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Freshwater turtles (Testudines: Pleurodira) in the Upper Cretaceous of Chilean Patagonia



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ABSTRACT

We describe remains of freshwater turtles from the Upper Cretaceous of Chilean Patagonia. The fossils, which comprise isolated shell fragments and incomplete appendicular bones, were recovered from meandering fluvial deposits of the Dorotea Formation (upper Campanian–Danian), in the Río de Las Chinas Valley, Magallanes region. These remains represent the first records of Upper Cretaceous pan-chelid pleurodiran turtles in the Magallanes-Austral Basin. The shell fragments show a strong ornamentation of irregular polygons distributed over their entire external surface, and one of the peripheral plates is narrow and elongated. These features are consistent with traits described in *Yaminuechelys*, a chelid genus from the Upper Cretaceous and Paleogene of Argentinian Patagonia. In addition, the suprapygal plate presents sulci that mark the limits of the vertebral scute 5 and the marginal scutes 12 as in *Yaminuechelys sulcipeculiaris*. This finding represents the southernmost record of a species conferred to *Yaminuechelys*, extending the distribution of this genus to the Magallanes-Austral basin during the Campanian–Maastrichtian.

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1. Introduction

Continental turtles have been present in what is now South America since the late Triassic (de la Fuente et al., 2014). The oldest known representative is the australochelyid *Palaeochersis talampayensis* from the Upper Triassic of the Los Colorados Formation in Argentina (Rougier et al., 1995; Sterli et al., 2007). One of the best represented continental turtle groups in South America is Pan-Chelidae (Maniel and de la Fuente, 2016; Vlachos et al., 2018). This lineage integrates the crown group Chelidae and pleurodiran turtles closely related to it (Joyce et al., 2004). Chelidae is a clade of freshwater turtles whose record is very diverse in South America, especially in Argentina (Maniel and de la Fuente, 2016). Pan-Chelidae appeared in South America in the Early Cretaceous, period in which this lineage had their first peak of diversity (de la Fuente et al., 2011; Vlachos et al., 2018; Krause et al., 2019). In the Late Cretaceous there were more peaks of diversity, specifically in the Coniacian and Maastrichtian, as well as various extinction events (Vlachos et al., 2018). This is attributed to a differential impact of the extinction event at different latitudes, which apparently was lower at high latitudes, where chelids were distributed during the

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Mesozoic (Askin, 1988; Alegret et al., 2012; Witts et al., 2016; Vlachos et al., 2018). Unlike other turtle groups, such as pelomedusoids, panchelids did not have a significant impact during the mass extinction event that occurred at the K-Pg boundary, and some clades that appeared in the Maastrichtian survived and formed the basis for the diversity of chelids that currently exists in South America (Vlachos et al., 2018). The highest abundance and diversity of Late Cretaceous turtles has been recorded in the La Colonia Formation (Campanian-Maastrichtian, Chubut Province), much of which corresponds to chelids (Gasparini and de la Fuente, 2000; Gasparini et al., 2015; Oriozabala et al., 2020). For the Paleogene, the main records are concentrated in Argentina, especially in the Chubut and Río Negro provinces, where different genera and species of chelids have been documented, such as Hydromedusa casamayorensis, Salamanchelys palaeocenica, Yaminuechelys maior and indeterminate chelids (Broin and de la Fuente, 1993; de la Fuente and Bona, 2002; Bona and de la Fuente, 2005; Bona, 2006; Bona et al., 2009; Maniel and de la Fuente, 2016). In the Eocene there was a significant expansion to the north of the Chelidae family (Broin and de la Fuente, 1993; Vlachos et al., 2018). Vlachos et al. (2018) mention that in the Bartonian chelids expanded to at least 10° S, and subsequently they are not below 40° S, and that during the Neogene chelids are present in all latitudes between 10° N and 40° S. In the Neogene, the number of South American records increases considerably, with findings in Argentina, Bolivia, Brazil, Colombia, Peru, Uruguay and Venezuela, represented by several nominal species including Chelus colombiana, Chelus/Emys macroccocygeanus, Phrynops geoffroanus and other taxa such as Hydromedusa cf. H. tectifera and Acanthochelys indet., in addition to other more fragmentary records (Wood, 1976; Barbosa Rodrigues, 1982; Gasparini et al., 1986; de la Fuente, 1992; Broin and de la Fuente, 1993; Kischlat, 1993; Sánchez-Villagra et al., 1995; Perea et al., 1996; Oliveira and Romano, 2007; Cadena et al., 2008, 2015; Cadena and Jaramillo, 2015a, 2015b; Ferreira et al., 2016; Maniel and de la Fuente, 2016), which shows that the definitive pattern of distribution of South American Chelids began to be established during this period. For the Pliocene and Pleistocene, records are concentrated in Argentina and Brazil, where chelids as Acanthochelys cosquinensis, Hydromedusa tectifera, Phrynops hilarii have been identified (de la Fuente, 1986, 1992; Maciel et al., 1996; Maniel and de la Fuente, 2016), in addition to other remains determined as Hydromedusa cf. H. tectifera (de la Fuente, 1992) and Phrynops sp. (Hirooka, 1991; de la Fuente, 1997). In South America there are currently 22 species of chelids distributed in the genera Acanthochelys, Platychelys, Rhinemys, Phrynops, Mesoclemmys, Hydromedusa and Chelus (Vlachos et al., 2018).

The objective of this work is to present the first remains attributable to freshwater turtles of the Chelidae family, found in outcrops of the Dorotea Formation (late Campanian–Danian), in Chilean Patagonia. Some of these remains are conferred to *Yaminuechelys*, a genus that until now had only been registered in Argentina (de la Fuente et al., 2001; Bona and de la Fuente, 2005; Oriozabala et al., 2020). This is the first confirmed record of chelid turtles in Chile. At the same time, this finding represents the southernmost record of cf. *Yaminuechelys* sp. known to date.

2. Locality and geological setting

The Late Cretaceous strata of the Última Esperanza Province are deposits of the Magallanes-Austral foreland basin. This basin was formed during the Andean compressional orogenesis associated with the initial break-up of Gondwanaland (Biddle et al., 1986; Wilson, 1991; Mella, 2001; Fildani et al., 2003). These sediments were deposited in a north-south elongated basin parallel to the Andes fold-thrust belt system (Macellari et al., 1989; Fildani et al., 2009; Romans et al., 2011), which extends north to south across the current political boundary between Chile and Argentina.

The Upper Cretaceous succession includes three formations in

ascending order: The Cerro Toro Formation (Cenomanian–Campanian; Katz, 1963; Hubbard et al., 2008; Daniels et al., 2019), the Tres Pasos Formation (Campanian–lower Maastrichtian; Romans et al., 2009; Hubbard et al., 2010; Auchter et al., 2016; Daniels et al., 2018) and the Dorotea Formation (upper Campanian-Danian; Schwartz et al., 2016; Gutierrez et al., 2017; Daniels et al., 2018; George et al., 2020).

The Dorotea Formation is interpreted as a shoreface coastal environment, with a tidal influenced delta (Covault et al., 2009; Hubbard et al., 2010; Vogh et al., 2014; Schwartz and Graham, 2015; Manriquez et al., 2019). It is composed of sandstones of different grain sizes, frequent conglomerate lenses, thin beds of calcareous sandy concretions and mudstones. In addition, this unit contains abundant fossils of marine invertebrates (bivalves and gastropods, among others), bone fragments including the remains of dinosaurs, marine reptiles and mammals and also mudstones with fossil plant imprints (Katz, 1963; Cortés, 1964; Schwartz and Graham, 2015; González, 2015; Manríquez et al., 2019).

The Dorotea Formation is exposed on the eastern flank of the Río de Las Chinas Valley (50° 42' 42.72" S/72° 32' 29, 08" W). This valley is part of the Estancia Cerro Guido, located northwest of the Torres del Paine National Park, in the northern sector of the Última Esperanza Province, Magallanes and Chilean Antarctic Regions (Fig. 1). This locality has a high potential for paleontological research due to the great diversity of flora and fauna from the late Cretaceous that has been recognized in recent years (Cisterna et al., 2014; Soto-Acuña et al., 2014, 2016a, b; Jujihara et al., 2014; Fernández-Jiménez et al., 2016; Mansilla Vera et al., 2016; Trevisan et al., 2016; Lobos et al., 2016, 2018; Garrido et al., 2016, 2018; Pino et al., 2016, 2018; Suazo Lara et al., 2017, 2018; Leppe et al., 2018; Ortíz et al., 2018; Manríquez et al., 2019; Trevisan et al., 2020). The turtle shell fragments described here were found in the "Saurópodo sector" (Fig. 1). These remains were recorded in two sections of the stratigraphic column in Saurópodo sector; SP-1 and SP-17 (Fig. 2), located in the central part of the valley. In the first site, the fossils are preserved in a fine to medium-grained sandstone level with trough cross-bedding, of upper Campanian age. In the other locality, the strata are composed of sandy mudstones with fine-grained sandstone lenses, of lower Maastrichtian age (between 71.7 \pm 1.2 Ma and 74.9 \pm 2.1 Ma U-Pb maximum depositional age; Gutiérrez et al., 2017).

3. Materials and methods

The studied material corresponds to isolated shell and appendicular bone fragments. The fossils were collected in the Saurópodo sector, Río de Las Chinas Valley (Fig. 1) during expeditions realized in February of the years 2015–2019. At section SP-1, turtle remains were found in association with sauropod and anuran bones. In the section SP-17, they were found associated with abundant remains of saurischian and ornithischian dinosaurs, mammals, and anurans.

The sedimentological studies were carried out during the same expeditions. This work resulted in the elaboration of 6 stratigraphic columns in detail to build a general column (Fig. 2). The facies analysis was presented by Manríquez et al. (2019).

For identification, the material was compared with turtle fossils published in the literature. The nomenclature of the shell plates and appendicular fragments follows Walker (1973), and Pritchard and Mortimer (1999).

Institutional abbreviations: CPAP, Colección de Paleobiología de Antártica y Patagonia, INACH (Chilean Antarctic Institute), Punta Arenas, Chile.

4. Systematic paleontology

Reptilia Laurenti, 1768 (*sensu* Modesto and Anderson, 2004). Testudines Batsch, 1788 (*sensu* Joyce et al., 2004). Pleurodira Cope, 1865



Fig. 1. Location of the study area. The sections where turtle remains were found are indicated. The distribution of the outcrops corresponding to the Tres Pasos, Dorotea and Man Aike formations is also illustrated.

Pan-Chelidae Joyce et al., 2004 Pan-Chelidae indet. (Fig. 3)

Material: CPAP 5941, Distal fragment of right humerus; CPAP 5942, distal end of right femur.

Locality, horizon and age: Saurópodo sector. Section SP-17 (upper Campanian–lower Maastrichtian) in Manríquez et al. (2019). Río de Las Chinas Valley, Dorotea Formation (late Campanian–Danian), Última Esperanza Province, Magallanes y Antártica Chilena Region, Chilean Patagonia. Thickness [m]

370

360

350

340

330

320 308

Lithology

Mud

Clay

Formation





Fig. 2. Stratigraphic column in the Saurópodo area of the Cerro Guido-Río de las Chinas Valley Complex, with the levels of turtle fossil records.

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Fig. 3. Pan-Chelidae indet. A, CPAP 5941, distal fragment of right humerus, A1: ventral view; A2: dorsal view; A3: anterior view; A4: posterior view; A5: articular view. B, CPAP 5945, distal fragment of left femur, B1: dorsal view; B2: ventral view; B3: posterior view; B4: anterior view; B5: articular view. Scale bar: 10 mm. Abbreviations, ca: capitellum; es: ectepicondylar sulcus; fc, fibular condyle; fl: flange; tc, tibial condyle; re: radial epicondyle; tr: trochlea; ue: ulnar epicondyle.

Description: CPAP 5941 (Fig. 3, A1-A5) corresponds to the distal portion of a right humerus. This fragment is dorsoventrally flattened and expanded mediolaterally. In ventral view, the capitellum and the trochlea are separated by a proximodistally orientated groove. The capitellum corresponds to the articulation surface for the radius, while the trochlea articulates with the ulna (Walker, 1973). The capitellum is smaller and mediolaterally narrower than the oval-shaped trochlea and projects farther ventrally, which is more evident in articular view. A broad muscle insertion site extends over the ventral surface of the capitellum and the trochlea where the triceps brachii, tractor radii, extensor radii and brachialis inferior muscles are anchored (Walker, 1973), as in Yaminuechelys maior (Bona et al., 2009), although the groove that separates the capitellum from the trochlea is more marked in the latter species. There is a small foramen in this area, interpreted as vascular. The dorsal surface is flat. In dorsal view, there is a longitudinal ectepicondylar groove at the medial border. This groove deepens distally and passes through the distal epiphysis. The radial epicondyle is rounded, well-developed and positioned dorsal to the level of the capitellum and trochlea. The ulnar epicondyle is blunt and lessdeveloped than the radial condyle. CPAP 5941 is similar to a distal fragment of a left humerus described by Gasparini and de la Fuente (2000), which these authors referred to Chelidae indet. The main similarities include a markedly marginally positioned ectepicondilar groove and the presence of a depressed area on the articular surface. CPAP 5941 also resembles the distal end of the humerus of Hydromedusa casamayorensis (Maniel et al., 2018) and Yaminuechelys maior (Bona et al., 2009), since this portion of the humerus is also dorsoventrally flattened and broad in both of these species. The same morphology is also shared with Prochelidella portezuelae (de la Fuente, 2003) and the pan-chelid Linderochelys rinconensis (de la Fuente et al., 2007).

CPAP 5942 (Fig. 3, B1-B5) corresponds to the distal portion of a left femur. The element is mediolaterally expanded and dorsoventrally flattened. The dorsal surface of the element is slightly convex. The articular condyles can be observed on the ventral surface. The tibial condyle is well-developed and projects markedly ventrally in articular view. The fibular condyle is smaller than the tibial and is not expanded

ventrally. A broad and shallow longitudinal depression separates the tibial condyle from the medial edge of the element, which continues proximally in the form of a ridge. CPAP 5942 resembles the distal fragment of a right femur described by Gasparini and de la Fuente (2000) that these authors referred to Chelidae indet. Both are laterally expanded and possess a tibial articular surface that is larger than the fibular articular surface. CPAP 5942 is also very similar to the distal fragment of a left femur of Yaminuechelys sulcipeculiaris illustrated in Oriozabala et al. (2020). In both elements, the tibial condyle is more developed than the fibular and projects farther distally. In contrast, Bona et al. (2009), mention that the distal portion of the Yaminuechelys maior femur has subequal tibial and fibular condyles. Also, the distal epiphysis is distinctly separated from the rest of the element by a flange in both fragments (in the illustration of the femur of Yaminuechelys sulcipeculiaris only the ventral view can be seen), and the surface of the bone bears striations that run along it longitudinally.

Remarks: The subcircular cross-section of the humerus and femur diaphyses, together with the dorsal bending of both elements and the distal flattening of the epiphysis of the humerus, are typical traits observed in pan-chelid turtles (Maniel and de la Fuente, 2016). However, the lack of true synapomorphies in the material precludes a more specific taxonomic identification. The appendicular bones described in this work present general similarities with the same elements referred to Chelidae that have been found in outcrops of similar age in the Patagonia of Argentina, therefore the Chilean material probably belongs to the same family. However, the incompleteness of the material prevents their referral to a particular genus.

Chelidae Lindholm, 1929.

Yaminuechelys de la Fuente et al., 2001.

Type species: *Yaminuechelys gasparinii* de la Fuente et al., 2001, Río Negro Province, Argentina, late Campanian–early Maastrichtian.

cf. Yaminuechelys sp.

(Fig. 4)

Material: CPAP 3040a, a suprapygal plate; CPAP 3010b, an eighth right costal plate; CPAP 3040c, a seventh right peripheral plate; CPAP 4944, a distal fragment of costal plate; CPAP 5943, left peripheral plate 11; CPAP 4945, a possible pygal plate.

Locality, horizon and age: Saurópodo sector. CPAP 3040a-c and CPAP 5943 are from section SP-1 (Campanian) in Manríquez et al. (2019); CPAP 4944 and CPAP 4945 are from section SP-17 (upper Campanian–lower Maastrichtian) in Manríquez et al. (2019). Río de Las Chinas Valley, Dorotea Formation (late Campanian–Danian), Última Esperanza Province, Magallanes y Antártica Chilena Region, Chilean Patagonia.

Description: Specimen CPAP 3040a (Fig. 4, A1-A2) corresponds to a suprapygal plate. This plate lacks most of its anterior portion. The preserved portion allows to distinguish three sides; two lateral and one posterior. In some of the species of the genus Yaminuechelys the suprapygal plate has a sub-pentagonal shape. This trait has been described in the holotype of Yaminuechelys gasparinii (de la Fuente et al., 2001), in an incomplete shell of Yaminuechelys cf. gasparinii (de la Fuente et al., 2010) and in Yaminuechelys sulcipeculiaris (Oriozabala et al., 2020). The incomplete preservation of the suprapygal plate CPAP 3040a prevents verifying if this element had a subpentagonal shape similar to that described in other species of the genus Yaminuechelys, although the preserved portion suggests a shape similar to the suprapygal plate of those species. The dorsal surface is strongly ornamented with irregular polygons, which vary in shape. There are triangular, square, pentagonal and approximately rounded polygons. Two sulci are also observed on the dorsal surface, which are approximately perpendicular to each other. In addition, the suprapygal plate bears a longitudinal sulcus that separates both marginals 12 in the midline, and a horizontal sulcus that separates the vertebral scutes 5 and both marginal scutes 12. The pattern of these sulci is very similar to that observed in the suprapygal plate of Yaminuechelys sulcipeculiaris (Fig. 3E in Oriozabala et al., 2020). The visceral surface of CPAP 3040a is mostly smooth, with stretch marks radiating from an anterior bulge. Lateral to this bulge, a series of shallow ridges and stretch marks are observed, which are especially evident near the right anterolateral border. These marks probably represent part of the iliac scars; the articulation surface for the ilium, which is a synapomorphy of Pleurodira (Gaffney and Meyland, 1988).

Specimen CPAP 3040b (Fig. 4, B1-B2) corresponds to a right eighth costal plate. It is a lateromedially expanded element. In dorsal view, the ornamentation of this fragment is similar to what is described in costal plates of the Anacleto Formation MAU-Pv-N-475 referred to Yaminuechelys aff. maior (de la Fuente et al., 2015), consisting of multiple well-marked irregular polygons. However, the polygons on the lateral half of the dorsal surface are mediolaterally elongated. In this surface the sulci that delimit the epidermal scutes are observed. Medially, a laterally convex sulcus is observed, which delimits the lateroposterior portion of the vertebral scute 4. Another sulcus is arranged mediolaterally, which contacts the lateral edge of the sulcus that delimits the vertebral scute 4. This sulcus marks the boundary between the pleural scute 4 and the vertebral scute 5. In visceral view, a preserved part of the dorsal rib can be observed. In its medial portion, the rib curves dorsally, similar to what is observed in the eighth costal plate of Yaminuechelys sulcipeculiaris (Fig. 3F in Oriozabala et al., 2020). Laterally, the rib progressively flattens and expands anteroposteriorly. The visceral surface lacks ornamentation but bears a series of longitudinal stretch marks.

Specimen CPAP 4944 (Fig. 4, E1-E2) corresponds to a distal fragment of a costal plate, which preserves part of its lateral margin. In dorsal view, the fragment shows ornamentation that covers its entire surface, formed by irregular polygons of up to five sides. Most polygons are mediolaterally elongated. The lateral margin is convex in dorsal view and dorsoventrally thin in medial view. In visceral view, a portion of the rib is preserved, which is broad anteroposteriorly and extends to the lateral margin of the element. The lateral end of the rib is preserved, suggesting a loose contact between costal and peripheral bone, which is a diagnostic feature of the chelid turtles (Lapparent de Broin and de la Fuente, 2001). The surface of the rib shows several longitudinal grooves.

Specimen CPAP 3040c (Fig. 4, C1-C6) corresponds to a right peripheral plate of the bridge, probably the seventh. The plate is narrow and not expanded laterally, but it is expanded posteriorly, as is described in Yaminuechelys maior (Bona et al., 2009). The peripheral plate is approximately twice as long as it is wide. The lateral edge of the element is dorsoventrally short, while the medial edge is taller dorsoventrally. The entire external surface (both dorsal and ventral surfaces) is ornamented with irregular polygons. The shape of the polygons varies between triangular, square, pentagonal and approximately circular. The dorsal surface is concave. This surface retains part of the groove that marks the boundary between two marginal scutes (in this case marginal 6 and 7). This groove is slightly inclined towards the anterior end. The medial border of the dorsal surface is approximately straight. The ventral surface is convex. As in the dorsal surface, there is a mediolaterally disposed sulcus, which marks the boundary between two marginal scutes. The medial border of the ventral surface is robust and concave in the middle and becomes increasingly convex towards the anterior and posterior ends. The lateral margin of the peripheral plate is broken, which prevents the description of its profile. The medial surface of the element is concave. The rib socket is present on this surface. In medial view, the element is anteriorly wider dorsoventrally than towards its posterior end. In anterior and posterior views, the element is dorsally concave and ventrally convex. In anterior view, the lateral edge is curved towards the dorsal. The posterior portion of the lateral border is not preserved. In anterior view, the element is dorsoventrally higher than in posterior view.

Specimen CPAP 5943 (Fig. 4, D1-D6) corresponds to a left peripheral plate, probably the eleventh, based on the thickness of the plate in cross section, and also because the pocket for the rib is not observed. In dorsal view, the element is partially eroded in certain areas, but the ornamentation formed by small irregular polygons and granules is clearly distinguishable. There is a sulcus between two marginals scutes that runs through the element mediolaterally. The most medial portion of this sulcus faces proximally, then continues towards the lateral edge of the plate, with its most lateral portion slightly curved anteriorly. In ventral view, the plate preserves ornamentation formed by small irregular polygons distributed over the entire surface. As on the dorsal surface, a slightly inclined mediolateral sulcus between two marginals scutes is present, running from medial towards lateral with a slight anterior inclination. The lateral margin of the ventral surface is almost straight. The medial edge of the dorsal surface is more extended medially than that of the ventral surface, which is straight along its entire length. In anterior and posterior views, the ventral surface is convex, while the dorsal surface is almost flat. A wide concavity separates the medial edges of the dorsal and ventral surfaces.

Specimen CPAP 4945 (Fig. 4, F1-F3) corresponds probably to a peripheral plate 10 or 11, or it could even be a pygal plate. Its exact position is difficult to determine because none of its edges is preserved, also obscuring the original shape. In dorsal view, the element presents an anteroposterior sulcus between marginal scutes (possibly the marginal scutes 12). This sulcus is slightly curved and bifurcates into two shorter furrows that extend towards the anterior edge of the plate. The ornamentation of the dorsal surface consists of irregular polygons, similar to those of the other plates previously described. This ornamentation is very tenuous and is only visible in some areas of the dorsal surface, probably because of erosion. In anterior view, an oval concavity can be observed on the anterior surface, which is closed in both ends. This plate is bordered by strong ventral and dorsal edges, the latter being quite eroded. The anterior margins of the dorsal and ventral surfaces converge slightly posteriorly, decreasing the dorsoventral height of the element. In ventral view, the anterior edge is slightly concave. The anterior margin of the dorsal surface extends farther anteriorly than that of the ventral surface. The ventral edge is bordered by a shallow and relatively wide groove. The element lacks ornamentation on its ventral surface. In cross-section, the plate is triangular, with the dorsal edge more extended than the ventral and separated by a



(caption on next page)

Fig. 4. cf. *Yaminuechelys* sp. A: Schematic reconstruction of the shell of *Yaminuechelys gasparini* with the interpretation of the position of the CPAP 3040a-c, CPAP 4943, and CPAP 5943 plates (modified from de la Fuente et al., 2001). CPAP 3040a, suprapygal plate and schematic representation. B1: dorsal view; B2: visceral view. CPAP 3040b, right eighth costal plate and schematic representation, C1: dorsal view; C2: visceral view. CPAP 5943, right peripheral plate (probably the eighth) and schematic representation, D1: dorsal view; D2: ventral view; D3: medial view; D4: lateral view; D5: anterior articular view; D6: posterior articular view. CPAP 5943, left peripheral plate (eleventh) and schematic representation, E1: dorsal view; E2: ventral view; E3: lateral view; E4: medial view; E5: anterior articular view; E6: posterior articular view. CPAP 4944, fragment of costal plate and schematic representation, F1: dorsal view; F2: visceral view. CPAP 5945, pygal plate and schematic representation. G1: dorsal view; G3: medial view. Scale bar: 10 mm. In the schematic representations the sulci and scutes are represented. The ornamentation was not represented. Abbreviations, asr: articular surface for the rib, is: iliac scar, od: oval depression; r: rib; su: sulcus. MA6: marginal scute 6; MA7: marginal scute 7; MA11: marginal scute 11; MA12: marginal scute 12; PL4; pleural scute 4; V4; vertebral scute 4; V5: vertebral scute 5.

concavity due to the oval concavity arranged longitudinally in the medial surface.

Remarks: Specimens CPAP 3040a-c were originally identified by Alarcón-Muñoz et al. (2016) as a single individual of chelonioid turtle, since the fragments were found in situ within an area of less than 50 cm² and some of them fit together, forming larger pieces (the costal plate CPAP 3040b). However, the preservation of the fragments indicates that the pieces were transported. For example, the anterior and posterior borders of the peripheral plate CPAP 3040c were covered in sediment, indicating that CPAP 3040a-c had probably been buried and is preserved as an isolated element. This means that the material cannot be assigned to a single individual with certainty. Virtually all the plates described are ornamented with polygons, which is a feature attributed to some species of Chelidae (Broin, 1987). Interestingly, the peripheral plate CPAP 5945 is larger and more robust compared to the other described plates, which suggests that it belongs to a turtle of considerable size.

5. Discussion

5.1. Taxonomic affinities

The turtle remains described in this work show the presence of at least one freshwater turtle taxon that was part of the vertebrate assemblage in the Río de Las Chinas Valley. With respect to the humeral and femoral fragments, it is only possible to identify them at a suprafamiliar taxonomic level, mainly based on their cross section, despite presenting similarities with the same elements of chelids found in Argentinian Patagonia. In general, isolated chelonian appendicular elements cannot be identified at a generic or specific level. A more exclusive identification requires more complete or more diagnostic elements, such as cervical vertebrae, cranial material, or more complete carapacial remains (for examples see Walker, 1973; Maniel and de la Fuente, 2016; Oriozabala et al., 2020). On the other hand, plate ornamentation allows a more precise identification than isolated appendicular elements.

Most of the shell fragments found in the Río de Las Chinas Valley present strong ornamentation on their dorsal surface formed by irregular polygons, in some cases combined with granulation. The presence of ornamentation has been described in the Triassic genera Proganochelys and Proterochersis and in the Upper Jurassic pan-pleurodiran genus Notoemys, consisting of weakly developed polygons (Lapparent de Broin and Molnar, 2001). Broin (1987) and Lapparent de Broin and Molnar (2001) suggested that ornamentation consisting of dorsal and ventral polygons radiating from a center possibly constitutes a primitive feature in Chelidae, which is present in almost all members of this group. Pan-Chelidae appeared in Gondwana at least as early as the Early Cretaceous and the group is currently represented in South America by 22 living species (Rhodin et al., 2017), making them not only the most geographically widespread, but also the most diverse group of turtles on the continent (Souza, 2005; de la Fuente et al., 2014). Extant chelid species are divided into two groups based on the number of the cervical series (which consists of eight vertebrae) relative to the length of the dorsal series (formed by 10 vertebrae). The different taxa are either considered neck shorter than the thoracic vertebrae, or neck longer than thoracic vertebrae. Representatives of both groups are present in South America and Australasia, the two areas of the family's current distribution (Holley et al., 2019). Although several morphological phylogenies indicate that long-necked chelids form a monophyletic group (e.g.: Gaffney, 1977; Bona and de la Fuente, 2005; Maniel et al., 2018), the phylogenetic value of this character is doubtful since analyses based on molecular data produce a contrasting phylogenetic hypothesis. Molecular phylogenies (e.g.: Seddon et al., 1997; Guillon et al., 2012; Pereira et al., 2017) suggest that the South American and Australasian chelids form two monophyletic groups, in which certain taxa evolved a long neck independently. Additionally, two recent morphological analyses (de la Fuente et al., 2017; Holley et al., 2019) have also failed to recover a monophyletic long-necked group. Recently, Holley et al. (2019) carried out a total-evidence phylogenetic analysis using a combination of morphological and molecular data, whose results coincide with those of the molecular studies. In view of the currently available information, a scenario where the long neck within Chelidae would be shared by taxa with a single common long-necked ancestor seems unlikely.

The oldest known record of a pan-chelids from the Aptian of Argentina (de la Fuente et al., 2011; Krause et al., 2019), in which there is no evidence of having presented ornamentation on the shell as in later pan-chelids (see de la Fuente et al., 2011). The ornamentation becomes more common in the Upper Cretaceous (Lapparent de Broin and Molnar, 2001). The ornamentation constituted by polygons is particularly developed in the genera *Chelodina, Hydromedusa* and *Pseudemydura* and is variably developed in *Phynops* and *Emydura* (Lapparent de Broin and Molnar, 2001). The presence of conspicuous ornamentation formed by polygons and in some cases, granules, and the loose contact between costal and peripheral bones allows the assignation of the shell fragments from the Río de Las Chinas Valley to Chelidae (Gasparini and de la Fuente, 2000; Lapparent de Broin and de la Fuente, 2001).

According to Bona et al. (2009), the general design of the shell ornamentation varies between chelid species. Within the Chelidae, the shell fragments can be referred to the *Hydromedusa-Chelodina* group, based on the pattern of polygonal shapes (Bona and de la Fuente, 2005; de la Fuente, 2007). In the genera *Chelodina* and *Pseudemydura*, the polygons are distributed on the entire surface of the plates, but they tend to be rounded (Lapparent de Broin and Molnar, 2001), whereas the polygons generally have three or more well-defined sides and many of them are markedly elongated on the shell fragments from the Río de Las Chinas Valley.

Bona and de la Fuente (2005), and Bona et al. (2009) indicate that a strong ornamentation constituted by polygons is a diagnostic feature of the genus *Yaminuechelys*, characteristic of the species *Yaminuechelys* gasparinii (de la Fuente et al., 2001) and *Y. maior* (Bona and de la Fuente, 2005). *Yaminuechelys* is a genus of pleurodiran turtles of the Chelidae family whose remains have been found in Argentinian Patagonia, with a temporal range from the Upper Cretaceous to the Paleocene (Maniel and de la Fuente, 2016). *Yaminuechelys gasparinii* was described based on a complete specimen from the upper Campanian–lower Maastrichtian of the Allen Formation (de la Fuente et al., 2001). Another species of the genus, *Yaminuechelys maior*, was described based on remains found in Paleocene strata of the Salamanca Formation (Bona and de la Fuente, 2005). Additionally, de la Fuente et al. (2015) referred the postcranial elements of two specimens found



Fig. 5. Formations of the Neuquén, San Jorge Gulf and Magallanes-Austral basins, with records of *Yaminuechelys* spp. (modified from Fitzgerald et al., 1990, Leanza and Hugo., 2001; Hechem and Strelkov, 2002; Nullo et al., 2006; Carignano and Varela., 2011; Foix et al., 2014; Tunik et al., 2015; Manríquez et al., 2019; George et al., 2020).

in the lower-middle Campanian of the Anacleto Formation, northwest of Argentinean Patagonia to the species *Yaminuechelys* aff. *maior*. (Fig. 5).

Yaminuechelys gasparinii presents a characteristic design especially evident in the costal and neural plates, which consists of dichotomous furrows and polygons distributed over the entire surface of the plates, without opening towards the edges of the plates or towards the sutures. In contrast, the decoration of the plates in Yaminuechelys maior consists of thick and deep lines that give rise to large and small polyhedral shapes that are well defined in the central region of the plates, but are open or combine with lines near the edges and close to sutures (Bona et al., 2009). While there is a combination of large and small polygons in the ornamentation pattern of Yaminuechelys maior, in Yaminuechelys gasparinii the size of the polygons is relatively uniform (Bona and de la Fuente, 2005). The ornamentation observed in the isolated chelid shell fragments of the Río de Las Chinas Valley resembles that of Yaminuechelys gasparinii, since no open polygons are observed towards the edges or near sutures. Additionally, as in Yaminuechelys gasparinii, the polygons are relatively uniform in size. A third species of the genus was recently described, which shares the same ornamentation pattern of the other two species. The taxon was named Yaminuechelys sulcipeculiaris by Oriozabala et al. (2020) based on partial shells, vertebrae and appendicular elements from the La Colonia Formation (Campanian-Maastrichtian), in the Chubut Province of Argentina. A part of the material on which this new species was erected had been preliminarily described by Gasparini et al. (2015), who referred it to Yaminuechelys aff. Y. gasparinii.

There are at least two other features on the plates that suggest affinity with *Yaminuechelys*. One of them is the shape of the peripheral plates of the bridge. The probable seventh right peripheral plate CPAP 3040c is narrow and not expanded laterally, but is expanded posteriorly, which is described in *Yaminuechelys maior* and *Hydromedusa tectifera* (Bona et al., 2009).

Due to the incomplete preservation of the suprapygal CPAP 3040a plate, it was not possible to verify if this plate had a sub-pentagonal contour, as described in *Yaminuechelys gasparinii* (de la Fuente et al., 2001), *Yaminuechelys sulcipeculiaris* (Oriozabala et al., 2020), and in an incomplete shell referred to *Yaminuechelys* cf. gasparinii by de la Fuente et al. (2010). However, as in the suprapygal plate of *Yaminuechelys sulcipeculiaris*, CPAP 3040a bears a longitudinal midline sulcus that marks the limit between both marginal scutes 12, and a horizontal sulcus that marks the limit between the vertebral scute 5 and the marginal scutes 12. Oriozabala et al. (2020) mention that the location of the sulcus between the vertebral scute 5 and the marginal scutes 12

varies between different species of *Yaminuechelys*. In *Y. maior* and in *Y.* aff. *maior*, this sulcus is arranged in the pygal bone (Oriozabala et al., 2020) and the same has been described in *Y. gasparinii* and *Y. cf. gasparinii* (de la Fuente et al., 2001, 2010). In contrast, in *Yaminuechelys sulcipeculiaris* this sulcus does not cross through the pygal bone, but is arranged in the suprapygal bone, so it was considered a diagnostic feature of this species (Oriozabala et al., 2020). The fact that this trait is present in the Chilean specimen suggests a greater affinity for *Y. sulcipeculiaris* than for the other species of the genus *Yaminuechelys*.

Although the ornamentation pattern and morphology described in the isolated plates agree with what has been described for *Yaminuechelys*, it is not possible to assign them with certainty to this genus, since it is not possible to corroborate the presence of several of the diagnostic characters related to the morphology of the carapace and the cervical vertebrae (de la Fuente et al., 2001, 2015; Bona and de la Fuente, 2005; Bona et al., 2009). Therefore, the turtle remains from the Río de Las Chinas Valley are only conferred to *Yaminuechelys*, until the recovery of additional diagnostic material allows definitive identification.

The deposits of the Río de Las Chinas Valley in which the turtle remains were found date from the upper Campanian to the lower Maastrichtian (SP-1 and SP-17 sections), with U-Pb maximum depositional age between 78 ± 1.8 Ma and 71.7 ± 1.2 Ma (Schwartz et al., 2016; Gutiérrez et al., 2017; Manríquez et al., 2019). This age makes cf. *Yaminuechelys* sp. from the Río de Las Chinas Valley contemporary with *Yaminuechelys gasparinii*, whose remains date back to the lower Campanian-Maastrichtian interval (de la Fuente et al., 2001), with *Yaminuechelys* aff. *maior*, described from the lower–middle Campanian of the Anacleto Formation (de la Fuente et al., 2015), and with *Yaminuechelys* sulcipeculiaris of Campanian-Maastrichtian age (Oriozabala et al., 2020).

Isolated fossil shell fragments referred to the genus *Yaminuechelys* based on the type of ornamentation have been found in different Cretaceous–Paleogene outcrops in Argentinian Patagonia (Maniel and de la Fuente, 2016). de la Fuente et al. (2001) list several localities in the provinces of Mendoza, Río Negro, Chubut and Neuquén where isolated plates with preserved ornamentation have been found, which can be referred to *Yaminuechelys* or aff. *Yaminuechelys* spp. (see Fig. 6 and figures and its descriptions in Staesche, 1929; Broin and de la Fuente, 1993; Alcober et al., 1995; Bona et al., 1998; Heredia and Salgado, 1999; Leanza and Hugo, 1999; Gasparini and de la Fuente, 2000). González Riga (1999) recognizes several ornate isolated plates belonging to chelids from the Loncoche Formation (Upper Cretaceous), Mendoza Province. Previtera and González Riga (2008) mention the

finding of a pygal and two anterior peripheral plates with strong ornamentation formed by irregular polygons. Based on this ornamentation and their thickness, these plates were assigned by these authors to cf. Yaminuechelys. At the same time, Previtera and González-Riga (2008) consider a peripheral plate described by González Riga (1999) as comparable to the chelid plates that they assign to cf. Yaminuechelys. Gasparini and de la Fuente (2000) identify several shell fragments ornamented with small irregular polygons found in outcrops of the La Colonia Formation (Upper Cretaceous), north of the Chubut Province. Bona et al. (2009) refer several shell fragments to the species Yaminuechelys cf. major collected in Danian sediments of the Roca Formation (Río Negro Province), which show the same ornamentation pattern as those from the La Colonia Formation. Isolated shell fragments found in outcrops of the Salamanca Formation (Lower Paleocene), in Punta Peligro, were assigned at first to Osteopygis sculptus and ?Najadochelys maior by Staesche (1929) and later reassigned to Yaminuechelys maior by Bona (2004) and Bona and de la Fuente (2005).

Most of these isolated plates were referred to Yaminuechelys based on their morphology and ornamentation. However, it is possible to use other tools that help identify isolated turtle plates. Jannello et al. (2016) studied the histology of isolated plaques referred to Yaminuechelys. These authors found that the pattern of sculpturing of Yaminuechelys differs from that reported in other ornamented turtles, which could constitute a feature derived from this genus, and that the presence of resorption lines associated with the maintenance of the ornamentation is a particular feature reported only in Yaminuechelys. These authors propose that these traits could serve as a taxonomic signal for Yaminuechelys. Therefore, histological analyzes can help to identify more accurately isolated plaques referred to Yaminuechelys based on their external morphology.

5.2. Paleoenvironment

Extant members of the Chelidae family often inhabit freshwater systems such as lakes, rivers, streams and lagoons in both South America and Australasia (Pritchard and Trebbau, 1984; Bona et al., 2009). A vast majority of fossil chelids appear to have inhabited freshwater environments, since their remains are usually found in sedimentary strata of continental origin, and the morphology of their shells and limbs resembles that of extant chelids (Bona and de la Fuente, 2005; de la Fuente, 2007). Currently, genera such as Phrynops preferentially inhabit ponds, marshes, lagoons and slow flowing to fast flowing streams. Some species of Phrynops (e.g. P. hilarii) share habitat with the chelid Hydromedusa tectifera, especially in La Plata River Basin in Argentina, Brazil, Paraguay and Uruguay (de la Fuente, 1986; Derocco et al., 2005). Hydromedusa tectifera is a chelid considered a sister taxon of Yaminuechelys (Bona and de la Fuente, 2005) and is a typical inhabitant of freshwater systems (Iverson, 1992; Cabrera, 1998; de la Fuente et al., 2014). However, unlike other extant chelids, H. tectifera also lives in intertidal estuaries and seems to tolerate brackish waters (Frazer, 1986; de la Fuente, 1999). As these extant chelids, Yaminuechelys lived in freshwater environments (de la Fuente et al., 2001, 2015; Bona and de la Fuente, 2005). Yaminuechelys aff. maior, Yaminuechelys gasparinii and Yaminuechelys cf. gasparinii were found in sediments deposited in freshwater environments (Filippi et al., 2011; Filippi and Garrido, 2012; de la Fuente et al., 2010; Oriozabala et al., 2020). The remains of Y. maior are typically found in sediments deposited in intertidal environments (Bona et al., 1998; Bona and de la Fuente, 2005), which indicates that this species may have tolerated similar environmental conditions as H. tectifera (Maniel and de la Fuente, 2016). As in the case of Y. maior, the deposits in which the remains of Y. sulcipeculiaris were discovered have a marine influence (Gasparini et al., 2015; Oriozabala et al., 2020), suggesting that this species could also have tolerated brackish water. Finally, histological studies of shell fragments referred to the genus Yaminuechelys have also reinforced the interpretation of this genus as a freshwater turtle (Jannello et al., 2016).

The presence of fossil bones of anurans (Suazo Lara et al., 2017, 2018) and dinosaurs (Kaluza et al., 2018) in the same deposits in which turtle remains are preserved suggests that cf. *Yaminuechelys* sp. lived in a freshwater system. This paleoenvironmental interpretation agrees with the sedimentological evidence, which indicates that the depositional environment was continental, associated to meandering fluvial deposits with floodplain facies (Schwartz et al., 2016; Manríquez et al., 2019).

5.3. Geographic distribution of Chelidae

Extant representatives of Chelidae inhabit freshwater environments of southern Gondwana, specifically in South America and Australasia (Pritchard and Trebbau, 1984; Broin, 1987; Broin and de la Fuente, 1993; Iverson, 1992; Bona et al., 2009). The oldest fossil record of this pan-chelid lineage corresponds to Prochelidella cerrobarcinae, from the Lower Cretaceous (Aptian) of Argentina (de la Fuente et al., 2011; Krause et al., 2019). On the other hand, the oldest records of pan-chelid turtles in Australasia date back to the Upper Cretaceous of Australia (Gaffney, 1981; Lapparent de Broin and Molnar, 2001; Smith, 2010; Bell et al., 2019a, 2019b) and the Oligocene of Tasmania (Warren, 1969), where Chelidae are still present to this day (Gasparini and de la Fuente, 2000). Holley et al. (2019) mention that the fragmentary nature of the Australian specimen described by Smith (2010), together with the absence of synapomorphies did not allow its inclusion in a phylogenetic analysis, making it difficult to carry out evolutionary and paleobiogeographic interpretations concerning pan-chelids. These authors discuss the main phylogenetic positions that Upper Cretaceous Australian pan-chelids could have had, and their possible impact on the evolutionary relationships of pan-chelids. On the one hand, there is the possibility that Australian pan-chelids are stem-chelids, and that in this case these pan-chelids would be part of a monophyletic group that currently consists only of South American species, or that Australian pan-chelids and stem-chelids are successive paraphyletic groups with respect to crown-chelids. According to Holley et al. (2019) these hypotheses could affect the position of the basal nodes, taking the origin of Pan-Chelidae and Chelidae further back. As an alternative, Holley et al. (2019) mention the possibility that the Australian pan-chelids of the Upper Cretaceous are crown-chelids. In this case, Holley et al. (2019) mention two possible phylogenetic positions: that they are located in the stem of the Australasian clade, or that they are located in the stem of the South American clade. According to these authors, in these cases, there could be an impact at the time of origin in the Australasian, South American, and Chelidae clades.

The current distribution of Chelidae in South America, Australia and New Guinea indicates that the group probably originated in southern Gondwana (Pritchard, 1984; Pritchard and Trebbau, 1984; Broin and de la Fuente, 1993; Holley et al., 2019). Currently, the Chelidae family has a wide distribution in South America, only being absent in Chile. Parsimony analysis of endemism carried out by Ippi and Flores (2001) establishes two endemic areas, one that covers the Amazonian biogeographic province (Cabrera and Willink, 1980), in which species such as Chelus fimbriata, Mesoclemmys dhali, M. gibbus, M. nasutus, M. raniceps, M. zuliae and Platemys platycephala are present and a second area that partially covers Paraná and the Pampean and Atlantic provinces (Cabrera and Willink, 1980), where species such as Phrynops hilarii, P. williamsi and Hydromedusa tectifera are distributed. This analysis suggests that the pattern of areas of endemism is not random, but is a probable consequence of historical and ecological factors that affected the biota of South America (Ippi and Flores, 2001). Vlachos et al. (2018) mention that some chelid clades that survived the mass extinction in the K-Pg boundary established the bases for the current diversity of this family in South America, whose members dispersed in South America mainly during the Eocene and Neogene, until reaching their current distributions. Recent studies have shown that for some

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Chelidae species associated with the second area of endemism, such as *P. hilarii* and *H. tectifera*, the southern distribution limit has reached higher latitudes principally as a consequence of recent climatic alterations (Derocco et al., 2005; Guerrero and Agnolin, 2016; Lerzo et al., 2019).

Until now, the Cretaceous record of Chelidae was restricted to findings in Argentinean Patagonia, which range from the Aptian to the Maastrichtian (Maniel and de la Fuente, 2016; Vlachos et al., 2018) and from Cenomanian of Australia (Smith, 2010; Bell et al., 2019a,2019b). Chelids are the dominant component in the chelonian faunas recorded in continental Cretaceous outcrops of Patagonia, whose main diversity peaks were in the Aptian-Albian (Lower Cretaceous) and in the Coniacian and Maastrichtian (Upper Cretaceous) (Gasparini and de la Fuente, 2000; Maniel and de la Fuente, 2016; Vlachos et al., 2018).

The southernmost Mesozoic occurrence of Chelidae known so far was reported by Goin et al. (2002) in outcrops of the Mata Amarilla Formation (Upper Cretaceous, Coniacian) and by Novas et al. (2019) in Chorrillo Formation (upper Campanian-lower Maastrichtian), both in Santa Cruz Province, Argentina. Goin et al. (2002) mention the finding of shell plates belonging to at least two species of chelids, with affinity to the *Phrynops* and *Chelus* groups. On the other the chelid material reported by Novas et al. (2019) consist on fragmentary shell plates of indeterminate taxonomic affinities. The finding of shell fragments of cf. *Yaminuechelys* sp. in the Río de Las Chinas Valley and the chelid turtles from Chorrillo Formation, Santa Cruz Province, Argentina (Novas et al., 2019) extends the distribution of the Chelidae family farther south and at the same time constitutes the southernmost report of the genus.

Although the available evidence is still scarce, it seems that chelids represent an important component of the Upper Cretaceous continental turtle fauna of the southwestern margin of Gondwana, mainly in the Coniacian and Maastrichtian, judging by the relative abundance of their remains in strata of that age in Argentina and Chile (Maniel and de la Fuente, 2016; Vlachos et al., 2018). On the other hand, the presence of the genus *Yaminuechelys* in Upper Cretaceous deposits of Argentinean Patagonia and of cf. *Yaminuechelys* sp. in the Southern Magallanes-Austral Basin of Chilean Patagonia constitutes evidence for the presence of similar components in the freshwater turtle faunas of the two regions (Fig. 6).

5.4. Other records of continental turtles in Chile

The record of continental turtles in Chile is very scarce and fragmentary, which makes generic and specific determinations difficult (Otero, 2015). The first record was published by Casamiquela et al. (1969) from Pichasca, Coquimbo Region in Northern Chile. These remains were found in outcrops of the Estratos de Quebrada La Totora, which, according to stratigraphic correlations and radiometric dates obtained from underlying and overlying units, can be constrained to the upper Albian–Cenomanian (Pineda and Emparán, 2006; Pineda and Calderón, 2008). The material corresponds to two peripheral plates, a fragment of plastron and several fragments of plates of indeterminate position which lack diagnostic features that would allow their identification (Otero, 2015). These turtle remains were found associated with sauropod bones (Casamiquela et al., 1969) in strata that represent debris flows in a floodplain environment (Otero, 2015).

Another finding was reported by Otero et al. (2012) in middle-late Eocene strata (Malumián and Caramés, 1997) of the Río Turbio Formation (Feruglio, 1938; *sensu lato.*; emend. Hünicken, 1955; *sensu* Malumián and Caramés, 1997), located in Sierra Dorotea, Magallanes Region. The material consists of plastron and xifiplastron fragments, as well as other plates of indeterminate position. According to the authors, the elements do not possess enough information that would allow their more precise identification, although they suggest that the remains could correspond to continental turtles, an interpretation based on the robustness of the elements. An important detail is that Otero et al. (2012) described ornamentation in the plates, composed of polygons of variable shape and regular size, that are oriented mediodistally. These remains were attributed to Chelidae indet. in Sterli et al. (2015).

6. Conclusions

We describe the presence of freshwater pleurodiran turtles from the Upper Cretaceous of the Magallanes (=Austral) Basin. The ornamentation of the studied shell fragments and the loose connections between costal and peripheral bones allows their referral to Chelidae. It consists of three or more sided polygons that are distributed along the entire surface of the plates, which allows us to refer the fragments to the cf. *Yaminuechelys* sp. Until now, this genus had only been recorded in the Upper Cretaceous–Paleocene interval of Argentinean Patagonia. The presence of chelids, together with other faunistic components such as anurans and dinosaurs, suggests that the strata in which these remains were preserved had been deposited in a freshwater (meandering fluvial) environment, an interpretation which is consistent with the sedimentological evidence. The material reported in this work represents the southernmost record of *Yaminuechelys* and the Chelidae family to date.

Research in the Río de Las Chinas Valley is beginning to reveal a great biological diversity, both in terms of flora and fauna. This information is valuable in understanding the evolution and distribution of the biota that existed in the southernmost regions of South America at the end of the Mesozoic, as well as the distribution of certain extant biotic components in the land masses that formerly constituted Gondwana.

Credit author statement

Jhonatan Alarcón-Muñoz: investigation, formal analysis, conceptualization, methodology, software, resources, writing - review & Editing, Sergio Soto-Acuña: conceptualization, methodology, software, resources, validation, supervision, writing - review & Editing, Leslie M. E. Manríquez: validation, software, formal analysis, investigation, writing - review & Editing, Roy A. Fernández: software, investigation, writing - review & editing, Dániel Bajor: investigation, writing - review & editing, Validation, Juan Pablo Guevara: investigation, review & editing, Felipe Suazo Lara: investigation, writing - review & editing, Marcelo A. Leppe: validation, investigation, supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Fig. 6. Schematic extension and distribution of Patagonian basins in South America (modified from Biddle et al., 1986; Náñez and Malumián, 2008; Scasso et al., 2012). Upper Cretaceous and Paleogene localities with findings referred to *Yaminuechelys* are represented (see Staesche, 1929; Broin and de la Fuente, 1993; Heredia and Salgado, 1999; Leanza and Hugo, 1999; González Riga, 1999; Gasparini and de la Fuente et al. 2000; de la Fuente et al., 2001, 2010; 2015; Bona and de la Fuente, 2005; Bona et al., 2010; Previtera and González Riga, 2008; Gasparini et al., 2015; Maniel and de la Fuente, 2016; Novas et al., 2019; Oriozabala et al., 2020). 1: Ranquil Có, 2: Calmu Có, 3: Puesto Norambuena, 4: Puesto La Rinconada, 5: Cañadón Amarillo, 6: Lago Pelegrini-Cinco Saltos, 7: Sierra Portezuelo, 8: Valle de La Luna Rojo, 9: Paso Córdoba, 10: Cerro Blanco, 11: El Abra, 12: Laguna Cari Laufquén Chica, 13: Los Alamitos, 14: Cerro Bayo, 15: Cerro Bosta, 16: La Colonia, 17: Cerro Hansen, 18: Punta Peligro, 19: La Anita, 20: Río de Las Chinas Valley.

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