

New chelid turtles of the lower section of the Cerro Barcino formation (Aptian-Albian?), Patagonia, Argentina

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ABSTRACT

A new chelid species (*Prochelidella cerrobarcinae* nov. sp.) are described from the Aptian-Albian? Puesto La Paloma Member, Cerro Barcino Formation, northern of Chubut Province, Argentina. The basal section of this member, which bears the turtle remains, is composed of tuffaceous mudstones with plane parallel lamination, asymmetrical ripples and a chert intercalation suggesting sub-aqueous deposition in a relatively shallow lacustrine environment. *Pr. cerrobarcinae* nov. sp. is represented by post-crural remains of several specimens that not only represents the oldest pleurodiran chelid record in the world but, together with the chelid remains of Albian Lightning Ridge, New South Wales, Australia, indicates that chelid diversification began well before the final fragmentation of southern Gondwana.

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1. Introduction

Patagonia has yielded some of the richest Cretaceous turtle faunas known to date (de Broin and de la Fuente, 1993; de la Fuente, 2007, and references therein; Gaffney et al., 2007; Sterli and de la Fuente, 2011). Diverse turtle faunas are well known from the Late Cretaceous of northern and central Patagonia, mainly represented by pleurodiran chelids and pelomedusoids, and meiolaniids as subordinate components of these faunas (de Broin, 1987; de Broin and de la Fuente, 1993; Lapparent de Broin and de la Fuente, 2001; de la Fuente, 2003; de la Fuente et al., 2001, 2010). However, Early Cretaceous turtles are poorly represented in Patagonia; few localities, such as Los Leones Hill (Albian, Lohan Cura Formation) and Turtle Town (Aptian-Albian?, Cerro Barcino Formation), have yielded chelids and a single stem Cryptodira (Lapparent de Broin and de la Fuente, 2001; Gaffney et al., 2007).

Here we describe chelid remains of a new species of the genus *Prochelidella* (Lapparent de Broin and de la Fuente, 2001), obtained from shallow lacustrine facies of the Aptian-Albian? Puesto La

Paloma Member, Cerro Barcino Formation of the Chubut Group, at Los Chivos Hill, Chubut Province, Argentina. These turtle remains not only represent the oldest pleurodiran chelid record in the world but, together with the chelid remains of Albian Lightning Ridge, New South Wales, Australia (Smith, 2009, 2010), indicate that chelid diversification began well before the final fragmentation of southern Gondwana.

1.1. Institutional abbreviations

MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

1.2. Anatomical abbreviations

ABD, abdominal scale; AN, anal scale; ast + cal, astragalus-calcaneum; caud. ver., caudal vertebrae; CER, cervical scale; co, costal bone; ento, entoplastron; epi, epiplastron; FE, femoral scale; fem, femur; GU, gular; hyo, hyoplastron; hypo, hypoplastron; HU, humeral scale; IG, intergular scale; il sc, iliac scar; isch sc, ischial scar; MAR, marginal scale; meso, mesoplastron; mt, metatarsal; ne, neural bone; nu, nuchal bone; PEC, pectoral scale; per, peripheral bone; ph, phalanx; PL, pleural scale; pub sc, pubis scar; py, pygal bone; ra, radius; spy, suprapygal bone; ti, tibia; ul, ulna; VER, vertebral scale; xi, xiphoplastron.

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2. Geological setting

The Somuncurá-Cañadón Asfalto Basin is located in northern Patagonia, including the southern sector of Río Negro Province and the northern sector of Chubut Province, Argentina (Fig. 1a). It overlies a Paleozoic–Mesozoic crystalline basement and was created by early Middle Jurassic tensional efforts linked to Gondwana breakup (Figari and Courtade, 1993; Cortiñas, 1996; Dalla Salda et al., 1999; Silva Nieto et al., 2002). This tectonic tension triggered the development of stratovolcanoes aligned with the Gastre Fault System (Coira et al., 1975; Rapela et al., 1991) and subsequent deposition of a volcanic-sedimentary substrate assigned to the Lonco Trapial Formation (Lesta and Ferello, 1972). During the late Middle Jurassic-Early Cretaceous, continental deposition occurred in half-grabens located in the western part of the basin (Silva Nieto et al., 2002). These asymmetrical troughs were mainly filled by siliciclastic, carbonate, and evaporite sediments included within the Cañadón Asfalto (Callovian-Kimmeridgian) and Cañadón Calcáreo (Kimmeridgian-Hauterivian) formations (Proserpio, 1987; Volkheimer et al., 2009). Both lithostratigraphic units record different types of continental environments: lakes, alluvial fans, deltas and rivers, with intercalations of basaltic flows and pyroclastic sediments in the older formation (Cabaleri and Armella, 1999; Cabaleri et al., 2005; Volkheimer et al., 2009).

The overlying Cretaceous deposits are laterally more extensive, having accumulated during sag conditions (Figari and Courtade, 1993; Silva Nieto et al., 2002). These deposits belong to the Chubut Group, which is composed of the Los Adobes and Cerro Barcino formations (*sensu* Codignotto et al., 1978). The Los Adobes Formation (Barremian) is composed of reddish channel-like conglomerates interbedded with tabular mudstones and scarce tuffs deposited in a fluvial environment (Codignotto et al., 1978; Allard et al., 2009). The Cerro Barcino Formation (Aptian-Santonian) is mainly composed of sheet-like tuffaceous strata and channeled sandstones, which were deposited in alluvial environments with high pyroclastic influx (Codignotto et al., 1978; Manassero et al., 2000; Cladera et al., 2004). The Cerro Barcino Formation can be divided in five informal members using the dominant coloration of the strata. In ascending order, they are: Puesto La Paloma (green), Cerro Castaño (reddish), Las Plumas (pinkish and reddish), and Puesto Manuel Arce (gray). In some sectors of the basin, the Las Plumas Member is capped by greenish yellow tuffs denominated the Bayo Otero Member. Cenozoic deposits include siliciclastic and pyroclastic sediments deposited in marine, estuarine, and continental settings; which have received different denominations in different geographical sectors (Ardolino et al., 1999; Malumán, 1999). Voluminous basaltic layers also constitute the Cenozoic geological record of the basin (Ardolino and Franchi, 1993).

The turtle specimens presented here were collected in Los Chivos Hill (north-central Chubut Province; Fig. 1b) from the basal part of the Puesto La Paloma Member (Cerro Barcino Formation). In accordance with the biostratigraphic data from the Cañadón Calcáreo and Cerro Barcino formations (Musacchio, 1972; Musacchio and Chebli, 1975; Volkheimer et al., 2009) an Aptian-Albian? age is assigned to the Puesto La Paloma Member. Although recently, Rauhut et al. (2003) have suggested a Hauterivian-Barremian age for this member, this age is not supported by the data mentioned above.

At Los Chivos Hill, the Puesto La Paloma Member (42 m thick) is primarily composed of sheet-like, fine-grained tuffs with small amounts of medium-grained sandstones, mudstones and chert (Fig. 1c). The lowermost 7.20 m of the section (referred herein as basal part), which bears the turtle remains, comprises tuffaceous mudstone strata with a chert intercalation near the top; mudstones are massive by bioturbation in the base and pass upward to levels with plane parallel lamination or asymmetrical ripples. Later of 2 m covered,

there is a 4.5 m interval (denominated herein as middle part) of well-sorted, medium-grained sandstones with planar tabular cross-bedding at the base, and low-angle cross-bedding with intralamina inverse grading at the top. The remaining part of the section (upper part) is mainly composed of massive or plane parallel laminated, fine-grained reworked tuffs comprising bodies with irregular and slightly erosive bases and plane to undulating tops; there are scarce intercalations of apedal tuffaceous paleosoils without horizontal zonation and massive tuffs with accretionary lapilli.

The described succession was originated in a continental setting with significant pyroclastic influx. Particularly, the basal part of the section represents shallow lacustrine sedimentation including settling from a suspension, migration of asymmetric ripples and silica precipitation (e.g. Talbot and Allen, 1996; Nakayama and Yoshikawa, 1997). The middle part of the section was deposited by aeolian processes such as migration of 2-D dunes and translation of waves with low-angles of rise (e.g. Kocurek, 1996; Mountney, 2006). The upper part of the section mainly records remobilization of pyroclastic substrates by unconfined fluvial streams and, less frequently, volcanic ash fall deposits and soil development (Cas and Wright, 1987; Umazano et al., 2008).

3. Systematic and description of specimens

3.1. Systematic

Systematic Paleontology

Testudines Batsch, 1758

Chelidae Lindholm, 1929

Prochelidella Lapparent de Broin and de la Fuente, 2001

Type species. *Prochelidella argentinae* Lapparent de Broin and de la Fuente, 2001, figured in Lapparent de Broin and de la Fuente, 2001, Fig. 3.

Pr. cerrobarcinae new species

Diagnosis [Etymology: "cerrobarcinae" from Cerro Barcino Formation.]

Diagnosis: A small chelid turtle with a carapace characterized by a wide nuchal bone and a wide cervical scale. The first neural has a narrow contact with the nuchal bone. The neural series is complete and almost continuous, with the suprapygial bone. The mesoplastra are short, wide, laterally-placed, and crossed by the humeropectoral sulcus. The plastral bridge extends from the posterior part of the third peripheral bone and first costal to the seventh peripheral. *Pr. cerrobarcinae* differs from *Pr. argentinae* in the absence of contact between neural 2 and costal 1, in the absence of strong free rib extremity of the costal 1 in the peripherals 3–4, in the more posteriorly placed axillary buttress, and in the shape and proportions of the first and the second marginal scales. *Pr. cerrobarcinae* differs from *Pr. portezuelae* in its smaller size, the absence of contact between neural 2 and costal 1, the U-shaped anterior plastral lobe, the straight and convergent margins of the posterior plastral lobe, and the plastral formulas (ABD > IG > PEC = HU).

Holotype: MPEF – PV 3287, the cast and bones of the anterior margin of a carapace. Referred specimens: MPEF – PV 3288, the cast and bones of a plastron in visceral view attached to bridge peripheral bones; MPEF – PV 3289, a plastron in visceral view attached to remains of bridge peripheral bones with bad preserved femora; MPEF – PV 3290, a partial carapace in visceral view, and the cast and bones of the posterior plastral lobe; MPEF – PV 3291, remains of left anterior costal cast and bones; MPEF – PV 3292, cast and bones of a carapace; MPEF – PV 3293, a posterior carapace (bones and scales); MPEF – PV 3294, cast and bones in visceral surface of the posterior carapace extreme; MPEF – PV 3295, is

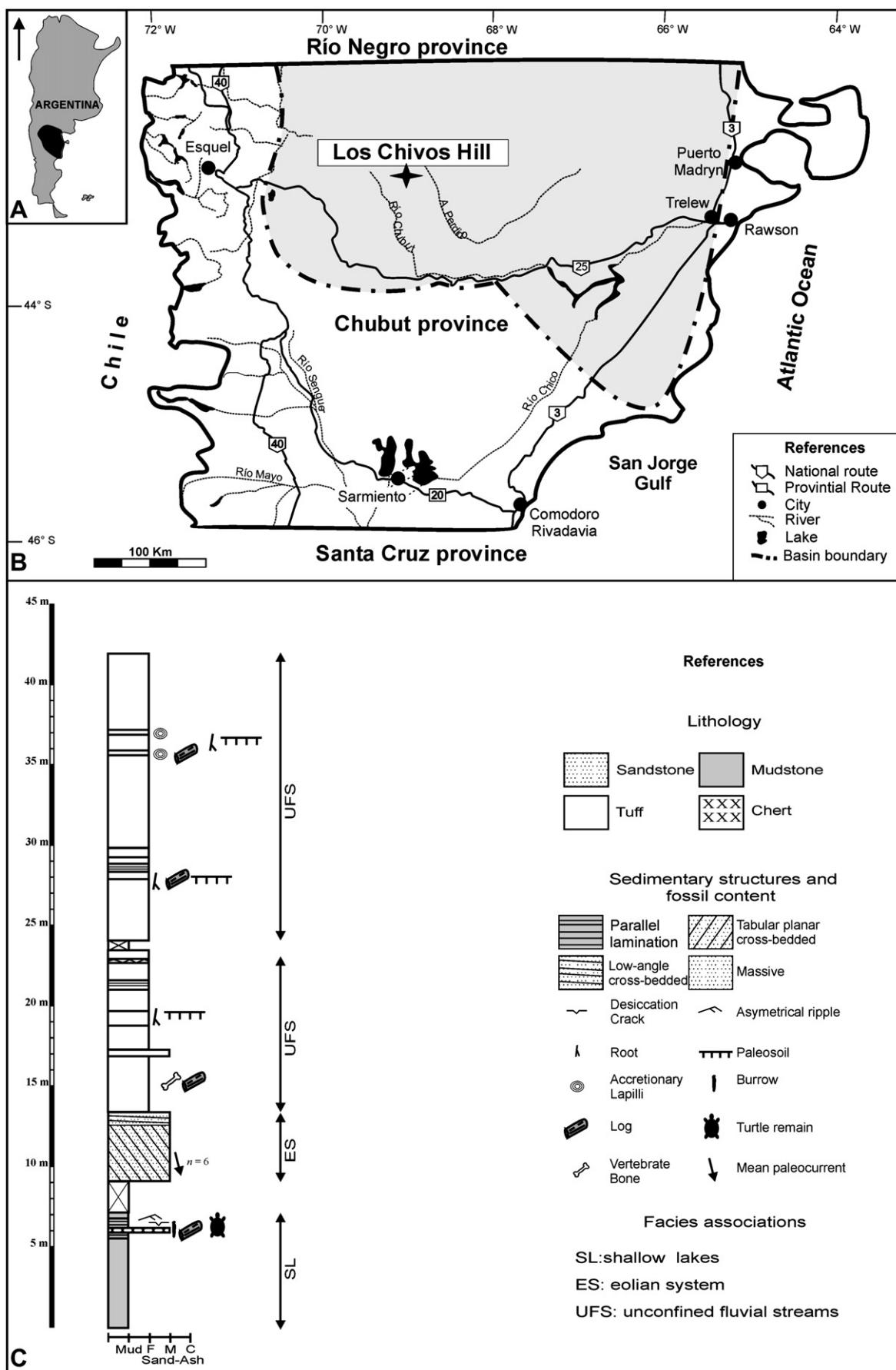


Fig. 1. (a) Location of the Somuncurá-Cañadón Asfalto Basin. (b) Position of the Los Chivos Hill Locality (Chubut Province). (c) Measured sedimentary log of the Puesto La Paloma Member (Cerro Barcino Formation) at Los Chivos Hill.

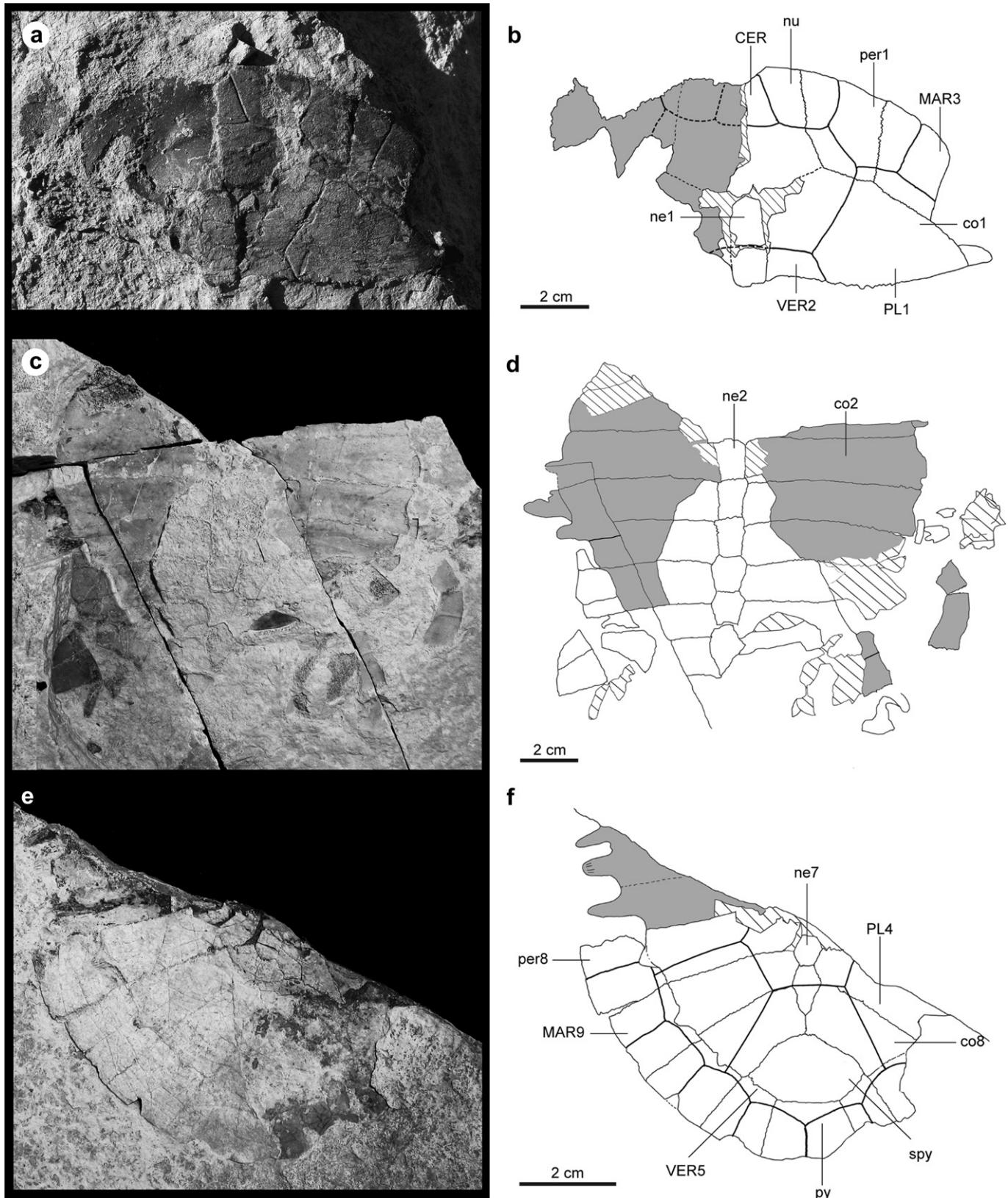


Fig. 2. *Prochelidella cerrobarcinae* nov. sp. (a–b) Anterior part of carapace (MPEF-PV 3287, holotype). (a) Picture. (b) Drawing. (c–d) Middle part of carapace (MPEF-PV 3292). (c) Picture. (d) Drawing. (e–f) Posterior part of carapace (MPEF-PV 3293). (e) Picture. (f) Drawing.

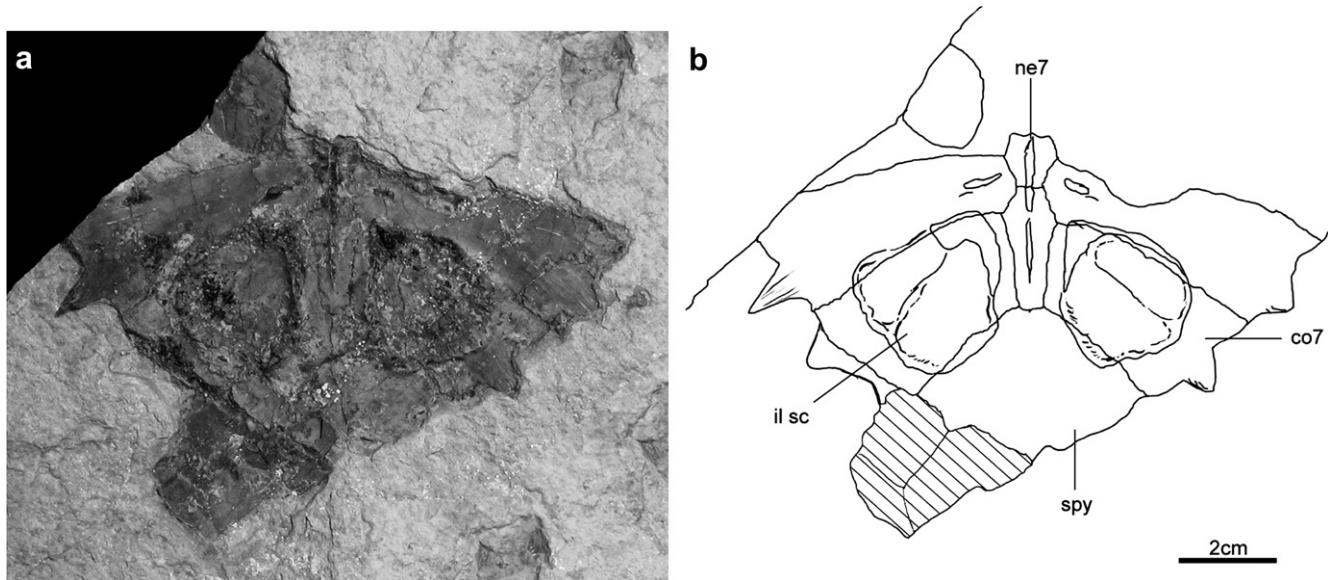


Fig. 3. *Prochelidella cerrobarcinae* nov. sp. (a–b). Posterior part of carapace in visceral view (MPEF-PV 3294). (a) Picture. (b) Drawing.

a partially preserved plastron in ventral view; MPEF – PV 3296, the cast of the posterior lobe extreme; MPEF – PV 3297, remains of pelvic bones cutted in longitudinal section.

Occurrence: Los Chivos Hill. Puesto La Paloma Member, Cerro Barcino Formation (Aptian-Albian?).

3.2. Comparative description

3.2.1. Carapace bones

The chelids found at Los Chivos Hill are small (estimated carapace length 160 mm in MPEF – PV 3293), equivalent in size to adult specimens of *Acanthochelys radiolata*. However, the elongation of the anterior border of the carapace in MPEF – PV 3287 is moderate, as seen in *Prochelidella* species.

The anterior part of the carapace in slab MPEF – PV 3287 is low and wide, with a slight nuchal notch (Fig. 2a, b). The carapace ornamentation consists of dense microvermiculation with rounded ridges and locally fine sulci delimiting irregular polygons. The nuchal bone is wider than long. The first neural bone is rectangular and longer than wide. Contrary to *Pr. argentinae* Lapparent de Broin and de la Fuente, 2001 (Bajo Barreal Formation) and *Pr. portezuelae* de la Fuente, 2003 (Portezuelo Formation) the second neural does not seem to contact costal 1. The 7 remaining neural bones are preserved in MPEF-PV 3992, 3993, and 3994 (Fig. 2c–f). The outline of these bones is roughly hexagonal (not inverted). The neural series continues to the suprapygal bone in the visceral view of the carapace that appears in the slab and counter slab of MPEF-PV 3294. However, in slab MPEF-PV 3293, the last neural bone (pentagonal in shape) is slightly separated from the suprapygal by the distal portion of the eight costal bones in dorsal view (Fig. 2e, f). The odd series is ended by a subpentagonal suprapygal and a short trapezoidal pygal. As is typical in turtles eight pairs of costal bones are present in *Pr. cerrobarcinae* nov. sp. The first costal bones are the larger ones (MPEF-PV 3287), the remainder costal bones are shorter than the first ones, and are preserved in MPFV-PV 3992 (first to seventh) in dorsal view, and in MPEF-PV 3293 in dorsal view (fourth to eighth) or in visceral view (seventh to eighth) in MPEF-PV 3294. The lateral margin of the peripheral bones is upward from

peripheral 2 to peripheral 77. On the visceral surface in MPEF-PV 3294, there are suboval ilium scars over the antero-lateral margin of suprapygal, most of the eight costal bones, and the distal margin of the seventh costals (Fig. 3a, b).

3.2.2. Carapace scales

In *Pr. cerrobarcinae* nov. sp. the cervical scale is trapezoidal and slightly wider than long and the first marginal scale is trapezoidal in shape and the second pentagonal MPEF-PV 3287 as in *Pr. portezuelae* (Fig. 2a, b). Only the right pleural scale (MPF-PV 3287), the third left pleural, and the fourth pleural scales (MPEF-PV 3293) are recognized (Fig. 2e, f). The first and large pleural extends over the proximal extreme of the first and second peripheral bones and the distal extreme of first and second costals. The fourth pleural scale extends over the centro-lateral ends of the seventh costal, the distal and proximal ends of the sixth and eighth costal bones, respectively, and medial ends of peripherals eighth to tenth. The first vertebral scale is wide anteriorly reaching the proximal part of the first peripheral bone, and narrows posteriorly (Fig. 2a, b). The intervertebral sulcus crosses the first neural bone and the sulcus between vertebral 4 and 5 crosses the last hexagonal neural bone, the eighth. The first vertebral scale is wider than the second (MPEF-PV 3287), while the fifth vertebral scale is wider than the fourth (MPEF-PV 3293). These features are consistent with the chelid condition: narrowed vertebral 2–4 (Lapparent and de la Fuente, 2001). The posterior sulcus of the fifth vertebral scale is slightly rounded and notched (as in *A. spixii* and *A. pallidipectoris*) and not straight (as in *A. radiolata*). The posterior marginal scales do not overlap the costal and suprapygal bones (Fig. 2e, f).

3.2.3. Plastral bones

The plastron is partially preserved in four specimens, but the ventral surface is exposed in only one (MPEF-PV 3295).

Among Los Chivos Hill specimens, the plastron is small (estimated length 155 mm in MPEF-PV 3295) (Fig. 4a, b). The narrow anterior plastral lobe is U-shaped, which outline is slightly different from that of *Pr. portezuelae*, which is subquadrangular. In these *Prochelidella* species, the narrow anterior lobe is in contrast with the enlarged lobes of *Acanthochelys pallidipectoris* and *Phrynos gibbus*. As is typical in chelids, the plastral bridge lobe is considerably shorter at its base (axillo-inguinal distance) than the anterior and

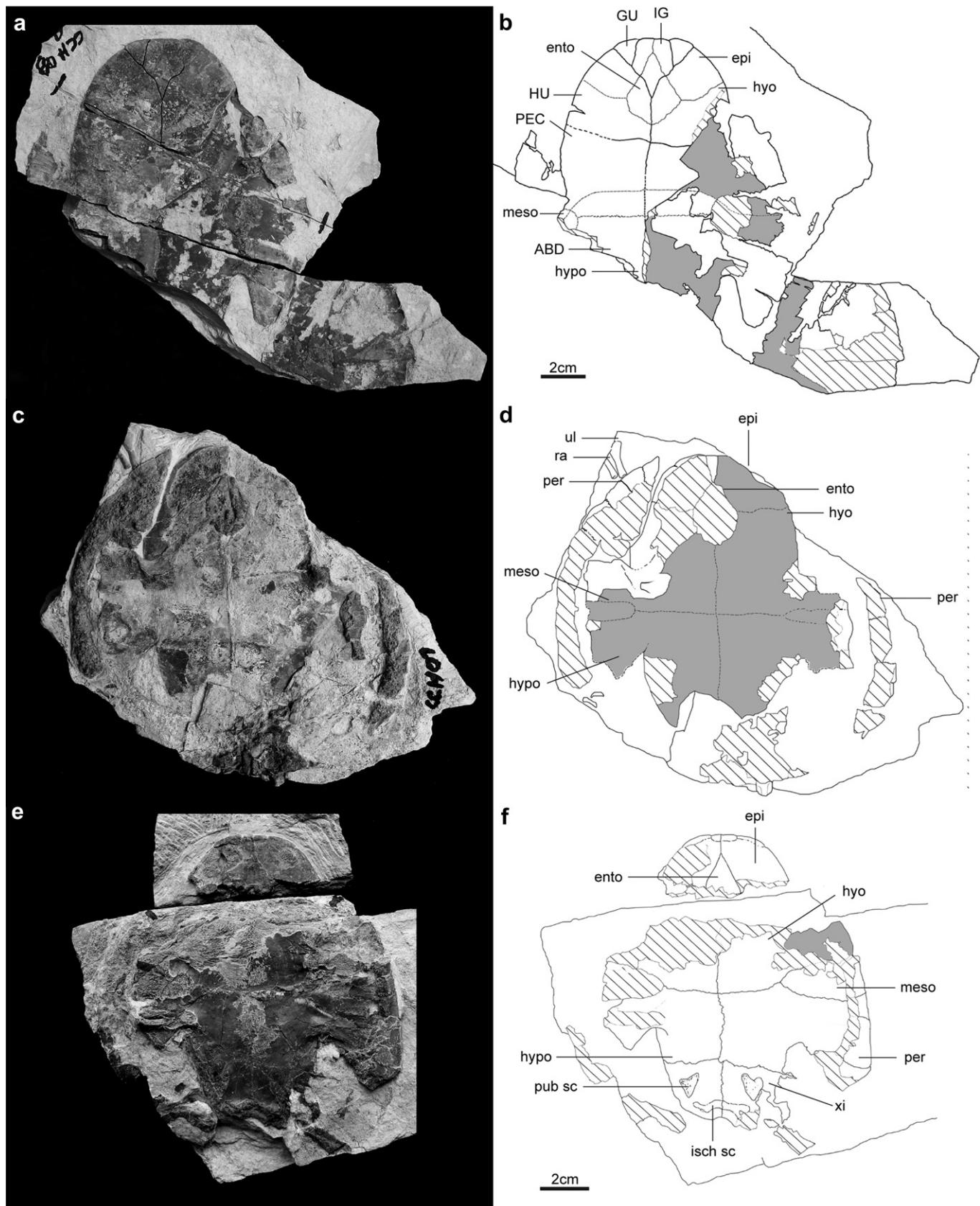


Fig. 4. *Prochelidella cerrobarcinae* nov. sp. (a–b) Plastron in ventral view (MPEF-PV 3295). (a) Picture. (b) Drawing. (c–d) Internal mold of plastron (MPEF-PV 3288). (c) Picture. (d) Drawing. (e–f) Plastron in visceral view (MPEF-PV 3289). (e) Picture. (f) Drawing.

posterior lobes. The medial length of the epiplastron in ventral (MPEF-PV 3295) and visceral view (MPEF-PV 3288–3289) are much shorter than those of the entoplastron (Fig. 4 a–f). The entoplastron is roughly subtriangular in shape, with a curved posterior margin. In ventral view (MPEF-PV 3295) the entoplastron is covered by integular and humeral scales. In specimens MPEF-PV 3295, 3288, and 3289, the outline of a short and wide lateral mesoplastra included between the hyo and hypoplastra are observed. The lateral margins of the posterior plastral lobe are straight and converge toward the anal notch, contrary to *Pr. portezuelae*, which has convex lateral margins. The posterior ends of xiphoplastron (MPEF-PV 3290, 3296) are acute xiphoplastral tips that delimits a deep U-shaped anal notch. In MPEF-PV 3289 the oval pubic and the elongated ischium scars are recognized on plastral visceral view.

3.2.4. Plastral scales

In MPEF-PV 3295, the ventral surface of the plastron shows a plesiomorphic scale pattern, including a simple gular-intergular scheme with gular scales on the epiplastra and a relatively large intergular scale and the humeropectoral sulcus running posterior to the entoplastron. The pectoroabdominal sulcus crosses the wide, short mesoplastra (Fig. 4a, b). The plastral formula recognized in the ventral surface of the anterior plastron (ABD > IG > PEC = HU) differs from the plastral scheme present in the holotype of *Pr. portezuelae* (see Table 1).

3.2.5. Other post-cranial remains

Remains of the left radius and ulna are preserved in MPEF-PV 3288 (Fig. 4c, d), while MPEF-PV 3290 exhibits two poorly preserved caudal vertebrae, remains of the proximal ends of the left and right femora, the right tibia, the right astragalus–calcaneum, and three right metatarsals and phalanxes (Fig. 5a, b). Among these bones the tibia and the astragalus–calcaneum are preserved in relatively good condition. As is typical in turtles the tibia (MPEF-PV 3290) is a stout bone and has an expanded head with a single and broad articular head in its proximal end, while its distal end expands slightly. A longitudinal cnemial crest extends along the dorsal surface of the tibial head and onto its shaft. A large astragalus–calcaneum is slightly displaced from the natural position and it is overlapped on the left peripheral 11. These bones are associated to 3 metatarsals and 3 phalanxes. The pelvic girdle is partially preserved in MPEF-PV 3297 and it is represented by the left girdle that is cut in longitudinal section. As is typical in pleurodiires the lateral process of the pubis and a broad surface of the ischium are attached by suture with the xiphoplastron.

4. Discussion

4.1. Taxonomic remarks

The shell morphology (Fig. 6) and pelvic girdle of *Pr. cerrobarcinae* nov. sp. are comparable with those of chelid pleurodiran turtles. The

ilium, pubis, and ischium are connected by suture to the shell, which is a recognized synapomorphy of Pleurodira (see Gaffney et al., 1991, and references therein). This condition associated with the presence of a cervical scale (MPEF-PV 3287), a short and wide mesoplastra crossed by humeropectoral sulcus (MPEF-PV 3295), and loose carapace–plastron and pleuro–peripheral contacts (MPEF-PV 3288, 3290, 3293, and 3294) allow these specimens to be assigned to the family Chelidae (see Lapparent de Broin and de la Fuente, 2001).

The anatomy of the anterior carapace of the new species described here (holotype MPEF-PV 3287; Fig. 6) fits with the diagnostic characteristics of the genus *Prochelidella* Lapparent de Broin and de la Fuente 2001. MPEF-PV 3287 exhibits the following synapomorphies recognized for *Prochelidella*: a wide, low carapace with slight nuchal notch, moderate elongation of the anterior border of the carapace, a nuchal bone anteriorly and posteriorly widen, and a rectangular neural 1 (Lapparent de Broin and de la Fuente, 2001; de la Fuente, 2003).

The genus *Prochelidella* included until now two named species: *Pr. argentinae* (type species of the genus) from the Bajo Barreal Formation (Cenomanian–Santonian?, Bridge et al., 2000; Genise et al., 2007) and *Pr. portezuelae* from the Portezuelo Formation (late Turonian–early Coniacian; Leanza, 1999; Hugo and Leanza, 2001; Leanza et al., 2004). *Pr. argentinae* was named by Lapparent de Broin and de la Fuente (2001: 466–467) on the basis of a specimen consisting of the anterior margin of a wide and low carapace. These authors also suggested that it might be related to extant species of the genus *Acanthochelys* (Gray, 1873) on the basis of the small size and decoration characterized by a dense microvermiculation with rounded ridges. However, this species retains plesiomorphic characters such as a wide and short nuchal bone and cervical scute, the presence of neurals, short and wide mesoplastra and a more advanced axillar process, which, as suggest by Lapparent de Broin and de la Fuente (2001), distinguishes it from the extant species of the genus *Acanthochelys*. The specimens described here are similar in size to the holotype of *Pr. argentinae* and smaller than the holotype of *Pr. portezuelae*. This later species is the best known species of the genus *Prochelidella* and is known through an anterior carapace margin, an almost complete plastron and six cervical vertebrae (atlas, third or four opisthocoelus, fifth biconvex, sixth procoelus, seventh biconcave, and eighth biconvex). The morphology of these cervical centra fits well with the cervical formulas characteristics of chelid turtles [1(1), (2(1), (3(1), (4(1), (5(1), 6(1)), 7(1), (8(1)] among pleurodiires, as proposed by Williams (1950). The third and new species *Pr. cerrobarcinae* also exhibits posterior parts of the carapace that were not present in *Pr. argentinae* and *Pr. portezuelae*. Among specimens MPEF-PV 3292, 3293, and 3294, the neural bone series is complete and almost continue in dorsal view and contiguous with the suprapygial bone in visceral view. This condition is present in some extant specimens of *Hydromedusa maximiliani* (see Wood and Moody, 1976), but is not typical in chelid turtles, where the reduction of neural bones is the rule (see Pritchard, 1988). The

Table 1
Characters comparison among *Prochelidella* named species.

Characters/species	<i>Pr. argentinae</i>	<i>Pr. cerrobarcinae</i>	<i>Pr. portezuelae</i>
Carapace size	small (190 mm)	small (135–180 mm)	moderate (270 mm)
Contact between neural 2 and costal 1	present	absent	present
Anterior marginal scales outline	1st and 2nd marginal scales subrectangular in shape	1st marginal scale trapezoidal in shape, 2nd pentagonal	1st marginal scale trapezoidal in shape, 2nd pentagonal
Marked growth annuli	yes	no	no
Strong free rib extremities of the costal 1	yes	no	no
Anterior plastral lobe	?	U-shaped	subquadangular
Posterior plastral lobe	?	hypo-xiphoplastral lobe margin straight and convergent	hypo-xiphoplastral lobe margin strong curved
Plastral formulas	?	ABD > IG > PEC = HU	FE > ABD = HU = IG > AN = PEC

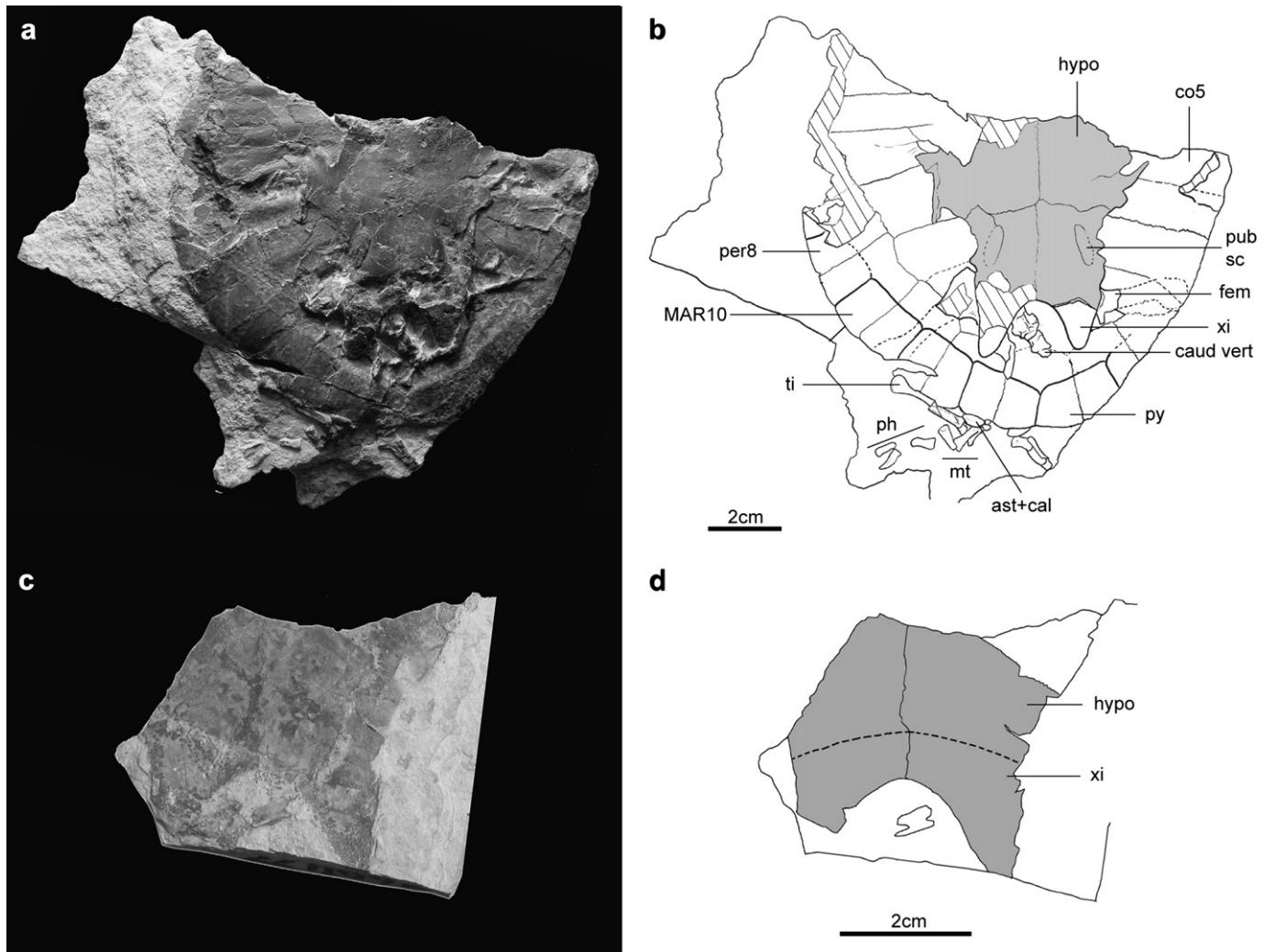


Fig. 5. *Prochelidella cerrobarcinae* nov. sp. (a–b) Mold of plastron in visceral view and carapace in ventral view (MPEF-PV 3290). (a) Picture. (b) Drawing. (c–d) Mold of posterior part of plastron (MPEF-PV 3296). (c) Picture. (d) Drawing.

main differential characters among *Pr. cerrobarcinae* nov. sp. and the other named species of *Prochelidella* are included in Table 1.

4.2. Paleobiogeographic remarks

The extant side-necked turtles comprise the Pelomedusoides and Chelidae, which have been separated on the basis of morphological and molecular data (Gaffney, 1977, 1991; Pritchard, 1979; Bull and Legler, 1980; Gaffney and Meylan, 1988; Seddon et al., 1997; Georges et al., 1998; Lapparent de Broin, 2000). Between them, the family Chelidae is a monophyletic group with extant species distributed across South America and Australasia (Pritchard and Trebbau, 1984; Iverson, 1992). The oldest fossil chelids are known from the Aptian-Albian? in Patagonia (this article) and from the Albian in Australia (Smith, 2009, 2010), as well as the Oligocene in Tasmania (Warren, 1969). The present disjointed distribution, the early fossil record of this family, and several peculiarities of extant chelids noted by Pritchard (1984) (e.g., that tropical chelids have a surprising tolerance to cold temperatures and, contrary to other reptiles, chelids exhibit great diversity toward the southern extreme of their range), suggest a much older biogeographical and phylogenetic history on southern Gondwanan landmasses.

The paleogeography of southern Gondwana (Fig. 7) has a complex history that was summarized by Woodburne and Case (1996). Geophysical and geological evidence suggests that at least as early as the Late Cretaceous, the Antarctic Peninsula was yet contiguous with southern South America (Grunow, 1992; Lawver et al., 1992; Shen, 1995). Furthermore, there are evidences for continuous subduction between terminal South America, along the Antarctic Peninsula and western Marie Byrd Land (portion of West Antarctica lying east of the Ross Ice Shelf and the Ross Sea and South of the Pacific Ocean) to Campbell Plateau (a large submarine plateau south of New Zealand), South Chatham Island (over 800 km east of southern New Zealand) and New Zealand during the Late Cretaceous (Grunow, 1992; Lawver et al., 1992; Bradshaw et al., 1995; LeMasurier and Landis, 1995; Smith, 1995; Storey, 1995). On the other hand, the separation of the New Zealand Region (including Campbell Plateau and South Chatam Island) and Australia from the remaining southern Gondwana could have happened by about 85–70 Ma (Lawver et al., 1992, Fig. 11) and about 80 Ma, respectively (Veevers and Li, 1991).

The differentiation of chelid turtles (from pelomedusoids) appears to have begun before the final break up of Southern Gondwana as evidenced by the early fossil record of chelids in the Aptian-Albian? of Patagonia (Los Chivos Hill) and in the Albian of

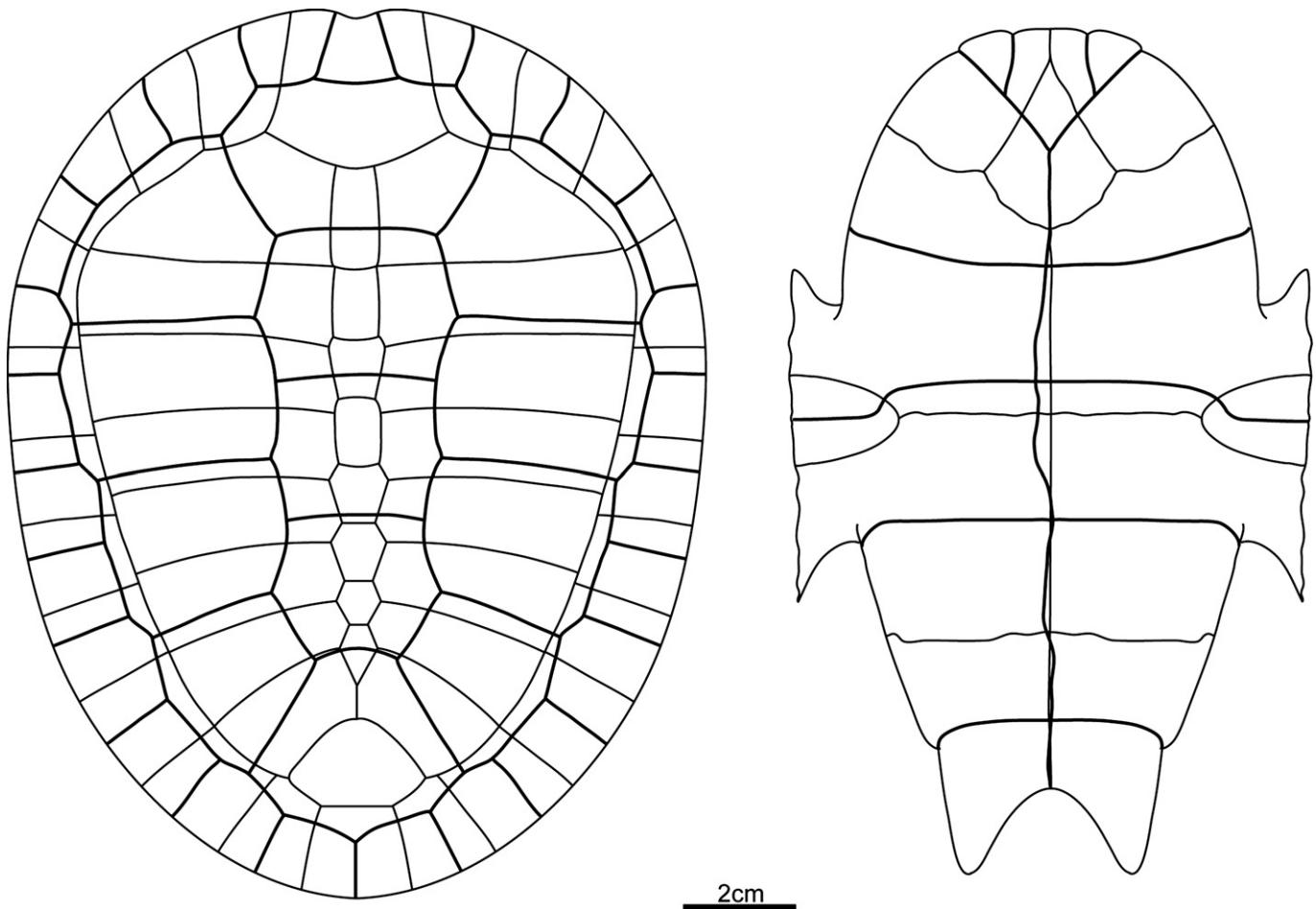


Fig. 6. Carapace and plastron reconstruction of *Prochelidella cerrobarcinae* nov. sp.

New South Wales, Australia (Smith, 2009), and the record of pelomedusoids (chelid's sister taxa) as early as Aptian-Albian in Niger and Brazil (de Broin, 1980; Gaffney et al., 2006, and references therein). Furthermore, in Campanian – Maastrichtian strata of Patagonia, the occurrence of isolated cervical vertebrae with similar morphology to that of some extant Australasian short-necked chelids (e.g., *Emydura*, *Elseya*), also supports the proposed statement (de Broin and de la Fuente, 1993, plate 1, 2–3). These data are

consistent with the occurrence of other tetrapods including monotremes in the early Paleocene faunas of Patagonia (Pascual et al., 1992) and ratites in late Eocene faunas of Seymour Island (Antarctic Peninsula) (Tambussi et al., 1994). The occurrence of these tetrapods in Patagonia, the Antarctic Peninsula, and Australia might be the result of a much older, widespread Southern Gondwana distribution of these taxa prior to the Late Cretaceous times.

Summarizing, *Pr. cerrobarcinae* n. sp. is the oldest chelid species, recovered from shallow lacustrine facies of the Aptian-Albian? Puesto La Paloma Member, Cerro Barcino Formation of the Chubut Group, at Los Chivos Hill, Chubut Province, Argentina. This species not only represents the oldest pleurodiran chelid record in the world but, together with the chelid remains of Albian Lightning Ridge, New South Wales, Australia (Smith, 2009, 2010), indicate that chelid diversification began well before the final fragmentation of southern Gondwana.

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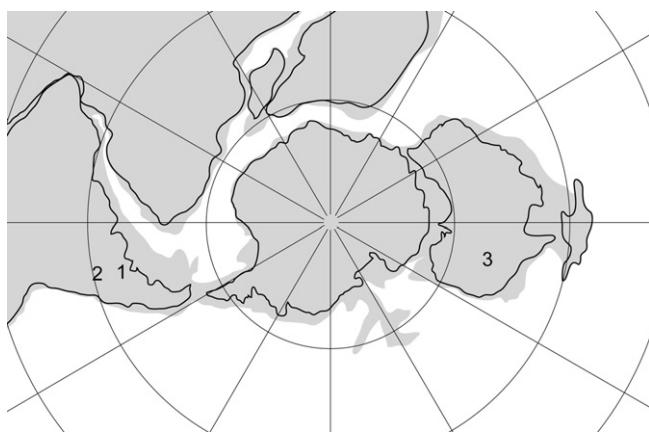


Fig. 7. Early Cretaceous paleogeographic map modified from Smith et al. (1981). 1, Cerro Los Chivos; 2, Cerro Los Leones; 3, Lightning Ridge.

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References

- Allard, J.O., Paredes, J.M., Giacosa, R.E., 2009. Fluvial Dynamics, Alluvial Architecture and Palaeohydrology of Axial Andean Transverse Drainage Systems in an Extensional Setting: Los Adobes Formation (Aptian), Cañadón Asfalto Basin, Argentina Acta geológica Lilloana. Proceedings of the 9º International Conference on Fluvial Sedimentology, San Miguel de Tucumán, 12–13.
- Ardolino, A.A., Franchi, M.R., 1993. El vulcanismo cenozoico de la Meseta de Somuncurá. Provincias de Río Negro y Chubut Actas 12º Congreso Geológico Argentino y 2º Congreso de Exploración de Hidrocarburos, 225–235, Buenos Aires.
- Ardolino, A.A., Franchi, M., Remesal, M., Salani, F., 1999. El volcanismo en la Patagonia extra-andina. In: Caminos, R. (Ed.), Geología Argentina. Servicio Geológico Minero Argentino, Buenos Aires, pp. 579–612.
- Batsch, A.J.C.K., 1758. Versuch einer Anleitung, zur Kenntnis und Geschichte der Thiere und Mineralien. Akademische Buchhandlung, Jena, 528 pp.
- Bradshaw, J.D., Weaver, S.D., Pankhurst, R.J., Story, B.C., 1995. New Zealand superterranea recognized in Marie Byrd Land and Thurston Island. In: VII International Symposium Antarctica Earth Sciences Abstract Siena, Italy, 60.
- Bridge, J., Jalfin, G., Georgieff, S., 2000. Geometry, lithofacies and special distribution of Cretaceous fluvial sandstone bodies, San Jorge Basin, Argentina, outcrop analog for the hydrocarbon-bearing Chubut Group. Journal of Sedimentary Research 70, 341–359.
- Bull, J., Legler, J., 1980. Karyotypes of side-necked turtles (Testudines: Pleurodira). Canadian Journal of Zoology 58, 828–841.
- Cabaleri, N.G., Armella, C., 1999. Facies lacustres de la Formación Cañadón Asfalto (Caloviano-Oxfordiano), en la quebrada Las Chacritas, Cerro Cóndor, provincia de Chubut. Revista de la Asociación Geológica Argentina 54, 375–388.
- Cabaleri, N.G., Armella, C., Silva Nieto, D., 2005. Saline lakes of Cañadón Asfalto formation (Middle upper Jurassic), Cerro Cóndor, Chubut province (Patagonia), Argentina. Facies 51, 350–364.
- Cas, R.A.F., Wright, J.V., 1987. Volcanic Successions: Modern and Ancient. Allen and Unwin, London, 528 pp.
- Cladera, G., Limarino, C.O., Alonso, M.S., Rauhut, O., 2004. Controles estratigráficos en la preservación de restos de vertebrados en la Formación Cerro Barcino (Cenomaniano), provincia del Chubut. Revista de la Asociación Argentina de Sedimentología 11, 39–55.
- Codignotto, J., Nullo, F., Panza, J., Proserpio, C., 1978. Estratigrafía del Grupo Chubut, entre Paso de Indios y Las Plumas Chubut. Actas 7º Congreso Geológico Argentino: 471–480, Neuquén.
- Coira, B., Nullo, F.E., Proserpio, C.A., Ramos, V.A., 1975. Tectónica de basamento de la región occidental del Macizo Nordpatagónico (provincias de Río Negro y del Chubut). Revista de la Asociación Geológica Argentina 30, 361–383.
- Cortiñas, J.S., 1996. La cuenca de Somuncurá-Cañadón Asfalto: sus límites, ciclos evolutivos del relleno sedimentario y posibilidades exploratorias Actas 13º Congreso Geológico Argentino y 3º Congreso de Exploración de Hidrocarburos, 147–163, Buenos Aires.
- Dalla Salda, L., Varela, R., Cingolani, C., 1999. El basamento pre-gondwánico del centro-oeste del Macizo Nordpatagónico. In: Caminos, R. (Ed.), Geología Argentina. Servicio Geológico Minero Argentino, Buenos Aires, pp. 107–112.
- de Broin, F., 1980. Les tortues de Gadofaoua (Aptien du Niger); aperçu sur la paléobiogeographie des Pelomedusidae (Pleurodira). Mémoires de la Société Géologique de France 139, 39–46.
- de Broin, F., 1987. The late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Part IV Chelona. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Paleontología 3, 131–139.
- de Broin, F., de la Fuente, M.S., 1993. Les tortues fossiles d'Argentine: synthèse. Annales de Paléontologie 79, 169–232.
- de la Fuente, M.S., 2003. Two new pleurodiran turtles from the Portezuelo formation (Upper Cretaceous) of northern Patagonia, Argentina. Journal of Paleontology 77, 559–575.
- de la Fuente, M.S., 2007. Testudines. In: Gasparini, Z., Coria, R., Salgado, L. (Eds.), Patagonian Mesozoic Reptiles. Indiana University Press, Bloomington, Indiana, pp. 50–86 (Chapter 3).
- de la Fuente, M., Lapparent de Broin, F., de Manera de Bianco, T., 2001. The oldest and first nearly complete skeleton of a chelid, of the *Hydromedusa* group (Chelidae, Pleurodira), from the Upper Cretaceous of Patagonia. Bulletin de la Société Géologique de France 172, 237–244.
- de la Fuente, M.S., Barbieri, R., Chafrat, P., 2010. Una tortuga Chelidae (Testudines: Pleurodira) de cuello largo en el Grupo Neuquén, Río Negro, Argentina. Significado cronológico y paleobiogeográfico. Andean Geology 37, 398–412.
- Figari, E., Courtade, S., 1993. Evolución tectosedimentaria de la cuenca Cañadón Asfalto, Chubut, Argentina Actas 12º Congreso Geológico Argentino y 2º Congreso de Exploración de Hidrocarburos, 66–77, Mendoza.
- Gaffney, E.S., 1977. The side-necked turtle familia Chelidae: a theory of relationships using sharing characters. American Museum Novitates 2620, 1–28.
- Gaffney, E.S., 1991. The fossil turtles of Australia. In: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., Rich, T.H. (Eds.), Vertebrate Paleontology of Australasia. Pioneer Design Studio, Melbourne, pp. 703–716.
- Gaffney, E.S., Meylan, P., 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.), The Phylogeny and Classification of Tetrapods. Clarendon, Oxford, pp. 157–210.
- Gaffney, E.S., Meylan, P.A., Wyss, A.R., 1991. A computer assisted analysis of the relationships of the higher categories of turtles. Cladistics 7, 313–335.
- Gaffney, E.S., Tong, H., Meylan, P., 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae and Araripemydidae. Bulletin of the American Museum of Natural History 300, 6–697.
- Gaffney, E.S., Rich, T.H., Vickers-Rich, P., Constantine, A., Vaca, R., Kool, L., 2007. *Chubutemys*, a new eucryptodiran turtle from Early Cretaceous of Argentina, and the relationships of the Meiolaniidae. American Museum Novitates 3599, 1–35.
- Genise, J.F., Melchor, R.N., Bellosi, E.S., González, M.G., Krause, M., 2007. New insect population (Pupichnia) from the upper Cretaceous of Patagonia, Argentina. Cretaceous Research 28, 545–559.
- Georges, A., Birrell, J., Saint, K.M., McCord, W., Donnellan, S.C., 1998. A phylogeny for side-necked turtle (Chelonia: Pleurodira) based on mitochondrial and nuclear gene sequence variation. Biological Journal of the Linnean Society 67, 213–246.
- Gray, J.E., 1873. Observations on chelonians, with descriptions of new genera and species. Annals and Magazine of Natural History 11, 289–308.
- Grunow, A., 1992. Creation and destruction of Wedell Sea floor in the Jurassic. Geology 21, 647–650.
- Hugo, C.A., Leanza, H.A., 2001. Hoja Geológica 3969-IV. General Roca, provincias del Neuquén y Río Negro. Instituto de Geología y Recursos Naturales. SEGEMAR, Boletín 308, 1–71.
- Iverson, J.B., 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Privately Printed, Richmond, Indiana.
- Kocurek, G., 1996. Desert aeolian systems. In: Reading, H.G. (Ed.), Sedimentary Environments: Processes, Facies and Stratigraphy. Blackwell Science, Oxford, pp. 125–153.
- Lapparent de Broin, F. de, 2000. The oldest pre-Podocnemidid turtle (Cheloniidae, Pleurodira), from the early Cretaceous, Ceará state, and its environment. Treballs del Museu de Geologia de Barcelona 9, 43–95.
- Lapparent de Broin, F. de, de la Fuente, M.S., 2001. Oldest world chelid (Cheloniidae, Pleurodira) from the Cretaceous of Patagonia. Comptes Rendus de l'Académie des Sciences de Paris 333, 463–470.
- Lawver, L.A., Ghaghani, L.M., Coffin, F.M., 1992. The development of paleoseaways around Antarctica. American Geophysical Union Antarctic Research Series 65, 7–30.
- Le Masurier, W.A., Landis, C.A., 1995. Environment of breakup and timing of mantle plume activity record by the West Antarctic erosion surface. In: International Symposium Antarctic Earth Sciences. Abstract, Siena, Italy, p. 242.
- Leanza, H.A., 1999. The Jurassic and Cretaceous Terrestrial Beds from Southern Neuquén Basin. Argentina. Field Guide. Instituto Superior de Correlación Geológica, INSUGEOL. Serie Miscelánea, 4, 1–30.
- Leanza, H.A., Apesteguía, S., Novas, F.E., de la Fuente, M.S., 2004. Cretaceous terrestrial beds from Neuquén Basin (Argentina) and their tetrapod assemblages. Cretaceous Research 25, 61–87.
- Lesta, P., Ferello, R., 1972. Región extra-andina de Chubut y norte de Santa Cruz. In: Leanza, A. (Ed.), Geología Regional Argentina. Academia Nacional de Ciencias, Córdoba, pp. 601–653.
- Lindholm, W.A., 1929. Revidiertes Verzeichnis der Gattungen der rezenten Schilskräten nebst Notizen zur Nomenklatur einiger Arten. Zoologischer Anzeiger 81, 275–272.
- Malumíán, N., 1999. La sedimentación en la Patagonia extra-andina. In: Caminos, R. (Ed.), Geología Argentina. Servicio Geológico Minero Argentino, Buenos Aires, pp. 557–612.
- Manassero, M., Zalba, P.E., Andreis, R., Morosi, M., 2000. Petrology of continental pyroclastic and epiclastic sequences in the Chubut group (Cretaceous): Los Altares-las Plumas area, Chubut, Patagonia Argentina. Revista Geológica de Chile 27, 13–26.
- Mountney, N.P., 2006. Eolian facies models. In: Posamentier, H.W., Walker, R.G. (Eds.), Facies Models Revisited. Society for Sedimentary Geology, Tulsa, pp. 19–83.
- Musacchio, E., 1972. Charophytas del Cretácico Inferior en sedimentitas chubutenses al este de La Herrería, Chubut. Ameghiniana 9, 354–356.
- Musacchio, E., Chebli, G.A., 1975. Ostrácodos no marinos y caróbitos del Cretácico Inferior de las provincias de Chubut y Neuquén. Ameghiniana 12, 70–96.
- Nakayama, K., Yoshikawa, S., 1997. Depositional processes of primary to reworked volcanics on an alluvial plain; an example from the Lower Pliocene Ohta tephra bed of the Tokai Group, central Japan. Sedimentary Geology 107, 211–229.
- Pascual, R., Archer, M., Ortiz Jaureguizar, E., Prado, E., Godthelp, H., Hand, S.J., 1992. First discovery of monotremes in South America. Nature 356, 704–706.
- Pritchard, P.C.H., 1979. Taxonomy, Evolution and zoogeography. In: Harless, M., Morlock, H. (Eds.), Turtles: Perspectives and Research. Wiley, New York, pp. 1–42.
- Pritchard, P.C.H., 1984. Evolution and zoogeography of south American turtles. Studia geologica Salmanticensis Volumen Especial 1. Studia Palaeochelonionogica 1, 225–233.
- Pritchard, P.C.H., 1988. A survey of neural bone variation among recent chelonian species, with functional interpretations. Acta Zoologica Cracoviensis 31, 625–686.

- Pritchard, P.C.H., Trebbau, P., 1984. The turtles of Venezuela. Contrib. Herpetology Soc. for Study Amphibians Reptiles 2, 1–403.
- Proserpio, C.A., 1987. Descripción geológica de la Hoja 44e, Valle General Racedo, provincia de Chubut. Boletín de la Dirección de Minería y Geología 201, 102 (Buenos Aires).
- Rapela, C.W., Dias, C.F., Franzese, J.R., Alonso, G., Benvenuto, A.R., 1991. El batolito de la Patagonia central: evidencias de un magmatismo triásico-jurásico asociado a fallas transcurrentes. Revista Geológica de Chile 18, 121–138.
- Rauhut, O.W.M., Cladera, G., Vickers-Rich, P., Rich, T., 2003. Dinosaurs remains from the Lower Cretaceous of the Chubut group. Argentina. Cretaceous Research 24, 487–497.
- Seddon, J.M., Georges, A., Baverstock, P.R., McCord, W., 1997. Phylogenetic relationship of chelid turtles (Pleurodira: Chelidae) based on mitochondrial 12S rRNA sequence variation. Molecular Phylogenetic and Evolution 7, 55–61.
- Shen, Y., 1995. A paleoisthmus between southern south America and Antarctic Peninsula during late Cretaceous and early Tertiary. In: 7th International Symposium on Antarctic Earth Sciences. Abstracts, Siena 345.
- Silva Nieto, D.G., Cabaleri, N.G., Salani, F., Coluccia, A., 2002. Cañadón Asfalto, una cuenca tipo “pull apart” en el área de cerro Cóndor, provincia del Chubut Actas 15º Congreso Geológico Argentino, 238–243, El Calafate.
- Smith, A.G., Hurler, A.M., Briden, J.C., 1981. Phanerozoic Paleocontinental World Maps. Cambridge University Press, Cambridge. 102pp.
- Smith, C.H., 1995. Mid-crustal conditions and processes during Cretaceous separation of Marie Byrd Land and New Zealand: evidence from Marie Byrd Land. In: International Symposium Antarctic Earth Science. Abstract, Siena, Italy 355.
- Smith, E.T., 2009. Turtle treasures from Opal fields of Lightning ridge, New south Wales. Turtle Simposium. In: Braman, D., Brinkman, D., Marion, C. (Eds.), Abstracts and Program. Special Publication of the Royal Tyrell Museum, Drumheller, pp. 167–168.
- Smith, E.T., 2010. Early Cretaceous chelids from Lightning Ridge, New South Wales Alcheringa 34, 375–384.
- Sterli, J., de la Fuente, M.S., 2011. A new turtle from La Colonia Formation (Campanian-Maastrichtian), Patagonia, Argentina with remarks on the evolution of vertebral column in turtles. Palaeontology 54, 63–78.
- Storey, B.C., 1995. Microplates and mante plumes in Antarctica. In: International Symposium Antarctic Earth Science. Abstracts, Siena, Italy 361.
- Talbot, M.R., Allen, P.A., 1996. Lakes. In: Reading, H.C. (Ed.), Sedimentary Environments: Processes, Facies and Stratigraphy. Blackwell Science, Cambridge, pp. 83–124.
- Tambussi, C., Noriega, J., Gazdzicki, A., Tatur, A., Reguero, M.A., Vizcaino, S., 1994. Ratite bird from the Paleogene La Meseta formation, Seymour Island, Antarctica. Polish Polar Research 15, 15–20.
- Umazano, A.M., Bellosi, E.S., Visconti, G., Melchor, R.N., 2008. Mechanisms of aggradation in fluvial systems influenced by explosive volcanism: an example from the upper Cretaceous Bajo Barreal formation, San Jorge basin, Argentina. Sedimentary Geology 203, 213–228.
- Veevers, J.J., Li, Z.X., 1991. Review of the sea floor spreading around Australia. II. Marine magnetic anomaly modeling. Australian Journal of Earth Sciences 38, 391–408.
- Volkheimer, W., Gallego, O.F., Cabaleri, N.G., Armella, C., Narváez, P.L., Silva Nieto, D.G., Páez, M.A., 2009. Stratigraphy, palynology and conchostracans of a Lower Cretaceous sequence at the Cañadón Calcáreo locality, extra-andean central Patagonia: age and paleoenvironmental significance. Cretaceous Research 30, 270–282.
- Warren, J.W., 1969. Chelid turtles from the Mid-Tertiary of Tasmania. Journal of Paleontology 43, 179–182.
- Williams, E., 1950. Variation and selection in the cervical central articulation of living turtles. Bulletin of the American Museum of Natural History 94, 505–522.
- Wood, R., Moody, R., 1976. Unique arrangement of carapace bone in the South American chelid turtle *Hydromedusa maximiliani* (Mikan). Zoological Journal of Linnean Society 59, 69–78.
- Woodburne, M.O., Case, J.A., 1996. Dispersal, Vicariance, and the late Cretaceous to early Tertiary Land Mammal Biogeography from south America to Australia. Journal of Mammalian Evolution 3, 121–161.