

THE TROPICAL TORTOISE *CHELONOIDIS DENTICULATA* (TESTUDINES: TESTUDINIDAE) FROM THE LATE PLEISTOCENE OF ARGENTINA AND ITS PALEOCLIMATOLOGICAL IMPLICATIONS

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INTRODUCTION

THE TERRESTRIAL tortoise clade *Chelonoidis* is endemic to the South American continent and nearby islands. Three continental species are currently recognized that inhabit three distinct habitats. The red-footed tortoise (*C. carbonaria*) and yellow-footed tortoise (*C. denticulata*) are often sympatric tropical to semi-tropical taxa, but the former taxon generally prefers open and wet savannahs, whereas the latter distinctly prefers permanent and wet forest cover. In contrast, the Chaco Tortoise, *C. chilensis*, is arid-adapted and lives along the eastern dry slopes of the southern Andes (Ernst and Barbour, 1989). The diverse group of generally dry-adapted tortoises from the Galapagos Islands is currently thought to be the gigantic sisters of *C. chilensis* (Caccone et al., 1999).

At present only *C. carbonaria* and *C. chilensis* are native to Argentina, reflecting the lack of sufficiently wet tropical forests in that country to permit the presence of *C. denticulata* as well. The Pleistocene Argentinean fossil record so far only produced remains that can be identified as *C. chilensis* and the remain of a now extinct giant tortoise (e.g., de la Fuente, 1997, 1999; Noriega et al., 2000, 2004). Large tortoises from South America were historically classified as *Geochelone*, but they likely represent extinct giant forms of *Chelonoidis* (Le et al., 2006).

Here we report a well-preserved tortoise plastron from the Late Pleistocene of Entre Ríos Province, Argentina, referable to *C. denticulata* (Fig. 1). This find is significant, because it was found approximately 800 km south of the extant, tropical range of this taxon (Vanzolini, 1994). Given the restricted habitat preferences of this taxon today, this find implies that wet-tropical forests once extended significantly further south on the South American continent.

The new specimen, CICYTTP-PV-R-1-268, is housed in the paleontological collections of the Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CICYTTP), Diamante, Argentina. Extant specimens of *C. denticulata* and *C. carbonaria* were examined at Yale Peabody Museum of Natural History (YPM) and the American Museum of Natural History (AMNH). The shell nomenclature used herein follows Zangerl (1969) and clade names follow Joyce et al. (2004).

Comparative Specimens.—*Chelonoidis denticulata* (AMNH 7043, 62587, 62589; YPM 11493, 14341, 17298). *Chelonoidis carbonaria* (AMNH 7042, 62583, 62585, 62588, 62590; YPM 10640, 10795, 12237, 13804, 13955, 14343).

SYSTEMATIC PALEONTOLOGY

TESTUDINES Linnaeus, 1758

TESTUDINIDAE Gray, 1825

TESTUDO DENTICULATA (Linnaeus, 1766) (synonym)

GEOCHELONE DENTICULATA (Williams, 1960) (synonym)

CHELONOIDIS DENTICULATA (Linnaeus, 1766)

(Fig. 2)

Description.—CICYTTP-PV-R-1-268 is represented by a nearly complete plastron with portions of the bridge peripherals (Fig. 2). The left half of the plastron is almost complete, only lacking small portions of the epiplastron, and is in contact with the ventral portions of the left bridge peripherals. The right half, in contrast, lacks portions of all elements with exception of the xiphiplastron. No right bridge peripherals are preserved. The plastron is significantly longer than wide with a length of 56 cm (including the anal processes) and a width of 22.5 cm. The sutures of the bony plates and scutes sulci can be identified easily.

Epiplastra.—The epiplastra form much of the anterior plastral lobe. They contact each other along the midline, the entoplastron posteromedially, and the hyoplastra posterolaterally. As usual in *Chelonoidis*, the anterior third of the anterior plastral lobe is upturned and the anterior rim of the epiplastra is thickened to form a distinct lip (Gaffney and Meylan, 1988, Joyce and Bell, 2004). However, due to damage to the relevant area, it is unclear if a significant visceral overhang of the epiplastral lip was present, although it is apparent that it was better developed than in *Manouria* spp. or *Gopherus* spp. At the level of the gular/humeral sulcus, the anterior plastral margin is slightly notched.

Entoplastron.—A large, diamond-shaped entoplastron is present that is surrounded by the epiplastra anteriorly and the hyoplastra posteriorly. Its ventral exposure is significantly larger than its dorsal exposure. Anteriorly, the entoplastron is clearly overlapped by the gular. In contrast, the humeropectoral sulcus only barely intersects the most posterior tip of this element.

Hyoplastra.—The hyoplastra are large elements that form the posterior portions of the anterior plastral margin. Laterally they contact four peripheral elements along a finely sutured contact. These four elements likely represent peripherals III through VI by comparison to other testudinids. A slim, only partially preserved axillary buttress that contacts peripheral III further supports the bridge (Joyce and Bell, 2004).

Hypoplastra.—The hypoplastra are large elements that approximate the hyoplastra in size and form about half of

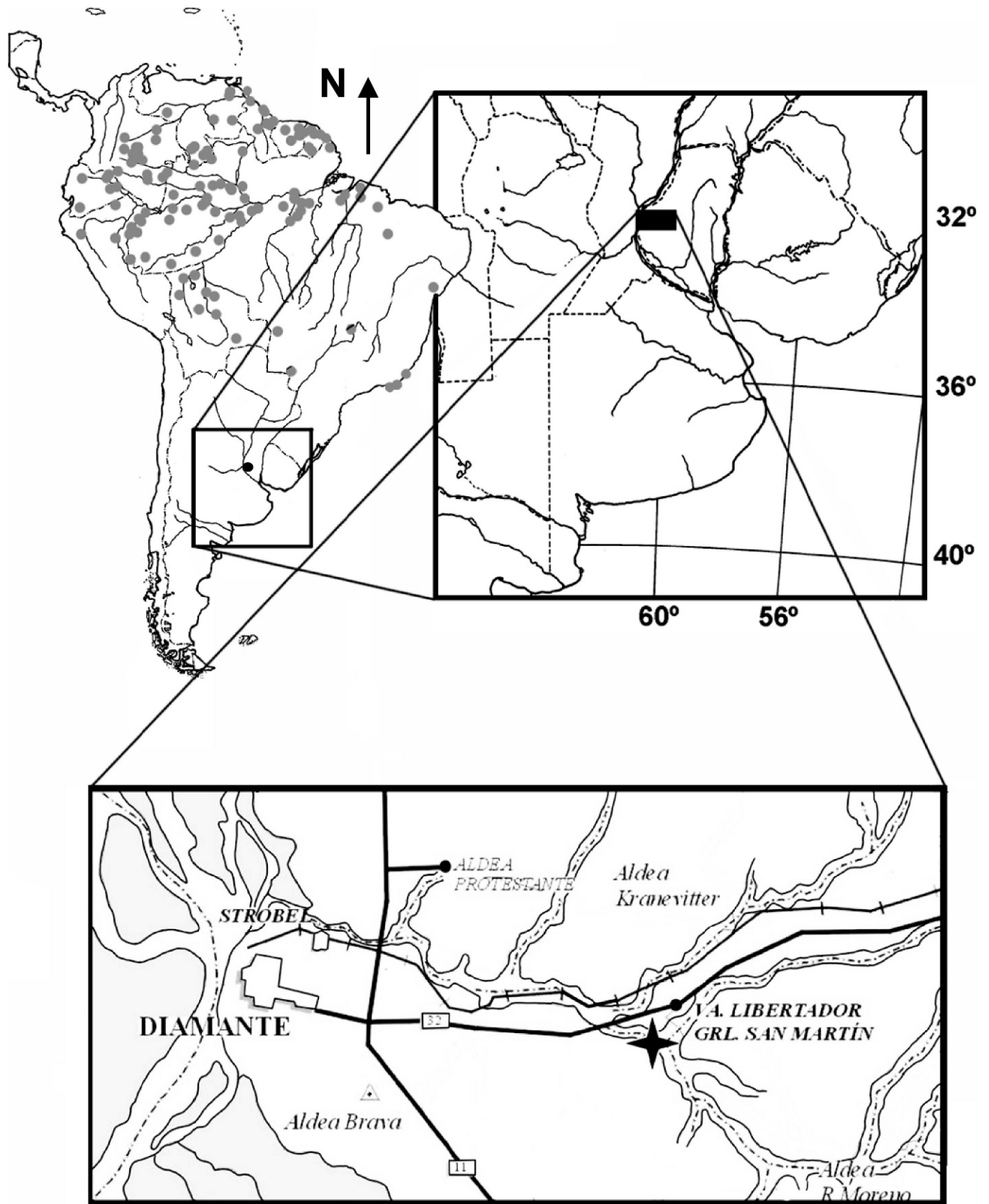


FIGURE 1—Geographic provenance of *Chelonoidis denticulata* (Linnaeus, 1766), CICYTTP-PV-R-1-268, from Entre Ríos Province, Argentina, South America (black circle); and recent distribution of *Chelonoidis denticulata* (grey circles), re-drawn from Iverson (1992).

the posterior plastral margin. They contact the hyoplastra anteriorly, the other hypoplastra medially, and the xiphiplastra posteriorly. Laterally, they are in contact with only two peripherals, here interpreted as peripherals VI and VII. As with the hyoplastra, a slim and only partially preserved buttress is present that articulates with what we interpret as peripheral VII.

Xiphiplastra.—The xiphiplastra are sub-rectangular elements that form the posterior half of the posterior plastral margin. At the level of the anal/femoral sulcus, the lateral margin is deeply notched. As in most tortoises, the skin sulcus runs parallel to the margin of the posterior plastral lobe and the area that was once covered by scutes in the living animal is heavily thickened all the way from the inguinal notch to a plateau formed anterior to the anal notch.

Peripherals.—Five peripherals are present that are here interpreted as being bridge peripherals 3 through 7. The anterior three of this series are in contact with the hypoplastron, whereas the posterior two are in contact with the hypoplastron. Although the dorsal aspects of the peripherals are missing, it is apparent that these elements do not have a lateral keel but rather are tall and flat elements, as in all derived tortoises.

Plastral Formula.—The plastral formula for CICYTTP-PV-R-1-268 is ABD > HUM <> FEM > GUL > ANAL <> PEC.

Gulars.—One pair of gulars covers the most anterior aspects of the epiplastra and extends posterior to partially cover the entoplastron. Dorsally, the gulars covered the greatly thickened anterior portion of the epiplastra, but due to damage it is uncertain if they helped form an overhanging lip. It is also unclear if the gulars were split, a diagnostic feature of *Chelonoidis denticulata* (Williams, 1960).

Humerals.—The humerals are the second biggest scutes to cover the plastron. Their anterior sulcus with the gulars is oblique but straight, but the posterior sulcus with the abdominals curves strongly to the anterior laterally. On the visceral side, the humerals cover part of the anterior plastral lobe, but this contribution diminishes posteriorly and disappears at the height of the axillary notch. Posterolaterally, the humerals contact the axillary scutes.

Pectorals.—Although the pectoral contribution to the midline sulcus is rather small, these scutes increase rapidly in size laterally. As a result, their anterior and posterior sulcus with the humerals and abdominals curve laterally to the anterior and posterior, respectively. The pectorals only slightly overlap the most posterior tip of the entoplastron. Anterolaterally, the pectorals contact the axillary scute.

Abdominals.—The abdominals are by far the largest plastral scutes. Both the anterior and the posterior contacts with the pectorals and humerals turn posteriorly along the lateral edges of these scutes. Posterolaterally, the abdominals contribute to the apparent rim of the posterior plastral lobe, but dorsally to that they contact the inguinal scutes, which form the actual rim of that lobe.

Femorals.—The femoral scutes generally have a squarish shape, although their lateral margin is distinctly convex. These scutes contribute a large portion to the posterior plastral margin. In the area of the femorals, the underlying hypoplastra are greatly thickened along the plastral rim. The femorals fully cover this thickening and their dorsal contribution onto the visceral surface increases posteriorly. In lateral view, the femorals are thus rather high and have a tall contact with the anteriorly positioned inguinals.

*Anal*s.—The anals cover the posterior third of the xiphiplastron and do not come close to the hypoplastral suture. Medially a deep anal notch separates them. In ventral view, both anals contact each other along a rather broad contact, but in visceral view they contact each other only slightly.

Marginals.—The ventral portions of six marginal scales can be identified in this specimen, which cover what remains of the left peripherals. Ventrally, the marginals do not overlap any of the plastral elements at all. Given that the peripherals are tentatively identified as numbers III through VII, the marginals correspondingly would represent numbers II through VIII.

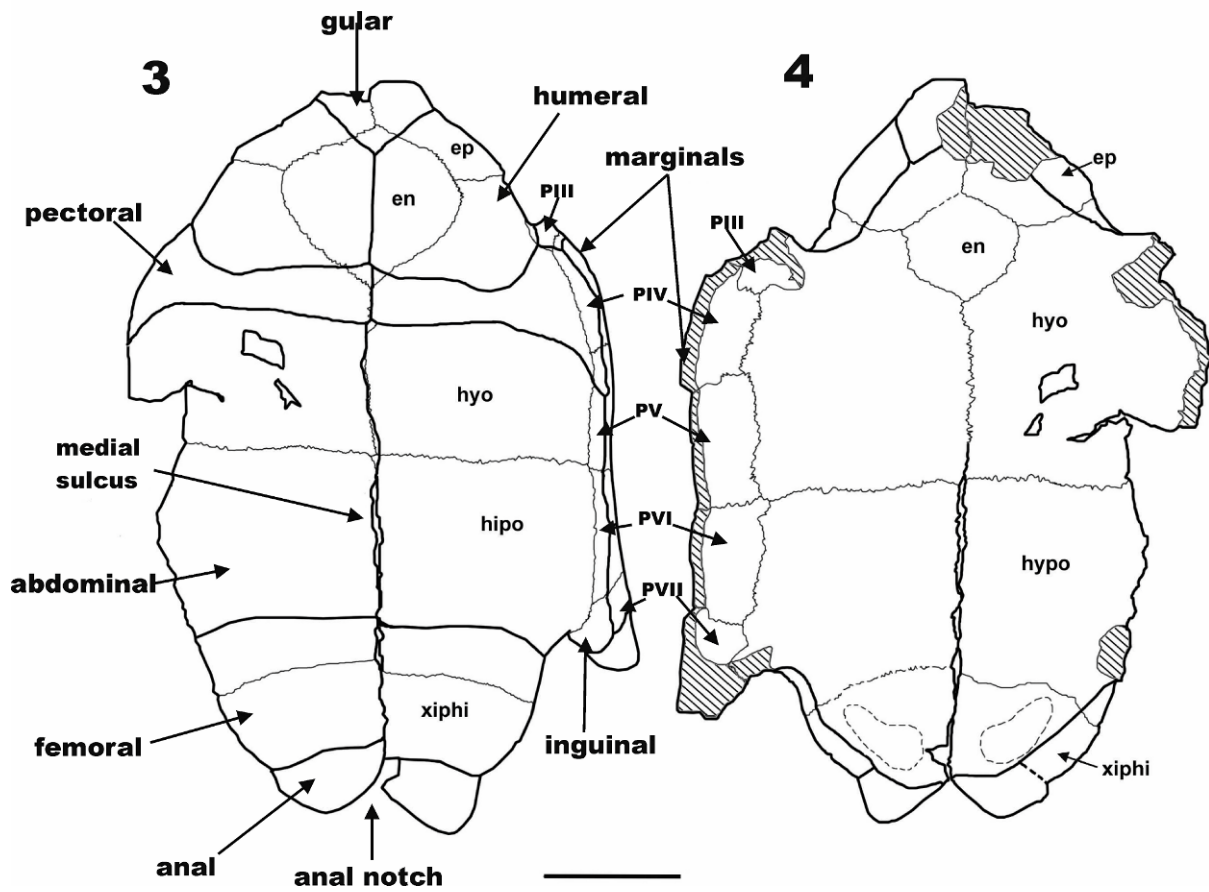
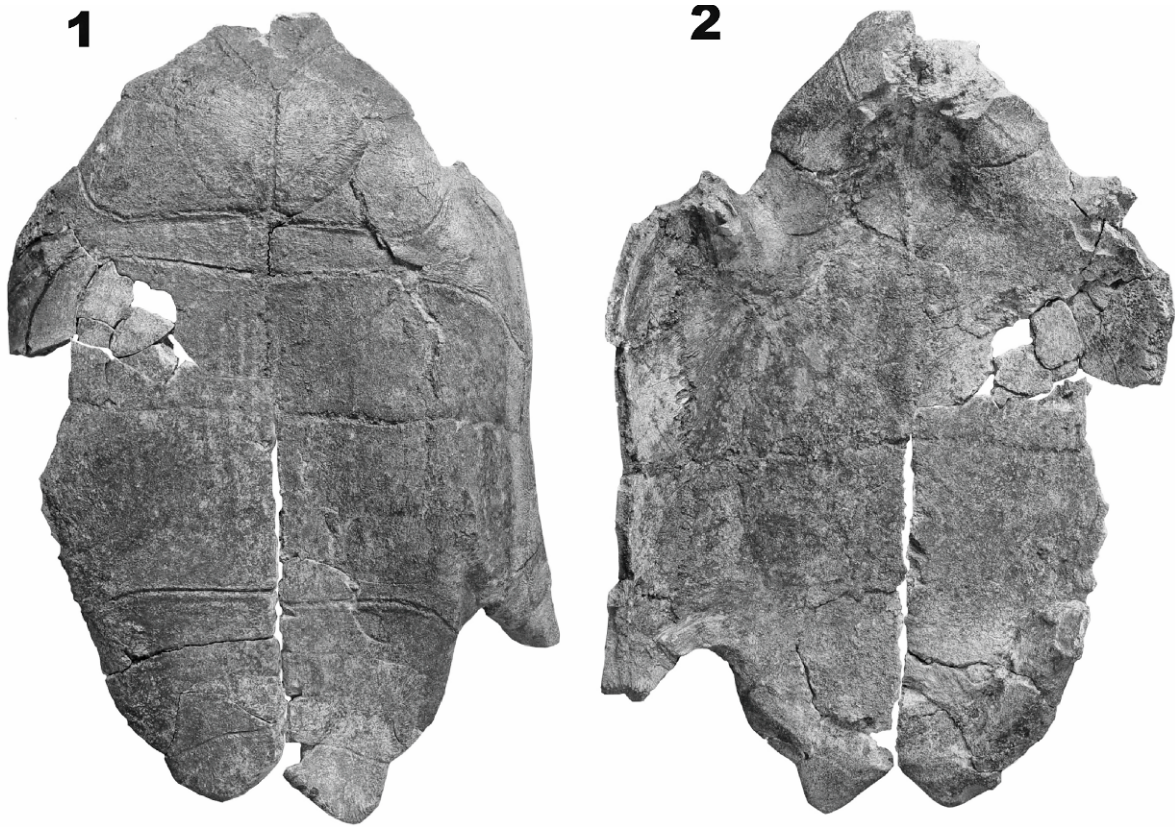
Inframarginals.—Axillary and inguinal scales are present. The axillary scale contacts the humeral medially, the pectoral posteriorly, and a marginal laterally, but its anterior border (the skin-scute sulcus) is less clear, making it uncertain clear how large this element was. An inguinal scute is clearly present on the left side, but it is hidden when observing the specimen from ventral view. Posteromedially this scute contacts the femoral, anterolaterally the abdominal, and laterally the marginal series.

Occurrence.—The fossil was recovered from the Arroyo Feliciano Formation, which crops out along major rivers and streams in Entre Ríos Province and forms the highest terrace (Iriando et al., 1985; Iriando, 1996). The locality is situated on the north bank of the Ensenada stream, 15 km east of Diamante city, Department of Diamante, Entre Ríos Province, Argentina (Fig. 1). Although affirmative, absolute dates are still lacking for this formation, paleontologists have repeatedly referred it to Isotope Stage V, which corresponds to the last interglacial period, approximately 120,000 yr B.P. (Tonni, 2004; Noriega and Tonni, 2007). Associated mammalian finds allow referral to the Lujanian Stage/Age, which corresponds to a Late Pleistocene age as well (Cione and Tonni, 1999; Noriega et al., 2004).

DISCUSSION

Systematic Assessment.—Although CICYTTP-PV-R-1-268 consists of a plastron only, it nevertheless can be identified clearly as a representative of the Testudinidae based on the absence of mesoplastra and extragulars, the presence of axillaries and inguinals (i.e., the reduction of the inframarginals to two pairs), the presence of tall, laterally unkeeled peripherals, and thin axillary and inguinal buttresses (Crumly, 1985; Gaffney and Meylan, 1988; Joyce and Bell, 2004). Within that clade, assignment is more difficult, in part because unique plastral characters have not yet been worked out for testudinids. However, the great size of the specimen, lack of hinges, presence of a well-developed epiplastral overhang and medially separated gulars, and particularly great thickening of the posterior plastral rim combined with the resulting height of the inguinal/femoral contact diagnose this specimen as belonging to the clade formed by *Chelonoidis carbonaria* and *Chelonoidis denticulata*.

Among extant taxa, *Chelonoidis carbonaria* and *Chelonoidis denticulata* are each other's closest relatives (Caccone et al., 1999; Le et al., 2006), and they are morphologically similar. Externally, these taxa are most easily distinguished by their unique coloration, which is reflected in their vernacular names (i.e., red-footed and yellow-footed tortoises, *C. carbonaria* and *C. denticulata*, respectively). However, large size, anteriorly projecting gulars, lack of any significant mid-body constriction, and especially the presence of a small inguinal scute (Williams, 1960; Pritchard and Trebau, 1984; Ernst and Barbour, 1989; Hagan, 1989), clearly allow referral of CICYTTP-PV-R-1-268 to *C. denticulata* or the stem-lineage thereof. The encroachment of the gulars upon



the entoplastron and the sub-equal midline length of the humerals and femorals are atypical for this species, but Williams (1960, page 2) already noted while discussing the diagnoses of two species that “recognition of species is never to be made on any single supposed key character but on the balance of characters in the character complex. If determination of species is made on total characters, no individual should be at all doubtful or difficult to place.” Although large *C. denticulata* are rare in the wild, this specimen is well within the known size range for this taxon and outside the known size range for *C. carbonaria*. This represents the first known fossil remain of this taxon.

Paleobiogeographical and paleoenvironmental implications.—The fossil specimen of *Chelonoidis denticulata* reported herein belongs to a diverse vertebrate paleofauna recorded from the Late Pleistocene Arroyo Feliciano Formation. Non-mammalian elements include remains referable to *Trachemys* cf. *dorbigni* (de la Fuente et al., 2002), a gigantic isolated neural referable to *Chelonoidis*, several teeth of *Caiman* sp., and the condor-like bird *Geronogyps reliquus* (Noriega et al., 2004; Ferrero and Noriega, in press). The rich associated mammalian fauna of at least 35 taxa mostly resembles classic Lujanian assemblages known from the Pampean region further to the south (Late Pleistocene-Early Holocene; Biozone of *Equus* (*Amerhippus*) *neogeus* Lund 1840; see Cione and Tonni, 1999).

Although many mammal fossils correspond to the Pampean region, the presence of taxa with tropical Brazilian affinities, such as the pampathere *Holmesina paulacoutoi* (Scillato-Yané et al., 2002, 2005) and the mustelid *Pteronura brasiliensis* (Prevosti and Ferrero, 2008), indicate that this region had distinct, more tropical influences as well (Noriega et al., 2004; Ferrero and Noriega, in press). In particular, the pampathere *Holmesina paulacoutoi* is thought to have lived in relatively humid environments and to have eaten soft vegetation, different from species of *Pampatherium*, which were more arid-adapted and likely consumed hard and abrasive grasses (De Iuliis et al., 2000; Scillato-Yané et al., 2005). Likewise, the giant otter *Pteronura brasiliensis* is an indicator of tropical lentic freshwater rivers, streams, swamps and ponds, with preference for riverbanks surrounded by gallery forests or closed vegetation (Prevosti and Ferrero, 2008). Combined with the habitat preferences of living tapirs and the strictly tropical, humid environmental needs of *Chelonoidis denticulata*, this suggest that around 120,000 BP Entre Rios consisted of subtropical savannahs that alternated with humid forested areas along the major water courses or marshes (Ferrero and Noriega, in press). The presence of the climatically sensitive tortoise *Chelonoidis denticulata* furthermore implies that temperatures were significantly warmer during the last interglacial as well.

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FIGURE 2—*Chelonoidis denticulata* (Linnaeus, 1766) plastron, CICYTTP-PV-R-1-268. 1, ventral view; 2, dorsal view. Graphic representation of the plastron. 3, ventral face with indication of bony plates and scutes; 4, dorsal face with indication of bony plates. Abbreviations: en, entoplastron; ep, epiplastron; hyo, hyoplastron; hypo, hypoplastron; xiphi, xiphiplastron, PIII – VII, peripheral bones III to VII. Scale bar equals 10 cm.

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