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Juliana Sterli^a & Marcelo S. De La Fuente^b

^a Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100 Trelew, Chubut Province, Argentina

^b CONICET and Museo de Historia Natural de San Rafael, Parque Mariano Moreno s/n, 5600 San Rafael, Mendoza Province, Argentina

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RE-DESCRIPTION AND EVOLUTIONARY REMARKS ON THE PATAGONIAN HORNED TURTLE *NIOLAMIA ARGENTINA* AMEGHINO, 1899 (TESTUDINATA, MEIOLANIIDAE)

JULIANA STERLI^{*1} and MARCELO S. DE LA FUENTE²

¹Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100 Trelew, Chubut Province, Argentina, jsterli@mef.org.ar;

²CONICET and Museo de Historia Natural de San Rafael, Parque Mariano Moreno s/n, 5600 San Rafael, Mendoza Province, Argentina, mdelafu@gmail.com

ABSTRACT—The main objective of this paper is to undertake a detailed re-description of the neotype (skull and lower jaw) and the referred material (postcranial remains) of *Niolamia argentina*. Additional preparation of this material has revealed previously unrecognized details of the cranial and postcranial skeleton, including the recognition of additional cranial scales, bone sutures, and foramina, the presence of a distinct ornamentation on the skull roof, and the identification of several new inner skull structures. Importantly, the additional preparation shows detailed carotid artery anatomy: the entrance of the carotid artery lies posteriorly in the pterygoids, runs anteriorly and bifurcates into the cerebral and palatine arteries within the basisphenoid, and is not covered ventrally by the pterygoids. In addition, the pterygoids are placed in a ventral position with respect to the basisphenoid and an intrapterygoid slit, a character diagnostic of Meiolaniidae, is present. We corroborate that *Crossochelys corniger* is a junior synonym of *Nio. argentina*. Following our preferred phylogenetic hypothesis, South American and Australian taxa related to or belonging to Meiolaniidae and *Mongolochelys efremovi* from the Upper Cretaceous of Mongolia form a monophyletic group, implying that the origin and diversification of this lineage predated the complete break up of Pangea in the Early to Middle Jurassic. The presence of a ghost lineage between this clade and Cryptodira, extending from the Middle Jurassic to the Early Cretaceous, supports this assessment.

INTRODUCTION

Meiolaniids are a peculiar and bizarre group of extinct turtles bearing cranial horns and frills, caudal rings, and tail clubs, and they were restricted to South America (?Late Cretaceous to Eocene) and Australasia (Oligocene to Holocene). Since the discovery of the first meiolaniid, *Meiolania platyceps* Owen, 1886, the relationships of meiolaniids with other turtles have been controversial. They have been considered to be related to both living groups of turtles, Pleurodira (Boulenger, 1887, 1889) and Cryptodira (Huxley, 1887; Baur, 1889a, 1889b; Gaffney et al., 1991; Gaffney, 1996), and even to lie outside the crown group (Joyce, 2007; Sterli, 2010). The meiolaniid record from South America is restricted to Patagonia, Argentina. Turtle remains closely related to or referred to Meiolaniidae in Patagonia are known from Lower Cretaceous to Eocene rocks. The related species *Chubutemys copelloi* Gaffney et al., 2007, is from the Aptian of the Cerro Barcino Formation (Gaffney et al., 2007) and *Patagoniaemys gasparinae* Sterli and de la Fuente, 2011, is known from the Campanian–Maastrichtian of the La Colonia Formation (Sterli and de la Fuente, 2011). The remaining South American Cretaceous meiolaniid turtles are fragmentary postcranial specimens, including appendicular bones, one isolated horn, and caudal vertebrae or carapace plates, all of which are tentatively assigned to Meiolaniidae. These fragmentary remains are known from the Campanian–Maastrichtian Allen, La Colonia, and Los Alamitos formations (Broin, 1987; Broin and de la Fuente, 1993; Gasparini and de la Fuente, 2000). Another meiolaniid allegedly from the Cretaceous is *Niolamia argentina* Ameghino, 1899 (Ameghino, 1899, 1906; Woodward, 1901), but its exact age and geographic location are unknown (see below). Finally, meiolaniid material

from the Eocene is represented by several specimens, including a skull identified as *Crossochelys corniger* Simpson, 1937, from the Cañadón Hondo locality, a tail ring identified as Meiolaniidae indet. from Mr. Acosta Fields, and several fragments of indeterminate meiolaniid from the Cañadón Vaca locality. All Eocene material is from the Sarmiento Formation and is from the Casamayoran South American Land Mammal Age (SALMA) (Simpson 1937, 1938; Escribano and Abril, 1987; de la Fuente and Fernández, 1992; Broin and de la Fuente, 1993).

The *Nio. argentina* specimens from the La Plata Museum (MLP 26–40, 26–41, 26–42, 26–43, and 26–44) have an enigmatic history and little is known about where and by whom they were found or the age of the sediments. At the time of the discoveries, in the 1890s, two competing groups, F. Ameghino's and F. P. Moreno's teams, were doing field work in Patagonia, and they attempted to hide information from each other, resulting in the loss of records. The first mention of *Nio. argentina* was made by Florentino Ameghino (1899), in which he coined the species name, but he neither designated a holotype, diagnosed the species, nor figured the specimen. This specimen is thought to have been discovered by his brother Carlos Ameghino in the ?Cretaceous–Paleogene Guaranitic Formation in the region of the Sehuen and Chubut rivers (Ameghino, 1899). Later that year, the director of La Plata Museum, Francisco P. Moreno (1899), communicated Santiago Roth's discovery of a tail ring, carapace, and skull remains of a new turtle “pertaining to a form like the chelonian of the Pleistocene of Queensland, described by Owen [meaning *Meiolania platyceps*]” (Moreno, 1899:25). Moreno's (1899) short communication was the first to show a picture of the skull and lower jaw of *Nio. argentina*. Two years later, Woodward (1901) published a short anatomical description with pictures of the tail ring, partial carapace, both scapulae, skull, and lower jaw of the turtle previously photographed by Moreno (1899). It is interesting to note the nomenclatural confusion around the species

^{*}Corresponding author.

name of Roth's specimen. Woodward (1901:176) pointed out "It may be appropriately named, following Ameghino, *Miolania* [sic] *argentina*." There are two mistakes in the binomen. First, the genus name proposed by Ameghino (1899) was *Niolamia*, not *Miolania*. Second, it is apparent that Moreno (1899) and Woodward (1901) were referring to the Australian meiolaniid genus *Meiolania* Owen, 1886, but simply misspelt it as *Miolania*. The nomenclatural confusion was resolved when Simpson (1938) proposed the skull described by Woodward (1901) and housed in the Museo de La Plata as the neotype of *Niolamia argentina*; an assignment followed by subsequent authors (Gaffney, 1983, 1996; de la Fuente and Fernández, 1992; Sterli, 2010), and in the present contribution.

The confusion regarding the locality and age of *Nio. argentina* also stems from the dispute between Moreno and Ameghino. Ameghino (1899:10) mentions that the turtle remains came from the "Formación guaraníca del Sehuen y del Chubut" (Guaranitic Formation from Sehuen and Chubut), but Woodward (1901) mentions that Roth collected extinct reptiles in association with mammals from the "red sandstone, supposed to be of Cretaceous age" (Woodward, 1901:169). To make matters even more confusing, Ameghino (1906) pointed out that Roth's locality is located three kilometers northwest of Colhué-Huapi Lake (now known as Muster Lake) in outcrops yielding a *Notostylops* fauna, which is identified within the Casamayoran SALMA (Middle Eocene). The Museo de La Plata collection label accompanying the remains of *Nio. argentina* mentions the locality as Cañadón Blanco and the age as Cretaceous. However, the exact location of the Cañadón Blanco locality found by Roth cannot be determined, other than that it is somewhere within Chubut Province, Argentina. Furthermore, the mammalian fauna found at the Cañadón Blanco locality indicates that the locality is Eocene to Early Oligocene in age (45–22 Ma) (Simpson, 1967; Reguero et al., 2003). Further preparation of an *Nio. argentina* skull allowed us to recover sediments from its nasal cavity. The sediment is a white, poorly consolidated tuff, inconsistent with Woodward's (1901:169) claim that the material was found in a Cretaceous "red sandstone." However, the Sarmiento Formation (25 Ma; Eocene–Miocene) (Bellosi, 2010) in Chubut Province is dominated by a similar white tuff, indicating an Eocene–Miocene age for the *Nio. argentina* neotype.

Additional meiolaniid remains from Patagonia include the holotype of the Eocene *Crossochelys corniger* collected by the American Museum of Natural History during the Scarritt Patagonian expeditions at the Cañadón Hondo locality, Chubut Province (Simpson, 1937, 1938). These turtle remains were found with the crocodylomorph *Sebecus icaeorhinus* Simpson, 1937, birds, mammals, and other vertebrates in the Sarmiento Formation (Simpson, 1937). In the same paper in which he described *C. corniger*, Simpson (1938) proposed that the skull housed in the Museo de La Plata and described by Woodward (1901) should be regarded as the neotype of *Nio. argentina*. There is no mention of meiolaniid turtles from Patagonia for the next 50 years until Gaffney's (1983) detailed descriptions of several South American meiolaniid skulls, including *C. corniger*, but excluding *Nio. argentina*. Later, in Gaffney's (1996) review of Meiolaniidae, he proposed that *C. corniger* is a juvenile of *Nio. argentina*, making the former a junior synonym of the latter.

The main objective of this paper is to present detailed descriptions of the neotype and referred material of *Nio. argentina*. A detailed description of this material is important because it is the most complete meiolaniid presently known from Patagonia. Furthermore, Gaffney states (1996:75), "...since Woodward, no-one (including the present author) working on meiolaniids has reexamined the type skull of *Niolamia argentina*. Simpson worked under the further handicap of using Anderson's skull reconstruction for comparative purposes and not actual specimens of *Meiolania platyceps*." Thus, a description of this important material is long

overdue. In addition, the phylogenetic position of *Nio. argentina* among meiolaniids and of Meiolaniidae among remaining turtles are also discussed. These analyses indicate the presence of long ghost lineages (Middle Jurassic to Early Cretaceous) between the clade leading to Meiolaniidae and Cryptodira (sensu Joyce et al., 2004). This long lineage implies that the differentiation of meiolaniid-like taxa and other clades predated the breakup of Laurasia and Gondwana.

Institutional Abbreviations—AM, Australian Museum, Sydney, Australia; AMNH, American Museum of Natural History, New York, U.S.A.; MLP, Museo de La Plata, La Plata, Argentina.

Anatomical Abbreviations—A–G, I₁–I₃, J₁, J₂, K, X–Z, horns and scales; **acp**, acromial process; **ani**, apertura narium interna; **asa**, articular surface for articular; **ass**, articular surface for splenial; **bo**, basioccipital; **bs**, basisphenoid; **cc**, canalis cavernosus; **CER**, cervical scale; **cl**, cavum labyrinthicum; **co**, condylus occipitalis; **com**, condylus mandibularis; **cp**, crista pterygoidea; **cr**, cartilaginous rider; **csa**, canalis semicircularis anterior; **csH**, canalis semicircularis horizontalis; **cso**, crista supraoccipitalis; **ct**, cavum tympani; **den**, dentary; **epi**, epipterygoid; **exo**, exoccipital; **facnv** (VII), foramen anterior canalis N. vidiani; **fccA**, foramen carotici cerebri anterior; **fccp**, foramen carotici cerebri posterior; **feng**, foramen externum N. glossopharyngei; **fja**, foramen jugulare anterior; **fjp**, foramen jugulare posterior; **fm**, foramen magnum; **fna** (VI), foramen N. abducentis; **fnh** (XII), foramen N. hypoglossi; **fon**, foramen orbito-nasale; **fpcci**, foramen posterior canalis carotici interni; **fpp**, foramen palatinum posterior; **fr**, frontal; **fst**, foramen stapedio-temporale; **g**, glenoid cavity; **ha**, hiatus acusticus; **ica**, incisura columella auris; **ipts**, intrapterygoid slit; **lar**, labial ridge; **lir**, lingual ridge; **M**, marginal scale; **mx**, maxilla; **na**, nasal; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pf**, prootic foramen; **PL**, pleural scale; **pmx**, premaxilla; **po**, postorbital; **pr**, prootic; **pra**, prearticular; **prf**, prefrontal; **pt**, pterygoid; **pto**, processus trochlearis oticum; **qj**, quadratojugal; **qu**, quadrate; **rlp**, recessus labyrinthicus prooticus; **SC**, supracaudal scale; **so**, supraoccipital; **sq**, squamosal; **ssc**, surface for suprascapular cartilage; **sur**, surangular; **V**, vertebral scale; **vnc**, vidian nerve canal; **vo**, vomer.

SYSTEMATIC PALEONTOLOGY

TESTUDINATA Klein, 1760 (sensu Joyce, Parham, and Gauthier, 2004)

MEIOLANIIDAE Boulenger, 1887

NIOLAMIA Ameghino, 1899

Type Species—*Niolamia argentina* Ameghino, 1899.

Emended Diagnosis—Same as for type species.

NIOLAMIA ARGENTINA Ameghino, 1899

(Figs. 1–13)

Crossochelys corniger Simpson, 1938: pp. 222–241; figs. 1–9.

Neotype—MLP 26–40, a skull (Simpson, 1938). We consider a lower jaw housed in the same collection (no number) to be part of the neotype because the occlusion with the upper jaw is perfect.

Referred Specimens—MLP 26–41, left scapula; MLP 26–42, right scapula; MLP 26–43, carapace remains; MLP 26–44, tail ring; AMNH 3161, disarticulated skull remains assigned originally to *Crossochelys corniger* (Simpson, 1938; see Discussion).

Emended Diagnosis—*Niolamia argentina* belongs to the clade Testudinata because it has a complete shell enclosing the pectoral girdle. It differs from other stem Testudines by the presence of an extensive squamosal/supraoccipital contact and an extensive contribution of the supraoccipital to the dorsal skull roof. It can be distinguished from *Mongolochelys efremovi* Khosatzky, 1997, in that squamosal and supraoccipital bones form posterior and

posterolateral horns, and the medial plate of pterygoids is separated ventrally from the basisphenoid to form the intrapterygoid slit. It is differentiated from other meiolaniids by: a scale A that is significantly larger than in any other meiolaniid and in contact with scale X; D scales not contacting on the midline, separated by a large scale X; scale H absent; scale D in contact with scale F; triturating surface with only two ridges (labial and lingual ridges); undivided apertura narium externa and nasomaxillary sinus absent; spines on the posterolateral border of the carapace present; supracaudal scale present; broad pygal embayment. Differs from *Meiolania platyceps* Owen, 1886, in that: the triturating surface is wider in the anterior (premaxilla) and posterior ends and narrower in the medial portion of the maxilla; the lingual ridge is expanded and forms a wide surface; pterygoid not covering foramen caroticum basisphenoidale; the quadrate participates in the foramen stapedio-temporale; nasal bones projecting beyond rest of skull; scale B projecting posterolaterally, and not recurved as in *M. platyceps*; scale D area protruding more than in *M. platyceps*; scale X rectangular in *Nio. argentina*, rhomboidal in *M. platyceps* and *Warkalanina carinaminor* Gaffney et al., 1992. Similar to *Ninjemys oweni* (Woodward, 1888) in: having scales A–C forming a large shelf at back of skull; scale X not separating G scales in adults; Y scale partially separating G scales anteriorly; tail rings closed ventrally; but differing from *Nin. oweni* in the development of a more extensive area covered by scales A–C in *Nio. argentina*.

Distribution—Cañadón Blanco (following MLP collection label information) and Cañadón Hondo localities, Chubut Province, Argentina. Late Cretaceous (following MLP collection information and Woodward, 1901) or Paleogene (according to the age assigned to the mammalian fauna found in Cañadón Blanco locality [Simpson, 1967] and the presence of a white tuff commonly found in the Sarmiento Formation in the nasal cavity of the neotype).

MATERIALS AND METHODS

The specimens (MLP 26–40, 26–41, 26–42, 26–43, and 26–44) were covered by asphalt and glued with mastic that completely obscured the cranial sutures, ornamentation, and foramina. Asphalt and mastic were mechanically removed using an air scribe and other tools. In addition, the basicranium was separated from the rest of the skull.

DESCRIPTION

Skull

Description of the skull morphology is based primarily on MLP 26–40 and, where specified, complemented with information from AMNH 3161.

Skull Roof—Our preparation of the neotype (MLP 26–40) of *Niolamia argentina* revealed previously unknown details of the ornamentation of the dermatocranium and of some postcranial remains. The dermal bones of the skull, lower jaw, carapace, and the tail ring have a fine ornamentation formed by small pits (Figs. 1A, 2–4, 12, 13). On some parts of the skull, for example in the posterior part, the pits become larger than the anterior ones (Figs. 1A, 2, 3). On the lower jaw, the outer surface of the dentary is heavily pitted and grooved (Fig. 4) as in *Meiolania platyceps* (Gaffney, 1983).

In previous reports on the anatomy of *Nio. argentina* there was no mention of skull sutures: Woodward (1901) recognized bones based on their topological positions, but did not identify sutures between them. As in *M. platyceps*, only a few sutures are recognized in the adult skull roof of *Nio. argentina* (Figs. 1A, 2A, 3, 5). The absence of sutures might correspond to the fusion of the sutures as result of a highly ankylosed skull. The only recognized sutures of the adult skull

roof are the midline sutures between the premaxillae, nasals, and frontals, and the suture between the prefrontal and the postorbital (Figs. 1A, 2A, 3). In ventral view, however, more sutures are recognized. The sutures between supraoccipital-parietal, parietal-frontal, frontal-postorbital, frontal-prefrontal, prefrontal-postorbital, vomer-prefrontal, palatine-maxilla, and palatine-vomer are evident, as well as the medial suture between the frontals and parietals (Fig. 5). In the juvenile specimen of *Nio. argentina* (AMNH 3161), the sutures are open; consequently, the bones of the skull are discrete and not tightly sutured or fused one to the other as in the adult specimen. This condition allows us to follow the sutures among frontals, parietals, squamosals, supraoccipital, prootic, quadrate, and pterygoid.

The medial suture between both nasals (MLP 26–40) is seen in the anterior part of the skull in dorsal view (Figs. 1A, 2A, 3). The sutures with the remaining elements are not seen in the adult specimen. However, the suture with the frontal could be inferred in the juvenile specimen AMNH 3161. This suture extends almost perpendicular to the sagittal plane. The nasal dorsally surrounds the apertura narium externa. As was mentioned by Woodward (1901) and Gaffney (1983, 1996), *Nio. argentina* has a single narial opening (Fig. 2A), as opposed to the divided one in *M. platyceps* or *Ninjemys oweni*. As in *M. platyceps*, there is a distinctive bony lip recessed slightly from the margin of the apertura narium externa in *Nio. argentina*. This bony lip is closed ventrally and likely built up of premaxillary bones. The nasals project slightly anteriorly beyond the anterior margin of the premaxilla (Fig. 3), but not as much as in *Nin. oweni*. The nasals are covered by scale Z (Figs. 1A, 2A, 3). The nasals form the roof of the fossa nasalis and associated structures (i.e., paranasal sinuses) that, as in *M. platyceps*, form a well-developed cavity in *Nio. argentina*. The nasomaxillary sinus described for *M. platyceps* (Gaffney, 1983) is not present in *Nio. argentina*.

The prefrontal of *Nio. argentina* (MLP 26–40) has, as in many turtles, two portions: a horizontal portion that forms part of the skull roof and a vertical portion. The horizontal portion forms the anterodorsal rim of the orbit, which is completed posteriorly by the postorbital (Figs. 1A, 2A, 3, 5). In *Nio. argentina*, as in most turtles, the horizontal plates of the prefrontal do not meet in the midline because they are separated by the frontals. The prefrontal-postorbital suture is seen in dorsal view and it extends perpendicular to the dorsal orbital margin. In ventral view, the posteromedial contact with the frontal is seen. The vertical flange forms the descending process that separates the fossa nasalis from the fossa orbitalis and forms the posterior rim of the apertura narium interna. As in *M. platyceps* and other turtles (i.e., stem and cryptodiran turtles), the descending process contacts the vomer medially, forming the border of the fissura ethmoidalis, and the palatine laterally (Figs. 1B, 5). The suture with the vomer is recognized on the right side, but the suture with the maxilla is not seen (Figs. 1B, 5). However, it is clear that the descending process reached the maxilla anteroventrally. The outline of the foramen orbito-nasale can be seen in the right ascending process, but its shape and the bones that form the margin of the foramen are difficult to determine (Figs. 1B, 5).

The frontal forms part of the anterior portion of the skull roof. The medial suture between both frontals is seen in *Nio. argentina*, extending along the midline (MLP 26–40 and AMNH 3161; Figs. 1A, 2A, 5). The sutures with other bones are not seen in dorsal view in the adult skull, but they are visible in ventral view (Fig. 5) and in the juvenile skull (AMNH 3161). The frontal contacts the nasal anteriorly, the prefrontal and the postorbital laterally, and the parietal posteriorly (Fig. 5). The frontal of *Nio. argentina*, as in *M. platyceps*, is excluded from the orbit (Fig. 1A). The frontal forms the roof of the sulcus olfactorius, the posterior portion of the fissura ethmoidalis, and the posterior part of the fossa nasalis (Fig. 5). On the ventral surface of the frontal of *Nio. argentina* a low parasagittal ridge separating the sulcus

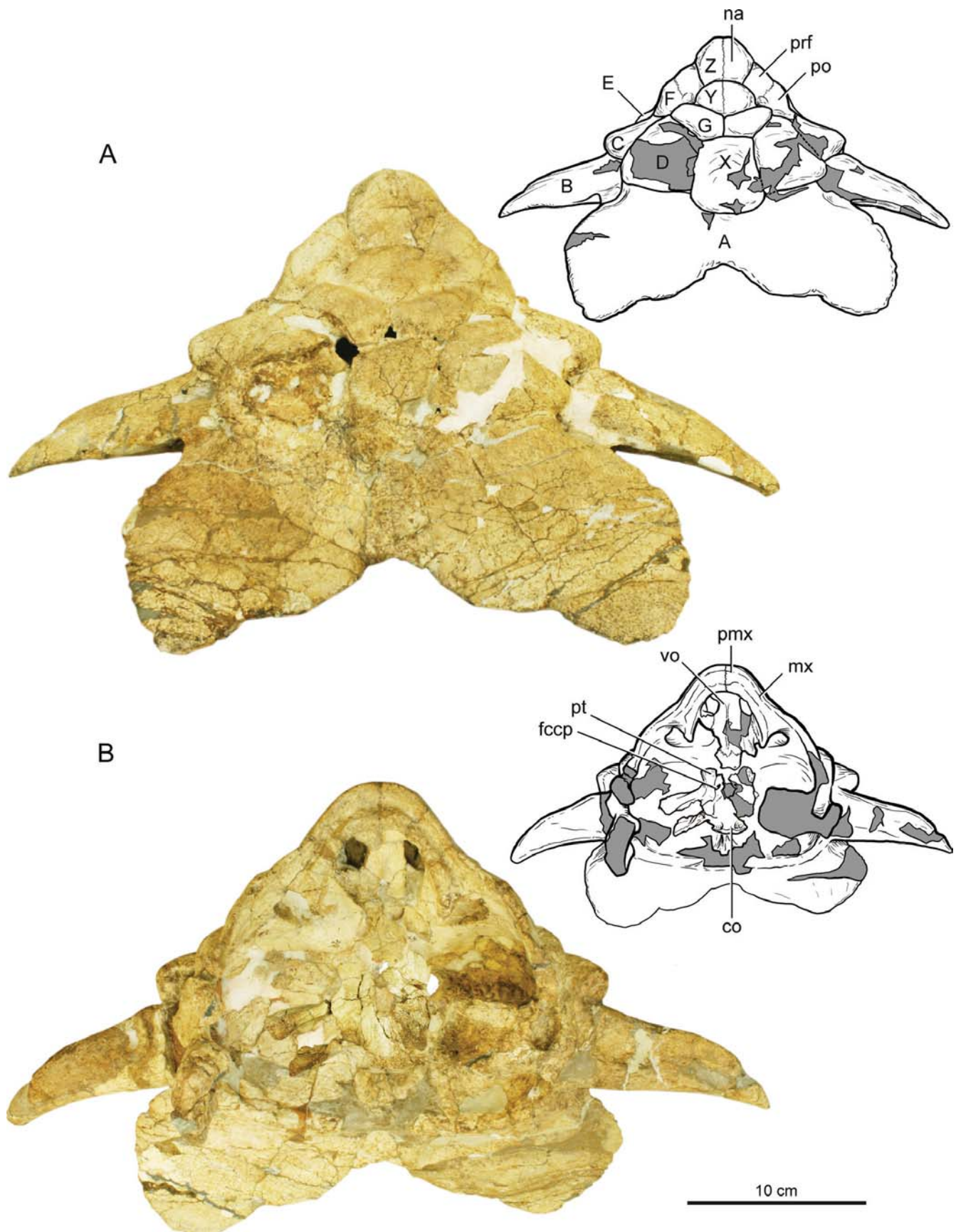


FIGURE 1. *Niolamia argentina* Ameghino, 1899. MLP 26–40, skull. Photographs and interpretive drawings of **A**, dorsal, and **B**, ventral views. (Color figure available online).

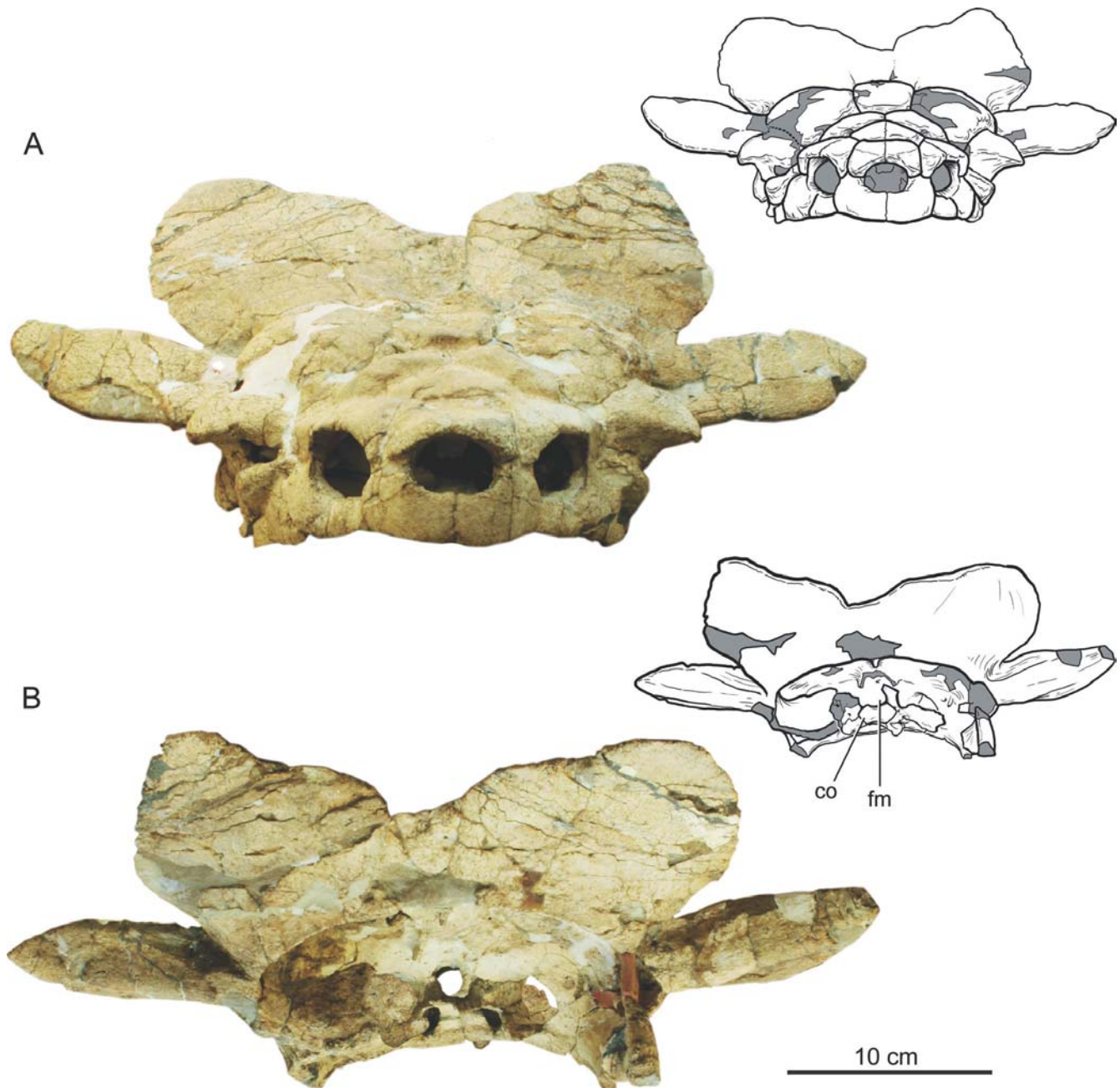


FIGURE 2. *Niolamia argentina* Ameghino, 1899. MLP 26–40, skull. Photographs and interpretive drawings of **A**, anterior, and **B**, posterior views. (Color figure available online).

olfactorius and the fossa orbitalis can be seen (Fig. 5). This ridge is almost non-existent near the contact with the parietal (contrary to the condition seen in *M. platyceps*) and becomes taller anteriorly near the contact with the prefrontal where they form the posterior portion of the fissura ethmoidalis. The fossa nasalis of *Nio. argentina* is a large structure and the sulcus olfactorius is very reduced (Fig. 5), as in *M. platyceps* and testudinids. Dorsally the frontals are covered, at least, by the unpaired scale Y (Figs. 1A, 3).

The parietal of *Nio. argentina* (MLP 26–40; Figs. 1, 2A, 3, 5) has, as in all turtles, a horizontal and a vertical plate (Gaffney, 1979a). The horizontal plate forms part of the skull roof and the

dorsal part of the cavum cranii, whereas the vertical plate forms the processus inferior parietalis, which laterally closes the cavum cranii and might close the foramen N. trigemini in a manner similar to that seen in some turtles (Gaffney, 1979a). Although the sutures of the parietal bone are not discernible in dorsal view of the adult skull of *Nio. argentina*, some of them are visible in ventral view (Fig. 5), including the medial suture between both parietals, the anterior suture with the frontal, the lateral suture with the postorbital, and the posterior suture with the supraoccipital. In the juvenile skull (AMNH 3161), the parietal-squamosal suture is also visible in the posterolateral corner of the skull. As in *M. platyceps*, the suture between the parietal and the supraoccipital

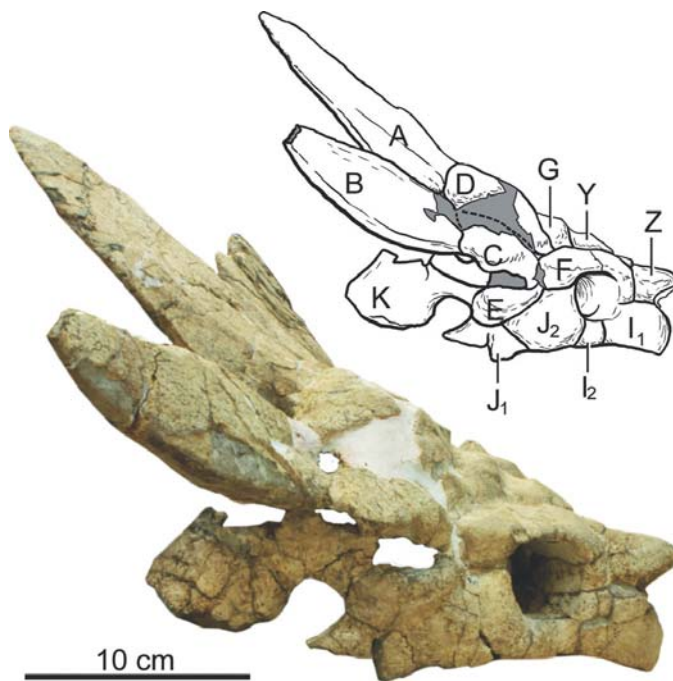


FIGURE 3. *Niolamia argentina* Ameghino, 1899. MLP 26–40, skull. Photograph and interpretive drawing of right lateral view. (Color figure available online).

of *Nio. argentina* is an overlapping suture, with the supraoccipital situated below the parietals. The descending process of the parietal is broken on both sides of *Nio. argentina*, and as a result, the extension and whether it closed the foramen N. trigemini cannot be determined. The ventral surface of the parietals of *Nio. argentina* is preserved and the dorsal region of the encephalon can be inferred (Fig. 5). In the posterior-most part of the parietals, there is a concavity that can be correlated with the convexity identified as the cartilaginous 'rider' of *Bothremys* sp. and, in the endocasts of *Plesiobaena antiqua*, the convexity that housed the cartilaginous anterior end of the supraoccipital (Gaffney, 1977, 1982). Anterior to the 'rider' the encephalon of *Nio. argentina* expands laterally (Fig. 5). This expansion could have housed the cerebral hemispheres in life (Gaffney, 1982). *Niolamia argentina* has no temporal fenestrae in the adult skull. Simpson (1938) interpreted *C. corniger* as having temporal fenestrae; however, considering the juvenile aspect of AMNH 3161, we believe these fenestrae are open sutures among supraoccipital, squamosal, and parietal bones in early stages of ontogeny that are later closed in adult specimens. Although some specimens of *M. platyceps* have some kind of temporal fenestra, Gaffney (1983) considered this intraspecific variation exaggerated by post-mortem damage.

Unfortunately no sutures of the bones forming the cheek margin are visible (Fig. 3). However, it is clear that in *Nio. argentina* the cheek margin is continuous, not showing any kind of emargination as seen in other meiolaniids (Fig. 3). Comparisons of the cheek region of *Nio. argentina* with *M. platyceps* (Gaffney, 1983) suggest that the jugal (MLP 26–40; Figs. 1B, 2A, 3, 5) could be located between the orbit and the cavum tympani and likely formed the posteroventral rim of the orbit. Like the jugal, the sutures of

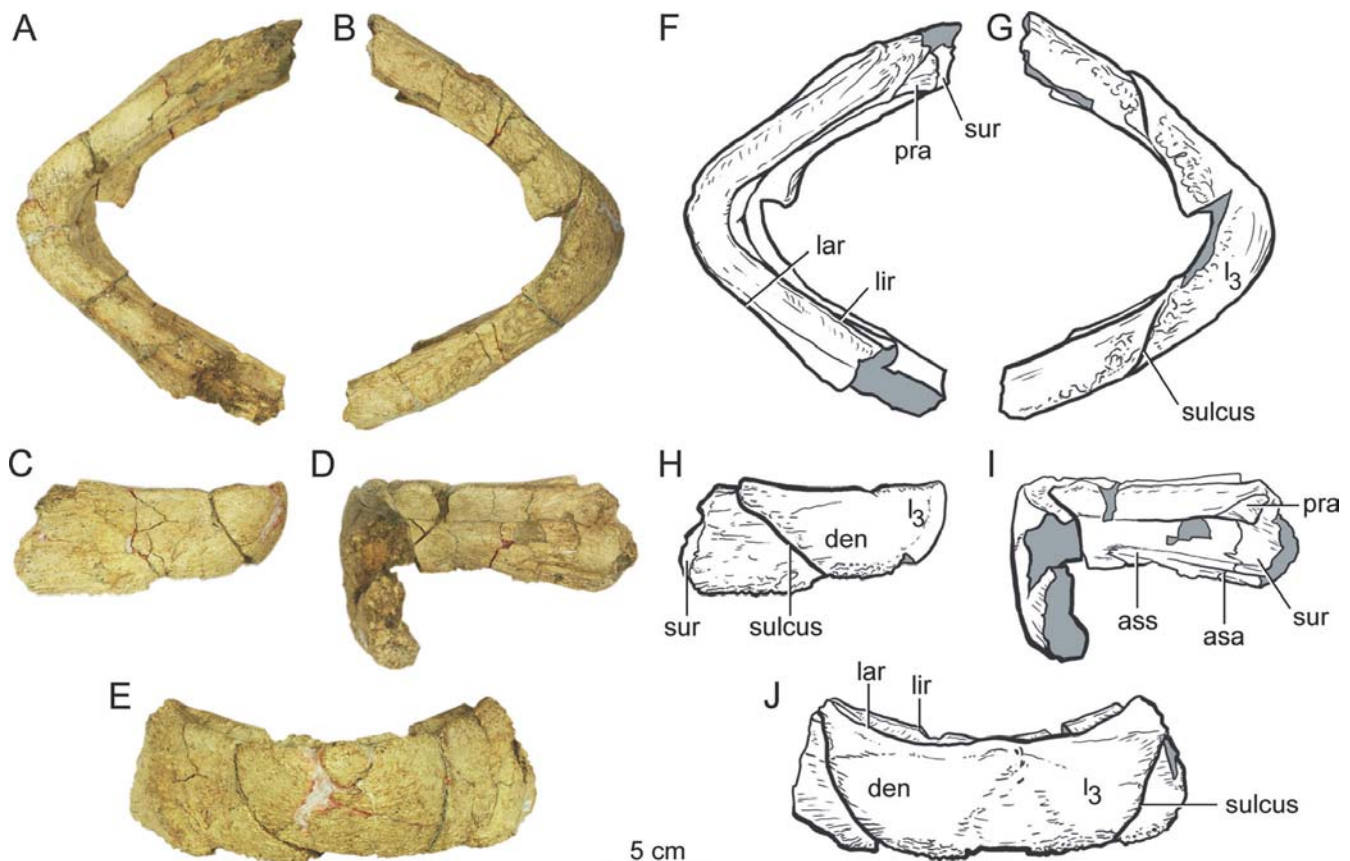


FIGURE 4. *Niolamia argentina* Ameghino, 1899. MLP 26–40, lower jaw. Photographs (A–E) and interpretive drawings (F–J). A, dorsal, B, ventral, C, right lateral, D, medial, and E, anterior views. F, dorsal, G, ventral, H, right lateral, I, medial, and J, anterior views. (Color figure available online).

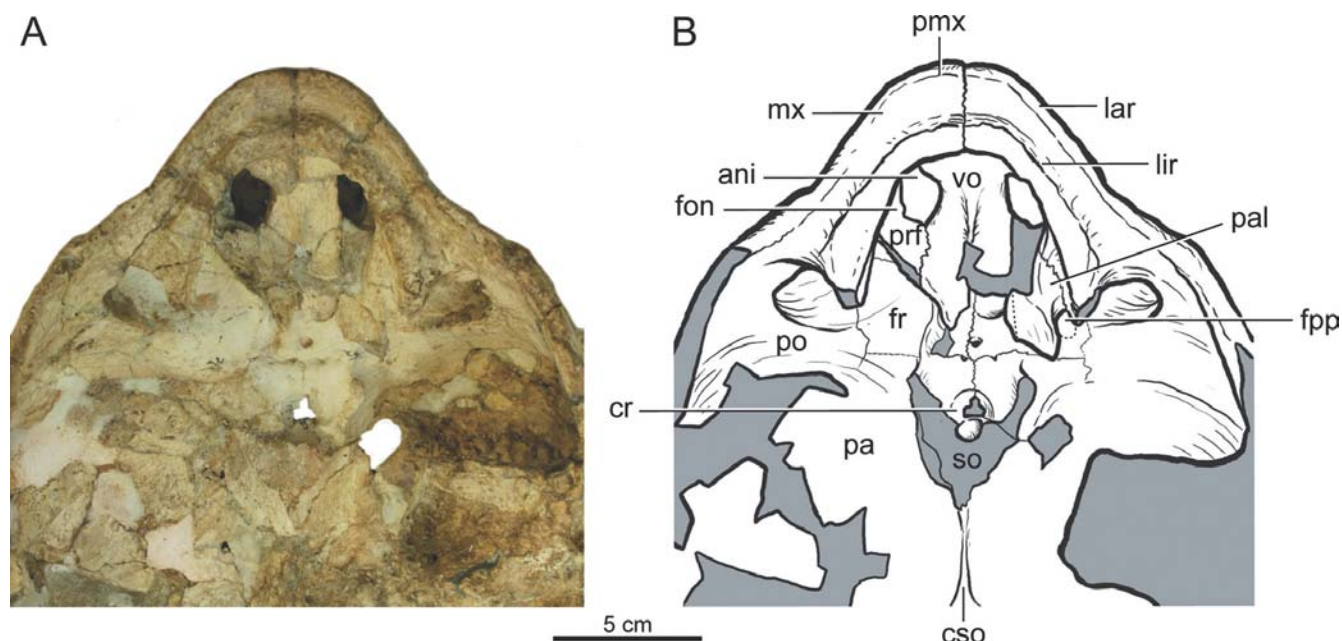


FIGURE 5. *Niolamia argentina* Ameghino, 1899. MLP 26–40, skull. **A**, photograph and **B**, interpretive drawing showing detail of anterior part of the ventral view with the basicranium removed. (Color figure available online).

the quadratojugal are not visible in *Nio. argentina* (MLP 26–40; Figs. 1B, 3). Comparing *Nio. argentina* with *M. platyceps*, the quadratojugal likely formed part of the anterior rim of the cavum tympani.

The sutures of the squamosal bone are not visible in the adult skull of *Nio. argentina* (MLP 26–40; Figs. 1–3). Following the contact surface seen in the juvenile skull AMNH 3161, the squamosal contacts the supraoccipital medially, the parietal anterolaterally, and the postorbital laterally. The remaining contacts are inferred based on comparisons with *M. platyceps* (Gaffney, 1983). As in all meiolaniids, the dorsal exposure of the squamosal of *Nio. argentina* is large, forming the posterolateral part of the skull roof, the dorsolateral portion of the cavum tympani, the lateral part of the frills, and the horn (Figs. 1–3). The development and morphology of the frill and the horn of *Nio. argentina* are similar

to that of *Nin. oweni*. The portion of the squamosal forming the frill is bent posteriorly and upwards compared to *Nin. oweni* (Figs. 1–3). The horn is triangular in cross-section. Both species differ from other meiolaniids in that the horns are bent posteriorly. The frill is more developed in *Nio. argentina* than in *Nin. oweni* (see Gaffney, 1992). The squamosal of *Nio. argentina* is covered dorsally by scales A, B, C, E, and J2 (Fig. 1A). Comparisons between the juvenile and the adult skull of *Nio. argentina* show the horn in the juvenile is a small protuberance, indicating that it grew laterally and posteriorly in the adult.

The only recognizable suture of the postorbital (MLP 26–40; Figs. 1, 2A, 3, 5) is with the prefrontal. In ventral view, it is clear that the postorbital contacts the prefrontal anteriorly, the frontal anteromedially, and the parietal posteromedially (Fig. 5). Based on the juvenile specimen (AMNH 3161), the postorbital

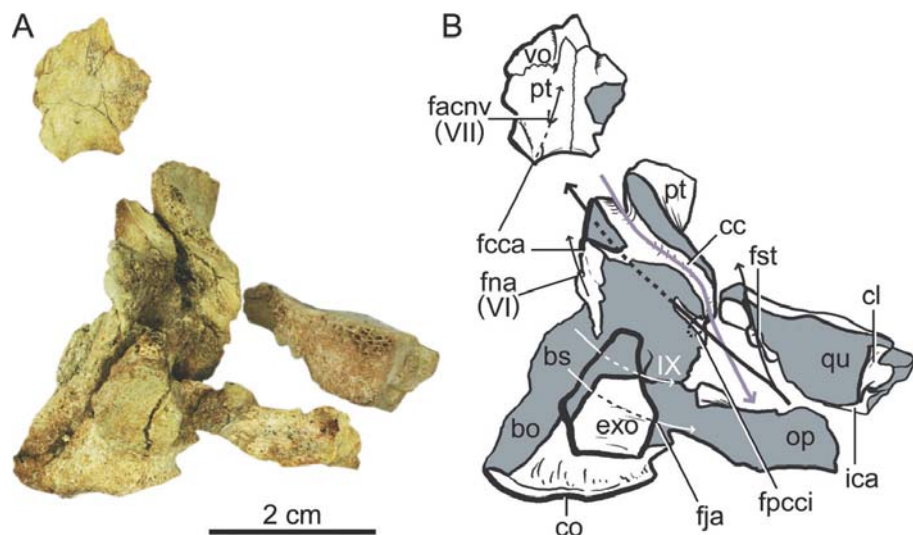


FIGURE 6. *Niolamia argentina* Ameghino, 1899. MLP 26–40, basicranium. **A**, photograph and **B**, interpretive drawing showing detail of dorsal view of the basicranium. Roman numeral indicates cranial nerve opening. (Color figure available online).

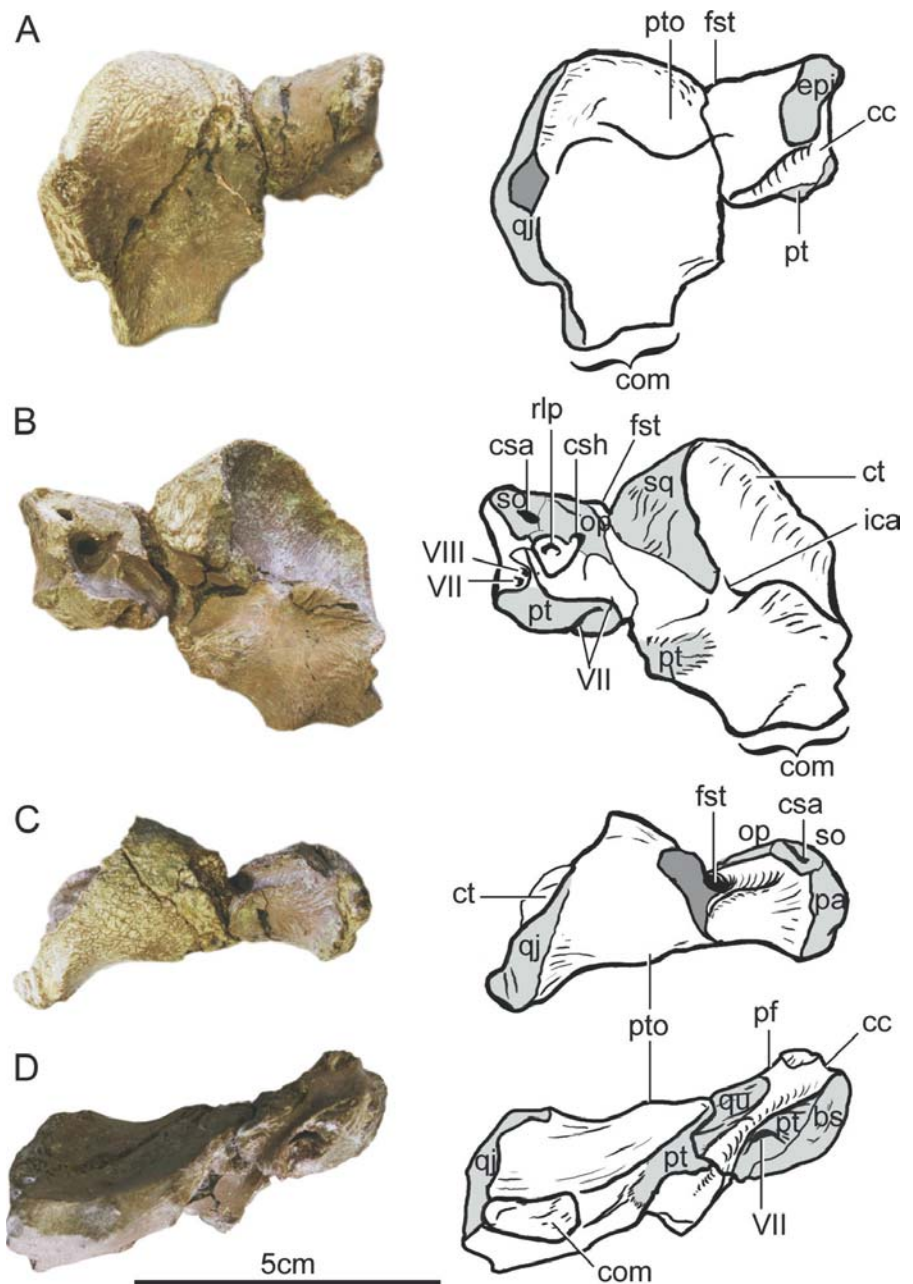


FIGURE 7. *Niolamia argentina* Ameghino, 1899. AMNH 3161, quadrate and prootic. Photographs and interpretive drawings of **A**, anterior, **B**, posterior, **C**, dorsal, and **D**, ventral views. Roman numerals indicate cranial nerve openings. Dark gray: broken surface. Light gray: contact surface. (Color figure available online).

also contacts the squamosal posteriorly, the parietal medially, and the frontal anteromedially. As in *M. platyceps*, the postorbital of *Nio. argentina* is of moderate size compared to other turtles (e.g., Chelydridae, Cheloniodea), with a comparatively well-developed dermal roof. The morphology of the postorbital of *Nio. argentina* is equivalent to that in other turtles, with a curved horizontal plate and a descending process, which separates, at least partially, the fossa orbitalis and the fossa temporalis inferior.

Palate—The medial midline contact between both premaxillae is preserved (MLP 26–40; Figs. 1B, 2A, 3, 5). The posterior contact with the maxilla is inferred. Posteriorly, the premaxilla contacts the vomer, but its exact suture is not visible (Fig. 5). The premaxilla forms the ventral border of the apertura narium externa (Fig. 2A), which in *Nio. argentina* is not divided as in *M. platyceps* and *Nin. oweni*. The premaxilla also forms the

floor of the fossa nasalis. In *Nio. argentina*, as in *M. platyceps*, the area of the premaxilla that forms the floor of the apertura narium externa is higher than the section forming the floor of the fossa nasalis. Whereas the triturating surface is described below for the maxilla, there is a noticeable groove between the labial and the lingual ridges that extends into the premaxillary portion (MLP 26–40; Fig. 1B). This could be due to the development of a lower hook at the symphysis in the lower jaw (see below for more detail). Contrary to the condition seen in *Nio. argentina*, the premaxillary triturating surface of *M. platyceps* bears an intermediate or accessory ridge, whereas in *Nin. oweni* there are two intermediate ridges. No parasagittal ridge is present in the triturating surface of *Nio. argentina* (Figs. 1B, 5), as is found between the accessory and labial ridge of *M. platyceps*. The foramen praepalatium is not visible in the preserved specimens.

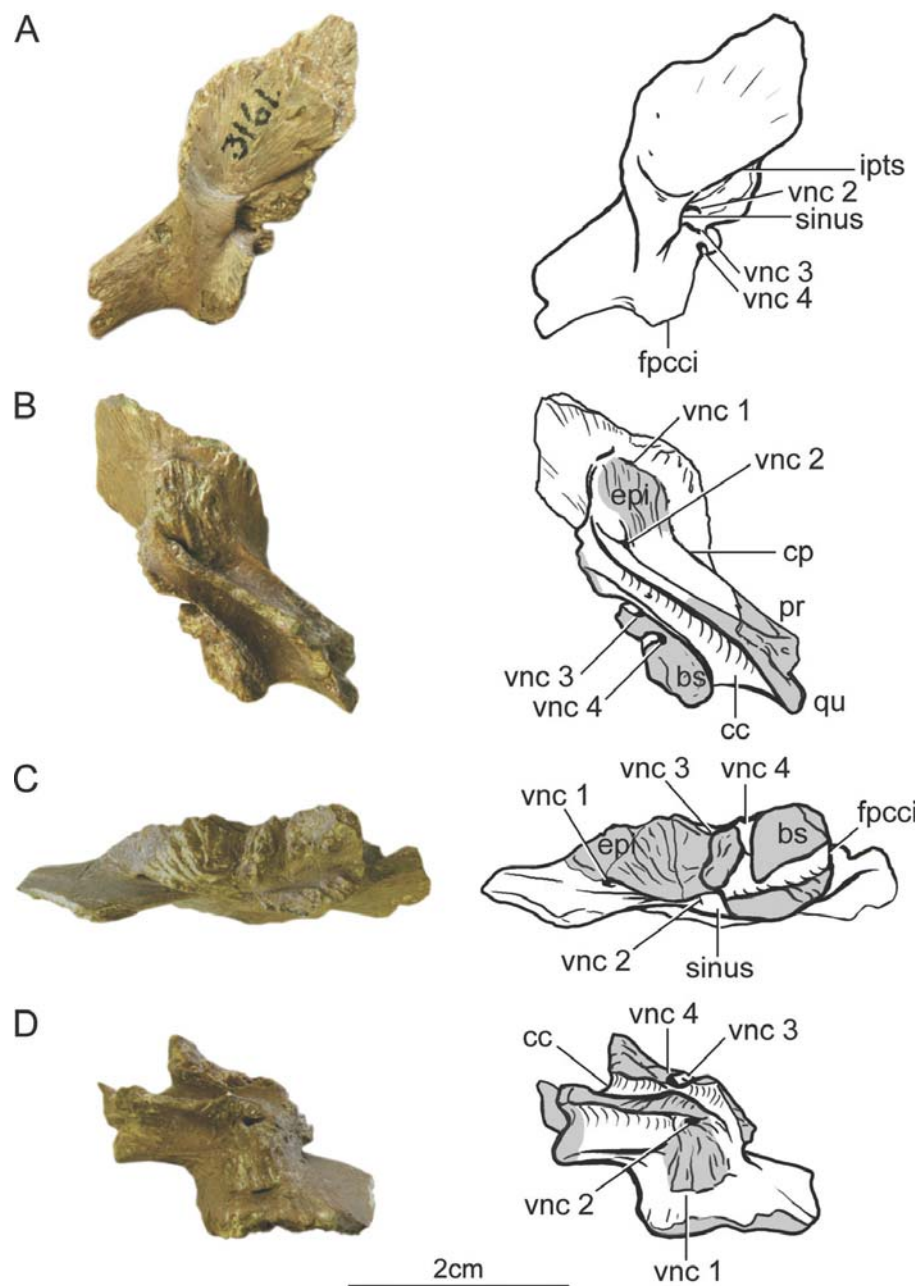


FIGURE 8. *Niolamia argentina* Ameghino, 1899. AMNH 3161, pterygoid. Photographs and interpretive drawings of **A**, ventral, **B**, dorsal, **C**, medial, and **D**, anterodorsal views. Light gray: contact surface. (Color figure available online).

The maxilla contacts the premaxilla anteriorly (MLP 26–40; Figs. 1B, 2A, 3, 5). The maxilla-palatine contact is located in the posteromedial portion of the maxilla, near the triturating surface (Fig. 5). Medially, the maxilla, together with the vomer and the prefrontal, forms the border of the apertura narium interna (Fig. 5). The maxilla has a dorsal process that contacts the prefrontal dorsally and separates the nasal cavity and the orbit. The separation between the nasal cavity and the orbit was previously noted by Woodward (1901). Contrary to *M. platyceps*, the nasomaxillary sinus is absent in *Nio. argentina*, and consequently the maxilla does not form the ventral half of this sinus. Ventrally, the triturating surface formed by the premaxilla and the maxilla only has two ridges, the labial and the lingual ridges (Figs. 1B, 5). The labial ridge is taller and sharper than the lingual ridge. The triturating surface is wider on the premaxilla, it narrows on

the medial part of the maxilla, and widens again on the posterior end. The lingual ridge is expanded and forms a wide surface. The maxilla of *M. platyceps* and *Nin. oweni* differs from *Nio. argentina* in the possession of accessory ridges between labial and lingual ridges. *Meiolania platyceps* has only one intermediate ridge, whereas *Nin. oweni* has two intermediate ridges (Gaffney, 1983, 1992). Although the sutures of the maxilla on the external surface of *Nio. argentina* are not visible, comparisons with *M. platyceps* indicate that it forms the anteroventral rim of the orbit.

The unpaired vomer (MLP 26–40; Figs. 1B, 5, 6) is a wide bone in *Nio. argentina* that contacts the premaxilla anteriorly, the prefrontal anterolaterally, the palatine posterolaterally, the pterygoid posteriorly, and most likely the maxilla anteriorly. As in other meiolaniids and testudinids (Gaffney, 1983), the vomer of *Nio. argentina* is an anteroposteriorly elongated element and together with the palate is arched dorsally (Figs. 1B, 5). In *Nio.*

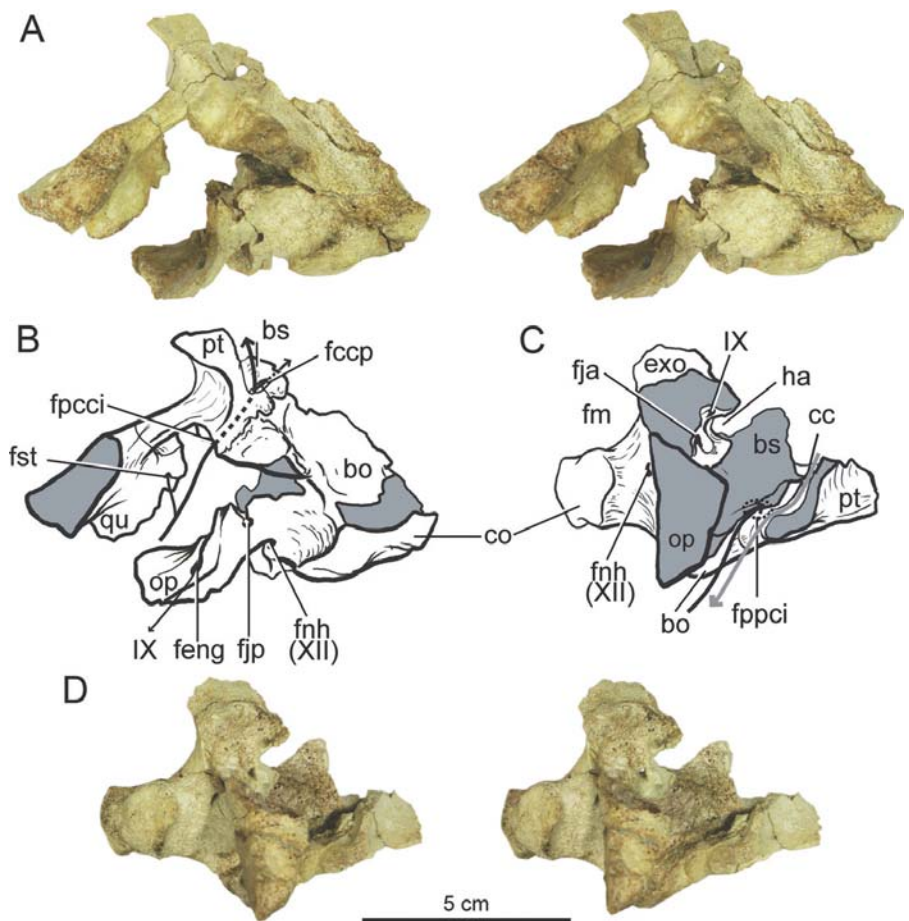


FIGURE 9. *Niolamia argentina* Ameghino, 1899. MLP 26–40, basicranium. **A**, stereophotograph, and **B**, interpretive drawing in ventroposterolateral aspect. **C**, interpretive drawing, and **D**, stereophotograph in right posterolateral aspect. Roman numerals indicate cranial nerve openings. (Color figure available online).

argentina, the vomer-prefrontal suture extends just subparallel to the axis of the vomer (Fig. 5). As noted by Woodward (1901), the vomer has a medial keel that becomes higher posteriorly (Fig. 5). The palatal troughs found on either this medial keel in *M. platyceps* are absent in *Nio. argentina*. The vomer of *Nio. argentina* forms the floor of the fossa nasalis and of the fissura ethmoidalis, and together with the maxilla and the prefrontal forms the rim of the apertura narium interna (Fig. 5).

Only a small portion of the left palatine is preserved (MLP 26–40; Figs. 1B, 5). The only sutures that could be identified are those with the maxilla anterolaterally and the vomer medially (Figs. 1B, 5). The remaining sutures are not visible, but it is assumed that the palatine contacted the prefrontal anteromedially and the pterygoid posteriorly, as in other turtles. It cannot be determined whether or not the palatine contacted the jugal. The palatine forms the floor of the orbital cavity. The palatine of *Nio. argentina* forms the medial border of the foramen palatinum posterius (Fig. 5). The anterior border of this foramen was likely formed by the maxilla.

In the adult skull of *Nio. argentina*, the only visible contact of the quadrate (MLP 26–40 and AMNH 3161; Figs. 3, 7) is with pterygoid; the remaining contacts are seen in the juvenile specimen (AMNH 3161). The quadrate contacts the prootic dorsomedially, the opisthotic dorsally, the quadratojugal laterally, the pterygoid ventrally, and the squamosal posterolaterally (Figs. 5, 7). As in all turtles, the quadrate forms the cavum tympani, which is a funnel-shaped structure in *Nio. argentina*. The portion of the quadrate between the cavum tympani and the foramen stapedio-temporale is thick and narrows medially to-

wards the contact with the prootic. In AMNH 3161, the presence of a processus trochlearis oticum is clearly visible (Fig. 7A, C, D). The prootic contributes to the processus trochlearis oticum. The foramen stapedio-temporale is also visible in AMNH 3161, and it is formed by the quadrate (contrary to *M. platyceps*) and the prootic and is oriented dorsally (Fig. 7C). Whether or not the incisura columella auris is open and the development of the cavum postoticum cannot be determined because of the preservational nature of the specimens (Fig. 7B). The condylus mandibularis is preserved in AMNH 3161 and as in other turtles is formed by two sections (Fig. 7D). The medial section is higher than the lateral section. Although the quadrate-squamosal suture is not recognized in *Nio. argentina*, the posterior part of the tympanic margin would be formed by the squamosal as in *M. platyceps*.

The epipterygoid bone is not preserved. However, the sutural surface for the epipterygoid is seen on the dorsal surface of the pterygoid in AMNH 3161 (Fig. 8B–D). The sutural surface is elliptical and occupies the anteromedial region of the pterygoid. The shape of the scar indicates the presence of a broad epipterygoid foot.

The preserved sutures of the pterygoid of *Nio. argentina* (Figs. 1B, 8, 9, 10A, B) are those with the other pterygoid medially, the vomer anteriorly, the quadrate laterally, the basisphenoid medially, the epipterygoid dorsally (AMNH 3161), the prootic dorsolaterally (AMNH 3161), and the basioccipital posteriorly. Laterally, the quadrate ramus of the pterygoid contacts the pterygoid ramus of the quadrate, forming both the anterior and ventral walls of the middle ear (Fig. 8). The poorly developed web of bone between the quadrate ramus of the

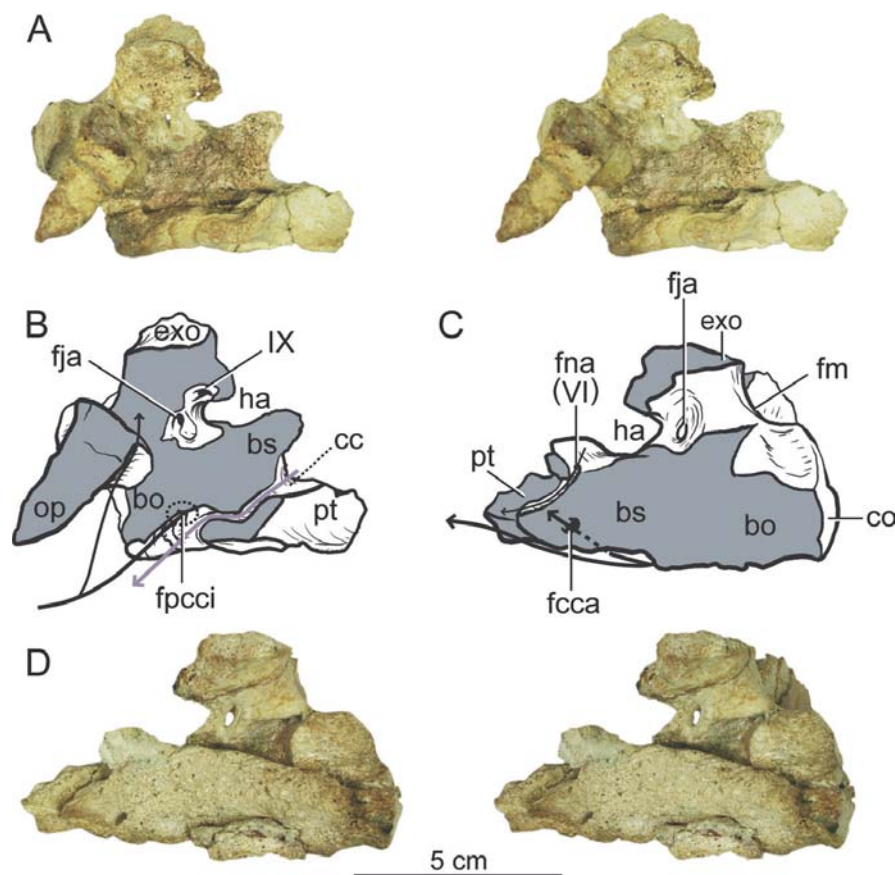


FIGURE 10. *Niolamia argentina* Ameghino, 1899. MLP 26–40, basicranium. **A**, stereophotograph and **B**, interpretive drawing of right lateral aspect. **C**, interpretive drawing, and **D**, stereophotograph in medial aspect. Roman numerals indicate cranial nerve openings. (Color figure available online).

pterygoid and its main body partially floors the cranioquadrate space in *Nio. argentina* and forms an enclosed canalis cavernosus. In ventral view, the pterygoid has an anterior horizontal plate that is located at a lower level than the basisphenoid, indicating the presence of an intrapterygoid slit characteristic of meiolaniids (Fig. 8A). The intrapterygoid slit was recognized previously by Woodward (1901:172) as a “transversely extended interpterygoid vacuity.” Unlike in *M. platyceps*, the anterior horizontal plate of the pterygoid does not ventrally cover the sinus containing the foramen carotici cerebri posterior (Gaffney, 1983). Because of the preservational nature of the specimen, the shape of the lateral pterygoid process cannot be established. Posterolaterally, anterior to the quadrate ramus of the pterygoid, there is a laterally facing teardrop-like concavity, likely for muscle insertion (Fig. 8A). Posteriorly, the pterygoid ventrally covers the tubera basioccipitalis formed by the basioccipital.

The following description is based on the pterygoid of AMNH 3161 because the inner structures are clearly preserved in this specimen (Fig. 8). Simpson (1938) recognized a pit (herein ‘sinus’) in the medial part of the pterygoid in AMNH 3161 where it must have contacted the basisphenoid. He described this sinus having “two small slit-like foramina on its medial notch and a large notch (foramen with participation of the basisphenoid) at its posteromedial edge” (Simpson, 1938:232). Simpson (1938) compares this sinus with that in baenids. The sinus in baenids is recognized as the foramen posterius canalis caroticus internus (Gaffney, 1972). Gaffney (1983) reinterpreted this sinus as having no homologue in *M. platyceps* and assuming that could be similar to the sinus described by Evans and Kemp (1975) for *Pleurosternon bullockii* (= *Mesochelys durlstoensis*) and Gaffney (1979b) for *Glyptops plicatulus*. Contrary to Gaffney’s (1983) in-

terpretation, we think the sinus found in *Nio. argentina* (AMNH 3161; Fig. 8A) is homologous to the foramen caroticum basisphenoidale of *M. platyceps* described by Gaffney (1983). This sinus is where the internal carotid artery (which entered the skull posteriorly via the pterygoid), two or three foramina containing branches of the vidian nerve (VII), and part of the foramen carotici cerebri posterior all converge. The internal carotid artery posteriorly enters the sinus through a foramen in the pterygoid (here named the foramen anterior canalis caroticus interni) and bifurcates within the sinus (Figs. 6, 9); the cerebral branch re-enters the skull through the foramen carotici posterior (Fig. 9A, B), whereas the palatine branch leaves the sinus and penetrates the skull through the intrapterygoid slit (Fig. 9).

There are several canals preserved in the pterygoid of AMNH 3161 (Fig. 8). Two dorsoventral canals (vnc1 and 2; Fig. 8) connect the canalis cavernosus with the sinus and two other canals extend posteroanteriorly (vnc3 and 4; Fig. 8). The anterior-most one of the last two (vnc3) connects the intrapterygoid slit (canalis caroticus lateralis) with the anterior border of the suture with the epipterygoid. The posterior-most one (vnc4) of the last two penetrates the pterygoid in the sinus and opens in the anterior part of the crista pterygoidea. These two posteroanterior canals (vnc3 and 4) were seen by Simpson (1938), but he was not able to assign them to any structure. All these canals are interpreted here as part of a complex vidian nerve system. As noted by Albrecht (1967), there are variations in the development of the vidian nerve system in the different turtles analyzed by him, and *Nio. argentina* would represent a complex case. Moreover, the foramina related with the vidian nerve system seem to be variable between the juvenile and the adult in *Nio. argentina*. In the adult specimen of *Nio. argentina*, the posterior entrance in the

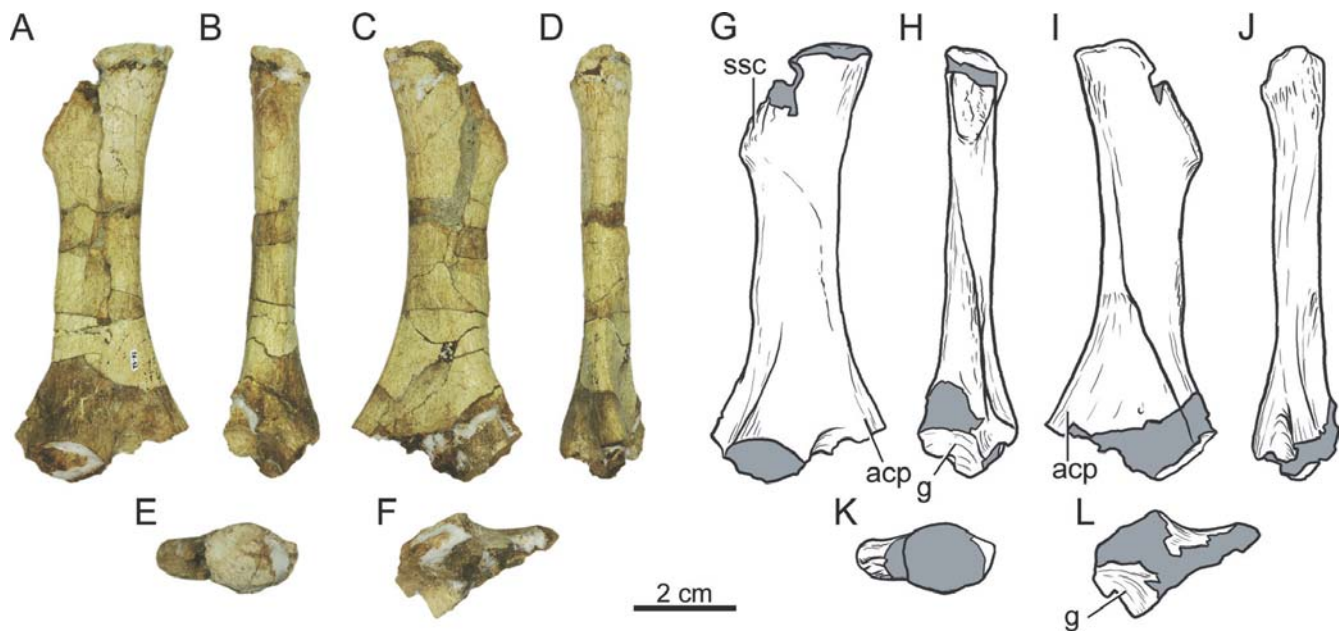


FIGURE 11. *Niolamia argentina* Ameghino, 1899. MLP 26–42, right scapula. Photographs (A–F) and interpretive drawings (G–L). A, anterior, B, ventral, C, posterior, D, dorsal, E, distal, and F, proximal views. G, anterior, H, ventral, I, posterior, J, dorsal, K, distal, and L, proximal views. (Color figure available online).

pterygoid of the anterior-most foramen of vidian nerve (vnc1) is seen in ventral view (Fig. 1B), but is not seen in the ventral view of the juvenile (Fig. 8). Gaffney (1983) described the N. vidiani (VII) in *M. platyceps* having in its own canal, but he did not mention the anterior path of the nerve. In the reconstruction of *M. platyceps* (Gaffney, 1983:fig. 45, part 2), however, a pair of foramina is drawn in the dorsal surface of the pterygoid, a location that is coincident with the foramina found in MLP 26–40 and AMNH 3161.

In dorsal view, there are two grooves in the pterygoid (Figs. 9B; 10A, B). The lateral groove is interpreted as the canalis cavernosus for the vena capitis lateralis. The medial groove is interpreted as the canalis carotici interni. The pterygoid partially covers the internal carotid before it splits into cerebral and palatine branches (Fig. 9A, B). The bifurcation of both branches likely occurred after the internal carotid leaves the canalis carotici interni at the level of the sinus in the basisphenoid (see below).

We agree with Woodward (1901:172) who noted that “the lateral margin of the pterygoid, though incomplete in both sides, exhibits no trace of the curious rolled-up lateral process so characteristic of existing Pleurodira.” That author was right in the sense that the lateral margins of the pterygoids are broken and there are no remains of the processus trochlearis pterygoidei in the preserved pterygoid. Woodward (1901:172) mentioned that “the pterygoid is connected with the parietal region by a small vertical lamina of bone on either side,” but the entire lateral wall of the cavum cranii is reconstructed in *Nio. argentina*.

Braincase—The supraoccipital of *Nio. argentina* (Figs. 1, 2) contacts the squamosal laterally and the parietal anteriorly. The supraoccipital and the parietal form an overlapping suture, with the supraoccipital extending ventral to the parietal for almost half of its length. The supraoccipital of meiolaniids has two portions, a horizontal plate exposed in the skull roof and a ventral process that forms the supraoccipital crest and the dorsal rim of the foramen magnum and of the cavum cranii. In *Nio. argentina*, the horizontal process, the distal part of the supraoccipital crest, and the posterodorsal part of the cavum labyrinthicum

and cavum cranii are preserved. The horizontal plate in *Nio. argentina* is well expanded laterally forming the posteromedial part of the frill in the skull roof. In ventral view, the supraoccipital crest of *Nio. argentina* is posteriorly directed well beyond the occipital condyle (Fig. 5). As pointed out by Woodward (1901), the supraoccipital crest is laminar and becomes broader in its contact with the skull roof. The structure of the inner ear is seen clearly in AMNH 3161. The supraoccipital forms the posterior roof of the cavum labyrinthicum, the recessus labyrinthicus supraoccipitalis. Dorsal to the hiatus acusticus (see the description of the opisthotic and the prootic) there is a canal that connects the cavum labyrinthicum and the cavum cranii. This canal is interpreted here as the foramen aqueducti vestibuli, which is formed by the supraoccipital of turtles and transmits the endolymphatic duct from the sacculus to the endolymphatic sac (Gaffney, 1979a). The canalis semicircularis posterior is preserved in AMNH 3161 connecting the recessus labyrinthicus supraoccipitalis with the recessus labyrinthicus opisthoticus (Gaffney, 1979a).

The contacts of the exoccipital (Figs. 6, 9, 10) are with the basioccipital ventrally and the opisthotic laterally. The dorsal part of the exoccipital is broken in both specimens, and consequently the contact with the supraoccipital is not preserved. In medial view, the foramen jugulare anterius is seen between the exoccipital and the opisthotic (Figs. 9C, D, 10). The foramen jugulare anterius connects the recessus scalae tympani and the cavum cranii, and formerly carried the vagus (X) and the accessory (XI) nerves and the vena capitis lateralis (Gaffney, 1979a). As in most turtles, the exoccipital of *Nio. argentina* forms, at least, the lateral border of the foramen magnum. Although the exoccipitals are broken dorsally, it can be estimated that the foramen magnum was taller than wide (Fig. 2B), as was described by Woodward (1901). The left exoccipital preserved in AMNH 3161 contributed to the formation of the condylus occipitalis. In the adult skull (MLP 26–40), the exoccipital seems to be fused with the basioccipital (Fig. 2B). The exoccipital in *Nio. argentina* is pierced by at least two foramina for the N. hypoglossi (XII) (Fig. 9). These

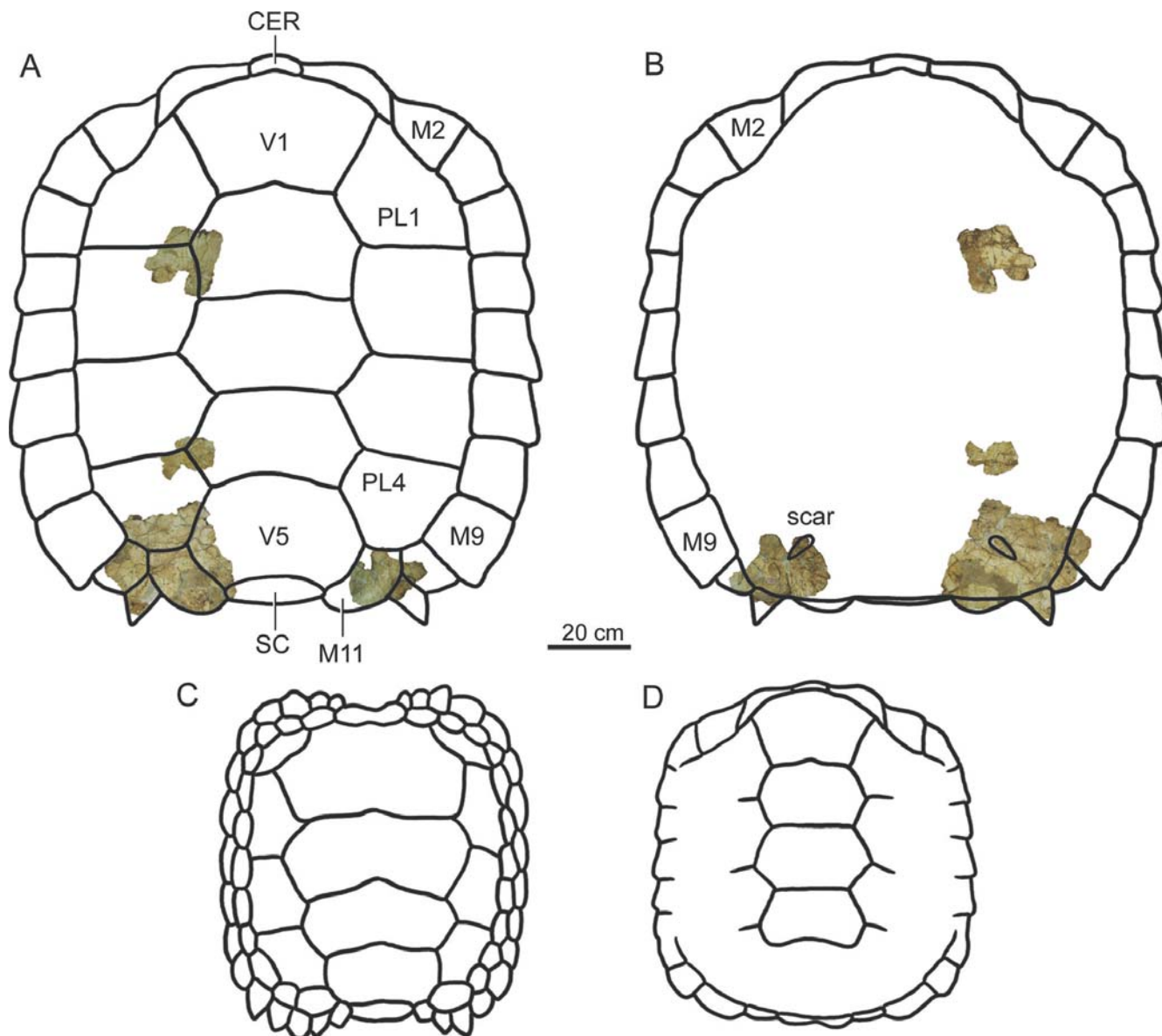


FIGURE 12. *Niolamia argentina* Ameghino, 1899. MLP 26–43, carapace remains. Reconstruction of the carapace of *Niolamia argentina* based on *Meiolania platyceps* and *Proganochelys quenstedti* (only scales are shown) in **A**, dorsal and **B**, ventral views. **C**, reconstruction of the carapace of *Proganochelys quenstedti* in dorsal view (only scales are shown; modified from Gaffney, 1990). **D**, reconstruction of the carapace of *Meiolania platyceps* in dorsal view (only scales are shown; modified from Gaffney, 1996). (Color figure available online).

foramina in *M. platyceps* “consist of two prominent foramina with a third much smaller one between the most anterior foramen N. hypoglossi and the foramen jugulare anterius in some specimens” (Gaffney, 1983:437).

The only visible suture of the basioccipital of *Nio. argentina* (MLP 26–40; Figs. 1B, 2B, 6, 9, 10) is with the pterygoid anterolaterally; the remaining contacts are inferred. The basioccipital contacted the basisphenoid anteriorly, the exoccipital dorsolaterally, and the opisthotic anterolaterally. Laterally, the basioccipital forms part of the floor of the cavum labyrinthicum and the cavum acustico-jugulare, as in *M. platyceps* (Gaffney, 1983). Because the basioccipital is missing in AMNH 3161 and it seems to be fused to the exoccipital in the adult skull (MLP 26–40), as in other turtles (Gaffney, 1979a), the exact contribution of each bone to the occipital condyle is not known. The occipital condyle

has a peanut-shaped outline (Fig. 2B). Its articular surface is different than that present in *M. platyceps*, in which three articular areas are roughly delimited (Gaffney, 1983). Ventrally, the basioccipital has a medial concavity that ends laterally in the basioccipital tubera (Figs. 1B, 9A, B). The dorsal surface of the basioccipital is broken preventing its description.

The inferred contacts of the prootic (Figs. 6, 7, 9C, D, 10) are with the pterygoid ventrally, the quadrate laterally, the supraoccipital dorsomedially, the parietal posteriorly, and the opisthotic posteriorly. As in all turtles, the prootic together with the opisthotic of *Nio. argentina* forms the cavum labyrinthicum and parts of the cavum cranii (Figs. 7B, 10). The canalis cavernosus is located in the anterior wall of the prootic (Figs. 7A, D, 9C, D, 10A, B). Dorsally and in the contact with the quadrate (Fig. 7A–C), the prootic forms the medial half of the foramen stapedio

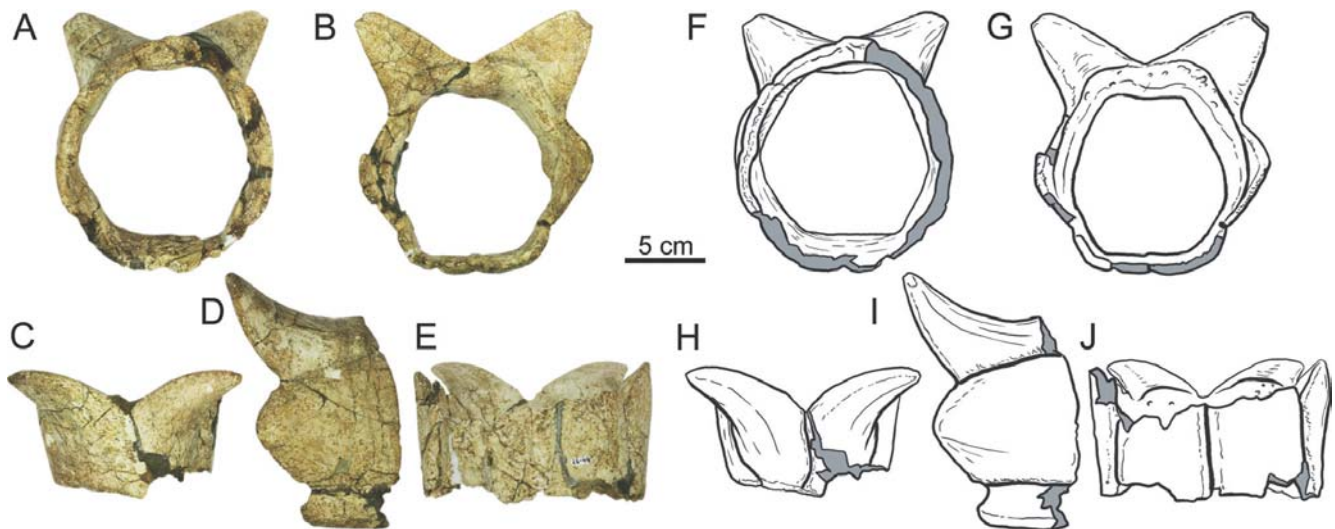


FIGURE 13. *Niolamia argentina* Ameghino, 1899. MLP 26–44, tail ring. Photographs (A–E) and interpretive drawings (F–J). A, anterior, B, posterior, C, dorsal, D, right lateral, and E, ventral views. F, anterior, G, posterior, H, dorsal, I, right lateral, and J, ventral views. (Color figure available online).

temporale (=CFA, canal for facial artery of Simpson, 1938). The anterior wall of the prootic of *Nio. argentina* is thickened and contributes in the formation of the processus trochlearis oticum (Fig. 7A, C, D). The recessus labyrinthicus prooticus is well preserved in AMNH 3161, allowing the following description of the inner ear (Fig. 7B). This recessus is connected to the recessus labyrinthicus supraoccipitalis through the canalis semicircularis anterior, and to the recessus labyrinthicus opisthoticus through the canalis semicircularis horizontalis (Gaffney, 1979a). In the medial wall of the prootic connecting the cavum labyrinthicum and the cavum cranii, there are two foramina for the N. acustici (VIII) and one foramen for the facial nerve (VII). In the ventral part of the prootic, there are two foramina, presumably for the facial nerve (VII) as well as a foramen pro ramo N. vidiani, as in *M. platyceps* (Gaffney, 1983).

The sutures of the opisthotic of *Nio. argentina* (Figs. 1B, 2B, 6, 9, 10A, B) are not seen but its contacts can be inferred from its structures. The opisthotic-exoccipital contact is indicated by the presence of the foramen jugulare anterius (Figs. 6, 9, 10A, B). The opisthotic has a well-developed processus paroccipitalis, which may contact the squamosal laterally. Ventrally, the opisthotic contacts the basisphenoid and the basioccipital. Anteromedially, the opisthotic forms the posterior border of the hiatus acusticus, bordered anteriorly by the prootic. Dorsal to the hiatus acusticus the foramen aqueducti vestibuli opens into the cavum cranii (see the description of the supraoccipital). The preservation of the opisthotic prevents a more detailed description of the structures formed by this bone, such as the processus interfenestralis, and whether the foramen jugulare posterior is surrounded by bone or not. According to Gaffney (1983:443), the “re-articulation of the right quadrate, prootic, and opisthotic of *Crossochelys* shows a strong similarity to *Meiolania platyceps* and suggest that the opisthotic entered the canalis stapedio-temporalis.” We agree with his interpretation.

Although Woodward (1901:172) recognized a “small basisphenoid,” we were unable to recognize sutures that would allow us to corroborate or refute that statement. The only known suture for the basisphenoid is that with the pterygoid (MLP 26–40; Figs. 1B, 6, 9, 10); the remaining ones are inferred. The basisphenoid contacts the basioccipital posteriorly and the prootic dorsally. As the basioccipital, the basisphenoid is a thick bone. In ventral

view, there is a pair of oval notches (‘sinus’ herein; the ‘foramen caroticum basisphenoidale’ of Gaffney, 1983) near the contact with the pterygoid, which exposes the canalis caroticus internus (Fig. 9A, B). Through this notch the bifurcation of the internal carotid in the cerebral and palatine branches is seen. The cerebral branch pierces the basisphenoid more anteriorly through the foramen carotici cerebri posterior (Sterli et al., 2010). The palatine branch leaves the canalis carotici interni through the sinus (=foramen caroticum basisphenoidale) and re-enters the skull through the intrapterygoid slit (Fig. 9A, B). Because the basicranium can be removed from the remaining parts of the skull, some inner structures could be seen. Anteriorly, the basisphenoid forms the sella turcica, the anterior extension of which cannot be determined because it is broken (Fig. 10C, D). Posterior to the sella turcica there is a tall dorsum sellae that is pierced by the abducens nerve (VI). The posterior opening of the abducens nerve is located in the dorsal and anterior surface of the basisphenoid, and opens anteriorly in the posterior wall of the sella turcica (Fig. 10C, D). Unfortunately, the clinoid processes are broken. In anterior view, the anterior opening of the abducens nerve is located more laterally than the anterior foramen for the cerebral artery (Fig. 10C, D). As in most adult turtles, the parasphenoid is not present as a distinct element.

Mandible—The most complete bone preserved is the dentary; remains of the prearticular and the surangular are also present (Fig. 4). Although Woodward (1901) recognized fragments of the articular and the angular, we were unable to confirm this observation.

Both dentaries of MLP 26–40 (Fig. 4) are preserved and they are fused at the symphysis (Woodward, 1901). A web of bone connects both dentaries behind and below the symphysis (Fig. 4A, B, F, G). In lateral view, the dentary has an ornamentation of pits and ridges that end posteriorly in knobs (Fig. 4B, C, G, H). Just anterior to the contact with the coronoid, there is a anteroventrally aligned groove (Fig. 4B, C, G, H), indicating the presence of a horny beak as suggested by Woodward (1901). The triturating surface is very simple, having only two ridges, the labial ridge and the lingual ridge (Fig. 4A, E, F, J). There is no accessory ridge as in *M. platyceps*. The lingual ridge is taller than the labial ridge and they remain parallel to each other along the entire triturating surface. Anteriorly, the lingual ridge does not

form a cusp as in *M. platyceps*; on the contrary, it is shorter than the labial ridge. Although the anterior tip of the labial ridge is broken, it has a dorsal projection, indicating the presence of an anterior hook. Just posterior to the triturating surface there is a roughened area where the coronoid bone contacted the dentary (Fig. 4A, F). In medial view, the sulcus cartilaginis meckelii remains open anteriorly, as in *M. platyceps*, but in *Nio. argentina* it seems to be even more open than in *M. platyceps*, because there is no ventral process on the dentary overhanging the sulcus (Fig. 4D, I). The splenial is not preserved, but it likely closed the sulcus cartilaginis meckelii posteriorly. In medial view, the roughened surface indicates the contacts with the splenial and the angular (Fig. 4D, I). At the midpoint of the dentary, the medial opening of the foramen alveolare inferius is present. In ventral view, the dentary widens posteriorly, and posterior to the sulcus for the horny beak the surface becomes smoother (Fig. 4B, G), probably for the insertion of the *M. adductor manibulae externus* (Schumacher, 1973).

Although no angular is preserved, there is a roughened surface and a groove in the lower part of the posteromedial end of the dentary that we interpret as the contact surface for the angular (Fig. 4D, I). Comparisons with the lower jaw of *M. platyceps* (MLP 26–40; Fig. 4) allows us to propose that a small portion of the surangular could be present at the posterior end of both rami in medial and lateral views (Fig. 4A, C, D, F, H, I). However, the poor preservation of these fragments precludes description of this bone. In medial view, at the posterior end of the right lingual ridge, there is a laminar bone that we identify as the remains of the prearticular (Fig. 4A, D, F, I).

Horns and Scales—Woodward (1901) recognized eight bosses in the skull of *Niolamia*, identified with the Roman numerals I to VII, plus one unnumbered. These bosses are coincident with the scale areas identified by Gaffney (1983) for meiolaniids in general and *Niolamia argentina* in particular. Gaffney (1983), following Simpson's (1938) nomenclature of cranial scales, renamed some bosses and identified some other scales not mentioned by Woodward (1901). The description of the cranial scales of *Nio. argentina* is based on specimens MLP 26–40 and AMNH 3161 (= *C. corniger* Simpson, 1937). In the following paragraphs we will describe the scale areas and compare them with previous studies. Scales B–K are paired, whereas scales A and X–Z are unpaired. Scale B (sensu Simpson, 1938; Figs. 1A, 2A, 3) was first recognized by Woodward (1901) as scale I. There are two B scales covering the laterally directed horn cores on each side of the skull. Scale B was likely even bigger in life (Gaffney, 1983). This horn is made up by the squamosal. The overall morphology (e.g., triangular shape) and orientation (directed more laterally than posterodorsally) of horn core B of *Nio. argentina* is more like that found in *Nin. oweni* than in *M. platyceps*. Scale B contacts scale A posteromedially, scale C medially, and D anteriorly. Our homology interpretation for scale B agrees with previous work (Woodward, 1901; Simpson, 1938; Gaffney, 1983, 1996).

Scale C ('scale VI' of Woodward, 1901; Figs. 1A, 2A, 3) is a paired scale located on the skull roof and on the lateral side of the skull above the cavum tympani. It is a small scale with a protuberance directed outwards and downwards. Scale C covers the squamosal and postorbital bones, and contacts scale B posteriorly, D medially, F anteriorly, E anteroventrally, and K posteroventrally.

Scale D ('scale III' of Woodward, 1901; Figs. 1A, 2A, 3) is a paired scale located on the posterolateral region of the skull roof, anterior to the frill. It is large, pentagonal in shape, and surrounded by scale A posteriorly, scale X medially, scale G anteromedially, scale F anterolaterally, and scales B and C laterally. The underlying bone of both scales D are not completely preserved, but it is apparent that the bone (parietal) is thickened in this region (Woodward, 1901) and has a convex surface. D scales do not meet each other along the midline in *Nio. argentina*, contrary to

the midline contact between these scales found in other meiolaniids (Gaffney, 1996). D scales are prevented from contacting each other along the midline due to the well-developed scale X, which contacts scale A.

Scale E ('boss VII' of Woodward, 1901; Figs. 1A, 2A, 3) is small and paired, and can be seen mainly in lateral view. This scale is strongly convex with a medial protuberance that points laterally. It is located just anterior to the cavum tympani and is surrounded by scale C dorsally, scale F anterodorsally, scale K posteriorly, and scales J1 and J2 ventrally. This scale covers the squamosal and likely the postorbital.

Scale F ('boss IV' of Woodward, 1901; Figs. 1A, 2A, 3) is paired, with each surrounding the upper half of the orbit. In dorsal view, scale F contacts scale C posterolaterally, scale D posteriorly, scale G posteromedially, scale Y medially, and scale Z anteriorly. In lateral view, scale F contacts scale E posteriorly, scale J2 posteroventrally, and scale I1 anteroventrally. Scale F covers at least the prefrontal and postorbital bones.

Although G scales (Figs. 1A, 2A, 3) were clearly seen in *Nio. argentina* prior to our work (e.g. Simpson, 1938; Gaffney, 1996), this scale was not described or numbered by Woodward (1901). Each scale G is pentagonal in shape, being broader than long. Both are located in the middle of the skull roof and contact one another along the midline. Scale G contacts scale Y anteromedially, scale F anterolaterally, scale D posterolaterally, and scale X posteromedially. This scale is convex, particularly so along the midline, where it ends in a midline protuberance. Scale G covers the parietal and frontal bones. Scale H (Figs. 1A, 2A, 3) is absent in *Nio. argentina* (in both the adult specimen, MLP 26–40, and juvenile, AMNH 3161).

Scale I was regarded by Gaffney (1983) as covering the premaxilla and maxilla, i.e., the anteroventral part of the snout bordering the anteroventral part of the orbit and the posteroventral margin of the apertura narium externa, in both *M. platyceps* and *Nio. argentina* (Gaffney, 1996:fig. 90). Further preparation of *Nio. argentina* allows the subdivision of scale I. We regard the anterior portion of scale I as scale I1 and the posterior portion as scale I2. As interpreted for scale I of *M. platyceps*, scales I1 and I2 in *Nio. argentina* represent the dorsal continuation of the horny rhamphotheca that covered the triturating surface (Gaffney, 1983). Scale I1 is probably unpaired and contacts scale Z dorsolaterally behind the apertura narium externa and scale I2 posteriorly. Scale I2 contacts scale I1 anteriorly and J2 posteriorly and forms the ventral rim of the orbit.

Gaffney (1983) identified scale J for *M. platyceps* as a large scale seen in lateral view covering the cheek of the skull between the orbit and the cavum tympani. Later, Gaffney (1996) identified two scales in *Nio. argentina* that have similar topological positions as scale J found in *M. platyceps*, and named the posterior scale J1 and the anterior scale J2, identifications with which we agree (Figs. 1A, 2A, 3). Scale J1 is located just anterior to the cavum tympani and contacts scale J2 anteriorly and scale E dorsally, and probably scale K posteriorly (the posterior portion of bone that is covered by scale J1 is missing in *Nio. argentina*). Scale J2 forms the posterior rim of the orbit and contacts scale I2 anteriorly, scale F anterodorsally, scale E posterodorsally, and J1 posteriorly. Scales J1 and J2 cover the jugal and the quadratojugal.

Scale K (Figs. 1A, 2A, 3) was identified by Gaffney (1996) for *Nio. argentina* as covering the posterodorsal part of the cavum tympani. We agree with his interpretation. Scale K contacts scale C dorsally, scale E anterodorsally, and probably scale J1 anteroventrally.

Scale A (Figs. 1A, 2A, 3) was identified by Woodward (1901) as the 'occipital crest' formed by laminar bosses fused together along the midline. Simpson (1938) identified this area as a posteriorly notched frill that was covered by scale A. This posterior directed frill extends upwards and projects posterior to the occipital condyle. The scale comparisons made by Simpson

(1938) were based on a model of *M. platyceps*, resulting in some erroneous interpretations (fide Gaffney, 1983). For example, whereas Simpson (1938) illustrates scale A as a paired element in *Nio. argentina* based on his interpretation of a *M. platyceps* cast (Anderson, 1925), he was not actually able to find the sulcus between both scales. Gaffney (1996) identified only one large scale area in the frill of *Nio. argentina* and in *M. platyceps*, but he was unsure whether scale A was paired or unpaired. Our preparation clearly shows there is no indication of a sulcus dividing the frill in *Nio. argentina*. Consequently we agree with Gaffney's (1996) interpretation that there is a single scale A in *Nio. argentina*. This scale contacts scales B, D, and X, anteriorly. *Niolamia argentina* differs from others meiolaniids in that scale A is in contact with scale X (see description of scale X). Because the dorsal sutures of the dermal roofing elements are hard to determine due to fusion of elements, the bones and their sutures below the scales are inferred based on comparisons with *M. platyceps* and the juvenile specimen of *Nio. argentina* (AMNH 3161), as well as from partially visible sutures visible in ventral view. Scale A covers the squamosal, the supraoccipital, and probably both parietal bones.

Scale X (Figs. 1A, 2A, 3) was identified by Woodward (1901) as the medial or interparietal boss (II), as scale 'a' by Simpson (1938), and as scale X by Gaffney (1996). Scale X is one of the largest scales in the skull roof of *Nio. argentina*. It is rectangular in shape, being longer than wide. Woodward (1901) suggested this scale has a concave surface, but this could be caused by post-mortem deformation. Contrary to that in *M. platyceps*, scale X in *Nio. argentina* is well developed, contacts scale A posteriorly, and thus is separated from both D scales. Scale X also contacts scale G anteriorly. Scale X is located on the parietal in *Nio. argentina*.

Scale Y (Figs. 1A, 2A, 3) was not mentioned or numbered by Woodward (1901). Simpson (1938) referred to it as scale 'b,' and Gaffney (1983) re-named it scale Y. This scale is located on the anterior region of the skull roof between the orbits. It is pentagonal in shape, pointing posteriorly and separating the anteromedial contact of the G scales, as in *Nin. oweni*, but in contrast to this scale in *M. platyceps*. It is surrounded by scale Z anteriorly, the F scales laterally, and the G scales posteriorly. The surface of this scale is convex, but less so than scale G or D. Scale Y covers at least part of the frontals. The dorsal exposure of scale Y is much smaller than in *M. platyceps*, where this scale is very large.

Scale Z (Figs. 1A, 2A, 3) was mentioned by Woodward (1901) as boss V, not named by Simpson (1938), and given its current name by Gaffney (1983). Scale Z is located in the anterior-most part of the skull (snout region) along the midline. In dorsal view, this scale is surrounded by the F scales posterolaterally and the Y scale posteriorly. In lateral view, scale Z contacts scale F posteriorly and scale I1 ventrally. This scale covers at least the nasals dorsally.

Scale I3 (Fig. 4) is not a true scale, but is the surface where the horny beak cover attaches to the anterior part of the lower jaw. We decided to identify it as scale I3, to be consistent with the description of a similar structure found in the skull (I1 and 2).

Postcranium

Pectoral Girdle—Both dorsal processes of the left and right scapulae are preserved in *Nio. argentina* (MLP 26-41 and 26-42; Fig. 11). Whereas Woodward (1901) identified MLP 26-41 as the right scapula and the MLP 26-42 as the left one, Gaffney (1996) identified the former specimen as the left and the latter as the right; we agree with Gaffney's (1996) interpretation. Only the proximal part of the acromion is preserved in MLP 26-42. This process joins the dorsal process in an angle greater than 90°, as in both testudinids (Walker, 1973) and *M. platyceps* (Gaffney, 1996). This angulation and the shoulder pattern, recognized in terrestrial turtles (long scapular prong and short coracoids) by Depecker et al. (2006), are correlated with the presence of a

domed shell and a mode of locomotion in which walking is predominant. This would be consistent with the development of a relatively deep shell in *Nio. argentina*, as is seen in *M. platyceps*. The left scapula is better preserved than the right side, and shows the original shape of shaft. The dorsal process is flattened anteroposteriorly. Laterally, in the medial part of the dorsal process, there is a tuberosity ('t. tuberosity' of Woodward, 1901) and from this point the dorsal process narrows (Fig. 11). Dorsal to this tuberosity, the scapular surface is rough, probably for the application of the suprascapular cartilage (Fig. 11A, G). Ventral to this tuberosity there is a small crest in the lateral side that is directed medially (Fig. 11B, C, H, I). The acromion is flattened, but breakage precludes determination of its full length (Fig. 11G, I). The glenoid cavity is partially preserved only in the right scapula, and nothing remains of the coracoid. The glenoid cavity faces posterolaterally (Fig. 11B, F, H, L).

Carapace—Several fragments represent the remains of the carapace (Fig. 12). Based on comparisons with *M. platyceps* and *Proganochelys quenstedti* Baur, 1887, the presumed calculated length of the carapace is 120 cm. Unfortunately, the general aspect of the carapace of *Nio. argentina* cannot be assessed with certainty because of the fragmentary nature of the specimen. We presume it was a domed carapace, as in testudinids, because they share a similar angle between the dorsal process of the scapula and the acromion (see the description of the scapula, above). The largest fragment of the carapace is flattened, perhaps as a consequence of taphonomic processes. The average thickness of carapacial remains is 1.5 cm, being thickest in the borders and thinner towards the midline. The position of only four of the 10 fragments within the carapace could be identified (Fig. 12A, B). Although the scale sulci are well preserved in the fragments, no sutures can be seen. We agree with Woodward's (1901) interpretation that the largest fragment is the left posterolateral corner of the carapace (likely representing costal 8 and peripherals 10 and 11). The general morphology of this fragment is more similar to this area in *Proganochelys quenstedti* (Gaffney, 1990) than in *M. platyceps* (Gaffney, 1996) (Fig. 12C, D). *Niolamia argentina* bears along its posterolateral edge a posterolaterally pointing spine, and along the midline it has a broad pygal embayment that is bordered anteriorly by what we interpret to be a supra-caudal scale (Fig. 12A, B). Accordingly, the sulci present in the posterior carapace fragment of *Nio. argentina* indicate the presence of vertebral scale V, pleural scale IV, marginal scales IX–XI, and a supracaudal scale. The presence of a supracaudal scale is also documented for *Proganochelys quenstedti* and the clade Testudinidae. Although the total number of marginal scales is unknown in *Nio. argentina*, we identified 11 marginals plus the scale covering the spine (Fig. 12A, B). Eleven marginals and a supra-caudal scale are also known in Testudinidae. Unfortunately, in *M. platyceps*, which is the only meiolaniid species in which an almost complete carapace is preserved, the number of marginal scales is unknown. The only specimen of *M. platyceps* that preserves the posterior margin of the carapace between peripheral X and midline (AM F61110) exhibits neither sutures nor sulci (Gaffney, 1996:21). Although Gaffney (1996:fig. 5) interpreted the presence of 11 pairs of marginal scales in his reconstruction of the carapace of *M. platyceps*, he recognized a marginal XII in a putative 11th disarticulated peripheral in another specimen (AM F81931). In ventral view towards the midline, a rugose surface is seen (Fig. 12B). Woodward (1901), following Boulenger's (1887) ideas of meiolaniids being pleurodiran turtles, identified this scar as the surface attachment for the ilium. However, the presence of this scar is also reported for a non-pleurodiran turtle, *Proganochelys quenstedti* (Gaffney, 1990:fig. 77). The scar in *Nio. argentina* could be also the broken surface of the thoracic rib 10 (and probably 9, as well). The internal border of the marginal scales indicates the scales become shorter anteroposteriorly towards the midline. The second largest fragment also represents the posterolateral border

of the carapace, but in this case from the right side (Fig. 12A, B). The two smallest recognizable fragments of the carapace of *Nio. argentina* are costal bones (because of the presence of the rib on the ventral surface). One is identified as the left costals 2 and 3, bearing vertebral scale II and pleural scales I and II, and the other as the left costal 6, bearing vertebral scale IV and pleural scales III and IV (Fig. 12A, B).

Tail Ring—The tail of meiolaniids was covered by tail rings, which overlap each other and form continuous protection for the tail. In *M. platyceps*, where the tail is well known, the distal rings fuse together and form a tail club (Gaffney, 1985). In contrast to the condition in *M. platyceps* (Gaffney, 1985:fig. 21), the caudal ring of *Nio. argentina* (MLP 26–44) is complete, has a hexagonal shape in anterior view (Woodward, 1901), and has two pairs of posterior projections dorsally and dorsolaterally (Fig. 13). The dorsal projections are larger and robust than the dorsolateral ones (Fig. 13). The posterior end overlaps the anterior end of the following ring, and the overlapping facets are preserved in this specimen (Fig. 13B, G). The tail ring was covered by six scales, four covering the mentioned projections, two more covering the ventral surface of the ring (Fig. 13). Woodward (1901:174) mentioned that a “part of a second caudal ring, of similar type” was also discovered. However, no second caudal ring was found in the MLP collection.

DISCUSSION

Meiolaniidae has its greatest diversity in Australasia, where six species have been described. The mainland Australian species are represented by *Warkalanian carinaminor* (?late Oligocene–early Miocene of Riverside Station, northwest Queensland), *Meiolania brevicollis* Megirian, 1992 (middle Miocene of Camfield Beds, Northern Territory), *Ninjemys oweni* (Pleistocene of southern Queensland), and indeterminate meiolaniids from Oligocene to Pleistocene localities (Gaffney, 1996). Two Pleistocene and one Holocene species have been described from three western Pacific islands that are situated on crustal plate of Gondwanan origin: *Meiolania platyceps* Owen, 1886, from Lord Howe Island; *Meiolania mackayi* Anderson, 1925, from Walpole Island, New Caledonia; and ?*Meiolania damelipi* White et al., 2010, from Efate Island (Vanuatu) (Owen, 1886; Anderson, 1925; White et al., 2010). In contrast, the diversity of named meiolaniid species in South America is very poor. According to Gaffney (1996) and this study, there is only the Patagonian *Nio. argentina*, which is probably of Eocene age.

Synonymy of *Niolamia argentina* and *Crossochelys corniger*

Crossochelys corniger was named and described in detail by Simpson (1937, 1938) who considered and then rejected the idea that it could be a juvenile. Gaffney (1983, 1996) interpreted *C. corniger* as a young individual of *Nio. argentina*, and declared the former species a synonym of the latter. Additional preparation of *Nio. argentina* and first-hand study of the holotype of *C. corniger* (AMNH 3161) allow us to corroborate Gaffney's synonymy. The elements shared between *C. corniger* and *Nio. argentina* are very similar to each other (e.g., skull scale pattern, bone morphology, and structures present), and differ in size and in other characters that may change during ontogeny (e.g., horn size, skull size, widely open sutures, and temporal fenestra). Because the observed differences could be the result of ontogeny or intraspecific variation, we corroborate Gaffney's statement that *C. corniger* is the junior synonym of *Nio. argentina*. In the following paragraphs we describe the similarities and differences between specimens MLP 26–40 and AMNH 3161.

Similarities—Although many sutures in the dorsal view of the skull roof of MLP 40–26 are not seen, the general morphology of the elements and their contacts (inferred from ventral view) can be compared directly with AMNH 3161. The elements common

to both specimens are the frontal, the parietal, the squamosal, the supraoccipital, the exoccipital, and the pterygoid. Comparisons of the first four elements will be based mainly on the scale pattern and the inner view of the parietal and frontal bones. The remaining bones, the exoccipital and the pterygoid, will be compared in general aspects, because these bones are poorly preserved in *Nio. argentina*.

The most conspicuous and comparable feature between MLP 40–26 and AMNH 3161 is the skull-scale pattern. Each species of meiolaniid has a characteristic scale pattern that differentiates it from others. In general, the pattern of scales (shape and relationships) seen in AMNH 3161 and MLP 26–40 seems quite similar and differs only in details, allowing us to consider that both belong to the same species. In AMNH 3161, non-paired scales Y and X and paired scales B, C, D, E, G, and J2 are distinguishable, and they are similar in shape, distribution, and contacts to those of MLP 26–40.

Regarding bones and their structures, the sutures between the frontal and the parietal with other bones can be inferred for AMNH 3161, and can be seen in ventral view in MLP 26–40. This comparison shows the outline of the frontal and the parietal and their structures in both specimens are very similar. The descending process of the parietal is anteroposteriorly extended, and the anterior border almost reaches the frontoparietal suture in both specimens. In the posteromedial part of the parietal, the cartilaginous ‘rider’ for the cartilaginous end of the supraoccipital (Gaffney, 1977) is also seen in both specimens and their shape and relative extension are similar. The frontal of both specimens has a descending process that contacts the palatine bone. Although the sutures of the exoccipital in MLP 26–40 are not evident, the shape of the foramen magnum of both specimens can be compared. In both, the foramen magnum is slightly triangular in shape with rounded apices, and is higher than wide. The pterygoid of both specimens is similar in shape and structures. Unfortunately, the pterygoid of MLP 26–40 is not as well preserved as in AMNH 3161, and consequently many structures seen in the latter specimen cannot be compared. As in other meiolaniids, the pterygoid in both specimens has its anterior process that is positioned below the plane of the basisphenoid and covers an intrapterygoid slit ventrally. In both specimens, the anterior process of the pterygoid does not prevent the ventral exposure of the foramen caroticum basisphenoidale. A peculiar feature observed in both MLP 26–40 and AMNH 3161 is the path of the N. vidiani (VII). In medial view, the pterygoid of *Nio. argentina* (AMNH 3161) has a vertical canal that connects the cavum labyrinthicum to the canalis caroticus internus, and interpreted by Simpson (1938) as the canalis for the nerve VII. It seems the N. vidiani exited the cavum labyrinthicum, ran through an ossified canal into the canalis carotici interni, and then exited the bone in the sinus (= foramen caroticum basisphenoidale sensu Gaffney, 1983). Then, the N. vidiani re-entered the cavum cranii through a paired opening in the anterior process of the pterygoid well seen in the ventral view of MLP 26–40 and recognizable also in AMNH 3161 (but not easily seen in ventral view).

Differences—Skull size is the most noticeable difference between AMNH 3161 and MLP 26–40. The skull of AMNH 3161 is almost one-quarter of the length of MLP 26–40, and there are similar differences in A and B horn size. In addition, the sutures in AMNH 3161 are open and form in the temporal region a kind of fenestra that was identified by Simpson (1938) as a true temporal fenestra. All of the mentioned characters change during ontogeny, consonant with the interpretation that AMNH 3161 is a juvenile specimen of *Nio. argentina*, as proposed by Gaffney (1983, 1996). The major differences between AMNH 3161 and MLP 26–40 are in the supraoccipital of the former, where there is a medial depression that could be interpreted as a sulcus between the two A scales (as was proposed in the original description by Simpson, 1938), and scale X has an anterior process

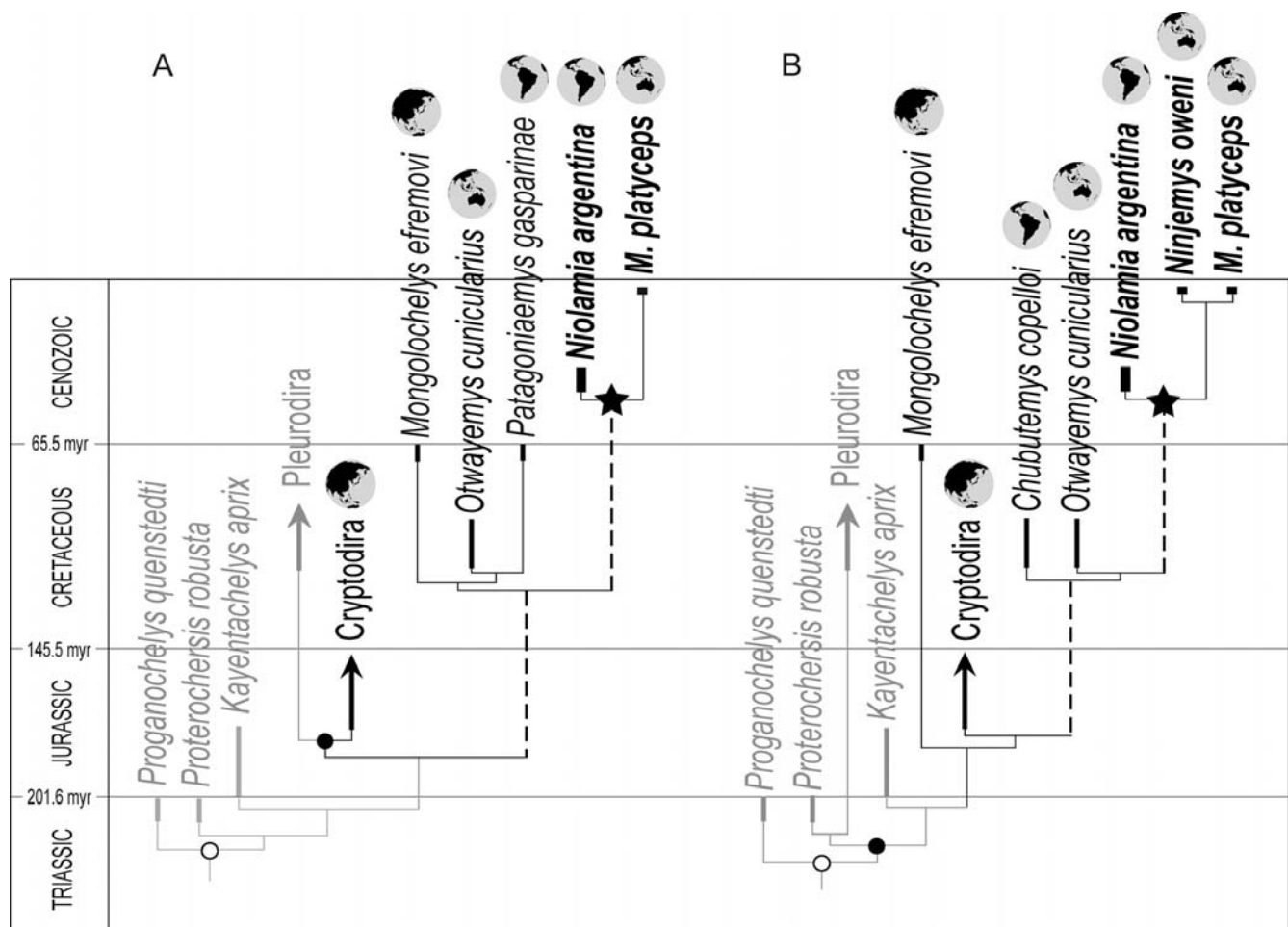


FIGURE 14. Phylogenetic hypotheses about the evolution of Meiolaniidae. **A**, Sterli and de la Fuente (2011) hypothesis. **B**, Gaffney et al. (2007) hypothesis. Dashed lines: ghost lineages discussed in the text. Thin vertical lines: ghost lineages. White circle: Testudinata (node-based definition). Black circle: Testudines (crown-group definition). Star: clade Meiolaniidae. In gray: taxa not considered in the discussion. In black: taxa discussed in the text.

that partially separates the posteromedial contact between both scales G. In MLP 26–40, there is no evidence of a paired scale A, and scale X does not prevent the medial contact between the G scales. In *Nin. oweni*, scale X has a small anterior process that slightly separates the posterior-most medial contact between both scales G, whereas in *M. platyceps* and *Warkalanina*, scale X has a rhomboidal shape, with one of the apices pointing anteriorly and separating the posteromedial contact of the G scales. Based on the phylogenetic position proposed for *Nio. argentina* (Gaffney, 1996; Sterli, 2010), if *C. corniger* is a juvenile, the absence of posteromedial contact of the G scales could be considered retention of a juvenile character in the adults (i.e., pedomorphosis) in *M. platyceps* and *Warkalanina*.

Phylogenetic Position of *Niolamia argentina*

The phylogenetic position of *Nio. argentina* among turtles was explored in two different contexts, one exploring the phylogenetic relationships among meiolaniids (Gaffney, 1996) and the other in a more inclusive phylogeny (Sterli, 2010; Sterli and de la Fuente, 2011). Although the phylogenetic position of the clade Meiolaniidae is controversial (Gaffney, 1996; Hirayama et al., 2000; Gaffney et al., 2007; Joyce, 2007), the position of *Nio. argentina* within Meiolaniidae is similar in Gaffney's and

Sterli's phylogenies (Fig. 14A, B). Because the phylogenetic position of Meiolaniidae among turtles exceeds the aim of this paper, we are going to focus our attention on the position of *Nio. argentina* itself. In both mentioned hypotheses, the Patagonian species *Nio. argentina* is recovered as the sister group of all the Australasian meiolaniids (Gaffney, 1996; Sterli, 2010; Sterli and de la Fuente, 2011). This phylogenetic hypothesis agrees with the stratigraphic record of meiolaniids, because *Nio. argentina* is the oldest member of the clade Meiolaniidae. The inclusion of the new information obtained after the preparation of *Nio. argentina* into a more inclusive phylogenetic analysis (Sterli and de la Fuente, unpubl. data) will allow further testing of the phylogenetic position of this species among meiolaniids.

Phylogeny, Ghost Lineages, and Paleobiogeography of Meiolaniidae and Related Taxa

Meiolaniid horned turtles are a monophyletic group of Testudinata (sensu Joyce et al., 2004) that were restricted to South America and Australasia during the Cenozoic (Gaffney, 1996, and references therein; White et al., 2010). Independent of which phylogenetic hypothesis is chosen, the calibration of the two main hypotheses of turtle evolution (Fig. 14) reveals an extensive ghost lineage for the clade Meiolaniidae that extends from the middle

Eocene to the Early Cretaceous (ca. 51 Ma). Moreover, the clade including Meiolaniidae and related taxa is also separated from Cryptodira by a long ghost lineage that extends ca. 47 Ma from the Early Cretaceous (oldest meiolaniid-like taxa) to the Middle Jurassic (oldest cryptodiran turtles as proposed by Danilov and Parham, 2006, 2008).

The presence of long ghost lineages between Gondwanan clades and exclusively non-Gondwanan clades is also observed in Notosuchia among crocodiles (Pol and Gasparini, 2007) and in Abelisauroida among theropods (Carrano and Sampson, 2008). Scarce outcrops of Middle and Late Jurassic non-marine rocks in Gondwana could be one of the plausible explanations for these similar patterns of ghost lineages in unrelated clades.

In addition, according to the preferred hypothesis followed here (Sterli and de la Fuente, 2011; Fig. 14A), Meiolaniidae and the clade formed by *Otwayemys cunicularius*, *Patagoniaemys gasparinae*, and *Mongolochelys efremovi* are recovered as sister groups. Such a close relationship among South American, Australian, and Mongolian taxa would imply a widespread distribution of this clade and related taxa prior to the fragmentation of Laurasia and Gondwana in the Early to Middle Jurassic (Hirayama et al., 2000). This is consonant with the presence of the ghost lineages subtending Meiolaniidae (Fig. 14A). The discovery of new fossil turtles in continental rocks of Middle Jurassic to Late Cretaceous age would help to complete this gap and illuminate the origin and diversification of this peculiar clade of turtles, the horned meiolaniids.

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