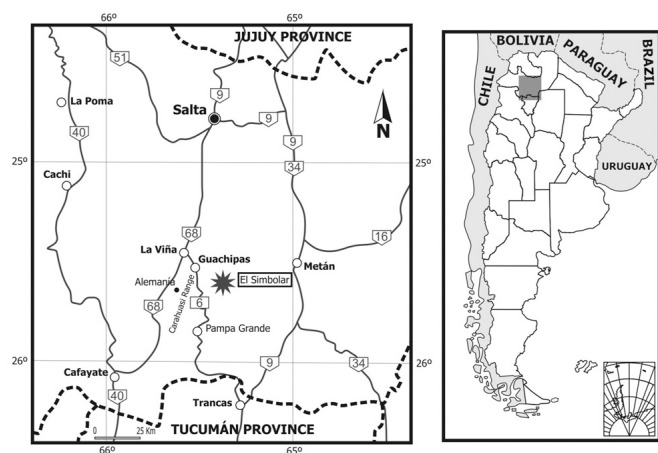


FIGURE 2. Map showing the location of El Simbolar (Salta Province, Argentina), where the material presented in this contribution was found.

well-developed upper canine, and the presence of a larger dorsal exposure of the frontal bone. Regarding archaeohyracids and advanced tyotherians, *Griphotherion* shares the following features with these groups: expanded hypocone areas on upper premolars, large facial extent of lacrimal bone, origin of masseter muscle as a flat area on the ventral border of the zygomatic arch, procumbent lower incisors, paralophid present on lower cheek teeth, entonoid mesially expanded and attached to the trigonid (isolating a fossettid), and premaxillomaxillary suture anteriorly directed on palate. Nevertheless, the new taxon differs from these groups by the following features: short external auditory meatus, low hypsodonty of postcanine teeth, reduced i1, strong dorsal edge of the zygomatic arch (continuous with the lambdoid crest), and mandibular foramen located at the level of the alveolar border.

## DESCRIPTION

### Skull and Mandible

The skull and mandibles present a moderate degree of deformation, with the sagittal plane sloped almost 30 degrees to the right. Despite this fact, most surfaces are well preserved, although the right side of the palate and most part of the basicranium are highly crushed. A crack crosses transversally the skull at the level of the posterior root of the zygomatic arch dorsally and the upper edge of the foramen magnum ventrally. The posterior portion divided by this crack is slightly displaced ventrally and laterally regarding the anterior portion.

The rostrum is short and ventrally curved. The orbit is relatively large, representing almost a third of the total skull length (Fig. 1A).

The facial and palatine processes of the premaxilla are reduced (Fig. 1A, B). The facial process of this bone has a roughly triangular shape. Rostrally, it forms the lateral wall of the narial aperture. The narial process of the premaxilla (see Billet et al., 2008) is absent. The premaxillomaxillary suture is straight and almost entirely vertical on the surface of the rostrum. The area of the palatine process is reduced and bears a small incisive foramen (Fig. 1B). The palatal segment of the premaxillomaxillary suture is oblique and extends rostrally from the I3 alveolus to the caudal edge of the incisive foramen.

The maxilla forms the sides of the rostrum, a major part of the zygomatic arch, and most of the palate (Fig. 1A, B). Dorsally, the maxilla makes contact with the nasal (nasomaxillary suture). Caudally, the maxilla makes contact with the frontal (frontomax-

illary suture), the lacrimal (lacrimomaxillary suture), and the jugal on the zygomatic arch (zygomaticomaxillary suture). The nasomaxillary suture is dorsally convex. The lateral surface of the maxilla is smooth and is pierced by the infraorbital foramen, which is located at the level of the third upper premolar (Fig. 1A). The frontomaxillary suture is formed by the contact between the frontal and a very small process of the maxilla located between the nasal and lacrimal. The anterior root of the zygomatic arch is rostrocaudally extended and the maxillary tuberosity is not prominent (Fig. 1B). In this area, the maxilla has a flattened ovoid space for attachment of the deep masseter muscle (see Turnbull, 1970) (Fig. 1B). This area is different from the condition observed in other paleogene taxa, such as *Colbertia*, *Notopithecus* Ameghino, 1897, and *Campanorco*, which present a much narrower zone for the attachment of this muscle. The zygomatic process of the maxilla forms the greater part of the ventral surface of the arch, and almost reaches the mandibular fossa. On the lateral surface of the arch, the zygomaticomaxillary suture is oblique and rostrocaudally extended. The maxilla is the most extended element of the osseous palate, being slightly vaulted. No foramina can be identified in this area. Finally, the maxilla forms a large part of the intraorbital wall and floor. The only visible suture in this area is a segment of the zygomaticomaxillary suture, which is straight and parallel to the ventral orbital rim.

The jugal bone is located on the lateral and dorsal surface of the zygomatic arch and, unlike the condition observed in taxa such as *Campanorco* and representatives of Mesotheriidae, is a very small, blade-like element (Fig. 1A). As in most Paleogene taxa (except Interatheriidae), it reaches the lacrimal dorsally and forms the rostroventral rim of the orbit, but the zygomaticolacrimal suture is not clearly visible. This bone is rostrocaudally extended.

The lacrimal bone is located dorsorostrally on the orbital rim (Fig. 1A). The semicircular facial process is relatively large. It makes contact rostrally and dorsally with the maxilla (lacrimomaxillary suture) and ventrally it seems to make contact with the jugal (see above). The lacrimal tubercle is vestigial and the lacrimal foramen is not visible. Presumably, the intraorbital process of the lacrimal is small, but the contacts and extent of this element are not clearly visible inside the orbit.

The nasal is a long and narrow element (Fig. 1A, C). The rostral end of this bone reaches the level of the first upper incisor. The width of the nasal is roughly constant rostrocaudally, without the conspicuous caudal expansion present in Notostylopidae and Archaeohyracidae. The frontonasal suture is sigmoid (rostrally concave on the lateral side and rostrally convex on the medial side). The rostral-most part of the suture reaches the level of the distal border of the third upper premolar.

The palatine bone forms the caudal third of the palate and the floor of the choanae (horizontal process of the palatine) (Fig. 1B). The palatomaxillary suture is rostrally convex and its rostral-most part is located at the level of the mesial edge of the first upper molar. Caudally, the palatine bears the postpalatine notch and the pterygoid apophysis of the palatine or ectopterygoid crest. The postpalatine notch (Fig. 1B) is very shallow and, as a result, the maxillary tuberosity is not prominent, as previously mentioned. Remarkably, the postpalatal platform, a structure reported as being present in all tyotherians (Billet et al., 2008, 2009; Billet, 2011), is absent in this taxon. The ectopterygoid crest (Figs. 1A, B and 3) is narrow and projects laterocaudally. The sphenopalatine suture is partially visible on the caudal side of the base of this crest. The surface of the horizontal process of the palatine is only preserved on the left side of the skull. The surface is smooth, and lacks any identifiable grooves or foramina. The choanae are slightly retracted behind the level of the distal edge of the third upper molar (Fig. 1B). The surface of the second process of the palatine, the intraorbital process, is badly damaged and no features are discernable.

The frontal presents a dorsal part and an intraorbital part. The dorsal part (Fig. 1A, C) is very extensive and represents a third of the total skull length. This condition is very different from that observed in taxa such as *Campanorco*, where the dorsal exposure of the frontal is reduced. The supraorbital foramen is small and is related to a rostral groove, which reaches the surface of the nasal (Fig. 1C). The postorbital process is large; this element is only preserved on the left side of the skull, where it points caudally (Fig. 1A, C). This condition is probably due to deformation. The temporal line (Fig. 1C) is short and converges with the one on the opposite side to form the rostral end of the sagittal crest. The caudal edge of the temporal line is roughly parallel to the coronal suture. The intraorbital part of the frontal is badly damaged. The only feature that can be clearly distinguished is the intraorbital aperture of the supraorbital foramen. This is larger than the dorsal aperture and is located near the dorsal orbital rim, towards the base of the postorbital process.

The parietal bone forms the caudal part of the skull vault (Fig. 1A, C). It makes contact rostrally with the frontal near the coronal suture, which presents a lateral part, on the orbitotemporal fossa, and a dorsal part, behind the temporal line. Here, the skull shows a strong postorbital constriction as in most Paleogene taxa (Fig. 1C). The parietal also presents a small rostral contact with the alisphenoid. The sagittal crest is also well developed along the entire length of this bone (Fig. 1A, C). The surface of the parietal is narrow and is laterally bounded by the squamosal suture, which is more or less straight rostrocaudally. This suture bears a large and deep fenestration on its caudal part (Fig. 1A, C). The occipitoparietal suture is short. A sharp lambdoid crest is present in this area, and it continues on the surface of the squamosal (Fig. 1A, C).

Ventrally, the pterygoid forms a small entopterygoid crest located on the medial surface of the ectopterygoid crest (Figs. 1B and 3). Only the right side crest is partially preserved. Although it is not complete, the position and the apparent development of this element make it similar to those of other Paleogene notoungulates, such as *Colbertia* and *Puelia* Roth, 1901.

The arrangement of the contacts between the different elements of the orbitotemporal fossa is only partially visible; nevertheless, it is clear that it resembles the scheme described for Archaeohyracidae in Billet et al. (2009). The orbitosphenoid (Fig. 1A) and the alisphenoid (Fig. 1A, B) are located on the ventromedial part of the skull and the orbitotemporal fossa. The contacts of the orbitosphenoid are not visible, but its location on the ventral part of the orbitotemporal fossa (which is also the narrowest part of the skull) can be inferred by the position of the sphenorbital fissure. The alisphenoid has a lateral part, on the orbitotemporal fossa, and a ventral part, on the mesocranium (the anterior zone of the basicranium). The lateral surface of the alisphenoid makes contact rostrally with the orbitosphenoid (intersphenoidal synchondrosis) and the frontal (sphenofrontal suture), dorsocaudally with the parietal (sphenoparietal suture), and caudally with the squamosal (sphenosquamosal suture). The sphenorbital fissure (Fig. 1A) is present on the contact with the orbitosphenoid. The medial wall of the fissure is formed by this last element, and the lateral wall is formed by the alisphenoid. This fissure is large, ventrodorsally extended, and rostrally concave in lateral view. The surface of the ventral part of the alisphenoid is considerably damaged. In the rostromedial part of this area there is a small point of contact with the palatine (sphenopalatine suture) on the base of the ectopterygoid crest. Caudally, adjacent to the rostral edge of the tympanic bulla, there is a well-developed sphenotympanic fissure (Figs. 1B and 3). Apparently, the ventral part of the sphenosquamosal suture is located on the medial side of the mandibular fossa, but this is not clear.

The basisphenoid forms the medial surface of the mesocranium and contributes to the roof of the choanae (Fig. 1B). The boundary between the basisphenoid and the alisphenoid is marked by

a longitudinal crest. The surface of the basisphenoid is damaged but is apparently smooth, without grooves or other features. The caudal contact of this element is the sphenoccipital synchondrosis. The skull is broken at this point, and the edge of the basisphenoid is ventrally displaced with respect to the surface of the basioccipital.

The squamosal bone (Fig. 1A, C) has two parts, the squama (or squamosal part) and the zygomatic part. The squama makes contact rostrally with the alisphenoid (sphenosquamosal suture), ventrally with the ectotympanic, and caudally with the occipital complex. Dorsally, this part overlaps the parietal, forming the squamosal suture. On the dorsal surface, the squama bears a small foramen located at the level of the mandibular fossa (Fig. 1C). This is probably the temporal meatus (see Gabbert, 2004). Ventrally, the squamosal forms the mandibular fossa, which is shallow and flat. Caudally to the mandibular fossa, the squamosal bears a small retroarticular process (Figs. 1B and 3). This process is rostrocaudally compressed and is almost indistinguishable from the external auditory meatus of the ectotympanic, forming a funnel-like structure together with this element (Fig. 3). This structure is also present in *Campanorco*. The retroarticular foramen (usually located between the retroarticular process and the external auditory meatus in other notoungulates) is not visible. Caudally to the auditory meatus, the squamosal is ventrally projected and forms the posttympanic process, which is not well developed. Laterocaudally, the squamosal has a roughly triangular area that bears the epitympanic sinus. This area lacks the usual inflation observed in other notoungulates (Fig. 1A, C). The lambdoid crest continues across this region until it reaches the area near the base of the jugular process. Caudally, on the occipital side of the skull, the occipitosquamosal contact is marked by the presence of a narrow, laterally concave mastoid foramen (Fig. 3). The zygomatic part of the squamosal forms the dorsal part of the zygomatic arch. Rostrally, this part makes contact with the jugal (temporozygomatic suture). On the dorsal surface of the zygomatic arch, the rostral-most end of the squamosal reaches the level of the third upper molar. Laterally, the area of contact with the jugal is roughly horizontal, and its caudal end is located at the level of the sphenotympanic fissure. Dorsally, the zygomatic part of the squamosal bears a sharp, well-developed postzygomatic crest. The caudal part of the crest is badly damaged, but it appears to extend as far as the lambdoid crest.

The ectotympanic bone forms the tympanic bulla and the external auditory meatus (Figs. 1B and 3). The bulla is balloon-like and ventrally prominent. The external auditory meatus is short and forms the funnel-like structure mentioned above. The location of the stylomastoid foramen and the vagina processus hyoidei (usually located between the meatus and the posttympanic process of the squamosal in notoungulates) is not visible.

The structures of the occipital complex are heavily damaged in this specimen. The basioccipital shows a weak crest along its sagittal line, which reaches the sphenoccipital synchondrosis rostrally. The basioccipital surrounds the tympanic bulla laterally, and also forms the caudal boundary of these elements. This bone bears the jugular foramen, which is a narrow aperture located on the caudal edge of the bulla (Figs. 1B and 3). Mediocaudally to the jugular foramen there is a single circular hypoglossal foramen (Figs. 1B and 3), which is adjacent to the occipital condyle. This last structure is damaged on both sides of the skull. The occipital surface of the skull is deformed and broken in caudal view. The surface is badly damaged and its features are not visible. The jugular process is narrow and short (similar to the morphology observed in *Simpsonotus* and *Colbertia*), and laterally compressed. This last condition is probably related to diagenetic deformation (Figs. 1B and 3).

The mandible (Fig. 1D-F) presents a strong, completely fused symphysis (Fig. 1D). The mandibular body is slender in dorsal view. There are four mental foramina on the left mandibular body: below the lower canine, below the first lower premolar,

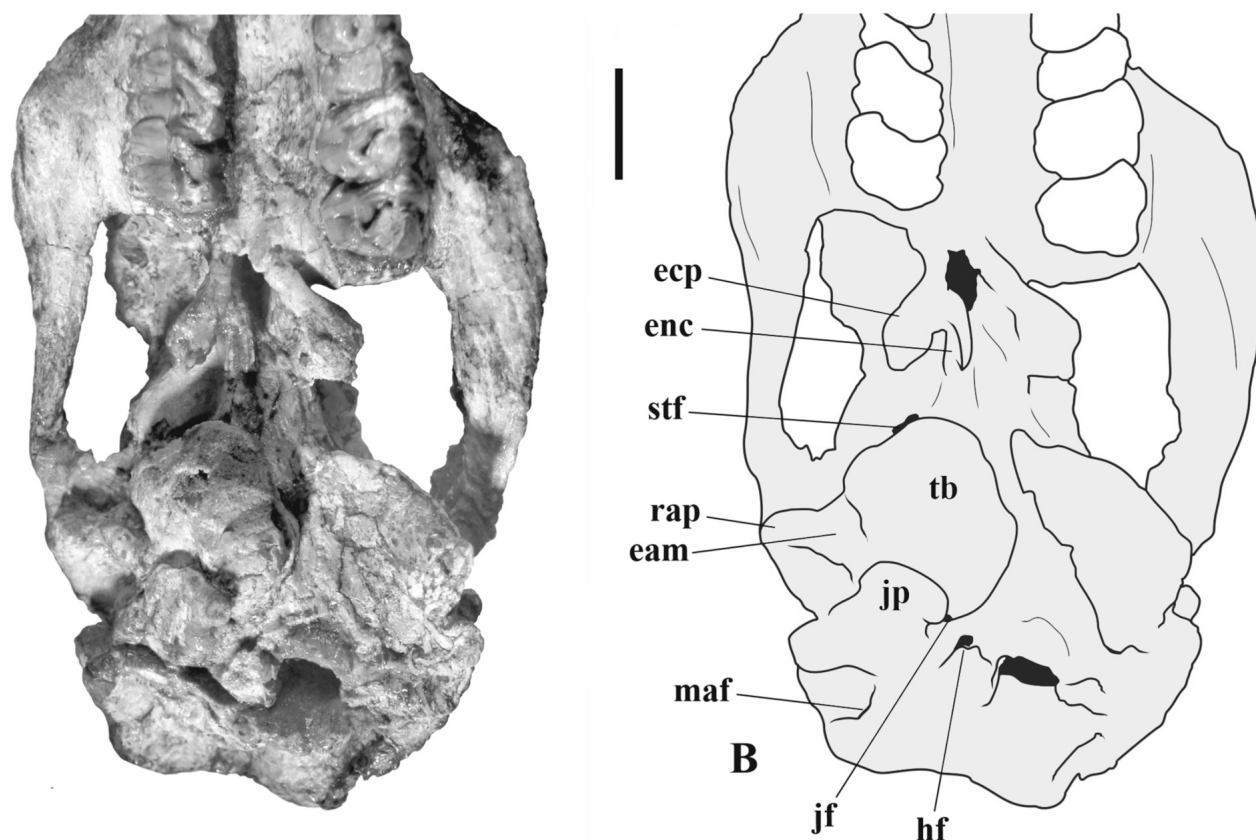


FIGURE 3. *Griphotherion peiranoi*, PVL 5903, holotype. Basicranium in ventral view. **Abbreviations:** eam, external auditory meatus; ecp, ectopterygoid crest; enc, entopterygoid crest; hf, hypoglossal foramen; jf, jugular foramen; jp, jugular process; maf, mastoid foramen; rap, retroarticular process; stf, sphenotympanic fissure; tb, tympanic bulla. Scale bar equals 1 cm.

at the distal edge of the second lower premolar, and at the distal edge of the fourth lower premolar (Fig. 1F). On the right mandibular body only two mental foramina are visible, one below the lower canine and the other below the fourth lower premolar. The medial aspect of the mandibular body shows a well-developed mylohyoid groove, with the ventral border marked by a robust crest.

The mandibular ramus is well developed rostrocaudally. The coronoid process represents roughly 25% of the total height of the ramus. This process is thin and caudally bent (Fig. 1E, F). The coronoid crest is weak.

The mandibular notch is deep (Fig. 1E, F). The articular process is damaged on both sides (Fig. 1E, F). This process shows a small lateromedial expansion.

The angular process is the most developed process in the ramus (Fig. 1E, F). It is well developed caudally and markedly exceeds the level of the articular process. This process also shows a small ventral expansion. The masseteric line is not well developed. The masseteric fossa, located on the lateral wall of the process, is very shallow. The area for attachment of the pterygoid muscles is visible on the medial wall of the angular process, and is deeper than the masseteric fossa. The mandibular foramen is located on the rostral edge of the pterygoid fossa, at the same level of the alveolar row. The aperture of the foramen is caudally oriented.

## Dentition

**General Aspects**—The dentition is brachydont and complete (no teeth are absent or markedly reduced with respect to the

primitive notoungulate formula). Therefore, the dental formula is 3/3, 1/1, 4/4, 3/3 (Fig. 4). There are small spaces between the anterior upper and lower teeth (incisors and canines), with the space between the I1 and the I2 being especially notable. The presence of all of the permanent teeth and the advanced wear degree (showing that no tooth had recently erupted at the time of death of the individual) indicate that the specimen is an adult. The incisive-canine row is reduced relative to the mesiodistal length of the premolar-molar row. This difference is particularly conspicuous in the lower teeth. Dental measurements are detailed in Table 1.

## Upper Dentition

The first upper incisor is clearly larger than the I2 and I3. The labial side of the tooth is slightly convex, whereas the lingual is concave. The crown is chisel-like. This morphology differs greatly from the remaining upper incisors, which are roughly triangular in labial view. There are no cingula in this tooth. The enamel layer is thinner on the lingual side of the tooth.

The I2 is slightly smaller than the I1 and the I3. This tooth is leaf-shaped, as are the I3 and the upper canine. The apex of the I2 crown is located mesially. The distal part of the crown is expanded and bears a slight concavity on the lingual side, where an incipient cingulum is also present.

The I3 is very similar in size and morphology to the I2. The tooth also presents a small cingulum on the lingual side, near the neck of the crown.



TABLE 1. *Griphotherion peiranoi*, PVL 5903, holotype—measurements (in mm) of the teeth.

Upper teeth														
Measure	I1		I2		I3		C							
	L	R	L	R	L	R	L	R						
Mesiodistal length	3.55	3.29	2.96	2.70	3.10	3.07	3.47	—						
Width	2.04	2.13	2.10	1.88	1.98	2.12	2.48	—						
Measure	P1		P2		P3		P4		M1		M2		M3	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R
Mesiodistal length	3.14	—	4.10	4.33	4.40	4.61	4.48	4.42	4.86	4.59	6.56	6.33	6.71	6.57
Width	2.82	—	5.40	5.37	5.74	5.62	6.28	6.18	6.67	6.12	8.20	8.04	7.83	6.61
Lower teeth														
Measure	i1		i2		i3		c							
	L	R	L	R	L	R	L	R						
Mesiodistal length	1.21	1.37	1.74	1.93	2.14	1.92	2.55	2.34						
Width	1.53	1.37	2.15	1.78	1.91	1.62	1.95	1.67						
Measure	p1		p2		p3		p4		m1		m2		m3	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R
Mesiodistal length	1.81	2.28	3.52	4.02	4.11	4.07	4.29	4.10	4.34	3.90	5.69	5.56	8.06	8.16
Width	1.80	1.65	2.56	2.26	2.93	2.66	3.06	3.03	3.71	3.28	4.33	4.42	4.28	4.37

Abbreviations: **L**, left; **R**, right.

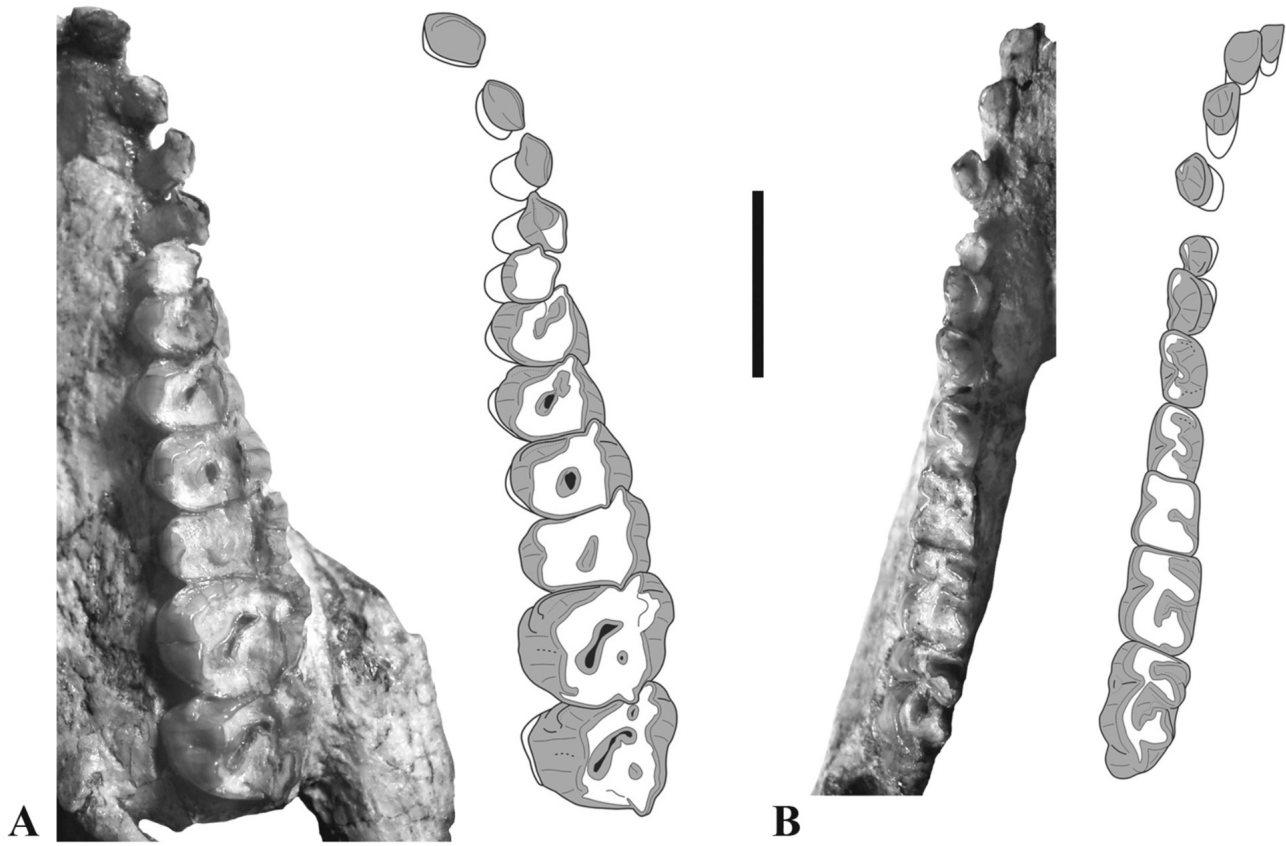


FIGURE 4. *Griphotherion peiranoi*, PVL 5903, holotype. **A**, upper dentition in occlusal view; **B**, lower dentition in occlusal view. Gray areas indicate distribution of enamel. Scale bar equals 1 cm.



The morphology of the upper canine is similar to that of the I2 and I3, but the crown is larger. The lingual cingulum is also more developed on this tooth. A wear facet is present on the distal half of the crown apex.

**Upper Premolars**—The size of the premolars increases progressively from the P1 to the P4. The premolars also become progressively more molariform toward the P4; this last condition is evident, among other features, by the expansion of the hypocone area.

The first upper premolar is a very small single-rooted tooth. The crown is very low and worn. In the sequence of dental eruption the first premolar appears before the remaining permanent premolars and molars (Hitz et al., 2006; Billet and Martin, 2011, and references therein). Although a wear surface is visible in this tooth (produced by occlusion during an earlier stage of the eruption sequence of the specimen), the growth in height of the adjacent permanent teeth was greater and, therefore, the P1 was no longer in contact with the lower teeth at the time of death of the individual. The morphology of the P1 is much simpler and otherwise very different from the other premolars. The paracone is the highest cusp, and it bears a small parastyle on its mesial side. The parastyle is located lingually to the paracone. The protocone is a small and low cusp. There are two cingula. The mesiolingual cingulum is well developed, whereas the distolingual cingulum is smaller. The two cingula surround the protocone mesially and distally. The P1 alveolus is located in a marked invagination of the maxilla, which represents a unique feature of this taxon.

The second upper premolar is much larger than the P1. The crown is relatively high compared to those of the other teeth. The labial wall of the ectoloph is convex. The columns of the paracone and metacone are visible in this wall, and the two are almost fused. The apices of these cusps are the highest points of the crown. Mesially there is the parastyle, which is more developed than in the P1. This is also exposed on the labial side, so its position is the typical one for notoungulates. This cusp is well developed and clearly differentiated from the paracone by a conspicuous labial sulcus. The metastyle is very small, nearly absent. The protocone is small and low. The protoloph is interrupted by a deep mesiolabial fossette, resembling the condition observed in some representatives of *Notohippidae*. The central fossa is also deep and oblique, and is connected to the mesiolabial fossette. There are small distal and mesial cingula.

The third upper premolar is similar to the P2. The paracone and metacone are subequal. The columns of these cusps are almost fused on the labial wall of the tooth. A narrow, shallow sulcus separates the two columns. The parastyle is well developed. This cusp is separated from the paracone by a deep sulcus and overlaps the distolabial corner of the P2 (in occlusal view). In this tooth, the protocone is higher than those of the anterior premolars. The protoloph is complete, and unites the protocone and parastyle. The central fossa is deep and oblique. This fossa is connected to the mesiolabial fossette, which is very shallow (unlike the same structure observed in the P2) and presents an arrangement roughly similar to that observed in *Notopithecus*. The mesial cingulum is well developed and located near the neck of the tooth. The distal cingulum is small and is incorporated into the crown.

The fourth upper premolar is the largest of the premolar series. The arrangement and development of the paracone and metacone are very similar to that seen in the other premolars described above (except the P1), although the sulcus that separates both columns is slightly deeper. The parastyle is somewhat larger in this premolar. This cusp clearly overlaps the P3 and is separated from the paracone by a deep sulcus. The metastyle is more conspicuous than in the other premolars. The protocone is a well-developed cusp and its mesiolingual wall is angulate. The deep central fossa is rounded and, apparently, it was closed in early stages of wear. The mesiolabial fossette is absent. The mesial cin-

gulum is more developed than in the P3, and the distal cingulum is not visible.

**Upper Molars**—The first upper molar is heavily worn and much smaller than the other molars. The mesiodistal length is 25% less than that of the M2, and the labiolingual length is 20% less. Due to advanced wear, the crown of the tooth is clearly transverse in occlusal view, unlike those of the other molars, and many features of the crown have been erased. The paracone and metacone are subequal. Unlike those of the premolars, these cusps are well separated by a wide sulcus. The parastyle is small but it clearly overlaps the P4. The sulcus that separates this cusp from the paracone is shallow. The metastyle is very small. The protocone and hypocone are also subequal and are separated by a conspicuous lingual sulcus. The central fossa is oblique and very shallow. The mesial and distal cingula are not visible, probably because of wear.

The second upper molar is clearly larger than the M1. The paracone and metacone present well-developed columns on the labial wall, separated by a wide and deep sulcus. The parastyle is small and is separated from the paracone by a wide but shallow sulcus. It overlaps the distolabial part of the M1. The metastyle in the M2 is more developed than that of the M1. The protocone is a large cusp. Its mesiolingual corner is angulate in occlusal view. The hypocone is smaller but is well developed. The central fossa is oblique. Its distolingual end is rounded and its mesiolabial end is acute. There are no cristae on the lingual face of the ectoloph. The circular distolabial fossette is very small and shallow. The crochet (a characteristic loph in notoungulates) is wide and labially curved. The protoloph is wide and oblique. The metaloph is narrower and transverse. Both lophs are connected by wear on the lingual edge, isolating the central fossa. The mesial cingulum is well developed. This cingulum forms a pocket-like structure on the mesiolingual corner of the protocone. The distal cingulum is slightly narrower than the mesial one, and is located higher on the crown. This cingulum has become partially merged with the metaloph by wear.

The third upper molar is less worn than the M2. In contrast to the proportions seen in most Paleogene notoungulate genera, this molar is about the same size as the M2 and is quadrangular in occlusal view. The paracone and metacone are well developed and are separated by a wide labial sulcus. There is an enamel fold near the base of the labial wall of the crown, similar to a small cingulum. The parastyle is proportionally larger in this tooth than in the M2. This cusp overlaps the distolabial corner of the anterior tooth and is separated from the paracone by a weak sulcus. Unlike in the first and second molars, the metastyle is large and projects distally in occlusal view, a feature also observed in taxa such as *Notopithecus* and *Archaeohyrax* Ameghino, 1897. The protocone is clearly angulate on its mesiolingual corner. The hypocone is smaller than the protocone but is still well developed and not vestigial, in contrast to those described in other Paleogene notoungulate taxa. The central fossa is oblique and deep. Unlike in the M2, the mesiolabial end of the fossa is rounded. A mesiolabial fossette is present in this molar, although it is very small. The distolabial fossette is slightly larger and circular. As both fossettes are present, this molar exhibits the characteristic 'face pattern' of typotherians. The crochet is curved labially and presents a small crista that penetrates the central fossa near its mesiolabial end. The protoloph is straight and oblique. The metaloph is transverse. The two lophs are united lingually and the central fossa is closed. The mesial cingulum is similar to that observed in the M2. The distal cingulum has become merged with the metaloph by wear.

### Lower Dentition

Some of the anterior lower teeth are reduced and slightly procumbent. The chisel-like first lower incisor is a very small

tooth, and is the smallest tooth in this taxon. Its mesiodistal length is 40% less than that of the i2. The labial side of the tooth is convex and presents a vertical wear facet near the tip of the crown. The lingual side presents a small enamel fold near the base of the crown.

The second lower incisor is morphologically similar to the i1, but larger. The labial side is convex, whereas the lingual side is slightly concave. A vestigial lingual cingulid is present.

The third lower incisor is similar to the previous teeth but the crown is asymmetric, with a small mesial projection. The lingual cingulid is well developed.

The lower canine is very similar to the i3 in size and morphology but the crown presents a higher degree of asymmetry and the lingual cingulid is more developed. This tooth is separated from the adjacent teeth by short diastemata.

**Lower Premolars**—As in the upper dentition, the p1 is a low-crowned tooth, with a higher degree of wear than the other premolars. The mesiodistal length of the p1 is 50% less than that of the p2, and the morphology of the crown is much more simple. The p1 is single rooted and the apex of the crown presents a mesial main cusp projected distally by a crest. There are no other clear features on the crown, and cingula are absent.

The morphology of the second lower premolar is similar to the pattern usually seen in some Paleogene notoungulates. The talonid and trigonid are vaguely differentiated and the tooth has two roots. The crown bears a main cusp (protoconid) located near the center of its mesiodistal length. Two small crests project from this cusp. The mesial crest is equivalent to a protocristid and the distal one is equivalent to an oblique cristid. There is a continuous lingual cingulid on the lingual wall of the tooth.

The third lower premolar presents two differentiated cusps on its crown. The larger one is located mesiolabially and is equivalent to a protoconid. A small paracristid projects from this point and then turns towards the lingual side of the premolar and merges with a small mesiolingual cingulid. The other cusp is located distolingually and is equivalent to a metaconid. This cusp is linked to the protoconid by a vestigial protocristid. The oblique cristid extends distally from the distolabial wall of the metaconid. This cristid surrounds a deep socket in the area of the talonid basin. There are no cusps on the talonid. There is a deep sulcus on the labial wall of the premolar that separates the trigonid and the talonid. Unlike in the p2, the lingual cingulid is vestigial.

The fourth lower premolar presents the higher degree of complexity in the premolar row. The protoconid is proportionally more developed in this tooth. This is connected to a paracristid, which is transversely developed as in the lower molars. The mesiolingual cingulid is small and is connected to the paracristid. The metaconid is almost equal in size to the protoconid. Both cusps are linked by a narrow protocristid. The oblique cristid is low, and projects from the central extension of the protocristid. It is connected to the hypolophid, which terminates in a small cusp (probably the entoconid). The talonid basin is deep and narrow. The labial sulcus separating the talonid and the trigonid is deep.

**Lower Molars**—The first molar is clearly smaller than the others. Its mesiodistal length is roughly 30% less than that of the m2. This tooth is heavily worn. The surface of the trigonid is smaller than that of the talonid in occlusal view and the area does not present any visible features. The oblique cristid emerges from the central region of the protolophid, which is clearly oblique in occlusal view. Few features are visible on the talonid. The entoconid is mesially expanded. It makes contact with the distal wall of the metaconid and isolates a small and very shallow talonid fossettid. The labial sulcus is well developed toward the apex of the crown, but is very weak and almost disappears towards the neck.

The second lower molar also shows heavy wear, but less than in the m1. The occlusal surface of the trigonid is much smaller than that of the talonid. The protoconid is located near the mesial edge of the tooth and is connected to a transverse paracristid, which is

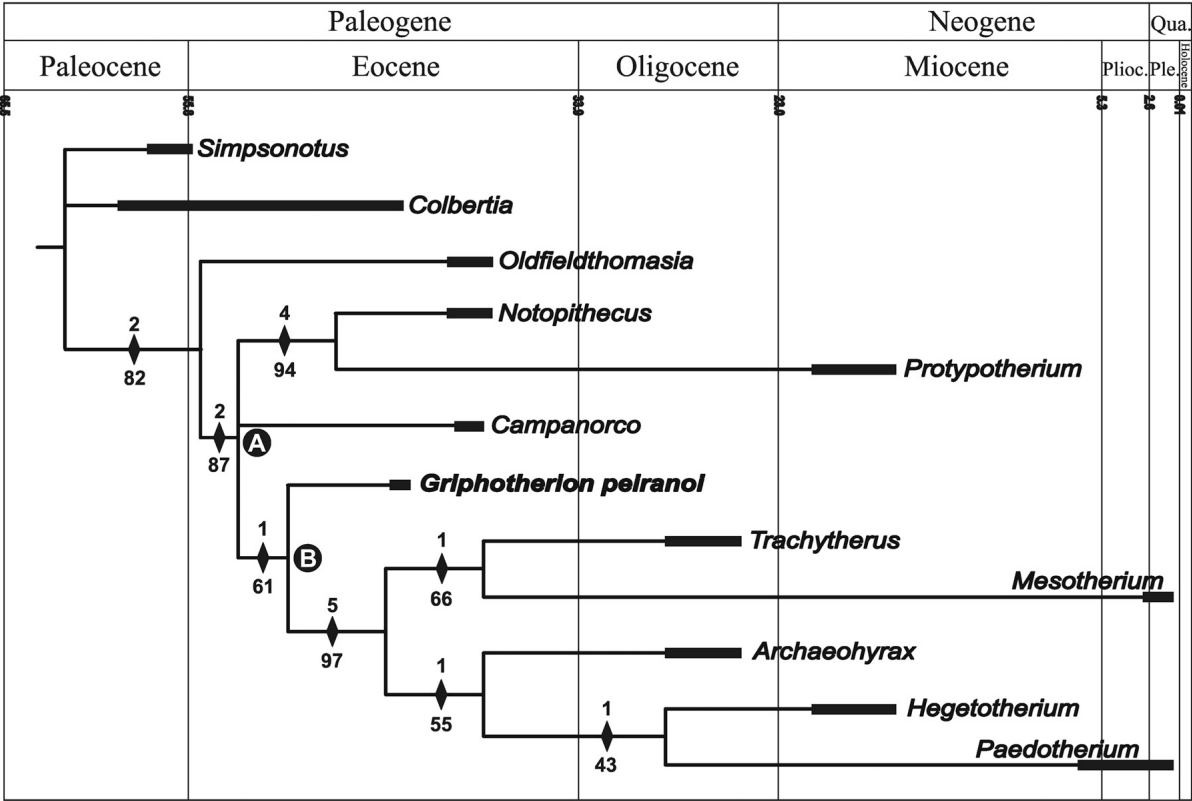
contiguous with a small mesiolingual cingulid. The metaconid is well developed. The paraconid (i.e., the small cusp present adjacent to the mesial wall of the metaconid in several basal forms of Notoungulata) is absent on the mesial edge of the metaconid (this may be due to wear). The oblique cristid arises from the medial part of the protolophid. It is contiguous with the hypolophid, which curves sharply towards the hypoconulid. The entoconid is well developed and mesially expanded by means of a roughly quadrangular process. This process closes the talonid basin and encloses a shallow fossettid, which is mesiodistally elongated. The labial sulcus is deep and well developed. The development of the entoconid is similar to that observed in early Archaeohyracids, such as *Punahyrax bondesioi* Reguero et al., 2008, and early diverging mesotheriids (see Billet et al., 2008).

The third lower molar is the largest of the molar series. The trigonid is proportionally smaller than those of the other molars. The morphology of the m3 trigonid is very similar to that observed in the m2 but the general degree of wear is less. The paralophid is more highly developed, the metaconid shows a mesial bulge that is probably equivalent to the base of the paraconid, and the protolophid is more transverse. The oblique crista arises from the medial region of the protolophid and is slightly angulate. The hypoconid cannot be differentiated in occlusal view. As is typical in Paleogene notoungulates, the m3 hypoconulid is greatly enlarged and projects distally. The hypoconulid is separated from the hypoconid by a labial talonid sulcus. Lingually, a low crest extends from the hypoconulid to the entoconid and encloses a small valley located between the two cusps. The morphology of the entoconid is similar to that observed in the m2, but the talonid fossettid is deeper. The labial sulcus that separates the trigonid and the talonid is deep and narrow, and this sulcus bears a basal cuspule. The general arrangement of this tooth is very similar to that observed in the Eocene archaeohyracid *Punahyrax* Reguero et al., 2008.

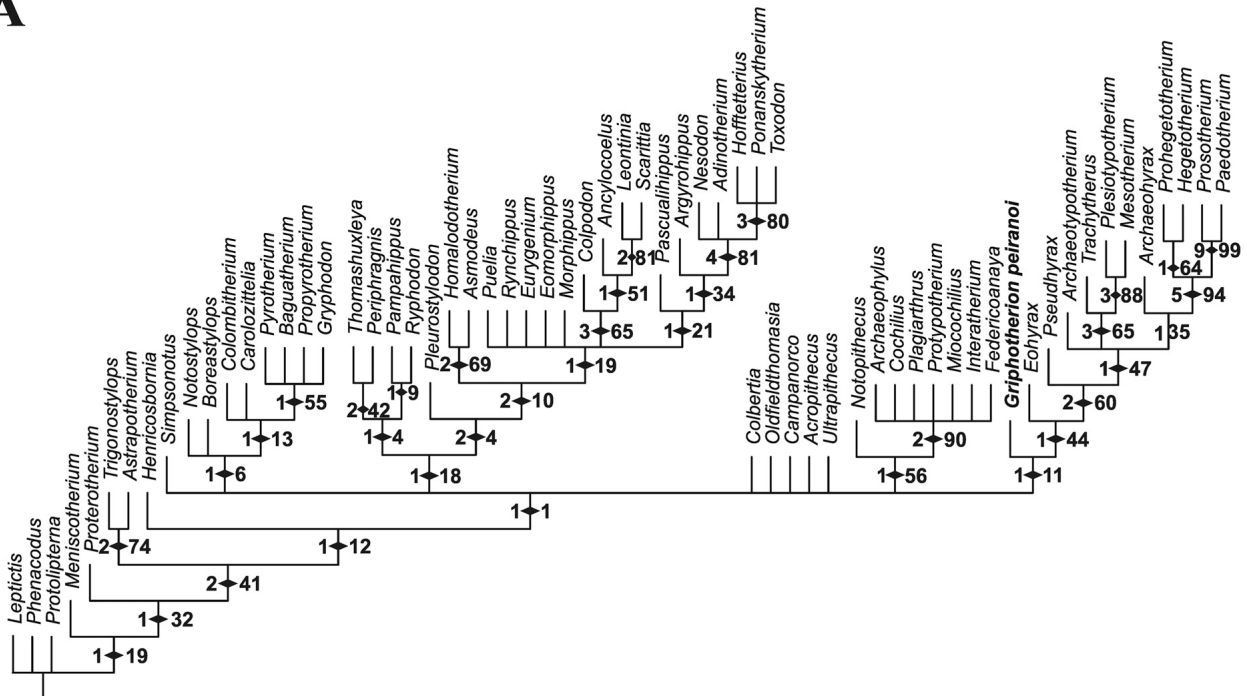
## PHYLOGENETIC ANALYSIS

The analysis performed resulted in two trees (49 steps). The strict consensus is shown in Figure 5A along with the support indices calculated for it. The most basal Typotheria in the tree are the genera *Colbertia* and *Oldfieldthomasia* Ameghino, 1901, both traditionally considered to be members of the Oldfieldthomasiidae. In the consensus presented here these two genera form a paraphyletic clade, which is consistent with recent studies that have described the family as paraphyletic (López, 2008; García López, 2009). *Griphotherion peiranoi* is included in a clade of derived typotherians. The most basal node of this clade (node A) is a polytomy that includes the Interatheriidae (represented by two taxa in this analysis), the Eocene informal taxon *Campanorco* (also from the Lumbrera Formation), and a monophyletic group of 'rodent-like' notoungulates that includes *G. peiranoi* as the most basal taxon (node B). Node A is supported by the following two unambiguous synapomorphies: high rostrum (more than three times the height of the anterior teeth) (character 15, state 1), and anterior root of zygomatic arch rostrocaudally expanded (character 23, state 1). Node B is supported by three unambiguous synapomorphies: expanded hypocone area on P2–3 (character 5, state 1), large facial extent of lacrimal bone (character 17, state 1), and origin of the masseter muscle as an expanded flat area on the ventral edge of the zygomatic arch (character 24, state 1).

The more extensive analysis conducted using the matrix published by Billet (2010) resulted in 1512 trees (366 steps). The strict consensus is shown in Figure 5B. This tree shows a lower degree of resolution than the results reported by Billet (2010) in the original analysis, with Typotheria and Toxodontia now included in the same polytomy. Nevertheless, the similar positions and relationships given for *Griphotherion peiranoi* in both



A



B

FIGURE 5. Phylogenetic position of *Grphotherion peiranoi*. **A**, strict consensus of analysis of several tyotherian taxa indicating their temporal range and location of nodes A and B (see text). Upper numbers on nodes indicate Bremer support values; lower numbers on nodes indicate Jackknife values; **B**, strict consensus of analysis based on data matrix of Billet (2010). Left numbers on nodes indicate Bremer support values; right numbers on nodes indicate Jackknife values.

analyses are remarkable. The new taxon is located as the sister group of a clade that includes representatives of Mesotheriidae, Archaeohyracidae, and Hegetotheriidae. Although the number of taxa is lower, the arrangement of this group is very similar to that of node B in our first analysis, where *G. peiranoi* is also shown as being closely related to the above-mentioned families. The monophyletic group that includes *G. peiranoi* and the ‘rodent-like’ notoungulates is supported by the following synapomorphies: procumbent lower incisors, mesial lophid (paralophid) present on the lower cheek teeth, entolophid less transverse and merged with the trigonid, lingual connection of lophids on lower cheek teeth isolating a trigonid-talonid fossettid, premaxillary-maxillary suture on palate oriented anteriorly, posterodorsal extremity of maxilla reaching posterior extremity of nasal, large facial extension of the lacrimal towards the nasal bone, and retroarticular process fused or appressed to the crista meatus and/or external auditory meatus along its entire length, thereby defining a channel for the postglenoid foramen.

### DISCUSSION

The specimen PVL 5903 presents a specific set of features that support its status as a new notoungulate taxon. Moreover, this new species presents an unusual combination of characteristics in the context of the Paleogene faunas, which prevent it from being included in any of the known families of the order known from this time period: Henricosborniidae, Notostylopidae, Oldfieldthomasiidae, Campanorciidae, Archaeohyracidae, Archaeopitheciidae, and Interatheriidae (see the section Diagnosis [following *GRIPHOTHERION PEIRANOI*, sp. nov.] for a list of these characteristics). Because of this, we refrain from placing it within the above-mentioned families. However, it must also be mentioned that there are some features that indicate that *G. peiranoi* could belong to the Archaeohyracidae (e.g., slightly enlarged I1, expanded anterior root of the zygomatic arch, and expanded entoconid isolating a talonid fossettid). Moreover, as was previously mentioned, the morphology of the third lower molar of *G. peiranoi* is very similar to that of *Punahyrax bondesioi*, a basal archaeohyracid from northwestern Argentina. However, the characteristics mentioned are also present in other taxa (e.g., Mesotheriidae and Hegetotheriidae), and do not represent sufficient evidence to support inclusion of the new species in this family. Furthermore, the early attainment of hypsodonty, a feature typical of archaeohyracids (Croft et al., 2003), is absent in *Griphotherion*. The teeth of the new species, although higher than those of other Paleogene taxa such as *Colbertia*, are undoubtedly brachydont (which also is an important feature that prevents the inclusion of *Griphotherion* in advanced typotherians such as mesotheriids and hegetotheriids). Other notable differences regarding the Archaeohyracidae are the high level of development of mesiolabial fossettes and the presence of strong cingula and a poorly developed parastyle in the upper molars. Finally, it must also be noted that some authors have questioned the integrity of the family Archaeohyracidae (Billet et al., 2009; Reguero and Prevosti, 2010). In a phylogenetic analysis performed by Billet et al. (2009), a clade of ‘late archaeohyracids’ (excluding forms such as *Eohyrax* Ameghino, 1901, and *Pseudohyrax* Ameghino, 1901) was diagnosed by a single derived feature, the presence of minute incisive foramina. This feature is present in *G. peiranoi*, but also in basal forms such as *Oldfieldthomasia* (see Billet et al., 2009). Additionally, the results of the analysis of these authors also show a clade of ‘late archaeohyracids’ and hegetotheriids diagnosed by the presence on an anteriorly shifted carotid foramen. This character is absent in *Griphotherion*, as well as in mesotheriids.

The position of the new taxon in the analyses performed is remarkable because it is located as an outgroup to the ‘rodent-like’ notoungulates, i.e., mesotheriids, archaeohyracids, and hege-

theriids. Notably, the Eocene notoungulate *Campanorco* is part of a basal polytomy and its relationship with the advanced Typotheria remains unclear in the analyses using both our matrix and Billet’s (2010) matrix. *Campanorco inauguralis* Bond et al., 1984, is a species that has not been formally described, recorded from the upper levels of the Lumbra Formation (Lumbra superior). This taxon has been included in some of the previous analyses as a member of the Typotheria. Reguero et al. (1996:56) defended that *C. inauguralis* should be integrated in a monophyletic group along with Mesotheriidae, Archaeohyracidae, and Hegetotheriidae, and that this species was “the perfect structural ancestor for the advanced ‘rodent-like’ notoungulates.” Later, Reguero (1999) applied the name Typotherioidea to the group Mesotheriidae + Archaeohyracidae + Hegetotheriidae. *Campanorco* was included as a sister taxon of Typotherioidea, forming the clade Typotheria sensu Reguero (1999), from which Oldfieldthomasiidae, Archaeopitheciidae, and Interatheriidae were excluded (Reguero et al., 1996; Reguero and Castro, 2004). Finally, Reguero and Prevosti (2010) presented a phylogeny of Typotheria in which the term Typotherioidea is retained, but with *C. inauguralis* included within that group. The monophyletic group *Campanorco* + Mesotheriidae + Archaeohyracidae + Hegetotheriidae was not seen in the analyses reported here, and the arrangement of the members of Typotherioidea is different, because archaeohyracids form a polyphyletic group in the second analysis of the present study. However, it should be pointed out that the position of *Campanorco* in a basal polytomy near the group *Griphotherion* + Mesotheriidae + Archaeohyracidae + Hegetotheriidae indicates that a closer relationship with these clades is not unambiguously supported, but should not be discarded.

The positioning of *Griphotherion* as sister taxon of the ‘rodent-like’ notoungulates is very important in terms of assessment of the Paleogene fossil record in northwestern Argentina. Basal groups such as henricosborniids and notostylopids are recorded from this region. In the case of henricosborniids, the genus *Simpsonotus* is the most basal notoungulate for which cranial osteology is known. Other families traditionally referred to as typotheres, such as Interatheriidae, Archaeohyracidae, Oldfieldthomasiidae, and Campanorciidae (not formally described), have also been recorded, along with the Toxodontia Notohippidae, Isotemnidae, and Leontiniidae. In most cases, the representatives of these families recorded in northwestern Argentina present generalized morphologies (Bond, 1981; Vucetich and Bond, 1982; Bond and López, 1993; López and Bond, 1995; García López, 2009), which has positioned them as basal groups in some phylogenies (Reguero et al., 1996, 2008; García López, 2009). In other cases, the most ancient representatives for some of these families were recorded (Bond and López, 1995; Deraco et al., 2008; Reguero et al., 2008). This notable presence of basal forms indicates that northwestern Argentina was an important region of early diversification for many notoungulate lineages, an idea already supported by other authors (e.g., Reguero et al., 2008). The record of *Griphotherion peiranoi* and its positioning as a basal form in the line of ‘rodent-like’ notoungulates, which underwent adaptive radiation during the last part of the Paleogene and most of the Neogene, is consistent with this perspective.

### CONCLUSIONS

*Griphotherion peiranoi* is a new genus and species of Paleogene notoungulate recorded in the levels of the Eocene Lumbra Formation known as the lower Lumbra, in the province of Salta in northwestern Argentina. This new taxon is a small-sized herbivore, which possesses a unique combination of traits that prevent its inclusion in other previously established notoungulate families. Nevertheless, the phylogenetic analyses performed indicate that this taxon was close to the ancestry of the ‘rodent-like’

notoungulates (Mesotheriidae and 'Hegetotheria') that evolved from Oligocene onwards in South America.

This finding adds to the already substantial and important body of notoungulate fossil records from the Lumbrera Formation. It also supports the perspective that northwestern Argentina played an important role as a region of early diversification for several lineages of this remarkable order of endemic South American ungulates.

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APPENDIX 1. List of characters and character states used in the phylogenetic analysis of typotherian taxa. All characters were treated as unordered.

- (1) First upper incisor: small and subequal to I2 (0); mesiodistal length and crown height greater than I2, but not particularly developed (1); very developed and robust (2). (Modified from Cifelli, 1993)
- (2) Development of diastemata between anterior teeth: absent (0); present (1). (Croft et al., 2003; Billet et al., 2009)
- (3) Crown of I1: parallel between them (0); converging to the apex (1). (Modified from Cifelli, 1993)
- (4) Anterior teeth (between I1 and P1): well differentiated (incisor-like and premolariform) (0); similar morphology, all incisor-like (1).
- (5) Hypocone area on P2–3: not expanded (0); expanded (1) (modified from López, 2008)
- (6) Hypsodonty on molariforms: brachydont, generally low lophs (0); tendency to mesodonty, higher lophs (1); protohypsodont or euhypsodont (2). (Modified from Croft et al., 2003)
- (7) Lingual face of upper teeth: one-lobed (labial flexus absent in occlusal view) (0); bilobed (1); trilobed (2).
- (8) Hypocone on M3: vestigial or absent (0); present, well developed (1).
- (9) Metastyle on M3: poorly developed (0); distally prominent (1).
- (10) Lower incisors: subvertical or moderately procumbent (0); strongly procumbent (1). (Modified from Billet, 2010).
- (11) Relative size of trigonid and talonid on m2: trigonid smaller than talonid (0); subequal (1).
- (12) Lingual face of lower molars: clearly divided by a well-developed sulcus (0); flat or with vestigial sulcus (1). (Modified from Croft et al., 2003)
- (13) Fossettoid on m2–3 talonid: absent (0); present (1) (Modified from Croft et al., 2003)
- (14) Length of the rostrum: short (0); clearly elongate (1).
- (15) Height of the rostrum: low, less than three times the height of I2–P1 (0); high, three or more times the height of I2–P1 (1).
- (16) Dorsocaudal extremity of maxillary contacting nasal: does not reach posterior extremity of nasals (0); does approximately reach posterior extremity of nasals (1); reaches much further than posterior extremity of nasals (2). (Billet, 2010)
- (17) Large facial extent of lacrimal toward nasal bone: absent (0); present (1). (Billet, 2010)
- (18) Medial platform of palatines expanding palate posteriorly and fully continuous with it: absent (0); present (1). (Billet, 2010)
- (19) Development of the meatal crest: weak or absent (0); well developed and usually long (1).
- (20) Development of the external auditory meatus: short (0); long (1).
- (21) Tympanic bulla: balloon-like and prominent (0); reduced (1).
- (22) Jugular process (paraoccipital process): slender and short (0); robust and long (1).
- (23) Anterior root of zygomatic arch: not expanded rostrocaudally (0); clearly expanded rostrocaudally (1) (Cifelli, 1993)
- (24) Origin of the deep masseter muscle: small and elongate area on the ventral border of the zygomatic arch (0); expanded and flat area on the ventral border of the zygomatic arch (1). (Cifelli, 1993)
- (25) Descending process of the zygomatic arch: absent or weak (0); well developed (1).
- (26) Jugal: well developed, usually reaching lacrimal (0); reduced and blade-like, reaches lacrimal (1); reduced, separated from lacrimal and confined to the middle part of the zygomatic arch (2).
- (27) Mandibular body: low, roughly two times the height of p2–3 at that level (0); high, more than two times the height of the p2–3 at that level (1).
- (28) Retroarticular process and external auditory meatus: recognizable as separated elements (0); fused in a cup-like structure (1).