A new meiolaniform turtle from the Maastrichtian of Northern Patagonia, Argentina

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Meiolaniformes are a group of chelonians including the famous horned-turtles *Niolamia argentina* (Patagonia) and *Meiolania platyceps* (Australia). In South America, the Late Cretaceous meiolaniforms are represented by two named taxa: *Patagoniaemys gasparinae* coming from Campanian–Maastrichtian beds of the La Colonia Formation, Chubut province, and *Trapalcochelys sulcata* from the Campanian–Maastrichtian beds of the Allen Formation, Río Negro Province. The aim of the present contribution is to describe a new meiolaniform chelonian coming from the Upper Cretaceous (Maastrichtian) Los Alamitos Formation, at Río Negro Province, Argentina. The material is represented by a partial basicranium, incomplete carapace and fragmentary postcranial bones (MPMIK 1839/P/33) belonging to a new species *Patagoniaemys aeschyli*. To this new species we refer all the material previously referred as indeterminate meiolaniid, meiolaniform and cf. *Niolamia* sp., coming from the same site and locality, and described by different authors since the 1980s. This new species differs from the type species *P. gasparinae*, particularly by the presence of longitudinal ridges in the nuchal bone. We also include brief comments about meiolaniform palaeobiogeography and the impact of K/Pg extinction event in Patagonian chelonians.

Key words: Testudinata, Meiolaniformes, Los Alamitos Formation, Maastrichtian, Cretaceous, Patagonia, Argentina.

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Introduction

Meiolaniformes represent a group of turtles that includes the well-known horned species *Niolamia argentina* (Patagonia) and *Meiolania platyceps* (Australia). Uncontroversial meiolaniforms are known from Early Cretaceous to Pleistocene times in southern landmasses, including South America, Australia, and New Caledonia (Sterli 2015). In addition, several authors support that the Late Cretaceous *Kallokibotion bajazidi* from Romania and *Mongolochelys efremovi* from

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Mongolia (Nopcsa 1923; Khozatskii 1997), among others, should be included among Meiolaniformes (Ckhikvadzé 1987; Hirayama et al. 2000; Joyce 2007; Sterli 2008; Anquetin 2011; Sterli and de la Fuente 2011a, b, 2019; Sterli et al. 2013; but see Joyce et al. 2016 and Pérez-García and Codrea 2018). The increasing number of extinct turtles potentially related to Meiolaniidae highlights the fact that the group was very diverse and that it had a long and complex evolutionary history.

Until recently, the better-known meiolaniform was the derived clade, the Meiolaniidae, from the Cenozoic, with its most iconic species, *Meiolania platyceps* described in great detail by Gaffney (1983, 1985, 1996). In South America, Late Cretaceous meiolaniforms are known from two described species: *Patagoniaemys gasparinae*, which originates from the Campanian–Maastrichtian deposits of the La Colonia Formation in Chubut Province (Sterli and De la Fuente 2011a), and *Trapalcochelys sulcata*, found in the Campanian–Maastrichtian strata of the Allen Formation in Río Negro Province (Sterli et al. 2013). Recently discovered specimens of *Patagoniaemys gasparinae* makes this species the most complete non-meiolaniid meiolaniform from Gondwana (Sterli et al. 2021; Oriozabala et al. 2025).

In addition, some scattered remains of several indeterminate meiolaniforms were described from several localities in Patagonia, indicating that the clade is far more abundant and geographically widespread than previously thought (Broin 1987; Broin and de la Fuente 1993; Gasparini and de la Fuente 2000; Sterli et al. 2013, 2021; Sterli 2015; Moyano-Paz et al. 2022). Particularly, Broin (1987) recognized the occurrence of meiolaniids (nowadays recognized as meiolaniforms, see Sterli et al. 2013) in the Maastrichtian beds of the Los Alamitos Formation, at Nueva Poupée farm (Los Alamitos farm at that time), which constitute the first Cretaceous meiolaniforms recognized in South America. She supported the idea that the specimens (consisting of a humerus and isolated carapace fragments and bones) were closely related to the Cenozoic Patagonian meiolaniid, *Niolamia argentina*. Later, Broin and de la Fuente (1993), Gaffney et al. (2007), and Sterli et al. (2013) recognized new fragmentary meiolaniform specimens from the same locality and age. Because of their isolated and fragmentary nature, all the specimens remained as indeterminate Meiolaniformes.

The aim of present contribution is to describe a partial carapace, cranial, and postcranial bones belonging to an associated meiolaniform specimen coming from the Maastrichtian beds of Los Alamitos Formation, at Nueva Poupeé farm, Río Negro Province, Argentina. The new specimen belongs to a new species of the genus *Patagoniaemys*, which sheds light on the still poorly known Late Cretaceous record of meiolaniforms.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:8C16458D-1D80-4B4C-8957-21010FB6769E

Institutional abbreviations.—MACN-Pv RN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional Paleovertebrados-Río Negro, Buenos Aires, Argentina; MPMIK, Museo Provincial “María Inés Kopp”, Valcheta, Río Negro, Argentina.

Other abbreviations.—SQS, shareholder quorum subsampling.

Geological setting

The specimens here described come from the base of Cerro Cuadrado (41° 57’13.5” S 66° 19’ 20.3” W; 582 m a.s.l.), at Nueva Poupée Farm (ex Los Alamitos Farm), approximately at 60 km from Arroyo Ventana locality, Valcheta Department, Río Negro Province, Patagonia, Argentina (Fig. 1A, B). The fossil bearing bed is a non-calcareous pelitic facies from the lower section of the Los Alamitos Formation (sensu Andreis 1987; see Fig. 1C, D). This bed contains almost all the microvertebrates found in the Formation (Bonaparte et al. 1984; Bonaparte 1987). The specimens described here were found together with abundant microvertebrates, including diverse fishes, anurans, snakes, sphenodonts, chelid turtles, birds, sauropods, theropods and hadrosaurid teeth, and abundant sauropod eggshells, as well as an unprecedented mammalian diversity (see Bonaparte et al. 1984; Albino 1987, 2000; Báez 1987; Bonaparte 1987, 2002; Broin 1987; Cione 1987; Powell 1987; Apesteguía 2005; Agnolín and Martinelli 2009; Gómez 2016; Rougier et al. 2021; Rozadilla et al. 2021; Agnolín et al. 2024; Panzeri et al. 2024).

Material and methods

Mechanical preparation.—The specimen was prepared using mechanical methods. The carapace was excavated and placed into two plaster jackets, which were prepared in two main stages. On the first stage a pin vise with a tungsten needle was used, removing small fragments of sediment containing some scattered materials of small vertebrates, taking advantage of the small fragments of the sediment, with the aim of getting close to the carapace elements while removing and protecting the delicate and small vertebrate remains. A second stage consisted of preparing the carapace materials using air scribes, particularly Micro Jack 3 and 4 and also the pin vise with a sharp tungsten needle and a 45° chisel shaped needle to give some detail. Because of the

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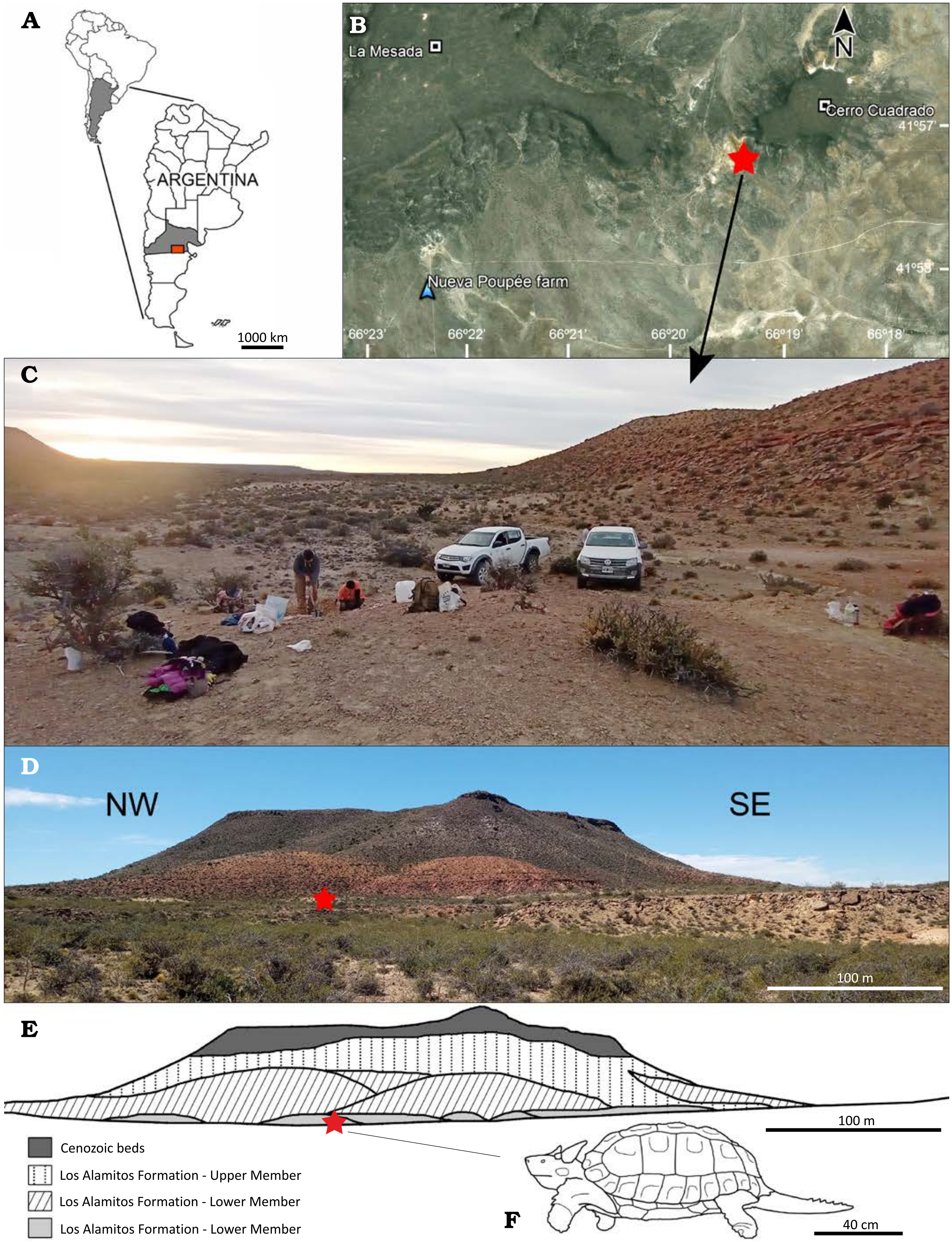
Fig. 1. **A**. Map showing geographic location of the study area within Argentina. **B**. Satellite map showing the location of Cerro Cuadrado. **C**. Photograph of the site showing the excavation work. **D**. Panoramic photograph of the discovery site. **E**. Line diagram showing outcrops in the type section of the Los Alamitos Formation southwest of Cerro Cuadrado. The red star marks the find site. **F**. Reconstruction of *Patagoniaemys aeschyli* sp. nov. (artwork by NRC)


A
ARGENTINA
1000 km
B
La Mesada
N
Cerro Cuadrado
41°57'
41°58'
Nueva Poupée farm
66°23'
66°22'
66°21'
66°20'
66°19'
66°18'
C
D
NW
SE
100 m
E
100 m
Cenozoic beds
Los Alamitos Formation - Upper Member
Los Alamitos Formation - Lower Member
Los Alamitos Formation - Lower Member
F
40 cm

fragmentary state of the carapace, cyanoacrylate adhesives were applied when needed. Long bones and vertebrae were prepared mechanically with air scribes Micro Jack 3 and 4.

Comparisons.—The specimens were compared to other meiolaniforms from Patagonia, Australia, and Asia. Those comparisons were based on firsthand observations by JS (*Chubutemys copelloi*, *Patagoniaemys gasparinae*, *Trapalcochelys sulcata*, specimens from Los Alamitos (*Peligrochelys walshae*, *Niolamia argentina*, *Gaffneylania auricularis*, *Otwayemys cunicularius*, and *Meiolania platyceps*), photographs (*Mongolochelys efremovi*), and the literature (Gaffney 1983, 1985, 1996; Gaffney et al. 1998, 2007; Sterli and de la Fuente 2011a, 2013, 2019; Sterli 2015; Sterli et al. 2013, 2015).

For the diversity analysis, we downloaded the data from the Paleobiology Database on August 25, 2025 (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app71-Agnolin_etal_SOM.pdf). We downloaded the species diversity count (SOM 1) from Patagonia listing the Argentinean provinces of Mendoza, Neuquén, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego. The Chilean Patagonia was not included because there are no species recognized in the Cretaceous–Paleogene. The time rule used was “major”. We also downloaded the list of occurrences at species level to account for the list of species recognized in each time bin (SOM 2). We calculated three diversity estimates following Vlachos (2024; and references therein): raw species diversity, range-through species diversity, and shareholder quorum subsampling (SQS). SQS was applied to account for uneven sampling intensity among time bins, as it standardizes samples based on coverage (the proportion of true diversity represented in a sample) rather than on the absolute number of occurrences or individuals. Coverage was calculated for each time bin. The SQS correction was calculated using the divDyn package (Kocsis et al. 2019, 2022) in R (R Core Team 2024) that calculates the SQS as in Alroy (2014). We used the sampled-in-bin richness (divSIB in the divDyn package; Koscis et al. 2022) and the SQS-corrected for 0.2 quorum levels (SOM 3). The diversity curves were calculated in Excel and subsequently edited in Adobe Illustrator for graphical purposes only to improve clarity and readability.

Systematic palaeontology

Testudinata Klein, 1760

Meiolaniformes Sterli & de la Fuente, 2013

Genus *Patagoniaemys* Sterli & de la Fuente, 2011a

Type species: *Patagoniaemys gasparinae* Sterli & de la Fuente, 2011a; Chubut Province, Argentina, Campanian–Maastrichtian.

Patagoniaemys aeschyli sp. nov.

Fig. 2–4.

ZooBank LSID: urn:lsid:zoobank.org:pub:8C16458D-1D80-4B4C-8957-21010FB6769E

Etymology: In reference to Aeschylus (525–455 BC), an ancient Greek writer often described as the father of tragedy. During a visit to the city of Gela (Italy), he was killed outside the city by a tortoise dropped by an eagle, which had mistaken his bald head for a rock suitable for shattering the shell.

Holotype: MPMIK 1839/P/33 (Figs. 2, 3, 4A_1–A_{10}, C_1–C_{10}), associated specimen including the posterior-most part of the basicranium formed by the basioccipital and parts of both exoccipitals, anterior margin of the dorsal carapace with part of the nuchal, right peripherals 1–4 and left peripherals 1–3 and part of right costal 1, three posterior peripherals, plastral bridge from the right side, including partial left hyoplastron, two highly incomplete neural arches of anterior cervical vertebrae, incomplete cervical 4, two incomplete centra of posterior cervical vertebrae, two fused thoracic vertebral centra, ?ilium, right pubis, and distal end of left humerus. The specimen was recovered partially articulated at a very restricted area (approximately 1 m^2) and was collected by members of our team during a fieldtrip in 2022.

Type locality: Cerro Cuadrado (41°57’13.5” S, 66°19’20.3” W; 582 m a.s.l.), Valcheta department, Río Negro Province, Argentina.

Type horizon: Los Alamitos Formation, Maastrichtian, Upper Cretaceous.

Material.—MPMIK 1839/P/34, isolated caudal vertebra (Fig. 4B); MACN-RN 36, left humerus (Broin 1987: pl. 1: 1); MACN-RN 37, bridge peripheral (Broin 1987: pl. 1: 2); MACN-RN 38, left anterior peripheral (Broin 1987: pl. 1: 3); MACN-RN 39, left bridge peripheral (Broin 1987: pl. 1: 4); MACN-RN 40, posterior peripheral (Broin 1987: pl. 1: 5); MACN-RN 41, left posterior peripheral (Broin 1987: pl. 1: 6); MACN-RN 63, peripheral 7 or 8; MACN-RN 64, right anterior peripheral 2 or 3; MACN-RN 66, fragment indet.; MACN-RN 67, fragment indet. or ?right bridge peripheral; MACN-RN 68, fragment indet.; MACN-RN 69, left peripheral 1 or 2; MACN-RN 70, peripheral indet.; MACN-RN 101, fragment of proximal end of left humerus; MACN-RN 709, fragment indet; MACN-RN 907, incomplete cervical 4 (Broin and de la Fuente 1993: fig. 5a–e); MACN-RN 908, incomplete cervical 8 (Broin and de la Fuente 1993: fig. 5f–j); MACN-RN 909, thoracic vertebra 10; MACN-RN 910, neural plate and waved costal; MACN-RN 918 fragment of right peripheral 1 or 2; MACN RN unnumbered, several caudal vertebrae. All from the type locality and horizon.

Diagnosis.—Large chelonian (maximum anterior carapace width about 60 cm, maximum inferred carapace length 80 cm). Referable to meiolaniforms by several features, namely the presence of small pits and grooves ornamenting carapace bones, anteriorly curved grooves among marginal scutes, opisthocoelous caudal vertebrae, and carapace-plastron connection through ligaments (Gaffney 1996; Hirayama et al. 2000; Sterli and de la Fuente 2013; Sterli et al. 2013). It is referred to *Patagoniaemys* by having a basioccipital with well-developed basal tubera with a concave surface between them, posteriorly flat occipital condyle, a shallowly notched anterior carapace margin, presence of a thickened bump on the posterior part of anterior marginal scutes, biconvex and

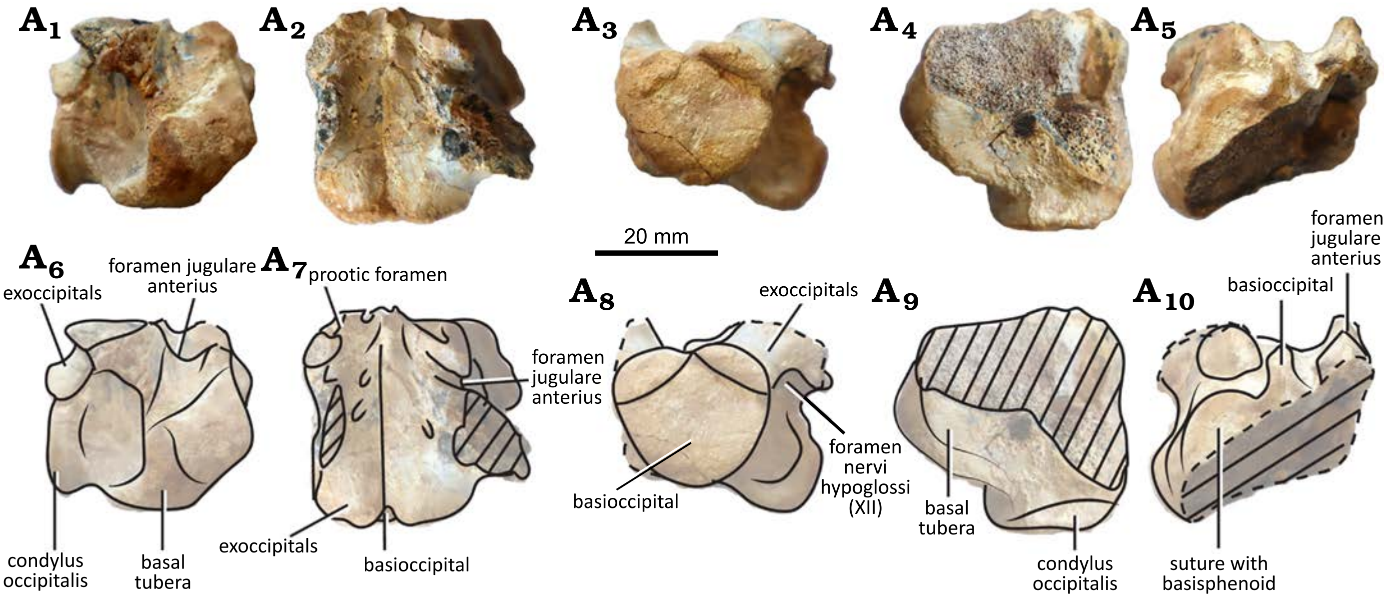


Fig. 2. Meiolaniform turtle *Patagoniaemys aeschyli* sp. nov. holotype (MPMIK 1839/P/33); Cerro Cuadrado locality, Argentina, Los Alamitos Formation Maastrichtian (Upper Cretaceous). Basioccipital in lateral (A_1, A_6), dorsal (A_2, A_7), posterior (A_3, A_8), ventral (A_4, A_9), and anterior (A_5, A_{10}) views. Photographs (A_1–A_5), explanatory drawings (A_6–A_{10}). The dashed areas correspond to missing parts.

narrow cervical 4 having a notably ventrally keeled centrum and disparate-sized articular surfaces with the anterior one bigger than the posterior one (Sterli and De la Fuente 2011; Oriozabala et al. 2025). *P. aeschyli* sp. nov. differs from the only previously known species of the genus, *P. gasparinae* in the presence of at least 5 longitudinal ridges on the nuchal bone (a feature unknown in other meiolaniforms) and the presence of a trapezoidal and narrow cervical scute with a posterior groove (lyra-shaped in contour in *P. gasparinae*; Oriozabala et al. 2025).

Description.—The description is based on the MPMIK 1839/P/33 (holotype) and MPMIK 1839/P/34 (caudal vertebra). Remaining specimens have been described elsewhere by previous authors (see de Broin 1987 and Sterli 2015).

Basicranium (Fig. 2): Only the posteriormost part of the basicranium is preserved. It is formed by the basioccipital and parts of the exoccipitals. In this part of the skull, the occipital condyle, the ventral rim of the foramen magnum, the basal tubera, and the foramina for the cranial nerve XII can be identified. The occipital condyle is kidney-shaped and it is formed by the basioccipital with contributions of both exoccipitals. The articular surface is flat. In ventral view, one of the basal tubera is preserved (the other is broken). The preserved basal tuber is well-developed latero-ventrally. In anterior view, the articular/sutural surface with the basisphenoid is partially preserved. In dorsal view, we can recognize at least two pairs of foramina nervi hypoglossi (cranial nerve XII), the foramen jugulare anterius (through which the cranial nerves X and XI exit the skull as well as the vena capitis cerebralis; Gaffney 1979), and the basis tuberculi basalis (where the bifid ligament of the medulla attaches; Kesteven 1910).

Carapace (Fig. 3): The anterior margin of the carapace is smoothly notched. The margins of the peripheral bones are gently dorsally curved (Fig. 3A_1–A_4). Preserved maximum anterior carapace width is about 60 cm, with an estimated total length of about 80 cm. The carapace is relatively thick at the base of the peripheral plates, where it shows a series of robust thick bumps, especially in the posterior parts of marginal (Fig. 3A_5, A_6). The external surface of the carapace ornamentation is composed of small pits and grooves.

Plates: The nuchal bone is incompletely preserved, but it was relatively wide and trapezoidal in contour (Fig. 3A_7, A_8). The preserved contacts are with peripheral 1 and costal 1 laterally. It has at least 5 longitudinal ridges, with the middle one the most prominent. Peripheral 1 is triangular or sub-trapezoidal in shape. It contacts peripheral 2 laterally, the nuchal medially, and costal 1 posteriorly. Peripheral 2 is rectangular, being longer than wide. It contacts peripheral 1 medially, peripheral 3 laterally and costal 1 posteriorly. Peripheral 3 is squarish and contacts peripheral 2 anteriorly, costal 1 posteromedially, and peripheral 4 posteriorly. The carapace peripheral bridge starts in this peripheral, where the axillary buttress abuts. Peripheral 4 is a bridge peripheral, rectangular in contour and C-shaped in cross-section. The only preserved contact is the anterior one with peripheral 3. Only right costal 1 is partially preserved. The preserved contacts are with the nuchal anteriorly and with peripherals 1 to 3 laterally. In ventral view, remains of the thoracic rib 2 are preserved and the sutural area for thoracic rib 1 is seen. The axillary buttress seems to extend over the costal 1.

Scutes: The cervical scute was present. Its posterior sulcus is not preserved, consequently its complete shape cannot be assessed. The lateral sulci converge anteriorly.

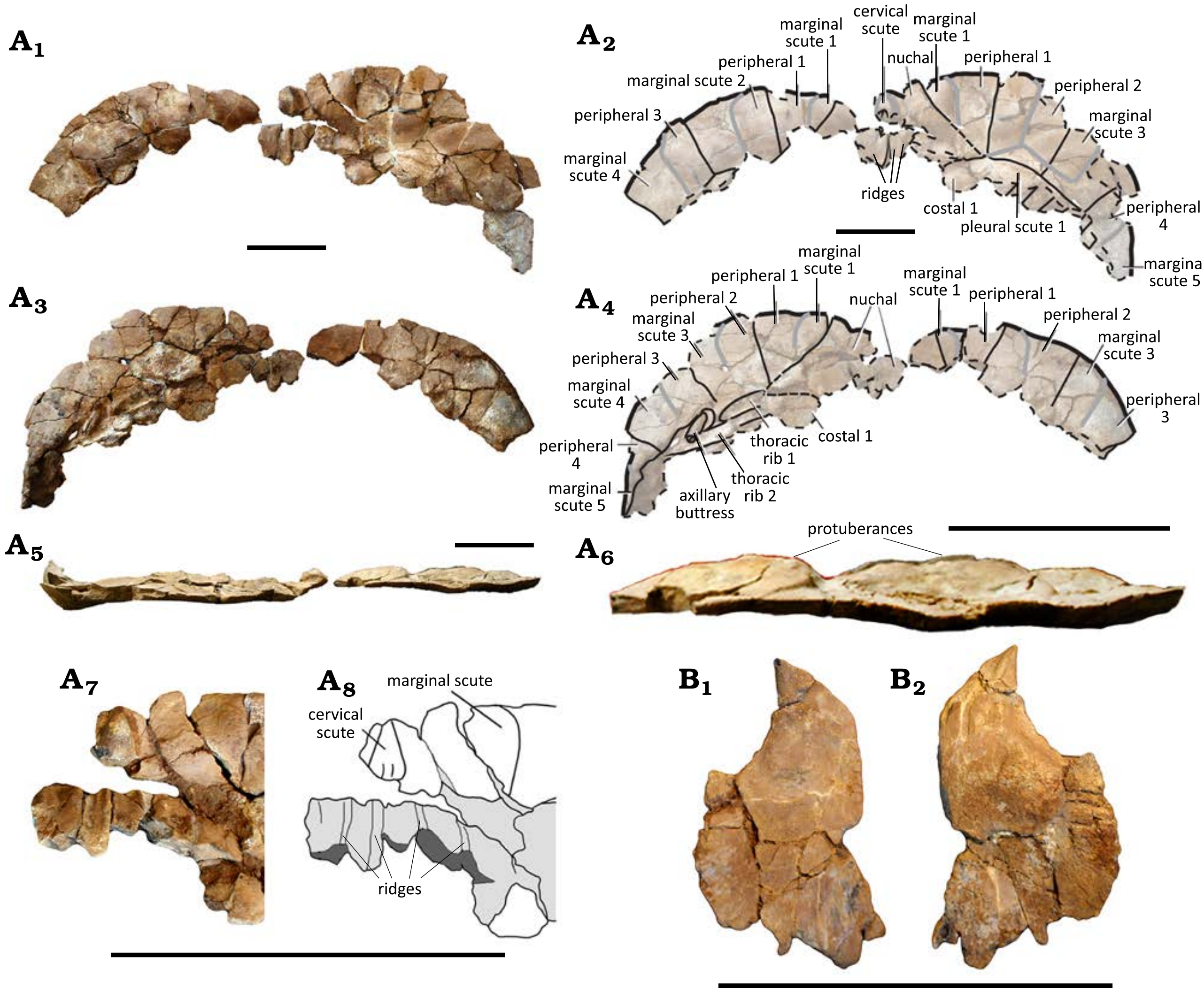


Fig. 3. Meiolaniform turtle *Patagoniaemys aeschyli* sp. nov. holotype (MPMIK 1839/P/33); Cerro Cuadrado locality, Argentina, Los Alamitos Formation Maastrichtian (Upper Cretaceous). **A**. Carapace; anterior border in dorsal (A_1, A_2) and ventral (A_3, A_4) views (grey lines, limits of the scutes; black lines, limits of the plates; dashed lines, possible limits of the plates), anterior view of the left side of the anterior margin (A_5), enlargement showing the protuberances that are typical of the genus (A_6), detail of the anterior margin in ventral view (A_7, A_8), showing the presence of longitudinal ridges that characterize the new species (light grey, nuchal bone; dark grey, broken surfaces). **B**. Left hyoplastron fragment in ventral (B_1) and visceral (B_2) views. Photographs (A_1, A_3, A_5–A_7, B), explanatory drawings (A_2, A_4, A_8). Scale bars 100 mm.

The cervical scute articulated on an inverted V-shaped protuberance made by the nuchal. Cervical contacted marginal 1 laterally, and probably vertebral 1 posteriorly. Only the lateral sulci of marginal 1 are preserved. Marginal 1 covered part of the nuchal and peripheral 1. The intermarginal sulci have a strong, anterior inflection in the rim of the carapace. Marginal 2 was squarish and contacted marginal 1 medially, marginal 3 laterally, and, at least, pleural 1 posteriorly. It covered the posterior part of peripheral 1, the tip of the nuchal, and the anterior part of peripheral 2. Marginal 3 covered the posterior part of peripheral 2 and the anterior part of peripheral 3. It contacted marginal 2 anteromedially, pleural 1 posteromedially, and marginal 4 laterally. Marginal 4 was rectangular and covered the posterior part of peripheral 3 and the anterior part of peripheral 4. It contacted marginal 3 anteriorly and marginal 5 posteriorly. Marginal 5 was covering the posterior part of peripheral 4. The only preserved contact was with marginal 4. The posterior part of marginals 1–3 covered bony protuberances of the underlaying plates.

Plastron: The hyoplastron forms part of the axillary buttress and is represented by a sheet of bone curving distally around the forelimb opening. Its incomplete nature does not clarify whether a plastral fontanelle was present (Fig. 3B).

Vertebral column: Two incomplete neural arches of cervical vertebrae have been preserved. There is no well-differentiated neural spine. A nearly complete centrum of cervical 4 is preserved (Fig. 4A). It is biconvex and is notably transversely compressed and shows a very prominent and narrow ventral longitudinal keel. The posterior condyle is

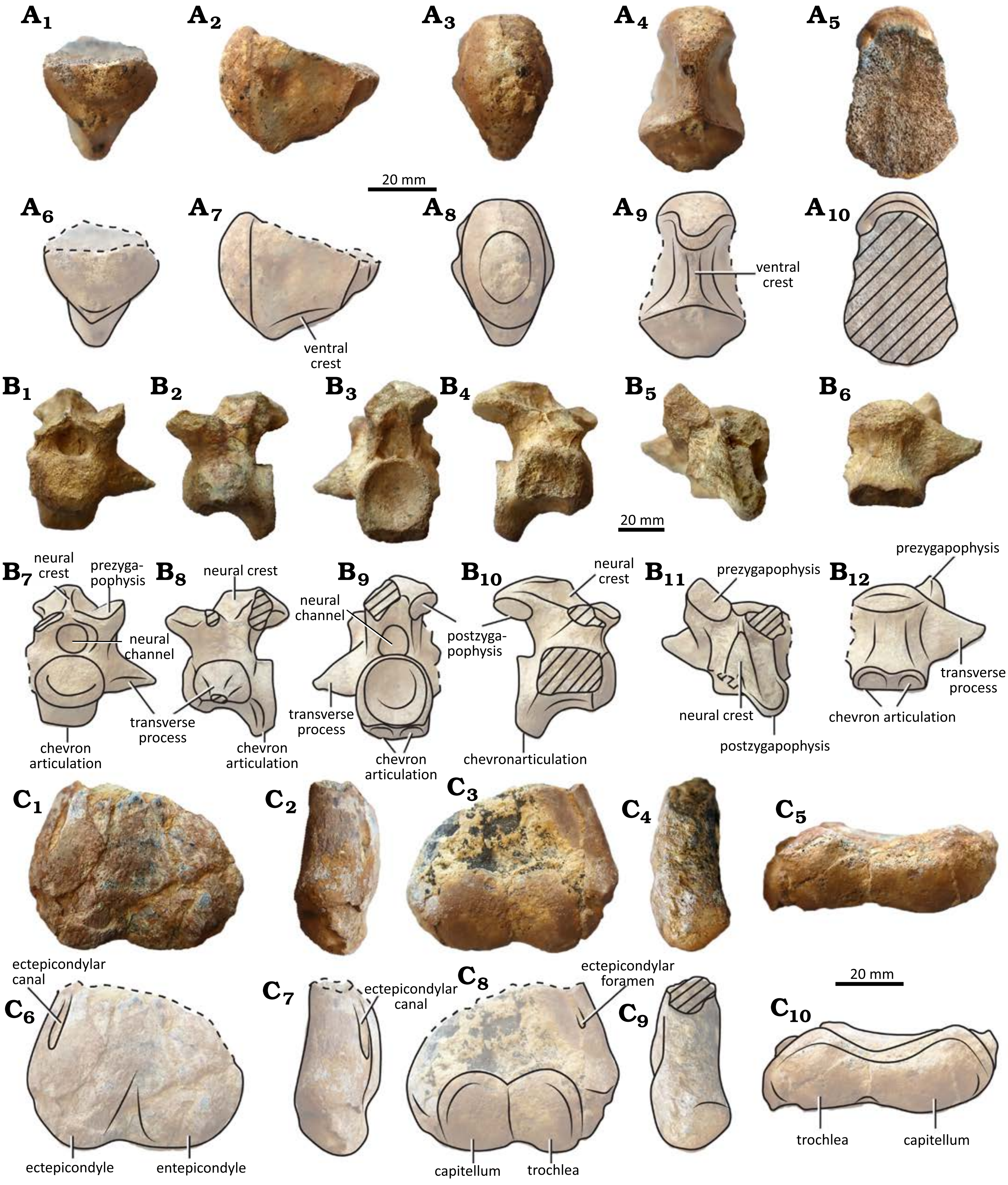


Fig. 4. Meiolaniform turtle *Patagoniaemys aeschyli* sp. nov., Cerro Cuadrado locality, Argentina, Los Alamitos Formation Maastrichtian (Upper Cretaceous). **A**. MPMIK 1839/P/33 (holotype), cervical vertebra 4 in anterior (A_1, A_6), lateral (A_2, A_7), posterior (A_3, A_8), ventral (A_4, A_9), and dorsal (A_5, A_{10}) views. **B**. MPMIK 1839/P/34, anterior caudal vertebra in anterior (B_1, B_7), right lateral (B_2, B_8), posterior (B_3, B_9), left lateral (B_4, B_{10}), dorsal (B_5, B_{11}), and ventral (B_6, B_{12}) views. **C**. MPMIK 1839/P/33 (holotype), distal end of left humerus in capitular (C_1, C_6), ulnar (C_2, C_7), intertubercular (C_3, C_8), radial (C_4, C_9), and distal (C_5, C_{10}) views. Photographs (A_1–A_5, B_1–B_6, C_1–C_5), explanatory drawings (A_6–A_{10}, B_7–B_{12}, C_6–C_{10}). The dashed areas correspond to missing parts.

ovoidal, higher than wide. The anterior condyle is wider than the posterior one, but as it is broken, its complete contour is unknown.

There are two incompletely preserved but strongly sutured (through synchondrosis) thoracic vertebral centra. They are longer than wide and hourglass-shaped in ventral view.

The caudal MPMIK 1839/P/34 is opisthocoelous (Fig. 4B). The centrum in ventral view is anteroposteriorly longer than transversely wide. The condyle is oval with its main axis horizontally oriented and the cotyle is almost round, slightly taller than wide. On its posteroventral edge, the wide and well-defined double articulation for the chevron is seen. There is a wide, longitudinal, ventral crest on the centrum. The transverse process is very thick and subquadrangular in cross-section at its base. It is subtriangular in contour and strongly anteriorly oriented. The neural crest is present but low.

Humerus: Only the distal end of a left humerus was found (Fig. 4C). The canal of the enclosed ectepicondylar foramen is seen in the capitular view. In the intertubercular view, it shows two distal condyles, one for the radius (capitellum) and one for the ulna (trochlea). The condyles are bulbous, subequal in size and extension. Both are separated by a narrow and shallow, but well-defined, intercondylar groove. The ectepicondylar foramen exits in the intertubercular view, next to the capitellum.

Remarks.—As outlined in the diagnosis and description, we consider this new species to present a combination of unique features sufficient to distinguish it from all other known taxa. The holotype preserves much of the anterior end of the carapace, a region that bears numerous diagnostic characters in meiolaniforms. Fortunately, Campanian–Maastrichtian meiolaniforms from Patagonia, namely *Trapalcochelys sulcata* and *Patagoniaemys gasparinae* include materials that could be directly compared with the material of the new species (Sterli et al. 2013; Oriozabala et al. 2025). Among meiolaniforms, *Patagoniaemys aeschyli* sp. nov. shares with *P. gasparinae* (Oriozabala et al. 2025), and probably *Trapalcochelys sulcata* and *Peligrochelys walshae*, a shallow notch in the anterior margin of the carapace. An anteriorly notched carapace is absent in the basal forms *Chubutemys copelloi* and probably *Otwayemys cunicularius* (Gaffney et al. 1998; Sterli et al. 2015). *Patagoniaemys aeschyli* sp. nov. shares with *P. gasparinae* the presence of thickened bumps on the posterior part of anterior marginal scutes, features absent in *Mongolochelys efremovi* (see Sukhanov 2000; Oriozabala et al. 2025). Otherwise, *Patagoniaemys aeschyli* sp. nov. and *P. gasparinae* share with *Mongolochelys efremovi* the presence of a wide, trapezoidal nuchal that almost prevents the contact of peripheral 1 and costal 1. The nuchal bone of *Patagoniaemys aeschyli* sp. nov. differs from *P. gasparinae* in the presence of at least 5 longitudinal ridges and the presence of a narrow cervical scute with a posterior groove, that strongly differs from the lyra-shaped contour present in *P. gasparinae* (Oriozabala et al. 2025).

Patagoniaemys aeschyli sp. nov. shares with *Otwayemys cunicularius* and *Mongolochelys efremovi*, a long thoracic rib 1 that reached or almost reached the axillary buttress. In *P. aeschyli* sp. nov. the bridge starts in peripheral 3 close to the anterior suture with peripheral 2, as in *M. efremovi*. In *Patagoniaemys gasparinae*, the axillary buttress reached peripheral 2 in one of the sides (JS personal observations). In spite of being not completely preserved, the low and wide carapace of *P. aeschyli* sp. nov. differs from that of derived meiolaniids (e.g., *Meiolania*) which show a strongly domed carapace (Gaffney 1996; Gaffney et al. 1992; Sterli and de la Fuente 2011a).

In *Patagoniaemys aeschyli* sp. nov., only one basal tuber of the basioccipital is completely preserved and well developed, whereas the other is broken. Based on the morphology and orientation of the preserved tuber, we infer that the original condition involved well-separated basal tubera with a concave surface between them, as observed in some specimens of *Peligrochelys walshae* (Sterli and de la Fuente 2019) and *Patagoniaemys gasparinae* (JS personal observations based on unpublished material). In contrast, some specimens of *Peligrochelys walshae* (e.g., MACN-PV CH 2017) exhibit a longitudinal ridge between the basal tubera. The occipital condyle of *Patagoniaemys aeschyli* sp. nov. is flat posteriorly as in *P. gasparinae* (JS personal observations based on unpublished material) and *Chubutemys copelloi* (Gaffney et al. 2007; Sterli et al. 2015). The occipital condyle in *P. aeschyli* sp. nov. is formed by the basioccipital and both exoccipitals. Due to the fusion of basioccipital and exoccipital in the condyle area, the contribution of the exoccipitals to the occipital condyle cannot be assessed for *Chubutemys copelloi*, *Peligrochelys walshae*, *Patagoniaemys gasparinae*, and *Mongolochelys efremovi*.

A common trait shared by *Patagoniaemys aeschyli* sp. nov., *P. gasparinae*, and *Peligrochelys walshae* is the biconvex and narrow cervical 4 having a notably ventrally keeled centrum and disparately-sized articular surfaces (Sterli and de la Fuente 2011a). In both *P. aeschyli* sp. nov. and *P. gasparinae* the anterior condyle of cervical vertebra 4 is dorsoventrally taller and transverse wider than the posterior one. In *Peligrochelys walshae* both condyles of cervical vertebra 4 are similar in shape and size (Sterli and de la Fuente 2019). This morphology differs from the box-shaped condition exhibited by species of *Meiolania* (Gaffney 1985).

Anterior caudal vertebrae in meiolaniforms are opisthocoelous and the posteroventral end of the centra houses the articular area for the chevrons. This morphology is observed in *T. sulcata*, *P. aeschyli* sp. nov., *P. gasparinae*, *Peligrochelys walshae*, *Mongolochelys efremovi* and in the meiolaniids *Gaffneylania auricularis* and *Meiolania platyceps*. The lack of complete and/or undeformed specimens makes comparisons among taxa difficult. Meiolaniforms also have an enclosed ectepicondylar foramen in the humerus. This condition is seen in *P. aeschyli* sp. nov., *P. gasparinae*, *Peligrochelys walshae*, *Mongolochelys efremovi*, *Gaffneylania auricularis*, and *Meiolania platyceps*.

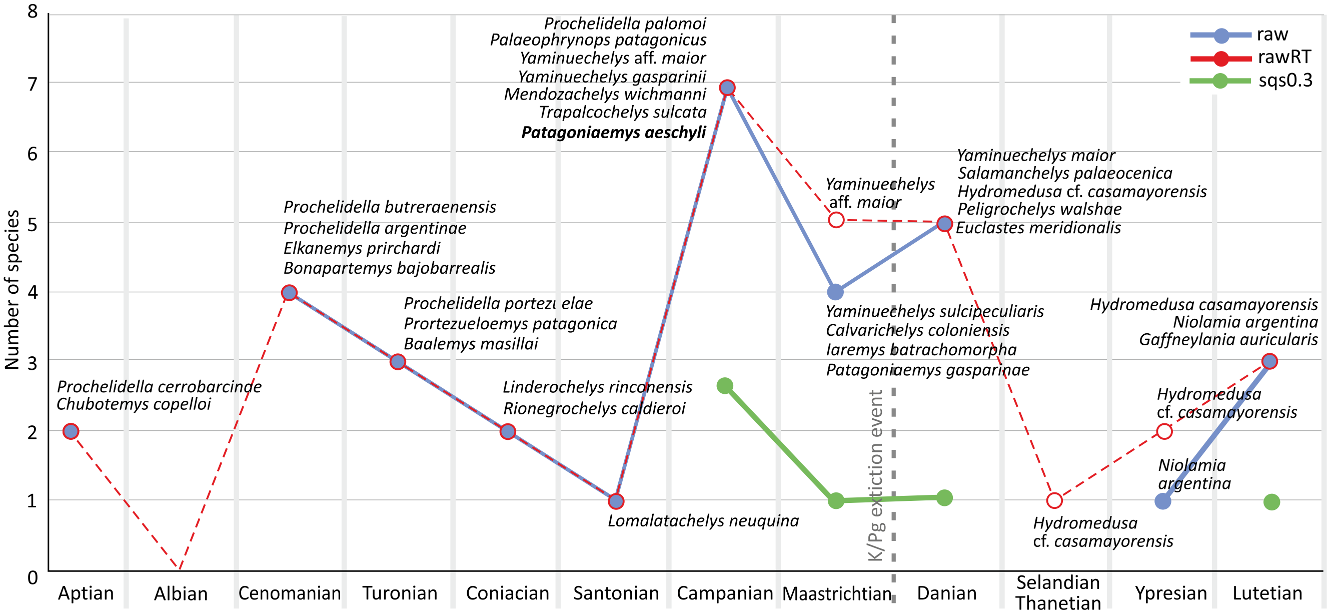


Fig. 5. Raw, range-through, and SQS 0.2 corrected species' diversity of turtles from the Cretaceous to the Paleogene in Patagonia. Data extracted from the Paleobiology Database (August 25, 2025).

The distal end of the humerus in *P. aeschyli* sp. nov. shows a narrow distal end with poorly developed epicondyles and separated distal condyles not forming a pulley-like continuous surface, features different from terrestrial chelonians, including meiolaniids in which the distal end of the bone forms a pulley-like articulation (Walker 1973; Nakajima et al. 2014; Krahl et al. 2019; see Gaffney 1996; Sterli et al. 2015). The ectepicondyle and entepicondyle are subequal in size and are much more transversely narrow than in *Peligrochelys walshae* (Sterli and de la Fuente 2019). Due to the fragmentary nature of the humerus in *P. aeschyli* sp. nov., no further comparisons are possible.

Stratigraphic and geographic range.—Cerro Cuadrado locality, Argentina, Los Alamitos Formation Maastrichtian (Upper Cretaceous).

Discussion

The discovery of meiolaniids in South America and Australia in the 19th century sparked a great debate. The discovery of such large and terrestrial forms on now separated landmasses was taken as a proof of ancient connection between the continents by Moreno (1899). This view was strongly criticized by Simpson (1938, 1939) who indicated that the common presence of meiolaniids was the result of parallel invasions from North America and Asia, respectively. Under this scheme, there occurred a single, or just a few, old biotic dispersal events between Australia and South America (e.g., Simpson 1980; Pascual et al. 1992; Szalay and Sargis 2001; Meredith et al. 2009; Wilf et al. 2013).

On the other hand, the common occurrence of basal meiolaniforms and derived meiolaniids in Patagonia and Australia is congruent with other faunistic evidence supporting the strong biotic ties between both landmasses during the Cenozoic (see Gaffney 1996; Beck 2012; Sterli et al. 2013; Ezcurra and Agnolín 2012; Agnolín 2024), and puts into question the occurrence of a single or a few dispersal events between both landmasses.

Vlachos et al. (2018) suggested that turtles in South America were seriously affected by the K/Pg mass extinction, in contrast with what is observed for North American turtles (e.g., Holroyd and Hutchison 2002; Hutchison and Holroyd 2003; Lyson et al. 2011; Holroyd et al. 2014). According to Archibald (1996), this turtle fauna includes a mix of extinct (Adocidae, Baenidae, Macrobaenidae, Pleurosternidae, Nanhsuingchelydidae) and extant (e.g., Chelydridae, Kinosternidae, Trionychidae) lineages, with most extinctions occurring in strictly terrestrial lineages, whereas aquatic ones were poorly affected by the K/Pg event. Explanations for such differences range from authors who suggested that the turtles were able to survive because aquatic environments are more heterogeneous than terrestrial ones, allowing some taxa to survive in natural refuges (Holroyd and Hutchison 2002), or contrarily, because they are much more stable and are not strongly affected by large-scale extinction events (Bakker 1977). In any case, aquatic and semiaquatic turtles seem to be more likely to survive mass extinctions. In the analyzed raw diversity of Cretaceous–Paleogene chelonians from Patagonia (Fig. 5), there is a peak of diversity in the Cenomanian with 4 species and then, the diversity drops during the “mid-Cretaceous”. In the Campanian, the diversity increases again to 7 species, then descends to 4 in the Maastrichtian, increasing slightly again in the Danian with 5 species. In the raw diversity diagram, the K/Pg extinction event is not remarkable, because the major drop is seen between the Campanian and

Maastrichtian. This drop, and later stabilization between the Maastrichtian and Danian, is also recovered in the range-through diversity and in the SQS 0.2 analysis (Fig. 5; SOM 3). Although raw and corrected diversities were used herein, it is interesting to note that Vlachos (2024) noticed that the coverage for the Campanian, Maastrichtian, and Danian is similar (0.88, 0.87, and 0.82, respectively).

In this regard, it is worth mentioning that similarities between chelonian assemblages of the uppermost Cretaceous (Maastrichtian Allen, La Colonia, and Los Alamitos Formations) and the Lower Paleocene (Danian Banco Negro Inferior of the Salamanca Formation and Roca Formation) strata are impressive (Fig. 5). In the Banco Negro Inferior, chelonians are represented by the chelids *Yaminuechelys maior* (Staesche, 1929), cf. *Hydromedusa* sp. and *Salamanchelys palaeocenica* Bona, 2006 (Bona and de la Fuente 2005; Bona 2006; Maniel and de la Fuente 2016), and meiolaniforms by *Peligrochelys walshae* (Sterli et al. 2015). All these forms have representatives in Maastrichtian deposits, including *Yaminuechelys* species (present in Allen, La Colonia, and Los Alamitos formations; Broin 1987; Broin and de la Fuente 1993; de la Fuente et al. 2014; Gasparini et al. 2015; Sterli et al. 2021). *Salamanchelys* is very similar to indeterminate chelids described for these Maastrichtian units (Bona 2006), cf. *Hydromedusa* sp. was also reported previously in latest Cretaceous assemblages (e.g., Broin 1987), and *Peligrochelys* is very closely related to *Patagoniaemys* (Sterli et al. 2015). This is also supported by the fact that at least two lineages of meiolaniform turtles survived the K/Pg boundary, one including derived meiolaniids and the other includes large basal meiolaniforms (e.g., *Patagoniaemys* and *Peligrochelys*; Sterli and de la Fuente 2013; Sterli et al. 2015).

The substantial number of taxa shared between diverse Maastrichtian localities and the Paleogene Punta Peligro site have been previously noted for plants, mammals and reptiles (Stiles et al. 2020; Agnolín 2024; Bravo et al. 2025). This pattern suggests that the K/Pg extinction event may not have severely impacted certain lineages, particularly chelonians, and further supports the interpretation that the Punta Peligro site represents one of the earliest Paleogene localities in South America (see del Campo et al. 2025).

Conclusions

The material from the Maastrichtian Los Alamitos Formation supports the recognition of Patagoniaemys aeschyli sp. nov. as a new basal meiolaniform that expands both the diversity and morphological disparity of the clade in the Late Cretaceous of Patagonia. The combination of cranial, vertebral, and humeral features (particularly the distinctive longitudinal ridges on the nuchal) substantiates the taxonomic validity of the new species and confirms the presence of at least two meiolaniform lineages in the latest Cretaceous of southern South America. the marked taxonomic continuity between Maastrichtian and Danian assemblages suggests that the K/Pg extinction event did not severely impact Patagonian turtles, supporting a scenario of lineage persistence and limited faunal turnover among southern chelonians.

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