A Review of the Fossil Record of South American Turtles of the Clade *Testudinoidea*

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Abstract

The fossil record of turtles of the clade *Testudinoidea* is generally poor in South America. Fossil tortoises (*Testudinidae*) are known from the Late Oligocene to Holocene, but they likely arrived from Africa during the Late Eocene or Early Oligocene. The fossil record of *Trachemys* (*Emydidae*) and *Rhinoclemys* (*Geoemydidae*) is restricted to the Pleistocene, but both lineages likely arrived in multiple waves over the course of the Neogene. Our taxonomic review of 12 named fossil testudinoids finds five nomina valida, two nomina invalida, four nomina dubia, and one nomen nudum.

Keywords

Phylogeny, biogeography, paleoecology, *Emydidae*, *Geoemydidae*, *Testudinidae*, *Trachemys, Rhinoclemmys, Chelonoidis*

Introduction

Testudinoidea is a clade of continental turtles that primarily consists of three subclades: *Emydidae*, which is mainly composed of North American species with the exception of *Emys orbicularis* in the Old World, *Geoemydidae*, which mainly includes Eurasiatic species with the exception of *Rhinoclemmys* in the New World, and *Testudinidae*, which has a worldwide distributed with the exception of Australia and Antarctica. In total, this cryptodiran crown clade represents more than half of all extant turtle species diversity (TTWG 2017).

Eleven species of *Testudinoidea* are currently recognized in South America: four species of *Testudinidae* (the continental *Chelonoidis carbonaria*, *Chelonoidis chilensis*, *Chelonoidis denticulata*, and the insular *Chelonoidis nigra* species complex), four species of *Emydidae* (*Trachemys adiutrix, Trachemys dorbigni, Trachemys ornata,* and *Trachemys venusta*), and five species of *Geoemydidae* (*Rhinoclemmys annulata*, *Rhinoclemmys diademata*, *Rhinoclemmys melanosterma*, *Rhinoclemmys nasuta*, and *Rhinoclemmys punctularia*) (for authorships, see TTWG 2017). By contrast, the fossil record of South American testudinoids is mostly restricted to late Oligocene to Recent testudinids (Broin 1991; Broin and de la Fuente 1993). This review recognizes only five valid species of extinct testudinoids from South America, all of which are testudinids referrable to *Chelonoidis* Fitzinger, 1835, in particular *Chelonoidis australis* (Moreno, 1889), *Chelonoidis gallardoi* (Rovereto, 1914), *Chelonoidis gringorum* (Simpson, 1942), *Chelonoidis hesterna* Auffenberg, 1971, and *Chelonoidis lutzae* Zacarías et al., 2013 (see also de la Fuente et al. 2014 for a recent summary). Extant continental Neotropical tortoises are mostly small to middle-sized, but the fossil record indicates the persistent presence of large tortoises from the late Oligocene to the latest Pleistocene. On the other hand, the record of geoemydids and emydids is fragmentary and restricted to the Pleistocene (Maciel et al. 1996; de la Fuente 1999; de la Fuente et al. 2002; Zacarías et al. 2014; Cadena et al. 2017).

The South American fossil record of testudinoids is heavily biased towards Argentina, which has yielded approximately half of fossil turtle

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occurrences and collections from South America to date (PaleoBiology Database, accessed December 2017). As a result, the history of discovery of fossil turtles in South America is in many ways parallel to that of Argentina, as recently summarized by de la Fuente and Sterli (2015).

At the beginning of 19th century, Weiss (1830) described and illustrated a new species of tortoise, *Testudinites sellovii*, from an unnamed Pleistocene horizon in Paysandú, Uruguay, which holds the record of being the first fossil turtle taxon named from South America. Additional, fragmentary material was later mentioned or described by Gervais (1877), Scalabrini (1884), Moreno (1889), and Rovereto (1914). The work of Simpson (1942) stands out by describing the new species "*Testudo*" *gringorum* from the Miocene of Chubut Province, Argentina, and by discussing the affinities of Neotropical tortoises. Following Simpson's work, the record of South America fossil testudinoids was regularly incorporated into global analyses, including the works of Williams (1950), Hoffstetter (1968), Pascual (1970), and Pascual and Odreman Rivas (1971). The work of Auffenberg (1971) is notable, as he described *Chelonoidis hesterna* based on well-preserved material from the middle-late Miocene of Huila, Colombia. The South American testudinoid fossil record was synthesized repeatedly by Auffenberg (1974), Gasparini and Báez (1975), Báez and Gasparini (1977, 1979), Estes and Báez (1985), Gasparini et al. (1986), de Broin (1991), and Broin and de la Fuente (1993). The number of researchers working on fossil turtles from South America has been increasing more recently, especially in the last decade. Important recent contributions that pertain to testudinoids include de la Fuente (1994, 1997a), Forasiepi et al. (2011), Zacarías et al. (2013), Cadena et al. (2015), and Oriozabala et al. (2018). For institutional abbreviations, see Appendix 1. Named fossil testudinoid genera from South America are listed in Appendix 2.

Phylogenetic Relationships

There are few works dealing with the phylogenetic relationships of fossil testudinoids from South America and the few that are available pertain to members of *Testudinidae* only. Representatives of *Emydidae* and *Geoemydidae* are scarce and poorly preserved, prohibiting any meaningful incorporation into a phylogenetic analysis.

The fossil emydids from South America have universally been attributed to the extant genus *Trachemys*, and in some cases to the species *Trachemys dorbignyi* (see Systematic Paleontology, below). The currently accepted species of *Trachemys* form a derived monophyletic clade within *Emydidae* (e.g., Pereira et al. 2017), a position that is generally accepted and well supported. All available geoemydid fossil material from South America is similarly referred to *Rhinoclemmys* (see Systematic Paleontology, below). Although there has been some debate in the past regarding the placement of *Rhinoclemmys* within *Testudinoidea* (e.g., Hirayama 1985; Yasukawa et al. 2001; Spinks et al. 2004), most recent molecular analyses agree that *Rhinoclemmys* forms a basal clade within *Geoemydidae* (e.g., Le and McCord 2008; Crawford et al. 2015; Pereira et al. 2017; Garbin et al. 2018).

All fossil representatives of *Testudinidae* from South America are considered members of the extant genus *Chelonoidis* (see Systematic Paleontology, below). The derived position of extant *Chelonoidis* within the clade *Geochelona* has long been well supported by morphological (Crumly 1982, 1984; Bour 1984; Gerlach 2001; Vlachos and Rabi 2017) and molecular (Caccone, Gibbs et al. 1999; Le et al. 2006; Fritz and Bininda-Emonds 2007; Pereira et al. 2017) analyses. With minor exceptions (e.g., Rodriguez and Diniz–Filho 2016), the monophyly of *Chelonoidis* is generally supported by recent molecular evidence as well (Pereira et al. 2017). Only few cladistic analyses exist that attempt to resolve the position of extinct South American testudinids. The cladistic analyses of de la Fuente (1994) and Zacarías et al. (2013) suggest that large-sized extinct tortoises from South America (i.e., *Chelonoidis australis*, *Chelonoidis gallardoi*, and *Chelonoidis lutzae*) are closely related to each other, that *Chelonoidis hesterna* is placed within the extant *Chelonoidis denticulata* + *Chelonoidis carbonaria* clade, and that *Chelonoidis gringorum* is sister to the extant *Chelonoidis chilensis* + *Chelonoidis nigra* clade (Figures 1, 2), but both analyses assume monophyly of extinct and extant *Chelonoidis* The inclusion of extinct *Chelonoidis* into a recent, global analysis of testudinid relationships, on the other hand, failed to recover them within *Chelonoidis*

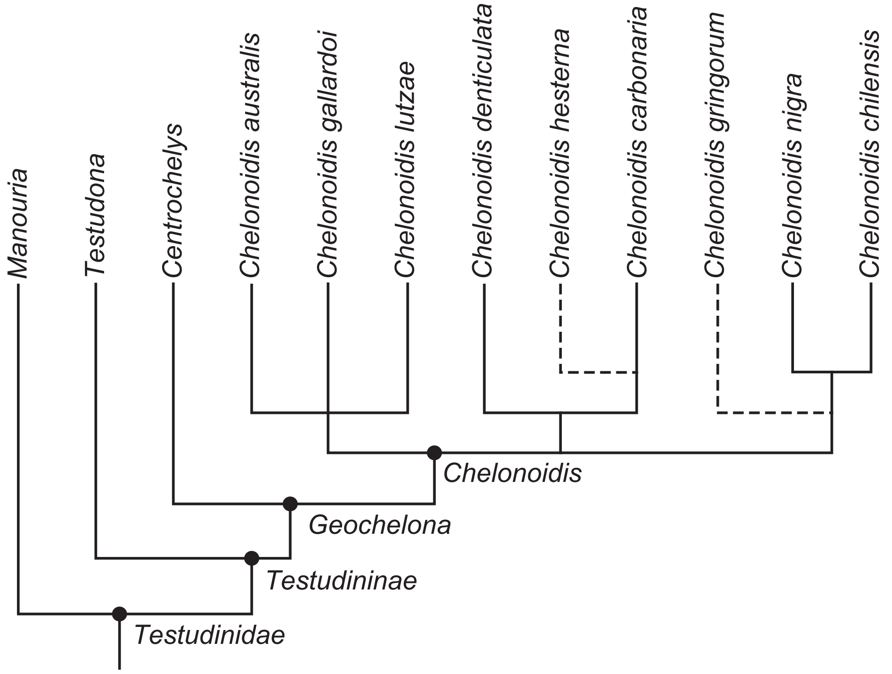

FIGURE 1. A phylogenetic hypothesis of valid testudinid taxa from South America. Solid lines indicate well-supported placement, whereas dashed lines indicate more tentative placements (see text for more details).

(Vlachos and Rabi 2017). This is most probably caused by the limited anatomical information that can be scored from most extinct taxa and the great variability of *Chelonoidis gringorum* (see de la Fuente 1994; Oriozabala et al. 2018). The phylogeny presented herein (Figures 1, 2) is a compilation of the results of the above-mentioned works, excluding *Chelonoidis* species from the West Indies region that are treated elsewhere (Vlachos 2018).

Paleoecology

Extant representatives of the testudinid clade *Chelonoidis* are adapted to wet tropical to seasonally dry terrestrial habitats, representatives of *Rhinoclemmys* to aquatic to semiterrestrial tropical habitats, and representatives of *Trachemys* to aquatic habitats in warm temperate to tropical environments (Ernst and Barbour 1989). The available fossil record of these groups in South America is highly limited, but the available anatomy in combination with depositional settings is broadly consistent with that of their extant relatives.

The recent study of Zacarías et al. (2014) concluded that the distribution of large-bodied extant tortoises (e.g., *Chelonoidis nigra*, *Centrochelys sulcata*, *Dipsochelys elephantina,* and *Cylindraspis peltastes*) is tightly controled by climate, as they only occur in tropical and subtropical zones. The presence of giant *Chelonoidis* in the Pleistocene of northestern Argentina is therefore significant, as it documents warmer conditions during that time (Manzano et al. 2009; Zacarías et al 2014). The presence of tortoises in the Miocene of Patagonia similarly attests to more favorable climatic conditions in the past, as tortoises are now absent in this part of the world (Oriozabala et al. 2018).

Paleobiogeography

The origin of South American tortoises (e.g., *Chelonoidis*) has been a matter of debate since the mid 20th century (see de la Fuente et al. 2014, for a recent review). Two main hypotheses characterize the debate. Tortoises either dispersed to South America from North America (e.g., Simpson 1942, 1943; Auffenberg 1971; de Broin 1991; Gerlach 2001) or they immigrated from Africa (e.g.,

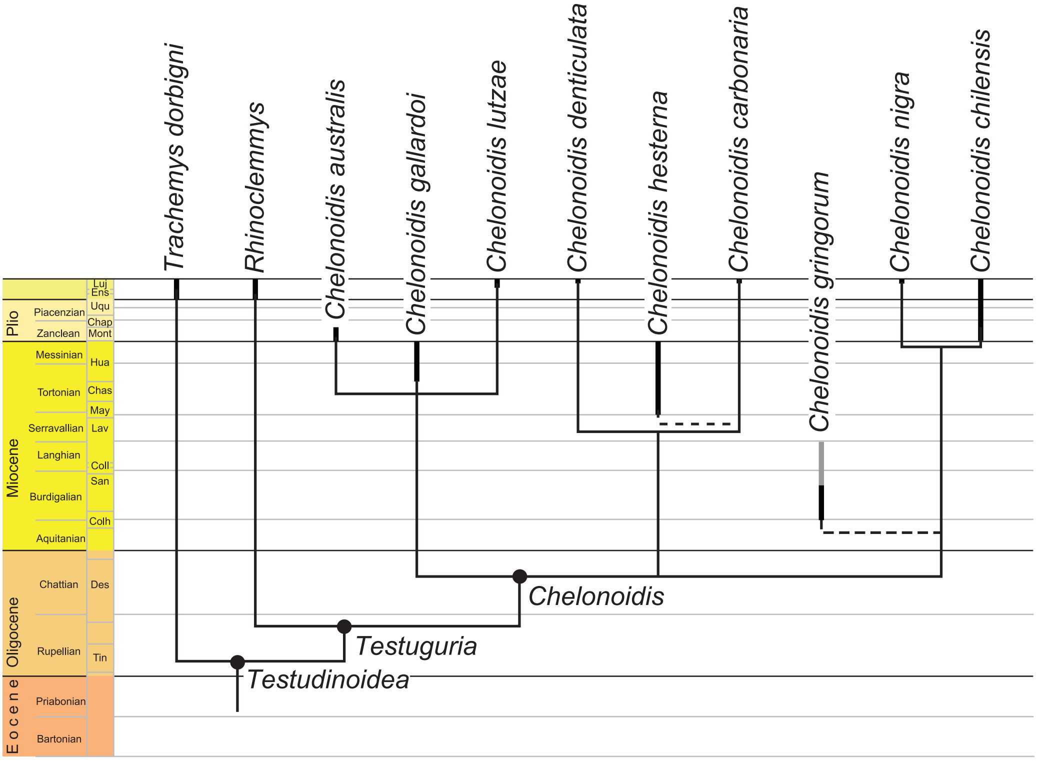

FIGURE 2. The stratigraphic distribution of valid testudinoid taxa from South America. Black lines indicate temporal distributions based on type material. Gray lines indicate temporal distributions based on referred material.

Simpson 1942; Crumly 1984). A single dispersal event is typically discussed, as most authors presume that South American tortoises are monophyletic, but Crumly (1984) suggested multiple invasions from North America, and perhaps also Africa, as he retrieved the group as polyphyletic. This debate recently received an important impulse from well-sampled molecular phylogenies that universally place *Chelonoidis* within the mostly African clade *Geochelona* (Le et al. 2006; Fritz and Bininda-Emonds 2007; Pereira et al. 2017). The comprehensive phylogeny of Vlachos and Rabi (2017) suggests that numerous extinct tortoises from North America may be representatives of *Geochelona* as well, but no close relationships are suggested with South American representatives. Incidentally, this phylogeny does not support the monophyly of South American tortoises, but this seems to be an artifact created by poor character sampling for various extinct South American tortoises (Vlachos and Rabi 2017). As the North American fossil record otherwise does not include any "native" members of *Chelonoidis*, but only some Neotropical tortoises in the West Indies that dispersed from South America to the North during the Pleistocene (Vlachos 2018), all available evidence favors a single, transoceanic dispersal event of tortoises from Africa to South America. The oldest available fossil tortoise remains from South America imply that this dispersal event must have taken place no later than the late Oligocene (Deseadan SALMA; Lapparent de Broin 1991; Figure 3), but molecular calibration studies suggest that this event already took place during the late Eocene-early Oligocene (Lourenço et al. 2012) or late Eocene (Pereira et al. 2017). Tortoises have a great potential to disperse across oceans, as they have an impermeable integument combined with a high floating capacity (Pritchard 1984). Transoceanic island colonizations have otherwise been documented for tortoises for the Galápagos Archipelago

Figure 3. The geographic distribution of fossil testudinoid turtles in South America. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations*: AC, Acre; AM, Amazonas; BA, Buenos Aires; CB, Córdoba; CC, Chaco; CH, Chubut; CN, Corrientes; CQ, Chusquisaca; CT, Catamarca; ER, Entre Ríos; FM, Formosa; LP, La Pampa; MZ, Mendoza; PI, Piura; RG, Rio Grande do Sul; RJ, Rio de Janeiro; RN, Río Negro; SA, Santa Cruz; SC, Santa Cruz; SF, Santa Fé; SJ, San Juan; TA, Tarija.

(e.g., Caccone, Gibbs et al. 1999; Caccone et al. 2002; Rusello et al. 2005), Madagascar (Caccone, Amato et al. 1999), and various West Indian Ocean islands (Williams 1950, 1952; Bour 1984, 1987; Austin and Arnold 2001; Austin et al. 2003). The implied transoceanic dispersal of tortoises from Africa to South America during the Paleogene therefore appears to be unproblematic.

The origin of South American *Emydidae* is universally accepted to be North American, as the South American representatives of *Trachemys* are nested deeply in molecular phylogenies within North American species of *Trachemys* (e.g., Pereira et al. 2017). *Rhinoclemmys*, on the other hand, holds a basal position within *Geoemydidae* (see above), and is reconstructed to have an Asian origin (Pereira et al. 2017). Thus, dispersal from North America as an intermediate step from Asia is plausible for geoemydids as well. The timing of these dispersal events has been a matter of debate, as it is unclear if these turtles colonized South America before, during, or after the final closure of the Central American Seaway. Using a relaxed molecular clock, Fritz et al. (2012) proposed that the ancestor of *Trachemys dorbigni dorbigni* and *Trachemys dorbigni adiutrix* arrived in South America in the latest Miocene (ca. 6Ma), which coincides with the formation of the Panama Island Archipelago (Woodburne 2010), prior to the emergence of the Panamanian Isthmus. *Trachemys ornata callirostris* and *T. ornata chichiriviche*, on the other hand, appear to have invaded South America during the Pleistocene (Fritz et al. 2012). Le and McCord (2008) similarly suggested that various *Rhinoclemmys* colonized South America at least four times, often prior to the closing of the Isthmus as well. These interpretations therefore differ from previous hypotheses suggesting that all *Trachemys* and *Rhinoclemmys* species are recent invaders to South America that used the emerging land bridge to expand towards the south only during the Pliocene or Pleistocene (e.g., Savage 1966; Pritchard and Trebbau 1984; Vanzolini and Heyer 1985; Moll and Moll 1990; Seidel and Jackson 1990; Vanzolini 1995; de la Fuente et al. 2002). As the fossil record of both clades is restricted to the Pleistocene in South America, it contributes little to this discussion. It is notable, however, that these two lineages have not yet been reported from the well-sampled middle Miocene locality of La Venta, Colombia (Figure 3).

Systematic Paleontology

Valid Taxa

The following section includes a full list of all herein-recognized named species of fossil *Testudinoidea*. See Appendix 4 for the hierarchical taxonomy of named fossil *Testudinoidea* as described in this work.

Testudinoidea Fitzinger, 1826

Phylogenetic definition. Following Joyce et al. (2004), the name *Testudinoidea* refers to the crown clade arising from the last common ancestor of the testudinid *Testudo graeca* Linnaeus, 1758, the emydid *Emys orbicularis* (Linnaeus, 1758), and the geoemydid *Batagur baska* (Gray, 1831).

Diagnosis. Testudinoids are herein diagnosed relative to other turtles by the extensive covering of the plastral scutes on the visceral side of the plastron, presence of axillary and inguinal scutes only, well-developed axillary and inguinal buttresses, presence of musk duct foramina, a biconvex eighth cervical vertebra, and a curved iliac blade with a double origin for the M. iliotibialis.

Emydidae Bell, 1825

Phylogenetic definition. Following Joyce et al (2004), the name *Emydidae* is herein referred to the crown clade arising from the last common ancestor of the emydine *Emys orbicularis* (Linnaeus, 1758) and the deirochelyine *Chrysemys picta* (Schneider, 1783).

Diagnosis. Emydids can be diagnosed as testudinoids based on the full list of characters provided for that clade above. Members of *Emydidae* are differentiated relative to other testudinoids by the absence of musk ducts and associated musk duct foramina, wide rib heads, a broad costo-vertebral tunnel, presence of paired marginals XII, and the expansion of vertebral V onto the pygal.

Comments. *Emydidae*, the so-called pond turtles, form a quite diverse clade of turtles with more than 50 species, distributed mainly in the New World, with the exception of the presence of *Emys orbicularis* in Europe (TTWG 2017). The emydids of the New World are mainly distributed in North America (TTWG 2017) and have a decent fossil record documented (Vlachos 2018). In South America, Emydidae is only represented by *Trachemys* Agassiz, 1857. The fossil record of *Trachemys* in South America is rather scarce, and the majority of records are only identifiable as *Trachemys* sp. (de la Fuente 1997b, 1999; Cabrera and Luna 2011; Zacarias et al. 2014). A relatively complete shell is available, however, from the Late Pleistocene of Entre Rios Province, Argentina, referrable to *Trachemys dorbigni* Duméril and Bibron, 1835 (de la Fuente et al. 2002).

Geoemydidae Theobald, 1868

Phylogenetic definition. Following Vlachos (2018), the name *Geoemydidae* is referred to the most inclusive crown clade that includes *Geoemyda spengleri* (Gmelin, 1789), but not *Emys orbicularis* (Linnaeus, 1758) or *Testudo graeca* Linnaeus, 1758.

Diagnosis. Geoemydids can be diagnosed as members of *Testudinoidea* based on the full list of characters presented for that clade above. Members of *Geoemydidae* are differentiated from other testudinoids by the presence of musk ducts and associated musk duct foramina, wide rib heads, a narrow costo-vertebral tunnel, and paired marginals XII that expand onto suprapygal II.

Comments. *Rhinoclemmys* Fitzinger, 1835, is the only clade of extant geoemydid turtles in the New World. A recent combined analysis of molecular and morphological data provided strong evidence for the monophyly of *Rhinoclemmys* and its basal position within *Geoemydidae* (Le and McCord 2008). Although this clade likely originated in the Paleogene (Le and McCord 2008; Pereira et al. 2017), its fossil record is poor.

In a brief list of Brazilian turtles, Campos and de Broin (1981) reported *Rhinoclemmys* from the Pleistocene of the San Jose de Itaborai Basin, Rio de Janeiro, Brazil. The authors did not provide any details regarding the morphology of this material, and we here therefore disregard this report. Oliveira and Romano (2007) more recently reported Pleistocene tortoises from the same basin, but made no reference to *Rhinoclemmys*. Seymour (2015) similarly mentioned a Pleistocene record of a geoemydid from Talara, Peru, but this material is disregarded here as well, as it remains undescribed and unfigured. In contrast, Cadena et al. (2017) recently figured and described carapace and plastral bones of an indeterminate species of *Rhinoclemmys* from the Pleistocene Tablazo Formation of Santa Elena Province, Ecuador. As this material is poorly dated, only little information can be obtained regarding the likely dispersal of *Rhinoclemmys* from North to South America.

Testudinidae Batsch, 1788

Phylogenetic definition. Following Joyce et al. (2004), the name *Testudinidae* is herein referred to the crown clade arising from the last common ancestor of *Testudo graeca* Linnaeus, 1758, *Manouria emys* (Schlegel and Muller, 1844), but not any emydid, geoemydid, or platysternid.

Diagnosis. Representatives of *Testudinidae* can be differentiated from other testudinoids by a skull with extensive temporal emargination, the presence of a median maxillary ridge, the presence of a well-developed ridge throughout the length of the vomer, the presence of neural differentiation consisting of octagonal and quadrangular neurals, good coincidence between the costo-peripheral suture and pleuro-marginal sulcus, fusion of the marginals XII into a supracaudal, narrow and thin rib heads, narrow costo-vertebral tunnel, presence of a well-developed epiplastral lip, short pectorals, lack of an overlap of the entoplastron by the humero-pectoral sulcus, and fused femoral trochanters.

Chelonoidis Fitzinger, 1835

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

Diagnosis. *Chelonoidis* can be diagnosed as a member of *Testudinidae* based on the full list of characters provided for that clade above. *Chelonoidis* can be differentiated from other testudinids based on the presence of a median maxillary ridge in the palate, the absence of the cervical scute, presence of a hexagonal neural I with short posterolateral sides, contact between pleural III and marginal VI, a large entoplastron, pectoral scutes that are narrower medially, but expanded distally.

Comments. Some valid species of *Chelonoidis* from the *Chelonoidis nigra* species complex in the Galápagos Archipelago became extinct in modern times, such as *Chelonoidis abingdonii* (Günther, 1877) and *Chelonoidis phantastica* (van Denburgh, 1907) (see TEWG 2015, and references therein). These taxa are not included herein. Fossil occurences of *Chelonoidis* in the West Indies are treated in Vlachos (2018). Olson and David (2014) recently suggested that the genus name *Chelonoidis* should be considered masculine, and as such introduced several mandatory changes in species-group names of *Chelonoidis* because of the gender agreement rule. We herein follow the traditional treatement of *Chelonoidis* as feminine. The reasoning to support this conclusion will be presented elsewhere.

Chelonoidis australis (Moreno, 1889) (= *Testudo praestans* Rovereto, 1914 = *Chelonoidis santafecina* Agnolin, 2004)

Taxonomic history. *Testudo australis* Moreno, 1889 (new species); [*Testudo australis*] Williams 1950 (nomen nudum); *Chelonoidis australis* = *Testudo praestans* de la Fuente 1988 (new combination and senior synonym); *Chelonoidis australis* = *Testudo praestans* = *Chelonoidis santafecina* de la Fuente 2005 (senior synonym).

Type material. MLP 26–400 (holotype), a partial carapace (de la Fuente 1988, pl. 44; de la Fuente 1997a, figs. 9–12).

Type locality. Atlantic coast between Monte Hermoso and Punta Alta, Buenos Aires Province, Argentina (de la Fuente 1988); Monte Hermoso Formation, Montehermosan SALMA, Early Pliocene (de la Fuente 1988).

Referred material and range. Early Pliocene, Monte Hermoso Formation, Montehermosan SALMA, Buenos Aires Province, Argentina (type material of *Testudo praestans* Rovereto, 1914 and *Chelonoidis santafecina* Agnolin, 2004).

Diagnosis. *Chelonoidis australis* can be diagnosed as a member of *Testudinidae* based on the presence of alternating quadrangular/octagonal neurals II–V with corresponding alternating costals, coincidence of the costo-peripheral suture with the pleuro-marginal sulci, well-developed axillary buttresses that make contact with the costal bones viscerally, and a well-developed epiplastral lip. *Chelonoidis australis* is here attributed to *Chelonoidis* based on biogeographic considerations. *Chelonoidis australis* can be distinguished from extant members of *Chelonoidis*, but is similar to the fossil *Chelonoidis gallardoi*, in the development of vertebral gibbosities and from extant species of the *Chelonoidis nigra* complex by having relatively wide anterior and posterior plastral lobe with elongated gular and anal scutes.

Chelonoidis australis differs from *Chelonoidis gallardoi* in carapacial proportions, the absence of pleural gibbosities, a wider epiplastral lip, and a less-developed anal notch.

Comments. Moreno (1889) described and named two species of tortoises from the Pliocene of Argentina, *Testudo australis* and *Testudo formosa* (see below). *Testudo australis* was identified as a nomen nudum by Williams (1950:25) because "the original descriptions have not been seen," a conclusion followed by Auffenberg (1974), but this reasoning is insufficient. De la Fuente (1988, 1997a) more recently identified the type material of *Testudo australis* in the collections of MLP and listed a number of characters that distinguish *Chelonoidis australis* from *Chelonoidis gallardoi* (also see below). A recent revision of these characters concluded that some of these differences might be preservational artifacts (e.g., the gibbosities on the costals of *Chelonoidis gallardoi*, the shape and relative dimensions of the carapace) or related to sexual dimorphism (e.g., plastral concavity, the degree of development and thickness of the epiplastral and xiphiplastral extremities, variation in the development of the anal notch, and the shape of femoro-anal sulcus), as shown, for example, in specimens of the European tortoise *Titanochelon bolivari* (Pérez–García and Vlachos 2014). Even if the specimens attributed to these taxa represent male and female individuals, their incompleteness does not allow further comparisons (e.g., absence of the neural series in *Chelonoidis gallardoi*). We here tentatively treat these two species as distinct based on temporal considerations. The preserved carapacial elements of "*Testudo*" *praestans* Rovereto, 1914, allow its recognition as a junior synonym of *Chelonoidis australis* (see "*Testudo*" *praestans* below). The hereby-referred plastron complements the known anatomy of *Chelonoidis australis*. The plastron shows clear testudinid affinities, in particular the presence of a well-developed epiplastral lip, and most probably belongs to a female individual, as it is flat, the anal notch is weakly developed, and the xiphiplastral extremities poorly developed.

Chelonoidis gallardoi (Rovereto, 1914)

Taxonomic history. *Testudo gallardoi* Rovereto, 1914 (new species); *Geochelone gallardoi* Auffenberg 1974 (new combination); *Chelonoidis gallardoi* de la Fuente 1988 (new combination).

Type material. MACN 5206 (holotype), a partial shell of an adult individual (Rovereto 1914, pls. 8.6, 10.1; de la Fuente 1988, pl. 42–43; de la Fuente 1997a, figs. 2–8).

Type locality. Andalhuala, Catamarca Province, Argentina (Rovereto 1914); Andalhuala Formation, Huayquerian SALMA, Tortonian–Messinian, late Miocene (Riggs and Patterson 1939; Marshall and Patterson 1981).

Referred material and range. No material has been referred to date.

Diagnosis. *Chelonoidis gallardoi* can be diagnosed as a member of *Testudinidae* based on the presence of neural differentiation, coincidence of costo-peripheral sutures with pleuro-marginal sulci, the fusion of the twelfth marginal scutes, and presence of a well-developed epiplastral lip. It is here referred to *Chelonoidis* based on biogeographic considerations. *Chelonoidis gallardoi* differs from *Chelonoidis australis* by the presence of gibbosities on both neural and costal bones, by the estimated length/width ratio of the carapace, the presence of a deep anal notch, and the relative proportions of anterior and posterior plastral lobes. It further differs from the extant *Chelonoidis nigra* complex by having wider anterior and posterior plastral lobes and by having more elongate gular and anal scutes.

Comments. In addition to "*Testudo*" *praestans* (see above), "*Testudo*" *gallardoi* is one of two extinct testudinids named by Rovereto (1914) from the late Miocene of Catamarca Province, Argentina, but, as noted by de la Fuente (1988, 1997a), it appears that Rovereto (1914) did not take into account the previous description of extinct testudinids from Monte Hermoso by Moreno (1889; "*Testudo*" *australis* and "*Te.*" *formosa*) in nearby Buenos Aires Province. A revision of the type material of "*Te.*" *gallardoi* by de la Fuente (1988, 1997a) provided evidence regarding the validity of this taxon as a member of *Chelonoidis* and characters that differentiate it from the similarly sized *Chelonoidis australis*. However, most of these differences may be artifacts based on preservation and/or sexual dimorphism (also see *Chelonoidis australis,* above). One of the valid characters that might support the distinction of this taxon is the presence of gibbosities on the costal bones. However, the presence of this character should be reassessed with caution, as large amounts of plaster distort the true morphology of this specimen. As such, the distinction of this taxon is herein only confirmed tentatively based on temporal considerations. The available morphological information is limited for this species. As a result, its phylogenetic position was largely unresolved in the analysis of Zacarías et al. (2013) at the base of *Chelonoidis*. The presence of neural gibbosities, however, appears to be a character that is otherwise present in the large continental members of *Chelonoidis*, at least in the cases where it can be observed with confidence. Although these gibbosities can be also partially verified in *Chelonoidis lutzae* from Argentina (Zacarías et al. 2013, fig. 3, 1–3), they are probably not present in the giant *Chelonoidis* sp. figured by Sánchez-Villagra and Scheyer (2010) from Colombia. This character is only present in small and middle-sized extant *Chelonoidis* as individual variation (see Williams 1950). However, in small to middle-sized extinct species of *Chelonoidis*, the Galápagos tortoises, and extinct Neotropical tortoises from the West Indies, these gibbosities are absent. Given that the Afrotropical *Impregnochelys pachytestis* Meylan and Auffenberg, 1986, shows similar gibbosities, whereas the Nearctic large testudinids do not, this character may provide some support for the African origin of some South American tortoises. However, the utility of this character is yet to be examined in a global cladistic analysis.

Chelonoidis gringorum (Simpson, 1942)

Taxonomic history. *Testudo gringorum* Simpson, 1942 (new species); *Geochelone gringorum* Williams 1950 (new combination); *Chelonoidis gringorum* de la Fuente 1988 (new combination).

Type material. AMNH 3366 (holotype), a partial carapace and plastron (Simpson 1942, figs. 1–2; de la Fuente 1988, pl. 36; de la Fuente 1994, figs. 2a–c, 3a–c).

Type locality. South side of the Chubut Valley, between Gaiman and Dolavon, Chubut Province, Argentina (Simpson 1942);

upper section of the "Patagonian" (= Gaiman Formation of Mendia and Bayarsky 1981), late Colhuehuapean SALMA, Burdigalian, early Miocene.

Referred material and range. Early Miocene, Colhuehuapean SALMA, Chubut Province, Argentina (referred material of de la Fuente 1988, 1994; and Broin and de la Fuente 1993); early Miocene, Colhuehuapien SALMA, Río Negro Province, Argentina (*Chelonoidis* cf. *gringorum* of de la Fuente 1988; and Broin and de la Fuente 1993); early Miocene, Santacrucian SALMA, Santa Cruz Province, Argentina (Chelonii indet. of Broin and de la Fuente 1993); middle Miocene, Colloncuran SALMA, Chubut Province, Argentina (referred material of Oriozabala et al. 2018).

Diagnosis. *Chelonoidis gringorum* can be diagnosed as a member of *Testudinidae* based on the full list of shell characters listed for that clade above and as a member of *Chelonoidis* based on the absence of a cervical scute. *Chelonoidis gringorum* can further be diagnosed as a member of the *chilensis* group by the presence of an usually thin shell that is broad and depressed with lateral convex sides, a wide posterior plastral lobe, and anteroposteriorly narrow inguinal scar. *Chelonoidis gringorum* differs from *Chelonoidis chilensis* by the lack of contact between the inguinal and femoral scutes on the ventral side of the plastron, the presence of an inguinal groove ventrally located between the base of the posterior plastral lobe and the hypoplastral inguinal pillar of the bridge, and by the expansion of the posterior process of the ischium.

Comments. *Testudo gringorum* was named by Simpson (1942) based on a specimen that was given to him during the 1933 Scarritt Expedition to Patagonia. This expedition targeted the upper section of "Patagonian" (e.g., late Colhuehuapean SALMA, early Miocene) outcrops exposed along the southern portions of the Chubut River valley in Chubut, Argentina. The locality provided by Simpson (1942) is not precise, as it refers to a wide region were Sarmiento Formation outcrops are exposed. Subsequent work (see Referred material) has since been able to confirm the presence of this taxon in the region. Williams (1950), Loveridge and Williams (1956), and Auffenberg (1971, 1974) included *Testudo gringorum* in the genus *Geochelone*, but de la Fuente (1988, 1994) more recently referred it to *Chelonoidis*. Auffenberg (1971) considered *Chelonoidis gringorum* to be ancestral to *Chelonoidis chilensis*, while Lapparent de Broin (1991) believed it to be related to an unnamed taxon from the late Oligocene of Bolivia. The type material of *Chelonoidis gringorum* is indeed similar to the Bolivian taxon in the presence of elongated gular scutes that cover the anterior region of the entoplastron. This character shows some variability within *Chelonoidis*, as *Chelonoidis denticulata* and the *Chelonoidis nigra* complex usually have short gulars that do not reach the entoplastron. The type and referred specimens of *Chelonoidis gringorum* further confirm, and expand, this variability (summarized and updated in Oriozabala et al. 2018). Recent phylogenetic analyses recovered *Chelonoidis gringorum* as sister to the Bolivian taxon, either outside or within crown *Chelonoidis* (de la Fuente 1994), or as the sister group of the clade formed by *Chelonoidis chilensis* and *the Chelonoidis nigra* complex (Zacarías et al. 2013). *Chelonoidis gringorum* is the southernmost testudinid known worldwide.

Chelonoidis hesterna Auffenberg, 1971

Taxonomic history. *Geochelone hesterna* Auffenberg, 1971 (new species), *Geochelone* (*Chelonoidis*) *hesterna* Auffenberg 1974 (new combination); *Chelonoidis hesterna* de la Fuente 1988 (new combination).

Type material. UCMP 40200 (holotype), a near complete shell of an adult male tortoise, associated with a crushed skull and lower jaw, and some appendicular elements (Auffenberg 1971, figs. 1–2).

Type locality. San Nicolás (UCMPV locality V-4536), 3 km northeast of Villavieja, Huila, Colombia (Auffenberg 1971; Wood 1997); Cerbatana gravel sandclays, Villavieja Formation, Honda Group, Laventan SALMA, middle-late Miocene (Flynn et al. 1997; Wood 1997).

Referred material and range. No material has been referred to date.

Diagnosis. *Chelonoidis hesterna* can be diagnosed as a representative of *Testudinidae* and *Chelonoidis* based on the presence of a median maxillary ridge in the palate and the full list of shell characters listed for those clades above. *Chelonoidis hesterna* can further be diagnosed as a member of the *Chelonoidis carbonaria* complex through the development of a narrow and high shell with parallel edges when viewed from above and a narrow posterior plastral lobe. *Chelonoidis hesterna* differs from *Chelonoidis carbonaria* through the presence of a smoother shell, a straight bridge, a proportional shorter anterior plastral lobe, gular scutes that do not reach the entoplastron, humeral scutes that expand onto the epiplastra, an entoplastron that is longer than wide, and a humeral scute that is longer along the midline than the femoral scute.

Comments. *Chelonoidis hesterna* was named by Auffenberg (1971) based on a partial shell and a referred partial skull from the Miocene of Laventa Fauna of Colombia. Wood (1997) later reported that these two specimens do not originate from the same locality and suggested that the skull belongs to another, larger species, to which he referred a partial shell, the so-called Creutzberg specimen (Wood 1997). This specimen was first mentioned by Sánchez-Villagra (1993) and refigured in Sánchez-Villagra and Scheyer (2010; with some parts shown as reconstructed). The mentioned difference in size alone is not sufficient to properly distinguish the two taxa, and in the absence of an available description of the comparable parts, we are not able to confirm this proposed distinction. Regardless, even if the Creutzberg shell belongs to a new species, it is not possible to refer the skull of Auffenberg (1971) to it. As such, we herein include tentatively the information from the skull under *Chelonoidis hesterna*. According to Auffenberg (1971), *Chelonoidis hesterna* is ancestral to the *Chelonoidis denticulata* + *Chelonoidis carbonaria* group, but closer to the former species. The close relationship of these three species is supported by the analyses of de la Fuente (1994) and Zacarías et al. (2013). In the analysis of de la Fuente (1994), it is recovered in a polytomy with *Chelonoidis carbonaria* and *Chelonoidis denticulata*, whereas in Zacarías et al. (2013), *Chelonoidis hesterna* is the sister to *Chelonoidis carbonaria*. Auffenberg (1971) suggested that *Chelonoidis hesterna* is a basal species of the *carbonaria* group from which the two extant species are derived as a result of the development of a great savannah in the Amazonian region at the end of the Miocene.

Chelonoidis lutzae Zacarías et al., 2013

Taxonomic history. *Chelonoidis lutzae* Zacarías et al., 2013 (new species).

Type material. CTES PZ7391 (holotype), carapace and plastron, both scapulae, right coracoids, both humeri and femora (Zacarias et al. 2013, figs. 31–5, 41–2, 51–7).

Type locality. Toropí Creek, 10 km south of Bella Vista, Corrientes Province, Argentina (Zacarías et al. 2013); upper section of lower member of the Toropí Formation (Zacarías et al. 2013), Lujanian SALMA, late Pleistocene.

Referred material and range. No material has been referred to date.

Diagnosis. *Chelonoidis lutzae* can be diagnosed as a member of *Testudinidae* based on the presence of fused femoral trochanters and the full list of shell characters listed for that clade above and as a member of *Chelonoidis* based on the absence of cervical scute. *Chelonoidis lutzae* differs from other *Chelonoidis* in the presence of a large sub-rhomboidal entoplastron with a distal projection that is crossed by the pectoral scute.

Comment. This recently named taxon is the most complete and well-preserved large tortoise from Argentina, allowing the documentation of numerous characters used to infer the phylogenetic position of the Argentinian large tortoises. The morphology of the plastron clearly distinguishes this taxon from known *Chelonoidis* (see Diagnosis). According to the phylogenetic analysis of Zacarías et al. (2013), *Chelonoidis lutzae* is recovered as sister to *Chelonoidis australis* (if *Chelonoidis gallardoi* is pruned) and all large continental extinct tortoises are recovered in an unresolved polytomy with the two primary *Chelonoidis* subclades (*nigra*+*chilensis* and *carbonaria*+*denticulata*). Note, however, that monophyly is forced due to the inclusion of a single outgroup.

Invalid and Problematic Taxa

Chelonoidis santafecina Agnolin, 2004
nomen invalidum
(objective junior synonym of *Testudo praestans* Rovereto, 1914; subjective junior synomym of *Chelonoidis australis* [Moreno, 1889])

Taxonomic history. *Chelonoidis santafecina* Agnolin, 2004 (new species); *Chelonoidis australis* = *Testudo praestans* = *Chelonoidis santafecina* de la Fuente 2005 (junior synonym).

Type material. MACN 5195 (holotype), a partial carapace and an almost complete plastron (Agnolin 2004, fig. 1). The holotype was erroneously listed as MACN 10113 by Agnolin (2004).

Type locality. Near Monte Hermoso, Buenos Aires Province, Argentina (Rovereto 1914); Monte Hermoso Formation, Montehermosan SALMA, Early Pliocene (de la Fuente 1997a).

Comments. Agnolin (2004) named *Chelonoidis santafecina* based on a partial shell that he reported to originate from the late Pleistocene Carcarañá Formation of Santa Fé Province, Argentina. Shortly after, de la Fuente (2005) exposed several issues with this new taxon. In particular, Agnolin (2004) erroneously assigned the collection number MACN 10113 to the type material of *Chelonoidis santafecina*, when in fact this number belongs to another specimen previously described as *Chelonoidis* sp. from the Pleistocene of Río Carcarañá (de la Fuente 1988, 1997b). In addition, the material described by Agnolin (2004) is already the type material of *Testudo praestans* (cataloged as MACN 5195), a species named by Rovereto (1914). The type locality of *Chelonoidis santafecina* is therefore the lower Pliocene Monte Hermoso Formation of Monte Hermoso, Buenos Aires Province, Argentina, and *Testudo praestans* Rovereto, 1914 is the objective junior synonym of *Testudo praestans*. We here otherwise recognized *Chelonoidis santafecina* as a subjective junior synonym of *Chelonoidis australis* (see above).

Chelys patagonica Wieland, 1923
nomen dubium

Taxonomic history. *Chelys patagonica* Wieland, 1923 (new species); *Chelus patagonica* Kuhn 1964 (unjustified emendation); [*Chelys patagonica*] Joyce and Faux 2008 (nomen dubium).

Type material. YPM VP 000351 (holotype), a partial carapace (Joyce and Faux 2008, fig. 1).

Type locality. Near Puerto Militar, Bahía Blanca, Buenos Aires Province, Argentina (Wieland 1923); precise stratigraphic location unknown, possibly Miocene (Wieland 1923).

Comments. Wieland (1923) casually named *Chelys patagonica* based on an unfigured, partial shell from Buenos Aires Province, Argentina. Simpson (1942) later suggested that Wieland did not intend to name a new species but only to provide "a purely arbitrary name of convienience" (Wieland 1923:14), noted testudinid features, but also suggested that the type specimen was perhaps lost. Wood (1976) later agreed with these sentiments and further noted uncertainty in the generic allocation of this specimen by Wieland (1923). Joyce and Faux (2008) more recently re-located the type specimen, provided figures and a description, and confirmed its testudinid nature. With regard to the validity of this name, Joyce and Faux (2008) further concluded that "it is impossible to know what Wieland intended" (Joyce and Faux 2008:802), but that if Wieland (1923) indeed wanted to name a new species this name would have to be considered available under the Code. We here conclude that Wieland (1923) indeed intended to name a new taxon, as he places the name in italics, as opposed to several nonitalicized usages of informal taxonomic names. We further concur with the views expressed by Joyce and Faux (2008) of the testudinid affinities of this specimen, to which we add the clear contact of pleural III with marginal VI, a character shared by the members of *Geochelona* and *Chelonoidis,* of course. However, as Joyce and Faux (2008) correctly note, this specimen lacks diagnostic features. As such, *Chelys patagonica* is here considered to be a nomen dubium.

Testudinites sellovii Weiss, 1830
nomen dubium

Taxonomic history. *Testudinites sellovii* Weiss, 1830 (new species); *Testudinites sellouwi* Moreno, 1889 (incorrectly spelled species epithet); *Testudo sellowii* Paula Couto 1948 (new combination; incorrectly spelled species epithet); *Geochelone* (*Chelonoidis*) *sellowi* Auffenberg 1974 (new combination; incorrectly spelled species epithet); [*Chelonoidis sellovii*] TEWG 2015 (new combination, nomen dubium).

Type material. MNB R.2480 (syntype series), eight shell fragments (Weiss 1830, pl. 5).

Type locality. Paso de Catalán, Río Queguay, Paysandú, Uruguay (Weiss 1830); Pleistocene (Ubilla et al. 2004).

Comments. *Testudinites sellovii* is based on fragmentary shell remains from the Pleistocene of Uruguay. The type material preserves little anatomical information. The gulars are short and do not cover the entoplastron. This character is found in some members of *Chelonoidis*, but also many other representatives of *Pan-Testudinidae*. Based on our personal observations of the type material, we conclude that the available morphology otherwise overlaps with that of *Chelonoidis chilensis,* but the Chaco tortoise is much smaller in size. As larger size is insufficient to recognize a valid species, we agree with TEWG (2015) and Vlachos et al. (2018) that this taxon should be regarded as a nomen dubium. It is clear that Weiss (1830) intended to name a new genus, not just a wastebasket for fossils of the extant genus *Testudo*, and so the generic name *Testudinites* should not be excluded by the provisions of Art. 20 (ICZN 1999) (contra TEWG 2015). However, as this name has not been used as valid in the last 150 years, it should be regarded as a nomen oblitum and not given priority over *Chelonoidis* (Art. 23.9.2, ICZN 1999). The subsequent emendations of the specific name by Moreno (1889; *sellouwi*), Paula Couto (1948; *sellowii*), and Auffenberg (1974; *sellowi*) are unjustified emendations (TEWG 2015).

Testudo elata Gervais, 1877
nomen dubium

Taxonomic history. *Testudo elata* Gervais, 1877 (new species); *Geochelone elata* Auffenberg 1974 (new combination); [*Testudo elata*] Campos and de Broin 1981 (nomen dubium).

Type material. MNHN uncat. (syntype series), a fragment of a dentary, two partial limb bones, and a plastral fragment (Gervais 1877, pl. 7). These specimens are most probably lost, as we were unable to find them in the collections or in the catalog of MNHN.

Type locality. Acre, Brazil (Gervais, 1877); Solimões Formation, late Miocene (Latrubesse et al. 2010).

Comments. The bone remains upon which Gervais (1877) based *Testudo elata* are highly fragmentary and preclude any detailed taxonomic determination. In fact, it is difficult to even confirm testudinatan affinities for most of the specimens based on the published information. Indeed, only one figured fossil (Gervais 1877, pl. 7.4) can be confirmed to be a shell fragment, but further identification is not possible. This name was considered to be a nomen dubium by Campos and de Broin (1981) and Oliveira and Romano (2007), a conclusion followed herein as well.

Testudo formosa Moreno, 1889
nomen dubium

Taxonomic history. *Testudo formosa* Moreno, 1889 (new species); [*Testudo formosa*] Auffenberg 1974 (nomen dubium).

Type material. MLP uncat. (syntype series), remains of a carapace and an almost complete plastron (Moreno 1889; not figured). Most probably these specimens are lost, as we were unable to find them either in the collections or in the catalog of MLP.

Type locality. Atlantic coast between Monte Hermoso and Punta Alta, Buenos Aires Province, Argentina (Moreno 1889); Monte Hermoso Formation, Montehermosan SALMA, Early Pliocene (de la Fuente 1988).

Comments. Moreno (1889) named *Testudo formosa* based on material from an unnamed locality near Monte Hermoso, Buenos Aires Province, Argentina. He provided a brief description of the carapace and the plastron of *Testudo formosa,* while noting similarities of the plastron with that of extant *Chelonoidis nigra* (his *Testudo nigrita*), in particular its flatness and the depth of the scute sulci. Considering the insufficient information provided by Moreno (1889) to characterize this tortoise and the fact that the type material appears to be lost, we concur with Auffenberg (1974) and de la Fuente (1988) that *Testudo formosa* is a nomen dubium.

Testudo paranensis Scalabrini, 1887
nomen nudum

Taxonomic history. *Testudo paranensis* Scalabrini, 1887 (new species); [*Testudo paranensis*] Williams 1950 (nomen nudum).

Type material. MPCNyAAS uncat. (syntype series), turtle shell fragments (Scalabrini 1887, unfigured). We were unable to find these remains in the collections or catalog of MPCNyAAS and they are therefore likely lost.

Type locality. Paraná River ravines, near Paraná, Entre Ríos Province, Argentina (Scalabrini 1887); conglomerado ósifero (i.e., bone conglomerate), Ituzaingó Formation, Upper Miocene (Cione et al. 2000).

Comments. Scalabrini (1887) named without a definition, description, or illustration a new tortoise, *Testudo paranensis*, from the ravines of Paraná River, near Paraná City, Entre Ríos Province, Argentina. The type material was initially supposed to be located in the Museum of the Province of Entre Rios, but our study of the material present at the current Museo Provincial de Ciencias Naturales y Antropológicas "Antonio Serrano" of Paraná reveals that this material is most probably lost. Williams (1950) and Auffenberg (1974) considered *Testudo paranensis* to be a nomen nudum, because it does not fulfill the availability criteria of the ICZN, a conclusion with which we concur. Auffenberg (1974) referred authorship of *Testudo paranensis* to Scalabrini (1884), but this is an error, as this article does not mention a tortoise.

Testudo praestans Rovereto, 1914
nomen invalidum
(objective sernior synonym of *Chelonoidis santafecina* Agnolin, 2004;
junior synonym of *Chelonoidis australis* [Moreno, 1889])

Taxonomic history. *Testudo praestans* Rovereto, 1914 (new species); *Geochelone preastans* Pascual et al. 1966 (new combination); *Chelonoidis australis* = *Testudo praestans* de la Fuente 1988 (junior synonym); *Chelonoidis australis* = *Testudo praestans* = *Chelonoidis santafecina* de la Fuente 2005 (junior synonym).

Type material. MACN 5195 (holotype), a partial shell (Rovereto 1914, figs. 69–70; de la Fuente 1988, pl. 45–46; de la Fuente 1997a, figs. 14–17).

Type locality. Near Monte Hermoso, Buenos Aires Province, Argentina (Rovereto 1914); Monte Hermoso Formation, Montehermosan SALMA, Early Pliocene (de la Fuente 1997a).

Comments. *Testudo praestans* is based on a partial shell from the Pliocene of Buenos Aires Province, Argentina (Rovereto 1914). Williams (1950) considered this taxon to be valid and suggested that it is perhaps the Pliocene descendant (= "representative" of Williams 1950) of the Miocene *Chelonoidis gringorum*, but de la Fuente (1988, 1997a) later suggested that it is synonymous with *Chelonoidis australis*. Although the two taxa are both known from fragmentary material only, the few comparable parts are similar by being large and by being decorated by carapacial gibbosities. The geographical and temporal proximity of the material referred to these taxa further corroborates their synonymy. We therefore here agree that "*Testudo*" *praestans* is a junior synonym of *Chelonoidis australis*. For the objective senior synonymy with *Chelonoidis santafecina,* see above.

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Appendix 1
Institutional Abbreviations

AMNH	American Museum of Natural History, New York, New York, USA
CTES	Paleozoología Corrientes, Facultad de Ciencias Exactas, Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina
MNB	Museum für Naturkunde, Berlin, Germany
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MLP	Museo de La Plata, La Plata, Argentina
MPCNyAAS	Museo Povincial de Ciencias Naturales y Antrapológicas "Antonio Serrano," Paraná, Argentina
UCMP	University of California Museum of Paleontology, Berkeley, California, USA
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

Appendix 2
Named South American Fossil Testudinoid Genera

Testudinites Weiss, 1830 (type species: *Testudinites sellovii* Weiss, 1830)

Appendix 3
Biogeographical Summary of South American Fossil *Testudinoidea*

Numbers in brackets reference Figure 3. *Abbreviation*: TL, Type locality.

Argentina

[1] Late Oligocene, Deseadan SALMA, Chattian; Cabeza Blanca, Chubut Province; *Testudinidae* indet. (Broin and de la Fuente 1993)

[2] Early Miocene, Colhuehuapean SALMA, Aquitanian–Burdigalian; Chubut River Valley, Chubut Province; *Chelonoidis gringorum* (TL) (Simpson 1942; de la Fuente 1988, 1994; Broin and de la Fuente 1993)

[3] Early Miocene, Colhuehuapien SALMA, Aquitanian–Burdigalian; Paso Córdova, Río Negro Province; *Chelonoidis gringorum* (de la Fuente 1988; Broin and de la Fuente 1993)

[4] Early Miocene, Santacrucian SALMA, Burdigalian; Pampa del Castillo, Santa Cruz Province; *Testudinidae* indet. (Chelonii indet. of Broin and de la Fuente 1993)

[5] Early–middle Miocene, Friasian–Colloncuran SALMA, Burdigalian–Langhian; Arroyo Seco de la Frazada, Mendoza Province; *Chelonoidis* sp. (middle and large sized) (Forasiepi et al. 2011)

[6] Early-middle Miocene, Friasian–Colloncuran SALMA, Burdigalian–Langhian; Zitro Mine, Mendoza Province; *Testudinidae* indet. (de la Fuente 1988; Broin and de la Fuente 1993)

[7] Early Miocene, Colloncuran SALMA, Langhian; Comallo, Río Negro Province; *Chelonoidis gringorum* (de la Fuente 1988; Broin and de la Fuente 1993)

[8] Early Miocene, Colloncuran SALMA, Langhian; Pilcaniyeu Viejo, Río Negro Province; *Chelonoidis* sp. (de la Fuente 1988; Broin and de la Fuente 1993)

[9] Middle Miocene, Colloncuran SALMA, Langhian; Collón Currá Formation, Chubut Province; *Chelonoidis gringorum*, *Chelonoidis* sp. (Broin and de la Fuente 1993; Oriozabala et al. 2018)

[10] Late Miocene, Chasicoen SALMA, Tortonian; Loma de las Tapias, San Juan Province; *Testudinidae* indet. (Contreras and Baraldo 2011)

[11] Late Miocene, Chasicoen–Huayquerian SALMA, Tortonian–Messinian; Arroyo Chasicó, Buenos Aires Province; *Testudinidae* indet. (Broin and de la Fuente 1993)

[12] Late Miocene, Huayquerian SALMA, Tortonian–Messinian; Huachipampa, San Juan Province; *Testudinidae* indet. (Broin and de la Fuente 1993)

[13] Late Miocene, Hayquerian SALMA, Tortonian–Messinian; Andalhuala–Chiquimil, Catamarca Province; *Chelonoidis gallardoi* (TL) (Broin and de la Fuente 1993; de la Fuente 1997a)

[14] Late Miocene, Hayquerian SALMA, Tortonian–Messinian; Salinas Grandes de Hidalgo, La Pampa Province; *Testudinidae* indet. (Broin and de la Fuente 1993)

[15] Late Miocene, Huayquerian SALMA, Tortonian–Messinian; Entre Ríos Province; *Testudinidae* indet. (*Testudo paranensis* of Scalabrini, 1887; Broin and de la Fuente 1993)

[16] Early Pliocene, Montehermosan SALMA, Zanclean; Montehermoso, Buenos Aires Province; *Chelonoidis australis* (TL) (including type material of *Testudo praestans* Rovereto, 1914), *Testudinidae* indet. (including type material of *Testudo formosa* Moreno, 1889) (de la Fuente 1988, 1997a)

[17] Early Pliocene, Montehermosan SALMA, Zanclean; Villa Bustos, Córdoba Province; *Chelonoidis* cf. *chilensis* (de la Fuente and Cabrera 1988; Broin and de la Fuente 1993)

[18] Early Pleistocene, Ensenadan SALMA, Calabrian; San Justo Department, Córdoba Province; *Chelonoidis* sp. (Zacarías and Luna 2013)

[19] Early Pleistocene, Ensenadan SALMA, Calabrian; Olivos, Buenos Aires Province; *Chelonoidis* sp. (de la Fuente 1988; Broin and de la Fuente 1993)

[20] Late Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Lavalle Department, Corrientes Province; *Chelonoidis* sp. (Zacarías and Luna 2013)

[21] Late Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Bella Vista Department, Corrientes Province; *Chelonoidis lutzae* (TL), *Chelonoidis* sp. (Broin and de la Fuente 1993; Noriega et al. 2000; Zacarías et al. 2013, 2014)

[22] Late Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Santa Lucia, Corrientes Province; *Chelonoidis* sp., *Trachemys* cf. *dorbigni* (Zacarías et al. 2014)

[23] Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Juntas de Fontana, Formosa Province; *Trachemys* sp. (de la Fuente 1999)

[24] Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Diamante City, Entre Ríos Province; *Chelonoidis denticulata* (Manzano et al. 2009)

[25] Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Río Coronda, Santa Fé Province; *Trachemys* sp. (de la Fuente 1999)

[26] Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; San Lorenzo, Santa Fé Province; *Chelonoidis* cf. *chilensis* (de la Fuente 1988, 1997b; Broin and de la Fuente 1993)

[27] Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Santa Fé Province; *Chelonoidis* sp. (de la Fuente 1988, 1997b; Broin and de la Fuente 1993)

[28] Late Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Playa del Barco, Buenos Aires Province; *Testudinidae* indet. (Broin and de la Fuente 1993)

[29] Late Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Cañada Las Achiras, Entre Ríos Province; *Trachemys dorbigni, Testudinidae* indet. (de la Fuente 1999; de la Fuente et al. 2002; Broin and de la Fuente 1993)

[30] Late Pleistocene–early Holocene, Lujanian SALMA, Calabrian–Tarantian; Mar Chiquita, Córdoba Province; *Trachemys dorbigni* (Cabrera and Luna 2011)

[31] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Quitilipi Department, Chaco Province, *Chelonoidis* sp. (Zacarías et al. 2011)

Bolivia

[32] Late Oligocene, Deseadan SALMA, Chattian; Quebrada Saguayo, Santa Cruz Department; *Chelonoidis* sp. (Broin 1991)

[33] Middle Miocene, SALMA unknown, Langhian–Serravallian; Quebrada Honda, Tarija Department; *Chelonoidis* sp. (Cadena et al. 2015)

[34] Late Pleistocene, Lujanian SALMA, Calabrian–Tarantian; Quebrada de Nuapua, Chuquisaca Department; *Chelonoidis* sp. (Hoffstteter 1968; Broin 1991)

Brazil

[35] Late Miocene, Huayquerian SALMA, Tortonian–Messinian; Pedra Preta, Alto Rio Juaruá, Acre State; *Testudinidae* indet. (Campos and Broin 1981), giant *Chelonoidis* sp. (Bocquentin and Negri 1991; Lapparent de Broin et al. 1993)

[36] Late Miocene, Huayquerian SALMA, Tortonian–Messinian; Alto Río Purus, Acre State; *Testudinidae* indet. (Campos and Broin 1981), a giant *Chelonoidis* sp. (Bocquentin and Negri 1991; Lapparent de Broin et al. 1993)

[37] Late Miocene, Huayquerian SALMA, Tortonian–Messinian; Alto Rio Acre, Acre State; *Testudinidae* indet. (Campos and Broin 1981), a giant *Chelonoidis* sp. (Bocquentin and Negri 1991; Lapparent de Broin et al. 1993)

[38] Late Miocene–early Pleistocene, SALMA unknown; Amazonas State; *Testudinidae* indet. (type material of *Testudo elata* Gervais, 1877)

[39] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Itaborai, Rio de Janeiro State; *Rhinoclemmys* sp., *Chelonoidis* sp. (Campos and Broin 1981)

[40] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Touro Passo, Rio Grande do Sul State; *Trachemys* sp. (Maciel et al. 1996)

[41] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Passo da Juquiri, Rio Grande do Sul State; *Chelonoidis* sp. (Maciel et al. 1996)

[42] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Arroio Seival and Sagna Borba, Rio Grande do Sul State; *Chelonoidis* sp. (giant) (Maciel et al. 1996)

[43] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Santa Victoria do Palmar, Rio Grande do Sul State; *Chelonoidis* cf. *carbonaria* (Maciel et al. 1996)

Colombia

[44] Early–middle Miocene, SALMA unknown; Península de la Alta Guajira, La Guajira Departement; *Chelonoidis* sp. (Cadena and Jaramillo 2015)

[45] Middle–late Miocene, Laventan–Hayquerian SALMA, Langhian–Tortonian; San Nicolas and La Venta, Huila Departement; *Chelonoidis hesterna* (TL), *Chelonoidis* sp. (giant) (Auffenberg 1971; Wood 1997; Sánchez-Villagra 1993; Sánchez-Villagra and Scheyer 2010)

Ecuador

[46] Pleistocene, SALMA unknown; Ataualpa, Santa Elena Province; *Rhinoclemmys* sp., *Geoemydidae* indet., *Testudinidae* indet. (Cadena et al. 2017)

[47] Pleistocene–Holocene, SALMA unknown; San José, Manabi Province, *Chelonoidis* sp. (Cantalamessa et al. 2001)

Paraguay

[48] Pleistocene, SALMA unknown; Bajo Chaco, Presidente Hayes Department; *Chelonoidis* sp. (Souberlich and de la Fuente 2011)

[49] Pleistocene, SALMA unknown; Villa Hayes District, President Hayes Department; *Testudinidae* indet. (Rios Díaz 2013)

Perú

[50] Pleistocene, SALMA unknown; Talara, Piura Department; *Geoemydidae* indet. (Seymour 2015)

Uruguay

[51] Pleistocene, SALMA unknown; Passo de Catalán, Paysandú Department; *Testudinidae* indet. (type material of *Testudinites sellovii* Weiss, 1830)

[52] Pleistocene, SALMA unknown; Rio Negro Department; *Chelonoidis* sp. (Berro 1927; Achaval, in de la Fuente 1994)

[53] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Artigas Department; *Chelonoidis* sp. (Ubilla et al. 2004)

[54] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Salto Department; *Chelonoidis* sp. (Ubilla et al. 2004)

[55] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Soriano Department; *Chelonoidis* sp. (Berro 1927)

[56] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Colonia Department; *Chelonoidis* sp. (Berro 1927)

[57] Late Pleistocene, SALMA unknown, Calabrian–Tarantian; Malo Creek, Tacuarembo Department; *Chelonoidis* sp. (Ubilla et al. 2004)

Venezuela

[58] Middle Miocene–early Pliocene, SALMA unknown, Langhian–Piacenzian; Urumaco Municipality, Falcón State; *Testudinidae* indet. (Sánchez Villagra and Scheyer 2010)

Appendix 4
Hierarchical Taxonomy of Named South American Fossil *Testudinoidea*

Testudinoidea Fitzinger, 1826
  Testudinidae Batsch, 1788

Chelonoidis Fitzinger, 1835
 Chelonoidis australis (Moreno, 1889)
 Chelonoidis gallardoi (Rovereto, 1914)
 Chelonoidis lutzae Zacarías et al., 2013
 Chelonoidis gringorum (Simpson, 1942)
 Chelonoidis hesterna (Auffenberg, 1971)

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