New evidence from the Palaeocene of Patagonia (Argentina) on the evolution and palaeo-biogeography of Meiolaniformes (Testudinata, new taxon name)

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Peligrochelys walshae gen. et sp. nov. is a new stem turtle closely related to the clade Meiolaniidae found in the Palaeocene levels of the Salamanca Formation (Maastrichtian–Danian) of central Patagonia, Chubut Province, Argentina. A phylogenetic analysis shows that *Peligrochelys walshae* forms a monophyletic group with *Mongolochelys efremovi*, a clade that, in return, is the sister group of a clade formed by *Patagoniaemys gasparinae*, *Otwayemys cunicularius*, *Kallokibotion bajazidi* and Meiolaniidae. Meiolaniidae is recovered deeply nested in a monophyletic group (Meiolaniformes, new taxon name) dominated by Gondwanan taxa (e.g. *Chubutemys copelloi*, *Patagoniaemys gasparinae*, *Otwayemys cunicularius* and *Peligrochelys walshae*), that also includes some notable Laurasian representatives (*Mongolochelys efremovi* and *Kallokibotion bajazidi*). The biogeographic scenario presented here supports the hypothesis that this group of turtles may have originated as early as the Early Cretaceous in the South American part of Gondwana. The long ghost lineage that extends below this clade suggests that it may have originated any time between the Early Jurassic and the Early Cretaceous, implying a Pangaean or Gondwanan origin for the clade, respectively. The phylogenetic scenario presented here shows that at least two lineages (*Peligrochelys walshae* and Meiolaniidae) of Meiolaniformes survived the K–P boundary extinction. Another interesting characteristic of meiolaniform turtles in the fossil record is their frequent association with another clade of strictly Gondwanan distribution, the pleurodiran clade Chelidae. This association is typically found in outcrops from the Early Cretaceous to the Eocene in central Patagonia, and in the Early Cretaceous and from the Miocene to the Pleistocene in Australia.

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Keywords: *Peligrochelys walshae*; phylogeny; K–P extinction; Chelidae; Meiolaniidae

Introduction

Meiolaniidae is a clade of extinct turtles restricted to the Cenozoic of Patagonia and Australasia, which includes bizarre turtles with cranial horns, frills and a tail club. As pointed out by Gaffney (1983, p. 364), these turtles form one of the most enigmatic clades of turtles and their origin and relationships with other turtles have been discussed controversially for centuries. Historically, meiolaniids have been described as being related to both living groups of turtles – Pleurodira (Boulenger 1887, 1889) and Cryptodira (Huxley 1887; Baur 1889a, b; Gaffney *et al*. 1991; Gaffney 1996) – or were even placed outside the crown (Joyce 2007; Sterli 2010; Sterli & de la Fuente 2011a), but only recently have other fossil turtles been allied with this group. Čkhikvadzé (1987) was the first to note similarities between meiolaniids, *Mongolochelys efremovi* (Khozatsky, 1997) and *Kallokibotion bajazidi* Nopcsa, 1923. The cladistic analysis of Hirayama *et al.* (2000) later grouped the Asian taxa *M*. *efremovi* and Sinochelyidae and the Australasian taxa *Otwayemys cunicularius* Gaffney, Kool,

Brinkman, Rich & Vickers-Rich, 1998 and Meiolaniidae into a monophyletic group. The recently discovered Patagonian turtles, *Chubutemys copelloi* Gaffney, Rich, Vickers-Rich, Constantine, Vacca & Kool, 2007 and *Patagoniaemys gasparinae* Sterli & de la Fuente, 2011a are also believed to be closely related with Meiolaniidae (Gaffney *et al.* 2007; Sterli & de la Fuente 2011a). The increasing number of extinct turtles potentially related to Meiolaniidae (Fig. 1) highlights the necessity for a more inclusive cladistic analysis that includes both meiolaniids and their entire putative sister taxa in order to explore the origin of and relationships within this peculiar clade of turtles.

This study was initiated by the finding of new turtle remains in Palaeocene outcrops of the Salamanca Formation at the Punta Peligro locality (Fig. 2) in central Patagonia (Chubut Province, Argentina). Punta Peligro has been the focus of intense fieldwork for more than 30 years. The most complete specimen presented here was found during fieldwork lead by Dr. José Bonaparte during a joint expedition of the Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina) and the Geology Department of the Universidad

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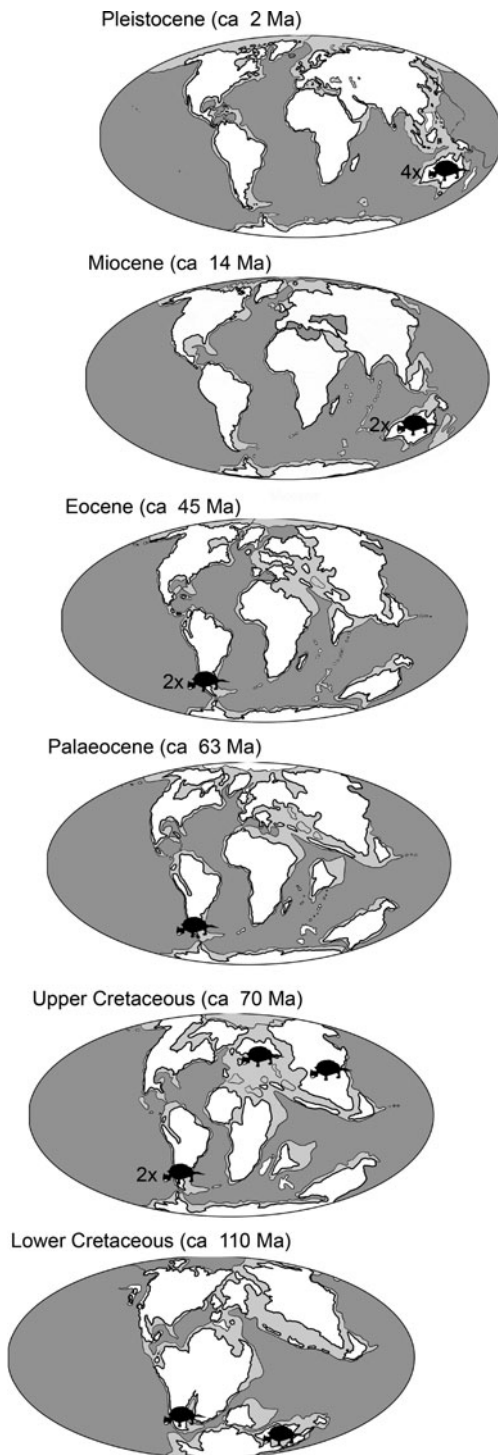*Corresponding author. Email: jsterli@mef.org.ar

Figure 1. Known meiolaniform diversity from the Lower Cretaceous to the Holocene. The number of known species for each place is represented by '2×' and '4×'. Lower Cretaceous: *Chubutemys copelloi* (Argentina) and *Otwayemys cunicularius* (Australia). Upper Cretaceous: *Patagoniameys gasparinae* and an unnamed new species (Argentina). Palaeocene: *Peligrochelys walshae* (Argentina). Eocene: *Niolamia argentina* and an unnamed new species (Argentina). Oligocene-Miocene: *Warkalania carinaminor* and *Meiolania brevicollis* (Australia). Pleistocene-Holocene: *Ninjemys oweni*, *Meiolania platyceps*, *Me. mackayi* and ?*Me. damelipi* (Australia and surrounding islands).

Figure 2. Location of Punta Peligro locality, Chubut Province, Argentina.

Nacional de la Patagonia San Juan Bosco between 1989 and 1991 (Bonaparte *et al*. 1993). Additional specimens were collected during subsequent field excursions led by Dr. Rosendo Pascual (Museo de La Plata, Argentina) in the 1990's and Dr. Guillermo Rougier (University of Louisville, USA) and the Museo Egidio Feruglio (Trelew, Argentina) in 2002 and 2004. The recently recovered remains represent a new genus and species, *Peligrochelys walshae* gen. et sp. nov., an extinct turtle related to the Gondwanan clade Meiolaniidae. The primary goals of this paper are to describe and name the new taxon from the Palaeocene of Patagonia, shed light on the origin of the clade Meiolaniidae, and discuss different aspects related to the palaeobiogeography of this clade and closely related taxa.

Geological setting

The Cretaceous to Cenozoic succession in the coastal area of the San Jorge Gulf (Chubut Province, Argentina) is represented by a Maastrichtian–Miocene sedimentary sequence accumulated in a regional context of a passive margin with episodes of epicontinental flooding and periods of Atlantic Ocean regression (Legarreta & Uliana 1994).

The Salamanca Formation was defined by Lesta & Ferello (1972) on the basis of the 'Salamancanéen' of Ihering (1903). This lithostratigraphic horizon is developed in the coastal region of San Jorge Gulf, in the area extending from Comodoro Rivadavia City to Bahía Bustamante. Its maximum thickness is 161 m at the Bajada de Hansen locality, where Andreis *et al*. (1975) defined the type section of the Salamanca Formation. According to Andreis *et al*. (1975), this formation can be divided into two members: Bustamante and Hansen. The Bustamante Member is characterised by limestones outcropping in the northern region of the gulf that represent the lateral facies of the transgression that accumulated in the Salamanca Formation. The Hansen Member crops out in the whole area, except for Pico Salamanca. This member includes the 'Banco Negro Inferior' (BNI) and the 'Banco Verde' beds. According to several authors (Simpson 1935; Andreis *et al*. 1975;

Legarreta *et al*. 1990; Bonaparte *et al*. 1993; Legarreta & Uliana 1994; Bond *et al*. 1995), these horizons are included in the upper section of the Salamanca Formation based on the lithological continuity and the sedimentation change above the BNI, showing an erosional unconformity between the BNI and the Río Chico Group. However, other researchers (Feruglio 1949; Marshall *et al*. 1981, 1997; Scillato-Yané & Pascual 1985) have included the BNI in the lower section of the Río Chico Group in the area of Punta Peligro, Cerro Redondo and Cerro Abigarrado.

According to Andreis *et al*. (1975), the upper section of Salamanca Formation (= Hansen Member) in the San Jorge Gulf area was accumulated under infra-littoral and transitional sea conditions. The sediments were accumulated in low energy environments yielded by submarine bars or littoral banks that had reduced the circulation in a sea with little differences between high and low tides. Based on foraminifera, Bertels (1975) assigned the upper levels of the Salamanca Formation to the Upper Danian. This hypothesis was supported by the $^{40}K/^{40}A$ isotopic age of 61 ± 5 Ma obtained from a vitreous tuff belonging to the Hansen Member at the Cañadón Hondo locality (Andreis 1977; Marshall *et al*. 1981). This age was subsequently corrected to 62.6 ± 5 Ma by Marshall (1982). Additionally, two more reliable radiometric ages sampled by Marshall *et al*. (1981) in two basaltic units at or just under the base of the Salamanca Formation yielded ages of 64.0 ± 0.8 Ma and 62.8 ± 0.8 Ma. Marshall *et al*. (1981, 1997) used these ages and palaeo-magnetic data to refer the overlaying BNI to polarity subchron C26r (= Danian Stage).

The Punta Peligro flora is composed of a rich diversity of angiosperms (36 leaf species, well-preserved angiosperms, flowers, fruit, seeds and pollen grains) and conifers recovered at Palacio de Los Loros locality (Salamanca Formation; Archangelsky & Zamaloa 1986; Iglesias *et al*. 2007). The palaeobotanical studies (using leaf-margin techniques) by Iglesias *et al*. (2007) suggest a mean annual temperature of 14.1 ± 2.6 °C and a mean annual precipitation of at least 115 cm ($+50/-35$ cm). These palaeoclimatic estimates (Iglesias *et al*. 2007) are also supported by the presence of various thermophilic groups [i.e. palm organs (Romero 1968; Archangelsky 1973), podocarps and alligatorids (Bona 2004)].

The Punta Peligro fauna comes from the basal levels of the BNI in the Hansen Member of the Salamanca Formation (Andreis *et al*. 1975). However, in the Cerro Hansen area, fragmentary or articulated remains of chelid turtles and crocodiles have been recovered below the BNI (Bona *et al*. 1998, fig. 2). The BNI levels are not restricted to Punta Peligro and are widely exposed in southeastern Chubut and northeastern Santa Cruz provinces (Bond *et al*. 1995). Despite the broad distribution of this lithological unit, the richest vertebrate record (particularly mammals) still derives from the Punta Peligro locality (Gelfo *et al*. 2009). The Punta Peligro fauna is composed of leptodactylid frogs, long- and short-necked chelids, meiolani-

form turtles, alligatorid crocodiles (Bonaparte *et al*. 1993; Broin & de la Fuente 1993; Bona & de la Fuente 2005; Bona 2006; this article), and a mixture of non-tribosphenic Gondwanan mammals, as well as mammals derived from the Laurasian boreosphenid stock represented by placentals and marsupials (Pascual *et al*. 1992; Bonaparte *et al*. 1993; Bond *et al*. 1995; Bonaparte & Morales 1997; Gelfo & Pascual 2001; Gelfo *et al*. 2007; Forasiepi & Rougier 2009).

Material and methods

A cladistic analysis was performed to evaluate the phylogenetic relationships of the new species of turtle presented here in particular and meiolaniform turtles in general. Meiolaniformes (new taxon name) is a stem based clade including all the taxa more closely related to *Meiolania platyceps* Owen, 1886 than to Cryptodira or Pleurodira. A dataset of 101 taxa and 240 morphological characters (see Online Supplementary Material Appendix 1) based on that of Sterli & de la Fuente (2011a) was enlarged for the present analysis. Seventeen taxa (including the new species presented here) and 88 characters were added to the Sterli & de la Fuente (2011a) matrix (see character descriptions in Online Supplementary Material Appendix 1). Four taxa (*Owenetta kitchingorum*, *Anthodon serrarius*, *Simosaurus gallardoiti* and *Sphenodon punctatus*) established the outgroup, while 97 taxa of extinct and extant turtles were considered as ingroup. *Sphenodon punctatus* was the taxon selected to root the analysis. All characters were weighted equally and some multi-state characters were ordered (7, 19, 27, 40, 42, 50, 52, 59, 67, 81, 82, 90, 99, 121, 139, 160, 177, 200, 214 and 215). In order to evaluate the phylogenetic relationships of turtles, two rounds of Tree Bisection-Reconnection (TBR) were performed and implemented in the phylogenetic program TNT (Goloboff *et al*. 2008a, b). In the first round, 1000 replicates of random addition sequences on Wagner trees were run. To find all possible most parsimonious trees (MPT), all trees in memory were subject to a second round of TBR. If more than one MPT was found, a strict consensus tree was calculated. Clade support was calculated using Bremer support and Jack-knife resampling with 1000 replicates. Jack-knife values are shown as Group present/Contradicted (GC) frequencies, calculated as the difference of frequencies of one group and all its contradicted groups (Goloboff *et al*. 2003).

In order to explore the historical biogeography of meiolaniform taxa, we applied the dispersal-extinction-cladogenesis (DEC) model created by Ree & Smith (2008). The DEC method is a model-based inference method for reconstructing the biogeographic history of certain clades on phylogenetic trees (Ree & Smith 2008) modelling lineage dispersal and local extinction in established areas through time (Ree *et al*. 2005). Additionally, the DEC model

includes the timing of the probability of the connection between areas and cladogenesis (Ree *et al*. 2005). The calibrated tree, area definition, and range constraints are available in the Online Supplementary Material Appendix 2.

Skull roof bones were observed under a Scanning Electronic Microscope (SEM) JEOL JSM-6460 using 15 Volts and 24 Pascals.

Institutional abbreviations

MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MEPF-PV: Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

Anatomical abbreviations

A–K, X–Z, horns and scales; acst, aditus canalis stapediotemporalis; bs, basisphenoid; cc, canalis cavernosus; cl, cavum labyrinthicum; co, condylus occipitalis; com, condylus mandibularis; csa, canalis semicircularis anterior; csh, canalis semicircularis horizontalis; ct, cavum tympani; ds, dorsum sellae; exo, exoccipital; fcca, foramen carotici cerebralis anterior; fccp, foramen carotici cerebralis posterior; feng, foramen externum N. glossopharyngei; fja, foramen jugulare anterius; fm, foramen magnum; fnab (VI), foramen N. abducentis; fnac (VIII), foramen for N. acustici; fnf (VII), foramen for N. facialis; fnh (XII), foramen N. hypoglossi; fo, fenestra ovalis; forb, fossa orbitalis; fo (V), foramen prooticum; fr, frontal; fst, foramen stapedio-temporale; ha, hiatus acusticus; ica, incisura columella auris; op, opisthotic; pa, parietal; pi, processus interfenestralis of opisthotic; pna (VIII), passage N. acustici (VIII); pr, prootic; prf, prefrontal; pt, pterygoid; pto, processus trochlearis oticum; qu, quadrate; rlo, recessus labyrinthicus opisthoticus; rlp, recessus labyrinthicus prooticus; solf, sulcus olfactorius; tb, tubera basioccipitalis.

Results

Cladistic analysis

One-hundred and twenty-trees of 901 steps (CI: 0.33; RI: 0.76) were found after two cycles of TBR in TNT (Goloboff *et al*. 2008a, b) and a strict consensus tree was calculated (Online Supplementary Material Appendix 1). The list of synapomorphies common to the 120 MPTs is shown in Online Supplementary Material Appendix 3. As our paper is focused only on a certain portion of the turtle tree, a simplified consensus tree is shown Figure 3.

In the strict consensus tree, the new species from Punta Peligro is recovered in the lineage leading to Meiolaniidae. The clade Meiolaniidae and related taxa (Meiolaniformes) in the present analysis is formed by ten species and is placed outside Testudines. Meiolaniformes is diagnosed in all MPTs by the presence of a large exposure of prefrontal
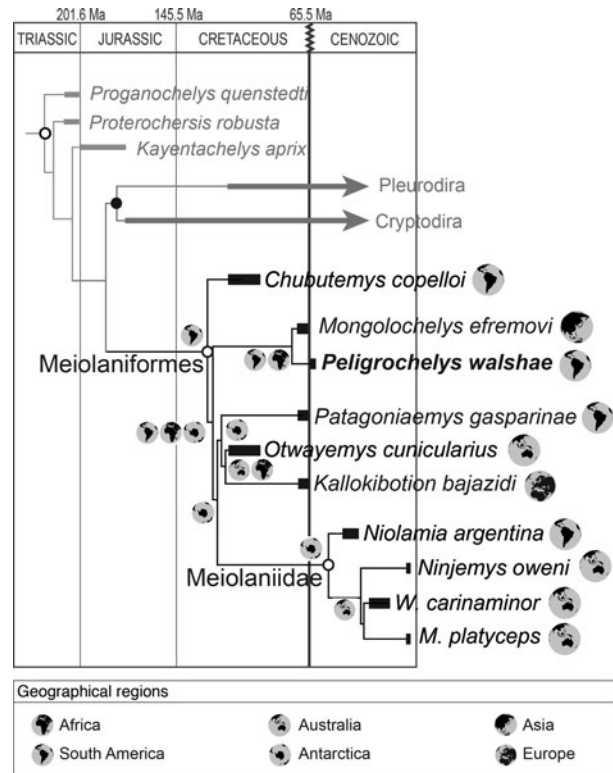

Figure 3. Phylogenetic relationships of *Peligrochelys walshae*. Simplified strict consensus of 120 trees of 901 steps. CI: 0.33, RI: 0.76. White circle: Testudinata. Black circle: Testudines.

(Character 7, prefrontal D), the absence of the frontal to the orbital rim (Character 10, frontal A), the presence of a processus pterygoideus externus like in *Proganochelys quenstedti* Baur, 1887 (Character 70, pterygoid L) and by the presence of a supraoccipital crest protruding posteriorly to the condylus occipitalis (Character 72, supraoccipital A). The clade is furthermore diagnosed in some trees by the absence of a vertical flange on the processus pterygoideus externus (Character 67, pterygoid I). *Chubutemys copelloi* is depicted as the sister group of all remaining meiolaniforms which share the contact between the squamosal and supraoccipital (Character 26, squamosal B), the presence of a tall and narrow ventral crest on the vomer (Character 46, vomer E) and the presence of a domed palate (Character 47, vomer F). The new turtle described here is depicted as the sister taxon of *Mongolochelys efremovi* by sharing the presence of a roughened area between the basisphenoid and basioccipital (Character 87, basisphenoid E). This clade is the sister group of the clade Meiolaniidae + the clade formed by *Kallokibotion bajazidi*, *Otwayemys cunicularius* and *Patagoniaemys gasparinae*, which is supported by the presence of ventral flooring of the cranioquadrate space by the quadrate, avoiding the ventral exposure of the prootic (Character 49, quadrate A), the incisura columella

auris enclosing the Eustachian tube (Character 53, quadrate F), the presence of a contact between the pterygoid and the basioccipital (Character 62, pterygoid D), the presence of a processus pterygoideus externus with parallel margins (Character 70, pterygoid L), and the presence of shortened humeri (Character 220, humerus E).

Meiolaniidae is supported by the following synapomorphies: contact between the quadratojugal and squamosal below the cavum tympani (Character 24, quadratojugal C); horns on the squamosal (Character 27, squamosal C); absence of an antrum postoticum (Character 52, antrum postoticum A), interpterygoid slit present (Character 60, pterygoid C); canalis carotici interni covered ventrally by bone posterior to the bifurcation in cerebral and palatine arteries (Character 98, canalis caroticum E); the arteria palatina enters the skull through the interpterygoid slit (Character 99, canalis caroticum F); foramen posterior canalis carotici interni formed by pterygoid (Character 100, canalis caroticum G); tail club present (Character 204, caudal A); and tail rings present (Character 208, tail ring A).

DEC model

As we primarily discuss in this paper the origin and evolution of meiolaniform taxa, we are going to focus our biogeographical study on this clade as well (Fig. 3). The ancestral areas of remnant nodes seen in Figure 1 are shown in Online Supplementary Material Appendix 4. The DEC model predicts that Meiolaniformes originated in South America. As the oldest members of this clade are from the Early Cretaceous of Patagonia (*Chubutemys copelloi*) and Australia (*Otwayemys cunicularius*), the clade Meiolaniformes should, therefore, be at least as old as the Early Cretaceous. However, as South America was part of Gondwana at that time, we argue that Meiolaniformes originated in Gondwana during the Early Cretaceous (or even earlier; see Discussion).

Systematic palaeontology

Testudinata *sensu* Joyce, Parham & Gauthier, 2004
Meiolaniformes new clade name

Definition. Meiolaniformes is the stem-based definition of Meiolaniidae. Meiolaniformes refers to all the taxa more related to *Meiolania platyceps* than to Cryptodira or Pleurodira in the phylogeny shown in Figure 3.

Referred taxa. Meiolaniformes contains the clade Meiolaniidae (which includes *Niolamia argentina* Ameghino, 1899, *Ninjemys oweni* (Woodward, 1888), *Warkalania carinaminor* Gaffney, Archer & White, 1992 and *Meiolania platyceps*) and their stem taxa *Chubutmys copel-*

loi, *Otwayemys cunicularius*, *Patagoniaemys gasparinae*, *Mongolochelys efremovi*, *Kallokibotion bajazidi* and *Peligrochelys walshae*. All taxa contained in Meiolaniformes are extinct.

Diagnosis. In all trees, Meiolaniformes are characterized by: prefrontal exposure large; frontal contribution to orbit absent; processus pterygoideus externus like in *Proganochelys quenstedti*; and crista occipitalis well developed beyond the foramen magnum. In some trees, Meiolaniformes are characterized also by the presence of vertical flange in the pterygoid present along all the lateral processes or completely absent.

Peligrochelys gen. nov.

Type species. *Peligrochelys walshae*

Etymology. From Peligro, the name of the locality, where this turtle was found and from *chelys*, Greek for turtle.

Diagnosis. As for the species.

Peligrochelys walshae sp. nov.
(Figs 4–9)

Etymology. *walshae*, in honour of María Elena Walsh, an Argentinean music composer, who wrote a famous song about a turtle named Manuelita.

Holotype. MACN-PV CH 2017, several skull bones (basisphenoid, basioccipital, right quadrate, right prootic, left opisthotic, a fragment of the right opisthotic, left exoccipital, right frontal, both postorbitals, fragment of left maxilla, fragments of both squamosals and other skull roof) and a left prezygapophysis.

Referred material. MPEF-PV 3975, basisphenoid and basioccipital; MPEF-PV 3976, right frontal; MACN-2018, left frontal.

Locality and horizon. Punta Peligro locality, 45 km north of Comodoro Rivadavia City, Chubut Province, Argentina (Fig. 2). Banco Negro Inferior, Salamanca Formation, Danian age (Lower Palaeocene).

Diagnosis. *Peligrochelys walshae* is a stem Testudines with the unique combination of the following features (asterisks denote autapomorphies): skull roof covered by scales; presence of a posterior wall separating the fossa orbitalis from the fenestra temporalis inferior; presence of a processus trochlearis oticum; cavum tympani well developed; presence of only one opening for the exit of the nervi hypoglossi (XII) in the exoccipital*; thick basicranium; presence of two concavities in the basioccipital delimited by the well-developed tubera basioccipitalis*; foramina carotici cerebralis posterior located close together; absence of a foramen posterior canalis carotici interni; and foramen carotici cerebralis anterior united forming a slit*. *Peligrochelys walshae* differs from the basal members of
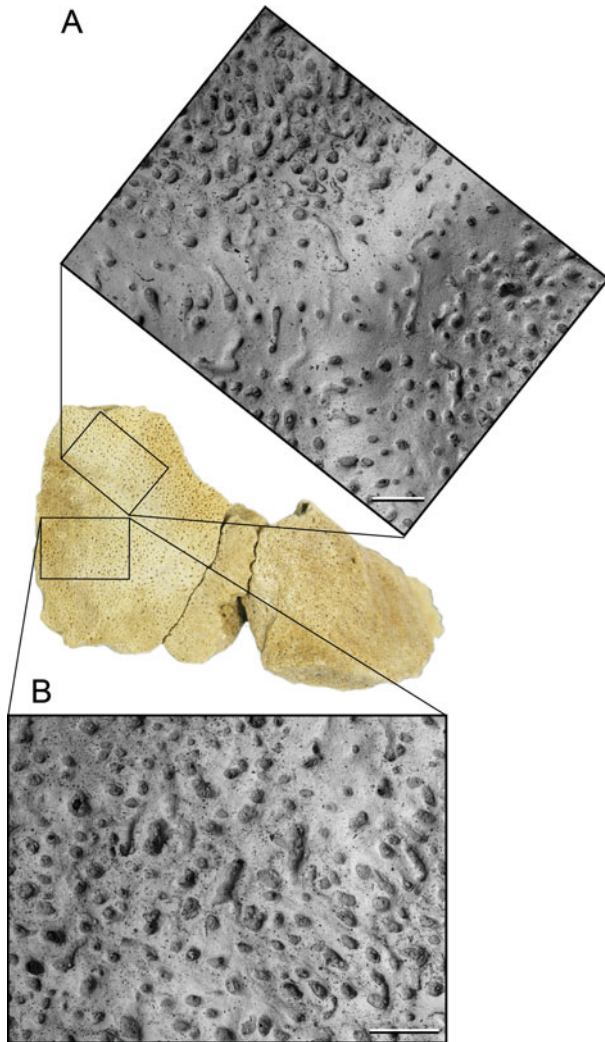
Figure 4. *Peligrochelys walshae*. MACN PV CH 2017, right frontal and right postorbital. Detail of the ornamentation of skull roof elements. **A**, SEM image at 15×; **B**, SEM image at 20×. Scale bar = 1 mm.

Testudinata (e.g. *Proganochelys quenstedti*, *Palaeocher-sis talampayensis* Rougier, de la Fuente & Arcucci, 1995, *Kayentachelys aprix* Gaffney, Hutchison, Jenkins & Meeker, 1987, *Condorchelys antiqua* Sterli, 2008) by the reduction of the processus interfenestralis of the opisthotic; absence of the processus basitrabecularis; and an enclosed canalis cavernosus. *Peligrochelys walshae* shares with other members of Meiolaniformes the presence of a large exposure of the prefrontal and the absence of the frontal in the orbital rim. *Peligrochelys walshae* shares with *M. efremovi* the presence of several scales F surrounding the orbit; presence of a roughened area in the basisphenoid that is continuous with the tubera basioccipitalis; presence of a deep concavity between the tubera basioccipitalis; and the presence of small knobs in the squamosal.

Description and comparisons

Only a few bones of the skull are preserved, mainly those of the basicranium and from the posterior part of skull roof. All the bones are disarticulated. In general, the bones are thick and robust. This is a turtle of relatively large size and the estimated skull length is approximately 10 cm.

Skull roof
The bones belonging to the skull roof are finely ornamented with small pits located very close to one another (Figs 4A, B). The pits are less abundant and less tightly packed in the sulci than in the surrounding parts (Fig. 4A). Some pits communicated with one another through shallow troughs (Fig. 4A).

Scales. As is typical in *Proganochelys quenstedti*, *Kayen-tachelys aprix*, *Kallokibotion bajazidi*, *Mongolochelys efre-movi*, meiolaniids and chelonioids, *Peligrochelys walshae* also possesses scales covering the skull roof, which leave sulci on the dermal bones of the skull. Unfortunately, only two bones of the skull roof (frontal and postorbital) have the scale pattern well preserved. Comparisons of the skull scale pattern in *M. efremovi* and Meiolaniidae allowed us to propose primary homologies for some of the scales. Here we follow the proposed primary homologies of Simpson (1938) and Gaffney (1996) as modified by Sterli & de la Fuente (2011b). The skull scale pattern seen in *P. walshae* (MACN PV CH 2017, 2018, MPEF-PV 3976) is very similar to that found in *M. efremovi*. In *P.* w*alshae*, scales F1, F2, F3, F4, G, H, J2, Y and Z are recognized (Figs 5A, B). All of scales recognized in *P. walshae* are paired, except for scale Y. Scales F1, F2, F3, J2 and H are located on the postorbital, while F4, G, Y and Z are located on the frontal and F1 on both bones (Figs 5A, B). Scales F1 to 4 are fused in meiolaniids and recognized as only one F scale. F1 is located on the postorbital and frontal, and may have reached the prefrontal as well (Figs 5A, B). It forms part of the orbital rim. It contacts scales F2, G and H posteriorly, F3 ventrally and F4 anteromedially. Only a small part of the scale F2 preserved on the posterior part of the postorbital (Figs 5A, B). Scale F3 is a small scale forming part of the posterior rim of the orbit (Figs 5A, B). It contacts scales F1 dorsally, F2 posterodorsally and J2 ventrally. The contact between scales G and Y is based on MACN-2018, because it is not clearly recognized in MACN-PV CH 2017 or MPEF-PV 3976. The scale G is located on the frontal and may have reached the postorbital as well (Fig. 5A). It contacts scales Y anteromedially, F1 laterally and F4 anteriorly; its remaining contacts are not preserved. Only a small fragment of scale H is preserved (Figs 5A, B). It is located between scales G and F1 on the postorbital. Only a small fragment of scale J2 is preserved on the postorbital (Figs 5A, B). It forms part of the posterior orbital rim and contacts scale F3 dorsally. Scale Y is
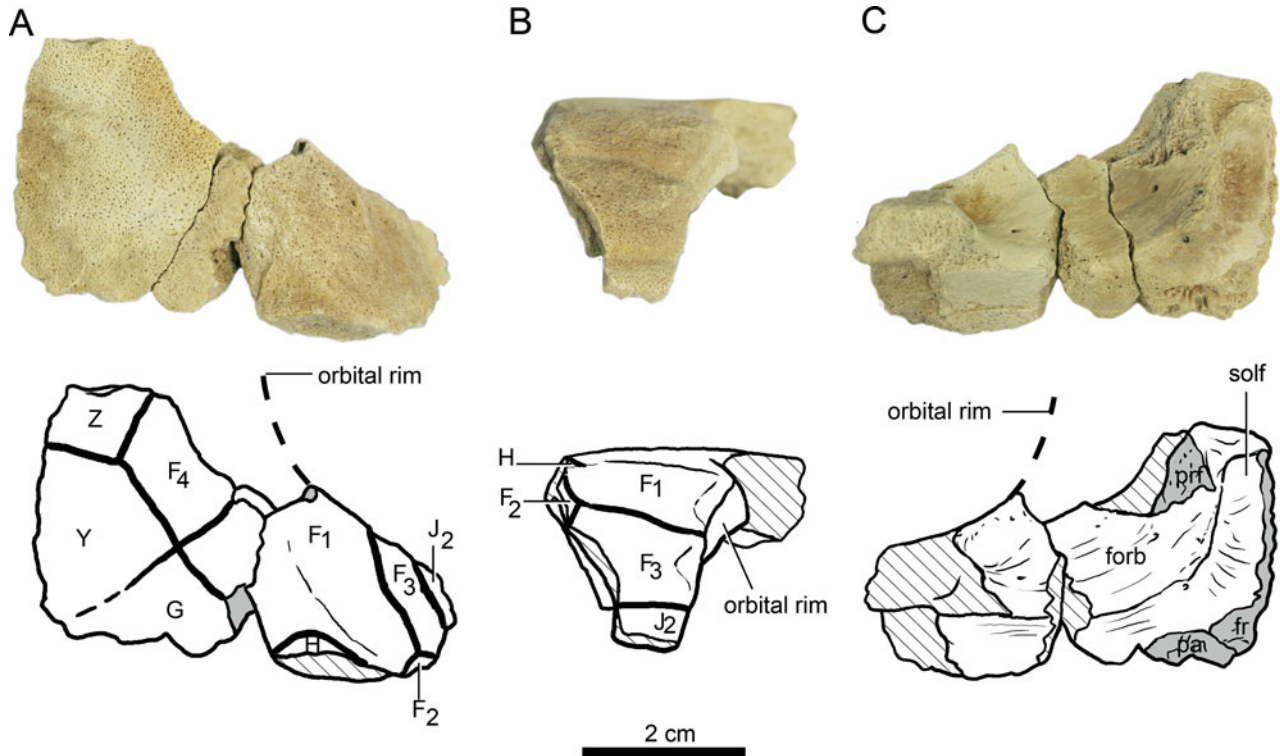
Figure 5. *Peligrochelys walshae*. MACN PV CH 2017, right frontal and right postorbital. **A**, Picture and drawing in dorsal view; **B**, Picture and drawing in right lateral view; **C**, Picture and drawing in ventral view.

unpaired (Fig. 5A), diamond shaped, and contacts scale Z anteriorly, scale F1 and F4 laterally, and scale G posteriorly. Finally, scale Z is located on the anterior part of the frontal and may have reached the nasal as well (Fig. 5A). It contacts scales Y posteriorly and F4 laterally. For comparisons with other taxa and homology statements, see the Discussion section.

Frontal. Three frontals are completely preserved (MACN-PV CH 2017, 2018, MPEF-PV 3976). It is a paired bone forming part of the skull roof. It contacted the postorbital laterally, and the prefrontal anterolaterally, the nasal anteromedially, the other frontal medially and the parietal posteriorly (Figs 5A, C). In ventral view, the frontal forms the roof of the fossa orbitalis laterally, the sulcus olfactorius medially, and part of the fossa nasalis anteriorly (Fig. 5C).

The frontal in *Peligrochelys walshae* does not contribute to the orbital margin (Figs 5A, C). This condition is also seen in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Mongolochelys efremovi* and meiolaniids (e.g. *Meiolania platyceps* and *Niolamia argentina*) among stem Testudines (Gaffney 1983, 1990, 1996; Sukhanov 2000; Sterli *et al*. 2007; Sterli & de la Fuente 2011b). Contrary to the condition seen in *M. efremovi*,, the suture with the nasal in *P. walshae* is perpendicular to the sagittal plane, instead of being tapered anteromedially.

Squamosal. Some skull roof fragments were recognized as part of the squamosal bones because they show small knobs resembling those present in the posterior part of the *Mongolochelys efremovi* skull. The fragmentary nature of the squamosal bones precludes any further description.

Postorbital. A big portion of the right postorbital and the lateral process of the left postorbital are preserved. The only preserved contact is that with the frontal medially (Figs 5A, C). It is probable that the postorbital contacted the prefrontal anteromedially as this contact can be deduced from the sutural surfaces of the postorbital and frontal (Figs 5A, C). The postorbital together with the prefrontal formed the dorsal rim of the orbit and the roof of the fossa orbitalis (Figs 5A, C). The postorbital of *Peligrochelys walshae* differs from that of *Patagoniaemys gasparinae* in the anterior extension of the horizontal plate and its participation to the orbital rim. In *P. walshae*, the anterior process of the postorbital is short and forms only the posteriormost margin of the orbit as in *Kallokibotion bajazidi*, while in *Pa. gasparinae*, like in *Mongolochelys efremovi* and *Niolamia argentina*, the postorbital has an extensive anterior process forming the medial part of the orbital rim. Another difference is the thickness of this element. In *P. walshae*, as in *M. efremovi* and Meiolaniidae, the postorbital is a much more robust element than in *Pa. gasparinae*. The postorbital in
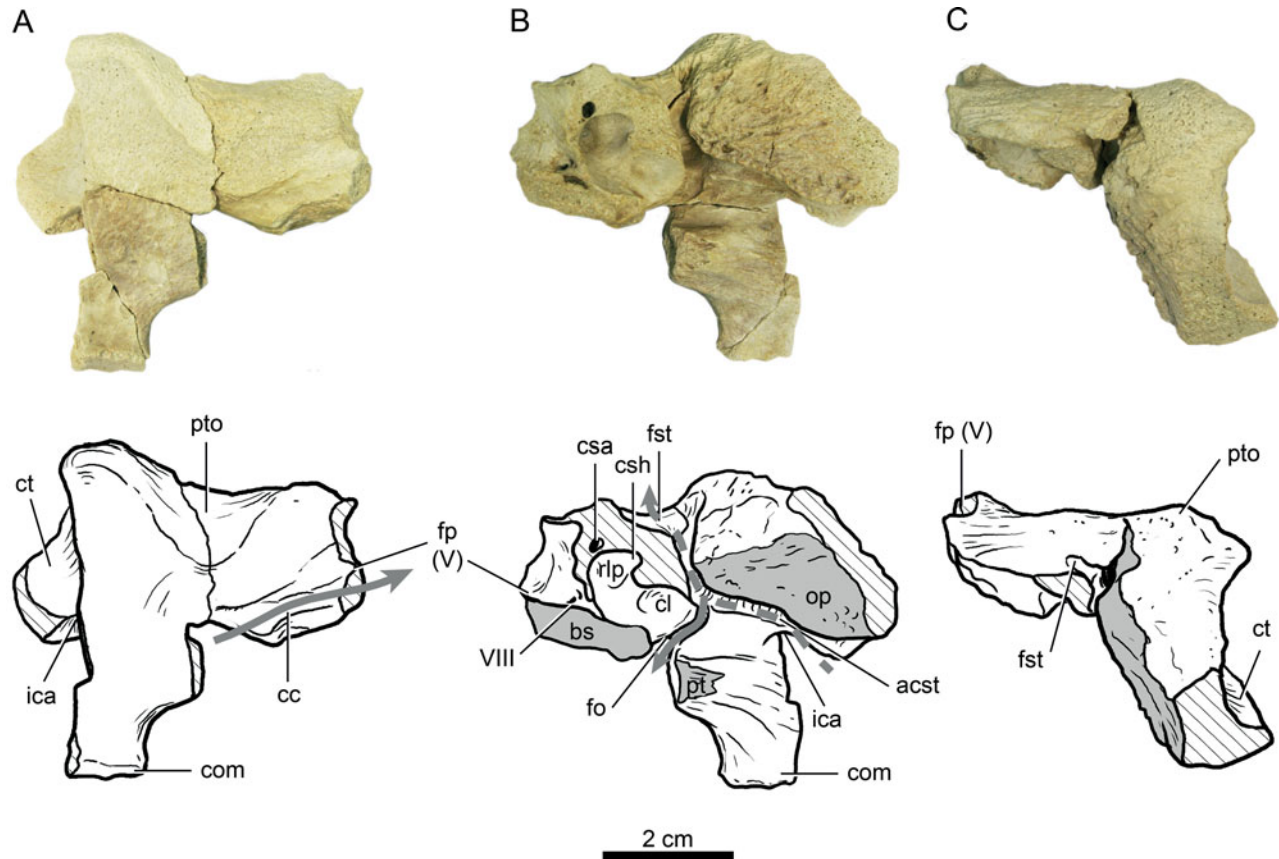
Figure 6. *Peligrochelys walshae*. MACN PV CH 2017, right quadrate and right prootic. **A**, Picture and drawing in anterior view; **B**, Picture and drawing in posterior view; **C**, Picture and drawing in dorsal view.

P. walshae as in meiolaniids, has a descending process probably connecting the jugal and maxilla and separating the fossa orbitalis posteriorly from the fossa temporalis inferior (Fig. 5C).

Palatal elements
Maxilla. Only the middle section of the left maxilla is preserved, and no contact surfaces are consequently preserved. Dorsally the maxilla forms the orbital margin, while ventrally the labial ridge of the triturating surface is found. The triturating surface is narrow, and a small lingual ridge is hinted at in the posterior part of the preserved maxilla. The labial ridge is much more developed than the lingual one. No auxiliary ridge is present in *Peligrochelys walshae*. The triturating surface of *Chubutemys copelloi* is narrower and steeper than the one present in *P. walshae* (MACN PV CH 2017) and the lingual ridge seems to be absent. In *Mongolochelys efremovi*, the triturating surface is more complex than in *P. walshae* and *C. copelloi*, because contrary to the condition recognized in these species in *M. efremovi* there are three ridges, the labial and the medial ridges being well defined and developed. There are also three ridges present in *Ninjemys oweni* and in *Meiolania*

platyceps (a high and well-developed labial ridge and two intermediate ridges, with the lingual ridge absent; Gaffney 1983). The triturating surface in *Niolamia argentina* has two ridges (labial and lingual). The labial ridge is taller and sharper than the rough and strong lingual ridge.

Palatoquadrate elements
Quadrate. The right quadrate is almost completely preserved, only lacking the most lateral part (Figs 6, 7). The quadrate preserves the contact surfaces with the prootic anteromedially and dorsally, with the pterygoid anteromedially and ventrally, and with the opisthotic posteromedially. On the anterodorsal surface of the quadrate, the processus trochlearis oticum is present as in Meiolaniidae and pancryptodiran turtles (Figs 6, 7). The processus trochlearis oticum in MACN-PV CH 2017 is also formed by the prootic (Figs 6, 7), as is the case in most turtles with a processus trochlearis oticum (Gaffney 1983). In posterior, ventral, and medial views of the quadrate the aditus canalis stapedio temporalis and the canalis cavernosus are seen (Figs 6A, B, 7A, B). The aditus canalis stapedio temporalis is also formed by the prootic anteriorly and the opisthotic posteromedially (as in Meiolaniidae *fide* Gaffney 1983 and
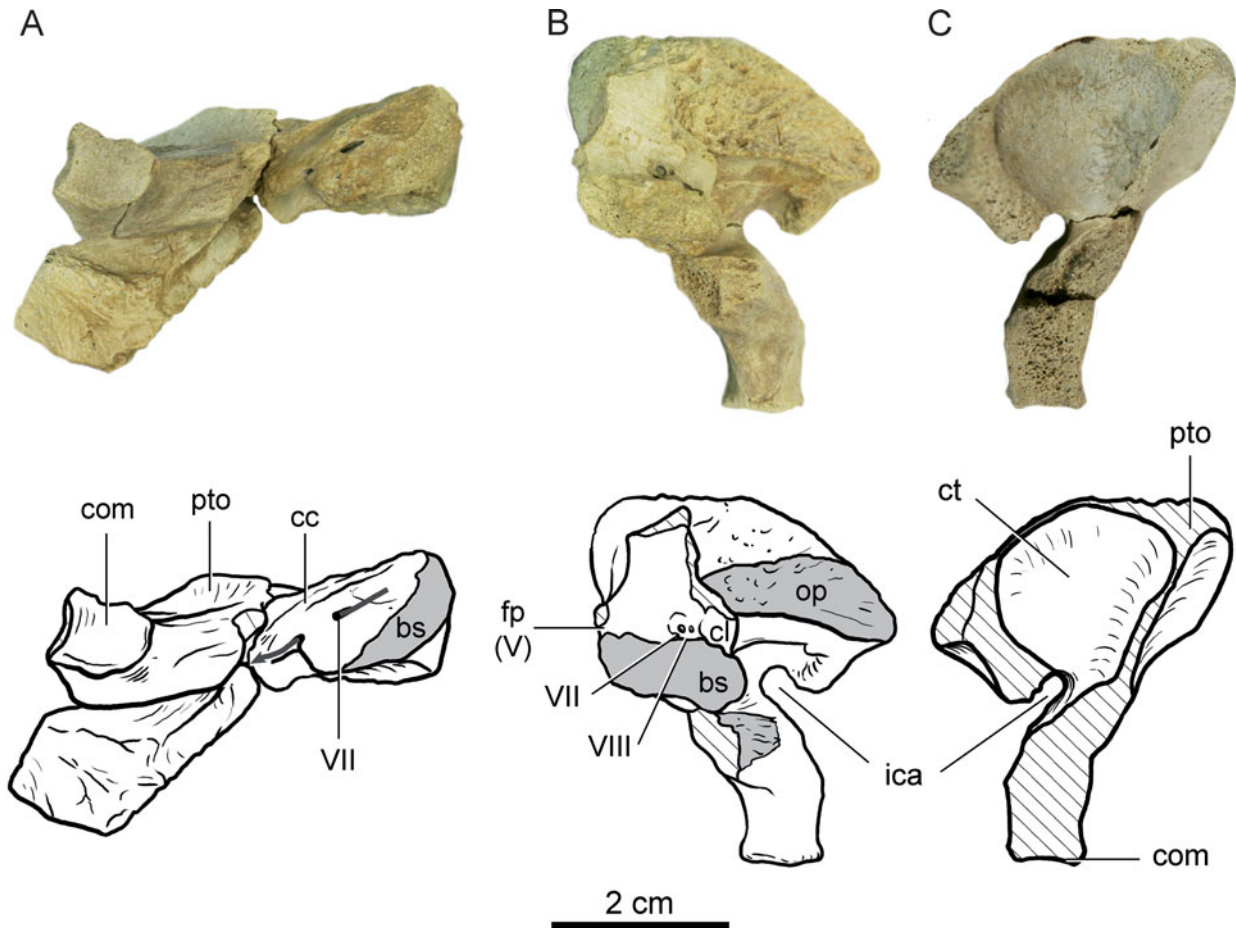
Figure 7. *Peligrochelys walshae*. MACN PV CH 2017, right quadrate and right prootic. **A**, Picture and drawing in ventral view; **B**, Picture and drawing in medial view; **C**, Picture and drawing in lateral view.

probably in *Mongolochelys efremovi*, pers. obs.). As in most Testudinata, the cavum tympani is fully developed; however, the presence of an antrum postoticum cannot be determined because this part of the quadrate and squamosal is missing (Fig. 7C). In meiolaniids, the antrum postoticum is not well differentiated from the cavum tympani (Gaffney 1983). The incisura columella auris seems to be open in *Peligrochelys walshae* (Fig. 7C). Ventrally the quadrate forms the condylus mandibularis of which only the proximal end is preserved in MACN-PV CH 2017 (Figs 6A, 7A). This fragment is wider than long and the surface is almost flat.

Braincase elements

Basisphenoid. The basisphenoid of *Peligrochelys walshae* is preserved almost completely in MACN-PV CH 2017 (Figs 8, 9) and MPEF-PV 3975. The only preserved contact of the basisphenoid is the posterior one with the basioccipital (Figs 8, 9). The contacts with the pterygoid and prootic are inferred based on the morphology of the

basisphenoid and comparison with other turtles. Contrary to the arrow-shaped basisphenoid in *Chubutemys copelloi*, the basisphenoid is quadrangular in *P. walshae* and in *Mongolochelys efremovi*. The basisphenoid and basioccipital are thick elements forming a robust braincase floor as in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *M. efremovi* and meiolaniids. In ventral view, the foramina carotici cerebralis posterior (*sensu* Sterli *et al*. 2010) are seen located very close to one other in the anterior region of the basisphenoid (Figs 8A, 9). These foramina might serve as the entrance for the arteria cerebralis. This arterial configuration is similar to *M. efremovi* and *Kallokibotion bajazidi*, as was suggested by Sterli *et al*. (2010), where the bifurcation of the internal carotid artery into its palatine and cerebral branches is not enclosed by bone and the internal carotid artery is not covered by the posterior part of the pterygoid. More anteriorly and dorsally the canals containing the right and left branches of the cerebral artery unite and are seen in anterior view as a narrow slit in *P. walshae* (Fig. 8B). In *K. bajazidi* and *M. efremovi*, both branches of the cerebral artery open in the dorsum sellae very close
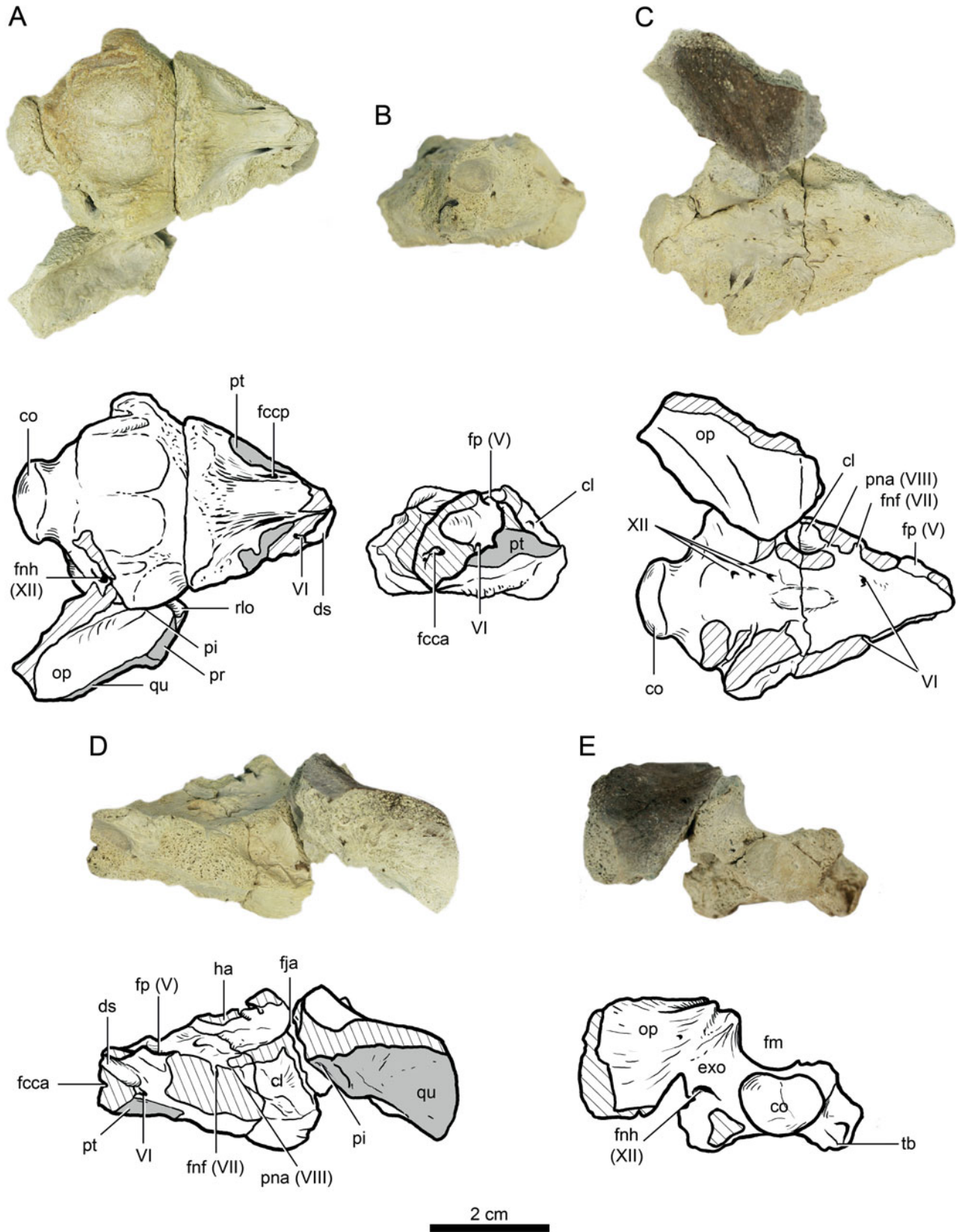
Figure 8. *Peligrochelys walshae*. MACN PV CH 2017, basisphenoid, basioccipital, left exoccipital and left opisthotic. **A**, Picture and drawing in ventral view; **B**, Picture and drawing in anterior view; **D**, Picture and drawing in lateroanterior view; **C**, Picture and drawing in dorsal view; **E**, Picture and drawing in posterior view.

Figure 9. *Peligrochelys walshae*. MACN PV CH 2017, basisphenoid, basioccipital, left exoccipital and left opisthotic. Picture and drawing in ventropostero-lateral view.

one to another. In *Meiolania platyceps*, both branches are separated by a column of bone (Gaffney 1983). In ventral view, posterior to the entrance of the cerebral arteries and in the contact with the basioccipital, there are paired roughened areas (Figs 8A, 9) interpreted as muscle attachment sites (Brinkman & Peng 1993) that are very similar to the structures so characteristic of *M. efremovi*. These roughened areas show continuity with the tubera basioccipitalis of the basioccipital (Figs 8A, 9; see below).

The nervi abducentis (VI) pierces the basisphenoid from the dorsal surface and exits anteriorly between the foramen carotici cerebralis anterior and the dorsum sellae in *Peligrochelys walshae* (Figs 8, 9). The dorsum sellae is a high structure, representing half of the basisphenoid thickness. The dorsum sellae is divided in two by a vertical medial ridge (Figs 8B, C). The basisphenoid also forms the ventral rim of the foramen prooticum (V) and foramen nervi acustici (VIII) (Figs 8B–D). In dorsal view, on the lateral side between the basisphenoid and the basioccipital, the hiatus acusticus communicates between the cavum cranii and the cavum labyrinthicum (Figs 8C, D). The degree of ossification of the hiatus acusticus cannot be determined in MACN-PV CH 2017 because of the nature of the specimen. In the dorsal surface, the crista dorsalis basioccipitalis is developed between the basisphenoid and the basioccipital (Fig. 8D).

Basioccipital. The basioccipital is almost completely preserved in *Peligrochelys walshae* (MACN-PV CH 2017 and MPEF-PV 3975). Like the basisphenoid, the basioccipital is a thick element. In ventral view, the paired tubera basioccipitalis of *P. walshae* are apparent (Figs 8A, 9) as in basal turtles and *Mongolochelys efremovi*, *Kallokibotion bajazidi* and Meiolaniidae. Between both tubera, a major concavity is present (Figs 8A, 9). This concavity is similar

to that present in *K. bajazidi*, *M. efremovi* and meiolaniids. In *P. walshae*, the major concavity is divided in the midline by a very low ridge that bifurcates posteriorly, outlining two concavities (Figs 8A, 9). The occipital condyle is triangular in shape and slightly wider than tall (Fig. 8E). The contribution of the exoccipitals to the condyle cannot be assessed because the sutures between those bones cannot be recognized (they might be fused as in most turtles; Gaffney 1979). The occipital condyle is separated from the main body of the basioccipital by a short neck (Figs 8A, D, 9). Like the basisphenoid, the bassioccipital forms the floor of the cavum labyrinthicum, the wall of the hiatus acusticus, and the crista dorsalis basioccipitalis (Figs 8C, D).

Exoccipital. Only a fragment of the left exoccipital is preserved (Figs 8A, D, E, 9). It is fused with the basioccipital ventromedially and the opisthotic laterally. The contact with the supraoccipital cannot be assessed with confidence because the supraoccipital is missing and sutural faces are unclear. In *Peligrochelys walshae*, there is only one opening for the nervi hypoglossi in the exoccipital (Figs 8A, E, 9), contrary to all other turtles where two or three openings are present (XII) (Gaffney 1979). Internally, however, this foramen is divided into two foramina, and even more internally, there are three openings into the cavum cranii (Figs 8C, D, 9). In medial view, the foramen jugulare anterius is visible anterodorsally to the most anterior hypoglossal foramen (Figs 8C, 9). The presence of an ossified foramen jugulare posterius separated from the fenestra postotica cannot be assessed because this area is broken in the preserved specimen of *P. walshae* (MACN-PV CH 2017). In *Kallokibotion bajazidi*, *Mongolochelys efremovi*, *Chubutemys copelloi* and some specimens of *Meiolania platyceps*, the fenestra postotica and the foramen jugulare posterius coalesce. As in all turtles, the medial border of the

exoccipitals forms the lateral rim of the foramen magnum (Fig. 8E). Because the exoccipital is broken, the outline of the foramen magnum cannot be assesed in detail. The exoccipital contribution to the occipital condyle cannot be estimated either because this bone is fused with the basioccipital (Fig. 8E). In posterior view, the exoccipital has an oblique crest running lateroventrally to dorsomedially which probably was continuous with the crista supraoccipitalis (Fig. 8E).

Prootic. The right prootic is preserved almost completely, while there is only a fragment of the left prootic. The only well-preserved contact of the prootic is that with the quadrate anterolaterally, while the remaining contacts are inferred (Figs 6, 7). The inferred contacts are with the opisthotic posteriorly, the parietal medially, the supraoccipital posterodorsally, the pterygoid and basisphenoid ventrally, and the epipterygoid anterodorsally.

In anterior view, the canalis cavernosus and the posterior rim of the foramen prooticum (V) are seen in the prootic (Figs 6A, B, 7A, B). In posterior view, a number of structures are apparent. The prootic forms the fenestra ovalis, together with the opisthotic (Fig. 6B). The cavum labyrinthicum and the recessus labyrinthicus prooticus and the canalis semicircularis anterior and horizontalis are also seen in posterior view (Fig. 6B). There is a thin ossified wall between the cavum labyrinthicum and the cavum cranii that is pierced by the facial nerve VII (one small foramen) and the acustic nerve VIII (two foramina) (Figs 6B, 7B). As it was described above, the prootic forms part of the canalis stapedio-temporalis (Figs 6B, C). In ventral view, a short and small channel with open ends is apparent ventrally to the canalis cavernosus through which the facial nerve (VII) runs (Fig. 7A). As in most turtles with a processus trochlearis oticum, the prootic contributes to the formation of the process together with the quadrate (Figs 6A, C, 7A).

Opisthotic. The left opisthotic is the better preserved of the two. The only preserved contact of the opisthotic is the medial one with the exoccipital (Figs 8A, C–E, 9). The other contacts can be inferred from the contact surfaces found on the opisthotics or the surrounding bones. The opisthotic contacts the quadrate and squamosal laterally and the prootic anteriorly (Figs 8A, C, 9). In ventral view, the trough leading to the foramen jugulare anterius is visible (Figs 8A, 9). This trough is also formed by the exoccipital. Anterior to the foramen jugulare anterius, remains of the processus interfenestralis of opisthotic are seen (Figs 8A, 9). The processus is recognized because the sulcus through which the nervi glossopharyngei (IX) runs, is apparent in ventral view (Fig. 9). The processus interfenestralis is broken but it is clear that it is not a robust process as in *Kayentachelys aprix* or *Condorchelys antiqua*. The anterior part of the processus interfenestralis of the opisthotic forms the posterior rim of the fenestra ovalis, which is completed anteriorly by the prootic (Fig. 9). The medial and dorsal part of the opisthotic forms the roof of the recessus labyrinthicus opisthoticus and its communication with the recessus labyrinthicus prooticus (in the prootic), the canalis semicircularis horizontalis (Fig. 8A).

Discussion

Primary homology of cranial scale pattern in turtles

The skulls of most turtles are covered by epidermal scales. However, not all scales leave the marks of their borders on the skull roofs. In this section, we focus our attention on scales that leave sulci on the cranial bone. This kind of cranial scales is common in several clades of turtles, such as cheloniids, testudinoids and several species of extinct turtles (like *Proganochelys quenstedti*, *Kayentachelys aprix* and meiolaniforms). The scale patterns of different extinct taxa have been described in detail (e.g. *Meiolania platyceps*, Gaffney 1983; *Pr. quenstedti*, Gaffney 1990; *K. aprix*, Sterli & Joyce 2007), but there has been no attempt to homologise scales across different taxa because patterns are often highly variable (like in *K. aprix*, *Kallokibotion bajazidi*, chelonioids, testudinoids). The only clade of extinct taxa, where the scales were first homologised and later tested in a cladistic frame was Meiolaniidae (Simpson 1938; Gaffney 1996). Comparisons among meiolaniids, related taxa and even *Pr. quenstedti* allowed us to expand the proposed homology of the meiolaniid skull scales to other taxa.

All members of the sister clade of Meiolaniidae have poorly preserved skull remains (e.g. *Patagoniaemys gasparinae* and *Otwayemys cunicularius*) or the skull scale patterns were not described or illustrated in detail (e.g. *Kallokibotion bajazidi*). Nonetheless, the preservation of scales in *Mongolochelys efremovi* and *Peligrochelys walshae* allow us to trace the scale pattern described for meiolaniids in these taxa. *Mongolochelys efremovi* and *P. walshae* have a very similar scale pattern, in terms of general morphology, location and relationships, to that of Meiolaniidae (Fig. 10). *Mongolochelys efremovi*, and probably *P. walshae*, share with Meiolaniidae the presence of single scales Y, X and A along the sagittal axis. Paired scales C, D, E, G, H, and K are also recognized in *M. efremovi* (and probably *P. walshae*) and Meiolaniidae. Contrary to Meiolaniidae, scales F, I, J and Z in *M. efremovi* and *P. walshae* are composed of several small scales. We can also trace the homology of some scales in *Proganochelys quenstedti*, where single scales X, Y and Z and paired scales D, G and H can be recognized. As in *M. efremovi* and *P. walshae*, scale F in *Pr. quenstedti* is formed by several small scales (Fig. 10). Contrary to Meiolaniidae and *M. efremovi*, *Pr. quenstedti* has a paired scale A (Fig. 10).

Optimization of this character in all MPTs indicates that the presence of cranial scales is plesiomorphic for all turtles.
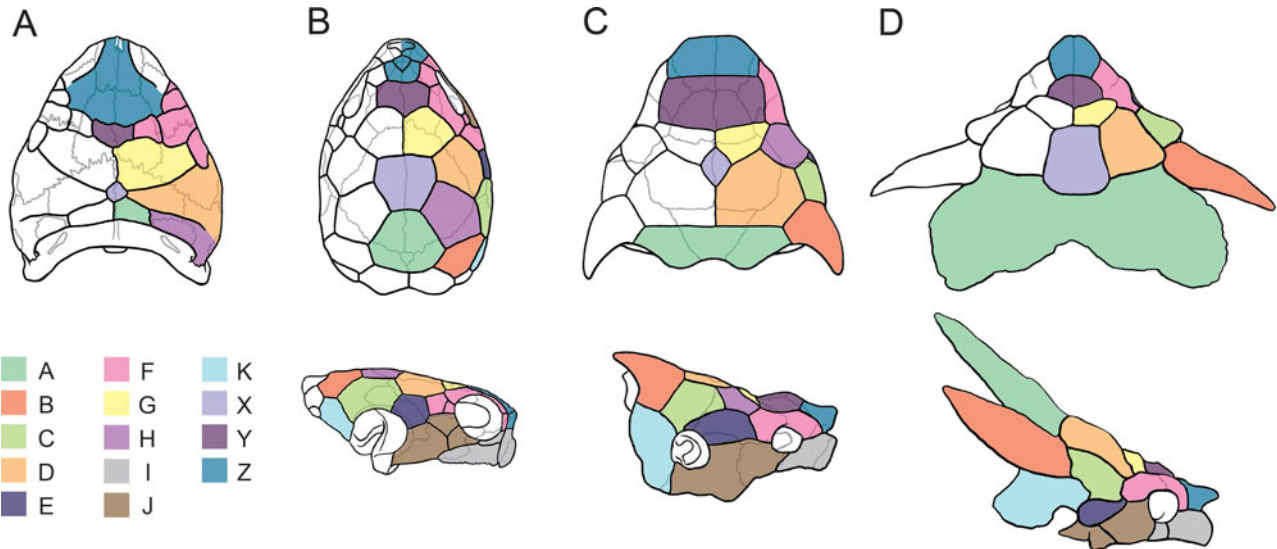
Figure 10. Primary homologies of scale patterns of skull roofs among turtles. **A**, *Proganochelys quenstedti* (modified from Gaffney 1990); **B**, *Mongolochelys efremovi* (modified from Sukhanov 2000); **D**, *Niolamia argentina* (modified from Sterli & de la Fuente 2011b); **C**, *Meiolania platyceps* (modified from Gaffney 1983).

In the lineage leading to Testudines, the capability to leave scale sulci on the skull roof has been lost once and then, depending on the optimization criterion (ACCTRAN or DELTRAN), was gained multiple times again (e.g. Pelomedusoides, Plesiochelyidae, Cheloniidae, Chelydridae; see Online Supplementary Material Appendix 5) or gained once and lost several times (e.g. Chelidae, *Platysternon megacephalum* Gray 1831, Sinemydidae and the clade formed by Testudinoidea + Kinosternoidea + Trionychia; see Online Supplementary Material Appendix 5).

Meiolaniformes: phylogeny and palaeo-biogeography

Meiolaniformes is a stem based clade including all the taxa more closely related to *Meiolania platyceps* than to Cryptodira or Pleurodira. The close relationship between *Mongolochelys efremovi* (= *Yumenemys* Bohlin, 1953 *sensu* Čkhikvadzé 1987), *Kallokibotion bajazidi* and meiolaniids was first suggested by Čkhikvadzé (1987). Khosatzky (1997) also noticed the similarity between *M. efremovi* and *K. bajazidi*. Hirayama *et al*. (2000) were first to include *M. efremovi* in a cladistic analysis wherein they identified *M. efremovi* and Meiolaniidae as monophyletic group and also as the sister group of *Otwayemys cunicularius* and Sinochelyidae. Joyce's (2007) more inclusive cladistic analysis also identified *M. efremovi* and Meiolaniidae as sister groups. In the cladistic analysis of Sterli & de la Fuente (2011a), more taxa potentially related to Meiolaniidae were incorporated into the dataset (e.g. *Chubutemys copelloi*, *O. cunicularius* and *Patagoniaemys gasparinae*)

and once again, Meiolaniidae was closely associated with *M. efremovi*, *O. cunicularius* and *Pa. gasparinae*.

In the present cladistic analysis, the inclusion of even more taxa related to or belonging to Meiolaniidae (e.g. *Ninjemys oweni*, *Warkalania carinaminor*, *Peligrochelys walshae*) and the inclusion of more characters (more than 80 compared to the dataset presented by Sterli & de la Fuente 2011a) allowed us to re-evaluate their phylogenetic relationships (Fig. 3). Meiolaniidae was recovered deeply nested in a monophyletic group (Meiolaniformes) dominated by Gondwanan taxa (e.g. *Chubutemys copelloi*, *Patagoniaemys gasparinae*, *Otwayemys cunicularius*, *P. walshae*), but including Laurasian representatives (*Mongolochelys efremovi* and *Kallokibotion bajazidi*) as well. The historical biogeographic analysis performed here (applying the DEC model), suggests that meiolaniforms originated at least during the Early Cretaceous in present day South America, which then formed part of Gondwana. It is interesting to note the long ghost lineage (ca. 60 Ma) below meiolaniforms, which extends from the Early Jurassic to the Early Cretaceous (Fig. 3). During those 60 Ma, the configuration of the continents changed drastically from a unique and continuous landmass, Pangaea, to two large landmasses, Laurasia and Gondwana. Depending on the exact timing of the origin of meiolaniforms (as denoted by its long ghost lineage), South America could have been part of Pangaea (Early Jurassic) or Gondwana (Middle Jurassic–Early Cretaceous). The former hypothesis supports the idea that meiolaniforms originated and diversified in the Early to Middle Jurassic before the breakup of Laurasia and Gondwana (Fig. 3; Hirayama *et al*. 2000; Sterli & de la Fuente 2011b). New discoveries in

Jurassic, Cretaceous and Early Palaeogene rocks may help to fill the gaps in the evolutionary history of this group of turtles.

The palaeobiogeography of meiolaniform taxa from the Early Cretaceous to the Palaeocene of Patagonia (Fig. 1) suggests that this group of turtles lived in high latitude (45–50°) environments with warm climates (Scotese 2002). This is in accordance with the calculated values of temperature and precipitation for the Palaeocene of Patagonia. Based on standard proxies of leaf-area and leaf-margin, Iglesias *et al*. (2007) estimated the mean annual temperature and the mean annual precipitation for the Salamanca Formation to be 14.1 ± 2.6 °C and 115 cm, respectively. This is in agreement with other fossil evidence in the Salamanca Formation including the presence of palms (Romero 1968; Archangelsky 1973), podocarps (Iglesias *et al*. 2007), and alligatorids, which require a minimum winter isotherm of 10 °C (Bona 2004). Considering all available proxies for climate estimation, Ortiz-Jaureguizar & Cladera (2006) and Iglesias *et al*. (2007) concluded the predominant biome in southern South America during the Early Palaeocene to be a tropical to subtropical moist forest.

Another compelling palaeo-biogeographical datum is the high frequency of association of two different clades of turtles in the Southern Hemisphere fossil record, the Chelidae (Pleurodira) and the Meiolaniformes. This association is typically found in outcrops from the Early Cretaceous to the Eocene in central Patagonia and from the Early Cretaceous and Miocene to the Pleistocene in Australia. In this sense, in the Early Cretaceous of Central Patagonia, the association is between the oldest chelid *Prochelidella cerrobarcinae* de la Fuente, Umazano, Sterli & Carballido, 2011 and the meiolaniform *Chubutemys copelloi*, found in the La Paloma Member of the Cerro Barcino Formation (Chubut Group) (Gaffney *et al*. 2007; de la Fuente *et al*. 2011). In the Upper Cretaceous, the association between several species of chelids and the meiolaniform *Patagoniaemys gasparinae* is registered in the La Colonia Formation (Campanian–Maastrichtian) (Gasparini & de la Fuente 2000; Sterli & de la Fuente 2011a) alongside the record of Chelidae indet. and Meiolaniidae indet. (actually, probably Meiolaniformes indet.) from the Los Alamitos and the Allen formations (Broin & de la Fuente 1993). The Palaeocene association between the chelids *Yaminuechelys maior* (Staesche, 1929) and *Salamanchelys paleocena* Bona, 2006 and the meiolaniform *Peligrochelys walshae* is recorded in the Palaeocene levels of the Salamanca Formation in Punta Peligro (Bona 2006; this article). The most recent association between chelids and meiolaniids in South America is between the chelid *Hydromedusa casamayorensis* de la Fuente & Bona, 2002 and *Niolamia argentina,* and a new meiolaniid species from the Eocene of the Sarmiento Formation (de la Fuente & Bona 2002; Sterli & de la Fuente 2011b).

The association of chelids and meiolaniform turtles in Australia starts in the Albian of Lightning Ridge, New South Wales (Smith 2009), while the chelids and meiolaniid turtles association begins in the Late Oligocene–Miocene, because there are no remains of meiolaniid turtles prior to the Eocene of Australia. The rich Eocene fauna of Redbank Plaine (Brisbane, Queensland) includes only freshwater chelids (*Chelodina alanrixi* Lapparent de Broin & Molnar, 2001, *Chelodina* sp. 2, *Chelodina* sp. 3, *Emydura s.l.* sp.1) (Lapparent de Broin & Molnar 2001). The Late Oligocene–Middle Miocene Etadunna Formation yielded remains of *Emydura* sp. and Meiolaniidae indet. (Gaffney 1981). The Early to Middle Miocene freshwater limestones of Riversleigh Station (northwestern Queensland) have yielded three taxa of side-necked chelids (*Pseudemydura* sp., *Chelodina* sp. and a member of the *Emydura* group) and a meiolaniid (*Warkalania carinaminor*). However, the chelids were found at the Rig and Gag sites (Gaffney *et al.* 1989), while the meiolaniid were discovered at the Pancake site (Gaffney *et al.* 1992). Gaffney (1981) recognized the association of *Emydura* sp. and meiolaniid tortoises in the middle Miocene Wipajiri Formation at the Leaf locality of Lake Ngapakaldi and in the Namba Formation at Lake Pinpa (South Australia). Remains of meiolaniids and chelids were recovered in The Canadian Lead (Gulgong, New South Wales), but Gaffney (1981) did not provide information about the likely associations of these specimens. Gaffney (1981) also pointed out the presence of chelid turtles (*Emydura* sp.) and meiolaniids in the Condamine River area (Queensland) in outcrops of the Chinchilla Sand Formation (Pliocene).

A more accurate phylogenetic scenario regarding chelid evolution, including both the previously mentioned extinct taxa and all the extant taxa, together with a detailed record of the ecological requirements of extant species of chelids, would result in better defined ecological parameters for extinct taxa. Once parameters are estimated for extinct chelids, the ecological requirements of meiolaniform taxa can be addressed. The fossil association of these two lineages requires further study for precisely this reason.

Survivorship of meiolaniform taxa to the K–P extinction

The survivorship of turtle taxa to the K–P extinction was evaluated considering mainly the fauna from the Northern Hemisphere. One of the most studied examples is the turtle fauna from the Northern Great Plains (North America). This fauna is considered among the richest in the world (Hutchison & Archibald 1986; Holroyd & Hutchison 2002), where 17 (Archibald 1996) or 23 species (Holroyd & Hutchison 2002) and eight families are represented. According to Archibald (1996), this turtle fauna includes a mix of extinct (Adocidae, Baenidae, Macrobaenidae, Pleurosternidae, Nanhsuingchelydidae) and extant (e.g.

Chelydridae, Kinosternidae, Trionychidae) lineages. The results obtained from these studies suggest terrestrial forms seem to be more prone to extinction than aquatic forms. For example, among the Northern Great Plains turtle fauna, most of the aquatic taxa have survived the K–P extinction and only the terrestrial Nanhsuingchelyidae, *Basilemys sinuosa* and few aquatic species (e.g. *Helopanoplia distincta*, *Gilmoremys lancensis*) are known to become extinct at the K–P boundary (Hutchison & Archibald 1986; Holroyd & Hutchison 2002; Lyson & Joyce 2009, 2010; Joyce & Lyson 2011). Differences in survival patterns across the K–P boundary between aquatic and terrestrial turtle species have been also previously documented (Archibald & Bryant 1990; Sheehan & Fastovsky 1992). One hypothesis to explain this difference has been recently proposed by Holroyd & Hutchison (2002), who have suggested that the aquatic environments have been more heterogeneous than terrestrial ones. The adaptation to fluctuating environments may be the main factor to understand the success of aquatic species compared to their terrestrial ones in surviving ecological changes at the K–P boundary (Holroyd & Hutchison 2002).

Contrary to previous studies, the present work is the first where the survivorship of the Sothern Hemisphere turtle fauna is evaluated in response to the K–P extinction. The phylogenetic scenario presented here suggests that at least two lineages of meiolaniform turtles survived the K–P boundary. In the Southern Hemisphere (Patagonia), the meiolaniform *Peligrochelys walshae* is a K–P boundary-surviving member of a lineage with closely related taxa in Laurasia, while Meiolaniidae (Australia and Patagonia) is a survivor lineage of exclusively Gondwanan taxa. Interesting to note is that the associated chelids show the same pattern as meiolaniforms: They have survived the K–P boundary. The long-necked chelid assigned to the genus *Yaminuechelys* (de la Fuente, Lapparent de Broin & Manera de Bianco, 2001), a close relative of the extant *Hydromedusa* Wagler, 1830, extends beyond the K–P boundary as well (de la Fuente *et al*. 2001; Bona & de la Fuente 2005). Although aquatic species seem to be more likely to survive mass extinctions, there are some peculiarities about the behaviour of the extant *Hydromedusa* that would help to explain why it could have survived the K–P extinction. *Hydromedusa tectifera* Cope, 1870 can survive extreme conditions: While generally restricted to freshwater, a few specimens of this species may inhabit brackish water and have epizoic barnacles (see Frazier 1986; de la Fuente 1999). Likewise, in the southern part of its range (Buenos Aires Province, Argentina), *H. tectifera* could hibernate underwater in small creeks by means of slowing down their metabolism (de la Fuente unpublished).

In this work, we compare the survival rates of chelids and meiolaniforms as a result of their particular association in the Southern Hemisphere. Although it is well known that the chelid turtles are aquatic in habit, the general assumption

that all Meiolaniformes are terrestrial is uncertain. Joyce & Gauthier (2004) demonstrated that the forelimb anatomy better reflects the ecology of extant turtles. Unfortunately, we only know the forelimb anatomy of two meiolaniforms *Meiolania platyceps* and *Mongolochelys efremovi*. It is known that *Me. platyceps* is terrestrial but there is no detailed description of *M. efremovi*, thereby not allowing its recognition as terrestrial or aquatic. On the other hand, all the remaining meiolaniforms (*Otwayanemys cunicularius*, *Patagoniaemys gasparinae*, *Kallokibotion bajazidi*, *Chubutemys copelloi* and even the meiolaniids *Warkalania carinaminor*, *Ninjemys oweni* and *Niolamia argentina*) have no forelimb preserved, precluding speculations about their palaeo-ecology. If Meiolaniformes prove to be a terrestrial group, the evaluation of their survivorship to the K–P extinction would be of great impact to comprehend the response of turtles to mass extinctions.

We believe that the discovery and description of more complete specimens, and of new forms belonging to these lineages (e.g. Chelidae, Meiolaniformes), will improve our knowledge regarding the origin, evolution, ecological requirements and palaeo-biogeography of these clades. Comparison of the survival patterns of Patagonian with North American turtle faunas will shed new light on one of the 'big five' mass extinctions.

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