Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujvp20

Tacuarembemys kusterae, gen. et sp. nov., a new Late Jurassic–earliest Cretaceous continental turtle from western Gondwana

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Published online: 04 Nov 2014.

To cite this article: Daniel Perea, Matías Soto, Juliana Sterli, Valeria Mesa, Pablo Toriño, Guillermo Roland & Jorge Da Silva (2014) Tacuarembemys kusterae, gen. et sp. nov., a new Late Jurassic–earliest Cretaceous continental turtle from western Gondwana, Journal of Vertebrate Paleontology, 34:6, 1329-1341, DOI: 10.1080/02724634.2014.859620

To link to this article: http://dx.doi.org/10.1080/02724634.2014.859620

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INTRODUCTION

Although turtles from Upper Jurassic–Neocomian continental deposits are common in Asia, Europe, and North America (e.g., Gaffney, 1979; Hirayama et al., 2000; Joyce, 2000; Sukhanov, 2000; Milner, 2004; Rabi et al., 2010; Joyce et al., 2011; Pérez-García and Ortega, 2011), they are virtually unknown in Gondwana. In South America, only the Early–Middle Jurassic Contorchelys antiqua Sterli, 2008, and an Aptian–Albian turtle fauna from Cerro Barcino, Argentina, and the Araripe Basin of Brazil are known (Gaffney et al., 2006, 2007; de la Fuente et al., 2011; Sterli et al., 2013).

Here we describe a new genus and species of turtle from the Tacuarembó Formation (Late Jurassic–earliest Cretaceous), which represents the oldest known turtle from Uruguay. Furthermore, this discovery begins to fill in the fossil record gap of continental turtles from the Jurassic to the Cretaceous in South America. Although the preserved remains of this new turtle are fragmentary, we considered that its significance regarding time, environment, anatomy, and taxonomy are worth exploring. Consequently, the main goals of this paper are to present, describe, and illustrate this new turtle, to explore its phylogenetic relationships in a global turtle data set, and to discuss the importance of this finding in the global context of turtle evolution.

Institutional Abbreviations—FC-DPV, Colección de Vertebrados Fósiles, Facultad de Ciencias, Montevideo, Uruguay; MGT, Museo de Geociencias de Tacuarembó, Tacuarembó, Uruguay.

Anatomical Abbreviations—ASN, anterior supernumerary scale; CB, cancellous bone; CO, costal plate; EC, external cortex; IC, internal cortex; MA, marginal scale; NE, neural plate; NU, nuchal plate; PC, peripheral plate; PL, pleural scale; R, ridges (perpendicular to the plate margins); SF, possible Sharpey’s fibers; SS, scale sulci; VE, vertebral scale.

GEOLOGIC SETTING

The sandstones that form the Tacuarembó Formation, which crops out in the southern region of the Paraná Basin (called the Norte Basin in Uruguay), were first described by Walther (1911). Bossi (1966) gave formational rank to these sedimentary deposits, and Bossi et al. (1975) further recognized lower and upper members. Perea et al. (2009) formalized this nomenclature by naming them Batoví and Rivera members, respectively. Perea et al. (2009) reviewed the paleontologic and chronostratigraphic knowledge of the Tacuarembó Formation, proposed a Late Jurassic–Early Cretaceous age for it, and identified the Priohybbodus arambourgi Assemblage Zone. Based on radiometric dates from the overlying basalt, the Tacuarembó Formation cannot be younger than the Haurtanian (Perea et al., 2001, 2009, and references therein).

Intensive field work carried out over the last couple of years in the Batovi Member (the only fossiliferous member of the unit) yielded abundant body fossils of bivalves, gastropods, conchostracans, hybodontids, ‘semionotids,’ actinistians, dipnoans, crocodyliforms, and theropod dinosaurs (see Perea et al., 2009).
Moreover, ichnofossils attributed to sauropod dinosaurs have been described recently (Mesa and Perea, 2010). Of particular interest are body fossils indicative of a Late Jurassic–Early Cretaceous age (Perea et al., 2001; Shen et al., 2004; Soto and Perea, 2008, 2010; Soto et al., 2012a, 2012b).

One of the most recent discoveries in the Batovi Member is an external partial mold of a carapace and associated shell bone fragments, described herein, that represent a new genus and species of turtle. The remains were recovered from fine-grained, pink-yellowish sandstones of mainly quartz composition. Bioturbation is common in the vicinity of the outcrop.

MATERIALS AND METHODS

The specimen is housed in the MGT. A sandstone block containing the fossil was isolated from the rock and protected by a plaster jacket. Then, the mold was prepared under a binocular microscope and completely reinforced with cyanoacrylate. A computed tomography analysis was made so as to reject or confirm the presence of bones potentially included in the sandstone block. Standard petrographic thin-sections of shell bone samples were prepared for histological analysis. The shell surface pattern was analyzed using a JSM-5900 LV scanning electron microscope (SEM). Taxonomic nomenclature in this paper follows Joyce et al. (2013). We added framework follows Perea et al. (2009).

Scheyer and Sander (2004) and Scheyer (2007). The stratigraphic framework follows Lyson et al. (2011), and histological terminology follows Scheyer and Sander (2004) and Scheyer (2007). The stratigraphic analysis is based on Sterli and de la Fuente (2013). We added Tacuarembemys kusterae and a character (anterior supernumerary scale) to the Sterli and de la Fuente (2013) data set, resulting in an augmented data matrix of 102 taxa and 241 characters, which was constructed in Mesquite (Appendix S1; Maddison and Maddison, 2007). All characters showing a clear morphcline were considered additive (22 in total; see Appendix S2). All characters were weighted equally. All cladistic analyses were performed in TNT (Goloboff et al., 2008a, 2008b). Two rounds of tree bisection reconnection (TBR) were performed. In the first round, the original Wagner tree is replicated and perturbed 1000 times using the TBR algorithm. All of the most parsimonious trees (MPTs) found in the first round were subjected to a second round of TBR to find all MPTs. Consistency (CI) and retention (RI) indices were calculated. Branch support is measured using Bremer support, jackknife, and bootstrap resamplings. Jackknife and bootstrap resamplings were obtained after 1000 replicates, and the values are shown as the difference in the frequency of a clade and the frequency when it is contradicted (GC values of Goloboff et al., 2003). If more than one MPT was found, a strict consensus was calculated. If the strict consensus was highly collapsed, the script written by Pol and Escapa (2009) was run in TNT to identify the rogue taxa and the precise causes (e.g., conflict of characters, lack of information, or both) for this behavior. To explore the evolution of certain characters, we mapped those characters using the TNT option of Optimize/Characters/Common mapping. Character numbers as in TNT (i.e., starting from 0). In Mesquite, character numbers are given as TNT number +1 (i.e., starting from 1).

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788, sensu Joyce, Parham, and Gauthier, 2004

TACUAREMBEMYS, gen. nov.

Etymology—From Tacuarembó Province, the area where the specimen was collected, and ‘emys,’ Greek for turtle.

Type Species—Tacuarembemys kusterae, sp. nov.

Diagnosis—As for type and only species.

Distribution—Upper Jurassic–?lowermost Cretaceous, Tacuarembó Province, northern Uruguay.

FIGURE 1. Map showing the locality from which MGT-1185, the holotype of Tacuarembemys kusterae, gen. et sp. nov., was collected.
presence of a deep nuchal notch, allowing vertebral 1 reaching the anterior rim of the carapace; it differs from those taxa, however, in the absence of highly ornamented shells, contact between neural 2 and costal 3, the presence of anterior supernumerary scales, and the shape of costal 1. It also differs from A. barretoi in the shape of the nuchal and from L. tenerensis in the shape of peripherals. It is different from Procirelrella cerrobobincae in the presence of nuchal notch, absence of cervical scale, presence of anterior supernumerary scale, and shape of vertebral 1. It differs from Sinemys lens Wiman, 1930, in the presence of marginal sulci on the peripherals only (at least in the anterior region of the carapace) and in the shape of the nuchal.

Autapomorphic characters of Tacuarembemys kusterae include carapace vaulted but not strongly convex, with a wide and well-developed nuchal notch (length/width = 0.30); a pair of triangular anterior supernumerary scales placed between marginal 1, vertebral 1, and pleural 1; wide nuchal plate with curved anterior and posterior borders; and narrow neural plates, with neurals 1 and 3–6 hexagonal and neural 2 rectangular in outline.

DESCRIPTION

The shell is represented by an external mold preserved in fine-grained sandstone, which reflects the morphology of the major part of the carapace (ca. two-thirds of it; see Fig. 2), as well as several disarticulated, mostly fragmentary carapace bones. Some of the most complete bones, such as costal 2 and neural 4 (Fig. 5), match the correlated regions of the mold. The estimated total shell length (straight sagittal length) is 180 mm (additional measurements in Table 1). The mold preserves the limits of scales and plates, but not the subtle shell surface ornamentation. This can be seen on the external surface of the bone fragments using a stereoscopic lens or a microscope (see below). The portion of the carapace mold posterior to neural plate 6 and the external borders posterior to peripheral 2 are not preserved (Fig. 2). Contrary to other continental Jurassic turtles (e.g., Kayentachelys aprix, Eileanchelys walldmani, Heckerochelys romani, xinjiangchelyids, sinemydids; Gaffney et al., 1987; Sukhanov, 2000, 2006; Matzke et al., 2004; Anquetin et al., 2009), the anterior border of Tacuarembemys kusterae is incised by a pronounced and deep nuchal notch. The deep nuchal notch resembles the one observed in Mongolochelys efernovi from the Upper Cretaceous of Mongolia and Naomichelys speciosa from the mid-Upper Cretaceous of North America (Khozatsky, 1997; Hirayama et al., 2000).

Macroscopically, the plates appear devoid of ornamentation (Figs. 3, 4A), except for small ridges that develop near the limits of the plates and are perpendicular to them. The external surface of a costal plate fragment was examined and small, randomly distributed pits are observed both microscopically (Fig. 4A) and using the SEM (Fig. 5). In thin-section, small, randomly distributed vascular canals were observed (Fig. 6). Although the general morphology of T. kusterae resembles that of N. speciosa, the lack of any remarkable ornamentation in the former differs notably from the pustulate ornamentation found in solenymydids (Lapparent de Braon and Murelaga, 1999; Joyce et al., 2011).

Plates

The nuchal plate is arch-shaped and wider rather than long. Its anterior margin is concave (due to a deep nuchal notch) and its posterior margin convex. It articulates with the first neural plate, the first pair of costal plates, and the first pair of peripheral plates. Half of its lateral sutures are not clear, and perhaps they were approximately coincident with the lateral borders of the first vertebral and first marginal scales.

The neural series is preserved from neural 1 to neural 6. Neural 1 is hexagonal and contacts with the nuchal, costals 1 and 2, and neural 2. Neural 2 is the smallest of the preserved neurals and is almost quadrangular, being slightly longer than wide. It contacts neurals 1 and 3 and costal 2 only. Neurals 3–6 are hexagonal. All are in contact with the previous and following neural and two costals (the corresponding costal and the anterior). Neurals 1 and 3–6 are subequal in size, with neural 3 slightly longer than the remaining neurals. The morphology and contacts of the neural series of T. kusterae is similar to those of Siamochelys peninsularis, a Middle Jurassic turtle from Thailand (Tong et al., 2002), but differ from those of stem turtles and N. speciosa (Gaffney et al., 1987; Hirayama et al., 2000).

The first pair of costal plates is wing-shaped and contacts peripherals 1–4. Costals 2–6 are roughly rectangular and much

| Abbreviations: D, maximum mold depth; L, maximum mold length; LASN, maximum length of anterior supernumerary scale; Leo, maximum length of costal plate; LM, maximum length of marginal scale; Lne, maximum length of neural plate; Lnu, maximum length of nuchal plate; Lpe, maximum length of peripheral plate; LPL, maximum length of pleural scale; NV, maximum length of vertebral scale; W, maximum width of costal plate; WM, maximum width of marginal scale; Wnu, maximum width of nuchal plate; Wve, maximum width of vertebral scale. |
|---|
| **TABLE 1.** Selected measurements (in mm) of MGT-1185. |
| **L** | 133 |
| **W** | 133 |
| **D** | 31 |
| **NNL** | 16.5 |
| **NNW** | 54 |
| **WNE1** | 38.5 |
| **LVE1** | 20.5 |
| **WVE2** | 35.5 |
| **LVE2** | 51 |
| **WVE3** | 39 |
| **LVE3** | 12 |
| **LME1** | 13 |
| **LME2** | 14.5 |
| **LME3** | 9.5 |
| **LM3** | 10.5 |
| **Lwu** | 31.5 |
| **Lnu** | 17.5 |
| **Wco1** | 49.5 |
| **Lco1** | 24 |
| **Wco2** | 58 |
| **Lco2** | 20 |
| **Lco3** | 20 |
| **Lco4** | 18.5 |
| **Lco5** | 18.5 |
| **Wne1** | 11 |
| **Lne1** | 16.5 |
| **Wne2** | 12 |
| **Lne2** | 14.5 |
| **Wne3** | 13 |
| **Lne3** | 19.5 |
| **Wne4** | 12 |
| **Lne4** | 13 |
| **Wne5** | 11 |
| **Lne5** | 18 |
| **Wpe1** | 23.5 |
| **Lpe1** | 20.5 |
| **LPL1** | 39 |
wider than long. The contacts with the neurals are described above. Due to the preservation of the specimen, contacts among costals 2–6 with the peripherals are missing. The presence or absence of costoperipheral fontanelles cannot be determined.

Whereas most of the peripheral plates are quite poorly preserved, the anterior ones (1–4) can be reconstructed on the basis of some sutures and the anterior morphology of the first costal plate (Fig. 2).

Peripheral 1 is part of the nuchal notch. It contacts with the nuchal, costal 1, and peripheral 2. Peripheral 2 contacts with peripherals 1 and 3 and costal 1, whereas peripheral 3 contacts with peripherals 2 and 4 and costal 1. The shell bone fragments (thickness up to 5.25 mm) represent mostly carapace remains, including the left costal 2 and the neural 4, whereas a few others probably belong to the bridge region of the plastron.

Scales

The cervical scale is absent in *T. kusterae*, which seems to be due to the deep nuchal notch and the short marginal scales. The cervical scale has been lost independently in different clades of turtles (e.g., pelomedusoids and testudinids). However, in a few (e.g., the pleurodiran turtle *Araripemys barretoi* from Aptian–Albian of Brazil; Meylan, 1996) the absence of the cervical scale correlates with the presence of a deep nuchal notch. In both pelomedusoids and testudinids, the absence of the cervical scale has been lost independently in different clades of turtles (e.g., pelomedusoids and testudinids). However, in a few (e.g., the pleurodiran turtle *Araripemys barretoi* from Aptian–Albian of Brazil; Meylan, 1996) the absence of the cervical scale correlates with the presence of a deep nuchal notch. In both pelomedusoids and testudinids, the absence of the cervical scale has been lost independently in different clades of turtles (e.g., pelomedusoids and testudinids). However, in a few (e.g., the pleurodiran turtle *Araripemys barretoi* from Aptian–Albian of Brazil; Meylan, 1996) the absence of the cervical scale correlates with the presence of a deep nuchal notch.

Vertebral 1 is trapezoid and covers the major part of the nuchal notch, the first half of neural 1, and part of costal 1. Vertebral 1 reaches the anterior border of the carapace at the level of the nuchal notch.

Vertebral 1 is trapezoid and covers the major part of the nuchal plate, the first half of neural 1, and part of costal 1. Vertebral 1 is the narrowest of the preserved series. Vertebrals 2–4 of *T. kusterae* are as wide as the pleurals (as in *S. peninsularis* and crown Testudines), differing from the wide vertebrals of stem Testudines (e.g., *Kayentachelys aprix*, *Condorchelys antiqua*, and *Indocheles spatulata*) and *N. speciosa* (Gaffney et al., 1987; Datta et al., 2000; Hirayama et al., 2000; Sterli, 2008). Vertebral 2 is larger than the first, hexagonal, and broader than long. It covers the posterior half of neurals 1 and 2, the anterior part of neural 3, and parts of costals 1–3. Vertebral 3 is similar in shape and size to the preceding vertebral; it includes posterior half of neurals 3 and 4, the anterior half of neural 5, and parts of costals 4–6. The contact between vertebrals 1 and 2, vertebrals 2 and 3, and vertebrals 3 and 4 is located in the first, third, and fifth neural plates, respectively. The presence of the sulcus between vertebrals 3 and 4 and crossing neural 5 is also present in *N. speciosa* and crown Testudines. In some stem Testudines (e.g., *K. aprix*, *I. spatulata*, *C. antiqua*, and *Eileanchelys waldmani*), this sulcus crosses neural 6 (Gaffney et al., 1987; Datta et al., 2000; Sterli, 2008; Anquetin et al., 2009).

A pair of subtriangular anterior supernumerary scales (sensu Lyson et al., 2011) is placed between vertebral 1, pleural 1, and marginal 1. We regard them neither as primarily homologous to the supramarginal scales, which are present in large numbers in some stem Testudines (e.g., *Proganochelys quenstedti* and *Protochersis robusta*; Joyce, 2007), nor to the supramarginals found in certain baenids along with anterior and posterior supernumerary scales (Brinkman and Nicholls, 1991; Lyson et al., 2011). A pair of anterior supernumerary scales was also documented for *N. speciosa*, *Boremys sp.*, *Solnhofia parsonsi*, and *Pleiochelys solodurensis*, among others (Bräm, 1965; Hirayama et al., 2000; Joyce, 2000; Lyson et al., 2011).

Pleural scales are as wide as long, and they cover much of the peripheral bones. Pleural 1 covers costals 1 and 2 and peripherals 2–4. Pleural 2 covers part of costals 2–4, and pleural 3 covers part of costals 4–6. The sulci between pleurals 1 and 2, 2 and 3, and 3 and 4 are located in costals 2, 4, and 6, respectively.

The anterior marginal scales are entirely included in the peripheral bones. Marginal scale 1 is small and roughly rectangular in shape, making contact with vertebral 1, the anterior supernumerary scale, and marginal scale 2. Although the cervical scale is absent, marginal scales do not contact each other in the midline, probably due to the deep nuchal notch present in *T. kusterae*. The left (right in the mold) marginal 1 and part of the marginals 2 and 3 are preserved, whereas the remaining marginal...
scales do not show their internal limits, nor do the pleural scales show their limits with them.

**Plate Histology**

Thin-sections of a costal plate allowed the assessment of the histological structure of *T. kusterae* (Figs. 4B, 6). The plates show a thick layer of cancellous bone framed by external and internal cortices of compact bone.

The external cortex is thick (thickness about 1.60 mm; Figs. 4B, 6) and well vascularized with primary vascular canals, which are roughly perpendicular to the plate surface and seldom branching. The external end of these vascular canals could be related to the pits observed in the SEM (Fig. 5). Conspicuous growth marks are not observed, although there may be a few faint ones. Possible Sharpey’s fibers can be observed (Fig. 6).

**FIGURE 3.** MGT-1185, shell bones of *Tacuarembemys kusterae*, gen. et sp. nov. **A**, **B**, paired neural plates; **A**, external and **B**, internal views. **C**, **D**, paired costal plate fragments; **C**, external and **D**, internal views. See text for anatomical abbreviations. Scale bars equal 10 mm.

**FIGURE 4.** Binocular lens photographs of costal plates of *Tacuarembemys kusterae*, gen. et sp. nov. **A**, external ornamentation pattern of a costal plate; **B**, natural transverse section of a costal plate. See text for anatomical abbreviations. Scale bars equal 1 mm.
The cancellous bone is thick (thickness about 1.68 mm; Figs. 4B, 6) and strongly vascularized. Primary osteons with lamellae and bone cell lacunae are concentrically arranged and widespread.

The internal cortex is thin (thickness about 0.88 mm; Figs. 4B, 6) and vascularized with scattered single primary vascular canals, and it is composed of parallel-fibered bone. Bone cell lacunae are arranged parallel to the plate surface. The boundary between the cancellous bone and the internal cortex is sharply demarcated.

**PHYLOGENETIC RESULTS**

After two rounds of TBR, 240 most parsimonious trees (MPTs) of length 905 steps were found (Fig. S1), with a CI of 0.335 and a RI of 0.763. A list of synapomorphies common to all MPTs is shown in Appendix S2. The strict consensus of all MPTs
shows a poorly resolved topology at the base of Testudines, but
in all MPTs T. kusterae is recovered inside Testudines (Figs. S1, S2). A big polytomy could be caused by the absence of informa-
tion or by a wildcard taxon (see below) jumping between differ-
ent positions in the MPTs. Consequently, we ran the script
written by Pol and Escapa (2009), which identified T. kusterae as
the most unstable taxon, jumping between two positions: (1) as
the sister taxon of crown Pleurodira and (2) as the sister clade of
Sinemys lens (see reduced consensus in Fig. 7). Following the
script, contradictory characters do not cause the alternate posi-
tion of T. kusterae and the scoring of several characters will help
to solve its phylogenetic position (see Fig. S3).

DISCUSSION

Phylogenetic Position of Tacuarembemys kusterae

Although Tacuarembemys kusterae behaves as a wildcard
taxon, the preserved characters allow us to place it inside
Testudines. Testudines is supported in this analysis by two
synapomorphies common to all MPTs: only one suprapygal
and small first thoracic rib, which are characters 136(0) and
200(2), respectively. These two characters are not preserved
in T. kusterae, but other scored characters preclude T. kus-
terae from being a basal stem Testudines. The presence of
the sulcus between vertebrals 3 and 4 on neural 5 (character
142) is a synapomorphy of the clade crownward to Che-
yungchelys, whereas the presence of narrow vertebral scales
(character 141) is a synapomorphy of the clade crownward to
Siamochelys peninsularis. In stem Testudines (e.g., Kayen-
tachelys aprix, Condorchelys antiqua, and Mongolochelys efre-
movi), vertebral scales are wider than pleural scales and the
sulcus between vertebrals 3 and 4 is located on neural 6. The
absence of shell sculpturing (character 123) positions
T. kus-
terae in the clade crownward to Plesiochelys etalloni. Although only 7.5% (18 of 241 characters) of the characters
are known for T. kusterae, those characters support referral
to Testudines. More specimens will hopefully bring more
information, in order to stabilize its phylogenetic position
among Testudines and thus permit a better understanding of
the evolution of this clade in Gondwana.

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FIGURE 7. Simplified reduced strict consensus of 240 most parsimonious trees of length 905 steps showing the alternative position of Tacuarembemys kusterae (stars) inside crown Testudines. Black circle: synapomorphy based definition of Testudinata (see Joyce et al., 2004). Open circle: crown group definition of Testudines (see Joyce et al., 2004). Gray circles: clades discussed in the text.
Character Evolution

MGT-1185 shows a combination of characters that are present in a variety of turtles, but there is no other turtle that exhibits all of them together, which justifies the recognition of a new taxon. The characters discussed below are characters that have been used for systematic purposes and that we consider worth discussing.

Wide and Deep Nuchal Notch—Although several taxa belonging to different clades show nuchal notches (Table 2, Fig. 8), only the cryptodiran Chirotetrachelys dumonii (Hauterivian–Aptian of Belgium and Spain; Pérez-García, 2012; Fig. 8A), the solemydid Naomichelys speciosa (Aptian–Campanian of North America; Hirayama et al., 2000; Joyce et al., 2011; Fig. 8B), and the nanhsiungchelyids Nanhsiungchelys wuchingensis and Zangerlia dzamunchondi (Upper Cretaceous of China and Mongolia, respectively; e.g., Sukhanov, 2000, and references therein; Fig. 8C) show a nuchal notch as pronounced as the one observed in T. kusterae. The absence of evident shell sculpturing is synapomorphic of the clade crownward from Plesiochelys etalloni (see Fig. 8D). Other continental Jurassic turtles (e.g., Kayentachelys aprix, Herrerocelys romani, Indochelys spatulata, and Stomochelys peninsularis) have a straight or nearly straight anterior border of the carapace. Although this feature has been excluded from recent (including the present) cladistic analyses, it is worth exploring in future analyses (see variation in Fig. S4).

Ornamentation (Character 123)—The T. kusterae material described does not show the diagnostic characters that would allow it to be reliably included in a specific clade within Testudines. Although there are two characters shared with Naomichelys speciosa, the ornamentation of the latter consists of “raised tubercles that easily dislocate from the surface” (Joyce et al., 2011:83), which is markedly different from the solemydid Naomichelys wuchingensis (Upper Cretaceous of China and Mongolia, respectively; e.g., Sukhanov, 2000, and references therein; Fig. 8C) show a nuchal notch as pronounced as the one observed in T. kusterae. Scale sulci are of different shape as well (Hirayama et al., 2000:fig. 3). In our cladistic analysis, the absence of evident shell sculpturing is synapomorphy of the clade crownward from Plesiochelys etalloni (see Fig. S5).

Absence of Cervical Scale (Character 137)—The absence of a cervical scale is a characteristic of T. kusterae, but it is not the only species in which this element has been lost (see Fig. S6). Although the cervical scale has been lost independently in several clades of turtles (e.g., pelomedusoids, testudinids, and Sinemys sp.), the morphology resulting from that loss is not the same in all cases. In testudinids and crown pelomedusoids, the cervical scale is absent but the anterior region of the carapace is not notched, resulting in the medial contact of both first marginals. In contrast, in T. kusterae, A. barretoi (Meylan, 1996; Fig. 8H), and Sinemys sp. (Brinkman and Peng, 1993), the anterior border is notched, the cervical is missing, but marginals 1 make no contact at the midline.

Anterior Supernumerary Scales (Character 138)—The presence of a pair of small, triangular anterior supernumerary scales, placed between marginal 1, vertebral 1, and pleural 1, is a rare feature in turtles, but present in T. kusterae. Comparable scales have also been observed in the baenids Boremys pulchra and B. grandis (Brinkman and Nicholls, 1991; Lyson et al., 2011), Stygiochelys sp. (Upper Cretaceous of North America; Brinkman and Nicholls, 1991; Lyson et al., 2011), and Eubaena sp. (Upper Cretaceous–Eocene of North America; Brinkman and Nicholls, 1991; Lyson et al., 2011), in Plesiochelys solodurensis (Late Jurassic of Europe; Bräm, 1965), and in the solemydid Naomichelys speciosa (Hirayama et al., 2000: fig. 3; see Fig. 8G). Boremys pulchra additionally preserves supramarginal and posterior supernumerary scales (Brinkman and Nicholls, 1991; Lyson et al., 2011). In some taxa (e.g., Solnhofia parsonsi; Joyce, 2000), there is only one (odd) supernumerary scale in the same position as the anterior supernumerary scale mentioned here. The presence of only one scale on one side of the shell is regarded as a shield abnormality (Zangerl, 1969; Pritchard, 2007). On the contrary, the presence of paired (bilaterally symmetric) anterior supernumerary scales seems to be relatively constant in some taxa (e.g., baenids) and seems not to be caused by shield abnormalities. The presence/absence of paired anterior supernumerary scales has been included in the present cladistic analysis, which shows (see Fig. S7) that the presence of anterior supernumerary scales appeared independently several times during turtle evolution.

Table 2. Comparison of taxa with conspicuous nuchal notches.

| Classification            | Taxon                              | NNL/NNW | Distribution          | Epoch          |
|---------------------------|------------------------------------|---------|----------------------|----------------|
| Xingjiangchelyidae        | Xingjiangchelys lautmarginalis      | 0.17    | China                | Middle Jurassic|
|                           | Xingjiangchelys lauschanensis      | 0.19    | Kyrgyzstan           | Middle Jurassic|
|                           | Annemys laiens                    | 0.08    | Mongolia             | Late Jurassic  |
| Macrobaenidae             | Ordosemys leios                    | 0.17*   | China                | Early Cretaceous|
| ?Adocidae (or Eucryptodira i.s.) | Shachemys baibolatica            | 0.08    | Uzbekistan           | Late Cretaceous|
| Cryptodira                | Nanhsiungchelys                   |         |                      |                |
|                           | Hanbogemys orientalis             | 0.18    | Mongolia             | Late Cretaceous|
|                           | Bulganemys jaganchobi              | 0.12    | Mongolia             | Late Cretaceous|
|                           | Zungerlia dzamunchondi             | 0.34    | Mongolia             | Late Cretaceous|
|                           | Nanhsiungchelys                   | 0.29    | China                | Late Cretaceous|
|                           | Jiangxichelys gonzhouensis         | 0.24    | China                | Late Cretaceous|
| Mongolochelyidae          | Mongolochelys eferenovi            | 0.22    | Mongolia             | Late Cretaceous|
| Lindholmydidae            | Gravenmyx barsboldi                | 0.08    | Mongolia             | Late Cretaceous|
| Solemydidae               | Naomichelys speciosa               | 0.34    | U.S.A., Canada       | Early Cretaceous|
|                           | Solenmys vermiculata              | 0.23    | Spain                | Late Cretaceous|
| Paracryptodira            | ‘Glyptops’ typocardium             | 0.18    | England              | Early Cretaceous|
| Cryptodira i.s.           | Chirotetrachelys dumonii           | 0.39    | Spain, Belgium       | Early Cretaceous|
| Pleurodirida              |                                    |         |                      |                |
| Bothremyidae              | Chupacabrachelys complexus         | 0.17    | U.S.A.               | Late Cretaceous|
| Araripeymyidae            | Araripeymys barretoi               | 0.24    | Brazil               | Early Cretaceous|
| Chelidae                  | Yamunaecheleyx maior               | 0.23    | Argentina            | Cenozoic (Pal)|
| Testudines i.s.           | Tacuarembyms kusteri, gen. and sp. nov. | 0.30 | Uruguay             | Late Jurassic–?earliest Cretaceous|

Nuchal notch length/nuchal notch width measured from Meylan and Gaffney (1991), Lapparent de Brin and Murelaga (1999), Hirayama et al. (2000), Sukhanov (2000), Milner (2004), Bona and de la Fuente (2005), Lehman and Wick (2010), Tong and Mo (2010), and Pérez-García (2012). Estimated measurements indicated with *. Abbreviations: Alb, Albain; Apt, Aptian; Ber, Berriasian; Cal, Callovian; Cam, Campanian; Hau, Hauterivian; Maa, Maastrichtian; NNL, Nuchal notch length; NNW, Nuchal notch width; Pal, Paleocene; San, Santonian; Tur, Turonian.
Vertebral/Pleural Scale Relationships (Character 141)—The presence of vertebral scales 2–4 that are wider than pleural scales is well known to be plesiomorphic for Testudines because it is present in basal turtles such as Proganochelys quenstedti, K. aprix, I. spatulata, and Condorchelys antiqua (Gaffney et al., 1987; Gaffney, 1990; Datta et al., 2000; Hirayama et al., 2000; Sterli, 2008). Contrary to the condition present in basal turtles, T. kusterae has narrow vertebral scales (condition present crownward to Chengyunchelys; see Fig. S8).

Sulcus Between Vertebrals 3 and 4 (Character 142)—In stem turtles such as K. aprix, C. antiqua, and Eileanchelys waldmani (Gaffney et al., 1987; Sterli, 2008; Anquetin et al., 2009), the sulcus between vertebrals 3 and 4 is located on neural 6. In contrast, the sulcus between vertebrals 3 and 4 crosses neural 5 in crown Testudines, N. speciosa (Fig. S9), and T. kusterae (Hirayama et al., 2000; Sterli and de la Fuente, 2013). This character was recovered in the present cladistic analysis as synapomorphic for the clade crownward to Siamochelys peninsularis (see Fig. S9).

Paleoecology

Histology can help infer the degree of aquatic adaptation in recent and fossil turtles (e.g., Ernst et al., 2006; Scheyer, 2007). Four categories were recognized by Scheyer (2007): I (terrestrial turtles), II (semiaquatic and mainly aquatic), III (fully aquatic), and IV (extreme adaptation to marine/aquatic environments). Plates of Tacuarembemys kusterae show a diploe structure (external cortex, cancellous bone, and internal cortex) that is indicative of categories I and II. The internal cortex is reduced in thickness, as in categories II and III. However, it represents half the thickness of the external cortex; i.e., disparity is not as great as in turtles of categories III and IV. Thus, this turtle is more likely to belong to category II (semiaquatic and mainly aquatic). Further evidence for the aquatic lifestyle is that the shell is dorsoventrally low; i.e., not strongly convex (e.g., see Sukhanov, 2000). All the preceding evidence agrees with the paleoenvironment proposed for the Tacuarembó Formation: permanent and temporary streams and lakes (Perea et al., 2001, 2009). However, doubts have been cast concerning the reliability of several means traditionally used to infer extinct turtle paleoecology (Benson et al., 2011).

Given the absence of cranial remains, nothing can be inferred about diet. If T. kusterae was durophagous, potential prey would have included some of the aquatic invertebrates (e.g., bivalves and gastropods) also found in the Batovi Member (see Martinez et al., 1993; Martinez and Figueiras, 1993; Shen et al., 2004). Abundant mollusk molds have been found close to the type locality.

The Continental Jurassic–Early Cretaceous Fossil Record of South American Turtles

Until the Middle Jurassic, the worldwide turtle record was dominated by stem Testudines of cosmopolitan distribution across Pangaea (e.g., Kayentachelys aprix, Condorchelys antiqua, Indochelys spatulata, Heckerochelys romani, and Eileanchelys waldmani). In accordance with the breakup of continental landmasses, the paleobiogeography of turtles increased in complexity, and the cosmopolitan distribution that had been dominant until the Middle Jurassic was replaced with Laurasian and Gondwanan distributions. Moreover, between the Middle Jurassic and...
FIGURE 9. Distribution of Late Jurassic and earliest Cretaceous turtle taxa discussed in the text. A, Oxfordian–Tithonian; B, Berriasian–Barremian. Based mainly on Hirayama et al. (2000), Lapparent de Broin (2000), and Sukhanov (2000). Paleogeographic maps after Ronald Blakey, Colorado Plateau Geosystems.
Late Jurassic, several (extant and extinct) clades originated and diversified (e.g., Cryptodira, Pleurodira, and Meiolani- forms; Sterli et al., 2012). However, Upper Jurassic continental deposits with vertebrates are scarce in Gondwana, and particularly in South America (Fig. 9A). For all of the above-mentioned reasons, this new turtle from Uruguay, though fragmentary, preserves valuable information from a key time in turtle evolution.

The components of the continental Upper Jurassic and Lower Cretaceous record of turtles in Gondwana and Laura- sia are notably different from one another. The Upper Jurassi- cian record of continental turtles of Gondwana is virtually nonexistent, because the Canadón Asfalto Formation (where Condorchelys antiqua Sterli, 2008, was found) has recently been radiometrically dated as Early-Middle Jurassic (Cúneo and Bowring, 2010). Fragmentary turtle remains from the Upper Jurassic of Ethiopia (labeled 'Testudinata indet.' in Fig. 9A) have been reported by Goodwin et al. (1999). If the proposed affinities with pelomedusoids, pleisochelyids, and/or solemyids (termed 'pleurosternids' by Goodwin et al., 1999) is confirmed, it would provide interesting paleobiogeographic implications. On the contrary, a large number of Early Creta- ceous taxa have been described from Gondwana. The oldest records of identified Cretaceous continental turtles from Gondwana come from the Barremian of Brazil (Gallo et al., 2009) and Morocco (Lapparent de Broin, 2000), the Aptian– Albian of Argentina (de la Fuente et al., 2007, 2011; Gaffney et al., 2007), and the Albian of Australia (Gaffney et al., 1998; Smith, 2010; Smith and Kear, 2013). Early Cretaceous chelonian faunas from Africa were dominated by panpelome- dans and pleurodiran turtles (Lapparent de Broin, 2000). Recent taxa of which are restricted to South America and Africa (Bonin et al., 2006), in the early Cretaceous Cretaceous chelonians from continental South America and Australia were dominated by the extinct meiolaniforms (Gaffney et al., 2007; Smith and Kear, 2013) and by panchelid pleurodiran turtles (de la Fuente et al., 2007, 2011; Smith, 2010), of which the latter are now restricted to South America and Austral- asia (Bonin et al., 2006). The list of Early Cretaceous South American turtles is completed with the Aptian–Albian San- tana fossils. However, the paleoenvironment of the Ararique basin is still debated due to the existence of both freshwater and saline deposits (Gaffney et al., 2006).

The Late Jurassic and Early Cretaceous continental turtle fauna from Laurasia was very different from that found in Gondwana (Fig. 9). Contrary to Gondwana, in Laurasia there is no evidence of the presence of crown Pleurodira and/or Meiolaniformes in the Upper Jurassic to Early Cretaceous. Besides, most of the components of the Early Cretaceous continental turtle fauna from Laurasia were already present from the Late Jurassic. That was not the case in Gondwana, possi- bly because of the scarcity of Upper Jurassic continental deposits. Continental environments from North America and Europe were dominated by pleurosternids, 'macrobaenids,' and solemyids (Gaffney, 1979; Brinkman et al., 2000; Joyce et al., 2011; Pérez-García and Ortega, 2011). A different sce- nario occurred in Asia, where one of the most diverse records of Late Jurassic to Early Cretaceous turtles can be found (Fig. 9). The Asian record was dominated by 'xinjiangchelyids,' 'sinemydids,' sinochelyids, pantrionychians, pantestudinoids, and the stem-testudine Sichuanchelys sp. (Sukhanov, 2000, and references therein; Danilov and Parham, 2007; Rabi et al., 2010, and references therein). In the present cladistic analysis, T. kusterae behaves as a wildcard taxon, and one of its alternative positions is as a sister clade of Sinemydtes. We are cautious in recognizing this position, and we prefer to wait for more complete specimens before regarding T. kusterae as a sinemyd.
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Submitted April 22, 2013; revisions received October 14, 2013; accepted October 22, 2013.

Handling editor: Sean Modesto.