

An alternative interpretation of small-bodied turtles from the “Middle Purbeck” of England as a new species of compsemydid turtle

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<https://zoobank.org/347E8CB2-6D5C-46C1-8269-C60629424822>

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Academic editor: Torsten Scheyer ♦ Received 14 April 2022 ♦ Accepted 9 August 2022 ♦ Published 17 August 2022

Abstract

A series of small-sized fossil turtles were collected from Beckles’ Pit, Durlston Bay, Dorset, United Kingdom in 1856 from a sediment package referable to the Early Cretaceous (Berriasian) Purbeck Group. The two primary accounts that previously documented these turtles concluded that they represent the juveniles of the coeval early pleurosternid *Pleurosternon bullockii*. A brief, third account, however, suggested that these may represent a new species of compsemydid turtle. We here highlight a series of discrete morphological characters that consistently distinguish the small-bodied turtles from Beckles’ Pit from large-bodied *Pleurosternon bullockii*, in particular the arrangement of the bones and scutes along the anterior margin of the shell. As these characters are otherwise used to diagnose new species of turtles, in particular compsemydids, and to establish the phylogeny of fossil turtles, we side with the latter interpretation and name a new taxon of early compsemydid, *Tongemys enigmatica* **gen. et sp. nov.** The early record of compsemydid is restricted to the Early Cretaceous of Europe, but is extremely fragmentary. We suggest that this may be a bias towards the collection and identification of small turtle remains, but also that a re-study of Early Cretaceous continental turtle faunas is likely to yield further material.

Key Words

Berriasian, Compsemydidae, Early Cretaceous, Paracryptodira, Testudinata, United Kingdom

Introduction

Late Jurassic (Tithonian) to Early Cretaceous (Berriasian) sediments of the Purbeck Group, which are broadly exposed along the southern coast of England, have yielded a particularly rich collection of fossil turtles over the course of the last two centuries (Owen 1842, 1853; Mantell 1844; Seeley 1869; Lydekker 1889a, b; Woodward 1909; Watson 1910a, b; Evans and Kemp 1975, 1976; Barrett et al. 2002). At present, at least five species are recognized as valid from these strata: the abundant pleurosternid *Pleurosternon bullockii* Owen, 1842, which is known from a single cranium and rich shell remains (Milner 2004; Evers et al. 2020; Guerrero and Pérez-García 2021a), the indeterminate paracryptodire *Dorsetochelys typocardium*

(Seeley, 1869) (Milner 2004; Pérez-García 2014), two helochelydrids, including “*Helochelydra*” *anglica* (Lydekker, 1889b) and an undefined form (Barrett et al. 2002; Joyce 2017) and the shell taxon *Hylaeochelys belli* (Mantell, 1844), which is a plausible thalassochelydian turtle, synonymous with the skull taxon *Dorsetochelys delairi* Evans & Kemp, 1976 (Anquetin and André 2020).

Lydekker (1889a) was the first to figure and describe the well-preserved, but crushed shell of a small-bodied turtle from the Middle Purbeck. The specimen was part of a collection that had been assembled by Samuel H. Beckles in what is now known to be part of the Marly Freshwater and Cherty Freshwater Members of the Purbeck Group (Sweetman et al. 2017, see below). Although Lydekker (1889a) noted numerous differences

with far larger specimens of *Pleurosternon bullockii* from the overlying Intermarine Member of the Purbeck Group, he ultimately concluded the small-bodied turtle to represent juveniles of that species, because he believed that subadult individuals would document an intermediate morphology. This conclusion was soon after reiterated by Lydekker (1889b), who attributed nearly two dozen additional small specimens from Beckles' collection to *Pleurosternon bullockii*. More than a century later, Lapparent de Broin and Murelaga (1999) listed a number of characteristics that distinguish the small-bodied material from Beckles' collection from large-bodied *Pleurosternon bullockii* and suggested that the small-bodied form might represent a new species of compsemydid turtle, but they refrained from naming it, likely because this was not the focus of their study. Guerrero and Pérez-García (2021b) recently figured and described most of the small-sized turtles available from the Beckles' collections. Similar to Lydekker (1889a) and Lapparent de Broin and Murelaga (1999), Guerrero and Pérez-García (2021b) highlighted numerous differences between these small-sized turtles and *Pleurosternon bullockii*, but sided with Lydekker (1889a) by interpreting the differences as ontogenetic. In our estimation, the analyses of Guerrero and Pérez-García (2021b) are insufficient to suggest conspecificity of the material at hand. Instead, the small-bodied turtles can readily be diagnosed as a new species of extinct turtle using a series of discrete characters otherwise used for this purpose. The primary goal of this contribution, therefore, is to name this taxon as a new species of fossil turtle, *Tongemys enigmatica* gen. et sp. nov. and to investigate its phylogenetic and biogeographic significance. All specimens discussed herein are housed at the Natural History Museum in London, United Kingdom (NHMUK).

Materials and methods

Geological settings

The vast majority of small-bodied turtles discussed herein (i.e. NHMUK PV OR 48262, 48263, 48263a, 48263c, 48263e, 48343, 48344, 48347 and 48354), including all specimens unambiguously referred to *Tongemys enigmatica* gen. et sp. nov., were explicitly listed by Lydekker (1889b) as originating from the collection of Samuel H. Beckles. The overall similarity of the remaining material referred herein (i.e. NHMUK PV OR 48264, 48345, 48351 and 48355) in their preservation and the adjacency of their catalog numbers make it highly plausible that these originate from this collection as well. This collection of fossil turtles was the by-product of an extensive excavation that had been carried out in search of mammalian remains under the supervision of Beckles in 1856 at Durlston Bay (Kingsley 1857) at a locality now known as "Beckles' Pit" (Milner 2004). To reach the target of this excavation, a single layer known as the mammal bed (bed DB 83 in the terminology of Clements 1993), Beckles had up to 16

m of overburden removed from an area of more than 650 m² (Kingsley 1857). It is unclear, however, if the resulting small-bodied turtles were collected from the mammal bed per se or from the overburden. The latter conclusion is supported by the heterogeneity of the matrix in which non-turtle specimens are preserved (Sweetman et al. 2017). We, therefore, conclude that these specimens either originated from the Marly Freshwater Member, which includes the mammal bed or the overlying Cherty Freshwater Member, the two members exposed at Beckles' Pit (Sweetman et al. 2017). These two Members are generally interpreted as representing lacustrine environments without marine influence. Among turtles, they otherwise yielded fragmentary helochelydrid remains (Barrett et al. 2002).

The best documented specimens of *Pleurosternon bullockii*, *Dorsetochelys typocardium* and *Hylaeochelys belli*, in contrast, originate from the overlying Intermarine Member (Milner 2004). This member is interpreted as ranging from lacustrine to lagoonal.

Although the exact location of the Jurassic-Cretaceous boundary within the Purbeck Group is still contentious, ammonite zonation, sequence stratigraphy and magnetostratigraphy suggest that the Marly and Cherty Freshwater Members are early Berriasian, while the Intermarine Member is middle to late Berriasian in age (Ogg et al. 1994).

Visualization

The best-preserved small-bodied turtles from Beckles' Pit were recently figured by Guerrero and Pérez-García (2021b). Although we here disagree with their interpretation of this material representing juveniles of *Pleurosternon bullockii*, we fully agree with their anatomical observations. To aid the reader, we, nevertheless, re-figure the two most telling specimens, NHMUK PV OR 48262/48265, the holotype (Fig. 1) and NHMUK PV OR 48343, the specimen with the best-preserved plastron (Fig. 2). In the rare instance where referred material provides important insights, we refer the reader to the figures of Guerrero and Pérez-García (2021b).

In the hope of recovering anatomical information from the ventral side of the holotype, which is covered in matrix, we subjected this specimen to high-resolution X-ray micro-computed tomography using a Nikon Metrology XTH 225 ST scanner at the NHMUK Imaging and Analysis Centre. The system set-up consisted of: a tungsten rotating reflection target; X-ray source set to 215 kV and 660 µA; source filtered with 1.5 mm of copper; detector gain of 24 dB; source-object distance of 358.7 mm and object-detector distance of 619.4 mm generating data with isotropic voxels with an edge length of 55.00 µm. Both parts of the specimen (NHMUK PV OR 48262 and 48265) were put together for the acquisition, which consisted of 4476 projections over a 360° rotation of the object, using the minimize ring artefact option of the instrument; each projection had a total integration time of 1 second resulting from 4 frame averaging of 250 msec

exposure each. 3D mesh models were generated using the software Amira 2020.2 (Thermo Fisher Scientific, Hillsborough, USA). Data segmentation was performed combining manual masking every sixth slice with the interpolation tool in the z-axis. The 3D mesh models were generated and exported as .ply-files. The images used in Fig. 1 were taken as screen shots from SPIERSview 3.1.0. The original set of coronal slices and the 3D mesh models are available at MorphoSource (<https://www.morphosource.org/projects/000434697>).

Comparisons

Our primary comparative sources are as follows: *Compsemys* (a.k.a. *Berruchelus*) *russelli* (Pérez-García, 2012) from the Paleocene of France, as described by Pérez-García (2012); *Calissounemys matheroni* Tong et al., 2022 from the Campanian of France, as described by Tong et al. (2022); *Compsemys victa* Leidy, 1856 from the Paleocene of New Mexico, as described by Gilmore (1919); *Peltochelys duchastelii* Dollo, 1884 from the Early Cretaceous (middle Barremian to early Aptian) of Belgium, as described by Joyce and Rollet (2020); *Pleurosternon bull-ockii* from the Early Cretaceous (Berriasian) of England, as described by Guerrero and Pérez-García (2021a); and *Selenemys lusitanica* Pérez-García & Ortega, 2011 from the Late Jurassic (Kimmeridgian) of Portugal, as described by Pérez-García and Ortega (2011).

Phylogenetic analysis

To investigate the phylogenetic relationships of compsemydids, we integrated *Tongemys enigmatica* gen. et sp. nov. into the paracryptodire character/taxon matrix of Rollet et al. (2021). The new turtle could be scored for 35 of 107 characters. The matrix was otherwise adjusted, by re-scoring the early compsemydids *Peltochelys duchastelii* and *Selenemys lusitanica* as “0,” not “1,” for characters 86 and 87, as they clearly do not exhibit extensive contacts between the inguinal and axillary buttresses with the costals, in contrast to the derived compsemydids *Compsemys russelli*, *Compsemys victa* and *Kallokibotion bajazidi*. The updated character taxon matrix is provided in the Suppl. material 1.

The expanded matrix was subjected to a parsimony analysis using TNT (Goloboff et al. 2008). Twenty-one characters (i.e. characters 6, 14, 16, 18, 27, 28, 31, 34, 39, 40, 41, 46, 48, 60, 63, 80, 88, 95, 97, 98 and 101) were run ordered because they form morphoclines. *Proganochelys quenstedtii* served as the outgroup. One thousand random addition sequences were followed by a round of tree bisection reconnection. Trees suboptimal by 10 steps and with a relative fit difference of 0.1 were retained as part of the first search. A tree-collapsing rule was implemented with a minimum length of 0. Our analysis under equal-weighting resulted in 48 most parsimonious trees

with 301 character-state transitions. The Pruned Trees function of TNT identified *Riodevemys inumbragigas* and *Scabremys ornata* as rogue taxa, which were subsequently removed. The 50% majority-rule tree is shown in Fig. 3. *Tongemys enigmatica* gen. et sp. nov. is retrieved as the most basal branching compsemydid.

Nomenclature

We use phylogenetic nomenclature throughout this manuscript. All names of taxa, including clades, are therefore highlighted using italics.

Systematic paleontology

Testudinata Klein, 1760

Compsemydidae Pérez-García et al., 2015

Tongemys enigmatica gen. nov.

<https://zoobank.org/92EBB8E9-9FDB-403E-A619-170CC9936568>

Type species. *Tongemys enigmatica* Joyce, Bourque, Fernandez & Rollet, sp. nov.

Tongemys enigmatica gen. et sp. nov.

<https://zoobank.org/5E4C6B25-01B6-4237-8C59-6DBC8DFBB978>

Figs 1, 2

Holotype. NHMUK PV OR 48262/48265, a near complete shell preserved on two separately catalogued slabs (Lydekker 1889a, fig. 3; Guerrero and Pérez-García 2021b, fig. 1a–c; Fig. 1).

Type locality. Beckles’ Pit, Durlston Bay, Dorset, United Kingdom; Marly Freshwater or Cherty Freshwater Members, Purbeck Group, early Berriasian, Early Cretaceous (see Geological Settings above).

Nomenclatural acts. This publication and its nomenclatural acts were registered at ZooBank on 2 August 2022, prior to publication. The LSID of the publication is urn:lsid:zoobank.org:pub:347E8CB2-6D5C-46C1-8269-C60629424822, that of the new genus LSID urn:lsid:zoobank.org:act:92EBB8E9-9FDB-403E-A619-170CC9936568 and that of the new species LSID urn:lsid:zoobank.org:act:5E4C6B25-01B6-4237-8C59-6DBC8DFBB978.

Etymology. The genus name, *Tongemys*, is formed in honor of Haiyan Tong, a paleontologist who has consistently contributed to the field of descriptive turtle paleontology and systematics over the course of the last three decades. The epithet, *enigmatica*, alludes to 150 years of taxonomic uncertainty obscuring the validity of this new taxon. The epithet is formed as a noun in apposition, not an adjective.

Diagnosis. *Tongemys enigmatica* gen. et sp. nov. can be diagnosed as a representative of *Compsemydidae* by its relatively small size (carapace length smaller than

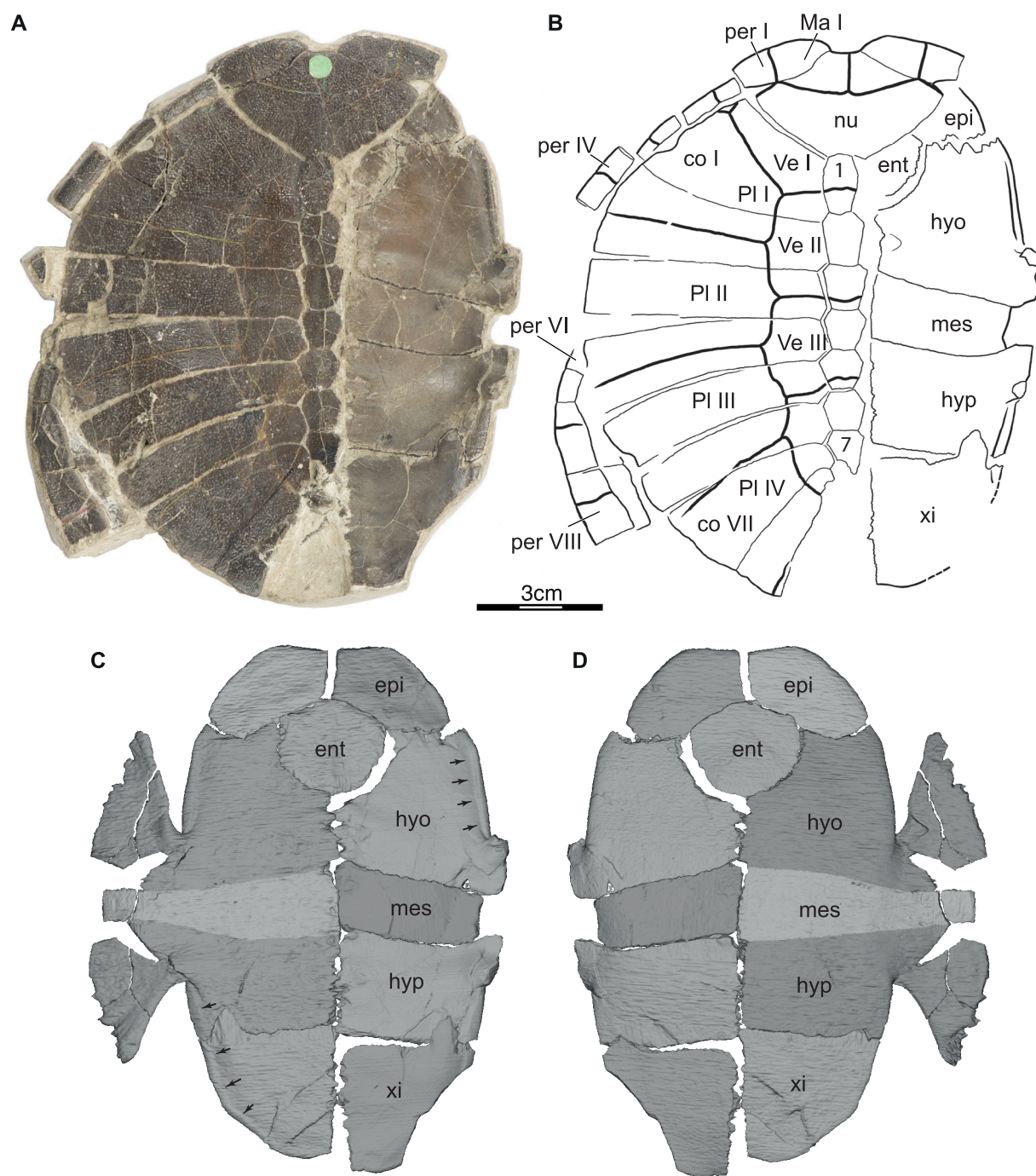


Figure 1. NHMUK PV OR 48262/48265, *Tongemys enigmatica*, holotype, Early Cretaceous (Barremian) of England: **A.** Photograph in dorsal view; **B.** Interpretive line drawing in dorsal view; **C.** 3D model of plastron in dorsal view; **D.** 3D model of plastron in ventral view. Abbreviations: co, costal; ent, entoplastron; epi, epiplastron; hyo, hyoplastron; hyp, hypoplastron; Ma, marginal scute; mes, mesoplastron; per, peripheral; Pl, pleural scute; Ve, vertebral scute; xi, xiphiplastron.

30 cm), a finely textured shell, a sutured bridge, the reduction to absence of a nuchal contribution to the anterior carapace margin, the reduction to absence of a contact between peripheral I and costal I resulting in a contact between the nuchal and peripheral II, the absence of a cervical and a posterolaterally sloping gular-humeral sulcus. *Tongemys enigmatica* gen. et sp. nov. differs from other compsemysids by the presence of a distinct nuchal notch, which is formed by an anterior protrusion

of peripheral I, a residual contribution of the nuchal to the anterior carapacial margin, a laterally expanded nuchal that is wider than costal I (also in *Selenemys lusitanica*), the convergence of the nuchal, peripheral I, peripheral II and costal I on to a single point, neurals II–VII as broad as long (also in *Compsemys russelli* and *Compsemys victa*), four-sided neural I (also in *Compsemys russelli* and *Compsemys victa*), narrow anterior peripherals (also in *Peltochelys duchastelii*) that are much wider than tall,

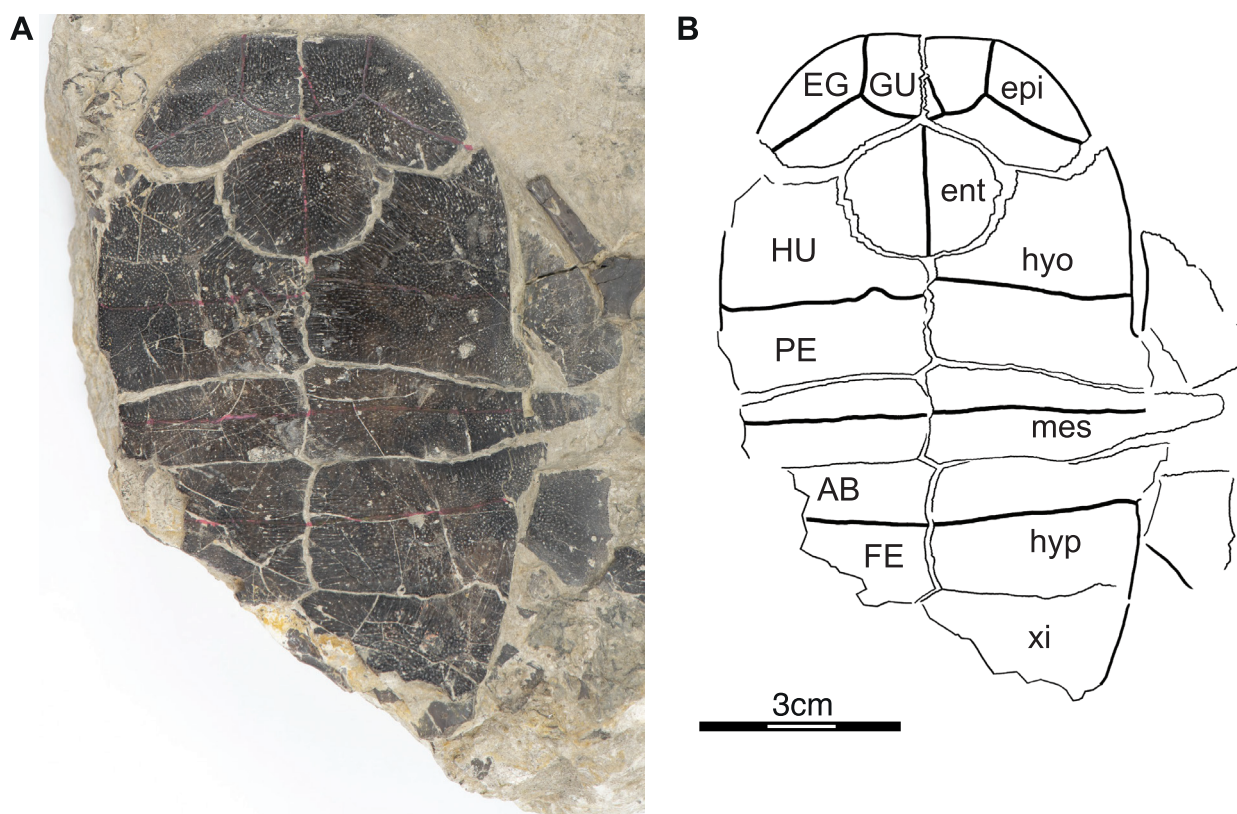


Figure 2. NHMUK PV OR 48343, *Tongemys enigmatica*, referred specimen, Early Cretaceous (Barremian) of England: **A.** Photograph in ventral view; **B.** Interpretive line drawing in ventral view. Abbreviations: AB, abdominal scute; EG, extragular scute; ent, entoplastron; epi, epiplastron; FE, femoral scute; GU, gular scute; HU, humeral scute; hyo, hyoplastron; hyp, hypoplastron; mes, mesoplastron; PE, pectoral scute; xi, xiphiplastron.

V-shaped peripherals in cross section, anterior and posterior to the bridge, a straight medial margin of costal VIII resulting in a trapezoidal space for the suprapyrgals (also in *Peltochelys duchastelii*), restriction of vertebral I to the nuchal and costals (also in *Selenemys lusitanica*), the convergence of vertebral I, marginal II, marginal III and pleural I on to a single point, development of a shallow anal notch only (also in *Selenemys lusitanica* and *Peltochelys duchastelii*), lack of a sinuous mid-line sulcus (also in *Peltochelys duchastelii*), a posterolaterally sloping gular/humeral sulcus that nearly crosses the epi-hyoplastral suture and restriction of gulars to epiplastra. The available material is not sufficient to allow differentiating *Tongemys enigmatica* from *Calissounemys matheroni*, but the latter appears to be larger and have a finer and more striated surface texture.

Referred material. The following specimens from the type locality are referred, based on their small size and the presence of a nuchal that is wider than costal I and that shows a reduced contribution to the anterior carapacial margin: NHMUK PV OR 48263, a carapacial disc lacking peripherals (Guerrero and Pérez-García 2021b, fig. 2d); NHMUK PV OR 48263c, the anterior half of a carapacial disk lacking the peripherals (Guerrero and Pérez-García 2021b, fig. 2b); NHMUK PV OR 48263e, a partial carapacial disk lacking peripherals (Guerrero and Pérez-García 2021b, fig. 2c); NHMUK PV OR 48264, a

carapacial disk lacking peripherals (Guerrero and Pérez-García 2021b, fig. 3b, c). The following specimens are referred, based on their small size and the presence of a laterally contracting mesoplastron: NHMUK PV OR 48343, a near complete plastron (Fig. 2; Guerrero and Pérez-García 2021b, fig. 4a); NHMUK PV OR 48344, a near complete plastron lacking much of the lobes (Guerrero and Pérez-García 2021b, fig. 4b); NHMUK PV OR 48347, a partial plastron lacking the anterior and posterior lobes (Guerrero and Pérez-García 2021b, fig. 4c); NHMUK PV OR 48355, a partial plastron lacking the anterior and posterior lobes (Guerrero and Pérez-García 2021b, fig. 3d); NHMUK PV OR 48354, a disarticulated shell lacking nuchal, peripherals and most of the anterior and posterior plastral lobes (Guerrero and Pérez-García 2021b, fig. 3a). The following specimens, also from the type locality, but too incomplete to yield much taxonomic information, are referred, based on their small size: NHMUK PV OR 48263a, a carapacial disk lacking the nuchal and the peripherals (Guerrero and Pérez-García 2021b, fig. 2a); NHMUK PV OR 48345, a heavily-eroded carapace (Guerrero and Pérez-García 2021b, fig. 1f); NHMUK PV OR 48351, a partially disarticulated carapacial disk lacking the nuchal and the peripherals (Guerrero and Pérez-García 2021b fig. 2e). Although all referred specimens are incomplete, all provide sufficient character evidence to assess their taxonomic referral.

Description.

Carapacial bones. The exact number of elements that comprise the carapace of *Tongemys enigmatica* is not known. No complete carapace is preserved, but the available material preserves a nuchal, eight neurals, eight pairs of costals, the anterior eight pairs of peripherals and one to two suprapygals. Three pairs of posterior peripherals and the pygal were likely present as well. Though incomplete, the shell looks to have been rounded, with exception of a distinct nuchal notch, which is framed by peripherals I (Fig. 1A, B). In the smallest specimens (e.g. NHMUK PV OR 48263a; Guerrero and Pérez-García 2021b, fig. 2a), elongate distal rib ends suggest that fontanelles were present, but in more skeletally mature specimens, including the holotype, the costals appear to contact the peripherals, with the exception of a minor gap between the nuchal, costal I and peripherals I and II (Fig. 1A, B). The surface of the shell is decorated by a fine texture consisting of small, evenly-spaced pits (Figs 1, 2). The holotype, one of the largest available specimens, has an estimate carapace length of 14 to 15 cm. Smaller specimens, such as NHMUK PV OR 48264, had an estimated carapace length of only 8 cm.

The nuchal is wide and hexagonal with long anterolateral and posterolateral contacts with peripheral I and costal I, a short anterior contribution to the margin of the shell and a short posterior contact with neural I (Fig. 1A, B). A lateral corner contact with peripheral II is interrupted by what looks to be a minute fontanelle. Among compsemymids, the nuchal of *Tongemys enigmatica* resembles that of *Selenemys lusitanica* by being wider than costal I, but differs by symplesiomorphically contributing to the anterior margin of the carapace. A clear lateral contact with peripheral II is present in all other compsemymids.

The available material suggests that eight neurals are present, of which the last is typically fused with the suprapygals. The former presence of an asymmetric, abnormal element in the holotype is hinted at by a notch at its posterior end (Fig. 1A, B). The variable fusion of neural VIII with suprapygal I is not only documented for other compsemymids, such as *Compsemys russelli*, *Compsemys victa* and *Selenemys lusitanica*, but also *Pleurosternon bullockii*. The neurals resemble those of *Compsemys russelli* and *Compsemys victa* by being nearly as wide as long. The holotype resembles *Compsemys russelli* and *Compsemys victa* by possessing a four-sided neural I, while the remaining parts of the sequence are hexagonal with symmetrically short anterior sides. The remaining specimens, though fragmentary, are consistent with this arrangement, with the exception of NHMUK PV OR 48263 (Guerrero and Pérez-García 2021b, fig. 2d), which resembles *Peltochelys duchastelii* by exhibiting a preneural, a hexagonal neural I with symmetrically short posterior sides and a square neural II. A square neural II also seems to have been present in *Selenemys lusitanica*.

Eight pairs of costals are present that are fully separated from their counterparts by the contiguous neural series (Fig. 1A, B). As in all turtles, the costals evenly fan out

from the anterior to the posterior. All costals have similar anteroposterior dimensions to one another, with the exception of costal I, which is considerably longer anteroposteriorly than costal II and costal VIII, which is much smaller and almost rudimentary relative to costal VII. The costals typically contact two neurals medially (see above). Costal I contacts peripheral II and III anterolaterally. A point contact may have existed with peripheral I anteriorly and peripheral IV posterolaterally. Costal VIII otherwise contacted the suprapygal complex posteromedially. The remaining contacts of the costals with the peripherals are not preserved.

The holotype is the only specimen to preserve a meaningful sample of peripherals (Fig. 1A, B). As in most species of compsemymids, peripheral I is located anterolaterally to the nuchal and the two bones broadly contact the entirety of one another. As a result, peripheral I lacks a posterior contact with costal I. This characteristic is present among all unambiguous compsemymids. In contrast to other compsemymids, however, peripheral I is not a wedge-shaped element that forms a rounded anterior carapace margin, but rather is a rectangular element that forms minor anterior protrusions that frame a narrow anterior nuchal notch. The anterior margin of peripheral II lines up with the anterior margin of costal I. A medial contact with the nuchal is, therefore, absent. A short contact between these two bones is present in *Selenemys lusitanica* and *Peltochelys duchastelii*, a more extensive one in *Compsemys russelli* and *Compsemys victa*. The remaining peripheral elements are disarticulated from the rest of the shell, likely because they were not tightly sutured to the costals. The peripheral III–IV and peripheral VIII–IX contacts, however, seem to have aligned with the costal I–II and costal VI/VII contacts. The anterior peripherals are notably narrow, like those of *Peltochelys duchastelii*. The CT data reveal that all available peripherals have a V-shaped cross section, not just the bridge peripherals. This is a previously under-reported characteristic not only apparent among other European compsemymids, such as *Peltochelys duchastelii*, but also the pleurosternid *Pleurosternon bullockii* (clearly visible in NHMUK PV R 1891) and the helochelydrid *Aragochoersis lignitesta* (Pérez-García et al. 2020).

The suprapygals are not preserved in the holotype (Fig. 1A, B). In three specimens, a single suprapygal is apparent that is fused with neural VIII (NHMUK PV OR 48263a, 48263 and 48354, Guerrero and Pérez-García 2021b, fig. 2a, c and fig. 3a, respectively). In two other specimens, two suprapygal elements are present, of which the anterior is fused with neural VIII (NHMUK PV OR 48351, 48264, Guerrero and Pérez-García 2021b, fig. 2e and fig. 3b and c, respectively). The fusion of the suprapygal element to neural VIII is alluded to by the unusual polygonal form of the resulting compound element, including angular concavities. The suprapygal elements in concert fill the triangular space between costals VIII. The medial margin of costal VIII is, therefore, straight, not stepped to account for differently-sized anterior and posterior suprapygals. A similar arrangement is seen in *Peltochelys duchastelii*.

Carapacial scutes. The carapace was likely covered by five vertebrals, four pairs of pleurals and twelve pairs of marginals (Fig. 1A, B). As in all other compsemeydids, but also *Pleurosternon bullockii*, a cervical is clearly absent. In the holotype, the intervertebral contacts are located over the middle of neural I, the posterior thirds of neural III and V and neural VIII (Fig. 1A, B). Other specimens generally agree, although minor deviations are apparent. As a more extreme abnormality, at least one specimen exhibits medially split vertebrals (NHMUK PV OR 48263c, Guerrero and Pérez-García 2021b, fig. 2b), also noted by Guerrero and Pérez-García 2021c (fig. 2c). Vertebral I is the broadest vertebral element. It has straight anterior contacts with marginal I, which jointly form a moderate convexity. Furthermore, it contacts the full length of marginal II anterolaterally, pleural I posterolaterally and vertebral II posteriorly. The near contact of vertebral I with marginal III hinders marginal II from broadly contacting pleural II, the condition seen in most other turtles. Vertebral I resembles that of *Selenemys lusitanica* by not lapping on to the peripherals. An overlap on to peripherals I and II is developed in *Compsemys russelli*, *Compsemys victa* and *Peltochelys duchastelii*. An overlap on to peripheral I only is exhibited in *Pleurosternon bullockii*. Vertebrals II to IV are hexagonal elements (Fig. 1A, B). They each have two lateral contacts with the adjacent pleurals and relatively straight anterior and posterior contacts with the adjacent vertebrals. Of the three, vertebral III is the widest, vertebral IV the narrowest. In the holotype, these vertebrals are distinctly narrower than the pleurals (Fig. 1A, B), but in the most juvenile specimens, they are wider (e.g. NHMUK PV OR 48263a, Guerrero and Pérez-García 2021b, fig. 2a). This differs significantly from the condition seen in *Pleurosternon bullockii*, where the vertebrals are much broader than the pleurals, even though all known individuals have a much greater size. The outlines of vertebral V are not well preserved in any specimen, but the holotype suggests that this element was about as wide as vertebral IV, but trapezoidal in outline, as its anterior sulcus with vertebral IV is narrow (Fig. 1A, B). This element appears to be particularly narrow in the holotype, as the vertebral V-pleural IV sulcus barely overlaps the most posterodistal portion of costal VIII, but is clearly located on costal VIII in other specimens. This is not confirmed to be regular by the remaining material (e.g. NHMUK PV OR 48263, Guerrero and Pérez-García 2021b, fig. 2d).

In the holotype, the interpleural sulci are straight, but, while the anterior two evenly cross costals II and IV (as in most turtles), the posterior one laterally crosses from costal VI on to costal VII (Fig. 1A, B). This unusual position is not seen in other specimens (e.g. NHMUK PV OR 48263, Guerrero and Pérez-García 2021b, fig. 2d).

The holotype best preserves the marginals (Fig. 1A, B). Marginal I is relatively broad and contacts its counterpart medially, marginal II laterally and vertebral I posteriorly. It evenly covers the medial two-thirds of peripheral I and the anterior portions of the nuchal. The median

intermarginal sulcus is symplesiomorphically located on the nuchal as in *Selenemys lusitanica*, but also *Pleurosternon bullockii*. Only remnants of the remaining intermarginal sulci are otherwise apparent. This, in return, suggests that the marginal-pleural sulcus was located near the peripheral-costal suture. In this regard, *Tongemys enigmatica* resembles other compsemeydids, but differs markedly from *Pleurosternon bullockii*, where the marginals broadly overlap the costals.

Plastral bones. The plastron consists of an entoplastron and paired epi-, hyo-, meso-, hypo- and xiphiplastron (Figs 1, 2). The plastral fore-lobe is relatively straight along the hyoplastral margin and has a transverse anterior margin, but otherwise is broadly rounded. The plastral hind-lobe is shorter than the fore-lobe and more evenly rounded. Only a shallow anal notch is apparent, as in *Selenemys lusitanica*. On the visceral side of the plastron, the skin-scutum sulcus is located just medial inside the margin of the plastron (see black arrows in Fig. 1C) and, therefore, lacks broad overlap, in contrast to the plastral hind-lobe of *Pleurosternon bullockii*. The space between the inguinal and axillary notches is significantly shorter than either lobe. There is no evidence of plastral fontanelles.

The epiplastron broadly contacts its counterpart along the mid-line, the entoplastron posteromedially and the hyoplastron along a posteriorly convex contact posteriorly (Figs 1, 2). The hyo-, meso- and hypoplastron jointly form the bridge region. Possible dorsal contacts of the wing-like axillary and inguinal buttresses with the carapace are unclear, even in the CT data, because the plastron is displaced relative to the carapace, but the lack of extensive sutural surfaces on the underside of the costals suggest that a contact would have been minor, if present at all. As in other compsemeydids and *Pleurosternon bullockii*, the plastral bones do not align to meet exactly at the mid-line. The mesoplastron narrows laterally to a tip. This condition is otherwise hinted at in *Selenemys lusitanica*. The mesoplastron is lacking in *Peltochelys duchastelii*. The hypoplastron is only about two-thirds the anteroposterior length of the hyoplastron. The xiphiplastron is attached to the hypoplastron along a transversely straight suture, which is stabilized on the visceral side by a pronounced process of the xiphiplastron that overlies the hypoplastron.

Plastral scutes. In NHMUK PV OR 48343, the only specimen that preserves the plastral scutes well, the plastron is covered by paired gulars, extragulars, humerals, pectorals, abdominals, femorals and presumably anals (Fig. 2). There is no evidence of inframarginals, but we cannot be certain of this observation. The gulars are large, blocky elements that do not overlap the entoplastron ventrally, but exhibit an asymmetric mid-line contact. Similar asymmetries are polymorphically developed in *Pleurosternon bullockii* as well. As in other compsemeydids, but not *Pleurosternon bullockii*, the extragular/humeral sulcus slopes posteriorly and may have even lapped on to the hyoplastron posterolaterally. There is no evidence of a deeply sinuous mid-line sulcus. The humeral-pectoral,

pectoral-abdominal and abdominal-femoral sulci are arranged relatively straight transversely. The humeral-pectoral sulcus is located mid-length between the entoplastron and the axillary notch, the pectoral-abdominal crosses the mesoplastron, and the abdominal-femoral laterally aligns with the inguinal notch. The anal-femoral sulcus is not preserved, but a telling break in the holotype suggests that it is orientated diagonally and did not cross on to the hypoplastron.

Discussion

Alpha taxonomy

The taxon represented by the small-sized turtle material recovered from Beckles' Pit has a somewhat unique taxonomic history, as authors have noted its morphological distinction ever since it was first reported in the 19th century, but either interpreted it as the juvenile morph of *Pleurosternon bullockii* nevertheless (Lydekker 1889a, b; Guerrero and Pérez-García 2021b) or as a new species of compsemydid (Lapparent de Broin and Murelaga 1999).

Although we here conclude that the turtles from Beckles' Pit represent a new species of compsemydid turtle, *Tongemys enigmatica* gen. et sp. nov., we agree that a number of characters are present that unite it with the coeval *Pleurosternon bullockii*, including a broadly similar surface texture, the number and arrangement of bones in the shell, a complete neural series, a four-sided neural I, the common fusion of neural VIII with suprapygal I, peripherals that are V-shaped anteriorly and posteriorly to the bridge, the absence of a cervical scute and a straight mid-line plastral sulcus. As our phylogenetic analysis cannot resolve the interrelationships of compsemydids, pleurosternids and baenids, it is unclear if these characters represent symplesiomorphies or homoplasies, although biogeographic arguments provide support for the former hypothesis, as early pleurosternids and compsemydids are best known from Europe.

In spite of the above listed similarities, we find considerable character evidence that distinguishes *Tongemys enigmatica* from *Pleurosternon bullockii*: much smaller size (a carapace length of ca. 15 cm versus ca. 55 cm); the development of a distinct nuchal notch that is framed by anterior protrusions of the first peripherals, instead of a rounded anterior margin; the near complete retraction of the nuchal from the anterior margin of the shell (ca. 20% of nuchal width contributes to the margin, instead of 50%), a nuchal that is laterally expanded to the approximate width of costal I resulting in a near contact of the nuchal with peripheral II which, in turn, hinders a clear contact between peripheral I and costal I, in contrast to a narrow nuchal and a broad contact between peripheral I and costal I; presence of neurals that are about as long as wide, not longer than wide; notably narrow peripherals; presence of a costal VIII that is significantly smaller than costal VII, not similar in size; a straight medial margin of

costal VIII resulting in a triangular space for the suprapygals, not an angular margin; restriction of vertebral I on to the costals, instead of a clear overlap on to peripheral I; a near contact of vertebral I with marginal III, resulting in a short, not expanded contact between marginal II and pleural I; marginals that are restricted to the peripherals, broad pleurals and narrow vertebrals, instead of wide marginals that lap on to the costals, narrow pleurals and broad vertebrals; a distance between the axillary and inguinal notch that is less, not greater than the length of the plastral lobes; plastral lobes with parallel, not evenly converging sides; absence, not presence of a deep anal notch; absence, not presence of broad scute overlap on the dorsal side of the plastral hind-lobe; laterally contracting mesoplastra, instead of rectangular elements; hypoplastron much shorter than hyoplastron, not equal in anteroposterior length; extragular-humeral sulcus not orientated transversely, but rather sloping posterolaterally to nearly contact the epiplastral-hyoplastral suture; and restriction of the gulars to the epiplastron, instead of overlapping the entoplastron.

The vast majority of characters listed above were noted by Guerrero and Pérez-García (2021b), but attributed to ontogeny, as they felt that most differences pertain to proportions. While we agree with Guerrero and Pérez-García (2021b) that proportions change during the ontogeny of turtles, we disagree that this has been documented in literature for the shell of turtles beyond matter-of-fact statements. Indeed, we are only aware of very few morphometric studies that rigorously document shell growth for turtles beyond simple plots of length, width or height against age (e.g. Chiari and Claude 2011; Casale et al. 2017).

As part of their study, Guerrero and Pérez-García (2021b) gathered novel morphometric data from unambiguous *Pleurosternon bullockii* versus *Tongemys enigmatica*, in particular 2D landmarks that approximate the outlines of the nuchal, entoplastron, vertebral III and the anterior plastral lobe. In our estimation, the resulting principal component plots are insufficient to serve as taxonomy evidence for two primary reasons. First and foremost, the use of morphometrics of single shell elements for taxonomic purposes has never been used before and has not been tested by reference to known examples. Is it possible to distinguish extant species using these measurements, even closely related ones? If so, what patterns should we look for? Is this source of data sufficient to distinguish between taxonomic versus ontogenetic effects? These basic questions remain unanswered. As is, the small-bodied turtles variously plot within, outside or beyond the range of the large-bodied ones, which does not correspond to any particular hypothesis in a self-apparent way. Secondly, the nuchal, entoplastron, vertebral III and the anterior plastral lobe of the vast majority of turtles globally have a similar shape, being trapezoidal, lozenge-shaped, hexagonal and tongue-shaped, respectively. Therefore, we do not expect these elements by themselves to yield useful taxonomic data, in contrast perhaps to the morphometrics of all shell elements combined (e.g.

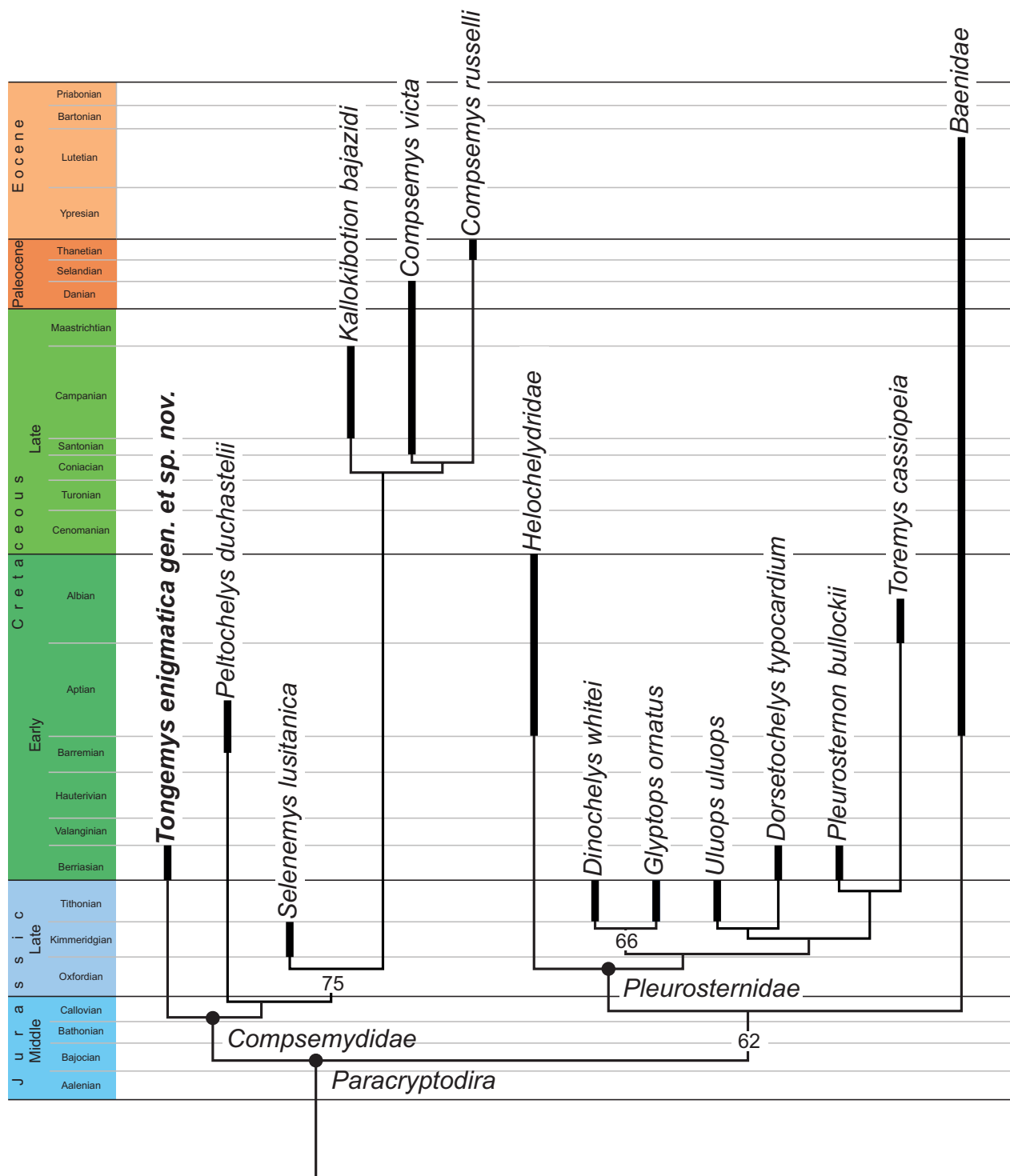


Figure 3. Time-calibrated 50% majority-rule tree obtained from the phylogenetic analysis under equal-weighting, without rogue taxa. Unless otherwise stated, all nodes were found in 100% of all trees.

Claude et al. 2003). Guerrero and Pérez-García (2021b) also plot regression scores of these elements against their centroid size, but here also we are unable to interpret the resulting graphs for the same reasons as listed above.

The available morphometric studies do highlight the tendency for the vertebral scutes to become relatively narrower during ontogeny, at least in the testudinid *Chelonoidis nigra* (Chiari and Claude 2011) and the cheloniid *Caretta caretta* (Casale et al. 2017). To explore if

this is universally true among turtles, we collected linear morphometric measurements from a series of eight extant turtles representing all major lineages (see Suppl. material 1 for data and plots). Although the available data are not sufficient to undertake meaningful statistical analyses, we find a notable gradual decrease in vertebral width is found in all species. In contrast to the morphometric data mentioned above, this observed morphometric trend explicitly favors the taxonomic distinctness of *Tongemys enigmatica*

and *Pleurosternon bullockii*, as the largest individuals of the smaller species have proportionally narrower vertebrals than the smallest individual of the latter species.

A number of studies exist that document ontogenetic variation in the shell of some extinct turtles (e.g. Brinkman 2003; Lichtig and Lucas 2015; Joyce et al. 2019; Garbin et al. 2019; Limaverde et al. 2020), but none observes ontogenetic trends among discrete characters beyond the closure of fontanelles or the loss of keels. Indeed, an underlying principle in fossil turtle taxonomy is that the shell of turtles more or less faithfully represents their species and are not influenced by ontogeny beyond changes to the level of ossification. Although we agree that this axiom has perhaps not been tested sufficiently, the very observation that no significant literature is available that might test this tenet is indirect confirmation that it seems to hold true. This is relevant for the taxonomic case at hand: if the turtle material from Beckles' Pit were juveniles of *Pleurosternon bullockii*, it would imply ontogenetic changes that far outpace what is normally observed between species, such as the relative contraction of the nuchal and vertebral I, which would cause the loss of contacts and the creation of others during ontogeny. Incidentally, all of the affected characters were used in the more recent literature to diagnose other compsemymid species as being distinct, including *Compsemys russelli*, *Peltochelys duchastelii* and *Selenemys lusitanica* (Pérez-García and Ortega 2011; Pérez-García 2012; Joyce and Rollot 2020). Therefore, we find it inconsistent to use these characters on the one side to diagnose new species, but to push them aside as an ontogenetic nuisance at other times. The turtle material from Beckles' Pit is easily distinguished from all other named compsemymids, particularly in the topological relationships of the nuchal and vertebral I relative to the surrounding elements and we feel justified in naming a new species, *Tongemys enigmatica*.

Tongemys enigmatica is intermediate in morphology between *Selenemys lusitanica* and *Peltochelys duchastelii*. This is supported by our phylogenetic hypothesis, which depicts them as a paraphyletic grade (see below). A notable difference with these species is the incomplete retraction of the nuchal from the carapacial margin and the retention of a mesoplastron, respectively. As such, we feel further justified in assigning our new species to a new genus as well.

Phylogeny, biogeography and paleoecology

Our phylogeny broadly corresponds to previous hypotheses (e.g. Rollot et al. 2021) by covering *Compsemys russelli*, *Compsemys victa*, *Kallokibotion bajazidi*, *Peltochelys duchastelii* and *Selenemys lusitanica* as members of *Compsemymidae*, in addition to the newly-added *Tongemys enigmatica*, which is recovered as the most basal representative of the clade (Fig. 3). The synapomorphies that unite this clade are the absence of cervicals, placement of marginal I mostly over peripheral I, absence of a contact between peripheral I and costal I and the presence of an

entoplastron that is broader than long. All compsemymids more derived than *Tongemys enigmatica* are united by the absence of the nuchal from the anterior margin of the carapace and the presence of a sinuous mid-line sulcus. The novel placement of *Kallokibotion bajazidi* as sister to *Compsemys russelli* and *Compsemys victa* is supported by the novel recognition that only these compsemymids possess extensive contacts of the axillary and inguinal buttresses with the overlying costals. This topology further supports the notion that the clade originated in Europe during the Late Jurassic, but secondarily dispersed to North America during an uncertain time (Joyce and Rollot 2020).

Guerrero and Pérez-García (2021b) noted that the material we refer to *Tongemys enigmatica* originates from a more lacustrine facies, while classic *Pleurosternon bullockii* originate from a setting with marine influence (see Geological settings above). As they concluded all material to represent the same taxon, they reasonably inferred that the juveniles of the species (i.e. *Tongemys enigmatica*) inhabited inland areas, while the adults (i.e. *Pleurosternon bullockii*) were more towards the shore. We conclude, instead, that two taxa are present and that these turtles occupied separate ecological niches. A more ponded, inland habitat for *Tongemys enigmatica* is consistent with the inferred habitat preferences of other basal compsemymids, as both *Selenemys lusitanica* and *Peltochelys duchastelii* were collected from formations otherwise known for their dinosaurs (Baele et al. 2012; Mateus et al. 2017).

At present, compsemymids are only known from three localities throughout the Late Jurassic and Early Cretaceous of Europe, despite a rich record of coeval dinosaurs, particularly in France, Germany and Spain. We suspect this is a taphonomic filter, as the three available forms are notably small in size (carapace length less than 20 cm) and, therefore, likely easily overlooked. We, nevertheless, suspect that careful study of existing collections will yield additional remains from across the continent.

Data availability

All specimens described herein are housed in the Paleontology Collections of the Natural History Museum, London, United Kingdom. The CT data and the 3D mesh models generated from it are available at MorphoSource (<https://www.morphosource.org/projects/000434697>).

Author contributions

WGJ designed the study. VF scanned the holotype using micro-CT. JRB obtained shell measurements of extant turtles. YR segmented CT data and exported 3D mesh models. WGJ photographed specimens, illustrated them and assembled figures. WGJ and YR assembled the character matrix and conducted phylogenetic analyses. WGJ, YR, JRB and VF prepared the manuscript and contributed to editing.

Competing interests

The authors declare that they have no conflicts of interest.

Financial support

This research was supported by a grant from the Swiss National Science Foundation to WGJ (SNF 200021_178780/1).

Acknowledgements

We would like to thank Michael Day (NHM) for providing access to the specimens that are the focus of this study and Coleman Sheehy and Dave Blackburn for access to the FLMNH Herpetology Collection. Julien Claude and Torsten Scheyer are thanked for meaningful insights that helped improve the quality of the manuscript.

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Supplementary material 1

File S1

Authors: Walter G. Joyce, Jason R. Bourque, Vincent Fernandez, Yann Rollot

Data type: shell measurement data (EXCEL file)

Explanation note: Extant Turtle Taxa; all measurements in mm taken direction from specimens; UF/H = University of Florida, Herpetology, Gainesville, Florida. Fossils; all measurements in mm taken indirectly using ImageJ; NHM = Natural History Museum, London, UK.

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