The LINNEAN SOCIETY of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2015, **174**, 519–548. With 16 figures

A new turtle from the Palaeogene of Patagonia (Argentina) sheds new light on the diversity and evolution of the bizarre clade of horned turtles (Meiolaniidae, Testudinata)

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Received 16 August 2014; revised 15 January 2015; accepted for publication 26 January 2015

In this contribution we present a new species of horned turtle, ***Gaffneylania auricularis*** **gen. et sp. nov.**, from the Paleogene of Patagonia. The specimens come from the lower section of the Sarmiento Formation (Middle Eocene) at Cerro Verde (Cañadón Hondo area, Province of Chubut, Argentina). The level containing turtles and crocodyliforrmes is located at the base of the section and it consists of laminated, fine tuffs interpreted as shallow pond sediments. It underlies another fossiliferous level comprising lenticular, massive sandstones bearing skeletal remains of mammals, referred by previous authors to the Casamayoran SALMA. *Gaffneylania auricularis* represents one of the most complete meiolaniids from South America found to date and it is distinguished from other meiolaniids by the presence of a peculiar half-moon-shaped, thick rim surrounding the cavum tympani, the presence of three cranial scutes K and an unenclosed canalis chorda tympani mandibularis, among others. This new species sheds new light on the evolution and palaeobiogeographical history of the clade Meiolaniidae in Australasia and South America during the Cainozoic. The break up of southern Gondwana provoked major global climatic changes during the Cainozoic that probably influenced the evolution of meiolaniid turtles. The co-evolution of meiolaniids with other amniotes (e.g. chelid turtles, mammals) suggests a common palaeobiogeographical history of those clades in southern Gondwana.

doi: 10.1111/zoj.12252

ADDITIONAL KEYWORDS: Casamayoran SALMA – Meiolaniformes – palaeobiogeography – phylogeny – Sarmiento Formation.

INTRODUCTION

Meiolaniidae, or horned turtles, is a bizarre group of turtles bearing cranial horns and frills, caudal rings, and a tail club that are restricted to the Eocene of southern South America and to the Oligocene, Neogene and Quaternary of Australasia (Australia and surrounding islands). Although Gaffney (1983, 1996), Gaffney & Meylan (1988) and Gaffney, Meylan & Wyss (1991) argued that Meiolaniidae is the sister group of the extant cryptodires, more recently other studies have referred this clade to the stem Testudines (Hirayama, Brinkman & Danilov, 2000; Joyce, 2007; Sterli, 2008; Sterli & de la Fuente, 2011a, 2013; Anquetin, 2012; Rabi *et al*., 2013; Zhou, Rabi & Joyce, 2014; Sterli, de la Fuente & Umazano, 2015). Meiolaniidae is deeply nested within Meiolaniformes, a clade recently defined by Sterli & de la Fuente (2013) and concluded to contain meiolaniids and the taxa *Chubutemys copelloi* Gaffney, Rich, Vickers-Rich, Constantine, Vacca & Kool, 2007, *Mongolochelys efremovi* Khosatzky, 1997, *Peligrochelys walshae* Sterli & de la Fuente, 2013, *Patagoniaemys gasparinae* Sterli & de la Fuente, 2011a, *Otwayemys*

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*Corresponding author. E-mail: jsterli@mef.org.ar *cunicularius* Gaffney, Kool, Brinkman, Rich, Vickers-Rich, 1998, and *Kallokibotion bajazidi* Nopcsa, 1923.

Meiolaniidae shows its greatest diversity in Australasia where at least five species have been named: *Warkalania carinaminor* Gaffney, Archer & White, 1992 from the ?Late Oligocene–Early Miocene of Riverside Station, north-west Queensland, *Meiolania brevicollis* Megirian, 1992 from the middle Miocene of Camfield Beds, Northern Territory, *Ninjemys oweni* (Woodward, 1888) from the Pleistocene of southern Queensland, *Meiolania platyceps* Owen, 1886 from Lord Howe Island and *Meiolania mackayi* Anderson, 1925 from Walpole Island (New Caledonia). By contrast, there is only one named species from South America, the Patagonian *Niolamia argentina* Ameghino, 1899 which is probably Eocene in age (Sterli & de la Fuente, 2011b). One of the objectives of the present paper is to present and describe a new species of Meiolaniidae from the Eocene of Patagonia. The specimens described here were found during fieldwork conducted in the austral summer of 2010 led by the palaeontologists Drs Pol and Sterli from MEF and Dr de la Fuente (Museo de Historia Natural de San Rafael, Argentina) in outcrops of the Sarmiento Formation in the Cañadón Hondo area (Chubut, Argentina). The second objetive is to explore the evolution of the clade in a phylogenetic and palaeobiogeographical context by gathering information from other clades, and the palaeogeography of southern Gondwana and from different palaeoclimatic proxies. As a result, extinction, dispersion and diversification patterns are recognized for the turtle fauna from the Cainozoic of Patagonia.

INSTITUTIONAL ABBREVIATIONS

MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

ANATOMICAL ABBREVIATIONS

aa, area articularis; ach, articulation with chevrons; ane, apertura narium externa; ang, angular; art, articular; bo, basioccipital; bs, basisphenoid; cap, capitellum; cc, canalis cavernosus; cctm, canalis chorda tympani mandibularis; CE, cervical scute; cl, cavum labyrinthicum; cm, condylus mandibularis; co, condylus occipitalis; csh, canalis semicircularis horizontalis; csp, canalis semicircularis posterius; ct, cavum tympani; den, dentary; dip, diapophysis; ds, dorsum sellae; dsc, drop-shaped concavity; ect, ectepicondyle; ectf, ectepicondylar foramen; ent, entepicondyle; epi, epipterygoid; exo, exoccipital; faccc, foramen anterius canalis carotici cerebralis; fana, foramen anterius nervi abducentis (VI); feng, foramen externum nervi glossopharyngei; fic, foramen intermandibularis caudalis; fja, foramen jugulare anterius; fm, foramen magnum; fme, fossa Meckelii; fnat, foramen nervi auriculotemporalis (V); fnh, foramen nervi hypoglossi (XII); fo, fenestra ovalis; for, foramen indet; fpccc, foramen posterius canalis carotici cerebralis; fpcci, foramen posterior canalis carotici interni; fpl, fenestra perilymphatica; fpo, fenestra postotica; fst, foramen stapedio-temporale; ha, hiatus acusticus; hh, humeral head; ica, incisura columella auris; ipts, intrapterygoid slit; K, cranial scute K; lar, labial ridge; lat, lateral process; MA, marginal scale; med, medial process; mx, maxilla; nc, neural channel; ncr, neural crest; nf, nutritious foramen; op, opisthotic; pa, parietal; pap, parapophysis; pe, peripheral bone; pf, prootic foramen; pi, processus interfenestralis; PL, pleural scute; pla, ovoid platform; pmx, premaxilla; prz, prezygapophysis; prar, processus retroarticularis; pro, prootic; pt, pterygoid; pto, processus trochlearis oticum; pz, postzygapophysis; qj, quadratojugal; qu, quadrate; rst, recessus scalae tympani; sq, squamosal; scor, suture with coronoid; sh, shoulder; sr, sulcus for the ramphotheca; ssp, suture with splenial; sur, surangular; sut, suture; tb, tuberculis basalis; thr, thoracic rib; tro, trochlea; tp, transverse process; ts, triturating surface; VE, vertebral scute.

GEOGRAPHICAL AND GEOLOGICAL SETTING

This study was performed in the Cañadón Hondo area (Fig. 1A, B), 65 km north-north-west from Comodoro Rivadavia City, Chubut Province, Argentina (Piatnitzky, 1931; Simpson, 1935; Andreis, 1977). The sedimentary sequence cropping out in this area corresponds to (from bottom to top) the Salamanca Formation, Río Chico Group, and Sarmiento and Chenque formations (Piatnitzky, 1931; Simpson, 1935; Feruglio, 1949; Andreis, 1977; Raigemborn *et al*., 2010). These units mainly crop out in incomplete sequences due to the frequent presence of common slides, and subordinate folds and faults.

The fossiliferous site is located in Rocas Gemelas near the Cerro Verde (Schaeffer, 1947). Two lateral sections are provided, 'Cerro Verde' and 'Pipe Rock', the latter located around 50 m to the east from the former (Figs 1B, 2, 3A–C). Beds cropping out show greenish colour and a general inclination of approximately 12° to the south-south-west. The lower 15 m of both sections is composed of massive, pyroclastic mudstones and fine tuffs. Intercalated, indurated cornices showing trough cross-bedding are present. Above these levels, the presence of silica is common, occurring as both interlayer bands and root endocasts (Fig. 3D, E).

At the Cerro Verde section, above the lowermost 15 m, fine and very fine tuffaceous sandstones occur. They

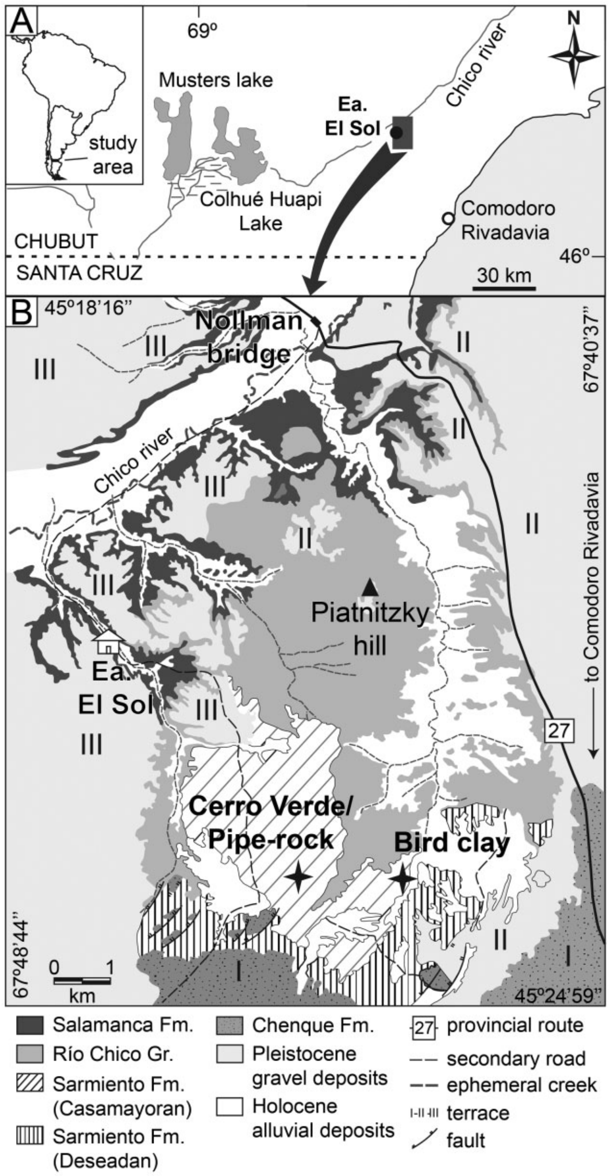

Figure 1. A, geographical location of the studied locality; B, simplified geological map of the Cañadón Hondo area (modified from Andreis, 1977; Pol *et al*., 2012).

display a tabular geometry. In the interval around 15–20 m, greenish, massive, tabular tuff contains skeletal remains of sebecid crocodyliforms (Pol *et al*., 2012) and meiolaniid turtles (the ones described herein). Above this level, a fine tuff with parallel lamination was deposited, containing crocodylomorph and chelid turtle remains. Immediately above these fossiliferous levels lenticular and massive sandstone occurs bearing relative large (> 5–10 cm) skeletal mammal remains, referred by previous authors (Simpson, 1935; Schaeffer, 1947; Andreis, 1977) to the Casamayoran South American Land Mammal Age (SALMA). In the interval around 22–25 m, a package of intercalated beds of fine and very fine tuffaceous beds were recognized. These beds show a gentle inclination (<5°) to the east. The Cerro Verde section culminates with 10–11 m of horizontally stratified, fine tuffs bearing small (< 2 cm) mammal remains, root traces, and passive-filled and meniscate burrows.

The uppermost 6 m of the Pipe Rock section is characterized by fine and massive tuffs, displaying tabular geometry and high degree of bioturbation and pedogenic structures (e.g. weakly to moderate granular structure, Fig. 3F). These beds bear a conspicuous ichnofabric composed of abundant vertical *Taenidium* and *Loloichnus* burrows (pipe-rock ichnofabric) (Krause, 2010) (Fig. 3G). These beds also contain moulds of pulmonate gastropods (*Strophocheilus* sp.) (Fig. 3H), rhizoliths and mammalian teeth remains (Fig. 3I).

The geometry and texture of the beds recorded from the Cerro Verde area are interpreted as fluvial facies, particularly channel (the only lenticular level) and floodplain (tabular beds). Reptilian fossils are contained in the laminated, fine tuffs interpreted as representing shallow ponds. The package of intercalated fine and very fine tuffs at Cerro Verde, above the channel, and those tabular, bioturbated-pedogenized beds at Pipe Rock, are interpreted as deposits of a proximal floodplain (e.g. levee deposits). Frequent rhizoliths, and poorly to moderate developed pedal structure support the presence of weakly developed palaeosols. Pedogenic processes probably obscured the preservation of primary structures (e.g. trough cross-bedding).

The greenish beds bearing frequent siliceous cement and nodules have been related to the '*Argiles Fissilaires*' (Koluel-Kaike Formation after Raigemborn *et al*., 2010), through lateral stratigraphic correlation. This hypothesis was formulated by Piatnitzky (1931), McCartney (1934) and Simpson (1935), but as typical facies of the Koluel-Kaike Formation (e.g. Krause, Bellosi & Raigemborn, 2010) are absent in Cañadón Hondo, further studies are necessary. On the other hand, facies corresponding to the Gran Barranca Member (Bellosi *et al*., 2010) have been recognized in Cañadón Hondo, overlying the greenish section. Fluvial facies were also recognized in the lowermost section of the Casamayoran beds at Cañadón Vaca, around 50 km to the west of Cañadón Hondo, underlying the Gran Barranca Member (Bellosi & Krause, 2014). In addition, beds bearing reptilian fossils were recorded in the sections Cañadón Hondo and Cañadón Vaca (Simpson, 1937). Thus, stratigraphic position, facies and fossil content support a probable equivalence of the Cerro Verde sections with the lowermost section of the Sarmiento Formation (Cañadón Vaca Member after Bellosi & Krause, 2014).

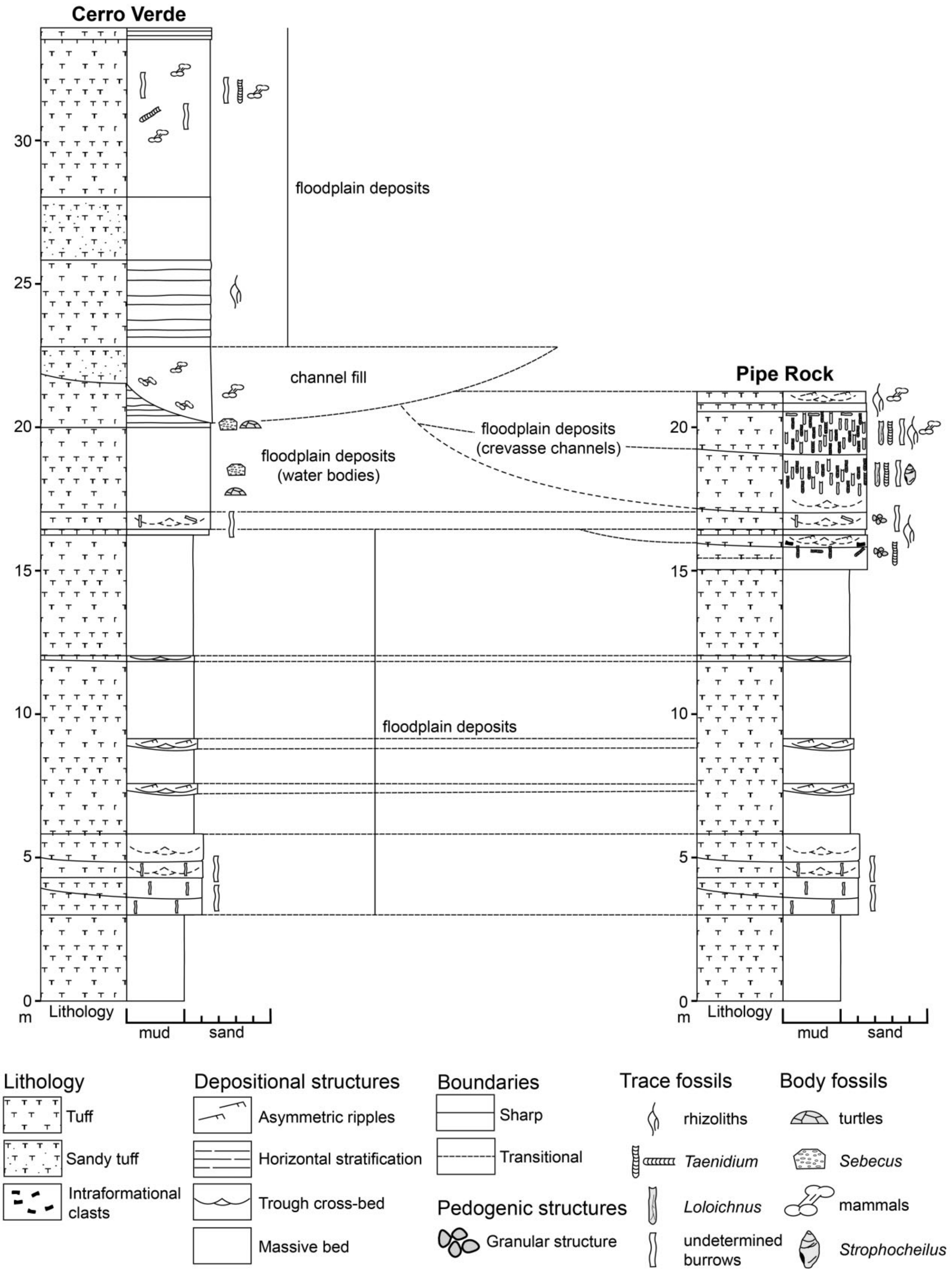

Figure 2. Sedimentological sections in the Cerro Verde area.

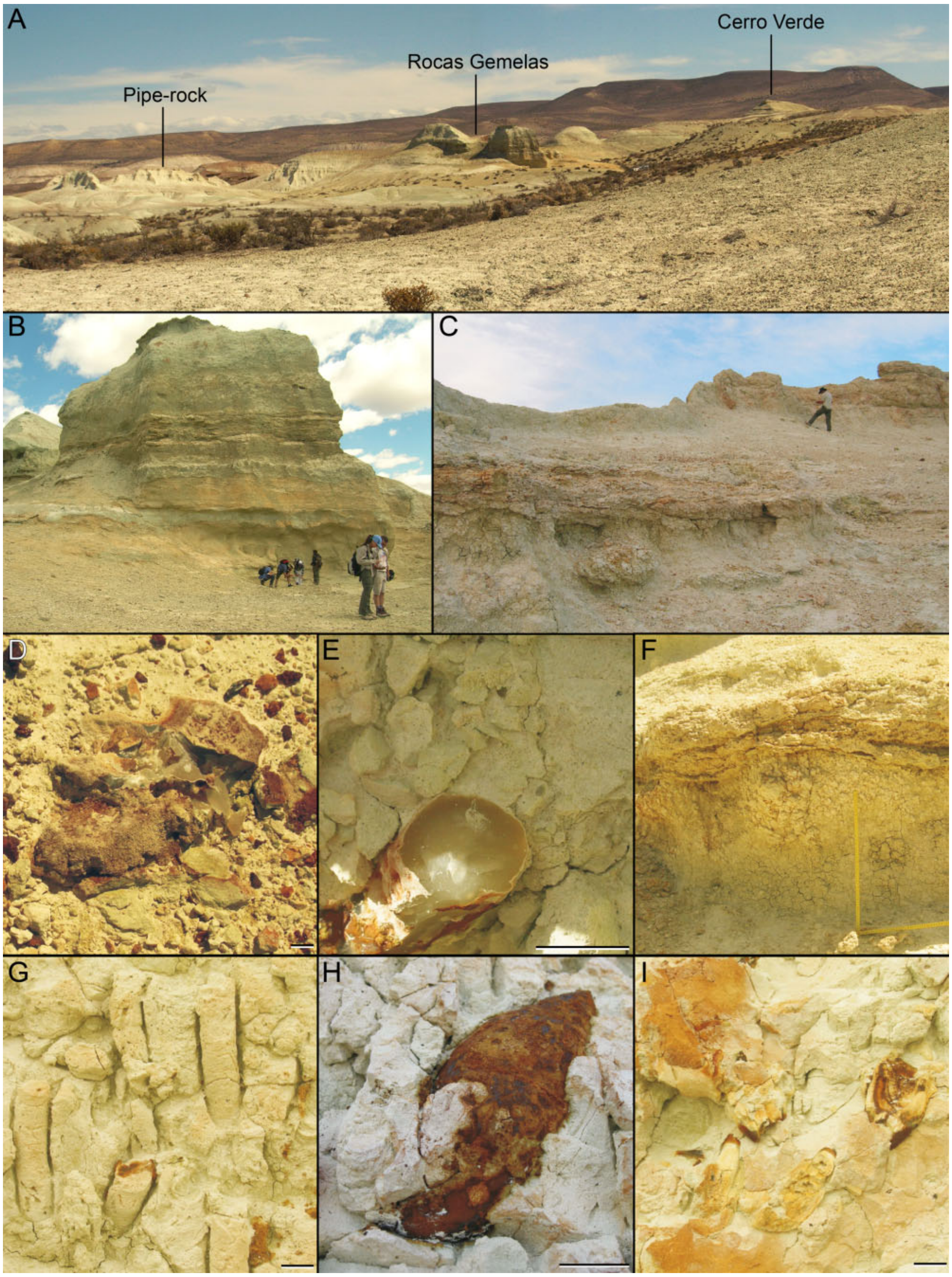

Figure 3. A, general view of the outcrops of the Sarmiento Formation in the middle–upper section at Cerro Verde area (viewed from north to south) (see also Pol *et al*., 2012, Fig. 2A). B, upper 15–20 m of the Rocas Gemelas section. The floor of this part of the outcrop corresponds to the fossiliferous level, just below the channel facies. C, upper 10 m of the Pipe-Rock section. The conspicuous pipe-rock ichnofabric occurs toward the top of the outcrop. D–E, silica in irregular nodules (F) and as rhizocretions (E). F, weakly developed palaeosol, displaying granular structure (vertical rule is around 30 cm). G, vertical burrows defining a pipe-rock ichnofabric. H, mould of pulmonate gastropod (*Strophocheilus* sp.). I, mammal tooth remains.

MATERIALS AND METHODS

Cranial nomenclature follows Gaffney (1979), Sterli *et al*. (2010) and Rabi *et al*. (2013), shell anatomy follows Zangerl (1969) and postcranial anatomy follows Gaffney (1990, 1996) and Sterli & de la Fuente (2011a). The anatomical comparisons and scoring of all meiolaniforms included in the matrix have been performed based on first-hand observations on the specimens (see Supporting Information 1), with the exception of

Mongolochelys efremovi, which was scored based on pictures kindly provided by Drs I. Danilov and W. G. Joyce. Additional information on *Chubutemys copelloi* is based on Gaffney *et al*. (2007) and Sterli *et al*. (2015), *Otwayemys cunicularius* on Gaffney *et al*. (1998), *Patagoniaemys gasparinae* on Sterli & de la Fuente (2011a), *Mongolochelys efremovi* on Khosatzky (1997), Sukhanov (2000) and Suzuki & Chinzorig (2010), *Kallokibotion bajazidi* on Gaffney & Meylan (1992), *Peligrochelys walshae* on Sterli & de la Fuente (2013), *Niolamia argentina* on Sterli & de la Fuente (2011b), *Ninjemys oweni* on Gaffney (1992), *Warkalania carinaminor* on Gaffney *et al*. (1992), *Meiolania brevicollis* on Megirian (1992), *Meiolania platyceps* on Gaffney (1983, 1985, 1996), and *Meiolania mackayi* on Anderson (1925).

Gaffneylania auricularis gen. et sp. nov. (Holotype MPEF-PV 10556 and referred specimens MPEF-PV 10557, 10558, 10559, 10560, 10561, 10571, 1778-1, 1778-2) was included in the data set of Sterli, Pol & Laurin (2013a), a matrix into which all named but not fragmentary meiolaniform turtles have been integrated. Including *G. auricularis*, the data set consists of 102 taxa (four outgroups and 98 in the ingroup) and 240 characters (see Supporting Information 2 and 3). Only the definition of character Dorsal rib A was modified in this analysis following recent observations (see Supporting Information 2). The same weight was applied to all characters and those characters showing a clear morphocline were ordered (21 in total, Supporting Information 2 and 3). The most parsimonious trees (MPTs) were saught using 1000 replicates starting from Wagner trees and perturbing those trees using the Tree Bisection Reconnection (TBR) algorithm, all as implemented in TNT software (Goloboff, Farris & Nixon, 2008a, b). In a second step, all the MTPs were subject to a second round of TBR to find all the possible MPTs. Consistency and retention indices (CI and RI) were also calculated in TNT. Branch support was calculated using Bremer support and jackknife and bootstrap resamplings also in TNT. Jackknife and bootstrap values were calculated using 1000 replicates and both absolute and difference of frequencies (GC of Goloboff *et al*., 2003). A strict consensus tree was calculated when more than one MPT was found. If a large polytomy was retrived in the strict consensus, the tool 'pruned trees' of TNT was used to detect the presence of wildcard taxa. After the recognition of wildcard taxa, a reduced strict consensus was calculated, showing the alternative positions of the pruned taxa using the command 'nelsen//' in TNT. The script developed by Pol & Escapa (2009) was also run to explore the characters that are causing the different positions of the wildcard taxa in the MPTs.

The biogeographical analysis was performed using the dispersal–extinction–cladogenesis (DEC) model created by Ree & Smith (2008). This method reconstructs the biogeographical history based on phylogenetic trees (Ree & Smith, 2008) and uses model-based inference to reconstruct lineage dispersal and local extinction in established areas through time (Ree *et al*., 2005). The DEC model also includes the probability of the connection between areas and cladogenesis through time (Ree *et al*., 2005). The calibrated trees, area definition and range constraints are available in Supporting Information 4–11.

CLADISTIC AND BIOGEOGRAPHICAL ANALYSES

The cladistic analysis resulted in 750 MPTs of 893 steps each (CI = 0.337, RI = 0.768). As more than one MPT was found, a strict consensus was calculated (Supporting Information 12–14). As there are some polytomies in the strict consensus, a reduced strict consensus was calculated (Supporting Information 15). The clade Meiolaniformes of the reduced strict consensus is shown in Figure 4. Using the tool Pruned trees of TNT, three unstable taxa were recognized: *Hangaiemys hoburensis*, *Patagoniaemys gasparinae* and *G. auricularis*. Although *G. auricularis*, the new genus and species described here, is identified as a wildcard taxon, this species takes different phylogenetic positions but always inside the clade Meiolaniidae

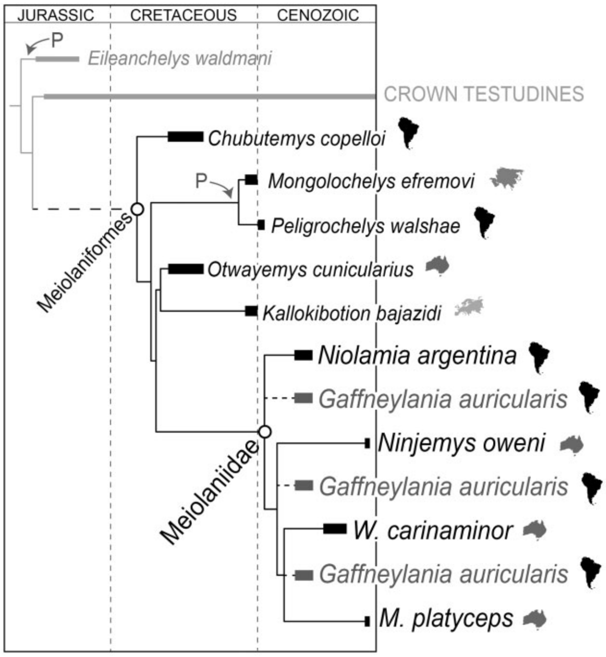

Figure 4. Reduced strict consensus of 750 MPTs of 893 steps each (CI = 0.337, RI = 0.768). The alternative position of ***Gaffneylania auricularis* gen. et sp. nov.** is shown with the dotted line. The alternativee position of *Patagoniaemys gasparinae* is shown with a P and an arrow.

(Fig. 4, Supporting Information 16). The clade Meiolaniidae is characterized by the following characters present in all trees (Supporting Information 17): quadratojugal–squamosal contact below cavum tympani (Quadratojugal C, character 23 in TNT), large posterolateral protuberances in the squamosal developed as horns (Squamosal C, character 26), presence of an intrapterygoid slit (Pterygoid C2, character 59), canalis carotici interni posterior to the bifurcation into palatine and cerebral arteries covered ventrally by bone (Canalis caroticum E, character 97), arteria palatina enters the skull through the intrapterygoid slit (Canalis caroticum F, character 98), and the entrance of the internal carotid to the skull is through the pterygoid (Canalis caroticum G, character 99); and the following characters present in some trees: antrum postoticum absent (Antrum postoticum A, character 51), transverse processes of the cervical vertebrae located in the anterior end of the centrum (Cervical vertebra A, character 182) and presence of a tail ring (Tail ring A, character 208). Bremer support for the clade is 3. As in previous analysis (Sterli & de la Fuente, 2011a; Sterli *et al*., 2013a, 2015) Meiolaniidae is nested inside the clade Meiolaniformes (when *Pa*. *gasparinae* is pruned from the strict consensus).

The alternative positions of *G. auricularis* among meiolaniids are not due to conflicting characters but because of the lack of information, as is shown in the result of the script of Pol & Escapa (2009) (Supporting Information 18). Unfortunately, there are few anatomical parts that are represented in *G. auricularis* and in other meiolaniids (such as *Nio. argentina*, *Nin. oweni*, *Warkalania carinaminor*). Furthermore, the internal relationships among meiolaniids were mainly established using cranial scute characters (Gaffney, 1996; Sterli *et al*., 2013a, 2015) and the tail rings, regions that are missing in *G. auricularis*.

The results of the DEC analyses are in agreement with the previous hypothesis presented by Sterli & de la Fuente (2013) for the palaeobiogeography of Meiolaniformes. In all the analyses (Supporting Information 19–21) Antarctica is depicted as the ancestral distribution of the lineage leading to Meiolaniidae. From there, meiolaniids dispersed to South America and Australasia (see more details in Discussion).

SYSTEMATIC PALAEONTOLOGY

TESTUDINATA KLEIN, 1760

MEIOLANIFORMES STERLI & DE LA FUENTE, 2013

MEIOLANIIDAE BOULENGER, 1887

***GAFFNEYLANIA* GEN. NOV.**

Derivatio nominis: Gaffney, named after Dr Eugene S. Gaffney in recognition of his enormous contribution in the understanding of the anatomy and phylogeny of turtles and especially for his work on meiolaniids. The etymology for *lania* is confusing. Originally, Owen (1858) described the first remains of meiolaniids as belonging to the land lizard *Megalania prisca* Owen, 1858. He provided the etymology of *Megalania* as: *Mega*, from the Greek word for great (Mέγας) and *lania* from the ancient Greek word from 'to roam about' (ἠλαίνω). Later, Gaffney *et al*. (1992) concluded that *lania* comes from the Latin *lanius* that means 'butcher'. In this case, we follow Owen (1858).

Type species: Gaffneylania auricularis

Locality: As for the species.

Horizon: As for the species.

Diagnosis: As for the species.

***GAFFNEYLANIA AURICULARIS* SP. NOV.**

Type specimen: MPEF-PV 10556, basicranium and other skull remains, almost complete lower jaw, carapacial and plastral remains, third cervical vertebra, four caudal vertebrae, complete left humerus, proximal end of right humerus, distal end of left ulna, femoral head, distal end of tibia, and several osteoderms.

Referred specimens: MPEF-PV 10557, carapacial remains; MPEF-PV 10558, carapacial remains; MPEF-PV 10559, carapacial remains; MPEF-PV 10560, 3rd cervical vertebra; MPEF-PV 10561, proximal end of right humerus; MPEF-PV 10571, osteoderm and shell fragment; MPEF-PV 1778-1, axis; MPEF-PV 1778-2, proximal caudal vertebra.

Derivatio nominis: auricularis, from auricle in reference to the half-moon shaped rim formed by the squamosal and quadratojugal that surrounds the cavum tympani of this species.

Locality: Rocas Gemelas, Cañadón Hondo, south-east Chubut Province, Argentina.

Horizon: Lower section of Sarmiento Formation, Casamayoran SALMA (Middle Eocene) (Simpson, 1935; Schaeffer, 1947; Andreis, 1977).

Diagnosis: Gaffneylania auricularis is referred to the clade Testudinata because it has a complete shell formed by interlocking dermal bones. It is diagnosed as belonging to Meiolaniidae due to the presence of a synapomorphy of the clade, the intrapterygoid slit (Canalis caroticum F, character 98). *Gaffneylania auricularis* shares with other meiolaniids the presence of a foramen posterius canalis carotici interni formed by the pterygoid (Canalis caroticum G, character 99), a ventrally open sinus (= fenestra caroticus of Rabi *et al*., 2013) where the internal carotid artery splits into the cerebral artery (piercing the basisphenoid) and the palatine artery (entering through the intrapterygoid vacuity) (Canalis caroticum D, character 96), a very thick basisphenoid and basioccipital, absence of a foramen dentofaciale majus, ornamentation in the dermal bones of the skull, lower jaw and shell consists of many small pits, strongly anteriorly curved marginal sulci in the carapace, presence of formed cervical and caudal vertebrae (Cervical articulation A, character 186), cervical centra as long as high or slightly longer than high (Cervical vertebra H, character 195), tall neural arches, presence of cervical ribs (Cervical rib A, character 181), and opisthocoelous caudal vertebrae (Caudal C, character 203). *Gaffneylania auricularis* shares with *Mei. platyceps* the robust humerus with well-expanded ends, short shaft (Humerus E, character 219), closed ectepicondylar foramen (Humerus A, character 215), and the presence of osteoderms. It differs from *Mei. platyceps* by the absence of a premaxillar dorsal process, ventrally open sinus (= fenestra caroticus of Rabi *et al*., 2013) where the internal carotid bifurcates into the palatine artery and cerebral artery (Canalis caroticum D, character 96), by the dorsum sellae only slightly overhanging the sella turcica, by the thin bony wall between the anterior foramina of the cerebral artery, by a very close exit of both rami of the cerebral arteries at the base of the high dorsum sellae in the posterolateral corner of the sella turcica, and by the absence of the accessory ridge in the triturating surface of the lower jaw. It shares with *Nio. argentina* that the foramen posterius canalis carotici cerebralis is not covered in ventral view by the pterygoids (Pterygoid C2, character 60). It differs from *Nio. argentina* by the shape of the occipital condyle, the shape and orientation of the squamosal horn, the angle between the rami of the lower jaw, by the presence of a medial symphyseal hook formed by the labial ridge, and because the labial ridge of the triturating surface of the lower jaw is taller than the lingual ridge. It is characterized by the following autapomorphies: a half-moon-shaped, thickened rim that is formed by the quadratojugal and squamosal bones that surrounds the cavum tympani, the presence of three K scutes (K1, K2 and K3) covering the moon-shaped rim, the shape of the occipital condyle, an ovoid occipital platform pierced by a foramen that is placed on both sides of the ventral portion of the occipital condyle, and a pair of basioccipital foramina placed in the midline of the skull between the condylus occipitalis and a posterior basioccipital depression, and by an unenclosed canalis chorda tympani mandibularis.

DESCRIPTION

SKULL

The description of the skull is based on the holotype (MPEF-PV 10556). The skull bones are extremely ankylosed and therefore do not allow the recognition of several sutures. Some sutures are clearly seen along their full path (e.g. the prootic–quadrate), some other sutures are recognized in some parts (e.g. the pterygoid–quadrate), while other contacts are inferred from the presence of certain structures (e.g. the prootic–opisthotic suture in ventral view).

Cranial scutes: There are no remains of the bones from the skull roof, and consequently there is no preservation of the dorsal scutes. However, three scutes are preserved in the rim surrounding the cavum tympani (Figs 5–8). The homology of these scutes with the scutes present in other meiolaniids is doubtful because in *Mei. platyceps* and *Nin. oweni* there are only two scutes in this region of the skull (scutes K and J from Gaffney, 1983). In *Nio. argentina* this area is damaged on both sides, but it is evident that it has two scutes J, J1 and J2, and only one scute K (Gaffney, 1983; Sterli & de la Fuente, 2011b). In *G. auricularis* we recognize three scutes surrounding the cavum tympani as the scute K formed by three parts, K1, K2 and K3 (Figs 5–8). Scute K1 is the most dorsal K scute and it is located entirely on the squamosal. Scute K2, by contrast, is located half on the squamosal and half on the quadratojugal. Scute K3 is the most ventral one and it is located in the quadratojugal.

Dermatocranium: No remains of prefrontal, nasal, frontal, jugal, postorbital or parietal are preserved.

Only the posterior portion of the left quadratojugal is preserved in the holotype (Figs 5, 6A, 7, 8). As in *Mei. platyceps* the quadratojugal contacts the squamosal below the cavum tympani and it is recovered as a

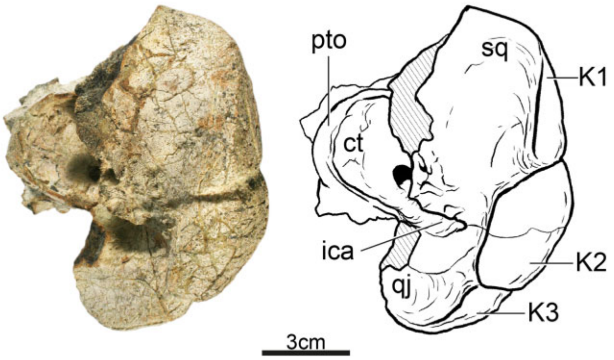

Figure 5. ***Gaffneylania auricularis*** **gen. et sp. nov.**, MPEF-PV 10556 (holotype). Photograph and drawing of the skull in left lateral view.

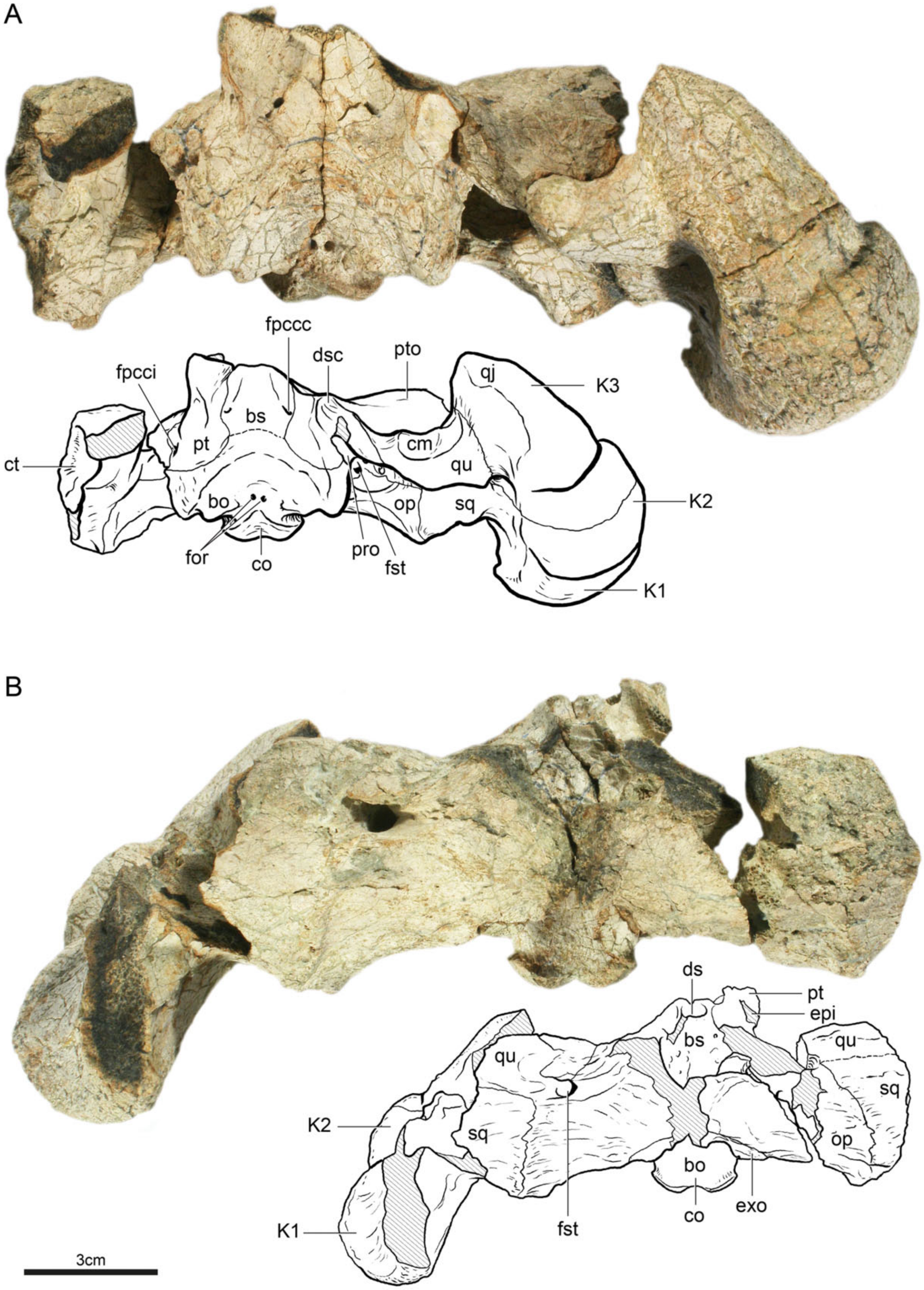

Figure 6. ***Gaffneylania auricularis*** **gen. et sp. nov.**, MPEF-PV 10556 (holotype). Photographs and drawings of the skull in ventral (A) and dorsal (B) views.

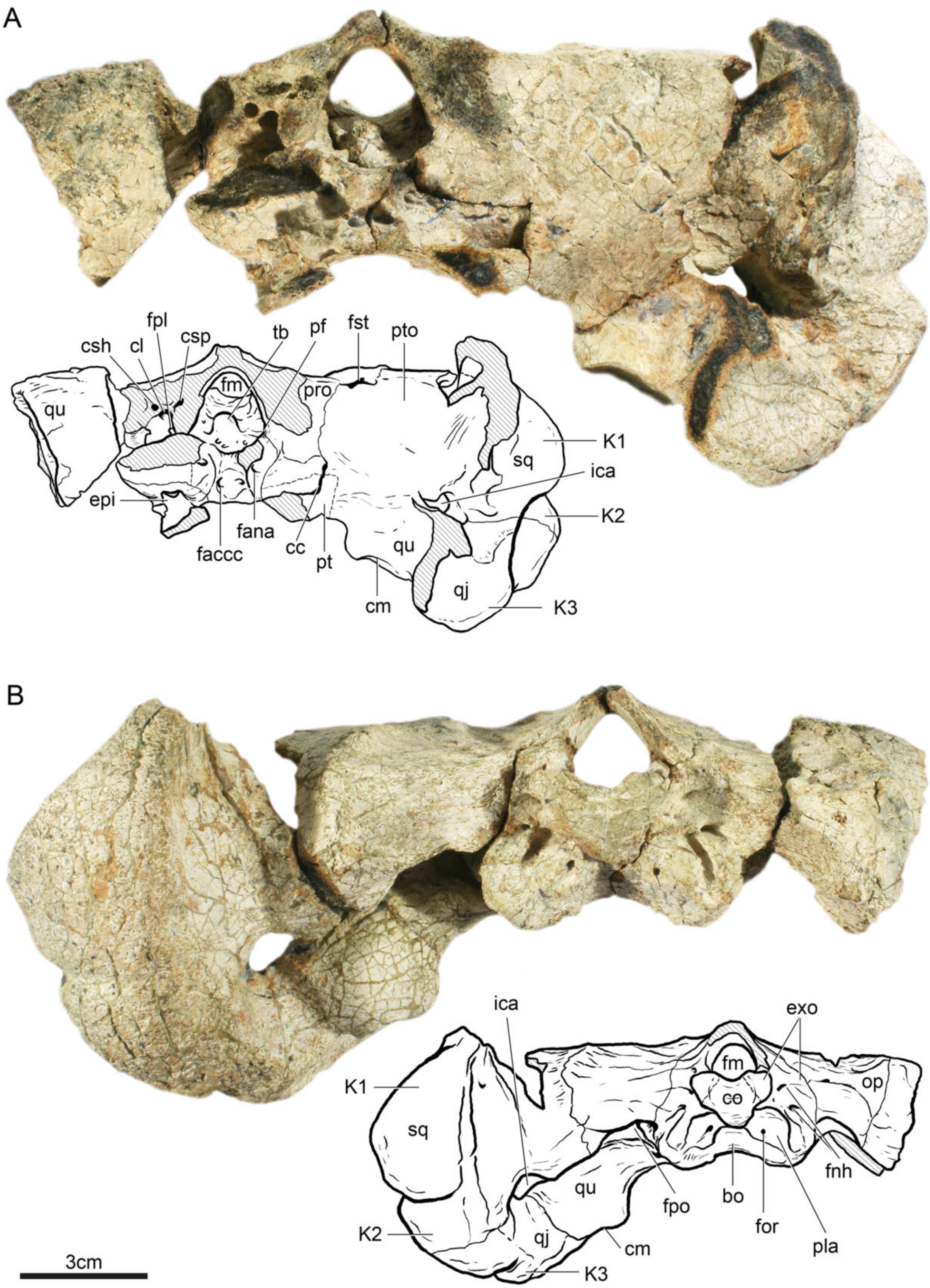

Figure 7. ***Gaffneylania auricularis* gen. et sp. nov.**, MPEF-PV 10556 (holotype). Photographs and drawings of the skull in anterior (A) and posterior (B) views.

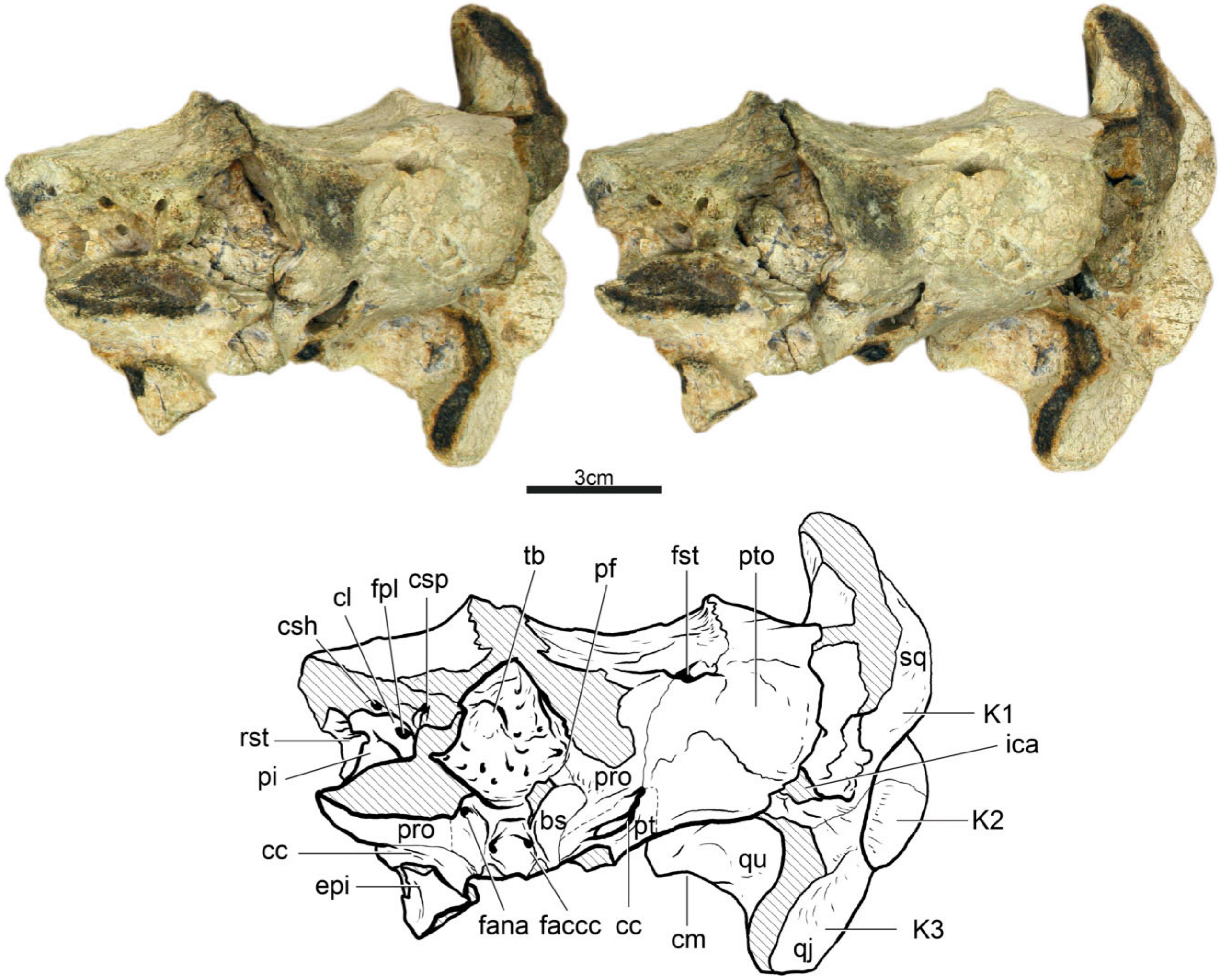

Figure 8. ***Gaffneylania auricularis* gen. et sp. nov.**, MPEF-PV 10556 (holotype). Stereophotographs and drawing of the skull in dorsoanterolateral view.

synapomorphy of Meiolaniidae in the cladistic analysis (Quadratojugal C, character 23). It is likely that this condition is present in other meiolaniids (i.e. *Niolania argentina*, *Ninjemys oweni*). The quadratojugal also contacts the quadrate medially. The other contacts of the quadratojugal are not preserved. The quadratojugal forms the anterior portion of the half-moon-shaped rim that surrounds posteroventrally the cavum tympani.

The left squamosal is preserved (Figs 5–8). It forms the posterodorsal part of the half-moon-shaped rim that posteroventrally surrounds the cavum tympani and the horn (Squamosal C, character 26). The squamosal also forms the posterodorsal part of the cavum tympani. As in *Mei. platyceps* the squamosal contacts the quadratojugal below the cavum tympani. The squamosal also contacts the quadrate medially. The remaining contacts of the squamosal are not preserved.

The presence of horns in the squamosal is a synapomorphy of Meiolaniidae (Squamosal C, character 26). The horn core B (Fig. 9) was found associated with the other cranial and postcranial remains herein described but its exact location on the skull cannot be assessed with certitude because it is broken at its base. Compared with *Nio. argentina*, the horn core B of this taxon is comparable in size and shape, but it is slightly smaller and curved slightly posterodorsally (Fig. 9A–C). The tip of the horn in this taxon is flat and blunt (Fig. 9C), while in *Nio. argentina* the horn ends in a pointed tip. In contrast to *Mei. platyceps*, but similar to *Nio. argentina*, the section of the horn is triangular (Fig. 9D). The triangular sections differ between *Nio. argentina* and *G. auricularis*. In the latter taxon the section is like an isosceles triangle with the short side facing dorsally (Fig. 9D), while in *Nio. argentina* is resembles a scalene triangle with its shortest side facing ventrally.

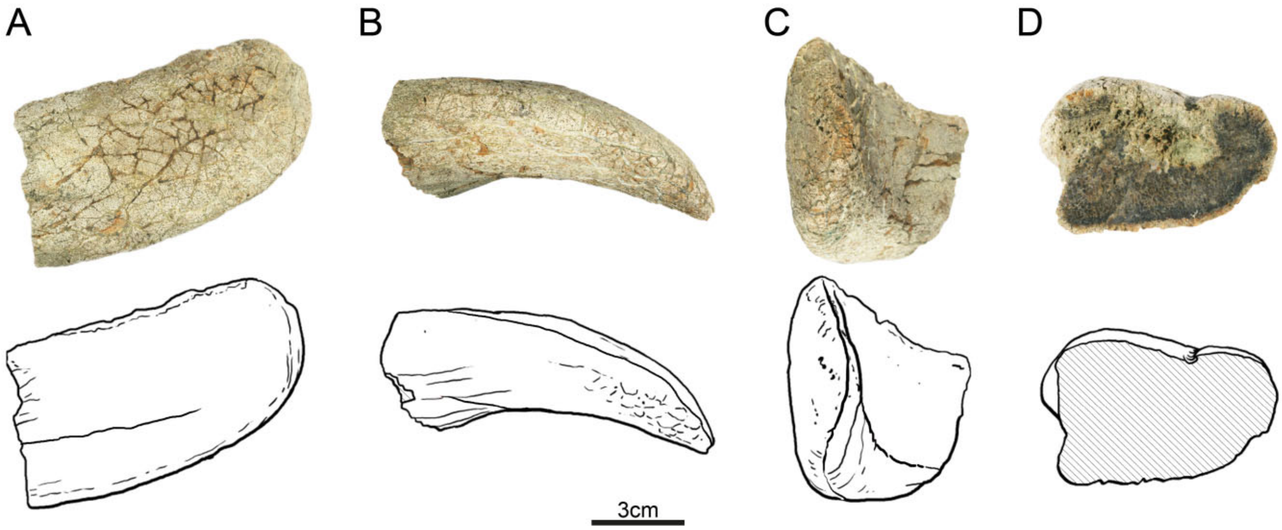

Figure 9. ***Gaffneylania auricularis*** **gen. et sp. nov.**, MPEF-PV 10556 (holotype). Photographs and drawing of the horn core B in anterior (A), ventral (B), lateral (C) and medial (D) views.

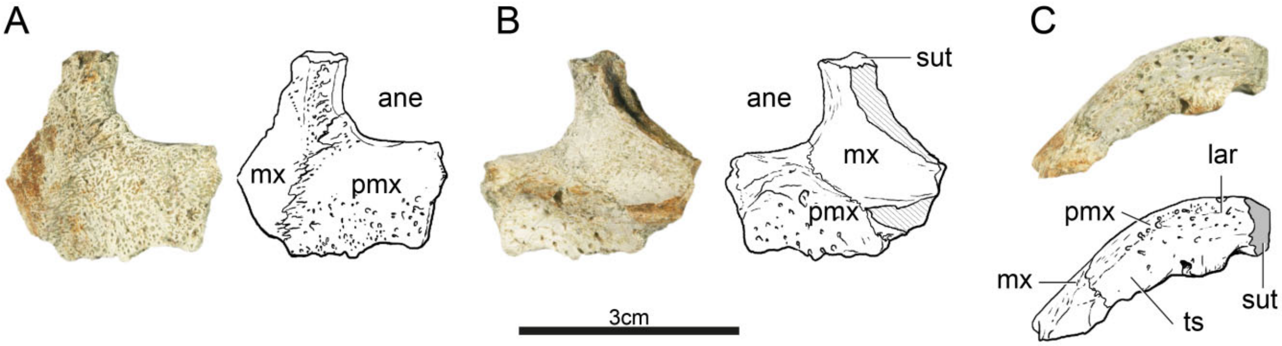

Figure 10. ***Gaffneylania auricularis*** **gen. et sp. nov.**, MPEF-PV 10556 (holotype). Photographs and drawings of the right premaxilla and maxilla in anterior (A), posterior (B) and ventral (C) views.

Palatal bones: There are no remains of the vomer or palatine. Only part of the right premaxilla is preserved (Fig. 10). It contacts the other premaxilla medially and the maxilla laterally through an oblique suture. The posterior, horizontal process of the premaxilla is missing. The premaxilla forms the ventral border of the apertura narium externa. In contrast to *Mei. platyceps*, but similar to *Nio. argentina*, the premaxilla of MPEF-PV 10556 does not have a dorsal process. In ventral view, the premaxilla forms part of the triturating surface. Only the labial ridge is preserved in MPEF-PV 10556 and comparisons with *Mei. platyceps*, *Nin. oweni* or *Nio. argentina* are therefore limited.

A part of the right maxilla is preserved as well (Fig. 10). The only preserved contact is the medial one with the premaxilla. Dorsally, the maxilla exhibits a sutural surface with the nasal or the prefrontal. Towards the posterior the maxilla is broken; possible contacts with the jugal or the nasal are not preserved. Consequently, it cannot be determined whether the naso-maxillary sinus was present. The maxilla forms the lateral border of the apertura narium externa. The portion of the maxilla that forms part of the triturating surface is broken in specimen MPEF-PV 10556.

Palatoquadrate bones: Both quadrates are preserved, the left one of which is more complete (Figs 5–8, 11). The quadrate contacts the prootic anteromedially, the pterygoid ventromedially, the quadratojugal lateroanteriorly, the squamosal posterior and posterolaterally, and the opisthotic posteriorly. The lateral aspect of the quadrate, as in most turtles, is funnel-shaped (Fig. 5). The cavum tympani is deep (Quadrate B + C, character 49), but there is no distinct antrum postoticum (Antrum postoticum A,character 51) or precolumellar fossa (Fig. 5) as in *Mei. platyceps* (Gaffney, 1983) or in *Warkalania carinaminor* (Gaffney *et al*., 1992). The anterior part

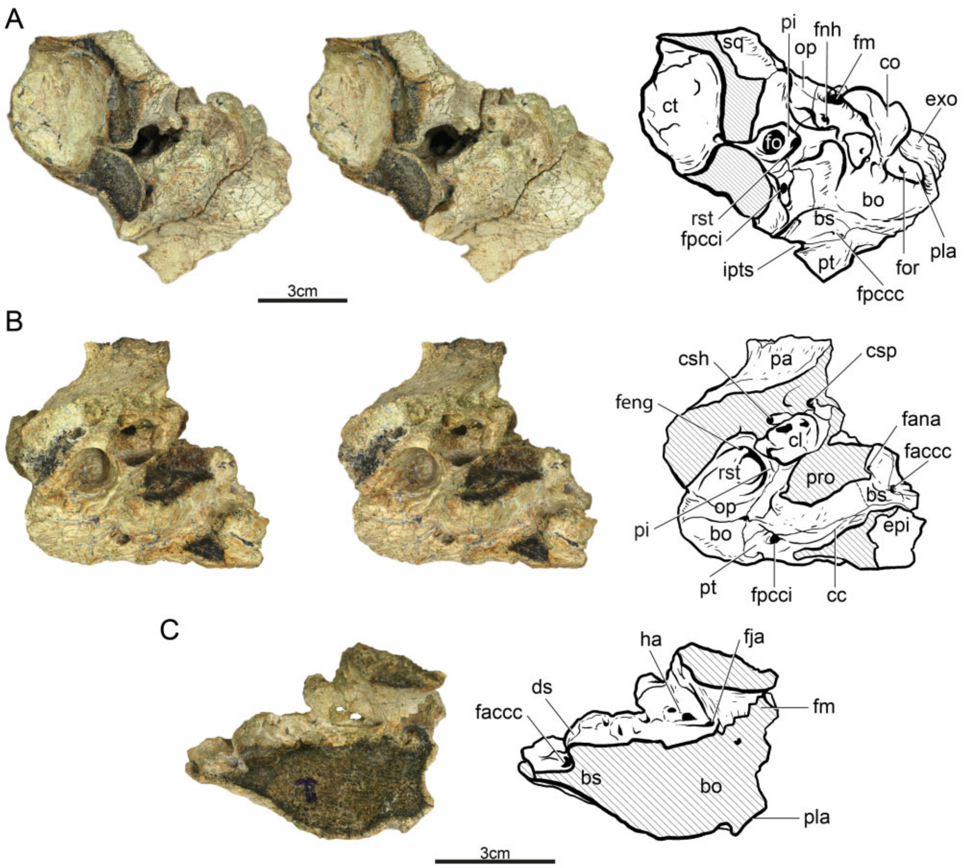

Figure 11. ***Gaffneylania auricularis*** **gen. et sp. nov.**, MPEF-PV 10556 (holotype). Stereophotographs and drawings of the skull in left ventroposterolateral (A) and right lateral (right quadrate removed) (B) views. Photograph and drawing of the skull in medial (C) view.

of the quadrate forms the entire processus trochlearis oticum (Figs 6, 7A, 7; Quadrate G, character 54). The medial part of the quadrate forms the anterior wall of the canalis cavernosus and the lateral wall of the canalis stapedio-temporalis. The canalis stapedio-temporalis ends dorsally in the foramen stapedio-temporalis, which is formed by the quadrate, prootic and opisthotic (Figs 7A, 8). This foramen is formed by the quadrate and prootic in *Nio. argentina* (Sterli & de la Fuente, 2011b) and by the prootic and opisthotic in *Mei. platyceps* (Gaffney, 1983). The incisura columella auris is closed in its most lateral part by the squamosal and the quadratojugal, but the quadrate portion of the incisura is not completely closed posteriorly (Figs 5, 7B). As in other meiolaniids (e.g. *Mei. platyceps* and probably in *Nin. oweni* and in *War. carinaminor* Gaffney, 1983, 1992; Gaffney *et al*., 1992), the incisura columella auris and the Eustachian tube are enclosed in bone in the external part of the cavum tympani (Quadrate F, character 52). In the anterolateral portion of the quadrate, the processus articularis ends in the condylus mandibularis (Figs 6A, 7A). The condylus mandibularis is rectangular, medio-laterally elongated and the surface is almost flat, as in *Mei. platyceps* (Gaffney, 1983). It is divided in two parts, the medial and the lateral. The lateral part is located below the medial one.

The base of the right epipterygoid is preserved (Figs 7A, 8), but the epipterygoid cannot be identified on the left side (Epiterygoid A, character 56). Due to the nature of the small fragment of the epipterygoid preserved on the right side, no detailed description is possible. The only preserved contact of the epipterygoid is with the pterygoid, ventrally (Figs 7A, 8).

Both pterygoids are preserved, although the right one is more complete (Figs 6A, 7A, 8, 11), only missing its anterior part. The preserved contacts of the pterygoid are with the basisphenoid posteromedially, the basioccipital posteriorly, the prootic dorsally, the epipterygoid dorsally and the quadrate laterally. In MPEF-PV 10556 (Figs 7A, 8A, 11A) the right pterygoid shows the presence of an intrapterygoid slit, a characteristic of meiolaniids (Pterygoid C2, character 59). As a consequence, the pterygoid is located in a lower level than the basisphenoid in this area (Pterygoid M, character 70). In contrast to *Mei. platyceps*, but as in *Nio. argentina*, the pterygoids in *G. auricularis* (Figs 6A, 11A) do not cover the sinus (= fenestra caroticus of Rabi *et al*., 2013) ventrally where the internal carotid bifurcates into the palatine and cerebral arteries (Pterygoid C2, character 60). In this sinus (= fenestra caroticus), the cerebral branch pierces the basisphenoid (Gaffney, 1983; Sterli *et al*., 2010; Sterli & de la Fuente, 2011b). In ventral view, at the level of the sinus (= fenestra caroticus), there is a drop-shaped concavity pointing anteriorly (Fig. 6A). This concavity could have served for the attachment of the muscle adductor mandibulae internus Pars pterygoideus posterior (muscular unit number 27 of Werneburg, 2011). In the posterolateral part of the pterygoid, near its suture with the basioccipital and the prootic, the foramen posterius carotici interni (fpcci, Sterli *et al*., 2010; Canalis caroticum G, character 99) is preserved (Figs 6A, B, 11). This foramen could also be recognized in *Mei. platyceps* (Gaffney, 1983) and in *Nio. argentina* (Sterli & de la Fuente, 2011b). Posteriorly, the pterygoid forms the entrance of the canalis cavernosus (Figs 7A, 11A), which runs along the dorsal part of the pterygoid between the pterygoid (anteriorly) and the prootic (posteriorly). Through this canal the vena capitis lateralis leaves the skull.

Basicranial bones: Due to the nature of the sutures in MPEF-PV 10556, the sutures of the supraoccipital are not recognizable (Figs 6B, 7). This bone might be fused with the exoccipitals. The characteristic contribution of the horizontal plate of the supraoccipital to the skull roof in meiolaniids is not preserved in MPEF-PV 10556; this area is broken.

Both exoccipitals are preserved (Figs 7B, 11A). The only clear suture of the exoccipital is the one with the opisthotic. It seems that the exoccipital and the basioccipital are fused. Perhaps the exoccipital is also fused with the supraoccipital. As in *Nio. argentina*, there are two large foramina nervi glossopharyngei in each exoccipital in *G. auricularis* (Figs 7B, 11A). Two large foramina and a third, much smaller, were described in *Mei. platyceps* (Gaffney, 1983). As is typical in turtles the exoccipital forms the lateral margin of the foramen magnum. As well, as in other turtles, the exoccipital probably contributes to the occipital condyle (Gaffney, 1979). The exoccipital of *G. auricularis* furthermore forms the posterior wall of the recessus scalae tympani and the posterior margin of the foramen jugulare anterius that connect this portion of the cavum acustico-jugulare with the cavum cranii (Figs 7B, 11A).

The basioccipital is a robust bone in *G. auricularis* and, together with the basisphenoid, is very thick in sagittal section (Fig. 11C). The basioccipital contacts the basisphenoid anteriorly, the pterygoid anterolaterally, the prootic dorsolaterally and anteriorly, the opisthotic dorsoposteriorly, and the exoccipital dorsally (Figs 6A, 7B, 11A, C). The basioccipital, together with the exoccipital, forms the condylus occipitalis. The occipital condyle has a triangular shape pointing ventrally, almost as wide as high (Fig. 7B). The outline and proportions of this condyle are different in other meiolaniids (e.g. it is subhexagonal two times wider than high in *Nio. argentina* and it is also subtriangular slightly wider than high in *Mei. platyceps*). As in *Mei. platyceps*, the occipital condyle of *G. auricularis* has three articular surfaces, two located above and separated by a shallow concavity and one located below in the midline. The main differences between the occipital condyle of *G. auricularis* and *Mei. platyceps* are that the medial articular facet of *G. auricularis* not only has a posterior but also a ventral development and that *G. auricularis* lacks the presence of a well-delimited concavity in the middle of the condyle as is characteristic of *Mei. platyceps* (Gaffney, 1983). In posterior view, on each side of the ventral portion of the condyle, there is an ovoid platform pierced by a foramen (Fig. 7B). This platform is unique among turtles. The function of this platform and the identity of the foramina are unknown. In ventral view a deep, semicircular concavity is seen (Figs 6A, 11A). Between this concavity and the occipital condyle there is a pair of foramina of unknown function. These foramina are also unique for this taxon. In dorsal view at the level of the contact with the basisphenoid, the basioccipital bears the basis tuberculi basalis (Gaffney, 1979) (Figs 7A, 8).

Both prootics are preserved in *G. auricularis* (Figs 6, 7A, 8, 11B, C). The left one is complete, while the right one is missing the dorsal part. The prootic is a thick, quadrangular element. The prootic contacts the quadrate laterally, the pterygoid anteriorly, the opisthotic posteriorly, the basisphenoid medially and perhaps the parietal dorsally (this contact is missing in this specimen). The prootic forms part of several structures of the skull. The prootic forms the anterior part of the inner ear (cavum labyrinthicum), which is completed posteriorly by the opisthotic (Fig. 11B, C). The entire rim of the fenestra ovalis is ossified, the prootic being the bone that closes it anteriorly (Fig. 11B, C). By contrast, in *Mei. platyceps* a small notch is recognized in the ventral margins of the prootic, and it was probably filled with cartilage in life (Gaffney, 1983). Dorsally the prootic forms the anterior rim of the foramen stapedio-temporalis (Figs 6B, 8). The foramen stapedio-temporalis is framed by the prootic anteriorly, the quadrate laterally and the opisthotic posteriorly. In anterior view, the prootic forms the posterior border of the prootic foramen (Figs 7A, 8). Due to breakage of the epipterygoid, the structure of the prootic foramen and the foramen nervi trigemini (V) cannot be assessed with certitude. In medial view the prootic forms the anterior wall of the hiatus acusticus, the wall separating the cavum cranii and the cavum labyrinthicum (Gaffney, 1979). The hiatus acusticus is highly ossified in this taxon (Fig. 11C) as in *Nio. argentina* and *Mei. platyceps* (Gaffney, 1983). Neither the fossa acustico-facialis, nor the foramen aquaducti-vestibuli, foramen nervi acustici and foramen nervi facialis are seen. In inner view, the prootic houses the recessus labyrinthicus prooticus where the ampullae and the anterior and horizontal semicircular canal are located.

Remains of both opisthotics are present, but only the left one is complete (Figs 6, 7B, 8, 11B, C). The opisthotic contacts the exoccipital medially, the squamosal laterally, the prootic anteriorly, the quadrate anterodorsally and the basioccipital ventrally. Its contacts with the supraoccipital or parietal cannot be seen. The opisthotic together with the prootic forms part of the inner (cavum labyrinthicum) and middle (cavum acustico-jugulare) ears (Figs 7A, 7, 11A–C). The recessus labyrinthicus opisthoticus is preserved in the opisthotic and houses the posterior ampullae and the posterior and horizontal semicircular canals (Figs 7A, 8, 11A) (Gaffney, 1979). The fenestra ovalis in this taxon is completely ossified (Fig. 11A, B). The processus interfenestralis of the opisthotic is a very thin strip of bone (Opisthotic D2, character 81) that reaches and fuses with the floor of the cavum acustico-jugulare (Fig. 11A, B). At the base, the processus interfenestralis of the opisthotic is pierced by the nervi glossopharyngei (IX) (Fig. 11A). The recessus scalae tympani and the cavum labyrinthicum are connected through the fenestra perilymphatica, which is located posterior to the processus interfenestralis of the opisthotic. In medial view, the opisthotic forms the posterior part of the well-ossified hiatus acusticus (Fig. 11C). Posterior to the hiatus acusticus, between the exoccipital and the opisthotic the foramen jugulare anterius is visible (Fig. 11C). The vagus (X) and the accessory (XI) nerves and the vena cerebralis posterior leave the skull through this foramen. The processus paraoccipitalis of the opisthotic is well developed in this taxon (Fig. 7B) as in *Mei. platyceps* (Gaffney, 1983). The middle ear has a posterior wall, which is built up by the opisthotic (Fig. 7B). The foramen jugulare posterius and the fenestra postotica are coalescent and formed by the opisthotic (Figs 7B, 11A). In dorsal view, the opisthotic forms the posterior rim of the foramen stapedio-temporale (Figs 6B, 8).

The basisphenoid is almost complete, only lacking the rostrum basisphenoidale (Figs 6, 7A, 8, 11A). This bone contacts the basioccipital posteriorly, the prootic laterally and the pterygoid ventrolaterally. Similar to the basioccipital, the basisphenoid is a very thick bone and it appears that both bones are fused because no suture is recognized between them (Fig. 11C). On its dorsal surface, along the contact with the basioccipital, the basis tuberculis basalis is present (Figs 7A, 8). As in *Mei. platyceps*, the dorsal surface of the basisphenoid is irregular with asymmetrical pits and grooves (Figs 7A, 8). Together with the basioccipital, the basisphenoid forms the ventral rim of the hiatus acusticus (Fig. 11C). Ventrally, in the basisphenoid the sinus (= fenestra caroticus) where the inner carotid exits the skull and where it bifurcates into the cerebral and palatine arteries is present (Figs 6A, 11A). The cerebral artery enters the skull through the foramen posterius canalis carotici cerebralis in this sinus (Sterli *et al*., 2010; Sterli & de la Fuente, 2011b; Rabi *et al*., 2013). The cerebral artery runs anteriorly through the basisphenoid and both branches exit very close to each other at the base of the high dorsum sellae in the posterolateral corner of the sella turcica (Figs 7A, 8). In MPEF-PV 10556 the two foramina are separated by a thin wall of bone, in contrast to the thick wall of bone present in *Mei. platyceps* (Gaffney, 1983). The nervi abducentis (VI) also pierces the basisphenoid (Figs 7A, 8). The entrance of the nervi abducentis to the basisphenoid is not seen, but the anterior exit is preserved. The nervi abducentis exits the basisphenoid laterodorsally to the foramen anterior canalis carotici cerebralis (Figs 7A, 8). Both processus clinoideus are broken in the specimen (Figs 7A, 8), so it is not possible to assess whether they were short as in *Mei. platyceps*. As in *Mei. platyceps* (Gaffney, 1983) the dorsum sellae of MPEF-PV 10556 is high and delimited on either side by a ridge (Figs 7A, 8). The dorsum sellae, in contrast to *Mei. platyceps* (Gaffney, 1983), overhangs the sella turcica by a small amount.

LOWER JAW

An almost complete lower jaw is available and only missed the right posterior part and both splenials and coronoids (Fig. 12). The external surface of the bones of the lower jaw is highly ornamented with ridges, grooves and pits (Fig. 12A, C–E). This ornamentation is also present in *Nio. argentina* and *Mei. platyceps*, although, at least in the last taxon, the ornamentation is restricted to the dentary and the anterior part of the surangular.

Dentary: Both dentaries are preserved, with the exception of the tip of the left dentary (Fig. 12). Both dentaries are fused at the symphysis (Fig. 12A; Dentary A, character 119). The dentary contacts the surangular posterolateraly, the angular posteroventrally, the coronoid posterodorsally, the prearticular posteromedially and the splenial medially (Fig. 12B–F). Although, both the splenial and the coronoid are missing in the specimen, the sutural surface is present on the dentary (Fig. 12B, F). The triturating surface of the lower jaw is formed entirely by the dentaries (Fig. 12C, F). As in *Nio. argentina*, there are only two ridges in the triturating surface, the labial and the lingual ridges. In *Mei.*

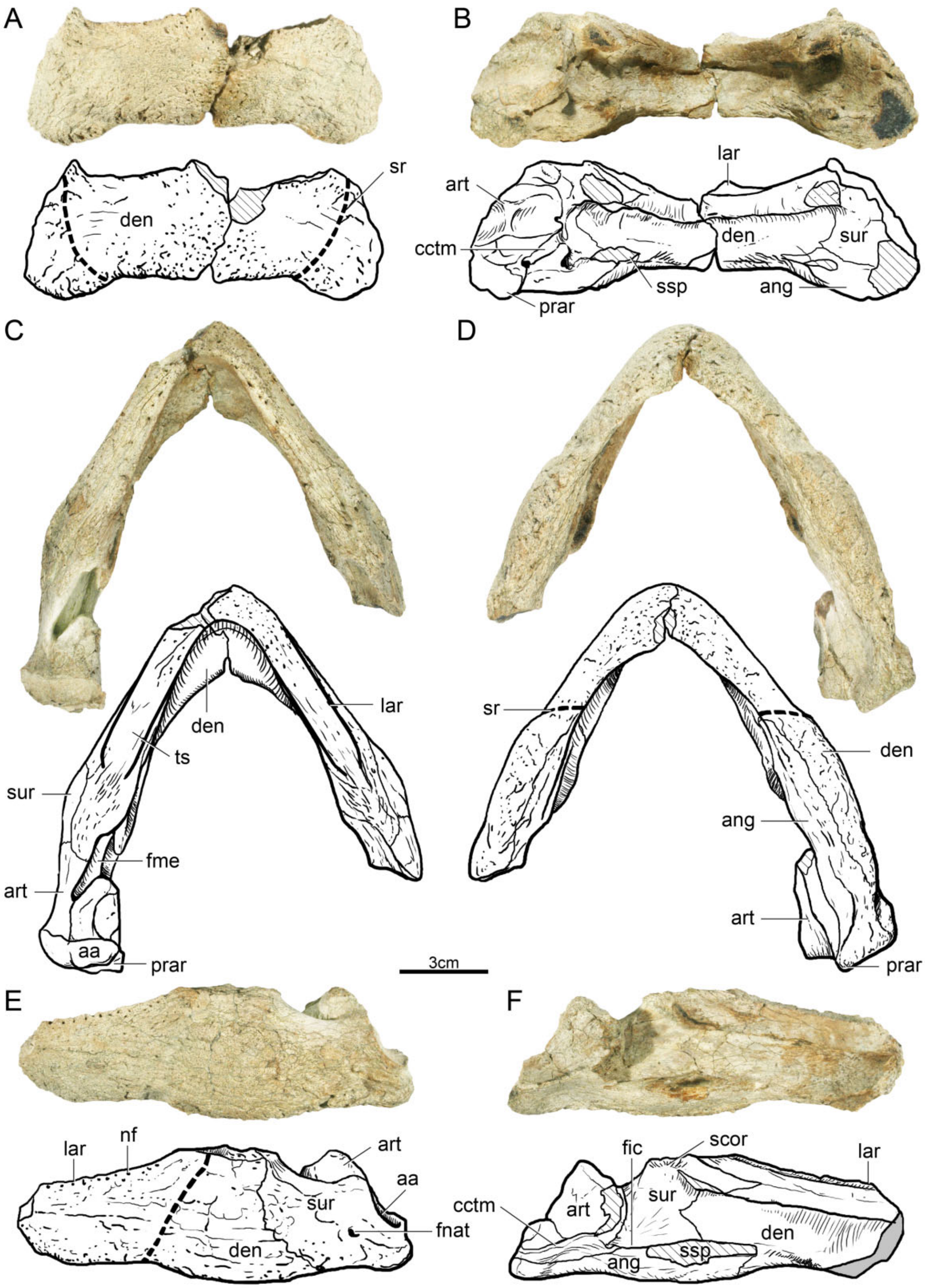

Figure 12. ***Gaffneylania auricularis* gen. et sp. nov.**, MPEF-PV 10556 (holotype). Photographs and drawings of the lower jaw in anterior (A), posterior (B), dorsal (C), ventral (D), left lateral (E) and medial (F) views.

platyceps, besides the labial and ligual ridges, an accessory ridge is described between them (Gaffney, 1983). In contrast to *Nio*. *argentina* and *Mei*. *platyceps*, the labial ridge is taller than the lingual ridge. Both ridges are almost parallel along their entire length with the exception of the anterior part, near the symphysis, where both ridges slightly converge (Fig. 12C). Also, at the bottom of both ridges there are many small nutritive foramina located on the external surface in the labial ridge and on the lateral surface in the lingual ridge (Fig. 12B). The surface between both ridges is concave. In contrast to *Nio. argentina*, the labial ridge of this taxon forms a medial hook at the symphysis (Fig. 12A). The foramen dentofaciale majus, located on the outer surface of the dentary in most turtles, is absent in *G. auricularis* (Fig. 12E). This foramen is also not recognized in other meiolaniids such as *Mei. platyceps*, *Nio. argentina* or *Nin*. *oweni*. The sulcus cartilaginis Meckelii is open for a small distance, because the anterior border of the splenial ends near the symphysis (Fig. 12B, F). In the posterior part of the dorsal margin of the sulcus cartilaginis Meckelii the foramen alveolare inferius is present. The canalis alveolaris inferior extends anteriorly covered by a thin layer of dentary.

Angular: The left angular is complete, while just the anterior portion of the right one is preserved (Fig. 12B, D, F). The sutures of this bone are not clear, but the contacts with other bones can be inferred by the presence of certain structures and comparisons with other meiolaniids. The angular contacts the prearticular dorsally, the dentary anteroventrally, the splenial anterodorsally and the surangular laterally (Fig. 12B, D, F). The angular forms the ventral border of the large foramen intermandibularis caudalis (Fig. 12B, F). A large foramen intermandibularis caudalis is also present in *Mei. platyceps* (Gaffney, 1983).

Surangular: Both surangulars are preserved (Fig. 12B–F). The left one is complete, while the posterior part of the right one is missing. The surangular forms the posteolateral part of the lower jaw. It contacts the dentary anteriorly, the articular medially, the coronoid anterodorsally and probably the angular (Fig. 12B–F). The surangular forms the lateral rim of the fossa Meckelii (Fig. 12B, F). The foramen nervi auriculotemporalis is present at the level of the area articularis mandibularis (Fig. 12E). The ramus cutaneus recurrens of the branch of the mandibular nerve (V3) enters the surangular through this foramen. This nerve leaves this bone anteriorly along an opening located in the medial surface of the surangular in the posterior portion of the fossa Meckelii.

Coronoid: Both coronoids are missing, but their presence can be inferred by the sutural surface left on the dentary and surangular (Fig. 12B, F).

Articular: Just the left articular is preserved (Fig. 12B, C, F). Unfortunately the sutures of this bone are not discernible, probably because all the posterior bones of the lower jaw are fused (as in *Mei. platyceps* and other turtles). The area articularis mandibularis could be also formed by other bones (e.g. surangular) in this taxon, but we describe this surface here. The area articularis mandibularis is a rectangular area, mainly concave, slightly subdivided into two subareas (Fig. 12B, C). It faces dorsoposteriorly and it is slightly inclined laterally. The medial part is larger, and anteroposteriorly longer than the lateral one. Posterior to the area articularis mandibularis there is a small processus retroarticularis that is longer in its medial portion (Fig. 12B). This process could be also formed by the angular. In the dorsal part of the medial surface of the retroarticular process there is a groove, which continues anteriorly along the medial surface of this bone and the prearticular (Fig. 12B, F). We interpret this groove as the unenclosed canalis chorda tympani mandibularis (Fig. 12B, F). In *Mei. platyceps* and most turtles this canal is enclosed by the articular and prearticular.

Prearticular: The posterior and anterior portions of the left prearticular are preserved, as well as a small anterior portion of the right one (Fig. 12B, F). The prearticular contacts the articular posteriorly, the angular ventrally and probably the coronoid dorsally (Fig. 12B, F). The prearticular forms the dorsal border of the foramen intermandibularis caudalis and the inner rim of the fossa Meckelii. In the medial surface of this bone the groove of the unclosed canalis chorda tympani mandibularis is preserved (Fig. 12B, F).

Splenial: Both splenials are missing, but their presence can be inferred by the suture surface left on the dentary (Fig. 12B, F). As in *Nio. argentina* the splenial almost reaches the symphysis anteriorly (Fig. 12B, F).

SHELL

The description of the shell is mainly based on MPEF-PV 10559, with complementary information from MPEF-PV 10557, MPEF-PV 10556 and MPEF-PV 10558. The most complete specimen (MPEF-PV 10559) is represented by several associated fragments. It is apparent that MPEF-PV 10559 is smaller than the holotype. *Gaffneylania auricularis* shows the main characteristics of meiolaniform shells: ornamentation consisting of many small foramina and strongly anteriorly curved marginal sulci (Fig. 13). The carapace bones are thin elements, but are thicker towards the periphery. The contact between the carapace and the plastron is loose, as it can be deduced from the distal ends of a hyoplastron or hypoplastron.

Carapace: Within the available specimens no remains of a pygal, suprapygals or neurals have been recognized, although the left portion of the nuchal is preserved in MPEF-PV 10559 (Fig. 13A). It is a large element forming the anteromedial rim of the carapace. It has a shallow nuchal notch, and the anterior border is serrated. This morphology is different from the anteriorly protruding nuchal margin seen in *Mei. platyceps* (see Gaffney, 1996; figs 5, 6, 11–22) and in *Kallokibotion bajazidi* (see Gaffney & Meylan, 1992) or the wide and deep nuchal margin seen in some meiolaniforms such as *Mon. efremovi* and *Pat. gasparinae* (see Sukhanov, 2000; Sterli & de la Fuente, 2011b; Sterli, de la Fuente & Cerda, 2013b). No natural borders of the nuchal (besides the anterior) are preserved in this specimen, and its contacts are therefore obscured.

Costals are represented mainly by MPEF-PV 10559, with the addition of MPEF-PV 10558 (right costal 1). There are remains of costals 1 (left MPEF-PV 10559 and right MPEF-PV 10558), left costal 3, left costal 4, at least one fragment of right costal 8 and several indeterminate costals. The distal end of two costals indicates that the costals and peripherals were separated by small fontanelles in some regions of the carapace. A similar condition is recognized in the carapace of *Chu. copelloi* and *Pat. gasparinae* (Sterli & de la Fuente, 2011a; Sterli *et al.*, 2015). In the ventral view of costal 1, thoracic ribs 1 and 2 are present. Unfortunately, poor preservation of the costals precludes any further description.

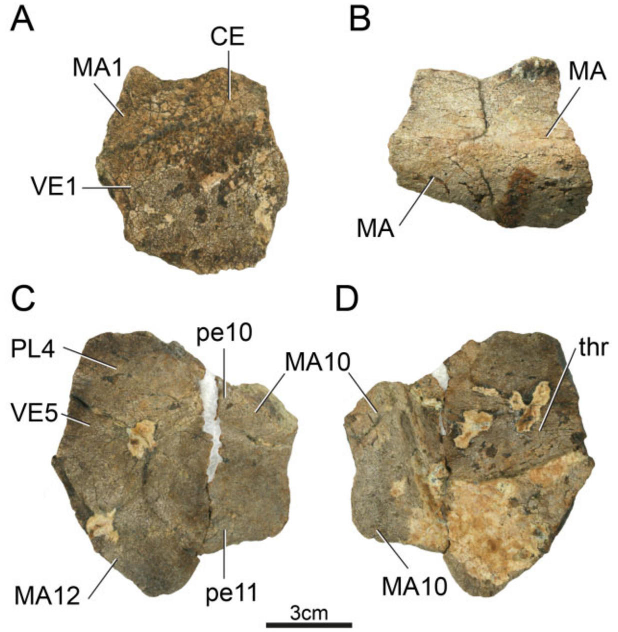

Figure 13. ***Gaffneylania auricularis* gen. et sp. nov.** Photographs of shell remains. A, left fragment of nuchal bone of MPEF-PV 10559 in dorsal view. B, bridge peripheral bone MPEF-PV 10556 (holotype) in lateral view. C, D, right peripherals 10 and 11 of MPEF-PV 10559 in dorsal (C) and ventral (D) views.

Peripherals are represented mainly by MPEF-PV 10559, with the addition of the left peripheral 2 (MPEF-PV 10558) and the right bridge peripheral of MPEF-PV 10556 (Fig. 13B). The preserved peripherals are right peripherals 3 and 4, left and right peripherals 5 or 6, left peripheral 7, left and right peripherals 8, left peripheral 9, and right peripherals 10 and 11 (Fig. 13C, D). Due to poor preservation of the specimen, the sutures of peripherals with other bones have not been preserved. Similar to the border preserved in the nuchal, the posterior peripherals (8–11) also show a serrated margin. The bridge is formed by peripherals 3–7, whereas in *Mei. platyceps* the bridge extends between peripherals 3 and 8 (see Gaffney, 1996, fig. 6). The preserved bridge peripherals are L-shaped. In some bridge peripherals, the peg for the rib is preserved. Compared with other meiolaniforms, these pegs are very narrow.

The left side of the cervical scute is preserved on the nuchal and it is broader than long (Fig. 13A). Parts of vertebrals 1–3 and 5 are preserved on the nuchal (Fig. 13A), the preserved costals and posterior peripherals (Fig. 13C). Due to the fragmentary nature of the shell, the shape and proportions of the vertebral scutes cannot be established. Pleurals 1–4 are preserved on the costals and posterior peripherals (Fig. 13C). Again, due to the fragmentary nature of the shell, the shape and proportions of the pleural scutes cannot be established. Almost all marginals are unknown, except marginal 10. The sulci between the marginal scutes are straight but near the border they bend strongly to the anterior (Fig. 13B). This is also seen in *Pat. gasparinae* (Sterli & de la Fuente, 2011a), *Trapalcochelys sulcata* Sterli *et al.*, 2013b (Sterli *et al.*, 2013b), *Mei. platyceps* (Gaffney, 1996) and *Mon. efremovi* (PIN 551-459-1). The ventral part of the marginals cover, only partially, the ventral part of the peripherals, suggesting that the visceral cavity was expanded (Fig. 13D). This condition is similar to the meiolaniid *Mei. platyceps* (Gaffney, 1996), but is different from other basal meiolaniforms such as *Chu. copelloi*, *Pat. gasparinae* and *Tra. sulcata*.

Plastron: The plastral remains are very fragmentary, preventing any detailed description. The description is based on MPEF-PV 10559, with complementary information from MPEF-PV 10556. Two fragments of the lateral left and right hypoplastra (MPEF-PV 10559) are preserved. The interdigitated distal ends of hyoplastron or hypoplastron (MPEF-PV 10559, 10556) show the loose connection between the carapace and the plastron. A loose connection along the bridge is also recognized in *Mei*. *platyceps* and in *Chu*. *copelloi* among meiolaniforms.

Only the sulcus between the abdominal and femoral scutes is preserved in the hypoplastra (MPEF-PV 10559). As in most turtles this scute is bent posteriorly at the base of the inguinal buttress.

VERTEBRAL COLUMN

Cervical vertebrae: The axis (Fig. 14A) and the third cervical vertebra (Fig. 14B) are the only preserved cervicals. The general morphology of these vertebrae resembles that of *Mei*. *platyceps* (Gaffney, 1985 and personal observations by J.S. on AM F 49141 and AM F 57984).

The axis (MPEF-PV 1778-1) is complete except for the left parapophysis (Fig. 14A). The centrum is strongly convex anteriorly and concave posteriorly. The anterior articular surface is wider than tall, while the posterior one is more quadrangular. Ventrally the centrum has a constriction just posterior to the anterior articular surface delimiting a ridge, which bifurcates posteriorly, and ends in the parapophysis. The neural arch of the vertebra is taller than the centrum. The diapophysis is located just posterior to the convex anterior articular surface. The prezygapophyses are strongly reduced and located at the base of the neural crest (in the middle of the neural canal) close to the diapophysis. The prezygapophysis faces dorsolaterally and articulates with the postzygapophysis of the atlas. The postzygapophysis is well developed and points ventrolaterally. Anteriorly the neural arch has a blunt process projecting further anteriorly than the centrum. The dorsal surface of this process is flat as in *Mei*. *platyceps* (Gaffney, 1985 and personal observations by J.S. on AM F 49141 and AM F 57984). Gaffney (1985) suggested this anterior process articulated with the underside of the skull just posterior to the crista supraoccipitalis. In some living turtles and in some extinct ones (Sterli & de la Fuente, 2011a), this anterior part of the neural arch is related to the M. collooccipitis (= M. obliquus capitis of Shah, 1963) that originates in the neural arches of cervicals 1–4, runs anteriorly, and inserts into the fascia temporalis posterostegalis located posteriorly in the squamosal, parietal and supraoccipital (Werneburg, 2011). Dorsally and between both postzygapophyses there is a concavity, probably for neck muscle attachment. The presence of diapophysis and parapophysis suggests that *G. auricularis* had double-headed cervical ribs and that at least cervical ribs 1 and 2 articulated with two cervical vertebrae. The axis of *G. auricularis* differs strongly from the axis of *Pat*. *gasparinae* in size and general morphology. The axis of *G. auricularis* is at least three times larger than that of *Pat*. *gasparinae*. In *Pat*. *gasparinae* the anterior and posterior articular surfaces of the centrum are not strongly convex and concave, respectively. In addition, the anterior process of the neural arch is a flat crest in *Pat*. *gasparinae*, while it is a blunt and robust process in *G. auricularis*.

The other preserved cervical vertebra is the 3rd (MPEF-PV 10556). This vertebra is mostly complete, but the right pre- and postzygapophyses and the left diapophysis are missing (Fig. 14B). The general morphology resembles that of *Mei*. *platyceps* (Gaffney, 1985 and personal observations by J.S. on AM F 49141 and AM F 57984). The centrum is robust, the anterior articular surface is round and strongly convex, and the posterior one is round and strongly concave. In ventral view, the centrum has an anterior constriction starting just posterior to the anterior articular surface. Posteroventrally the centrum has paired parapophyses. The neural arch is well developed, being as tall as the centrum. The diapophysis is located in the middle of the centrum. The prezygapophysis points mediodorsally. The neural arch has a small anterior crest located anteriorly to the postzygapophysis. Only the proximal edge of the left postzygapophysis is preserved and it faces ventrolaterally. Although the axis of *G. auricularis* and *Pat*. *gasparinae* is markedly different, there a few differences in cervical 3. As in the axis, *Pat*. *gasparinae* is much smaller than *G. auricularis* and the articular surfaces of the centrum are not well developed in *Pat*. *gasparinae*, differing notably from those of *G. auricularis*. Another difference is the absence of a well-developed ventral crest in *G. auricularis*.

Caudal vertebrae: Only four caudal vertebrae are known from *G. auricularis*, one anterior (Fig. 14C) and three mid or posterior (MPEF-PV 10556). All are opisthocoelous (Caudals B–D, characters 204–206) and have a posteroventral articulation for chevron bones (Chevron A, Character 207). The anterior caudal is a large, robust, almost complete element, although the left postzygapophysis and both transverse processes are missing. The general shape resembles that of the second to fourth caudal of *Mei*. *platyceps*. The centrum is strongly convex anteriorly and concave posteriorly. Posteroventrally it has two processes for the articulation with the chevrons. The neural arch is well developed and it is as tall as the centrum. The diapophysis is located in the middle of the centrum and points posterolaterally. The postzygapophyses are located more closely to one another than both prezygapophyses. The neural arch has a blunt process anterior to the postzygapophyses. The general morphology of this

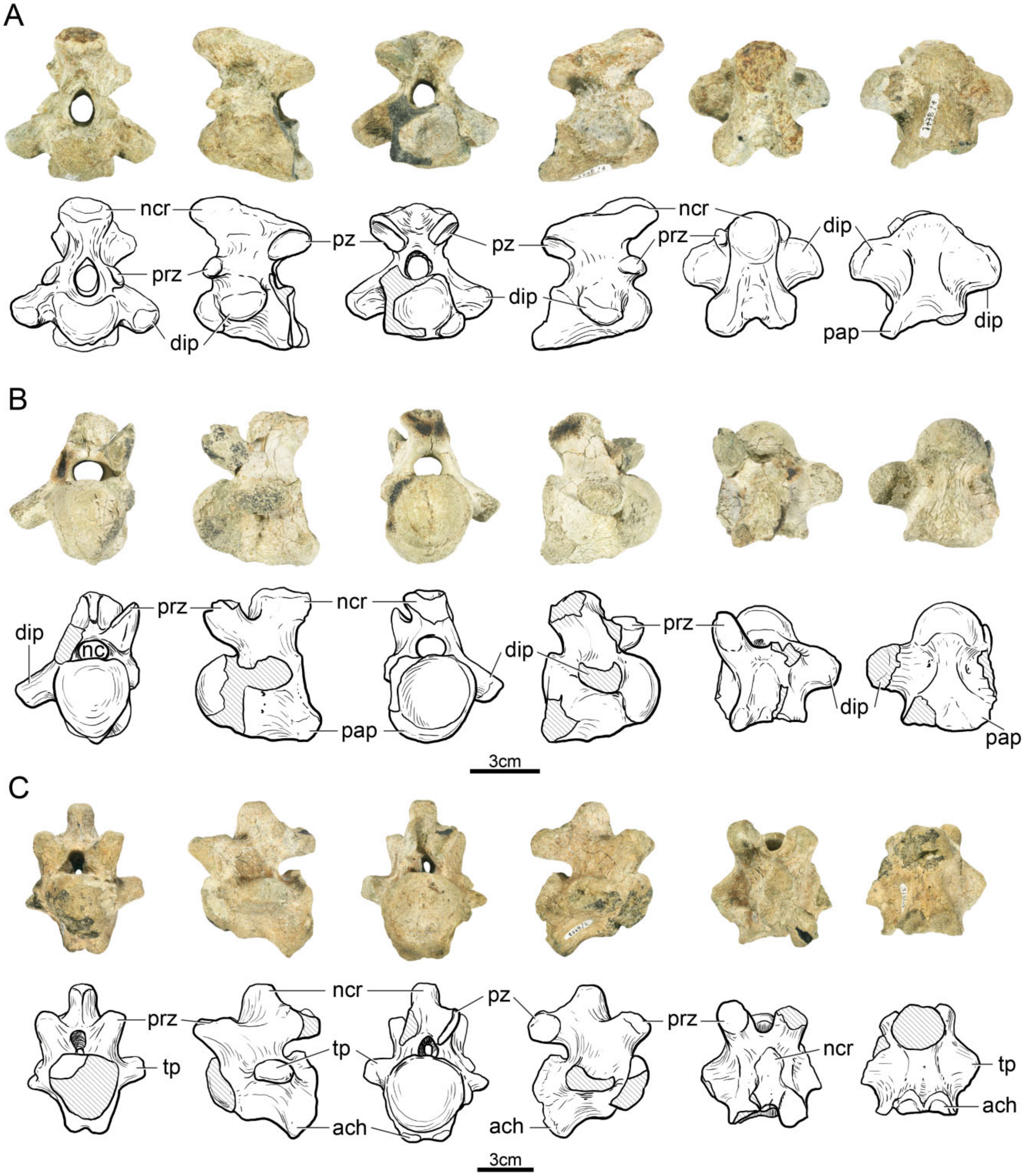

Figure 14. ***Gaffneylania auricularis* gen. et sp. nov.** Photographs and drawings of the axis MPEF-PV 1778-1 (A), cervical vertebra 3 MPEF-PV 10556 (holotype) (B) and a proximal caudal vertebra MPEF-PV 1778-2 (C) in anterior, left lateral, posterior, right lateral, dorsal and ventral views.

vertebra is similar to the anterior caudals of *Pat. gasparinae*, but that of *Pat. gasparinae* is much smaller. Two of the three medial vertebrae are broken and distorted. The undistorted vertebra is the smallest. The anterior and posterior articular surfaces are strongly convex and concave, respectively. The neural arch of this vertebra is almost gone. The base of the transverse process is preserved and is located in the middle of the centrum.

Forelimbs

The description of the humerus is based on the complete left humerus and on the proximal end of the right humerus of the holotype (Fig. 15). The humerus has both ends (epiphyses) well expanded (Humerus E, character 219) and almost in the same plane. Both ends are connected by a very short diaphysis that gives the aspect of a short and robust humerus (Fig. 15A; Humerus E, character 219). The general morphology of the humerus of *G. auricularis* resembles that of *Proganochelys quenstedti* Baur, 1887 (Gaffney, 1990 and personal observations on SMNS 16980), *Mei. platyceps* (Gaffney, 1996 and personal observations on AM F 57984 and AM F 16848) and the meiolaniform humerus described as cf. *Niolamia* (de Broin, 1987), and differs from the more slender humeri of extant turtles and *Palaeochersis talampayensis* Rougier, de la Fuente & Arcucci, 1995 (Sterli, de la Fuente & Rougier, 2007), *Mon. efremovi* (Suzuki & Chinzorig, 2010), *Kallokibotion bajazidi* (Gaffney & Meylan, 1992) and *Naomichelys speciosa* Hay, 1908 (Joyce, Sterli & Chapman, 2014). In the proximal end, the head and the medial and lateral processes are well defined (Fig. 15A). The head is ovoid, being taller than wide (Fig. 15A–E). Next to the head and towards the lateral process, a shoulder is present (Fig. 15A, B). The medial process is more developed than the lateral process as in *Mei. platyceps*. In ventral view, a deep, C-shaped intertubercular fossa is present (Fig. 15C, E). The distal end is built up by the ectepicondyle (anterior) and the entepicondyle (posterior) (Fig. 15A–D, F), two processes of similar size. A groove leading to the ectepicondylar foramen (Humerus A, character 215) is present on the dorsal surface of the ectepicondyle (Fig. 15A, D). The canal opens in the ventral surface of the humerus next to the capitellum (Fig. 15C). In ventral view, the distal end has two articulation facets, the anterior capitellum and the posterior trochlea (Fig. 15C, F). The capitellum articulates with the radius, and the trochlea with the ulna (Gaffney, 1990). Only the distal end of the right ulna (MPEF-PV 10556) is known for *G. auricularis*. The distal end in distal view has two convex surfaces. This end would articulate with the ulnare and intermedium (Gaffney, 1990).

Hindlimb

Two fragments of the femur and tibia are preserved in *G. auricularis*. The femur is represented just by the right head of the holotype (MPEF-PV 10556). The head is oval in shape, and longer than wide. Due to the fragmentary nature of the femur, no other characters can be described. Only the distal extreme of the tibia is preserved. In the distal end of the tibia a convex and flat surfaces are defined which articulate with the astragalocalcaneum.

Osteoderms

Nine osteoderms of *G. auricularis* have been recovered (MPEF-PV 10556, 10557 and 10571). They are all different in shape, size and robustness, and we assume they covered the limbs based on comparison with turtles with osteoderms preserved *in situ* (e.g. *Pro. quenstedti*, *N. speciosa*). All osteoderms in *G. auricularis* are single elements (not arranged in triads or in pairs as the tail and neck osteoderms of *Pro. quenstedti*). The biggest elements of *G. auricularis* are asymmetric and tear-shaped (Fig. 16A–C). In the ventral part they have an oval attachment site with the dermis and it ends in a free tip inclined at approximately 30° to the horizontal (Fig. 16B, C). The mid-sized elements are more symmetric and also tear-shaped (Fig. 16D, E). They also have a free tip and a ventral attachment site, but in this case it is rounded (Fig. 16E). The smallest elements (Fig. 16F, G) are not complete, but they seem to be disc-like elements with a broad ventral surface as the attachment site (Fig. 16G). Compared with *Pro. quenstedti*, it seems that the asymmetrical elements are located mainly in the flanks of the zeugopodium and the subcircular elements are located in the middle (Barrett *et al*., 2002). As in *Pro. quenstedti* but in contrast to *N. speciosa* and *Solemys vermiculata* de Lapparent de Broin & Murelaga, 1999 (de Lapparent de Broin & Murelaga, 1999; Barrett *et al*., 2002), all osteoderms in *G. auricularis* have no conspicuous ornamentation. However, the osteoderms of *G. auricularis* have the same small pits present in other dermal bones of the same taxon (e.g. shell remains, skull bones) as well as in other meiolaniforms (e.g. *Peligrochelys walshae*, *Mei. platyceps*).

DISCUSSION

Diversity

The clade Meiolaniidae is known from southern South America and Australasia (Australia and surrounding islands). The major diversity of this clade is found in Australasia where at least five species have been named ranging from the ?late Oligocene–early Miocene to the

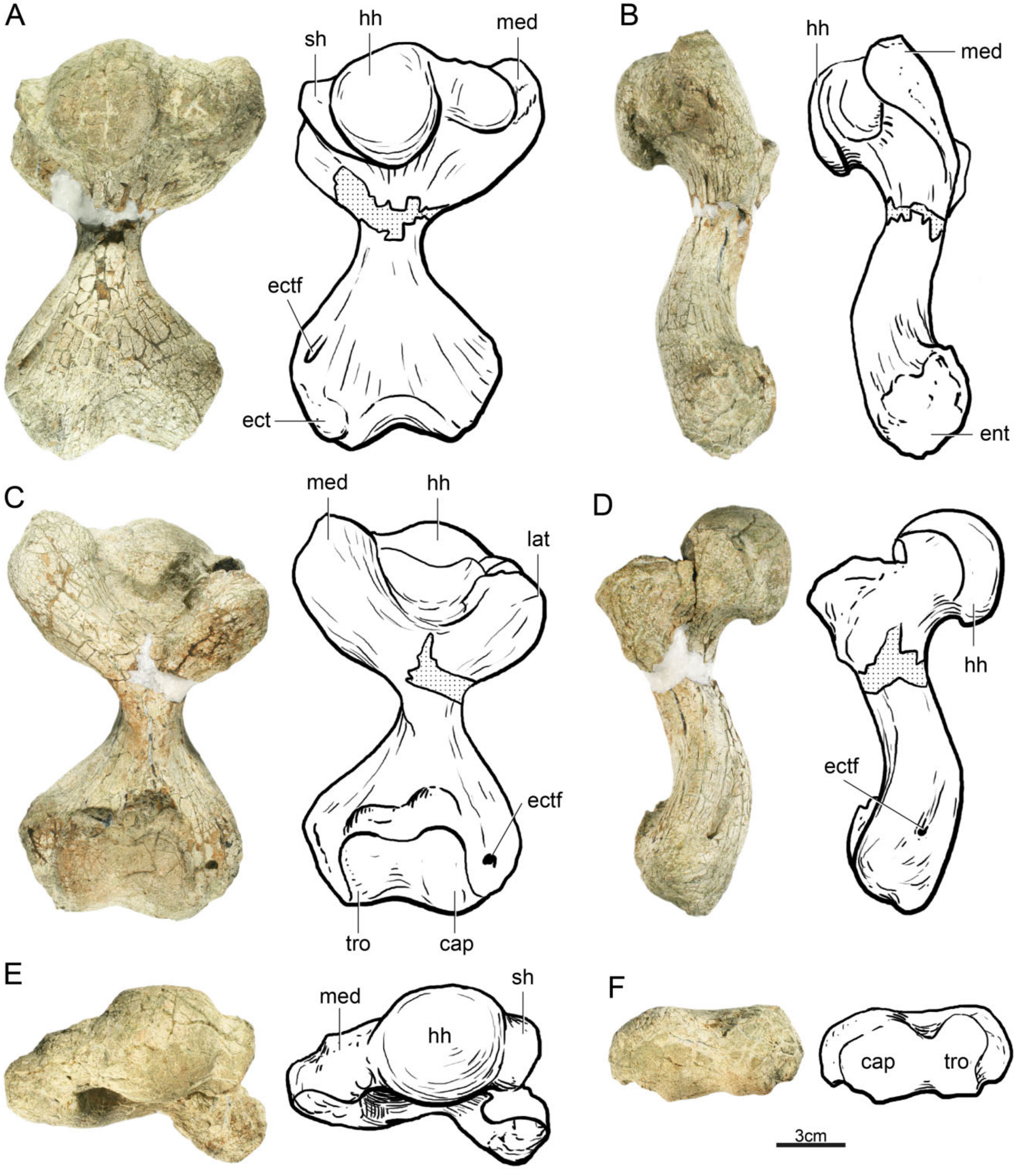

Figure 15. ***Gaffneylania auricularis*** **gen. et sp. nov.**, MPEF-PV 10556 (holotype). Photographs and drawings of the left humerus in dorsal (A), posterior (B), ventral (C), anterior (D), proximal (E) and distal (F) views.

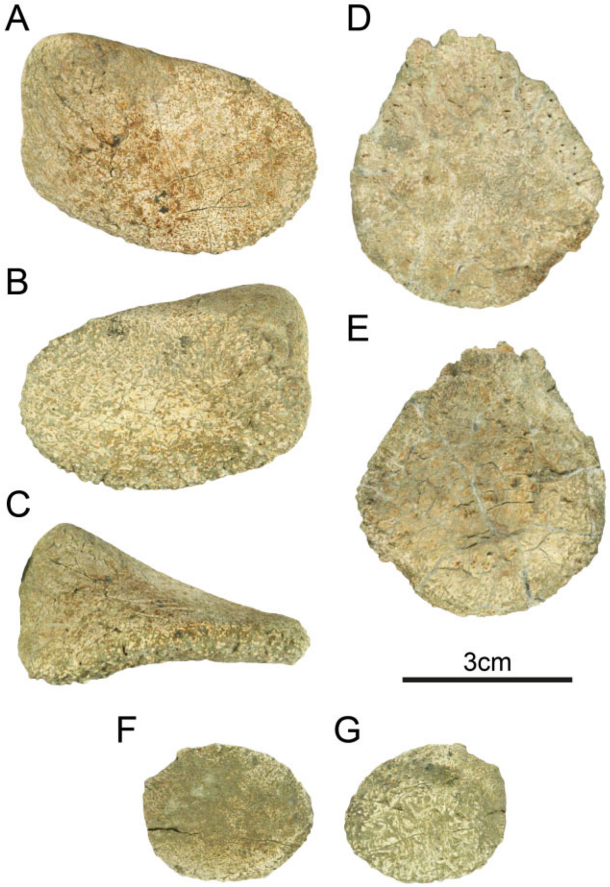

Figure 16. ***Gaffneylania auricularis* gen. et sp. nov.** Photographs of some osteoderms. A–C, asymmetric osteoderm MPEF-PV 10556 (holotype) in dorsal (A), ventral (B) and anterior (C) views. D, E, symmetric osteoderm MPEF-PV 10556 (holotype) in dorsal (D) and ventral (E) views. F, G, symmetric osteoderm MPEF-PV 10571 in dorsal (F) and ventral (G) views.

Quaternary *Warkalania carinaminor* (?late Oligocene–early Miocene of Riverside Station, north-west Queensland), *Meiolania brevicollis* (middle Miocene of Camfield Beds, Northern Territory), *Ninjemys oweni* (Pleistocene of southern Queensland), *Meiolania platyceps* (Pleistocene, Lord Howe Island) and *Meiolania mackayi* (Pleistocene, Walpole Island, New Caledonia). Recently another putative meiolaniid, ?*Meiolania damelipi* White *et al*., 2010, was found in Vanuatu Island (White *et al*., 2010), but the assignment of this species to Meiolaniidae has recently been questioned (Sterli, in press). By contrast, until now the diversity of meiolaniids in South America has been restricted to only one species, *Nio*. *argentina* from Chubut Province, Argentina. Even though the Patagonian *Crossochelys corniger* Simpson, 1937 was recognized by Simpson (1938) as a fully valid Meiolaniidae species, the revisions made by Gaffney (1983, 1996) and Sterli & de la Fuente (2011b) suggest that *Crossochelys corniger* is the junior synonym of *Niolamia argentina*. In this paper we present the second meiolaniid species from South America, *Gaffneylania auricularis*, which provides more information regarding the anatomy and diversity of this clade on this continent.

Meiolania platyceps is the most complete known meiolaniid so far. Although a beautiful dermal skull, tail ring and tail club are known for *Nin*. *oweni*, the basicranium and the remaining postcranial remains are missing (Gaffney, 1992). The other Australasian species are represented by even more fragmentary specimens. This is the case of *War*. *carinaminor* from Riversleigh (Australia), where only some skull fragments have been assigned to the species (Gaffney *et al*., 1992). Some other cranial and postcranial remains originated from Riversleigh were also mentioned by Gaffney *et al*. (1992), although he did not assign them to *War*. *carinaminor*. The middle Miocene *Mei*. *brevicollis* is known based on a few skull remains, three cervical vertebrae (second, fifth and sixth) and scarce shell fragments (Megirian, 1992). The Pleistocene *Mei*. *mackayi* is only known from horn cores, fragments of humeri and a tibia described by Anderson (1925). In this context, the discovery of the cranial and postcranial remains of *G*. *auricularis* is important. The Patagonian meiolaniids represent the oldest record of the clade, providing important information about the anatomy and evolutionary history of the clade. In addition to two meiolaniid species, Patagonia has revealed the existence of several species related to the clade Meiolaniidae, such as *Peligrochelys walshae* and *Chu*. *copelloi*, providing more data to explore the origin and evolution of the clade in southern Gondwana.

THE BREAK UP OF GONDWANA, CLIMATIC CHANGES, AND MEIOLANIID PALEOBIOGEOGRAPHY

Meiolaniidae is a clade distributed formerly in southern South America and Australasia. This distribution has also been observed in many other many kinds of organisms, allowing Morrone (2002, 2006) to recognize the Austral biogeogeographical kingdom, separated from the better known Holarctic and Holotropical kingdoms. The Austral kingdom of Morrone (2002, 2009) is formed by southern South America, south-eastern Australia, Tasmania, New Zealand, Antarctica, New Guinea and the southern tip of South Africa. The animals and plants distributed in this Austral kingdom are the result of the common history of all those continents in the geological past when all of them were closely related in the supercontinent Gondwana. There are many taxa exhibiting the same phylogenetic and distributional pattern that suggest a common past history: the angiosperm *Nothofagus*, lungfishes, helmeted frogs, madtsoiid snakes, chelid and meiolaniid turtles, ratite birds, monotremes and marsupials (e.g. Pascual *et al*., 1992; de Broin & de la Fuente, 1993; Woodburne & Case, 1996; Van Tuinen, Sibley & Hedges, 1998; Scanlon & Lee, 2000; Sanmartín & Ronquist, 2004; Scanlon, 2005; Sigé *et al*., 2009; Cione *et al*., 2011; de la Fuente *et al*., 2011; Gómez, Báez & Muzzopappa, 2011; Beck, 2012; Black *et al*., 2012). Sanmartín & Ronquist (2004) analysed 54 animal and 19 plant phylogenies to reconstruct the biogeographical history of the southern hemisphere. In this study Sanmartín & Ronquist (2004) concluded that the break up of Gondwana played an important role in the history of the distribution of the animals in the southern continents and that Antarctica acted as a frequent route of dispersal between southern South America and Australia. They also showed that the data provided by animals is congruent with the geological sequence of the break up of Gondwana, being: (Africa (New Zealand (southern South America + Australia))) (Sanmartín & Ronquist, 2004).

The palaeobiogeographical distribution of meiolaniids (Supporting Information 19–21; Sterli & de la Fuente, 2013) is generally in concordance with the biogeographical scenario proposed by Morrone (2002, 2006) and Sanmartín & Ronquist (2004). According to several phylogenetic analyses (Sterli & de la Fuente, 2013; Sterli *et al*., 2013a, 2015; present analysis) meiolaniids are recovered deeply nested in a monophyletic group dominated by Gondwanan taxa named Meiolaniformes. Following the analyses presented here and in Sterli & de la Fuente (2013) the clade Meiolaniformes would have been originally distributed in the southern part of the present-day South America and it would have originated sometime between the early Jurassic and the early Cretaceous. After the split of *Ch. copelloi*, the clade dispersed onto Antarctica (Supporting Information 19–21; Sterli & de la Fuente, 2013, fig. 3). Later, the palaeobiogeographical reconstruction suggests that some clades of meiolaniforms, including the clade Meiolaniidae, were distributed in the present-day Antarctica and then dispersed to other continents (i.e. South America, Australia). Unfortunately, until now, no remains of meiolaniform turtles, nor any other continental turtle, have been found in Antarctica.

The palaeobiogeographical scenario presented here and by Sterli & de la Fuente (2013) is plausible according to the palaeogeography and palaeoclimatic reconstructions obtained for southern South America, Antarctica and Australia for the Late Cretaceous, Palaeogene and Neogene. The separation of Gondwana started at 155 Mya approximately when South Africa started the detachment from Antarctica (Jokat *et al*., 2003). Until 90 or 80 Mya (Gaina *et al*., 1998) Antarctica, Australia, New Zealand/New Caledonia and South America remained connected. The origin of the South Tasman Sea, between South America/Antarctica and Australia/New Guinea, started in the Late Cretaceous (90 Mya) and complete separation occurred either in the early Eocene (50 Mya; Woodburne & Case, 1996) or in the late Eocene (35 Mya; Lawver, Gahagan & Dalziel, 2011). The connection between South America and Antarctica was lost in the Eocene–Oligocene boundary (33.9 Mya) with the opening of Drake Passage (Livermore *et al*., 2005). This event caused serious climatic changes worldwide, such as a drop in temperature and precipitation (e.g. Zachos *et al*., 2001; Merico, Tyrrell & Wilson, 2008). In Gondwana, this climatic event is well studied in South America (e.g. Bellosi & Krause, 2014) and in Australia (e.g. Martin, 2006; Kemp *et al*., 2014). In turn, this climatic change caused changes in the vegetation and consequently in the fauna. In South America, in particular in Patagonia, studies have mostly focused on the evolution of mammals (e.g. Pascual, 1984; Flynn & Wyss, 1998; Ortiz-Jaureguizar & Cladera, 2006; Pascual & Ortiz-Jaureguizar, 2007; Woodburne *et al*., 2014). Following previous authors, the evolution of mammals in South America can be divided into several phases, identified as SALMAs, ruled by the main climatic events that occurred during the Cainozoic. Goin, Abello & Chornogubsky (2010) identified the drastic change in the mammalian fauna in Patagonia occurred between the Late Eocene and Oligocene as the Patagonian Hinge in resemblance with the European Grande Coupure (Stehlin, 1909).

THE EXTINCTION OF TURTLES IN PATAGONIA DURING THE EOCENE

The fossil record of the clades Meiolaniformes and Chelidae (Pleurodira) in Patagonia spans from the Early Cretaceous to the Middle Eocene. The last records of meiolaniids and chelids in Patagonia are found in the Cañadón Hondo area (Chubut Province, Argentina) in outcrops of the Sarmiento Formation below beds with mammals suggesting the Casamayoran SALMA (early Middle Eocene). There are no records of turtles in any of the highly fossiliferous younger sediments of Gran Barranca (Barrancan SALMA; late Middle Eocene and Mustersan SALMA; latermost Middle–Late Eocene) or La Cancha (Tinguirirican SALMA; Early Oligocene). The turtle record in Patagonia starts again in the Deseadan SALMA (Late Oligocene–Early Miocene) with the discovery of fragmentary remains of probably terrestrial tortoises of the clade Testudinidae from Cabeza Blanca (Chubut, Argentina) (de Broin & de la Fuente, 1993). The ecological requirements (e.g. temperature, humidity) and behaviour of extant testudinids are very different from those of chelids, as revealed by their distribution and habitats. Extant chelids are aquatic turtles always associated with freshwater bodies under tropical and subtropical conditions and they are distributed throughout South America with exception of the coastal Andes and Patagonia (Iverson, 1992; de la Fuente, Sterli & Maniel, 2013). The southernmost discovery of chelids in South America was recorded during the Palaeocene in Punta Peligro (Chubut Province, Argentina; around 1000 km south of the distribution of the closest living species) and during the Eocene in the Cañadón Hondo area (also in Chubut Province; around 950 km south of the distribution of the closest living species) (Bona, 2006, and references therein). Otero, Soto-Acuña & Yury-Yañez (2012) presented the first record of turtles and crocodiles from Sierra Baguales (Magallanes Region, Chile; middle Eocene, Río Baguales Formation). Considering the description and the photographs shown by the authors, it is highly probable that the Testudines indet. they presented are indeed remains of chelids. If this assumption is confirmed, the record from Sierra Baguales would be the southernmost record of chelids in Patagonia, 1600 km south from the distribution of the closest living species of chelid. Unfortunately, meiolaniforms do not have extant representatives to be used for comparison. On the other hand, testudinids are terrestrial turtles and in South America testudinids are nowadays found in dry areas with scarce vegetation, savannahs, dry and humid forests and even rain forests (Ernst & Barbour, 1989; de la Fuente *et al*., 2013). The southernmost distribution of extant testudinids in South America is represented by *Chelonoidis chilensis*, which reaches Chubut Province (Argentina) (Iverson, 1992). In the fossil record, the southernmost record of testudinids in South America is represented by the finding in Cabeza Blanca (Chubut Province, Argentina) (de Broin & de la Fuente, 1993). Cabeza Blanca is located 400 km to the south from the distribution of the extant *Chelonoidis chilensis*.

Based on the geological and fossil record and the correlation with the palaeobiogeographical history of other groups (e.g. marsupials, hystricognath rodents, platyrhine monkeys), we propose that chelids and meiolaniids became extinct in Patagonia after the Middle Eocene when the climatic conditions were deteriorating, in particular becoming colder and drier (e.g. Zachos *et al*., 2001). This cooling trend in Patagonia was studied trough abiotic proxies that defined the presence of at least two hyperthermals in the Palaeocene–early Eocene and a period of drier conditions towards the middle Eocene (Krause *et al*., 2010; Bellosi & Krause, 2014; Raigemborn *et al*., 2014). Compared with the mammalian record, turtles became extinct before the Eocene–Oligocene extreme drop in temperature. This might be related to the fact that turtles are ectotherms and depend more on external temperature to perform metabolic activities (Dawson, 1975; Bennett, 1980; Bartholomew, 1982). Moreover, due to their ectothermia, diurnal reptiles could be particularly sensitive to climate changes (Barrows, 2011). Consequently if the temperature dropped beyond the range of temperatures at which turtles can attempt to regulate their body temperature they need to move to more temperate areas or if this change is faster than their migration or adaptation capabilities, they might become extinct (Hutchison, 1982). In this regard, meiolaniids became extinct in Patagonia, while chelids survived in lower latitudes (from Buenos Aires Province towards the north). After the extirpation of chelids and meiolaniids in Patagonia, there were approximately 15 Myr where there are no records of turtles in this region until the appearance of testudinids in the Late Oligocene. South American testudinids could have originated in Africa, as has been suggested by de la Fuente (1988, 1997), and is consistent with molecular and biogeographical studies (Le *et al*., 2006). A similar palaeobiogeographical scenario has also been proposed for the platyrhine monkeys and hystricognath rodents (Takai *et al*., 2000; Marivaux, Vianey-Liaud & Jaegger, 2004; Poux *et al*., 2006; Antoine *et al*., 2012; Kay, 2015).

AUSTRALASIAN RECORD OF MEIOLANIIDAE AND SURVIVORSHIP OF THE CLADE AFTER GLOBAL COOLING

Although Sterli & de la Fuente (2013) have presented a plausible palaeobiogeographical scenario for meiolaniforms, more evidence on other taxa (e.g. chelid turtles, madtsoiid snakes, marsupials, monotremes) is needed to develop a stronger hypothesis about the palaeobiogeography of southern Gondwana taxa. Following Sterli & de la Fuente's (2013) palaeobiogeographical scenario the clade Meiolaniidae may have originated in Antarctica and then dispersed to Patagonia and Australasia before the final separation of the three continents by the Late Eocene (Lawver *et al*., 2011). This hypothesis is somewhat in agreement with the palaeobiogeographical scenarios proposed for marsupials (Beck *et al*., 2008; Beck, 2012; Black *et al*., 2012). These authors proposed several hypotheses to explain the presence of marsupials in Australasia. This presence could be the result of a single or multiple dispersal events from South America to Australasia through Antarctica sometime during the latest Cretaceous or Palaeocene or, alternatively, the marsupial taxa were well spread in the three continents during that time span (Beck *et al*., 2008; Beck, 2012). At least up to now, the absence of turtles (and snakes and monotremes) and the scarce record of marsupials with Australasian affinities in the middle Eocene of the La Meseta Formation (Seymour Island, Antarctica) and the scarce fossil record of continental vertebrates in the Late Cretaceous–Palaeogene of Australasia (Black *et al*., 2012) obscure the palaeobiogeographical history of these clades during an important period for their evolution and distribution among the southern continents.

In accordance with the mammalian record in Australasia, the fossil record of turtles shows a large gap between the Late Cretaceous and the middle Eocene for chelids and Late Oligocene for meiolaniids (Gaffney, 1981; de Lapparent de Broin & Molnar, 2001). As was mentioned above, the meiolaniids survived in Australasia at least from the Late Oligocene to the Pleistocene–Holocene (Gaffney, 1996). Why did meiolaniids (and chelids) survive in Australasia after the worldwide cooling at the Eocene–Oligocene boundary? In contrast to South America, and particularly Patagonia, in Australasia there has been a balance between global cooling and its drifting northwards to warmer regions (McGowran *et al*., 2004). In this sense, although the global temperatures decreased since the middle Eocene climatic optimum (Bohaty & Zachos, 2003) the movement of Australia towards lower latitudes buffered these changes (McGowran *et al*., 2004). From the Late Cretaceous to the Eocene, Australia was connected to Antarctica. In this time period Australia was located at high latitudes with temperatures around 12 and 20 °C (McGowran *et al*., 2004). The opening of the South Tasmanian Sea (caused by the separation of Tasmania–Australia and Antarctica) and the Drake Passage (caused by the separation of South America and Antarctica) at the end of the Eocene (Lawver *et al*., 2011) allowed circulation of the circumpolar current (Zachos *et al*., 2001). The presence of this circumpolar current triggered the drop in the temperatures in Antarctica, initializing the rapid growth of ice sheets (Zachos *et al*., 2001). Although global temperatures declined after the Eocene–Oligocene boundary, the change in temperatures in the Australian continent was not as evident (at least in mid- and lower latitudes) because the continent was drifting northwards (McGowran *et al*., 2004). As global climate was becoming colder, Australasia was migrating towards lower latitudes, compensating for this cooling.

Note that temperatures (and latitude) were comparable during the Late Cretaceous–Early Eocene in Australia and Patagonia, although as far as we know there is no fossil record of turtles during that period in Australia. Consequently, we suggest that the absence of turtles duting that period could be a consequence of a gap in the fossil record per se because this is coincident with the gap in the fossil record also cited for mammals (Black *et al*., 2012) and other continental vertebrates (de Lapparent de Broin & Molnar, 2001; Scanlon, 2005).

ACKNOWLEDGEMENTS

We thank the owner of the farm where we performed the fieldwork, C. A. Cerbino, and D. Castro, I. Maniel, D. Pol, P. Puerta, M. Ramírez and B. von Baczko for their help during fieldwork. Special thanks to L. Reiner (MEF) who prepared the specimens. We thank the collection managers who allowed us to study the collections under their care: E. Ruigómez (MEF, Trelew), M. Reguero (MLP, La Plata), A. Kramarz (MACN, Buenos Aires), Y. Y. Zhen (Australian Museum, Sydney), I. Percival (Geological Survey New South Wales, Sydney), K. Spring and P. Wilson (Queensland Museum, Brisbane), T. Rich (Victoria Museum, Melbourne), S. Chapman (Natural History Museum, London), C. Mehling and E. Gaffney (AMNH, New York). The line drawings of the specimens were produced by J. González. Thanks to I. Werneburg for insight regarding cranial musculature. The Willi Hennig Society is thanked for the free availability of TNT. We are grateful to W. G. Joyce, D. Brinkman and an anonymous reviewer for their detailed and constructive reviews and P. Hayward for editorial work on the manuscript. This work was financed by PIP 112-200801-00795 and PICT 2013-0095 (M.S.d.l.F.), and PICT-2010-0646 and National Geographic Grant 8975-11 (J.S.).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Supporting Information 1. Taxa scored in the matrix.
Supporting Information 2. Matrix in nexus file with the MPTs.
Supporting Information 3. Matrix in tnt format.
Supporting Information 4. Summary of the biogeographical analysis using the DEC model.
Supporting Information 5. Calibrated tree number 1.
Supporting Information 6. Calibrated tree number 2.
Supporting Information 7. Calibrated tree number 3.
Supporting Information 8. File with the input data about dispersal constraints for DEC analysis.
Supporting Information 9. Lagrange file for tree number 1.
Supporting Information 10. Lagrange file for tree number 2.
Supporting Information 11. Lagrange file for tree number 3.
Supporting Information 12. MPTs in nexus file.
Supporting Information 13. MPTs in ctf.
Supporting Information 14. Strict consensus tree with all the taxa.
Supporting Information 15. Reduced strict consensus tree with three taxa pruned (*Patagoniaemys gasparinae*, *Gaffneylania auricularis* and *Hangaiemys hoburensis*). Bremer support, and bootstrap and jackknife resamplings.
Supporting Information 16. Reduced strict consensus tree showing the alternative position of pruned taxa: *Patagoniaemys gasparinae*, *Gaffneylania auricularis* and *Hangaiemys hoburensis*.
Supporting Information 17. List of common synapomorphies.
Supporting Information 18. Result of the script of Pol & Escapa (2009).
Supporting Information 19. Results of DEC analysis for tree number 1.
Supporting Information 20. Results of DEC analysis for tree number 2.
Supporting Information 21. Results of DEC analysis for tree number 3.