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A GIANT AMONG GIANTS: A NEW LAND TORTOISE FROM THE PLEISTOCENE OF THE ARGENTINE PAMPAS

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Abstract. Gigantism in terrestrial tortoises occurred frequently and convergently in different lineages of Testudinidae. Despite the fact that giant forms were geographically and stratigraphically widespread in South America, Pleistocene members are still very poorly known, most of them represented by fragmentary and unassociated materials. The aim of the present contribution is to describe *Chelonoidis pucara* n. sp., a new species coming from Upper Pleistocene beds of northern Buenos Aires province, Argentina. The new species is known by the anterior half of a plastron having a unique combination of apomorphic and plesiomorphic features. It is very large-sized (estimated carapace length about 1.7-1.8 meters), rendering it as the largest testudinid from South America, and placing it among the "supergigantic" tortoise phenotype. Like other supergigantic tortoises (which were up to now exclusively known in the Old World), the new species shows enlarged epiplastral projections, probably related to competition with other males. The ecological role of these "supergigantic" tortoises is also briefly discussed.

INTRODUCTION

The occurrence of giant tortoises in the Pleistocene of the Pampean Region was well known to 19th-century naturalists (e.g., Gervais 1867, 1877; Ameghino 1881, 1898; Moreno 1889). Since these first discoveries, remains of these giant Pleistocene tortoises were found in several fossiliferous sites in Argentina (see summary in de la Fuente et al. 2018; Fig. 1A). However, in the relatively well-prospected Buenos Aires province, despite of intensive fieldwork along more than a century, giant Pleistocene tortoises are known only from a couple of isolated plates from few localities (Lapparent de Broin & de la Fuente 1993; Pardiñas et al. 1996; de la Fuente 1999; Agnolín 2004, 2021; de la Fuente et al. 2018; Agnolín et al. 2024).

Despite the fact that these giant forms were geographically (and also probably stratigraphically) widespread throughout the province, and that giant carapaces should have had a high preservation potential, the specimens known up to the date are always fragmentary and dissociated, which has pre-

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cluded the identification, even at the generic level, of the giant tortoises that inhabited the Argentine Pampas.

During the revision of the paleontological collections at the Museo "Legado del Salado" in Junín City, Buenos Aires province, the authors found the anterior half of the plastron of a giant tortoise from Upper Pleistocene beds. The specimen is informative enough to recognize it as a new species and to confirm the generic affinities of this elusive chelonian. The aim of this contribution is to describe a new species of giant terrestrial tortoise based on this specimen, and to provide a brief overview of the Pleistocene record of giant tortoises in Argentina.

MATERIAL AND METHODS

References for terminology of plates and scutes follow the nomenclature of de la Fuente (1994, 1997a), whereas character-states of morphological traits follow those employed by Lapparent de Broin et al. (2006b). Drawings and photographs were based on the methodology of Zacarías et al. (2013, 2014). Scutes are marked in the drawings by a solid and continuous line, whereas osseous plates are marked by an irregularly, interdigitated line. For convenience, following Lapparent de Broin (1977), the first letter of the name of the osseous plates is capitalized, whereas the name of the keratinous scales is not.

We follow the nomenclature and taxonomy employed by Rhodin et al. (2015) with the modifications carried out by de la Fuente et al. (2018) and Joyce et al. (2021).

For continental South America, we recognize three extant species: the closely related *Chelonoidis denticulata* (Linnaeus, 1766) and *C. carbonaria* (Spix, 1824) (which form the *C. carbonaria* complex; Auffenberg, 1971), from wooded areas of northern and central South America, and the southern form *C. chilensis* (Cabrera 1998; Richard 1999) (see Fig. 1A). The number of species included within the *C. chilensis* clade is under debate, ranging from one to three different taxa; for the sake of simplicity, we recognize a single species, *C. chilensis*, following Fritz et al. (2012).

Locality and horizon

The specimen described here is housed in the Museo Legado del Salado (MLS), in Junín City, Buenos Aires province, Argentina. It was found in the Manantial de las Piedras stream, or Ascensión stream (see Fig. 1B), by Facundo Maranesi (a resident of the town of Ascensión) in January 2012. The exact location of the discovery was in a cliff of this stream (34°8'28.20"S, 61°2'12.92"W, Rojas department, Buenos Aires province, Argentina), 2.7 km northwest of the small village of La Beba, and 11 km northern of small town Ascensión (see Fig. 1C). This stream is a tributary of the Rojas River, which is part of the Arrecifes River basin. The stratigraphic unit containing the fossil is made up of greenish sediments, consisting of fine sand and clayey silt (Toledo et al. 2014). The fossil described was found at the top of this level, where rough calcretes appear, about 50 cm below the surface level. This level has been described in the surrounding basins of the Salto-Arrecifes, Salado, Luján, and Areco rivers, where it is referred to as the "Upper Green Luján Sequence" (see Fig. 1D-E), and is partially correlated to the Guerrero Member of the Luján Formation (Toledo 2010, 2011, 2017). In the valley of the Salto, Arrecifes, Areco and Luján rivers, ages between 16.5 ka and 13 ka were obtained for this

Fig. 1 - Locality and stratigraphical position that yielded *Chelonoidis pucara* nov. sp.

A) The map at the left shows the distribution of *C. chilensis* and *C. carbonaria* in Argentina (area of sympatry shaded in dark gray), with localities that yielded Pleistocene remains of terrestrial tortoises (see de la Fuente et al. 2018). 1, possible *Chelonoidis petrocellii* (cited as *Chelonoidis* cf. *C. chilensis* by de la Fuente 1997a, and *Chelonoidis* sp. by Agnolín 2004) Upper Pleistocene, Lujanian Stage, San Lorenzo, Santa Fé Province; 2, *Chelonoidis* sp. (see de la Fuente 1997a; first mention by Gervais 1867, 1877), Upper Pleistocene, Lujanian Stage, Carcarañá river, Santa Fé Province; 3, giant *Chelonoidis* sp. Upper Pleistocene, Lujanian Stage; Quitilipi Department, Chaco Province (Zacarías et al. 2011); 4, giant *Chelonoidis* sp. Upper Pleistocene, Lujanian Stage; Dique Los Quiroga, Santiago del Estero province (Agnolín 2004); 5, *Chelonoidis lutzae*, Upper Pleistocene, Lujanian Stage, Bella Vista Department, Corrientes Province (Noriega et al. 2000; Zacarías et al. 2013, 2014); 6, *Chelonoidis* sp. (Zacarías & Luna 2013; Zacarías et al. 2014), here regarded as *C. lutzae*; Upper Pleistocene, Lujanian Stage, Lavalle Department, Corrientes Province; 7, *Chelonoidis lutzae* (cited as indeterminates Testudinidae or *Chelonoidis* sp. by Broin and de la Fuente 1993; Noriega et al. 2000), Upper Pleistocene, Lujanian Stage, Arroyo Perucho Verna y Cañada Las Achiras, Entre Ríos Province; 8, *Chelonoidis petrocellii* Middle-Upper Pleistocene, Bonaerian Stage, Arroyo Frías, Buenos Aires Province (Agnolín 2021); 9, giant *Chelonoidis* sp., Lower-Middle Pleistocene, Ensenadan Stage, Olivos, Buenos Aires Province (Broin & de la Fuente 1993; Agnolín 2004); 10, giant tortoise, Pleistocene, Luján, Buenos Aires province (Moreno 1889); 11, giant tortoise, Pleistocene, Vitel creek (Moreno 1889); 12, *Chelonoidis pucara* (present contribution), Upper Pleistocene, Lujanian Stage, Manantial de las Piedras stream, Buenos Aires Province; 13, *Chelonoidis petrocellii* (cited as *Chelonoidis* sp. by Bogan et al. 2010), Upper Pleistocene, Lujanian Stage, Salto river, Buenos Aires Province; 14, giant *Chelonoidis* sp. (personal observation), Upper Pleistocene, Lujanian Stage, Laguna de Lobos, Buenos Aires Province; 15, giant *Chelonoidis* sp. (Agnolín et al. 2024), Middle-Upper Pleistocene, Bonaerian Stage, Punta Médanos, Cabo de San Antonio, Buenos Aires Province; 16, giant *Chelonoidis* sp. (Pardiñas et al. 1996), Upper Pleistocene, Lujanian Stage, Quequén Salado river, Buenos Aires Province; 17, giant *Chelonoidis* sp. (cited as Testudinidae indet. by Broin & de la Fuente 1993), Upper Pleistocene, Lujanian stage, Playa del Barco, Buenos Aires Province; 18, small-sized *Chelonoidis* sp., Lower-Middle Pleistocene, Ensenadan Stage, San Justo Department, Córdoba Province (Zacarías & Luna 2013); 19, *Chelonoidis lutzae* (cited as *Chelonoidis denticulata* by Manzano et al. 2009) Upper Pleistocene, Lujanian stage, Diamante City, Entre Ríos Province.

B) Map showing the Arrecifes river basin, with detail (red square) of the location of the Manantial de las Piedras stream.

C) Satellite image of the stream sector where the discovery was made.

D) Part of the plastron in situ.

E) Outcrop photograph of the Manantial de las Piedras stream with details of the stratigraphical levels of the Lujan Formation; LP, La Plata sequence; RL, Red Lujan sequence; UGL, Upper Green Lujan sequence (Bogan et al. 2008; Toledo 2010, 2011, 2017; Toledo et al. 2014; Toledo & Schewenninger 2014). The dashed lines indicate calcretes that can be correlated with the Puesto Callejón Viejo Paleosol.

F) Same levels as in D, but at the exact location of the discovery. The discoverer can be seen extracting the turtle.

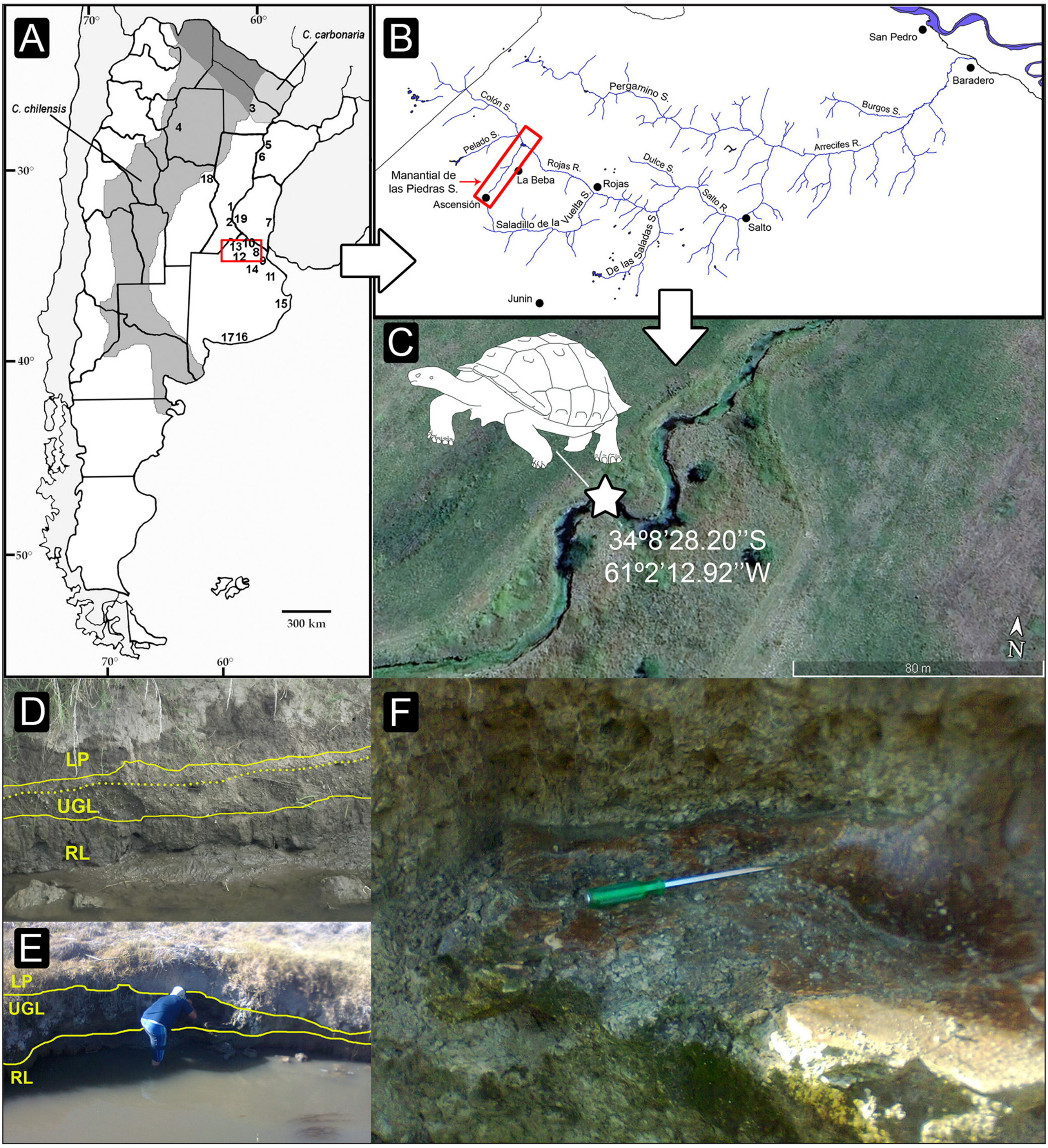

Fig. 1

unit, indicating that these levels correspond to the end of the Lujanian Stage (Upper Pleistocene; Bogan et al. 2008; Toledo et al. 2014; Toledo & Schewenninger 2014). Remains of *Glyptodon* sp., *Equus (Amerhippus)* sp. and indeterminate Lamini were found at the same level and locality. This level overlies reddish-brown loess levels, corresponding to the "Red Lujan Sequence", where ages ranging from 30 to 17.5 ka have been obtained in other localities of these basins (Toledo et al. 2014; Toledo & Schewenninger 2014; Toledo 2017). At these levels, remains of *Notiomastodon* and *Macrauchenia* were found in the Ascensión stream. Blasi et al. (2016, 2020), assigned this level to the MIS3. In this way, the levels that yielded the tortoise described here are younger than MIS3, corresponding to the end of the Lujanian Stage (< 20 ka).

Systematic Paleontology

Order **Testudines** Batsch, 1788
Suborder **Cryptodira** Cope, 1868
(*sensu* Joyce et al., 2021)
Family Testudinidae Batsch, 1788
(*sensu* Joyce et al., 2021)
Genus *Chelonoidis* Fitzinger, 1835
(*sensu* Joyce et al., 2021)

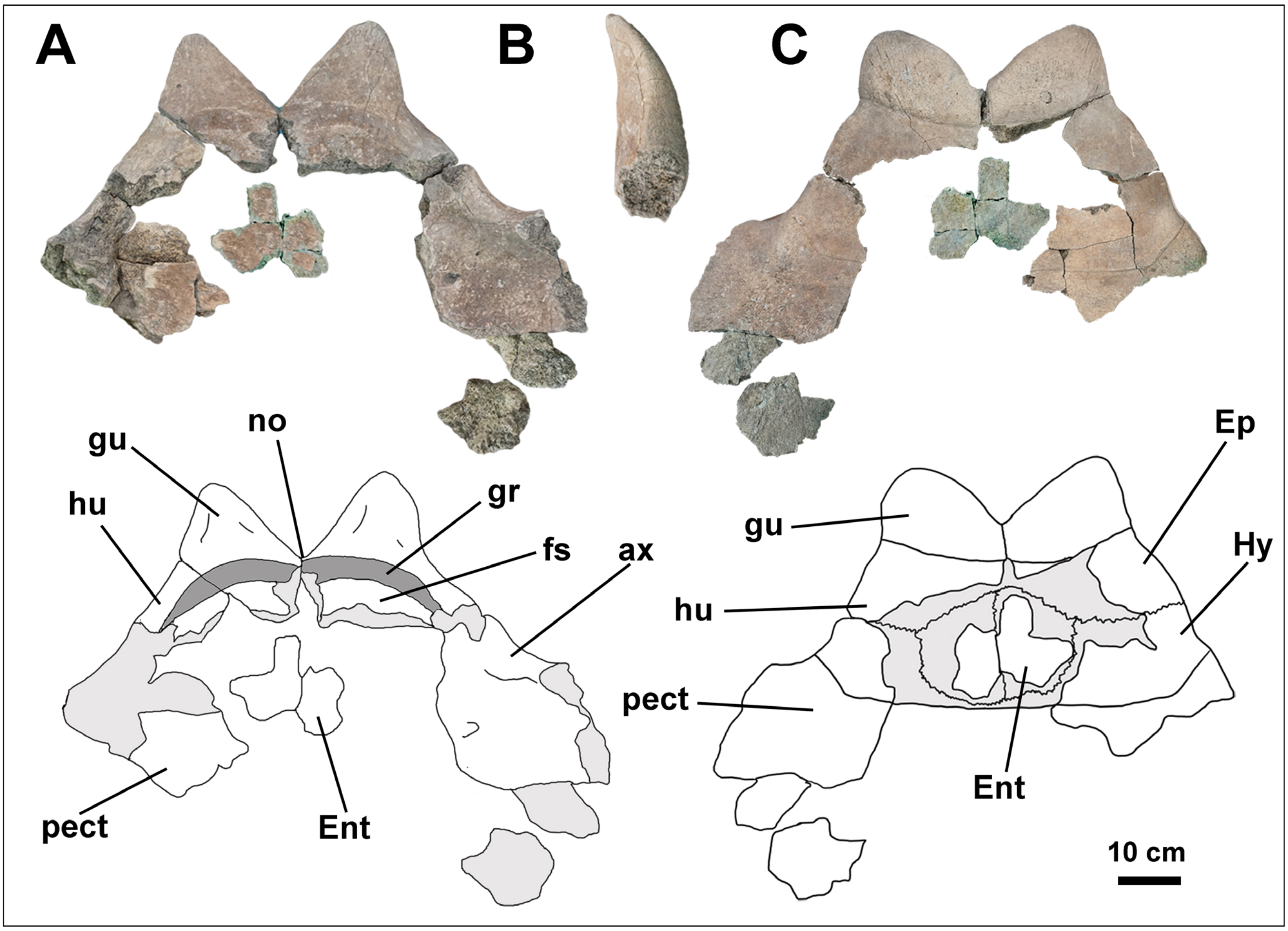

Fig. 2 - *Chelonoidis pucara* nov. sp. (MLS 227) anterior half of a plastron in A) visceral; and C) ventral views; B) lateral view of epiplastral projection and humeral scute, showing the absence of epiplastral lip and pocket.Abbreviations: ax, axillary buttress; fs, flattened surface below the epiplatron, showing the absente of epiplastral lip and pocket; gr, transverse shallow groove delimiting the posterior margin of the epiplastral eminence. Plates: Ent, entoplastron; Ep, epiplastron; Hy, hyoplastron. Scutes: gu, gular scute; hu, humeral scute; no, epiplastral notch; pct, pectoral scute. Scale bar: 10 cm.

Type species: *Testudo boiei* Wagler, 1830 = *Testudo carbonaria* Spix, 1824.

Chelonoidis pucara nov. sp.

Fig. 2

Etymology: The specific epithet comes from the Quechua adjective *pucara* o *pukara*, which means "fortification", alluding to the giant and very thick carapace.

Holotype: MLS 227, anterior half of the plastron of an adult male individual.

Type horizon: Upper Green Lujan Sequence, Lujan Formation (upper Lujanian Stage, Upper Pleistocene; see Toledo 2010, 2011, 2017, Toledo et al. 2014; Toledo & Schewenninger 2014).

Type locality: Manantial de las Piedras stream (or Ascension stream), 34°8'28.20"S, 61°2'12.92"W, Rojas department, Buenos Aires province, Argentina.

Diagnosis: Very large and thick-shelled terrestrial tortoise (estimated carapace length 1.7-1.8 meters long) lacking a gular pocket and epiplastral lip, with a strong "V" shaped and deeply divergent horn-like epiplastral projections; large entoplastron with straight midline suture; pectoral scute anteroposteriorly long, representing more than half the anteroposterior length of the humeral scute, and lateral margin of the humeral scute slightly sigmoidal.

Description

The plastron is represented by an incomplete anterior lobe including epiplastron, hyoplastron and a partial entoplastron. The preserved part of the plastron indicates that it was relatively long and narrow (as inferred from the preserved portion) suggesting that the carapace was cylindroid. The margins of the plastron are notably thick and form a strong buttress.

The epiplastron is robust and strongly dorsoventrally thickened (71.52 mm of maximum thickness at their base). The epiplastral lobes are strongly anteriorly extended, are prominent, and transversely wide, forming horn-like anterodorsally oriented projections. Dorsal and ventral margins of the lobes are notably convex, and the ventral surface lacks ridges or crests. An epiplastral notch is present, deep and subtriangular in contour. In visceral view the gular pocket is absent and there are no epiplastral lips. The epiplastral projections are posteriorly delimited by a shallow groove having a smooth surface. Posteriorly, there exists a gently concave surface that extends up to the entoplastron level.

The epiplastron is relatively short, being much shorter anteroposteriorly than the hyoplastron. The margins of the plastron between the levels of the gular and humeral scutes are gently convex and do not form a shoulder.

The entoplastron is represented by fragments. It is much thinner than the margins of the plastron. The midline suture is nearly straight.

The hyoplastron is notably thick, especially at the level of the axillary buttress. The latter is anteroposteriorly extended and contacts the dorsal caparace at a very low angle and forming very wide and shallow axillary notches. This suggests a wide anterior opening of the shell. The posterolateral surface of the hyoplastron shows is highly rugose, ornamented with deep pits, rugosities, and ridges.

The sulci separating the scutes are deep, well-defined, and not located on raised ridges. The gular scutes are subtriangular in shape and are posteriorly delimited by a gently convex gular groove. The gulars do not contact the anterior margin of the entoplastron. The gulo-humeral sulcus does not cross the entoplastron. The humeral scute shows a narrow overlap onto the hyoplastron in visceral view. The pectoral scute is anteroposteriorly extended is nearly as long (or even a little bit longer) than the humeral scute.

Measurements. Maximum plastral width at the base of the anterior lobe (at level of axillary notch): 60 cm; maximum transverse width at the base of the epiplastral horns: 36.92 cm; maximum dorsoventral thickness at the base of the epiplastral horn: 71.52 mm; maximum dorsoventral thickness of plastral margin at mid-length of the humeral scute: 49.23 mm; maximum dorsoventral thickness of entoplastron: 24.52 mm.

Comparisons

In spite of the incomplete nature of the only known specimen of *C. pucara* nov. sp., it preserves the anterior half of the plastron, including the epiplastral area, one of the most anatomically informative parts of the testudinid carapace (Auffenberg 1971; Broin 1977, 2003; Claude & Tong 2004; Lapparent de Broin 2002; Lapparent de Broin et al. 2006a,b; Pérez-García & Vlachos 2014; Pérez-García et al. 2016; Vlachos & Rabi 2018; Vlachos et al. 2020). This allows the recognition of the distinctiveness of the new species, as well as comparison with extant and extinct tortoises.

As mentioned above, all extant South American testudinids have been hypothesized to form a monophyletic clade referred to as *Chelonoidis* since the 1950s (Williams 1950). Historically, all South American fossil testudinids have been referred to *Chelonoidis*, mainly on geographical grounds (Auffenberg 1971). However, given the large morphological variability within this genus, it has been difficult to find characters that allow the referral of fossil remains to this taxon (Joyce & Faux 2008). Nevertheless, a combination of characters allows to refer MLS 227 to the genus *Chelonoidis*, including: short gular scutes, gular scutes posteriorly rounded, not forming a triangle, lack of an epiplastral lip, pocket, and backward thickening (these are present in some members of the genus), narrow gular and humeral scutes overlap in visceral view, perpendicularly oriented humero-pectoral sulcus, and pectoral scutes that are narrower medially but expanded distally (Claude & Tong 2004; Lapparent de Broin et al. 2006a,b; Vlachos & Rabi 2018; Vlachos et al. 2018). Furthermore, MLS 227 differs from the North American Pleistocene genus *Hesperotestudo* in several traits, including the absence of an epiplastral lip, gular pocket, and not strongly medially narrowed pectoral scutes (Meylan & Sterrer 2000). This combination of traits is unknown in any other testudinid lineage, and *C. pucara* nov. sp. may be confidentially referred to as *Chelonoidis*.

It is worth to mention that *C. pucara* differs from other giant testudinids, such as *Titanochelon schaefferi* (late Miocene of Greece; Vlachos et al. 2020), *Gigantochersina ammon* (Eocene-Oligocene of Egypt; Andrews 1906) and *Impregnochelys pachytectis* (Miocene of Kenya; Meylan & Auffenberg 1986) by having a very short humeral and very long pectoral scutes, in the absence of epiplastral lip and pocket, gular scutes not forming a “V”, and in the presence of horn-like epiplastral projections. In addition, *G. ammon* and *I. pachytectis* show the anterior lobe of the plastron notably transversely narrow (Andrews 1906; Meylan & Auffenberg 1986), and the later exhibits a very long and thick epiplastron and epiplastral lip, which are clearly absent in *C. pucara* nov. sp.

In spite of the fact that *C. pucara* nov. sp. is known from a partial plastron, its particular anatomy distinguishes it from any extant and extinct *Che-*

lonoidis species. Its large size and very thick plastral plates distinguish it at first sight from extant *Chelonoidis*, including those of the "*C. nigra* complex" (Galápagos Giant Tortoises) (see Pritchard 1979; Bour 1984; Pritchard & Trebbau 1984). The latter includes forms characterized by an anterior half of the plastron that is notably transversely narrow and with very thin plates (Arnold 1979; Pritchard 1979; Bour 1984; Pritchard & Trebbau 1984). Noriega et al. (2000) proposed that gigantism probably occurred more than once in Pleistocene testudinids from Argentine lowlands, with some forms being related to the *C. carbonaria* group and others to the *C. chilensis* group. On the other hand, Agnolín (2004) proposed that these giant tortoises belong to a single clade informally called "thick-shelled terrestrial tortoises" by Pritchard and Trebbau (1984), a criterion endorsed by other authors (e.g., Zacarías et al. 2013), and followed here. The thick plates and large size place *C. pucara* nov. sp. within the phenotypical group named by Pritchard and Trebbau (1984) as "thick-shelled tortoises" which includes extinct forms of South American extinct terrestrial tortoises of the genus *Chelonoidis*.

However, *C. pucara* nov. sp. differs significantly from all known thick-shelled tortoises in several anatomical details. One of the most important is the absence of an epiplastral lip and pocket, a condition regarded as plesiomorphic for tortoises, which is shared with members of the "*C. nigra*" and "*C. carbonaria*" complexes (Franz & Franz 2009). This flattened epiplastron contrasts with the complex condition of an elevated epiplastral shelf with an epiplastral lip, pocket, and backward thickening present in other thick-shelled members of the genus, including the giant forms *C. gallardoi, C. australis,* and *C. lutzae* (Claude & Tong 2004; Lapparent de Broin 2003; Lapparent de Broin et al. 2006a; Zacarías et al. 2013; Vlachos et al. 2018). Further, a relatively well-developed overhang of the epiplastron is known in *C. carbonaria* and *C. denticulata* (Manzano et al. 2009), as well as in *C. australis* (de La Fuente 1997b). On the other side, the visceral surface of the epiplastron in *C. pucara* nov. sp. is flat, and differs from the complex one observed in several Antillean *Chelonoidis* species (e.g., *C. dominicensis, C. alburyorum, C. gersoni*; Franz & Franz 2009; Albury et al. 2018; Viñola-López & Almonte 2022; in *C. carbonaria* and *C. denticulata* the sculpture is present but barely visible; Franz & Franz 2009). These species also differ by having very thin shell plates, and tongue-like gular/epiplastral projections which exhibit a strong epiplastral shelf that separates the gulars from the internal floor of the lobe (e.g., *C. cubensis, C. dominicensis, C. alburyorum*; Franz & Franz 2009; Albury et al. 2018; Viñola-López & Almonte 2022).

The anterior projection of the gular scute in *C. pucara* nov. sp. is also very short (see Fig. 3), which contrasts with extinct giant tortoises (de la Fuente 1997b; Zacarías et al. 2013). *C. denticulata, C. carbonaria* and *C. hesterna* differ in the much elongated and narrow anterior plastral lobe (related to the cylindroid carapace), and truncated epiplastral projections (Zacarías et al. 2013). When compared with *C. hesterna*, coming from Miocene deposits in Colombia, *C. pucara* resembles in the relatively short gulars and rounded posterior margins. It strongly differs in the shape of horn-like epiplastral projections, and the wider and shallower axillary notch (see Auffenberg 1971).

Chelonoidis pucara nov. sp. also differs from the giant Miocene-Pliocene *C. gallardoi* and *C. australis* by several features, including the enlarged pectoral scute resulting in posteriorly located pectoroabdominal groove, in the shallower axillary notches, and in the different shape of epiplastral prominences (de la Fuente 1997b). *C. pucara* nov. sp. differs from most South American tortoises (including giant thick-shelled ones), with exception of the Miocene *C. gringorum*, by the occurrence of separate gular and epiplastral lip more than twice as wide as long, strongly projecting and bifid anteriorly (Simpson 1942; de la Fuente 1994; Oriozabala et al. 2018). It should be mentioned that, in spite that the holotype specimen of *C. lutzae* is a male, it lacks the strong horn-like epiplastral projections observed in *C. pucara* nov. sp. (Zacarías et al. 2013, 2014).

Long gulars with converging lateral margins, and humeropectoral sulcus crossing the entoplastron are plesiomorphic features retained by *C. gringorum* (Lapparent de Broin 1991), which differ from the much shorter and nearly transversely oriented humeropectoral sulcus observed in *C. pucara* nov. sp. *Chelonoidis gringorum* also shows relatively narrow and deep axillary notches, which in *C. pucara* are much shallower and wide, a condition plesiomorphically retained by other tortoise lineages, including *Chelonoidis* of the "*nigra* group" (see Pritchard 1979; Bour 1984; Lapparent de Broin 1991).

The occurrence of a short pectoral scute is regarded as a feature shared by most testudinids, in-

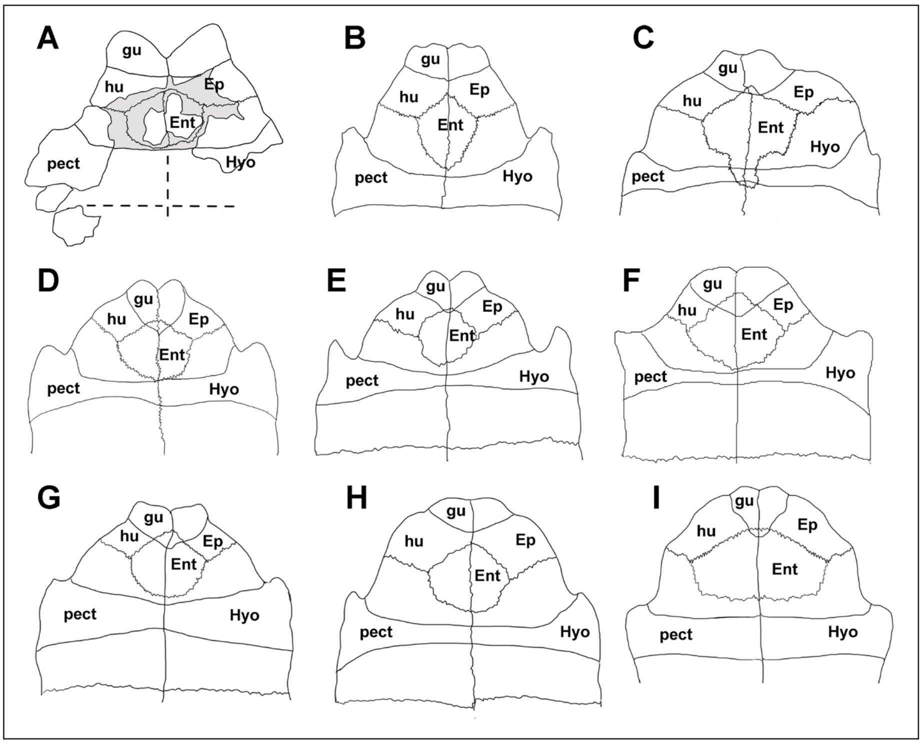

Fig. 3 - Anterior half of the plastron of selected tortoises of the genus *Chelonoidis* and *C. pucara* nov. sp. in ventral view. A) *C. pucara*; B) *C. hesterna* (modified from Auffenberg 1971); C) *C. lutzae* (modified from Zacarías et al. 2013); D) *C. gringorum* (modified from Simpson 1942); E) *C. chilensis*; F) *C. australis*; G) *C. carbonaria*; H) *C. denticulata* (modified from Pritchard and Trebbau, 1984); I) *C. meridiana* (modified from Vlachos et al. 2023).
Abbreviations:
Plates: Ent, entoplastron; Ep, epiplastron; Hyo, hyoplastron;
Scutes: gu, gular scute; hu, humeral scute; pct, pectoral scute. Not to scale.

cluding *Chelonoidis* species (Lapparent de Broin 1991; Claude & Tong 2004). However, *C. pucara* nov. sp. shows an elongated pectoral scute that is as long as, or anteroporteriorly longer, than the humeral scute. The Miocene species *C. meridiana* shows a proportionally long pectoral scute, which may constitute a plesiomorphic feature shared with *C. pucara* nov. sp. (Vlachos et al. 2023). However, it differs from *C. meridiana* by having a humeral scute being anteroposteriorly shorter and a pectoral scute being anteroposteriorly shorter (it represents approximately one-third of the medial length of the hyoplastra, whereas in *C. pucara* nov. sp. it represents less than half; Vlachos et al. 2023) and further differs in the absence of a epiplastral lip.

A feature that may be regarded as unique to *C. pucara* nov. sp. is its extensive epiplastral horn-like projections. In spite that the shape of epiplastral projections is sexually dimorphic in several species, none of the extinct and extant *Chelonoidis* species have such horn-like projections, with the single exception of the Miocene *C. gringorum* (Simpson, 1942) (de la Fuente 1994). Horn-like epiplastral projections or plastral forking occurs in members of different and unrelated tortoise groups, likely to have arisen independently (Arnold 1979), as in *Megalochelys* (Setiyabudi, 2009), *Hesperotestudo turgida* (Oelrich, 1957), *Centrochelys sulcata*, *Astrochelys yniphora* (Claude & Tong, 2004), *Chersina angulata* (Delfino et al., 2024), *Cylindraspis triserrata* (Kehlmaier et al., 2019) and some members of the basal form *Hadrianus* (Lapparent de Broin, 1977). The dorsoventral thickness at the base of such epiplastral projections in *Megalochelys atlas* is about 16.5 cm (Murchison 1868) whereas in *C. pucara* nov. sp. the maximum thickness is up to 7 cm. These epiplastral projections strongly extend anteriorly to the level of the anterior margin of the dorsal carapace. In life, these projections were covered by keratinous gular scutes, extending the spikes on *C. pucara* nov. sp. even more forward. It is clear that in *C. pucara* nov. sp. these were heavily built structures that, as in males of extant tortoises, may constitute formidable weapons that were used by them in shoving and fighting.

The recently described *Chelonoidis petrocellii* was found in Middle Pleistocene beds of northern Buenos Aires province (Agnolín 2021). This species was based on a very incompletely preserved thick-shelled carapace, including a partial anterior half of the plastron, which brings valuable, but limited anatomical information. A new, nearly complete carapace of this species was recently discovered, which brings new data on this poorly known taxon and allows to compare it in more detail with *C. pucara*. The new *C. petrocellii* specimen (MACN-Pv 20125) comes from a 7-meter-deep pit excavation for a septic tank made on Buenos Aires Formation beds (Middle Pleistocene) at Glew city, Buenos Aires

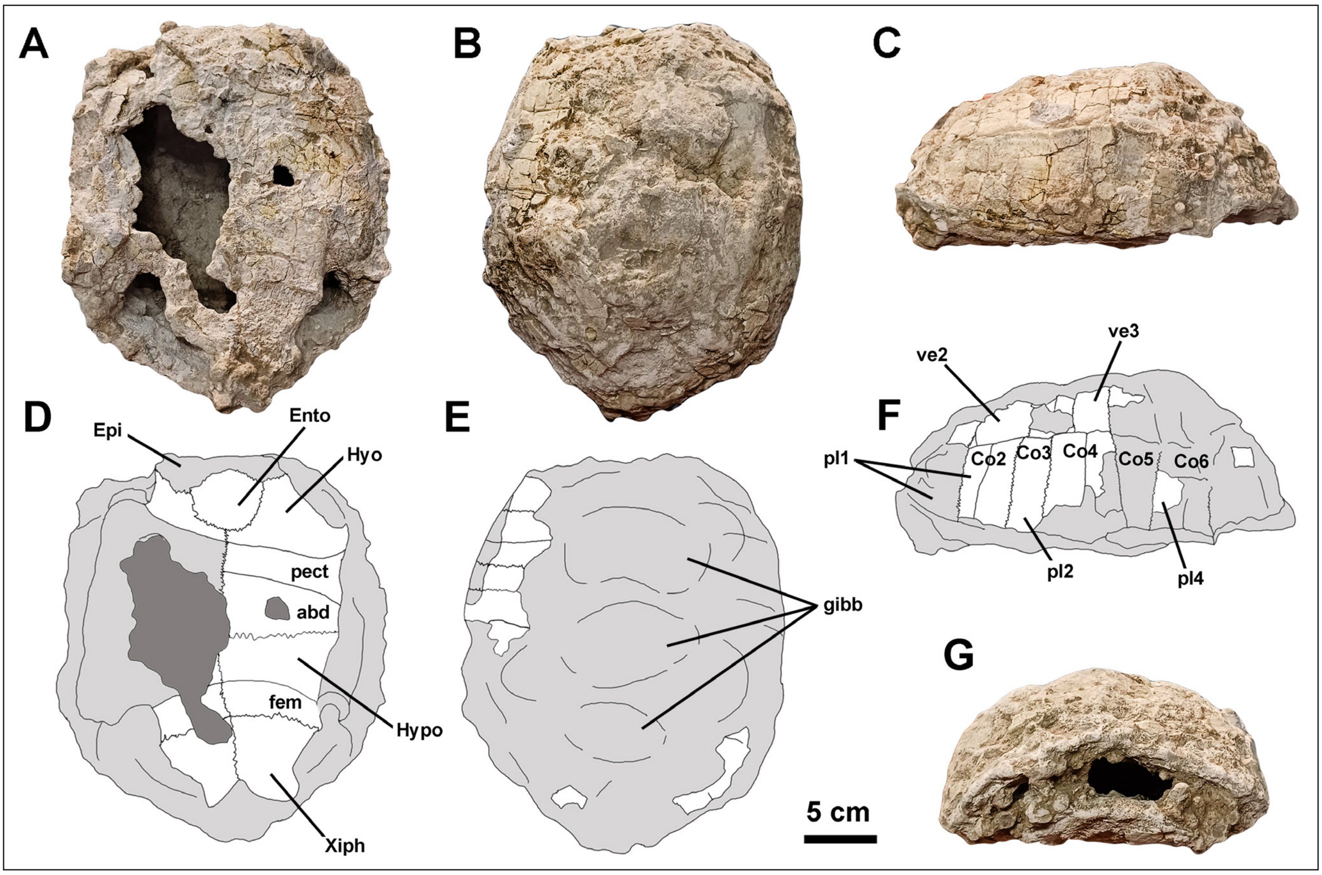

Fig. 4 - *Chelonoidis petrocellii* Agnolín, 2021, new specimen (MACN-Pv 20125) in A,D), ventral; B,E), dorsal; C,F), right lateral; and G), anterior views. Abbreviations. Plates: Co, costal; Ent, entoplastron; Ep, epiplastron; Hyo, hyoplastron; Hypo, hypoplastron; Xiph, xiphiplastron; Scutes: abd, abdominal; gu, gular scute; fem, femoral; hu, humeral scute; pect, pectoral scute; pl, pleural; ve, vertebral. Scale bar: 5 cm.

province. MACN-Pv 20125 has badly damaged anterior carapace margin and eroded outer surface of dorsal carapace plates, which results in that the anatomical information inferred from the preserved elements is relatively limited (see Fig. 4). However, the preserved epiplastron shows the characters present in the *C. petrocellii* holotype (MCA 2024), including the thickened anterior margin, and a thick epiplastral lip and pocket, a very large entoplastron and occurrence of acute and prominent free margin of anterior peripheral plates (Agnolín 2021; the latter absent in *C. carbonaria* and *C. denticulata*). The preserved parts of the holotype suggested that the carapace of *C. petrocellii* was low and transversely broad. The newly recovered specimen corroborates such inference. The new specimen shows complete ossification of the sutures and pointed xiphiplastral extremities, which indicate a mature male individual. It shows the typically alternating costal plates with odd ones being wider medially and even ones wider laterally observed in testudinids and the occurrence of vertebral and pleural carapace gibbosities (usually regarded as a possible synapomorphy of giant terrestrial *Chelonoidis*; Vlachos et al. 2023). Xiphiplastral extremities are very narrow and are separated by a deep and "V"-shaped anal notch. Based on this new evidence, it is not improbable that specimens which belong to the *C. chilensis* group and cited as *C. chilensis* by de la Fuente (1997a) and as *Chelonoidis* sp. by Agnolín (2004) from the late Pleistocene of Santa Fe province, may be also referred to this taxon.

Both the holotype and referred specimens of *C. petrocellii* differ from *C. pucara* nov. sp. on its much smaller size (carapace length about 27.5 cm), by the presence of a gular pocket partially overhanged by epiplastral lips, and by the truncate epiplastral projections (Agnolín 2021).

Testudinites sellovii was described by Weiss in 1930 based on poorly preserved and incomplete plates of a very large terrestrial tortoise coming from the late Pleistocene of Northwestern Uruguay. The specimen is so incompletely preserved that it is currently regarded as a *nomen dubium*. The anatomical information suggests that it may belong to the genus *Chelonoidis* (Vlachos et al. 2018), but the available materials do not allow us to make valuable comparisons with *C. pucara*. A few differences noted include straight external margin of the humeral and gular scutes with inferred subtriangular contour, having a posteriorly pointed tip (see Vlachos et al. 2018). In contrast, *C. pucara* nov. sp. shows a convex external margin and gular scute with poorly convex posterior margin, not strongly posteriorly extended. These few differences may be devoid of taxonomical value, but the poor information afforded by the only known specimen "*T. sellovii*", makes this species as an indeterminate testudinid.

In sum, the unique combination of characters makes *C. pucara* nov. sp. a very distinctive species. In addition to its unique features, it shows several plesiomorphic traits that are shared with basal testudinids, including poorly developed epiplastral lip and pocket, short pectoral scutes, and shallow axillary notches (Lapparent de Broin 1991; Claude & Tong 1994; Franz & Franz 2009; Vlachos et al. 2018). The unique combination of apomorphic and plesiomorphic traits makes the position of *C. pucara* nov. sp. within any lineage of the genus *Chelonoidis* very difficult to ascertain.

Discussion

The fossil record of tortoises in the Pleistocene of Argentina

South American testudinids were traditionally thought to have their origins in North American forms, and were hypothesized to have arrived into the continent by Miocene times (Simpson 1943; Williams 1950; Auffenberg 1971). However, new fossil findings indicate that testudinids were present in Patagonia at least from Oligocene, and probably Eocene times (Sterli et al. 2021), and phylogenetic analyses indicate that South American tortoises are deeply nested among African taxa within the Geochelona clade (Le et al. 2006; Fritz & Bininda-Emonds 2007; Lourenco et al. 2012; Pereira et al. 2017; Kehlmaier et al. 2017). Tortoises are known to have the ability to readily colonize oceanic islands by means of overwater dispersal from continental populations or other island groups (Le et al. 2006; Hansen et al. 2017; Albury et al. 2018; Kehlmaier et al. 2023). Large land tortoises are well-adapted to float and are buoyant due to their high lung-to-body mass ratio associated with their high-domed shells (Patterson 1973), and are frequently found floating in oceanic coasts (Gerlach et al. 2006). Gerlach et al. (2006) reported have barnacles and other marine epibionts in one of these floating tortoises, indicating that they spent in the marine water by at least six to seven weeks. Because of that, it is usually inferred that tortoises arrived to South America by means of rafting on floating islands (de la Fuente 1994, 1997b) as in New World monkeys and rodents (Kehlmaier et al. 2017). Alternatively, Agnolín (2024) proposed that these tortoises belonged to a biota shared by both continents, the "Atlantogea Biogeographical Province" (Ezcurra & Agnolín 2012), prior to their final separation, and that its occurrence in South America and Africa was not the result of transoceanic dispersal.

The record of giant tortoises in the lowlands of South America begins by the end of the 19th century with the first mention of a giant fossil tortoise by Paul Gervais in 1867 (p. 282). This author examined the fossil collections sold to the National History Museum of Paris by the fossil collector M. François Séguin and found a few pieces of a carapace that the collector informed was about 1.5 meters long and 1.2 wide (Gervais 1867, 1877). The specimen was from the Upper Pleistocene of the Carcarañá River, at Santa Fe province, Argentina. Regrettably, the specimen was destroyed during extraction, and thus, the carapace size indicated by the collector cannot be corroborated by Gervais. Ameghino (1881; p. 185) mentions the occurrence of fragmentary carapace remains of a very large terrestrial tortoise coming from late Pleistocene deposits at the Frías creek. Lately, Ameghino (1898; p. 707) refers the giant tortoise from the pampas to the species *Testudo elata* Gervais, 1867, which was then thought to come from Pleistocene beds in Brazil (Gervais 1867). In the Ameghino´s collection, there is a fragmentary plate belonging to a giant tortoise coming from southern Buenos Aires province, Farola de Monte Hermoso locality, which is labeled as *Testudo elata* (MACN A 1269). *Testudo elata* was coined by Gervais (1877) based on remains coming from supposed Pleistocene beds in an uncertain locality at Acre, Brazil. The species was based on not surely associated material coming from a very large tortoise that include a partial dentary, radius, ulna and a plastral fragment. Later analyses indicate that the beds which yielded *T. elata* were from the Soli-

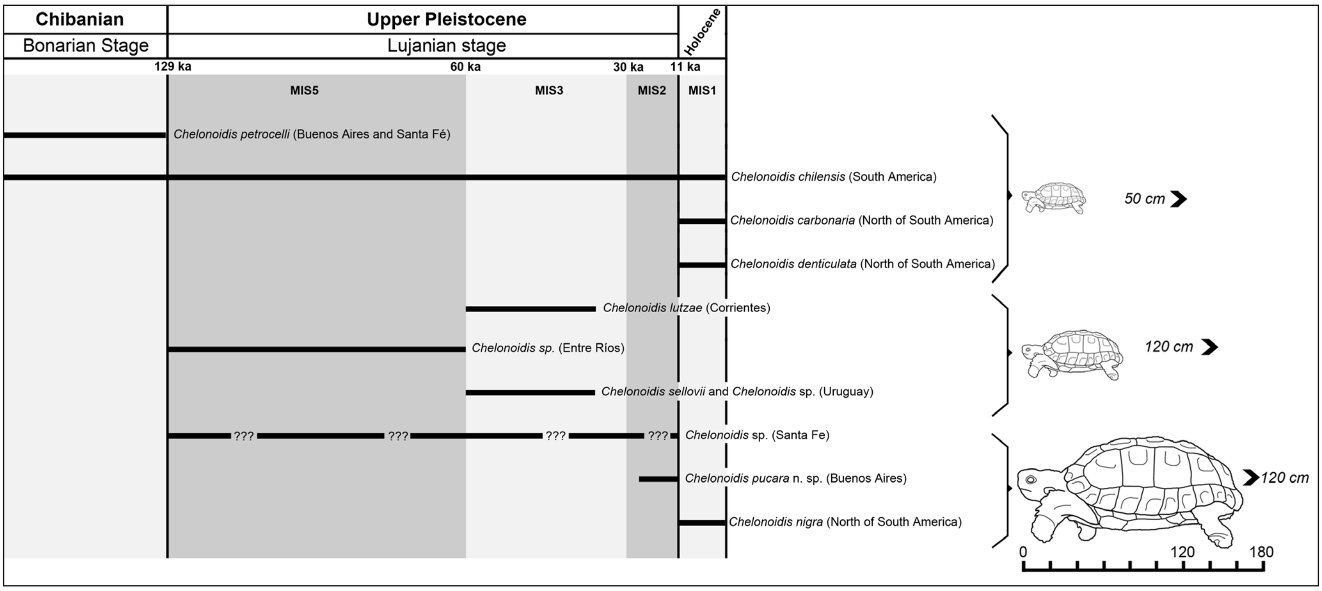

Fig. 5 - Chronostratigraphical distribution of Upper Pleistocene and Holocene *Chelonoidis* species from Argentina, and living species from South America. International stages are indicated following the International Chronostratigraphic Chart 2024/12. The South American stages follow Cione et al. (2015). Marine Isotope Stages (MIS) from South America follow the work of Gasparini et al. (2016). On the right side the relative size of different *Chelonoidis* species are indicated.

moes Formation (Late Miocene in age) and that the fragmentary nature of the specimen cannot allow to diagnose the species, and consequently should be considered a *nomen dubium* (de la Fuente et al. 2018).

More recently, Zacarías et al. (2013) described a partial carapace of a giant tortoise from Upper Pleistocene beds of the Toropí/Yupoí Formation, at Arroyo Toropí, Corrientes province, Argentina. The specimen is a giant form that they named as *C. lutzae*. The holotype of *C. lutzae* comes from beds corresponding to the MIS3, between 52 ka and 36 ka BP (Pacella et al. 2020). To this species, a partial carapace of a giant tortoise should be referred to, described as *Chelonoidis* sp. coming from the same site, and described by Noriega et al. (2000). Manzano et al. (2009) described a very large plastron coming from the late Pleistocene Arroyo Feliciano Formation, at Entre Ríos province, which the authors referred to the extant *C. denticulata*. They noted some features that were atypical for that species, including the invasion of the gulars into the entoplastron and the subequal length of the humeral and femoral scutes, features present in the *C. lutzae* holotype (Zacarías et al. 2013), a species to which we refer the specimen. From southern Entre Ríos province, at the Arroyo Perucho Verna, some authors reported, but do not illustrate, remains belonging to giant tortoises (Lapparent de Broin & de la Fuente 1993; Noriega et al. 2000). Noriega et al. (2000) reports a humerus coming from Arroyo Perucho Verna that is more robust than those belonging to Arroyo Toropí species (this is *C. lutzae*). However, the difference in robustness is not a very useful distinctive character, and may be regarded as intraspecifically variable. Thus, it is not certain that both are different species. The specimen referred to *C. denticulata* comes from the Salto Ander Egg Formation, corresponds to 100 ka (Brunetto et al. 2015), which is coincident with the age proposed for several *Chelonoidis* sp. from Arroyo Perucho Verna and Cañada Las Achiras (Noriega et al. 2000; Tonni, 2004; Ferrero, 2008; Ferrero & Noriega 2009, 2023), all belonging to the MIS 5 (Ferrero & Noriega 2023).

In all probability, the specimens described since the 19th century coming from Carcarañá River, at Santa Fe province may be referred to a different, larger species (Gervais 1877; de la Fuente 1997a, 1999; Agnolín 2004). Agnolín (2004) suggested the occurrence of more than one species occurring in the site, but this was due to the erroneous identification of epiplastral fragments. Regrettably, the Santa Fe records lack a precise stratigraphical position (Vezzosi 2015; Fig. 5).

In sum, *C. lutzae* could be considered the only giant tortoise occurring in Upper Pleistocene beds of Corrientes and Entre Ríos provinces, including previous mentions of indeterminate giant *Chelonoidis*, *C. denticulata* and *C. elata*. The specific status of specimens from Santa Fe is still uncertain, waiting for more complete specimens.

Agnolín (2004) reported a partial carapace of a very large *Chelonoidis* species coming from the late Pleistocene of Los Quiroga dam, Santiago del Estero province, Argentina. In spite of being incompletely preserved, the occurrence of gibbosities and strong carapace thickness, relates this specimen to other giant members of the genus (Agnolín 2004).

In the Buenos Aires province, there were several previous reports of isolated plates belonging to indeterminate giant *Chelonoidis* coming from the Lower Pleistocene of Olivos (de Broin & de la Fuente 1993; Agnolín 2004), Middle to Upper Pleistocene of Partido de la Costa (Agnolín et al. 2024), and Upper Pleistocene of Playa del Barco (de Broin & de la Fuente 1993), Quequén Salado river (Pardiñas et al. 1996) and Salto (Bogan et al. 2010). Moreno (1889) was the first author to indicate the occurrence of a giant tortoise in the Buenos Aires pampas, probably from Luján (a plate housed at that time at the MACN, but now lost), and a partial specimen found at the Vitel creek close to Chascomús city (probably housed at MLP, but now lost). Regrettably, Moreno does not describe the specimens in any detail. *Chelonoidis pucara* constitutes without any doubt the most informative specimen of a Upper Pleistocene tortoise described in Buenos Aires province. It is not improbable that Upper Pleistocene remains of very large tortoises identified as *Chelonoidis* sp. from this province, may prove to belong to this taxon. However, more material is needed to support this supposition.

Regarding small to medium-sized tortoises, fossils belonging to extant *C. chilensis* were reported for Córdoba (without proper geographical and stratigraphical data) and Santa Fe (late Pleistocene) provinces (Auffenberg 1969; de la Fuente 1997a; Vezzosi 2015), whereas *C. denticulata* was reported for the late Pleistocene of Entre Ríos province (Manzano et al. 2009). A fragment of carapace coming from the late Pleistocene of Salto locality, in Buenos Aires province was described by Bogan et al. (2010) and identified as being from a small member of the genus *Chelonoidis*, the size of *C. chilensis*. However, the identification of these specimens was put into question by previous authors, and were variously identified as belonging to indeterminate members of the genus *Chelonoidis* (see de la Fuente et al., 2018), to *C. lutzae* (see below) and to *C. petrocellii* (Agnolín, 2021; see below). Agnolín (2021) described *C. petrocellii* from the Middle Pleistocene of northern Buenos Aires province. This species was originally known by an incomplete carapace having notably thickened plates. Some specimens previously referred to as C. *chilensis* and indeterminate *Chelonoidis* (Agnolín 2005; Bogan et al. 2010) may be referred to this species (see below). *C. petrocellii* shows characters shared with giant thick-shelled tortoises, such as thickened carapace and plastron plates, and gibbosities on dorsal carapace, which are absent in small to medium-sized *Chelonoidis*. It is well-known that paedomorphosis and phylogenetic dwarfism and miniaturization occurred several times among testudinid lineages (Crumly 1984; Pritchard & Trebbau 1984). It is possible that *C. petrocellii* constitutes a phylogenetic dwarf of the giant thick-shelled line.

Summing up, *C. chilensis* and *C. denticulata* lack unambiguous Pleistocene reports in Argentina, and the only Pleistocene tortoises that can be clearly diagnosed are the medium-sized *C. petrocellii,* the large to giant *C. lutzae* and the supergiant *C. pucara*.

Supergigantism in South American tortoises

Lapparent de Broin (2002) pointed out the strong difficulties when calculating size in extinct testudinids. Following her recommendations and comments we include a tentative size extimation for *C. pucara* nov. sp. on the basis of available remains. Based on the preserved plastron, we can estimate carapace size of *C. pucara* nov. sp. by means of extrapolation with other large species of the genus *Chelonoidis*. Using the maximum transverse width at the base of the anterior lobe, and comparing it with extant species (e.g., *C. denticulata, C. carbonaria*; Pritchard & Trebbau 1984), extinct species (*C. hesterna*; Auffenberg 1971), and giant extinct forms [e.g., *C. australis* (maximum carapace length 95 cm, maximum transverse width at the base of the anterior lobe 35 cm, maximum carapace height 57 cm), *C. gallardoi* (maximum carapace length 98 cm, maximum transverse width at the base of the anterior lobe 40.5 cm, maximum carapace height 63 cm); de la Fuente, 1997b], the size of *C. pucara* nov. sp. may be conservatively estimated at 1.7-1.8 meters in maximum horizontal carapace length and 1.1 meters in maximum carapace height.

Large (between 55 and 100 cm) and giant (>100 cm) sizes were developed independently at different times and in disparate clades of the crown

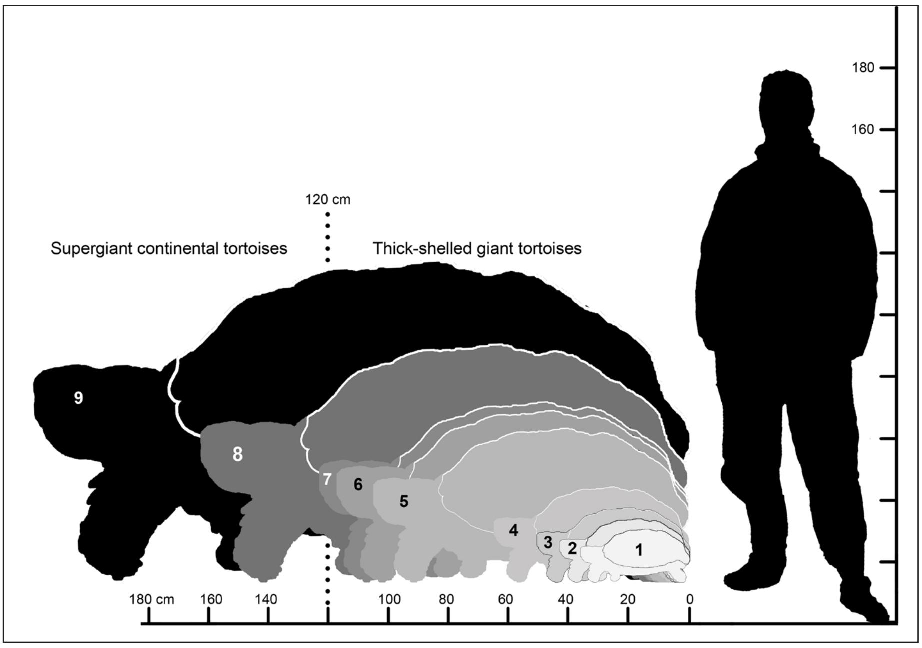

Fig. 6 - Schematic illustration of the different representatives of *Chelonoidis*, using the carapace length taken from the literature, compared to a 180 cm tall person. Number references: 1, *C. petrocellii* (27 cm; Agnolín 2021 and present work) and *C. hesterna* (28 cm; Auffenberg 1971); 2, *C. gringorum* (32 cm; Simpson 1942; Vlachos & Rabi 2018); 3, *C. chilensis* and *C. carbonaria* (43 and 40 cm, respectively; Ernst 1998; Vlachos & Rabi 2018); 4, *Chelonoidis denticulata* (50 cm; Vlachos & Rabi 2018); 5, *C. meridiana* (80 cm; Vlachos et al. 2023), *C. lutzae* from Corrientes and Entre Ríos provinces (83 and 85, respectively; Noriega et al. 2000; Zacarías et al. 2013), *Chelonoidis* sp. from Uruguay (85 cm; Ubilla et al. 2016; Vlachos et al. 2018); 6, *C. australis* (95 cm; de la Fuente 1997b); and *C. gallardoi* (98 cm; de la Fuente 1997b); 7, *C. nigra* (130 cm; Vlachos & Rabi 2018); 8, *C. pucara* n. sp. (175 cm; present work).

Testudinidae (Vlachos & Rabi 2018; Albury et al. 2018; Pérez García et al. 2020). In their classic work, Pritchard and Trebbau (1984) classified extant and extinct giant testudinids in several phenotypical classes. They include all giant South American tortoises within their "Group 8", the extinct "Thick-shelled giant tortoises". This category included tortoises with thickened shells and plastron, having maximum carapace lengths of about 120 cm, and found on most continents and many islands. Within this category were included all fossil giant tortoises of Miocene, Pliocene and Pleistocene of South America (de la Fuente 1997b; Agnolín 2004). However, the very large size of *C. pucara* (estimated maximum carapace length about 1.7-1.8 meters), that nearly duplicates those of "Thick-shelled giant tortoises", such as *C. meridiana* (maximum carapace length of 80 cm), *C. gallardoi* (maximum carapace length of 98 cm), *C. australis* (maximum carapace length of 95 cm) and *C. lutzae* (maximum carapace length of 83 cm) and falls outside this category (see Fig. 6). For such large species, Pritchard and Trebbau (1984) established the category "Supergiant continental tortoises" (Group 10). These very large taxa were restricted to the Pliocene-Pleistocene of Eurasia, particularly India, Indonesia and Spain (Pérez-García et al. 2017, 2020). This group includes the gigantic genus *Megalochelys*, with the species *M. atlas*, which has an average carapace length of about 175 cm (Vlachos & Rabi 2018).

These taxa are characterized by exaggerated development of the epiplastral spurs, and it is possible that the great size may be the evolutionary result of male combat and competition for females (Pritchard & Trebbau 1984). The ecological role of these enormous tortoises appears to be different from those inferred for "Thick Shelled Giants", and still remains uncertain.

Because tortoises are ectothermic animals, they cannot regulate their body temperature and depend on the environmental temperature to regulate their metabolism. Because of this, several authors suggested that tortoises may be useful to determine the temperature and past climate (Brattstrom 1961; Auffenberg 1971; Pritchard 1984). Testudinid occurrences have been regarded as indicative of xeric or semiarid (Auffenberg 1971; Pritchard 1984; Georgalis & Kear 2013) to tropical/semitropical climates (Hibbard 1960; Brattstrom 1961; Manzano et al. 2009; Zacarías et al 2014; Oriozabala et al. 2018; Vlachos et al. 2018). Other authors suggest that testudinids are not good indicators of temperature because today they are adapted to extreme conditions: they can survive very cold winters or dry and hot seasons and cold nights (Lapparent de Broin 2003; Agnolín 2021). Most of these authors based their conclusions almost relying on evidence from extant tortoise physiology and distribution, and inferred attributes of some extinct forms.

Extant members of the genus *Chelonoidis* occupy a wide range of habitats including savannas, xerophytic and open ecosystems, and wet tropical and subtropical forests (Fritts 1983; Ernst 1998; Ernst & Leuteritz 1999; Manzano et al. 2009; Vargas Ramírez et al. 2010; Wang et al. 2011). In the case of giant tortoises from Argentina, Zacarías et al. (2013) suggested that the extinct *C. lutzae* probably inhabited a wet and warm climate, in agreement with other paleontological and geological evidence. In their view, this lends some support to the view that giant tortoises are probably related to tropical to subtropical climates. In the same line, Fritts (1983) based on studies carried out in the Galápagos Islands found that tortoises from more xeric habitats had smaller body sizes while the ones inhabiting more mesic regions grew larger, being a response to ecological pressures like shade and food availability.

However, *C. pucara* occurs in a higher latitude (more than 600 kilometers south to the locality that yielded *C. lutzae*) in a stratigraphical unit that has a high number of paleontological and geological evidence indicating cold and arid environments (Tonni et al. 2003). It is well-known that some small to medium sized tortoises use burrows during the winter and hot parts of the summer for the avoidance of extremes of temperature (Woodbury & Hardy 1948; Richard 1999); where there are no great temperature hazards, tortoises do not burrow (Brattstrom 1961). In these areas where there is a marked seasonality and succulent food is available only during a certain time of the year, the tortoises emerge from their burrows only when the climate is suitable and the succulent food is available (Brattstrom 1961; Richard 1999). However, burrowing is not frequent for large forms, their range of geographic distribution being significantly more limited in periods with relatively low temperatures (Pérez-García et al. 2020).

Thus, if the supergigantic *C. pucara* inhabited such high latitudes with a semiarid climate having strong seasonality, which was the strategy of this chelonian for surviving to such a rough climate? Cadena et al. (2015) analyzed giant tortoise fossils from Bolivia and conclude that these taxa were probably more resilient than smaller ones and behaved like endotherms during basking by increasing their body temperature (Barrick et al. 1999, references therein) and retaining heat better in coolers areas. In the same sense, Georgalis and Kear (2013) proposed that the large body-size of these turtles confers an advantage for maintaining higher metabolic activity (through inertial homeothermy). The occurrence of *C. pucara* in semiarid environments gives some indirect support to this hypothesis, suggesting some kind of endothermy in these extinct taxa.

Scavenging and opportunistic predation are not uncommon in terrestrial tortoises, as a strategy to supplement their low-protein diet, providing an important source of nitrogen (Bjorndal 1989). In continental South America, the yellow-footed (*C. denticulata*) and particularly the red-footed (*Chelonoidis carbonaria*) tortoises are well-known by its generalistic habits, including high percentage of carrion on its diet (Castaño-Mora y Lugo 1979; Pritchard & Trebbau 1984; Gorzula & Señaris 1998; Mourthé & Casal 2017; Mattea & Allain 2020). Further, *C. carbonaria* was observed predating on small reptiles and even birds (Castaño-Mora y Lugo 1979; Pritchard & Trebbau 1984; Gorzula & Señaris 1998; Cabrera 2023). It is possible that supergigantic tortoises, such as *C. pucara*, may have had similar habits with opportunistic scavenging and predation. It was frequently proposed that the Pleistocene pampas ecosystem was imbalanced, due to the high percentage of herbivorous megamammals, when compared with the relatively few predators (Fariña 1996; Fariña & Blanco 1996; Fariña et al. 2013). This led some authors to suggest that there was a hidden predator or scavenger among the known fauna that go unnoticed, probably a ground sloth (Fariña 1996; Fariña & Blanco 1996; Tejada et al. 2021). In spite that we recognize that it is speculative, it cannot be discarded that the vacant scavenger or predatory niche of the Pleistocene Pampas may have been partially filled by supergigantic tortoises, such as *C. pucara*.

Late Pleistocene extinction of giant tortoises

Chelonoidis pucara is the youngest extinct tortoise from the Upper Pleistocene of Argentina. Cione et al. (2003) postulated that giant tortoise extinction at the end of the Pleistocene was the result of a combination of early human exploitation and extreme and frequent periodic climate which led to changes in temperature, humidity, and habitat modification. These changes, adversely impacted megamammals and also giant tortoises, that led these taxa to extinction, in a “Broken Zig-Zag effect”. Megamammals and giant-sized birds exhibit a combination of life-history traits that could make them highly vulnerable to environmental disturbances. In these taxa large body size correlates with many other ecological traits that factor in extinction risk, including delayed maturation, low-fecundity populations, slow reproductive rate, low population densities, low clutch size, and large individual home ranges (see Cione et al. 2009; Agnolín et al. 2022). Small litters, slow growth rates, late sexual maturity, long gestation and long intervals between litters, are less able to compensate for increased mortality and are therefore vulnerable to population extinction (Johnson 2002; Cione et al. 2009). Species with large home ranges are also very vulnerable to habitat loss and degradation and edge effect (Woodroffe & Ginsberg 1998; Cione et al. 2009; Agnolín et al. 2022).

The extinction of giant "thick-shelled" and supergiant terrestrial tortoises may be the result of similar causes. It is well-known that giant tortoises are easy to collect and process, and because of that, human range expansion is usually associated with regional and global overkill of these animals (Sandom et al. 2014; Rhodin et al. 2015). Further, in spite of the clear differences between the ecology of large birds and mammals, and the poikilotherm physiology of chelonians, the giant tortoises exhibit several features associated with gigantism, such as slow growth rates and delayed maturity, high hatchling and juvenile mortality rates, and large individual home ranges (see Rhodin et al. 2015). Thus, we infer that these traits may be responsible for giant tortoise extinction in South America.

CONCLUSIONS

The new species *Chelonoidis pucara* is very distinctive because of its unique combination of apomorphic and plesiomorphic features. The occurrence of long pectoral scutes, shallow and wide axillary notches, and poorly developed epiplastral lip and pocket are plesiomorphic traits absent as a whole in other *Chelonoidis* species. The very distinctive anatomy of the new species reinforces the great morphological disparity observed in extant members of the genus, and may lend some support to the view that *Chelonoidis* may include different generic entities (Crumly 1984; Rodrigues & Diniz Filho 2016; Vlachos & Rabi 2018). Its uniqueness also precludes recognition to which lineage within South American tortoises it belongs.

Gigantism occurred several times independently in testudinids, during the Pleistocene this occurred at least four times in America, including *Hesperotestudo osborniana* in North America and *Chelonoidis nigra* group and *C. lutzae* in South America (Vlachos & Rabi 2018), to which we here add *C. pucara*. Further, this new species represents the first member of the "Supergiant continental tortoises" class of Pritchard and Trebbau (1984) that inhabited America.

The ecological role of these supergiants remains uncertain. They are supposed to be strongly terrestrial forms having some kind of endothermy and that male combat and competition for females constitute remarkable behavioral traits of these forms. *C. pucara* is congruent with such inferences because of the oval and widely opened anterior carapace (as inferred by plastral shape) and by the occurrence of notably thickened and prominent epiplastral spurs. It is also suggested that *C. pucara* and other supergiants may have an important role as opportunistic scavengers and also occasional predators.

Together with *C. lutzae, C. pucara* constitutes the second valid species of giant tortoise from the Pleistocene of South America.

Data Availability Statement

The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

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