Structural variation of the masseter muscle in Typotheria (Mammalia, Notoungulata)

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Resumen: *VARIACIÓN ESTRUCTURAL DEL MÚSCULO MASETERO EN TYPOTHERIA (MAMMALIA, NOTOUNGULATA).* La gran diversidad morfológica del orden Notoungulata se expresa en rasgos notorios, como el tamaño corporal, incluyéndose aquí desde animales del porte de un pequeño roedor (*e.g., Punapithecus*) hasta formas de más de una tonelada (*e.g., Trigodon*). Se conocen además, diferentes casos de convergencia con otros placentarios, reconociéndose formas rodentiformes y otras similares a lagomorfos, perisodáctilos y artiodáctilos. Esta notable diversidad se expresa también en rasgos específicos, como la región auditiva y el aparato masticatorio. En este trabajo se presenta un análisis sobre la evolución estructural de la zona de origen del músculo masetero enfocada en el suborden Typotheria. Se seleccionó una muestra de 12 representantes de ese grupo más dos representantes de notoungulados tempranamente divergentes (Henricosborniidae y Notostylopidae). La muestra abarca un lapso de más de 43 Ma (Eoceno–Pleistoceno). Se establecieron tres condiciones principales relacionadas con el origen del masetero que muestran cierto ordenamiento temporal y filogenético. La Condición 0 (*e.g., Colbertia, Oldfieldthomasia*) se caracteriza por el origen puntual y restringido del masetero superficial y por una zona limitada para el masetero profundo, encontrándose exclusivamente en formas eocenas y siendo comparable al plan generalizado presente en ciertos marsupiales (*e.g., Didelphis*). La Condición 1 (*e.g., Notopithecus, Protypotherium*) presenta un masetero profundo de desarrollo limitado y un masetero superficial asociado a un proceso descendente conspicuo, mostrando similitudes con Lagomorpha (*e.g., Oryctolagus*). Finalmente, la Condición 2 (*e.g., Griphotherion, Typotheriodon, Hegetotherium, Paedotherium*) es la más compleja, mostrando un espectro de variaciones relacionadas con diferentes grados de hipertrofia del masetero profundo y reflejando similitudes a nivel superficial con ciertos roedores (*e.g., Sciuromorpha*). Esta perspectiva más focalizada muestra la complejidad alcanzada por los Notoungulata y es necesaria para obtener un cuadro más completo de la evolución del grupo, el cual brinda la oportunidad de estudiar la historia natural de un linaje de raíz mesozoica, sometido a aislamiento geográfico y sobreviviente casi hasta tiempos recientes.

Abstract: The great morphologic diversity of the order Notoungulata is evident in remarkable traits, such as the body size, and this group includes from small, rodent size animals (*e.g., Punapithecus*) to forms exceeding 1000 kg in weight (*e.g., Trigodon*). Moreover, several cases of convergence with other placentals are known within the group, with rodent-like and lagomorphs-like forms in Typotheria and animals similar to some Perissodactyla or Artiodactyla within Toxodontia. This remarkable diversity is also expressed in specific traits developed on certain parts of the skeleton, such as the auditory region or the masticatory apparatus. In this contribution we present an analysis on the structural evolution of the area of origin of the masseter muscle focused on the suborder Typotheria. A sample of 12 representatives of that group was selected, plus two representatives of early diverging notoungulates (Henricosborniidae and Notostylopidae). This sample covers a span of approximately 43 Ma (Eocene

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–Pleistocene). On each case, the relative development and arrangement of the different parts of the masseter was determined evaluating the area of the muscular scars remaining on the zygomatic arch and its anterior root. Three main conditions related to the origin of the masseter muscle were deduced, showing some temporal and phylogenetic arrangement. Condition 0 (*e.g., Colbertia, Oldfieldthomasia*) is characterized by a small origin of the superficial master and a small area for the deep master, is only present in Eocene representatives, and is comparable to the generalized plan present in some marsupials (*e.g., Didelphis*). Condition 1 (*e.g., Notopithecus, Protypotherium*) presents a moderately-developed deep master and an origin of the superficial masseter related to a conspicuous descendant process, being similar to some Lagomorpha (*e.g., Oryctolagus*). Finally, the condition 2 (*e.g., Griphotherion, Typotheriodon, Hegetotherium, Paedotherium*) is the most complex, showing a spectrum of variations related to different stages of hypertrophy of the deep masseter which reflex similarities to certain rodents (*e.g., Sciuromorpha*). This morphologic perspective shows the complexity achieved by the Notoungulata and brings a more complete frame on the evolution of this group, which represents one of the most characteristic elements of the South American fossil biota.

Key words: Structure. Masseter muscle. Typotheria. Notoungulata. Cenozoic. South America.

Palabras clave: Estructura. Músculo masetero. Typotheria. Notoungulata. Cenozoico. América del Sur.

Introduction

The order Notoungulata is one of the most representative elements of the endemic mammalian fauna of the Cenozoic from South America. The position of the clade within placental mammals remained elusive for more than a century; however, recent contributions have established their close relationship with Perissodactyla, forming the clade Panperissodactyla within Laurasitheria (Buckley, 2015; Welker *et al.*, 2015). Even so, relationships among the different families of Notoungulata remain in part unresolved and their position among other groups of South American ungulates (*e.g.*, Astrapotheria, Xenungulata, Litopterna, Pyrotheria) are still a topic of debate (Billet, 2010, 2011; Billet and Muizon, 2013; Kramarz *et al.*, 2017). Notoungulates are conspicuously present in most of the fossil assemblages of the Cenozoic and their record shows an evolutionary history marked by changes in morphology, taxonomic diversity, and exploration of ecologic niches (Simpson, 1967; García-Lopez, 2009; García-López and Powell, 2011; Giannini and García-López, 2014).

Paleobiological studies are of great importance since they bring a more comprehensive framework, necessary for the reconstruction of fossil communities. Regarding the order Notoungulata, some authors have already made important contributions in subjects such as paleodiet, body size, functional morphology, and ontogeny (Elissamburu, 2004, 2012; Shockey *et al.*, 2007, Croft and Weinstein, 2008; Billet *et al.*, 2009; Townsend and Croft, 2010; Cassini *et al.*, 2010, 2011; Scarano *et al.*, 2011; Cassini and Vizcaíno, 2012; McCoy and Norris, 2012; Armella *et al.*, 2016). Neverteheless, these studies are mostly focused on Neogene taxa, being the paleobiology of Paleogene representatives still poorly known.

Within the Notoungulata, the suborder Typotheria is particularly interesting, since it represents a clear example of evolutionary convergence with extant orders such as Lagomorpha and Rodentia (Simpson, 1967; Cerdeño and Bond, 1998; Croft and Anaya, 2006). This convergence is largely expressed in the arrangement of the muscles of the masticatory apparatus, which leads to the development of structures such as zygomatic plates and mandibular expansions.

Masseter muscles fulfill a fundamental role in mastication within mammals, forming the masticatory apparatus along with the temporal and pterygoid muscles (Turnbull, 1970; Crompton and Parker, 1978; Herring,

2007; Druzinsky *et al.*, 2011). This group of muscles has been classified in different ways by many authors. In this sense, one of the most complete and detailed surveys was performed by Turnbull (1970), who classified the masticatory apparatus in four groups according to the arrangements and relative development of each element. These groups correspond to carnivores, rodents, ungulates, and a generalized group (including forms like the metatherian *Didelphis*). In this classification is evident that the masticatory dominance of the different muscles reflexes the feeding habits of the animal; in this way, the predominance of the temporal muscle is characteristic of carnivores, whereas strong masseter and pterygoid muscles are more typical in herbivores (Herring, 2007).

In the present contribution we analyze the variation patterns in the zone of origin of the different parts of the masseter muscle in a sample of notoungulates. Although most of the analyzed forms represent families within Typotheria, some early-diverging taxa were included (*i.e.*, Henricosborniidae, Notostylopidae). From this, we bring a morphologic classification and discuss the related evolutionary and phylogenetic background.

Materials and methods

Functional characterizations mentioned in the text were performed based on the direct study of the mentioned taxa. In some cases, this analysis was helped with the consultation of specialized literature, particularly those contributions where craniodental traits were described for representatives of Notoungulata (*e.g.*, Scott, 1912; Simpson, 1948, 1967; Billet *et al.*, 2008, 2009; Billet, 2011; García-López, 2011; García-López and Powell, 2011). The selected sample comprehends 11 genera and is focused mainly on representatives of Typotheria. Additionally, two taxa of early diverging families of No-

toungulata (Henricosborniidae and Notostylopidae) where included in order to obtain an evolutionary and morphofunctional perspective on the basis of forms of poorly-differentiated ecomorphology. Within Typotheria, the sample includes taxa belonging to "Oldfieldthomasiidae", Interatheriidae, "Archaeohyracidae", Hegetotheriidae, and Mesotheriidae. Though some of these clades are paraphyletic clusters, the use of their names is maintained here for practical purposes. Table 1 shows the list of included genera, analyzed material, and contributions consulted.

The arrangement of the different parts of the masseter muscle was established analyzing the surface of the skull, in order to identity the structures usually associated to the origin of each muscular element. At this point, the nomenclature and morphological frame used was that proposed by Turnbull (1970). Likewise, specialized literature focused on extinct and extant mammals was consulted (*e.g.*, Cox and Jeffery, 2011; Crompton and Parker, 1978; Gambaryan and Kielan - Jaworowska, 1995; Russel, 1998; Getty, 2005; Herring, 2007; Druzinsky *et al.*, 2011; Evans and de Lahunta, 2013). Following Turnbull (1970), the masseter muscle is divided in three parts: superficial masseter (*pars superficialis*), deep masseter (*pars profunda*), and zigomaticomandibularis. Starting from this scheme, structures commonly associated to the origin of each part were individualized, and the development (based on the relative area) of each surface was qualitatively determined. Finally, three discrete categories were determined and named as Condition 0, 1, and 2.

Abbreviations

DMO, area for the deep masseter origin; SMO, area for the superficial masseter origin; ZMO, area for the zygomaticomandibularis origin.

Results

The three morphological conditions (Condition 0, Condition 1, and Condition 2) determined in this study are differentiated by the arrangement and relative development of the different parts of the masseter muscle. Likewise, there are variations regarding the relative position of some structures, particularly those associated to the origin of the superficial masseter and its position regarding the anterior root of the zygoma.

Condition 0

Genera included within this con-

dition are characterized by the presence of a vestigial tubercle associated to the origin of the superficial masseter (SMO) and a relatively small, narrow, and simple area for the origin of the deep masseter (DMO), without divisions for this part of the muscle. The zygomatic arch is usually gracile, with the anterior root small and laterally compressed. Four genera were included here: *Simpsonotus* (Henricosborniidae), *Colbertia* ("Oldfieldthomasiidae"), *Boreastylops,* and *Notostylops* (Notostylopidae).

Simpsonotus (figure 1A), recorded in the Mealla Formation (late Paleoce-
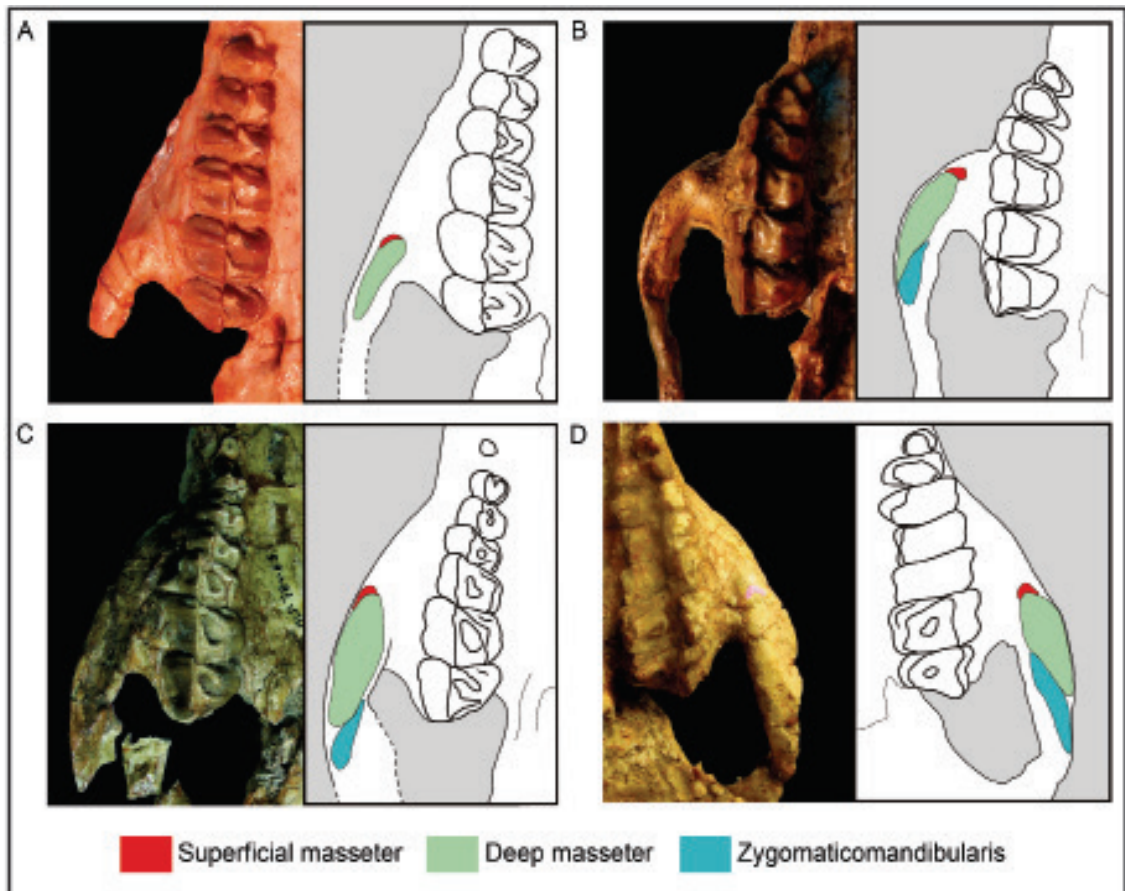
Figure 1. Taxa included in the Condition 0 and schematic interpretation of the area for the origin of the different parts of the masseter muscle. **A-** *Simpsonotus praecursor*, holotype (MLP 73-VII-3-11); **B-** *Notostylops murinus* (MACN-A 10494); **C-** *Boreastylops lumbrerensis*, holotype (MLP 78-V-6-5); **D-** *Colbertia lumbrerense* (PVL 4294). Not in scale. **/ Figura 1.** *Taxones incluidos en la Condición 0 e interpretación esquemática del área de origen de las diferentes partes del músculo masetero.* **A-** Simpsonotus praecursor*, holotipo (MLP 73-VII-3-11);* **B-** Notostylops murinus *(MACN-A 10494);* **C-** Boreastylops lumbrerensis*, holotipo (MLP 78-V-6-5);* **D-** Colbertia lumbrerense *(PVL 4294). Las imágenes no están en escala.*

ne of Jujuy Province, Argentina), presents a small SMO, associated to a very small tubercle located ventrally and laterally on the anterior part of the zygoma. This area is located at the level of the M2 in ventral view. On turn, the *pars profunda* of the masseter muscle is originated more ventrally on the zygomatic arch, in an anteroposteriorly elongated zone, located immediately posterior to the SMO.

Boreastylops and *Notostylops* (figure 1B, C) are forms with a considerably greater body size regarding other representatives of the Condition 0; nevertheless, they follow the same basic pattern. The *pars superficialis* of the masseter muscle rises from a small tubercle on the anterolateral surface of the anterior root of the zygomatic arch, at the level of the M2. The deep masseter rises posteriorly, in a narrow area that ends posteriorly on the anterior edge of the zone for the origin of the zygomaticomandibularis (ZMO), which is developed ventrally and internally on the body of the arch.

In *Colbertia* (figure 1D) the superficial maseter has it origin in a small and narrow elongated area located between the level of the M2 and the medial part of the M3 and bounded anteriorly by a small tubercle on the zygomatic root. This condition is very similar to that of *Simpsonotus*; nevertheless, in *Colbertia* the tubercle is slightly larger. This area is immediately adjacent to the mediolateral edge of the DMO, which is a narrow area that occupies two thirds of the zygomatic process of the maxilla. The ZMO is visible from the level of the middle length of the DMO to the zone adjacent to the mandibular joint. The ZMO is developed on the internal aspect of the zygomatic arch.

Condition 1

The two genera included within this group belong to the family Interatheriidae, and represent a pre-Deseadan form (*Notopithecus*; middle-late Eocene) and one Interatheriinae, a more specialized subfamily with euhypsodont members (*Protypotherium*; middle Miocene). The Interatheriidae were small to medium sized typotheres which show morphological convergences with woodchucks and hares. Additionally, one of the most remarkable synapomorphies of the family is the condition of the jugal bone on the zygomatic arch, which is excluded from the ventral and anterior orbital margin by a large zygomatic process of the maxilla (Cifelli, 1993; Hitz *et al.*, 2006). The maxilla also exhibits a conspicuous descendant process developed on the ventral part of the anterior root of the zygoma, which marks the SMO (although not included in this study, some interatheriids show a very developed process, such as *Interatherium*). In turn, the DMO is not particularly large (although in some cases it can be moderately large), differing from the Condition 2 described below.

In *Notopithecus* (figure 2A) the anterior root of the zygoma is moderately enlarged. The tubercle or descendant process is small and located at the level of the mesial edge of the M1 in ventral view. The superficial masseter rises in the descendant process and runs on the external edge of the zygoma, over a thin crest. Medially and posteriorly, the DMO, which is flat and shows well-marked edges.

Protypotherium (figure 2B) presents a more specialized arrangement than *Notopithecus*. The descendant process is larger in this case. The superficial masseter rises from this process, which bears a short posterior crest. The zygomatic process of the maxilla is larger and longer than in *Notopithecus*, relegating the jugal to the middle-posterior part
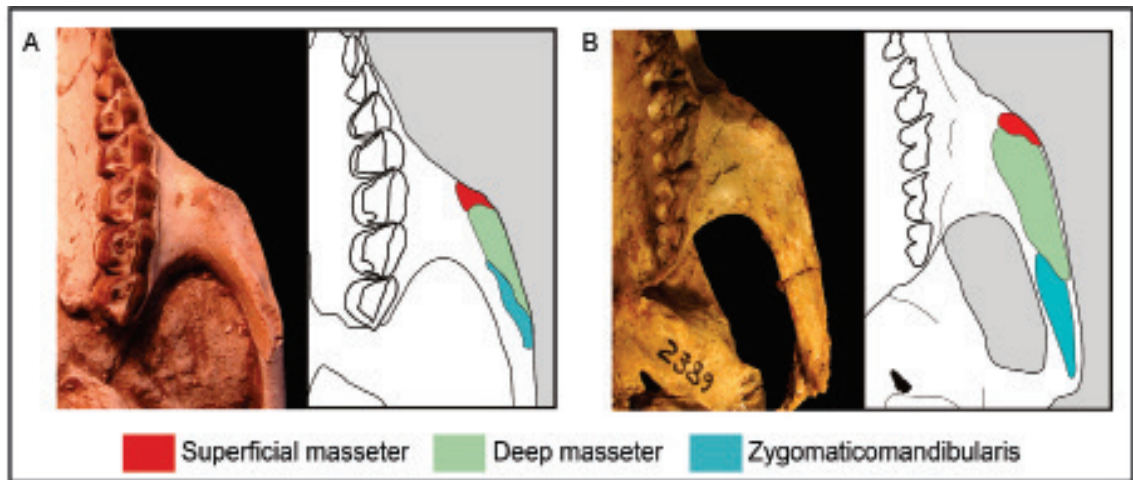
Figure 2. Taxa included in the Condition 1 and schematic interpretation of the area for the origin of the different parts of the masseter muscle. **A-** *Notopithecus adapinus* (MACN-A 10790); **B-** *Protypotherium australe* (PVL 2389). Not in scale. **/ Figura 2.** *Taxones incluidos en la Condición 1 e interpretación esquemática del área de origen de las diferentes partes del músculo masetero.* **A-** Notopithecus adapinus *(MACN-A 10790);* **B-** Protypotherium australe *(PVL 2389). Las imágenes no están en escala.*

of the arch. Two well-defined fossae (anterior and posterior) are visible on the ventral part of the zygomatic process. The anterior fossa is the DMO and is tear-shaped, with a sharp posterior edge. The posterior fossa is the ZMO. This is adjacent medially to the DMO and is located on the medial aspect of the arch reaching the area adjacent to the glenoid fossa.
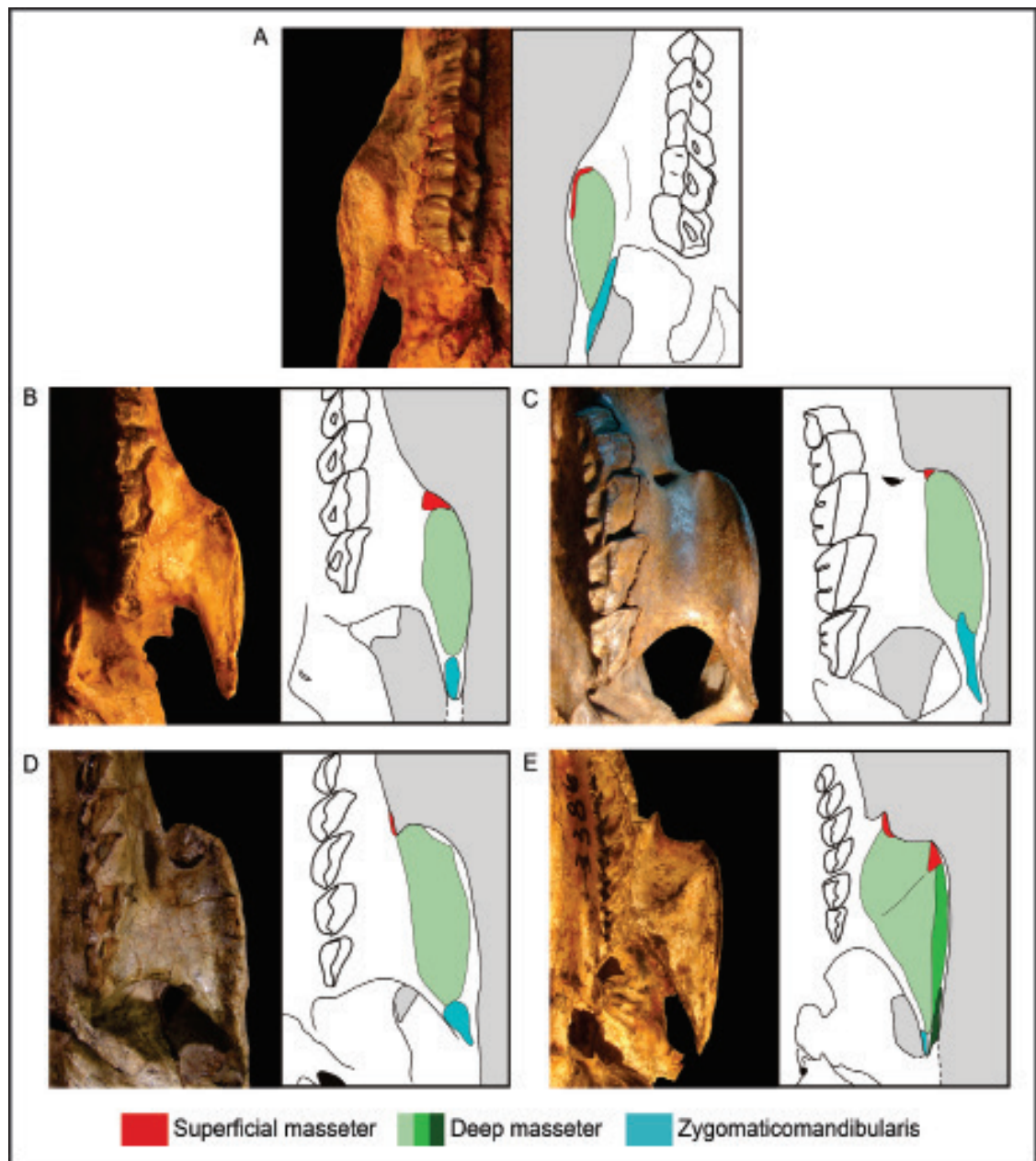
Condition 2

In this condition the anterior root of the zygomatic arch is highly developed or hypertrophied and laterally expanded. Moreover, this condition is characterized by the absence of a tubercle or descendant process associated to the SMO. Five genera were studied within this condition: an Eocene form of indeterminate family, although possibly linked to the ancestral branch leading to Hegetotheria (*Griphotherion*; see García-López and Powell, 2011), one "Archaeohyracidae" (*Archaeohyrax*), one Mesotheriidae (*Typotheriodon*), and two Hegetotheriidae (*Hegetotherium* and *Paedotherium*). In turn, there are differences among these genera regarding the position, origin, and subdivisions of the

masseter (that will be described below).

Griphotherion (figure 3A) shows the most basic arrangement within this condition. The zygomatic arch is robust and roughly parallel to the anteroposterior axis of the skull. The posterior root is narrow, with a smooth medial edge and a well - developed postzygomatic dorsal crest. The anterior root is expanded forming an incipient plate, mainly evidenced by a flattened ventral surface on the zygomatic process of the maxilla. This root is also expanded anteroposterioly, extending from the mesial edge of the M1 to the distal edge of the M3. The SMO is small and is located on the anteroexternal aspect of the zygomatic process, at the level of the M2. Although the position of the SMO is similar to that of the Condition 0, the main difference lies in the absence of an associated tubercle. Then, the SMO is only manifested as a narrow, elongated, and rugous surface. The DMO is a continuous surface, without the divisions observed in other genera within this condition (see below).

In *Archaeohyrax* (figure 3B), the basic pattern is similar to that in *Griphotherion*;

Figure 3. Taxa included in the Condition 2 and schematic interpretation of the area for the origin of the different parts of the masseter muscle. **A-** *Griphotherion peiranoi*, holotype (PVL 5903); **B-** *Archaeohyrax patagonicus*, holotype (MACN-A 52-617); **C-** *Typotheriodon extensum* (MACN-PV 2925); **D-** *Hegetotherium mirabile* (PVL 91); **E-** *Paedotherium typicum* (PVL 3386). **/ Figura 3.** *Taxones incluidos en la Condición 2 e interpretación esquemática del área de origen de las diferentes partes del músculo masetero.* **A-** Griphotherion peiranoi*, holotipo (PVL 5903);* **B-** Archaeohyrax patagonicus*, holotipo (MACN-A 52-617);* **C-** Typotheriodon extensum *(MACN-PV 2925);* **D-** Hegetotherium mirabile *(PVL 91);* **E-** Paedotherium typicum *(PVL 3386). Las imágenes no están en escala.*

nevertheless, the zygomatic plate is more laterally expanded, being similar to the development observed in Mesotheriidae and Hegetotheriidae. The SMO is located on the anterolateral aspect of the zygomatic arch and its posterior edge is marked by the contact between the jugal and the maxilla. The fossa for the DMO is located medially and posteriorly to the SMO. As for *Griphotherion*, there are no divisions in the DMO.

Condition 2 shows higher singularities in representatives of the Neogene, such as *Typotheriodon* (figure 3C), in which the zygomatic plate is much wider (laterally expanded) and its surface reaches the distal part of the M3. In these forms the SMO is located in a small surface below the lacrimal bone and laterally on the most basal part of the root of the zygoma (in ventral view). Then, the position of the SMO is more dorsal to that observed in *Griphotherion* and *Archaeohyrax*. The DMO is very developed, occupying most of the hypertrophied zygomatic plate. This part apparently shows two subareas, an internal or medial one, which is larger, and an external or lateral, being smaller and parallel to the latter. Posteriorly, the ZMO is narrow and reaches the jugal-squamosal contact. The described morphology is strongly homogeneous among the representatives of Mesotheriidae, and the same arrangement can be found in Quaternary forms such as *Mesotherium*.

Within Hegetotheriidae (figure 3D, E), the Condition 2 shows an even higher development of the zygomatic plate, and hence of the masseter muscle. The SMO is dorsal in the zygoma and is associated to a protuberance of the maxilla (very developed in some cases).

Hegetotherium, from the middle Miocene, shows the mentioned arrangement. The SMO is relatively small and is located on the posterodorsal area of the maxilla, adjacent to the nasal and anterior to the lacrimal bone. The DMO occupies most of the zygomatic plate; this is a continuous area and hence the muscle was very robust. Posteriorly, the ZMO is narrow and reaches the vicinity of the mandibular joint. Considering this arrangement, the pattern in *Hegetotherium* can be regarded as an "advanced variant" of that observed in *Archaeohyrax*.

In *Paedotherium*, a genus that inclu-

des rabbit-size forms from the Miocene and Pliocene, the condition shows the higher degree of complexity, whit subdivisions in the different parts of the masseter and particularly in the *pars profunda*. The SMO is a small irregular area located on a facial process of the maxilla (or horizontal spine; Billet, 2011) located adjacent to the anterior and dorsal end of the anterior zygomatic root and lateral to the infraorbital foramen. There is another wrinkled small area, located on the anterolateral surface of the arch. This secondary attachment surface (SAS) could be interpreted as an origin for an accessory branch of the superficial masseter; nevertheless, such trait must be considered with caution (see Discussion).

The DMO shows a remarkable development, indicating a high hypertrophy for this muscle. Moreover, the DMO is divided in three subareas distributed on a large zygomatic plate. The first subarea is the larger subdivision and is located on the anterior surface of the zygomatic plate, reaching dorsally the SMO. The second subarea is immediately posterior to the former and faces ventrally. It is smaller than the first subarea and both are separated by an oblique crest which anterolateral end reaches the SAS mentioned above. Finally, the third subarea is located adjacent to the posterolateral end of the zygomatic plate, being developed partially on the jugal bone. It is narrow and anteroposteriorly elongated, being the smallest of the three subareas.

Discussion

Turnbull (1970) included the order Notoungulata in the Specialized Group II of his classification ("ungulate-grinding" or "mill" type), which was integrated mainly by extant ungulates (Perissodactyla). However, this author stated on his contribution that the knowledge on the muscular

structure and functional characterization of Notoungulata was inadequate and that extensive surveys were not being developed at the time. At this point, and in accordance with the doubts expressed by Turnbull, the observations performed on the present contributions indicates that the inclusion of the entire order Notoungulata within the specialized group of modern ungulates implies inconsistencies related to different arrangements in the masticatory muscles and functional variations. Turnbull characterized his Specialized Group II as that in which "mill action, or grinding motion, predominates" (Turnbull, 1970: 160), and mentioned three masticatory movements associated: "fore-and-aft direction", "medial and lateral direction", and "vertical (orthal) direction". Morphological evidence (related to occlusal relief and arrangement of the temporomandibular joint) indicates that this combination of movements can be present in some notoungulates; however, other representatives of the order show marked singularities. Moreover, Turnbull's Specialized Group II presents a characteristic reduction of the temporal muscle combined to a great development of the masseter. This could be compared to the condition present in representatives of Pachyrukhinae or Mesotheriidae (here included on the Condition 2 and traditionally considered as "rodent-like" forms) but hardly to Paleogene forms (such as *Griphotherion* or *Colbertia*) or even certain Neogene genera (*e.g. Protypotherium*) which show a great development of the temporal muscle, associated to strong sagittal crests and, occasionally, moderate to low development of the masseter. In this sense, we consider that the order Notoungulata cannot be satisfactory included as a whole in just one of the morphologic groups proposed by Turnbull. Moreover, just one on the conditions here established,

the Condition 0, matches with one of the groups proposed by that author (precisely, the Generalized Group).

Comparisons and comments

As mentioned above, Condition 0 is restricted to Paleogene forms in which the masseter muscle shows a simpler arrangement (regarding other conditions here defined) and is not particularly hypertrophied. In turn, the temporal muscle is proportionally large in these forms.

Following the pattern and arrangement of the different parts of the masseter, Condition 0 can be considered as part of Turnbull's Generalized Group. This author included here extant representatives of Metatheria and Eutheria such as *Didelphis* (large American opossum) and *Echinosorex* (moonrat). In these animals the SMO is located on a usually small osseous protuberance developed ventrally on the anterior zygomatic root, just below the orbit. This protuberance can be part of both the maxilla and the jugal (as in *Didelphis*) or just the maxilla, and it is homologous to the vestigial descendant process or tubercle that represents the SMO in the representatives of the Condition 0.

As for the deep masseter, its origin is located on the ventral edge of the zygomatic arch (occupying a large portion of the body) in the representatives of the Generalized Group. Posteriorly the DMO reaches the ZMO. This arrangement is similar in the genera that were included in the Condition 0, and both the DMO and the ZMO are anteroposteriorly elongated.

Within the representatives of the Condition 0, the arrangement of the masticatory apparatus is particularly interesting for the family Notostylopidae. This clade (here represented by *Notostylops* and *Boreastylops*) includes forms that show a diastema (very large in some genera) separating the anterior incisors from premolars and molars

(or in some cases a strong reduction of the anterior premolars and the canine). This trait is commonly found in mammals with some kind of dental specialization (*e.g.*, hypsodonty) and implies a clear division between the function of incisors and postcanines during mastication (Hildebrand, 1974), as well as a dominance of the masseter and pterygoid muscles (Greaves, 2008). The case of Notostylopidae is notable, since the species of this family retain brachyodont postcanine teeth, enlarged (although not hypsodont) incisors, and well - developed (probably dominant) temporal muscles. In this sense, notostylopids show a singular combination of brachyodont teeth, a generalized arrangement of the masticatory apparatus, development of diastemata, and reduction of dental pieces. Considering the basal position of this family in the phylogenetic context of the Notoungulata, evidenced in different contributions (*e.g.*, Cifelli, 1993; Billet, 2010, 2011), these traits constitute remarkable characters. Additionally, dental and other cranial features of the Notostylopidae had lead to the proposal of some interesting phylogenetic affinities, not previously considered (*e.g.*, close relationship with the enigmatic clade Pyrotheria; see Billet, 2010, 2011).

Regarding Condition 1, this is observed in representatives of Interatheriidae, a family of Typotheria. These forms present a conspicuous descendant process developed on the anterior root of the zygomatic arch which can be particularly large in some cases, as in the genus *Interatherium*. In the analyzed taxa, the disposition of the masseter muscle represents a pattern similar to that of the Condition 0; nevertheless, in this case the descendant process were the SMO is present (hence homologous to the small tubercle or wrinkled area of the Condition 0) is conspicuous. Moreover, although not hypertrophied, the deep masseter shows also

a higher development, given the relative surface of the DMO.

The basic pattern characteristic of the Condition 1 can be compared to that present in the order Lagomorpha. Most representatives of this group present a lateral development of the anterior root of the zygoma and a conspicuous descendant process, referred as masseteric spine by Wible (2007). This structure, located on the ventral side of the zygomatic process of the maxilla, is homologous to the descendant process of the Interatheriidae (figure 4). However, a clear difference between these two clades is that the zygomatic process of the maxilla is shorter in Lagomorpha, being well developed in Typotheria and particularly in Interatheriidae. Moreover, one of the characters that define the family Interatheriidae is the isolation of the jugal from the ventral edge of the orbit, which is formed entirely by the maxilla (Cifelli, 1993; Hitz *et*
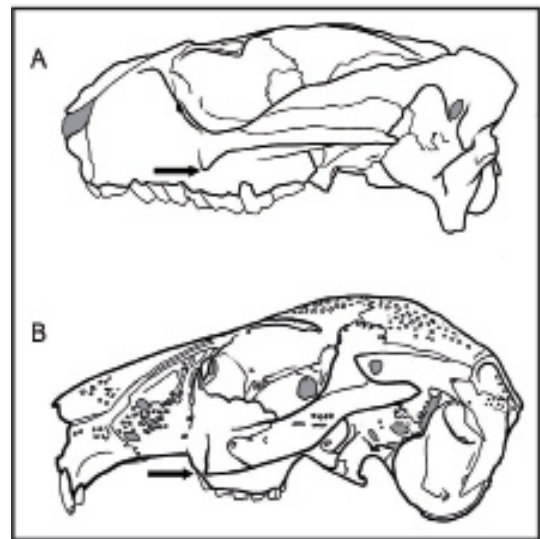
Figure 4. Lateral view of the skull in Interatheriidae and Lagomorpha. The horizontal arrow points to the masseteric spine. **A-** *Protypotherium australe*; **B-** *Romerolagus diazi* (modified from Wible, 2007). Not in scale. / **Figura 4.** *Vista lateral del cráneo en Interatheriidae y Lagomorpha. La flecha horizontal señala la espina masetérica.* **A-** Protypotherium australe; **B-** Romerolagus diazi *(modificado de Wible, 2007). Las imágenes no están en escala.*

al., 2006). In turn, lagomorphs generally had a well-developed jugal bone and the maxilla is restricted to the anterior part of the zygoma. The DMO is also similar in both groups; in Lagomorpha this area of origin runs posteriorly from the ventrolateral aspect of the jugal, while in Interatheriidae the DMO shows a similar arrangement but is located on the ventrolateral aspect of the maxilla.

Teeth functional adaptations also differ between Lagomorpha and Interatheriidae. The presence of diastema and a particular arrangement of the glenoid fossa (oblique and not strongly differentiated from the surrounding structures) are found in Lagomorpha (Wible, 2007). In turn, interatheriids usually do not present well-developed diastema (except for *Interatherium*), dentition turns from brachyodont in basal forms to hypsodont in post-Eocene genera, and the axis of the temporomandibular joint is clearly transverse. Thus, in this case is not possible to establish a clear correlation between the development of diastemata, the structural modifications of the masticatory apparatus, and the masticatory movements performed by these two groups.

Finally, some characters of the Condition 2 can be compared to protrogomorph and sciuromorph rodents, a fact consistent with the image of "rodent-like forms" traditionally applied to many of the taxa that we include here (particularly within Mesotheriidae and Hegetotheriidae). Nevertheless, the Condition 2 is more heterogeneous and complex than the previous conditions, covering a broader spectrum of comparisons. In a general sense, it includes representatives that show a great development of the anterior zygomatic root, exhibiting a wide surface for the insertion of the deep part of the masseter. In turn, the SMO differs between taxa recorded previously or poste-

riorly to the Eocene/Oligocene boundary. In *Griphotherion*, an Eocene typothere, the SMO is restricted to a small ventral area while in mesotheriids and non-pachyrukhine hegetotheriids it is located on the anterior and dorsal zone of the zygoma. Moreover, in Pachyrukhinae, the SMO is associated to a sharp process lateral to the infraorbital foramen. This process was referred as horizontal spine by Billet (2011), who confirms its homology regarding the descendant process of other notoungulates, based on the observation of basal pachyrukhines.

Notwithstanding the morphological variations expressed above, the most complex trait in Condition 2 is related to the great development of the DMO, which is laterally and dorsally expanded forming a structure that can be regarded as a zygomatic plate. In Paleogene taxa, such as *Griphotherion*, the DMO is relatively simple but in Neogene representatives of Mesotheriidae and Hegetotheriidae (and particularly in Pachyrukhinae) the DMO shows divisions that imply a great functional complexity for the deep masseter.

Development of zygomatic plates can be observed in other mammals, but Condition 2 can be particularly compared with vombatid marsupials and within Eutheria, certain rodent groups. Vombatidae (wombats) are herbivorous marsupials of the semiarid savannahs of Australia (Woolnough, 1998). Their diet includes mainly grasses (*e.g.*, *Poa*; Evans *et al.*, 2006). The presence of zygomatic plate, the development of diastemata, and euhypsodont teeth represent common traits between vombatids and pachyrukhines, the latter being included among the most specialized forms of the Condition 2. Crompton *et al.* (2008) described the control of mandibular movements in *Lasiorhinus latifrons* (a species of wombat) and characterized its masticatory apparatus. In their classification, the-

se authors named the superficial masseter as external superficial masseter, the deep masseter as internal superficial masseter, and the zygomaticomandibularis muscle as deep masseter. Following those authors the SMO of Vombatidae is located dorsally on the anterior root of the zygomatic arch. The DMO is wide and run posteriorly on the ventral edge of the zygoma. Finally, the ZMO is located posteriorly on the medial aspect of the arch. This arrangement is very similar to that present in Mesotheriidae and non - pachyrukhine hegetotheriids, and results in a comparable general morphology that can be appreciated when skulls are compared in ventral view (figure 5).

Regarding the comparison with rodents, several comments can be made when Condition 2 is considered. As we mentioned above, previous authors have usually noted the similarities between Neogene typotheres and rodents or even regarded these extinct taxa as "rodent-like" notoungulates (e.g., Elissamburu, 2004; Croft and Anaya, 2006; Reguero *et al.*, 2007; Cassini *et al.*, 2010). The masticatory apparatus in rodents is highly specialized, showing strong modifications of the masseter muscle (and a wide variety of morphologies within the order) affecting the morphology of the zygomatic arch and infraorbital foramen. Given the different arrangements derived from these complex adaptations, the masticatory apparatus in rodents vary from generalized forms that does not show strong modifications of the anterior zygoma and the infraorbital foramen (*e.g.*, Protrogomorpha, Sciuromorpha), to specialized conditions in which the infraorbital foramen is highly modified for the passage of rami of the masseter (*e.g.*, Hystricomorpha, Myomorpha). In this sense, similarities between the morphology in representatives of the Condition 2 and rodents are somewhat superficial, being limited to the development of a zygomatic plate (with the concomitant development of the corresponding part of the masseter), the presence of diastema, enlarged incisors, and hypsodonty. A deeper analysis
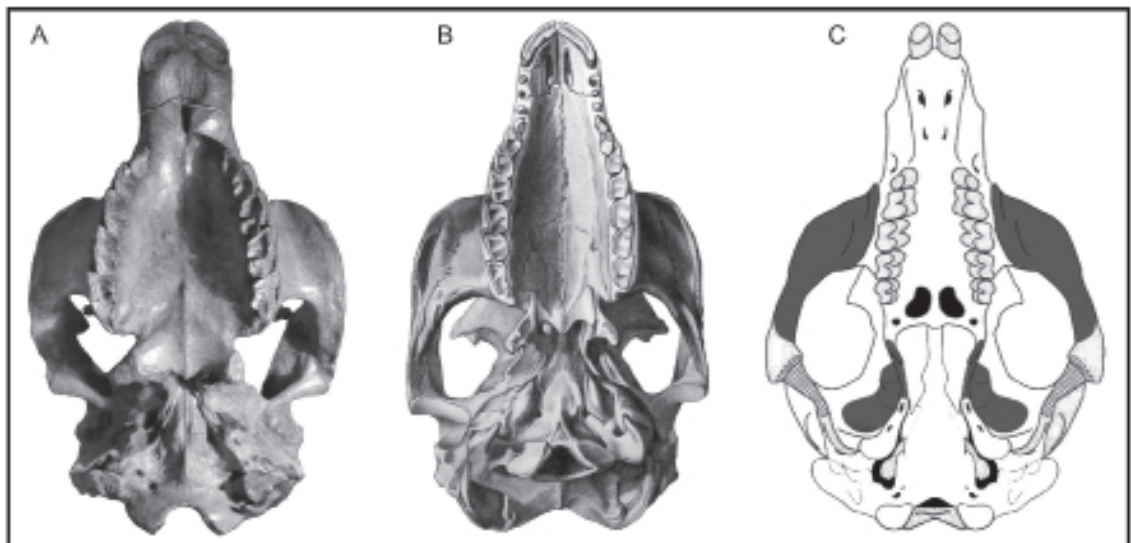

Figure 5. Ventral view of the skull in Mesotheriidae, Hegetotheriidae, and Vombatidae, showing the general morphology and the development of zygomatic plates. **A-** *Typotheriodon extensum* (MACN-PV 2925); **B-** *Hegetotherium mirabile* (modified from Scott, 1912); **C-** *Lasiorhinus latifrons* (modified from Crompton *et al.*, 2008). Not in scale. **/ Figura 5.** *Vista ventral del cráneo en Mesotheriidae, Hegetotheriidae y Vombatidae mostrando su morfología general y el desarrollo de placas cigomáticas.* **A-** Typotheriodon extensum *(MACN-PV 2925);* **B-** Hegetotherium mirabile *(modificado de Scott, 1912);* **C-** Lasiorhinus latifrons *(modificado de Crompton* et al.*, 2008). Las imágenes no están en escala.*

reveals a different disposition of the muscles, particularly regarding the superficial masseter. The SMO is always more dorsal in the rostrum of typotheres developing a zygomatic plate, being different from the morphology of most rodents, where the SMO is low and more anterior on the facial aspect of the maxilla. Additionally, the passage of fibers of the masseter through the infraorbital foramen is not present in representatives of the Condition 2 (or any other notoungulate).

Some superficial convergence can be also traced between the heterogeneous nature and increasing complexity of the muscular packages in Condition 2 and the variable arrangements exhibited by different rodent groups. For example, in beavers (*Aplodontia rufa*, Protrogomorpha) the muscular arrangement is far simpler than that present in animals like woodchucks (*Marmota monax*, Sciuromorpha) (Druzinsky, 2010) and squirrels (Turnbull, 1970). This increasing complexity is comparable to that observed from the Paleogene representatives of Condition 2 to the more specialized and post-Tinguiririican forms of the group. Nevertheless, evolutionary trends seem to be different between rodents and taxa included in Condition 2. In basal forms, such as *Griphotherion*, the development (although incipient) of a zygomatic plate was not parallel to the acquisition of dental specializations (*e.g.*, hypsodonty, diastemata, etc.). In that case, development of more complex muscles precedes morphological and functional modifications of the basic dental pattern of the order. In turn, in the generalized condition in rodents, as in *Aplodontia rufa*, the incipient zygomatic plate (with a muscular arrangement similar to that of *Griphotherion*) in combined with hypsodont teeth and development of diastemata (figure 6). In fossil protrogomorph genera, such as *Ischyromis* from the Oligo-
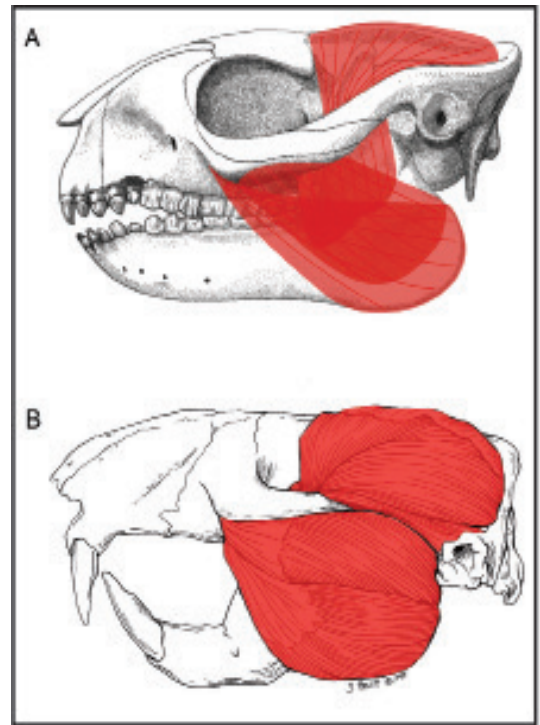
Figure 6. Comparisson of skull shape and general masticatory apparatus arrangement in lateral view between a basal notoungulate and a rodent. **A-** *Griphotherion peiranoi*; **B-** *Aplodontia rufa* (modified from Druzinsky, 2009). Not in scale. **/ Figura 6.** *Comparasión entre la forma del cráneo y la disposición general del aparato masticatorio entre un notoungulado basal y un roedor;* **A-** Griphotherion peiranoi*;* **B-** Aplodontia rufa *(modificado de Druzinsky, 2009). Las imágenes no están en escala.*

cene, dental and muscular traits are similar to the extant *Aplodontia* and hence different from the basal forms of the Condition 2. This is also observed in *Rhombomylus*, an Eocene genus proposed as sister group of Rodentia (Meng *et al.*, 2003). Both *Ischyromis* and *Rhombomylus* present a primitive pattern for the masseter muscle and an incipient zygomatic plate but develop diastemata and fully hypsodont teeth. Then, in this case dental specialization precedes hypertrophy and division of the masseter muscle, a trend that becomes evident in other groups (*e.g.*, Sciuromorpha).

Sciuromorph rodents, like *Marmota monax*, present a well-developed zygomatic plate but do not exhibit particular conver-

gences with taxa of the Condition 2, such as mesotheriids and pachyrukhines. Some traits can be identified as common to both morphologies, including hypsodont dentition, enlarged incisors, and presence of diastemata but, although there is hypertrophy of the deep masseter in both cases, the areas of origin are considerably different.

In summary, the pattern of attachment of the masseter muscle and different degree of dental specialization observed in Condition 2 is singular for these notoungulates and morphologic convergences with extant lineages are only superficially expressed. Therefore, the term "rodent-like" used for most typotheres indicating convergence with Rodentia cannot be considered extensively accurate. In this sense, both Condition 0 and Condition 2 show characters comparable to a relatively broad spectrum of groups, including clades outside Eutheria, such as Didelphidae and Vombatidae.

Finally, it is also worth noting that *Paedotherium* shows, besides the anterodorsal SMO, another attachment area located on the lateral and external surface of the arch, below and anteriorly to the orbit (see figure 3E). This presumably represents an additional punctual area for the attachment of a muscular bundle, indicating a subdivision of the superficial masseter (that would be divided in superior and inferior parts). Gambaryan and Kielan-Jaworowska (1995) described a similar division in the mesozoic multituberculates *Nemegtbaatar gobiensis* and *Catopsbaatar catopsdoides*; in these taxa the superficial masseter is divided in two rami (anterior and posterior) along the zygomatic arch. In turn, this kind of subdivision in the superficial masseter is not usual in extant mammals. Although more studies are needed in order to assess this possible trait in pachyrukhines, it certainly illustrates the high complexity achieved by this particular group of eutherians.

Conclusions

It is evident that the masticatory apparatus underwent a wide range of changes and specializations among notoungulates. This structural evolution shows some degree of independence from the acquisition of derived dental characters, although in some cases there is a trend toward an increasing complexity of the masticatory muscles associated to hypsodonty and development of other traits like diastemata.

Some of the arrangements exhibited by the analyzed taxa do not show evident morphological convergence regarding extant forms. In turn, certain Neogene genera show a clear convergence related to complex structures.

Certain morphological patterns were circumscribed to determinate families (*e.g.*, Interatheriidae, Notostylopidae) whereas others are phylogenetically widespread. The case of Condition 2 is notable, achieving a high degree of complexity and comprising a group of lineages whose radiation spans from the middle Paleogene to the end of the Neogene.

Acknowledgements

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Taxon	Specimens	References
Henricosborniidae		
Simpsonotus praecursor	MLP 73-VII-3-11 (holotype)	Pascual *et al.* (1978)
Notostylopidae		
Notostylops murinus	MACN-A 10499; MACN-A 10466	Simpson (1948)
Boreastylops lumbrerensis	MLP 78-V-6-5 (holotype); PVL 4261	Vucetich (1980)
Typotheria		
Colbertia lumbrerense	PVL 4183; PVL 4184 (1-2); PVL 4293; PVL 4294; PVL 4300; PVL 4607 (holotype); PVL 4608; PVL 6218; PVL 6227	. . . .
Interatheriidae		
Notopithecus adapinus	MACN-A 10790; MACN-A 10787	Simpson (1967)
Protypotherium australe	MACN-A 3882; PVL 2389	Scott (1912)
"Archaeohyracidae"		
Archaeohyrax patagonicus	MACN-A 52-617 (holotype)	
Hegetotheriidae		
Hegetotherium mirabile	PVL 91	McCoy and Norris (2012); Scott (1912)
Paedotherium typicum	MACN-PV 10178; MMMP 226-S; MMMP 698-S; PVL 3386	Cerdeño and Bond (1998)
Mesotheriidae		
Typotheriodon extensum	MACN-PV 2925	
Family indet.		
Griphotherion peiranoi	PVL 5903 (holotype)	García-López and Powell (2011)

Table 1. List of specimens and bibliographical sources. / **Tabla 1.** *Lista de especímenes y fuentes bibliográficas.*