

BASICRANIAL OSTEOLOGY OF *COLBERTIA LUMBRERENSE* BOND, 1981 (MAMMALIA: NOTOUNGULATA)



DANIEL A. GARCÍA LÓPEZ

Consejo Nacional de Investigaciones Científicas y Técnicas. Cátedra de Paleontología, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán. Miguel Lillo 205, T4000JFE San Miguel de Tucumán, Tucumán, Argentina. dgarcialopez@csnat.unt.edu.ar

Abstract. A description of *Colbertia lumbrerense* Bond (Mammalia, Notoungulata) is presented. This species is recorded in levels of the Lumbrera Formation (Eocene) in northwestern Argentina. Several specimens were collected; yet its cranial osteology has not been studied in detail. The new description provided herein is based on five specimens, including the type specimen. The external surface of the posterior zone of the skull in this species shows a generalized notoungulate morphology. The development of certain elements (external auditory meatus, meatal crest, epitympanic sinus) is similar to that observed in other Paleogene notoungulates such as *Simpsonotus* Pascual, Vucetich, and Fernández; *Brachystephanus* Simpson, Minoprio, and Patterson; and *Xenostephanus* Simpson, Minoprio, and Patterson. In spite of this generalized arrangement, the skull shows some distinctive features, particularly in the petrosal. Some traits of this bone are shared with *Dolichostylodon saltensis* García López and Powell, a notoungulate recorded in upper levels of the same formation. The morphology described in this study is consistent with recent phylogenetic analyses of Paleogene notoungulate taxa that place *C. lumbrerense* in a basal position.

Key words. Notoungulata. Paleogene. Basicranium. Osteology. Petrosal

Resumen. OSTEOLOGÍA DEL BASICRÁNEO DE *COLBERTIA LUMBRERENSE* BOND (MAMMALIA: NOTOUNGULATA). Se presenta una descripción de la anatomía craneal de *Colbertia lumbrerense* Bond (Mammalia: Notoungulata). Esta especie ha sido registrada en niveles de Formación Lumbrera (Eoceno) del noroeste argentino y, aunque se han colectado varios individuos, su osteología craneana no ha sido estudiada en detalle. Esta descripción está basada en cinco individuos, incluyendo el holotipo de la especie. La zona posterior del cráneo en esta especie muestra rasgos generalizados para los notoungulados. El desarrollo de ciertos elementos (meato auditivo externo, cresta meatal, senos epitimpánicos) es similar al observado en otros notoungulados paleógenos como *Simpsonotus* Pascual, Vucetich y Fernández, *Brachystephanus* Simpson, Minoprio y Patterson y *Xenostephanus* Simpson, Minoprio y Patterson. A pesar de esta morfología generalizada, el cráneo muestra peculiaridades significativas, como el petroso. Algunas características de este hueso son compartidas con *Dolichostylodon saltensis* García López y Powell, un notoungulado registrado en niveles superiores de la misma formación. Las observaciones llevadas a cabo en este estudio son consistentes con análisis filogenéticos recientes de taxones paleógenos que ubican a *C. lumbrerense* en una posición basal.

Palabras clave. Notoungulata. Paleógeno. Basicráneo. Osteología. Petroso

THE genus *Colbertia* Paula Couto, 1952, was recorded in the Paleogene of Brazil and Argentina. It includes two species of small-sized notoungulates, *i.e.*, *Colbertia magellanica* (Price and Paula Couto, 1950) and *Colbertia lumbrerense* Bond, 1981. The genus was originally referred to the family Oldfieldthomasiidae and related to *Maxschlosseria* Ameghino, 1901, from Patagonia, Argentina (Paula Couto, 1952; Bond, 1981) and *Brachystephanus* Simpson, Minoprio, and Patterson, 1962, from Mendoza, Argentina (Bond, 1981). Later, López and Bond (2003) and López (2008) proposed a new family, albeit not formally named yet, to include this genus and some other genera traditionally placed in Oldfieldthomasiidae (*e.g.*, *Maxschlosseria*, *Brachystephanus*).

Colbertia lumbrerense was recorded in rocks of the Lumbrera Formation (Eocene) in Salta Province, northwestern Argentina. These levels are known as Lumbrera inferior (lower Lumbrera) (del Papa, 2006; del Papa *et al.*, 2010).

Bond (1981) —based on several specimens— described in a general way the skull of this taxon.

In spite of noteworthy contributions offering descriptions of some Paleogene Patagonian genera, knowledge of the cranial anatomy of the Paleocene and Eocene species of Notoungulata is still incomplete. Simpson (1932, 1936, 1948, 1967) described Paleogene genera from Patagonia in detail. Simpson *et al.* (1962), in their description of the mammalian fauna of the Divisadero Largo Formation (Mendoza, Argentina), presented some data drawn from the cranial osteology of *Brachystephanus postremus* Simpson, Minoprio, and Patterson, 1962; *Xenostephanus chiotii* Simpson, Minoprio, and Patterson, 1962; and *Allalmeia atalaensis* Rusconi, 1946. Additionally, Paula Couto (1952), Pascual *et al.* (1978), and Vucetich (1980) described cranial features of Paleogene species from Brazil and northwestern Argentina.

New contributions to the knowledge of notoungulate

cranial osteology include Arnal and López (2006), who analyzed the auditory region of *Brachystephanus postremus*, and García López (2006), who presented a preliminary description of the basicranium of *Colbertia lumbrerense*. Billet *et al.* (2008; 2009) published detailed descriptions of notoungulates from the Oligocene beds of Salla (Bolivia). Finally, García López and Powell (2009) provided a description of different cranial features of *Dolichostylodon saltensis*, an Oldfieldthomasiidae also found in the Lumbrera Formation.

Herein is presented a description of the basicranium and the middle ventral cranial region of *Colbertia lumbrerense*. This description is complemented by specimens yet undescribed, summarizing previous observations by Bond (1981). The new specimens are very well preserved, thus allowing analysis and description of the cranial osteology to a detail not previously attained.

MATERIALS AND METHODS

All specimens studied come from Estancia Pampa Grande, Guachipas Department, Salta Province, Argentina. They were found in the lower beds of the Lumbrera Formation. This unit carries an important fossil content and numerous new taxa have been described from it (Vucetich, 1980; Bond, 1981; Pascual *et al.*, 1981; Bond and Vucetich, 1983; Bond and López, 1993; Babot *et al.*, 2002). The rich record of terrestrial mammals allows referring this formation to the Casamayoran South American Land Mammal Age (SALMA) (Vucetich, 1980; Bond, 1981; Pascual *et al.*, 1981). However, correlation with Patagonian faunas is still tentative.

All fossil material described herein is deposited in the Colección Paleontología de Vertebrados Lillo (PVL), Instituto Miguel Lillo (Tucumán, Argentina) and includes the five specimens listed below. The ontogenetic age of the specimens is based on emerged dental pieces and their degree of wear.

PVL-4607 (holotype of *Colbertia lumbrerense*). Skull and mandible of a young adult. The skull lacks the left zygomatic arch and the premaxilla on both sides. The dorsal surface is poorly preserved, particularly the skull vault. Some features of the basicranium are visible, but this region and the occipital zone are highly deteriorated.

PVL-4183. Almost complete skull of a young adult, lacking the right zygomatic arch and the premaxilla. The material is highly weathered. The basic morphology of some elements is still visible, but not so the sutures.

PVL-6218. Nearly complete but weathered skull of a young

adult. The left zygomatic arch is lost, but the right arch is well preserved; some surfaces of muscular origin are evident. **PVL-6227.** Fragment of the skull and mandibles of an adult. The fragment includes the posterior half of the skull, with part of the maxilla and the left zygomatic arch. The specimen is highly deformed, but the bone surface is well preserved. The left tympanic cavity is exposed and the tympanic aspect of the petrosal is visible. The cranial cavity is exposed dorsally, and the cerebellar and lateral aspects of the petrosals are also visible.

PVL-4300. Skull and mandibles of an old individual. The skull is nearly complete. All the surfaces are well preserved except for the palate and the anterodorsal part of the skull. The basicranium is well preserved. The internal cranial cavity is partially exposed as well as the cerebellar and lateral aspects of the petrosals.

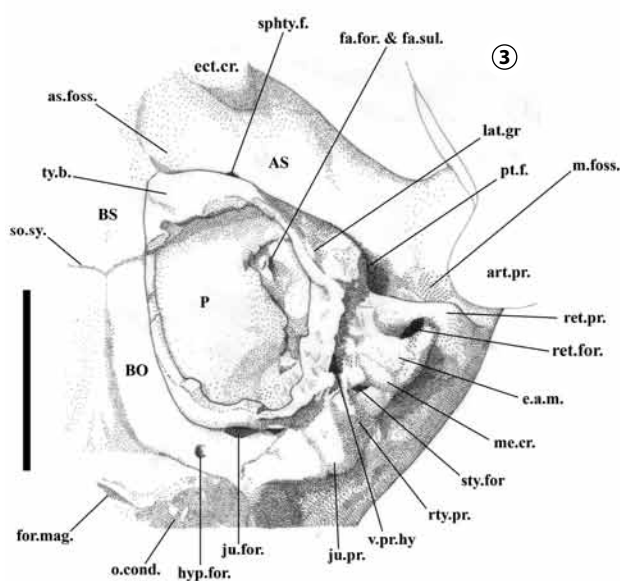
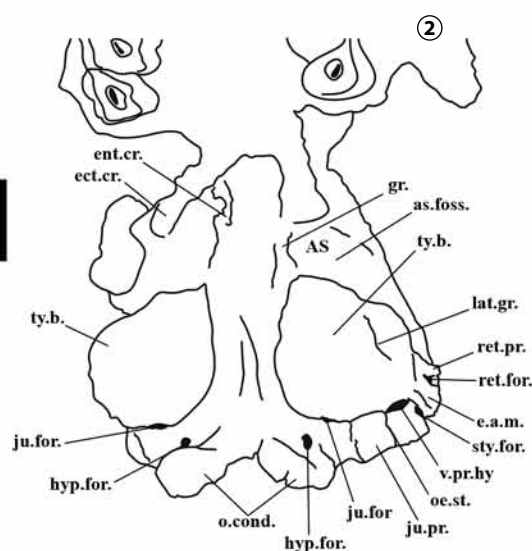
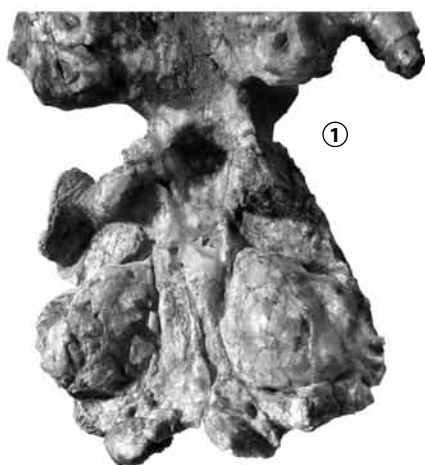
The anatomical terms used in this paper follow mainly the Nomina Anatomica Veterinaria. Other names drawn from the anatomical literature —focused on Notoungulata (*e.g.*, Gabbert, 2004; Billet *et al.*, 2008; 2009)— were used when appropriate. For descriptive purposes, and following Wible *et al.* (2004), the basicranium is described in two parts, anterior part or mesocranium and posterior part.

ANATOMICAL DESCRIPTION

Mesocranium

The mesocranium includes the anterior part of the basicranium, between the choanae and the anterior extent of the ear region (Wible *et al.*, 2004, 2009). This zone comprises part of the palatine, the pterygoid, and the basisphenoid and alisphenoid (fused), along with the choanae and the pterygoid crests (ectopterygoid and entopterygoid). The posterior limit of this region in *Colbertia* is the anterior border of the tympanic bulla.

Palatines form the floor of the choanae, which open at the level of the distal border of the third upper molar. This condition shows some variability in the studied specimens and in some cases the choanae are slightly behind the level of that molar (Fig. 1.1). Two pairs of pterygoid crests project posteriorly from the lateral borders of the choanae, the ectopterygoid crests and the entopterygoid crests, which form the lateral frame of the basipharyngeal canal (Figs. 1.1–2). Apparently, the ectopterygoid crests are formed by the palatine, but the surface of these structures is badly damaged and the elements involved are not visible. The entopterygoid crests are located on the medial wall of the ectopterygoid crests. These crests run posteriorly from the lateral borders



of the choanae. Crests are damaged in all the studied specimens; thus their features are not clearly visible. The roof of the basipharyngeal canal is wide (Fig. 1.1–2) and formed mainly by the basisphenoid in the most posterior part. Anteriorly, the surface is broken and not visible. The ventral surface of the basisphenoid is smooth and lacks the crests and longitudinal grooves observed in other notoungulates (Gabbert, 2004). However, there is a crest marking the boundary between basisphenoid and alisphenoid. The contact between basisphenoid and basioccipital (sphenoccipital synchondrosis) is located at the level of the anterior half of the medial edge of the bulla. This contact is transversal and irregular (Fig. 1.3).

The alisphenoid has its greater extension in the mesocranium (Fig. 1). It forms the entire lateral surface, from the pterygoid crests in the anteromedial end and the contact with the basisphenoid in the medial border, to the contact with the tympanic bulla posteriorly and the medial end of the mandibular fossa of the squamosal at the latero-posterior end. Three main features are present on the ventral surface of the alisphenoid, *i.e.*, a roughly triangular fossa, the sphenotympanic fissure, and the petrotympanic fissure. The fossa of the alisphenoid (Fig. 1.2–3) shows an anterior apex adjacent to the base of the pterygoid. Two crests diverge medially and laterally from this point. The medial crest runs anteroposteriorly, along the contact between basisphenoid and alisphenoid. The lateral crest is lower than the medial

Figure 1. *Colbertia lumbrerense* Bond, 1981. **1**, PVL-4300, posterior half of the skull in ventral view / mitad posterior del cráneo en vista ventral; **2**, scheme of the same image showing the elements of the basicranium / esquema de la misma imagen mostrando los elementos del basicráneo; **3**, drawing, based mainly on PVL-6227, of the left auditory region in ventral view / dibujo, basado principalmente en el ejemplar PVL-6227, de la región auditiva izquierda en vista ventral. **art.pr.**, articular process of mandible / proceso articular de la mandíbula; **AS**, alisphenoid / aliesfenoides; **as.foss.**, alisphenoid fossa / fosa del aliesfenoides; **BO**, basioccipital / basioccipital; **BS**, basisphenoid / basiesfenoides; **e.a.m.**, external auditory meatus / meato auditivo externo; **ect.cr.**, ectopterygoid crest / cresta ectopterygoidea; **ent.cr.**, entopterygoid crest (broken) / cresta entopterygoidea (rota); **fa.for. & fa.sul.**, facial foramen and facial sulcus / foramen facial y surco facial; **for.mag.**, foramen magnum / foramen magnum; **gr.**, groove for the auditory tube? / surco para el tubo auditivo?; **hyp.for.**, hypoglossal foramen / foramen hipoglosso; **ju.for.**, jugular foramen / foramen yugular; **ju.pr.**, jugular process / proceso yugular; **lat.gr.**, lateral groove on tympanic bulla / surco lateral sobre la bulla timpánica; **m.foss.**, mandibular fossa / fosa mandibular; **me.cr.**, meatal crest / cresta meatal; **o.cond.**, occipital condyle / cóndilo occipital; **oe.st.**, occipitosquamosal suture / sutura occipitoesquamosal; **P**, petrosal / petroso; **pt.f.**, petrotympanic fissure (hidden by the tympanic bulla) / fisura petrotimpánica (oculta por la bulla timpánica); **ret.for.**, retroarticular foramen / foramen retroarticular; **ret.pr.**, retroarticular process / proceso retroarticular; **rty.pr.**, retrotympanic process / proceso retrotimpánico; **so.sy.**, sphenoccipital synchondrosis / sincondrosis esfenoccipital; **sphty.f.**, sphenotympanic fissure / fisura esfenotimpánica; **sty.for.**, stylomastoid foramen / foramen estilomastoideo; **ty.b.**, tympanic bulla / bulla timpánica; **v.pr.hy.**, vagina processus hyoidei. Scale bars: 1 cm.

one, running anteromedially – posteromedially. It is pointed towards the mandibular fossa, but progressively weakens and then it disappears before reaching the fossa. The fossa is shallow and bowl-shaped; its anterior half (adjacent to the pterygoid crests) is deeper than the posterior half. Gabbert (2004) described a similar fossa for the Toxodontia and identified this structure as the scaphoid fossa, the zone of origin for the *tensor veli palatini* muscles. On the other hand, Billet *et al.* (2008; 2009) stated that this fossa is probably homologous to the pterygoid fossa of other ungulate mammals, which also receives the *pterygoideus medialis* muscle. Nevertheless, unlike the structure observed in *C. lumbrense*, both the scaphoid fossa and the pterygoid fossa are usually interpreted as trigonoid structures. For this reason, the true nature of this triangular fossa is considered unknown.

There are no grooves on the medial surface of the alisphenoid, although the presence of a longitudinal groove for the auditory tube (Eustachian tube) is usual in notoungulates (Pascual *et al.*, 1978; Gabbert, 2004; Arnal and López, 2006; Billet *et al.*, 2008, 2009). There is a notch over the ventral surface of the tympanic bulla that probably conveyed the auditory tube (this notch is described below). One of the specimens (PVL-4300) shows a low crest oriented anteroposteriorly that seems to be part of a groove, but this is difficult to confirm (Fig. 1.2).

There is a large, obliquely elongate foramen on the posterior border of the alisphenoid. This foramen is the sphenotympanic fissure (Fig. 1.3) according to Gabbert's terminology (Gabbert, 2004). Patterson (1936) and Simpson (1948) described this structure as the oval foramen, which is the exit of the mandibular branch of the trigeminal nerve (V_3). Later, Simpson (1967) mentioned this foramen as the *foramen lacerum medium*. I have not identified other foramina on the alisphenoid of *Colbertia lumbrense*. The sphenotympanic fissure is almost entirely surrounded by the alisphenoid, with only a little contribution from the tympanic bulla (that is, the ectotympanic) on the posterior edge.

There is a small notch near the posterolateral end of the alisphenoid, on the medial extent of the mandibular fossa (Fig. 1.3). This structure is the petrotympanic fissure (canal of Huguier *sensu* Billet *et al.* 2008, 2009), which is the exit of the *chorda tympani* nerve (Evans and Christensen, 1979; Novacek, 1993; Gabbert, 2004). The position and osteological relationships of the petrotympanic fissure in the specimens here studied are not clear, although in the specimens PVL-6227 and PVL-4300 this structure is associated to a small groove over the edge of the tympanic bulla. However, the

fissure is apparently located between the alisphenoid and the squamosal.

Posterior part of the basicranium

The posterior part of the basicranium is defined as the posterior region of the braincase floor (Wible *et al.*, 2004), from the anterior edges of the tympanic bullae and the mandibular fossae to the occipital condyles. This region includes several elements: ectotympanic (tympanic bulla and external auditory meatus), squamosal (mandibular fossa, retroarticular process, retrotympanic process), basioccipital, and other elements of the occipital complex (*e.g.*, occipital condyle, jugular process).

The tympanic bulla houses the tympanic cavity and covers the ventral surface (tympanic side) of the petrosal, which houses the inner ear. Since no evidence indicates that the bulla is formed by more than one element in *Colbertia lumbrense*, it is assumed in this work that this structure is formed only by the ectotympanic. The tympanic bulla is globular in lateral view. In ventral view (Figs. 1.1–3; 2.1) this structure is roughly subtriangular with an anteromedial apex (above the contact between the basisphenoid and the alisphenoid), a posteromedial apex (adjacent to the occipital condyle), and a posterolateral apex (at the proximal end of the external auditory meatus). The medial side (between the anteromedial and the posteromedial apex) contacts with the basisphenoid on the anterior third of this element and with the basioccipital on the two posterior thirds. The anterolateral side (between the anteromedial and the posterolateral apex) contacts mainly with the alisphenoid. In this zone, the inflation of the bulla obscures the contact between it and the alisphenoid and therefore the sphenotympanic fissure is not visible in ventral view of the skull. The anterolateral side contacts with the retroarticular (postglenoid) process of the squamosal at the lateral end. The posterior side (between the posteromedial and posterolateral apex) is associated to the jugular foramen (jugular fissure according to Gabbert, 2004) or posterior lacerate foramen (Billet *et al.*, 2008, 2009), to the jugular process, and to the retrotympanic process of the squamosal.

The external surface of the bulla is smooth. However, there is a very shallow lateral groove (Fig. 1.2–3). This groove is at the same level as an internal thickening of the bullar lateral wall where the tympanic crest is located. This crest is an osseous support along which a large part of the tympanic membrane is attached, thus marking the limit between the external ear and the middle ear cavity (Bloch and Silcox, 2001).

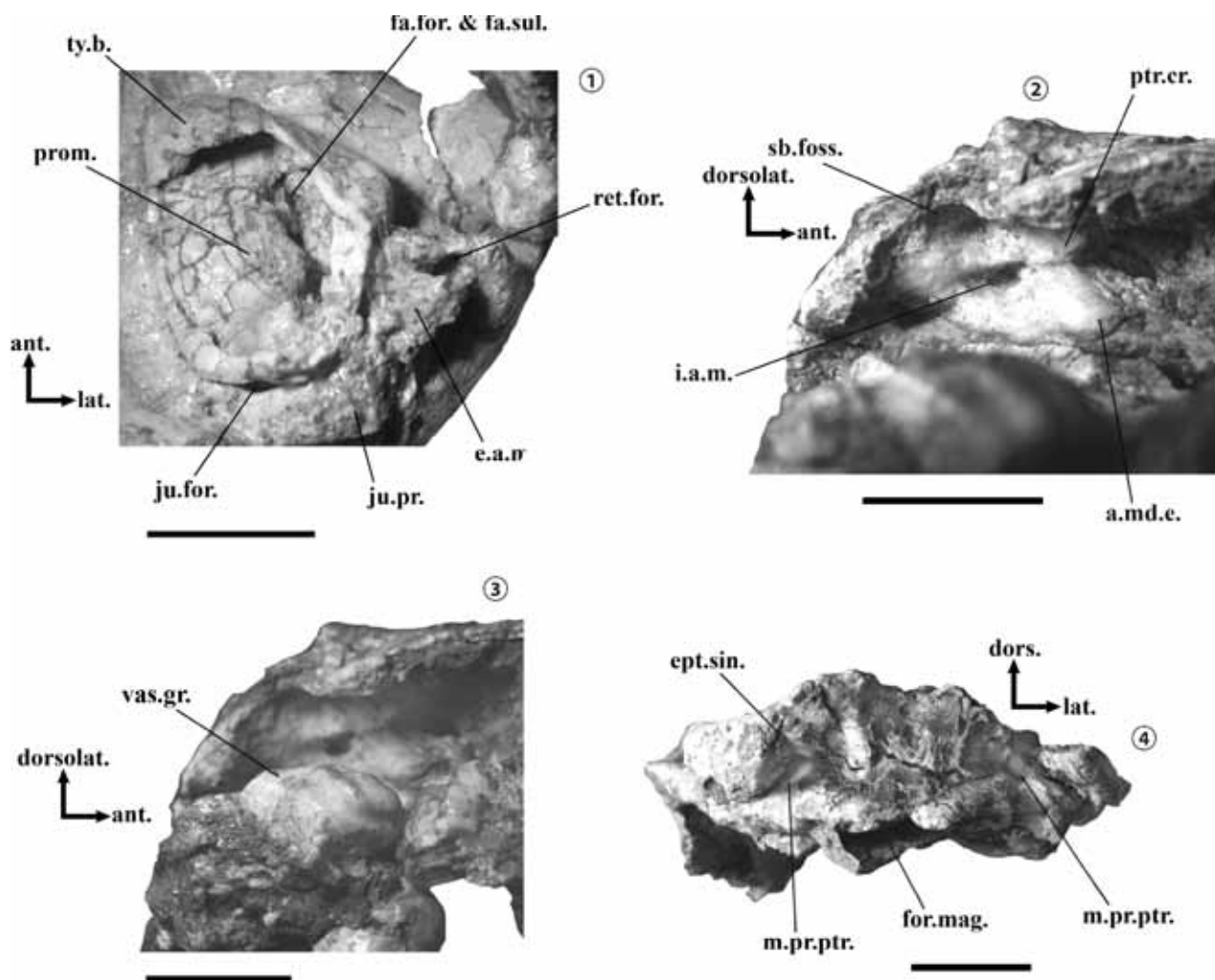


Figure 2. *Colbertia lumbrerense* Bond, 1981. **1**, PVL-6227, ventral view of left auditory region, with the tympanic view of petrosal partially exposed / *vista ventral de la región auditiva externa con la vista timpánica del petroso parcialmente expuesta*; **2**, PVL-4300, inner cranial cavity with the cerebellar view of petrosal exposed / *cavidad craneana interna con la vista cerebelar del petroso expuesta*; **3**, PVL-4300, inner cranial cavity with the squamosal view of petrosal partially exposed / *cavidad craneana interna con la vista escamosal del petroso parcialmente expuesta*; **4**, PVL-6227, posterior view of skull, showing the mastoid exposure of petrosal / *vista posterior del cráneo mostrando la exposición mastoidea del petroso*. **a.m.d.e.**, anteromedial end of petrosal / *extremo anteromedial del petroso*; **ant.**, anterior / *anterior*; **dors.**, dorsal / *dorsal*; **dorsolat.**, dorsolateral / *dorsolateral*; **e.a.m.**, external auditory meatus / *meato auditivo externo*; **ept.sin.**, epitympanic sinus / *seno epitimpánico*; **fa.for. & fa.sul.**, facial foramen and facial sulcus / *foramen facial y surco facial*; **for.mag.**, foramen magnum / *foramen magnum*; **i.a.m.**, internal auditory meatus / *meato auditivo interno*; **ju.for.**, jugular foramen / *foramen yugular*; **ju.pr.**, jugular process / *proceso yugular*; **lat.**, lateral / *lateral*; **m.pr.ptr.**, mastoid process of petrosal / *proceso mastoideo del petroso*; **prom.**, promontorium / *promontorio*; **ptr.cr.**, petrosal crest / *cresta petrosa*; **ret.for.**, retroarticular foramen / *foramen retroarticular*; **sub.foss.**, subarcuate fossa / *fosa subarcuata*; **ty.b.**, tympanic bulla / *bulla timpánica*; **vas.gr.**, vascular groove / *surco vascular*. Scale bars: 1 cm.

The internal cavity of the tympanic bulla has been studied in one specimen (PVL-6227) (Figs. 1.3; 2.1). Thickness of the bulla wall increases dorsally as it approaches the basicranium. The wall is also thicker on the lateral side of the bulla (at the location of the tympanic crest). Nevertheless on the medial side the wall becomes thinner, even at the contact with the basicranium.

Inside the bullar, near the anteromedial apex, there is a weak, vertical osseous structure. This is the only element that could be identified as a septum like those mentioned by

Patterson (1936) in some Typotheria. However, this element seems to be unattached to the bulla wall and no vestige of a septum was identified at the posterior zone of the cavity. Patterson mentioned the presence of vertical septa in typotherians and, based on this feature, he proposed a mixed origin for the bulla —*i.e.*, ectotympanic and entotympanic. The author mentioned a similar condition for the Toxodontia but established that the septum was horizontal in this group. Cifelli (1993) observed vertical septa only in Archaeohyracidae and Hegetotheriidae. The nature of the element present

in *Colbertia lumbrense* is uncertain, and it should be noted that none of the middle ear ossicles were identified. The fragility of the element present in *C. lumbrense* does not allow a better preparation. Therefore, until new material with a better preserved tympanic cavity is found, this element will remain unidentified.

The short and horizontal external auditory meatus runs posterolaterally and its surface is roughly flat (Figs. 1.2–3; 2.1). The meatal crest is a slight osseous ridge located longitudinally over the posterior surface of the meatus (Fig. 1.3). Morphology of the crest is similar to a structure observed in *Simpsonotus praecursor* Pascual, Vucetich, and Fernández, 1978, although in this case such a structure was identified only as an osseous ridge (not a meatal crest) and the meatus was described as flat and not crested (Pascual *et al.*, 1978). However, the similarity of the structure in both taxa is remarkable and it probably corresponds to a basal condition of the meatal crest. This crest is poorly developed in *Colbertia*, and is much weaker than in other Paleogene taxa like *Notostylops murinus* Ameghino, 1897. The external acoustic porus is located posteriorly and ventrally to the level of the mandibular fossa in lateral view. The porus is completely surrounded by the ectotympanic.

The mandibular fossa (squamosal) is a shallow cavity, with poorly defined anterior border. The posterior border of the fossa is formed by the anterior slope of the retroarticular process (Fig. 1.2–3); this slope is vertical, and the posterior limit of the fossa is abrupt.

The well-developed retroarticular process (formed by the squamosal) is adjacent to the external auditory meatus (Fig. 1.2–3); it is anteroposteriorly compressed and prominent in ventral view. The retroarticular process is well differentiated from the tympanic bulla and the external auditory meatus (Fig. 1.3).

The great development of the retroarticular (postglenoid) foramen is remarkable (Fig. 1.3). This foramen — which conveys the postglenoid vein — is a large, elongated oval aperture. In *Colbertia*, the external aperture of the retroarticular foramen is formed by the retroarticular process anteriorly (squamosal) and by the external auditory meatus posteriorly (ectotympanic). The foramen is latero-ventrally oriented and located anteriorly and ventrally to the acoustic porus.

The retrotympenic process (squamosal) is adjacent to the posterior edge of the external auditory meatus (Fig. 1.3); it is larger and wider than the retroarticular process, and contacts anteromedially with the posterolateral wall of the tympanic

bulla. Medially, the retrotympenic process is adjacent to the jugular process and both structures are separated by a groove where the occipito-squamosal suture is visible (Fig. 1.2).

The squamosal bears the epitympenic sinus on its posterolateral zone. Bond (1981) mentioned that the squamosal is “somewhat inflated” to form the epitympenic sinus in *Colbertia lumbrense*. However, the observations and comparisons carried out in this study indicate that this inflation is virtually absent. Nevertheless, the surface of the squamosal is broken in two specimens (PVL-4300 and PVL-6227) and the small interior cavities of the sinuses are visible. Externally, the wall of the sinuses shows the usual arrangement in notoungulates, adjacent laterally to the mastoid process of the petrosal (Gabbert, 2004) (Fig. 2.4).

There are two apertures near the retrotympenic process (Fig. 1.3). The lateral aperture is the stylomastoid foramen and the medial one is the *vagina processus hyoidei* (Patterson, 1932; Moore, 1981), also called tympanohyal recess (Billet *et al.*, 2008, 2009) or hyoid recess (Gabbert, 2004) in notoungulates. The stylomastoid foramen, the tertiary exit of the facial nerve (cranial nerve VII) in living mammals, is located between the posterior edge of the external auditory meatus and the anterior edge of the retrotympenic process. The aperture is smaller than the retroarticular foramen. The *vagina processus hyoidei* is an osseous sheath that surrounds the distal end of the tympanohyal, that projects from the sheath to articulate with the stylohyal (Moore, 1981), and is located anteromedially to the retrotympenic process, adjacent to the posterolateral wall of the tympanic bulla. It is a deep, slightly elongated cavity. A small osseous ridge separates the stylomastoid foramen from the *vagina processus hyoidei* (Fig. 1.2–3).

The elements of the occipital complex constitute the medial, posterior, and lateral surfaces of the basicranium. The jugular processes (Fig. 1.2–3; 2.1) are broken in all the studied specimens. Only the base is visible in PVL-4300 and PVL-6227. Features of the base indicate that the process was small and laterally compressed. The development is similar to that in *Simpsonotus praecursor* (Henricosborniidae) and is lesser than in those of other notoungulates like *Archaeohyrax patagonicus* (Ameghino, 1897) and *Notostylops murinus*.

The jugular foramen is located medially to the base of the jugular process and is adjacent to the posterior wall of the tympanic bulla (Fig. 1.2–3). This foramen conveys cranial nerves IX, X, and XI (glossopharyngeal, vagus, and accessory, respectively), and the internal jugular vein. The foramen is large and latero-medially elongate. The posterior

wall of the bulla forms a slope that is ventrally continuous with the anterior wall of the jugular foramen. The hypoglossal (condylar) foramen (exit of the hypoglossal nerve) is adjacent, medially and posteriorly, to the jugular foramen, near the base of the occipital condyle (Fig. 1.2–3). It is a single, small, and circular aperture. Apparently, the position of these foramina is very conservative and there is no marked variability among several notoungulate groups.

The occipital condyle is slightly elongated mediolaterally. There is an osseous ridge running from the anterior wall of the condyles on each side. Each ridge converges on the sagittal line forming a single ridge running longitudinally on the basioccipital and becoming sharper anteriorly (Fig. 1.3). Then the ridge disappears and (apparently) it does not continue on the basisphenoid. This ridge is present in other notoungulates and its development is variable among different taxa. In *Colbertia lumbrerense* it is longer than in *Oldfieldthomasia debilitata* and *Notostylops murinus*, and its extension is similar to that of *Archaeohyrax patagonicus*. According to Billet *et al.* (2009), who described this structure in an Oligocene archaeohyracid, this ridge separates two zones for the origin of the *recti capitis ventralis* muscles. The basioccipital does not present any other remarkable features and there are no foramina near the medial wall of the tympanic bulla.

Petrosal

The petrosal bone houses the inner ear structures (*e.g.*, the cochlea and the semicircular canals) (Wible *et al.*, 1995; Bloch and Silcox, 2001). This is a very complex bone, usually treated as a triangular pyramid with four views given its position of this bone in the skull, *i.e.*, ventral, dorsal, lateral, and posterior (MacIntyre, 1972; Wible *et al.*, 1995; Gabbert, 2004). In *Colbertia*, the tympanic (ventral) and cerebellar (dorsal) sides are better exposed and studied in greater detail, while the squamosal (lateral) and mastoid (posterior) views are just partially exposed.

Tympanic view. This view is partially exposed in PVL-6227 (the surface of the bulla is broken) (Fig. 2.1).

The medial tympanic surface of the petrosal (between the bullar wall and the medial edge of the promontorium) is narrower than the transversal extension of the promontorium. This condition differs from the wide medial margin described by Gabbert (2004) for the Toxodontia. Furthermore, the medial tympanic surface of the petrosal in *Colbertia lumbrerense* is smooth, without grooves or other structures.

The promontorium occupies a large surface of the tympanic view of the petrosal and is oriented anteromedially –

posterolaterally. The medial edge of this structure is not well developed, and the surface of the promontorium is slightly convex from the level of the vestibular fenestra to the medial margin of the petrosal. Therefore, the promontorium is not particularly prominent.

The vestibular fenestra (oval window) faces anterolaterally and is located anteriorly to the external auditory meatus. The cochlear fenestra (round window) is oriented laterally. There is a small fossa adjacent to the cochlear fenestra referred here to the stapedius fossa. The secondary facial foramen is anterior to the vestibular fenestra and opens inside a groove oriented posteriorly (the facial sulcus). This groove reaches the level of the anterior edge of the vestibular fenestra.

The *tegmen tympani*, the part of the petrosal which forms the rear (or, in this case, lateral) roof of the tympanic cavity (MacPhee, 1981), is not completely exposed. It seems to occupy a smaller surface than the promontorium.

There is a small foramen inside the tympanic cavity, on the posterior end. The edges of the foramen are formed by the ectotympanic (dorsally) and the petrosal (ventrally). The nature of this structure is not clear.

Cerebellar view. This view of the petrosal is exposed in PVL-4300 (Fig. 2.2) and PVL-6227. In both cases the surface is poorly preserved and small features (such as grooves) can not be observed. One of the most striking features in this zone is the great development of the anteromedial apex, which forms a large and smooth surface anterior to the internal auditory meatus. The subarcuate fossa and the petrosal crest (*crista petrosa*) are also large structures visible in this view. The subarcuate fossa is dorsal to the internal auditory meatus and is a deep circular cavity, slightly larger than the meatus. It houses the paraflocculus, a small lobe of the cerebellum (Rougier *et al.*, 1992; Wible *et al.*, 1995). The petrosal crest, the limit between the medial and posterior fossae of the cranial cavity, is very weak in *Colbertia lumbrerense* although it forms a prominent bulge on its medial third.

The internal auditory meatus is ventral and slightly anterior relative to the subarcuate fossa and contains two openings, the *foramen acusticum superius* (dorsal) and the *foramen acusticum inferius* (ventral). The *foramen acusticum superius* contains the primary exit of the facial nerve (the secondary facial foramen and the stylomastoid foramen are the other two passages), it is located dorsally and is smaller than the *foramen acusticum inferius*, which contains passages of the vestibulo-cochlear nerve (Wible, 1990). A thin horizontal ridge separates both foramina (this is nominated as the *crista transversa* in the Nomina Anatomica Veterinaria).

A horizontal ridge crosses the surface of the cerebellar view, from the posterior to the anterior edge, reaching the petrosal crest. This ridge separates the subarcuate fossa from the internal auditory meatus. It is very strong in all the examined petrosals and constitutes a remarkable feature of the cerebellar view.

Squamosal view. A conspicuous vascular groove (running dorsomedially – ventrolaterally over the dorsal and lateral surface of the petrosal) is the only visible feature on this view (Fig. 2.3). Gabbert (2004) mentioned a similar groove for the squamosal view of the petrosal in members of *Toxodontia* and established that “it probably conveyed an emissary vein from the dorsal cerebral vein”. He also mentioned that the groove seems to be directed into the retroarticular foramen. The path of the groove is similar in *Colbertia lumbrense*, but the spatial relationships with the foramina seem to be different than those observed by Gabbert. Therefore, at the moment it is not possible to determine the exact function of this groove in *C. lumbrense*, because many vessels can pass through the squamosal view of the petrosal (Wible *et al.*, 1995).

Mastoid view. This view is only visible (in posterior view) as a laterally compressed posterior process (Fig. 2.4). The posterior end of the process emerges over the medioventral edge of the mastoid foramen. It contacts laterally with the squamosal and medially with the occipital. This occipital exposure of the petrosal is then visible as a small osseous plate, well differentiated from the surrounding elements.

DISCUSSION AND CONCLUSIONS

Cranial characters, particularly those referred to the basicranium, are a valuable contribution to phylogenetic studies (Cifelli, 1993). *Colbertia* is recorded from rocks deposited during the Paleogene, the period when Notoungulata were most diverse (Bond, 1986; Cifelli, 1993; Croft *et al.*, 2008). The morphological study of this and other Paleogene taxa provides many elements for phylogenetic analyses and understanding of the evolutionary history of the order. Nevertheless, data on cranial osteology of Paleogene notoungulates are still scarce.

The basic structural pattern of superficial basicranial osteology in *Colbertia lumbrense* is generalized for a notoungulate. Position and osteological morphology of structures and foramina (*e.g.*, epitympanic sinus, *vagina processus hyoidei*, sphenotympanic fissure) show an arrangement comparable to that observed in other Paleogene notoungulate taxa. In this context, *C. lumbrense* shows some particular

similarities with *Simpsonotus* Pascual, Vucetich, and Fernández, 1978, from Jujuy Province, Argentina (Mealla Formation, Paleocene), the only genus of Henricosborniidae whose cranial osteology is known. These similarities are even more evident with *Simpsonotus praecursor*, the smallest and best known species of the genus. *C. lumbrense* and *S. praecursor* present short and horizontal external auditory meatuses, meatal crests reduced to small ridges on the posterior border of the meatuses, and slender jugular processes. Furthermore, the external inflation that indicates the presence of the epitympanic sinus is virtually absent in *S. praecursor* and *C. lumbrense*. Pascual *et al.* (1978) interpreted this fact as indicative of the absence of the sinus in *S. praecursor*. However, in *C. lumbrense*, although not prominent, the epitympanic sinus is present in the squamosal, and therefore the absence of the inflated morphology is not indicative of the absence of the sinus. It should be noted that the morphology of the ear region of *Simpsonotus* has been considered primitive (Pascual *et al.*, 1978) and that phylogenetic analyses performed on Notoungulata indicate that the henricosborniids are the most basal representatives within the order (Cifelli, 1993).

Some of the features mentioned above (*e.g.*, short meatal crest and auditory meatus) are also found in *Brachystephanus* and *Xenostephanus*. These genera were recently grouped with *Colbertia* in a separate, not formally named family, on the basis of dental synapomorphies (López and Bond, 2003; López, 2008). The globular tympanic bulla of *C. lumbrense* is also a feature shared with these taxa (López, 2008), although the degree of inflation in this species is generally lesser and seems to be variable in different specimens.

Recent phylogenetic analyses carried out on Paleogene notoungulates included in the families of the Typotheria-Hegotheria lineage used some of the above mentioned cranial characters (*e.g.*, bulla size, external auditory meatus length, meatal crest development) and placed *Colbertia lumbrense* as a basal taxon (López, 2008; García López, 2009). The observations derived from the present study and the similarities observed with Paleocene taxa support these hypotheses. According to this arrangement, most basal Paleogene taxa show short and horizontal external auditory meatuses, poorly developed or absent meatal crests, large tympanic bullae, and small epitympanic sinuses. The most derived morphology shows a long and more dorsally directed meatus, strong meatal crest, relatively smaller tympanic bulla, and a larger epitympanic sinus. However, a more detailed survey of cranial features is necessary to include taxa and characters in future phylogenies.

Although the pattern described for *Colbertia lumbrerense* could be considered generalized, some elements studied show distinctive features, particularly the petrosal. Information available on the external morphology of this structure in Notoungulata is even scantier than osteological descriptions of complete skulls. The petrosal is only mentioned in the osteological analysis of *Oldfieldthomasia* Ameghino, 1901, performed by Simpson (1936; 1967), the descriptions of several notoungulates made by Patterson (1936), the work of Gabbert (2004), and the recent contribution of Billet *et al.* (2008). However, analyses by Simpson (1936, 1967) are based on sections of the skull, and the superficial morphology of the petrosal is not described. Patterson (1936), on the other hand, described only the morphology of the promontorium and the position of the vestibular and cochlear fenestrae, and Billet *et al.* (2008) described only the cerebellar side of petrosal of the mesotheriid *Trachyterus alloxus* Billet, de Muizon, and Mamani Quispe, 2008. Gabbert (2004) was the only author that made a more detailed analysis of this bone. One of the most conspicuous differences in the tympanic view between the petrosal of *Colbertia lumbrerense* and the toxodontians described by Gabbert is the superficial morphology and extension of the promontorium. In *C. lumbrerense*, this structure is less prominent than in Toxodontia. Furthermore, there is no ventral process of the *tegmen tympani* and the lateral extension of this area is apparently shorter. In cerebellar view, *C. lumbrerense* presents a bulge on the middle part of the *crista petrosa*, a horizontal ridge that separates the subarcuate fossa from the internal auditory meatus, and a prominent anteromedial end. Neither the Toxodontia nor the mesotheriid *Trachyterus alloxus* show these features. However, they are all present in *Dolichostylodon saltensis*, an oldfieldthomasiid recovered from the same geologic unit as *Colbertia lumbrerense* (Lumbrera Formation) (see García López and Powell, 2009). Considering that *C. lumbrerense* was traditionally included within the Oldfieldthomasiidae, these similarities suggest phylogenetic significance. Nevertheless, the fragmentary knowledge on the petrosal morphology of Paleogene notoungulates does not yet allow clarification of this issue.

Finally, there is no clear indication of the path of the carotid artery in the basicranium of *Colbertia lumbrerense*. A small foramen is present on the posterior wall of the bulla, apparently formed by the ectotympanic and the petrosal. This foramen seems to open exteriorly near the jugular foramen, between this aperture and the jugular process. However, no clear evidence supports the identification of this struc-

ture as a carotid foramen, there is no groove on the surface of the promontorium, and the anterior region of the bulla is not fully exposed in the studied specimens.

ACKNOWLEDGEMENTS

I thank J. Babot and P. Ortiz for their valuable contributions to this paper, and S. Nanni for reading and correcting the English version. G. Rougier and G. López reviewed the manuscript and made valuable comments. I am indebted to A. Kramarz (Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina), J. Powell (Colección de Paleontología de Vertebrados Lillo, Tucumán, Argentina), and M. Reguero (Colección de Paleontología de Vertebrados del Museo de La Plata, La Plata, Argentina) for allowing me to examine fossil material under their care. Financial support was provided by the Consejo de Investigaciones de la Universidad Nacional de Tucumán (CIUNT) and the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET). This work was possible thanks to the institutional support of the Cátedra de Paleontología, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, and Fundación Miguel Lillo.

REFERENCES

- Ameghino, F. 1897. Mammifères crétacés de l'Argentine. (Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*). *Boletín del Instituto Geográfico Argentino* 18: 406–429, 431–521.
- Ameghino, F. 1901. Notices préliminaires sur les ongulés nouveaux des terrains Crétacés de Patagonie. *Boletín de la Academia Nacional de Ciencias en Córdoba* 16: 349–426.
- Arnal, M. and López, G. 2006. La región auditiva de *Brachystephanus postremus* Simpson, Minoprio y Patterson (Notoungulata, Oldfieldthomasiidae?) de la Formación Divisadero Largo, Mendoza, Argentina. *Ameghiniana* 43: 24R.
- Babot, M.J., Powell, J.E., and de Muizon, C. 2002. *Callistoe vincei*, a new Proboryhaenidae (Borhyaenoidea, Metatheria, Mammalia) from the Early Eocene of Argentina. *Geobios* 35: 615–629.
- Billet, G., de Muizon, C., and Mamani Quispe, B. 2008. Late Oligocene mesotheriids (Mammalia, Notoungulata) from Salla and Lacayani (Bolivia): implications for basal mesotheriid phylogeny and distribution. *Zoological Journal of the Linnean Society* 152: 153–200.
- Billet, G., Patterson, B., and de Muizon, C. 2009. Craniodental anatomy of late Oligocene archaehyracids (Notoungulata, Mammalia) from Bolivia and Argentina and new phylogenetic hypotheses. *Zoological Journal of the Linnean Society* 155: 458–509.
- Bloch, J.I. and Silcox, M.T. 2001. New basicrania of Paleocene-Eocene *Ignacius*: re-evaluation of the Plesiadapiform-Dermopterian link. *American Journal of Physical Anthropology* 116: 184–198.
- Bond, M. 1981. Un nuevo Oldfieldthomasiidae (Mammalia, Notoungulata) del Eoceno Inferior (Fm. Lumbrera, Grupo Salta) del NW argentino. *2º Congreso Latinoamericano de Paleontología* (Porto Alegre), *Anais* 2: 521–536.
- Bond, M. 1986. Los ungulados fósiles de Argentina: evolución y paleoambientes. *4º Congreso argentino de Paleontología y Bioestratigrafía* (Mendoza), *Actas* 2: 173–185.
- Bond, M. and López, G.M. 1993. El primer Notohippidae (Mammalia, Notoungulata) de la Formación Lumbrera (Grupo Salta) del Noroeste Argentino. Consideraciones sobre la sistemática de la Familia Notohippidae. *Ameghiniana* 30: 59–68.
- Bond, M. and Vucetich, M.G. 1983. *Indalecia grandensis* gen. et sp. nov. del Eoceno temprano del Noroeste Argentino, tipo de una nueva subfamilia de los Adianthidae (Mammalia, Litopterna). *Revista de la Asociación Geológica Argentina* 38: 107–117.
- Cifelli, R.L. 1993. The phylogeny of the native South American ungulates. In: F.S. Szalay, M.J. Novacek y M.C. McKenna (Eds.). *Mammal Phylogeny, vol 2: Placentals*. Springer-Verlag, New York, p. 195–216.
- Croft, D.A., Flynn, J.J., and Wyss, A.R. 2008. The Tinguiririca Fauna of

- Chile and the early stages of "modernization" of South American mammal faunas. *Arquivos do Museu Nacional, Rio de Janeiro* 66: 191–211.
- del Papa, C.E. 2006. Estratigrafía y paleoambientes de la Formación Lumbra, Grupo Salta, Noroeste Argentino. *Revista de la Asociación Geológica Argentina* 61: 313–327.
- del Papa, C., Kirschbaum, A., Powell, J., Brod, A., Hongn, F., and Pimentel, M. 2010. Sedimentological, geochemical, and paleontological insights applied to continental omission surfaces: a new approach for reconstructing an Eocene foreland basin in NW Argentina. *Journal of South American Earth Sciences* 29: 327–345.
- Evans, H.E. and Christensen, G.C. 1979. *Miller's Anatomy of the Dog*. Second Edition. W.B. Saunders Company. Philadelphia, London, Toronto, 1181 p.
- Gabbert, S.L. 2004. The basicranial and posterior cranial anatomy of the families of the Toxodontia. *Bulletin of the American Museum of Natural History* 285: 177–190.
- García López, D.A. 2006. El basicráneo de *Colbertia lumbrense* Bond, 1981 (Notoungulata, Oldfieldthomasiidae?). *9º Congreso Argentino de Paleontología y Bioestratigrafía* (Córdoba), *Libro de resúmenes*: 128.
- García López, D.A. 2009. [Notoungulados del Paleógeno del noroeste argentino: morfología y evolución. Tesis Doctoral. Universidad Nacional de Tucumán, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Tucumán, Argentina, 338 p. Unpublished.]
- García López, D.A., and Powell, J.E. 2009. Un nuevo Oldfieldthomasiidae (Mammalia: Notoungulata) del Paleógeno de la Provincia de Salta, Argentina. *Ameghiniana* 46: 153–164.
- López, G.M. 2008. [Los ungulados de la Formación Divisadero Largo (Eoceno Inferior?) de la provincia de Mendoza, Argentina: sistemática y consideraciones bioestratigráficas. Tesis Doctoral, Universidad Nacional de La Plata, Facultad de Ciencias Naturales y Museo, La Plata, Argentina, 415 p. Unpublished.]
- López, G.M. and Bond, M. 2003. Una nueva familia de ungulados (Mammalia, Notoungulata) del Paleógeno sudamericano. *Ameghiniana* 40: 60R.
- MacIntyre, G.T. 1972. The trisulcate petrosal pattern of mammals. In: T. Dobzhansky, M.K. Hecht, and W.C. Steere (Eds.), *Evolutionary biology* 6, Apple-Century-Crofts, New York, p. 275–303.
- MacPhee, R.D.E. 1981. Auditory regions of primates and eutherian insectivores. Morphology, ontogeny, and character analysis. *Contributions to Primatology* 18: 1–282.
- Moore, W.J. 1981. *The mammalian skull*. Cambridge University Press. Cambridge, 369 p.
- Novacek, M.J. 1993. Patterns of Diversity in the Mammalian Skull. In: J. Hanken y B.K. Hall (Eds.), *The skull. Volume 2. Patterns of structural and systematic diversity*, The University of Chicago Press, Chicago and London, p. 438–545.
- Pascual, R., Vucetich, M. R., and Fernández, J. 1978. Los primeros mamíferos (Notoungulata, Henricosborniidae) de la Formación Mealla (Grupo Salta, Subgrupo Santa Bárbara). Sus implicancias filogenéticas, taxonómicas y cronológicas. *Ameghiniana* 15: 367–390.
- Pascual, R., Bond, M., and Vucetich, M.G. 1981. El Subgrupo Santa Bárbara (Grupo Salta) y sus vertebrados, cronología, paleoambientes y paleobiogeografía. *8º Congreso Geológico Argentino* (San Luis), *Actas* 3: 743–758.
- Patterson, B. 1932. The auditory region of the Toxodontia. *Geological Series of the Field Museum of Natural History* 6: 1–27.
- Patterson, B. 1936. The internal structure of the ear in some notoungulates. *Geological Series of the Field Museum of Natural History* 6: 199–227.
- Paula Couto, C. de. 1952. Fossil Mammals of the Beginning of the Cenozoic in Brazil. Notoungulata. *American Museum Novitates* 1568: 1–16.
- Price, L.I. and Paula Couto C. de. 1950. Vertebrados terrestres do Eoceno na bacia calcárea de Itaboraí. *2º Congresso Panamericano de Engenharia de Minas e Geologia* (Rio de Janeiro), *Anais* 3: 149–173.
- Rougier, W.R., Wible, J.R., and Hopson, J.A. 1992. Reconstruction of the cranial vessels in the Early Cretaceous mammal *Vincelestes neuquenianus*: implications for the evolution of the mammalian cranial vascular system. *Journal of Vertebrate Paleontology* 12: 188–216.
- Rusconi, C. 1946. Nuevo mamífero fósil de Mendoza. *Boletín Paleontológico de Buenos Aires* 20: 2.
- Simpson, G.G. 1932. Skulls and brains of some mammals from the *Notostylops* beds of Patagonia. *American Museum Novitates* 578: 1–11.
- Simpson, G.G. 1936. Structure of a primitive notoungulate cranium. *American Museum Novitates* 824: 1–31.
- Simpson, G.G. 1948. The beginning of the Age of Mammals in South America. Part 1. Introduction. Systematics: Marsupialia, Edentata, Condylarthra, Litopterna and Notioprogonia. *Bulletin of the American Museum of Natural History* 91: 1–232.
- Simpson, G.G. 1967. The beginning of the Age of Mammals in South America. Part 2. Systematics: Notoungulata, concluded (Tyotheria; Hegetotheria, Toxodonta, Notoungulata *incertae sedis*); Astrapotheria Trigonostylopoidea; Pyrotheria; Xenungulata; Mammalia *incertae sedis*. *Bulletin of the American Museum of Natural History* 137: 1–259.
- Simpson, G.G., Minoprio, J.L., and Patterson, B. 1962. The mammalian fauna of the Divisadero Largo Formation, Mendoza, Argentina. *Bulletin of the Museum of Comparative Zoology at Harvard College* 127: 237–303.
- Vucetich, M.G. 1980. Un nuevo Notostylopidae (Mammalia, Notoungulata) proveniente de la Formación Lumbra (Grupo Salta) del noroeste argentino. *Ameghiniana* 17: 363–372.
- Wible, J.R. 1990. Petrosals of Late Cretaceous marsupials from North America, and a cladistic analysis of the petrosal in therian mammals. *Journal of Vertebrate Paleontology* 10: 183–205.
- Wible, J.R., Novacek, M.J., and Rougier, G.W. 2004. New data on the skull and dentition in the Mongolian Late Cretaceous eutherian mammal *Zalambdalestes*. *Bulletin of the American Museum of Natural History* 281: 1–144.
- Wible, J.R., Rougier, G.W., Novacek, M.J., and Asher, R.J. 2009. The eutherian mammal *Maelestes gobiensis* from the late Cretaceous of Mongolia and the phylogeny of Cretaceous Eutheria. *Bulletin of the American Museum of Natural History* 327: 1–123.
- Wible, J.R., Rougier, G.W., Novacek, M.J., McKenna, M.C., and Dashzeveg, D. 1995. A mammalian petrosal from the Early Cretaceous of Mongolia: implications for the evolution of the ear region and mammalian interrelationships. *American Museum Novitates* 3149: 1–19.

Recibido: 4 de septiembre de 2009

Aceptado: 31 de mayo de 2010