Wutuchelys eocenica n. gen. n. sp., an Eocene stem testudinoid turtle from Wutu, Shandong Province, China

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Abstract – We describe here a new turtle from the early Eocene of Wutu, Shandong Province, China. This turtle with a full row of well-developed inframarginal scutes is assigned to the basalmost testudinoids while stem testudinoids were believed to disappear by the Palaeocene–Eocene boundary. This account shows that stem testudinoids crossed this boundary in their original range. The first comprehensive phylogenetic analysis of stem and modern testudinoids performed here demonstrates that the stem testudinoids, previously placed in the family 'Lindholmemydidae', do not form a monophyletic group, and the two major clades of testudinoids (Emydidae and Geoemydidae + Testudinidae) split one from another well before the Palaeocene/Eocene boundary, prior to the Late Cretaceous.

Keywords: Testudines, stem Testudinoidea, Wutu, China, early Eocene, systematics

1. Introduction

Testudinoidea is the most diverse group of living turtles, which represents about half of the diversity of the order Testudines today (Claude & Tong, 2004; Lourenço *et al.* 2012). Known since the Mid Cretaceous, the early stages of the radiation in this group remain largely unknown, and the pre-Eocene fossil record is exclusively found in Asia, suggesting that they originated in this region during the Cretaceous. For a long time, all pre-Eocene stem testudinoid turtles have been assigned to the paraphyletic Lindholmemydidae (or more certainly polyphyletic; see Tong *et al.* 2016). This composite assemblage is characterized by a set of primitive characters and no apomorphy. Among the plesiomorphies of Lindholmemydidae, the presence of well-developed inframarginal rows makes them unique by comparison with the modern families. On the other hand, the modern families (Emydidae, Geoemydidae, Testudinidae and Platysternidae) almost all apparently start their fossil record in the Eocene in Asia, Europe and North America, while so-called Lindholmemydidae (testudinoids with inframarginals) disappeared from the fossil record before the Eocene. To date, none of these stem testudinoids has been reported after the Palaeocene/Eocene boundary, suggesting that

the stem testudinoids became extinct before that time. Here we report the first post-Palaeocene stem testudinoid turtles, discovered from the early Eocene of Wutu, in Shandong Province, China.

The first turtle remains from the early Eocene Wutu Formation were reported by Ye (1995). Based on the presence of a complete row of inframarginals and absence of the mesoplastron, Ye (1995) referred this juvenile turtle shell (IVPP RV 95001) to the family Dermatemydidae, but refrained from erecting a new taxon because of the absence of available characters of the carapace. Since that time, additional material has been discovered, including several incomplete shells and shell fragments collected by the Sino-Belgian expeditions in the Wutu coal mine in 2006 and 2008. In this paper we provide a re-examination of the shell described by Ye in 1995 and a systematic study of the new material collected by the Sino-Belgian team. In order to better understand the early stages of the testudinoid radiation, we conducted the first comprehensive phylogenetic analysis of the group, including most basal taxa. Since our analysis indicates that the members of the family Lindholmemydidae do not form a monophyletic group, we use the term 'stem testudinoids' instead of that family name throughout our paper.

Institutional abbreviations: IVPP – Institute of Vertebrate Paleontology and Paleoanthropology, Chinese

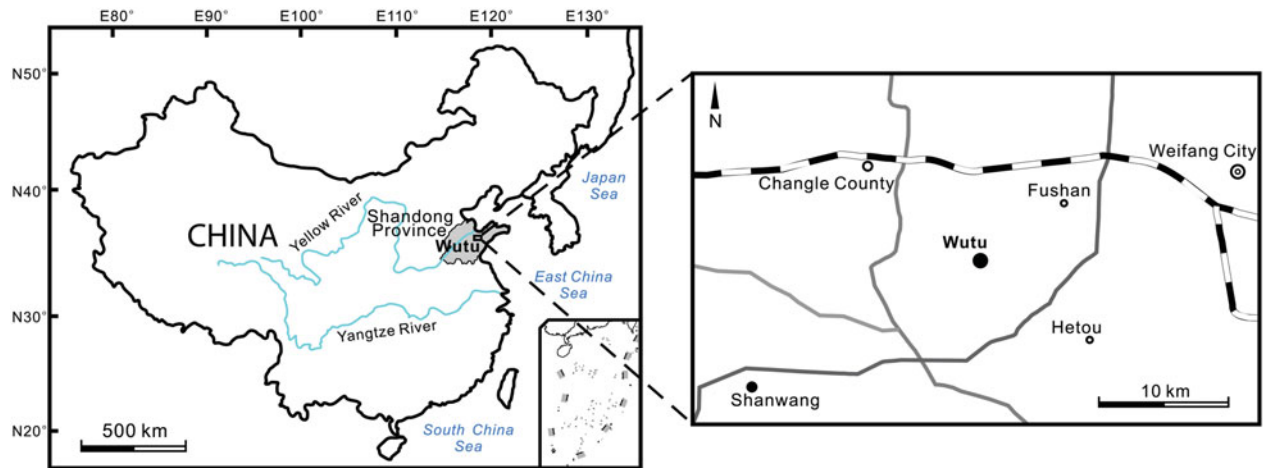†Author for correspondence: htong09@yahoo.fr

Figure 1. (Colour online) Map showing the location of the Wutu coal mine (modified from Zhang *et al*. 2016).

Academy of Sciences, Beijing; PEPZ (IBCAS) – Peking National Herbarium Paleozoological collection (Institute of Botany, Chinese Academy of Sciences), Beijing.

2. Geological setting

The new material was collected from the surface tailings of the Wutu coal mine near the town of Wutu, Linqu County, Shandong Province, China (Fig. 1), in 2006 and 2008. The Wutu Formation, which reaches *c*. 1000 m in thickness, was established by Geological Team No 121, Shandong Coal and Geology Exploration Bureau, in 1960 (Zhao, 1981). It consists of several members, namely from bottom to top: the lower coal-bearing Member, the oil shale Member, the middle coal-bearing Member (containing 12 coal beds) and the upper coal-bearing Member (Fig. 2).

The new specimens are fragmentary carapaces, some associated with plastron. The fossils were embedded in black shale at the contact of coal beds 5 and 7 from the middle coal-bearing Member at *c.* 250 m below the ground (Li *et al*. 2011; Fig. 2). The specimens collected are compressed, some of them being deformed.

The Wutu coal mine in the Wutu Basin of the Shandong Province is an important fossil locality. Mainly known for its mammal fauna that allows the Wutu Formation to be assigned to an early Eocene age (Tong & Wang, 1998), the site has also yielded the oldest Asian records of *Nuphar* (Nymphaeaceae) and *Prunus* (Rosaceae) based on well-preserved seeds (Chen, Manchester & Chen, 2004; Li *et al*. 2011). Although Beard & Dawson (1999) even proposed a late Palaeocene age for the fossil site, based on the presence of some primitive mammals with North American affinities such as the neoplagiaulacid multituberculate *Mesodmops dawsonae* and the carpolestid plesiadapiform *Carpocristes oriens*, it is now widely accepted to be of early Eocene age. The presence of a diversified mammal association (51 species) mainly including derived taxa belonging to modern orders such as

the hyaenodontan *Preonictis youngi*, the miacid carnivoran *Zodiocyon zetesios*, the perissodactyls *Pappomoropus taishanensis*, *Chowliia laoshanensis* and *Homogalax wutuensis*, and the artiodactyl *Wutuhyus primiveris* (Tong & Wang, 2006) clearly pertains to an Eocene age. Finally, the palynological assemblage from the Wutu Formation suggests a late Early Eocene to early Middle Eocene age with a warm temperate vegetation succession comprising mixed needle- and broad-leaved forests (Wang, Wang & Zhang, 2005; Zhang *et al*. 2016).

3. Material

The material studied herein consists of three partial shells and other shell fragments. This material is housed in the Institute of Botany, Chinese Academy of Sciences, Beijing, and Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing (see holotype and referred specimens).

The comparative material of pre-Eocene testudinoids includes all the taxa that are sufficiently well known to allow comparisons and phylogenetic analyses: *Anhuichelys* spp. from the Palaeocene of China (Tong *et al*. 2016); *Amuremys planicoctata* (Riabinin, 1930) from the Latest Cretaceous of Russia and China (Danilov *et al*. 2002); *Elkemys australis* Ye, 1974 from the Early Palaeocene of Guangdong, southern China (first-hand observation of H.T.; Ye, 1974; Danilov, Claude & Sukhanov, 2012); *Gravemys* (including *G. barsboldi* Sukhanov & Narmandakh, 1976 from the Late Cretaceous of Mongolia (Danilov, 2003) and *G. hutchisoni* Danilov, 2003 from Inner Mongolia, China (first-hand observation of H.T.; Danilov, 2003)); *Hokouchelys chenshuensis* Ye, 1974 from the Middle Palaeocene of Guangdong, southern China (first-hand observation of H.T.; Ye, 1974); *Hongilemys kurzanovi* Sukhanov & Narmandakh, 2006 (Sukhanov, 2000; Sukhanov & Narmandakh, 2006); *Lindholmemys elegans* Riabinin, 1935 and *L. martinsoni* from the Late Cretaceous of Uzbekistan and *L. occidentali*s from the Late Cretaceous of Mongolia (Riabinin, 1935; Nessov
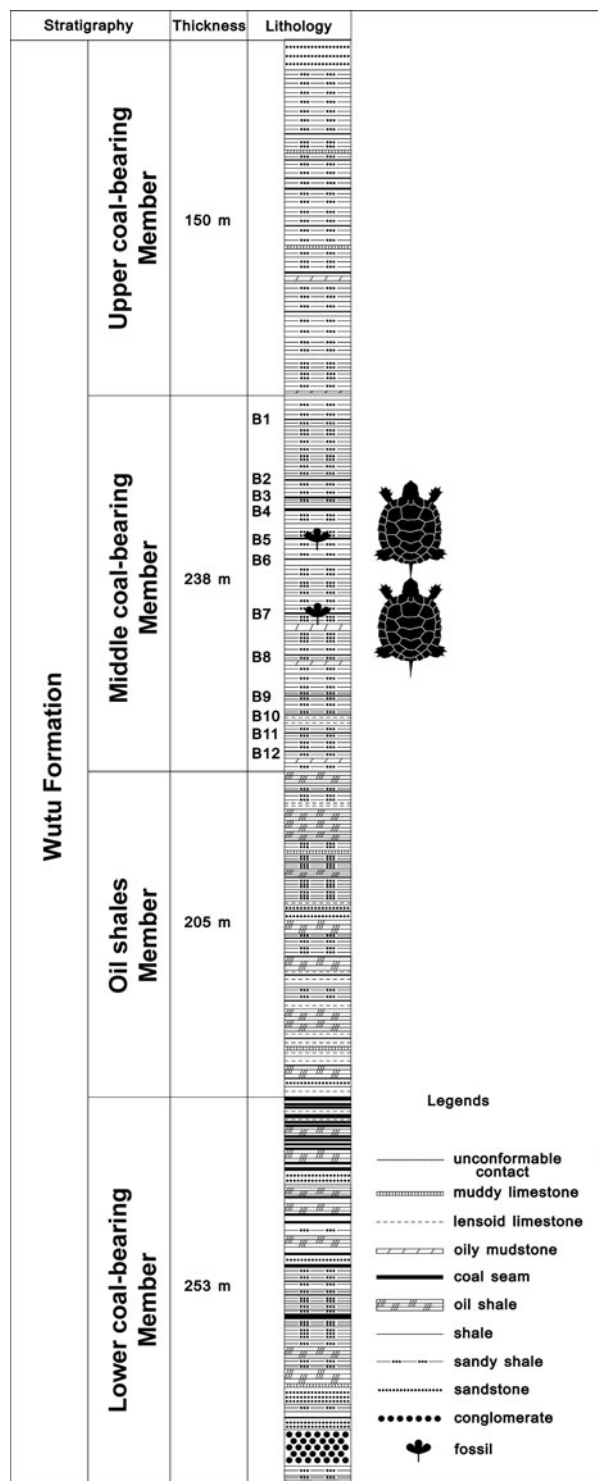
Figure 2. General stratigraphic column of the Wutu Formation, indicating fossil layers B5 and B7 where the fossil turtles come from (modified from Li *et al.* 2011).

& Krassovskaya, 1984; Danilov, 1999; Sukhanov, 2000; Danilov & Sukhanov, 2001); *Paramongolemys khosatzkyi* Danilov & Sukhanov, 2013 from the Late Palaeocene of Mongolia (Danilov & Sukhanov, 2013); *Pseudochrysemys gobiensis* Sukhanov & Narmandakh, 1976 (Sukhanov & Narmandakh, 1976; Danilov, Claude & Sukhanov, 2012); *Shandongemys dongwuica* Li *et al.* 2013 (first-hand observation of

H.T.; Li *et al.* 2013); *Tsaotanemys rugosus* Bohlin, 1953 from the late Early Cretaceous of Gansu, China (Bohlin, 1953); and the Palaeocene stem testudinoids which were previously assigned to the genus *Mongolemys*, but the generic assignment is doubtful: '*M.*' *tatarinovi* Sukhanov & Narmandakh, 1976; '*M.*' *reshetovi* Sukhanov & Narmandakh, 1976 and '*M.*' *trufanensis* Ye, 1974 (Sukhanov & Narmandakh, 1976; Danilov, 1999; Sukhanov, Danilov & Narmandakh, 1999; Danilov, 2003).

4. Systematic palaeontology

Testudines Linnaeus, 1758
Cryptodira Cope, 1868
Testudinoidea Batsch, 1788
Wutuchelys eocenica n. gen. n. sp.
(Figs 3–6)

Etymology: The genus name is from Wutu, the locality where the turtle specimens have been collected; the species name derives from the Eocene age of the specimen.

Holotype: PEPZ WT012, a partial shell with articulated carapace and plastron; the right one-third of both carapace and plastron and the anterior portion of the carapace are missing; the anterior end of the plastron is damaged and the xiphiplastra are disarticulated.

Referred specimens: PEPZ WT003, including three individuals (WT003a: a smaller carapace preserved mostly as imprint exposed in dorsal view; WT003b: a partial shell with very damaged carapace articulated with incomplete plastron, the plastron lacking both epiplastra and xiphiplastra; WT003f: a partial plastron); PEPZ WT006a–g: a fragment of plastron, exposed in dorsal view; PEPZ WT009: an isolated right peripheral 1; PEPZ WT010: a fragment of carapace; PEPZ WT013: a small shell preserved mostly as internal mould, only part of the carapace preserved and exposed in inner view; all from the type locality. IVPP RV 95001, an almost complete juvenile shell with articulated carapace and plastron. The shell is severely crushed dorsoventrally, so some plates are overlapping on one another and crushed and the neural series is not visible; the carapace lacking notably the nuchal and some peripherals. On the plastron, both epiplastra and the left xiphiplastron are missing; the entoplastron is damaged. The specimen has been further damaged since the description of Ye (1995); we are unable to completely restore the left xiphiplastron and the left bridge region.

Type locality and horizon: Wutu coal mine, Linqu County, Shandong Province, China; middle coal-bearing Member of Wutu Formation, Early Eocene.

Diagnosis: A stem testudinoid differing from all post-Eocene testudinoids by the presence of a full row of well-developed inframarginal scutes and differing from all other pre-Eocene stem testudinoids by the
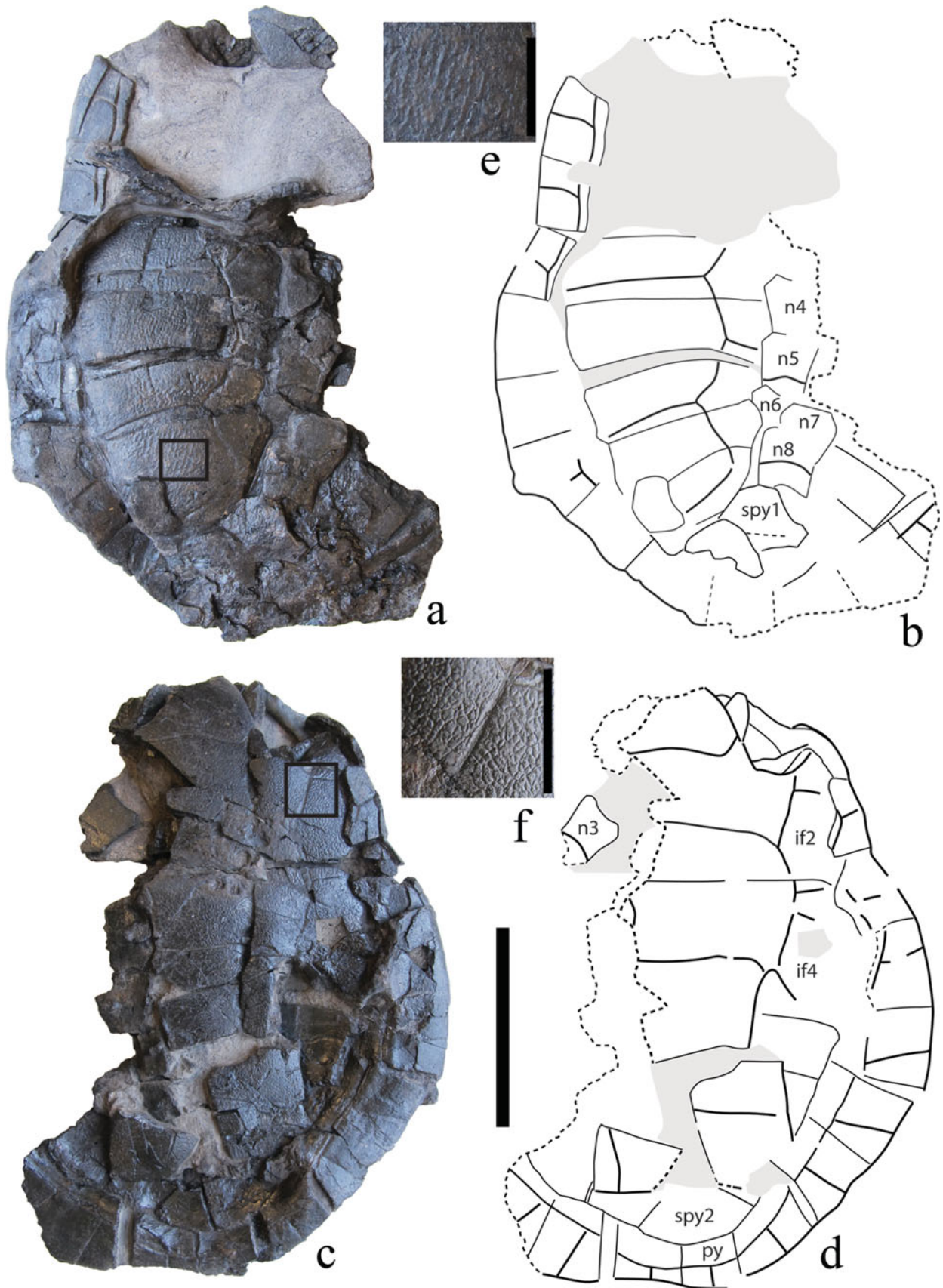
Figure 3. (Colour online) *Wutuchelys eocenica* n. gen. n. sp. PEPZ WT012 (holotype), shell in dorsal (a, b) and ventral (c, d) views and detail of the ornamentation on the carapace (e) and plastron (f). Scale bar = 5 cm (a–d) and 2 cm (e, f). Abbreviations: if, inframarginal; n, neural; py, pygal; spy, suprapygal.
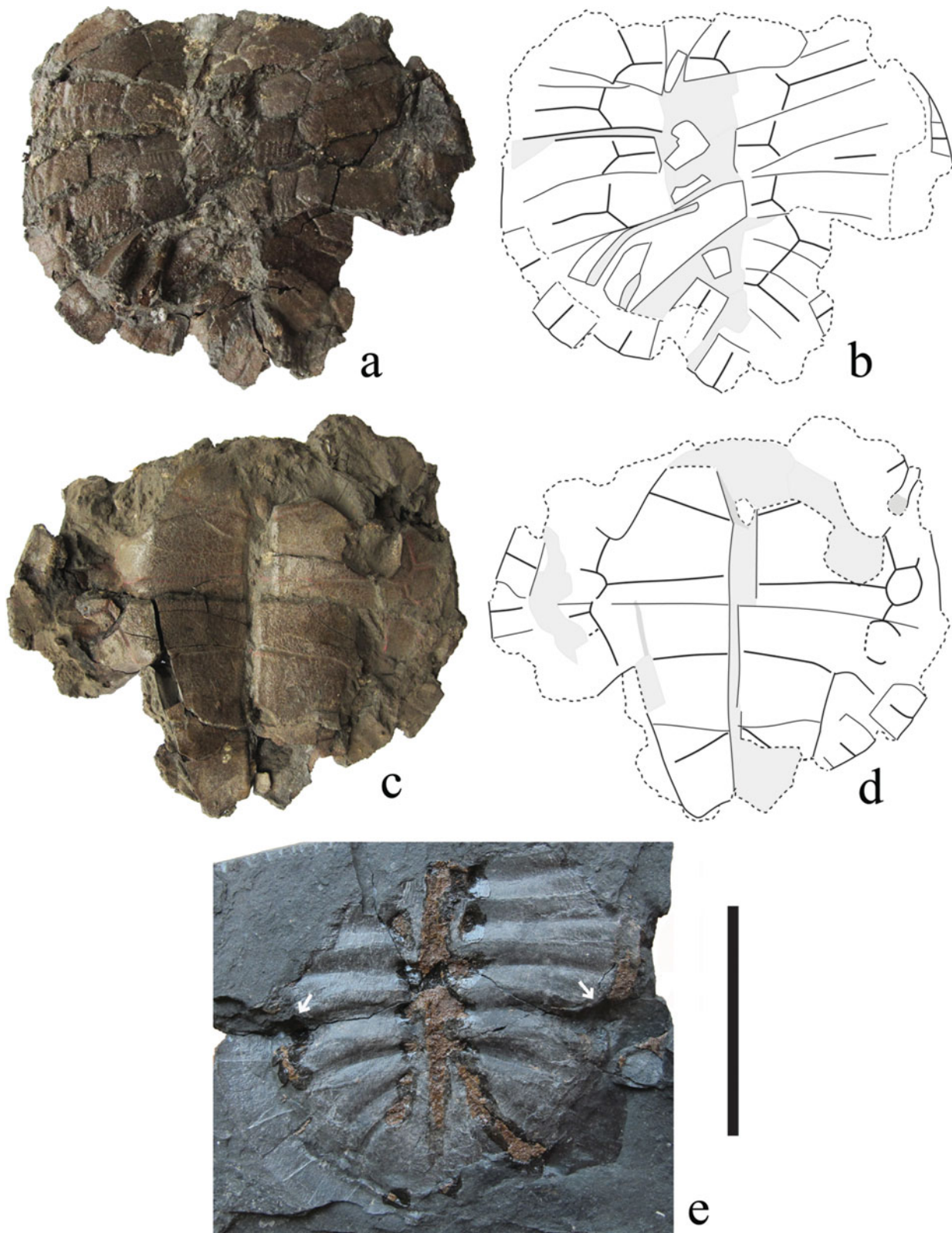
Figure 4. (Colour online) *Wutuchelys eocenica* n. gen. n. sp. a–d: IVPP RV 95001, a juvenile shell in dorsal (a, b) and ventral (c, d) views. (e) PEPZ WT013, internal mould of carapace. Arrows indicate the insertion site of the inguinal buttresses on the inner surface of costal 5. Scale bar = 5 cm.

following combination of characters: carapace oval in outline that is slightly expanded posteriorly, with a relatively large cervical notch; shell surface covered with a pronounced ornamentation, consisting of anteroposteriorly directed thin ridges and furrows on the carapace and fine vermiculate furrows on the plastron; vertebrals wider than long; trapezoidal vertebral 1 which is expanded anteriorly and reaching the second marginal scute; short bridge by comparison with most pre-Eocene testudinoids; large anal notch; round
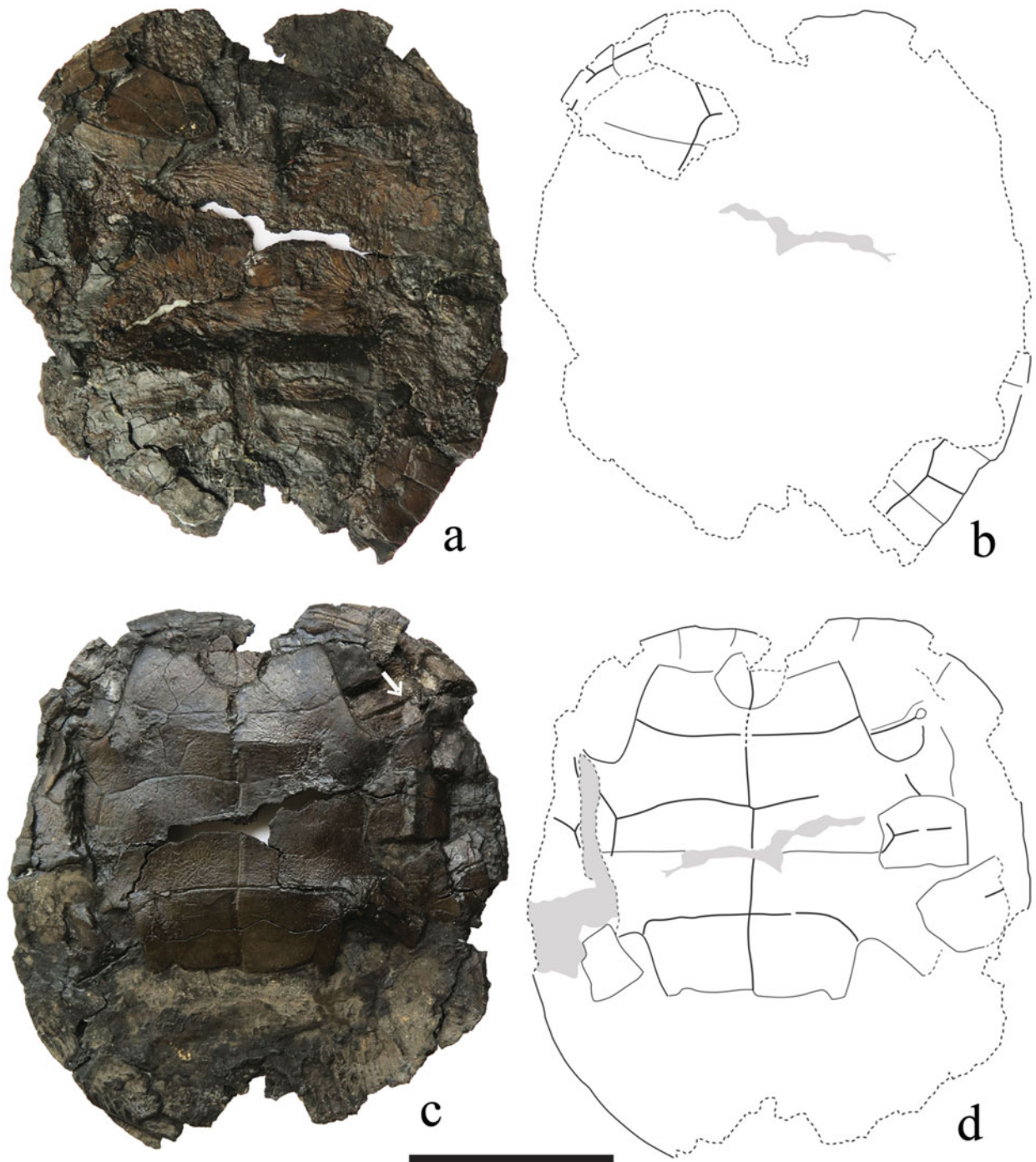
Figure 5. (Colour online) *Wutuchelys eocenica* n. gen. n. sp. PEPZ WT003b, a shell in dorsal (a, b) and ventral (c, d) views. Arrow indicates the insertion scar of the axillary buttress on the inner surface of costal 1. Scale bar = 5 cm.

entoplastron; humeropectoral sulcus located far anterior to the base of the anterior lobe of the plastron and posterior to the entoplastron, and four relatively wide inframarginals which are mainly located on the bridge and slightly extend onto the peripherals.

Measurements: see Table 1.

4.a. Description

Carapace: As preserved in PEPZ WT003b and PEPZ WT012, the carapace has a relatively wide oval outline

which is slightly expanded posteriorly. As all shells have undergone a dorsoventral crushing, the original height of the carapace is undeterminable. The cervical notch, partly preserved in PEPZ WT003b, is shallow and wide. There are no midline or lateral keels on the carapace, and the carapace margin is smooth without serration. The surface of the carapace is covered with clear ornamentation consisting of thin ridges and furrows, directed anteroposteriorly and slightly anteromedially (Fig. 2E). The damaged carapace of PEPZ WT003a, PEPZ WT003b and PEPZ WT013 exposes

Table 1. Measurements of *Wutuchelys eocenica* n. gen. n. sp. (in mm. Estimated complete value in parentheses)

	PEPZ WT012	PEPZ WT003b	IVPP RV95001
Carapace (length/width)	150(160)/115(140)	128(135)/115	85(110)/100(103)
Plastron (length/width)	125(135)/50(100)	80(105)/86	84(88)/80
Anterior lobe (length/width)	—	20(30)/57	21(25)/51
Bridge (length)	45	39	30
Posterior lobe (length/width)	50/—	15(36)/48	33/44
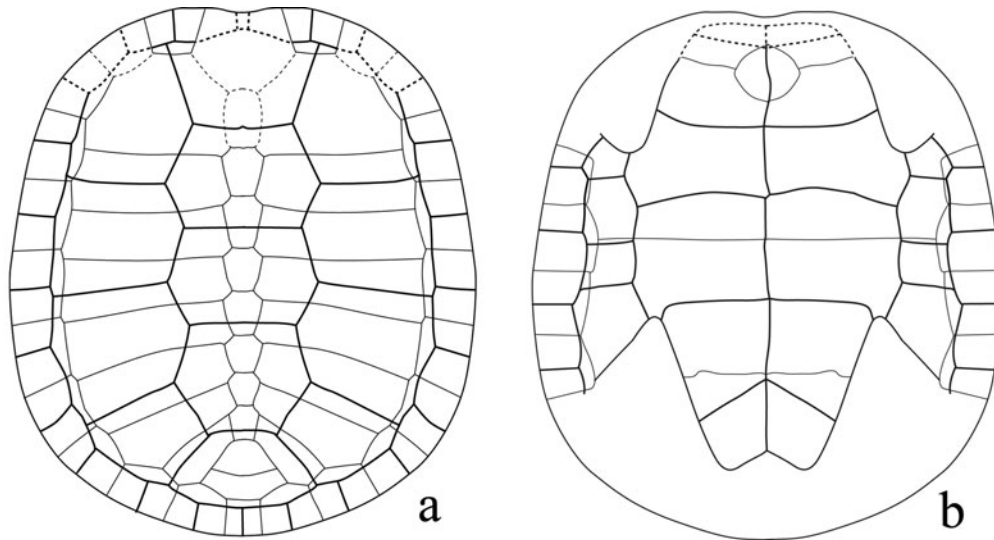
Figure 6. Reconstruction of carapace (a) and plastron (b) of *Wutuchelys eocenica* n. gen. n. sp.

the internal structure. On the inner surface of the costal 1, the second thoracic rib forms a sharp edge that extends laterally to end at an oval scar on the lateral part of the plate for the axillary buttress insertion (Fig. 5C, D). The inguinal buttresses insert on the lateral one-fourth of the costal 5 (Fig. 4E). The rib heads are not reduced.

The nuchal is not preserved. The incomplete neural series (neurals 3–8) is preserved in PEPZ WT012. Neural 3 is detached and turned over, so its dorsal surface is exposed on the ventral side of the shell. The preserved neurals are relatively narrow, hexagonal with short anterolateral sides. Neurals 3–5 are longer than wide. Neural 6 is not completely exposed, so its shape is unclear. Neurals 7 and 8 are crushed; it appears that neural 7 is roughly square and neural 8 is slightly longer than wide. Suprapygal 1 is almost complete, and is trapezoidal. Suprapygal 2 is damaged dorsally, but its ventral side is well preserved. It is large and appears wider than suprapygal 1. The pygal has the dorsal surface damaged, but its ventral side is almost intact; it is roughly square. The complete costal series are preserved in IVPP RV 95001IVPP RV 95001; and the left costals 3–8 and the right costal 7 are preserved in PEPZ WT012. Costal 1 is longer than costal 2. Peripheral 1 (PEPZ WT009) is trapezoidal with a long contact with costal 1. The right peripherals 4–11 are preserved in PEPZ WT012. Peripherals 4–6 are relatively narrow; peripherals 7 and those postward are wider.

The vertebrals are preserved in PEPZ WT012 and IVPP RV 95001. Vertebral 1, incomplete in IVPP RV 95001, is wide, with the lateral margins divergent anteriorly. PEPZ WT009 (an isolated peripheral 1) shows that vertebral 1 contacts marginal 2. Vertebrals 2 and 3 appear to be wider than long. The intervertebral sulci cross the first, third, fifth and eighth neurals respectively. The pleural scutes are as wide as the vertebrals. In PEPZ WT012, the interpleural sulci are located closer to the posterior margin of the costal, not at the mid-length as in IVPP RV 95001. We interpret this difference as intraspecific variation. The marginals are restricted in the peripherals, with the pleuromarginal sulci well distant from the costoperipheral suture.

Plastron: The plastron is loosely connected to the carapace. The plastron is broad with a wide and short bridge. The anterior lobe is relatively long and clearly wider than the posterior lobe. The posterior lobe is longer than the bridge, with straight lateral borders which are convergent posteriorly. The surface of the plastron is covered with clear ornamentation consisting of fine vermiculate furrows (Fig. 2F).

The epiplastron is not preserved. The entoplastron, incompletely preserved in PEPZ WT003b and PEPZ WT003f, appears to be almost circular. The hypoplastron has a similar bridge length to the hyoplastron but is longer than the latter at the midline. The xiphiplastron is longer than wide. The anal notch is large and deep.

The gulars are not preserved. The humeropectoral sulcus is located posterior to the entoplastron and far anterior to the line connecting the bottom of the

axillary notches. The pectoral is shorter than the abdominal. The femoroanal sulcus forms a wide angle which is located posterior to the hypoxiphiplastral suture in PEPZ WT012, but reaches the hypoxiphiplastral suture in IVPP RV 95001. A complete row of four inframarginals is preserved on both sides of IVPP RV 95001 and the left side of PEPZ WT012. The inframarginals are relatively wide and located mainly on the bridge, with the lateral border slightly extending onto the peripherals. They separate the plastral scutes completely from the marginal scutes. In PEPZ WT012, the inframarginals 1 and 3 are small while inframarginals 2 and 4 are much larger.

4.b. Comparisons

Based on the general morphology and ornamentation on the shell surface, all specimens from Wutu are referred to a single species. It is assigned to Testudinoidea because the axillary and inguinal buttresses contact the costal plates. It is outside of the clades Geoemydidae, Testudinidae, Platysternidae and Emydidae *sensu stricto*, all characterized by a reduction or a disappearance of inframarginal scutes. The general shell morphology of *Wutuchelys* is well comparable to the testudinoids from the Palaeocene and the Cretaceous of Asia.

Wutuchelys has a complete series of four relatively wide inframarginals which are mostly located on the bridge and slightly overlap the peripherals. The right inframarginals of PEPZ WT003b appear to be narrower, but this is due to the lateral shift of the plastron caused by crushing. This inframarginal morphology is different from the strong overlapping of the inframarginals scutes on the peripheral plates of *Elkemys*, *Gravemys* and *Hokouchelys* (Danilov, Claude & Sukhanov, 2012). Although *Mongolemys* and *Shandongemys* also have wide inframarginals which are restricted in the bridge, they are distinct from *Wutuchelys* in having only three inframarginals. The inframarginals of *Lindholmemys*, *Amouremys*, *Tsaotangemys*, *Hongilemys* and *Paramongolemys* are narrow. *Pseudocrysemys* has reduced inframarginal series, allowing, in some cases, the contact between the abdominal and the marginal scutes.

IVPP RV 95001 has wide vertebral scutes which may partly be due to the juvenile nature of the specimen. The vertebrals of holotype of *Wutuchelys* (PEPZ WT012) are incomplete. When reconstructed, vertebrals 2 and 3 would be slightly wider than long. This is different from the longer than wide vertebrals 2 and 3 in *Elkemys*, *Gravemys*, *Lindholmemys*, *Paramongolemys* and *Hokouchelys*. In other lindholmemydids, these vertebrals are as long as wide.

Vertebral 1 in *Wutuchelys* is wider than the nuchal plate with the anteriorly divergent lateral borders, resulting in the contact between vertebral 1 and marginal 2 as in some *Mongolemys* and *Paramongolemys* (Danilov & Sukhanov, 2013). In *Elkemys*, *Gravemys*, *Hokouchelys*, *Lindholmemys* and *Pseudocrhysemys*, vertebral 1 is narrower than the nuchal, contacting marginal 1.

The shell surface of *Wutuchelys* is covered with clear ornamentation, consisting of fine anteroposteriorly directed ridges and furrows on the carapace and vermiculate furrows on the plastron. *Elkemys*, *Hokouchelys* and *Paramongolemys* have a smooth shell surface. The ornamentation of *Shandongemys* consists of larger ridges, while that of *Amuremys* is more irregular and stronger.

Wutuchelys is a small turtle; the largest specimen has a carapace length of *c.* 16 cm. IVPP RV 95001 is a juvenile, with wider shell and open sutures. The largest specimen (PEPZ WT012) is likely an adult or sub-adult individual, with a more elongate shell. All specimens have a loose connection between the plastron and the carapace; the whole plastron is often pushed inward and sometimes laterally by crushing. This loose connection is reminiscent of living *Platysternon*. One additional important related feature of *Wutuchelys* is its short bridge. The bridge length / plastron width ratio in this taxon is *c.* 45 %. This ratio is even smaller in IVPP RV 95001 (38 %), likely due to the wider shell of the juvenile. Although *Shandongemys*, *Mongolemys* and *Tsaotanemys* also have a short bridge, with a bridge length / plastron width ratio of 50– 58 %, it is apparent that *Wutuchelys* has the shortest bridge among pre-Eocene testudinoids. *Elkemys*, *Gravemys* and *Hokouchelys* have the greatest ratio, ranging from 60 % to 73 %, which is also comparable to most geoemydids and testudinids.

The detailed comparisons between *Wutuchelys* and other genera of pre-Eocene stem testudinoids are summarized in Table 2. (Some poorly known taxa are not included: *Lindholmemys occidentali*s, '*Mongolemys*' *tatarinovi*, '*M.*' *reshetovi* and '*M.*' *trufanensis*.)

5. Phylogenetic analysis

The phylogenetic relationships of the basal testudinoids with modern families of the group (Emydidae, Geoemydidae, Testudinidae, Platysternidae) are not well understood. Molecular dating indicates that Emydidae and Testudinidae + Geoemydidae may have split during the Cretaceous (Lourenço *et al.* 2012), but this lacks support from the fossil record. To date, no comprehensive analysis has been run; only a few stem testudinoids have been included in the phylogenetic analyses (Claude & Tong, 2004; Cadena, Ksepka & Norell, 2013; Tong *et al.* 2016). In order to determine the phylogenetic relationships of *Wutuchelys*, a data matrix of 36 informative characters for 28 taxa, including 12 stem testudinoids, extends the work of Tong *et al.* (2016). *Chelydra*, *Ordosemys*, *Dermatemys* and *Claudius* are included for rooting the tree and testing the monophyly of the in-group.

Two analyses were run, one using only morphological characters and one constraining the relationship of living taxa using a molecular scaffold based on the phylogenies obtained by Crawford *et al.* (2015),

Table 2. Comparisons between *Wutuchelys eocenica* n. gen. n. sp. and other stem testudinoid taxa

Character/ taxon	*Wutuchelys eocenica*	*Shandongemys dongwuica*	*Mongolemys elegans*	*Elkemys australis*	*Gravemys barsboldi*	*Hokouchelys chenshuensis*	*Lindholmemys elegans*	*Amuremys planicostata*	*Tsaotanemys rugosus*	*Hongilemys kurzanovi*	*Paramongolemys khosatzkyi*
Carapace length	160 mm	225 mm	250-350 mm	*c.* 250 mm	280 mm	350 mm	250 mm	200-300 mm	About 130 mm	250 mm	290 mm
Shell height	—	Low	Moderate	Moderate	Moderate	High	High	?	High	Moderate	Moderate
Carapace shape	Oval, expanded posteriorly	Oval, not expanded posteriorly	Oval, expanded posteriorly	Oval, not expanded posteriorly	Oval, narrowed posteriorly	Oval, not expanded posteriorly	Oval, expanded posteriorly	Oval	Oval, not expanded posteriorly	Oval	Oval, expanded posteriorly
Carapace surface ornamentation	Present, antero-posteriorly directed thin ridges and furrows	Present and strong, coarse ridges and tubercles	Smooth or with sculpturing of tubercles and ridges	Smooth	With sculpturing of tubercles and ridges	Smooth	Smooth or with sculpturing of tubercles and ridges	Pronounced tubercles and ridges	Parallel ridges or small warts arranged into rows or fused to small irregular branching ridges	Smooth?	Smooth
Shell thickness	Thin	Thick	Thin	Thin	Moderate	Thick	Thick or thin	Thick	Thick	Thick	?
Cervical notch	Relatively large	Absent	Absent	Large	Large	Large	Weak	Weak	Weak	Weak	Absent
Vertebral 1 shape	Trapezoidal, Wide anteriorly	?	Trapezoidal, Wide anteriorly	Vase-shaped	Round	Vase-shaped	Rectangular, parallel lateral borders or vase-shaped	Vase-shape	Trapezoidal, Wide anteriorly	Round	Trapezoidal, Wide anteriorly
Vertebral 1/marginal 2 contact	Present	?	Present	Absent	Absent	Absent	Absent	Absent	Present	Absent	Present
Axillary buttresses	Moderate	Moderate	Weak	Weak to moderate	Moderate to strong	Strong	Strong	Moderate	?	?	Weak
Vertebral 2- 3 shape	Slightly wider than long	As wide as long	As wide as long	Longer than wide	Longer than wide	Longer than wide	As wide as long	As wide as long	As wide as long	As wide as long	As long as wide
Shape of anterior lobe	Relatively long? and wide	Short and wide	Relatively long and narrow	Short and wide	Short and wide	Short and wide	Short and wide	?	Short and wide	Relatively long and wide	Relatively long and narrow
Bridge length (Minimal length of bridge/plastron width)	Short (45%)	Short (50%)	Short to moderate (50–57%)	Long (60–70%)	Long, (60–72%)	Long (*c.* 73%)	Long (*c.* 65%)	?	Short (*c.* 53%)	Long (*c.* 65%)	Moderate (57%)
Contribution of hyoplastron and hypoplastron to the minimal length of bridge	Approximatively equal	Approximatively equal	Approximatively equal	Greater in hyoplastron	Greater in hyoplastron	Greater in hyoplastron	Approximatively equal	?	Approximatively equal	Approximatively equal	Approximatively equal

Table 2. Continued

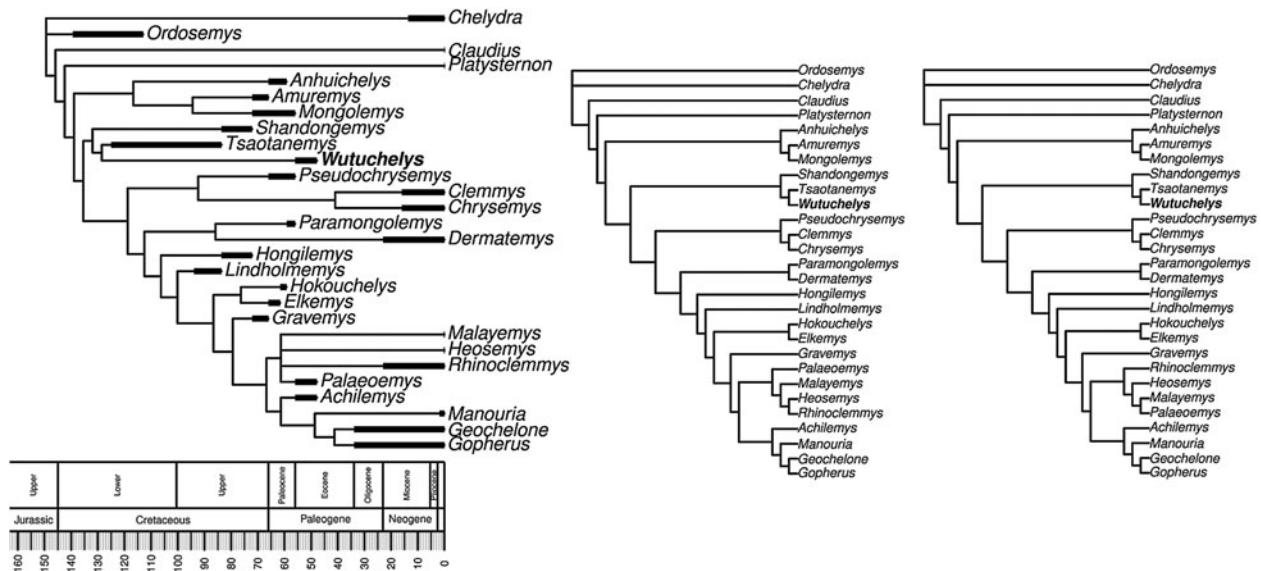| Character/ taxon	Wutuchelys eocenica	Shandongemys dongwuica	Mongolemys elegans	Elkemys australis	Gravemys barsboldi	Hokouchelys chenshuensis	Lindholmemys elegans	Amuremys planicostata	Tsaotanemys rugosus	Hongilemys kurzanovi	Paramongolemys khosatzkyi
Shape of posterior lobe	Relatively wide at the base, with straight backward convergent margins	Relatively wide at the base, with straight backward convergent margins	Narrow at the base, with straight nearly parallel lateral margins	Wide et the base, with convex lateral margins in femoral	Wide at the base, with straight backward convergent lateral margins	Relatively wide at the base, with lateral margins slightly convergent backward	Relatively wide at the base, with convex margins in femoral	?	Relatively wide at the base, with slightly convex lateral margins convergent backward	Relatively wide at the base, with lateral margins convergent backward	Relatively wide at the base, with straight backward convergent margins
Anal notch	Moderate	?	Shallow	Large	Large	Large	Shallow	?	Large	?	Shallow
Entoplastron	As wide as long	Wider than long	Longer than wide or as wide as long	Wider than long	Wider than long	Wider than long	Longer than wide or wider than long	As wide as long	As wide as long	As wide as long	Slightly longer than wide
Humeropectoral sulcus	Far anterior to the base of anterior lobe	Far anterior to the base of anterior lobe	Far anterior to the base of anterior lobe	Anterior to the base of anterior lobe	At the base of anterior lobe	Anterior to the base of anterior lobe	Close to the base of anterior lobe	Anterior to the base of anterior lobe	Posterior to the base of anterior lobe	Anterior to the base of anterior lobe	Anterior to the base of anterior lobe
Pectoral overlapping entoplastron	No	No	No	Yes	No	No	No	No	No	No	No
Inframarginals (number)	Wide (4)	Wide (3)	Wide (3)	Wide (4–5)	Wide (4)	Wide (4)	Narrow (3)	Narrow (?)	Narrow (4)	Narrow (3)	Narrow (3)
Inframarginals extending onto peripherals	Yes, slightly	No	No	Yes, strongly	Yes, strongly	Yes, strongly	Yes, slightly	No	No?	Yes, slightly	No

Figure 7. Strict consensus on the left and the two trees obtained for the unconstrained phylogenetic analysis.

Lourenço *et al*. (2012) and Guillon *et al*. (2012). Character description and distribution are given in Appendices 1 and 2. All characters except one were ordered, and all ordered multi-state characters were scaled so that those characters would not have a disproportionate effect above binary characters on phylogeny estimation. Parsimony analyses were performed under PAUP 4.0 b10 (Swofford, 1998) using random addition sequence, and the tree bisection–reconnection branch-swapping algorithm across 10 000 replicates.

The unconstrained analysis resulted in two equally parsimonious trees of 104.45 steps (Fig. 7). In this analysis, *Wutuchelys* is found in a clade with *Tsaotanemys*, which is the sister group of *Shandongemys*. *Platysternon* is at the base of the Testudinoidea radiation, but *Dermatemys* is found within the in-group with *Paramongolemys*, suggesting an important convergent pattern between Dermatemydidae and Testudinoids. Together with *Paramongelemys*, *Hongilemys*, *Lindholmemys* and *Hokouchelys*, *Elkemys* and *Gravemys* form a clade with Testudinidae and Geoemydidae. Emydidae and *Pseudochrysemys* form a monophyletic group, which is the sister group of this clade. *Amuremys*, *Mongolemys* and *Anhuichelys* form a clade which has an intermediate position between *Platysternon* and *Wutuchelys + Tsaotanemys + Shandongemys* clade. If we exclude the position of *Dermatemys*, the analysis is in agreement with the molecular scaffold with the exception of *Platysternon*, which is more basal. This first result suggests that Lindholmemydidae are polyphyletic, that *Anhuichelys* is in a more basal position than in Tong *et al*. (2016) and that based on the position of *Lindholmemys*, Emydidae split from Testudinidae + Geoemydidae before Turonian.

The analysis constrained by a molecular scaffold resulted in four equally parsimonious trees of 112.12 steps (Fig. 8). As in the unconstrained analysis, W*utuchelys* and *Tsaotanemys* are found in a basal

clade. *Platysternon* being constrained with Emydidae, some relationships change but several remain. *Hongilemys*, *Lindholmemys*, *Gravemys*, *Hokouchelys* and *Elkemys* are a sister group of Geoemydidae + Testudinidae. The position of *Paramongelemys* and *Shandongemys* is variable. Finally, *Pseudochrysemys* and Emydidae are a sister group of *Platysternon*, *Amuremys* and *Anhuichelys* in all instances. General conclusions are the same as in the unconstrained analysis, with a split between Emydidae + Platysternidae and Testudinidae + Geoemydidae before the Turonian, a basal position for *Wutuchelys*, and also a basal position for *Anhuichelys*, which become a convergent form with Testudinidae rather than rooting them.

Our phylogenetic analyses confirm some previous hypotheses. First of all, Lindholmemydidae are not monophyletic and this family should not stand for pre-Eocene Testudinoidea. Furthermore, two notable relationships are found in both constrained and unconstrained analyses. First, *Elkemys*, *Gravemys*, *Hokouchelys*, Geoemydidae and Testudinidae form a monophyletic clade. This relationship is supported by one exclusive synapomorphy (character 35: the contribution of the hyoplastron to the bridge length is greater than that of the hypoplastron) and three non-exclusive synapomorphies (character 33: a long bridge. This character is also present in *Anhuichelys* by convergence and some geoemydids by reversion. Character 18: a large anal notch and character 31: the presence of four inframarginals. These two characters also occur in the *Wutuchelys/Tsaotanemys* clade by convergence). It is noteworthy that the number of inframarginals and the contribution of the hyoplastron to the bridge relative to the hypoplastron are partially correlated to the bridge length, even though there is no complete match in the distribution of the different states. Within this group,
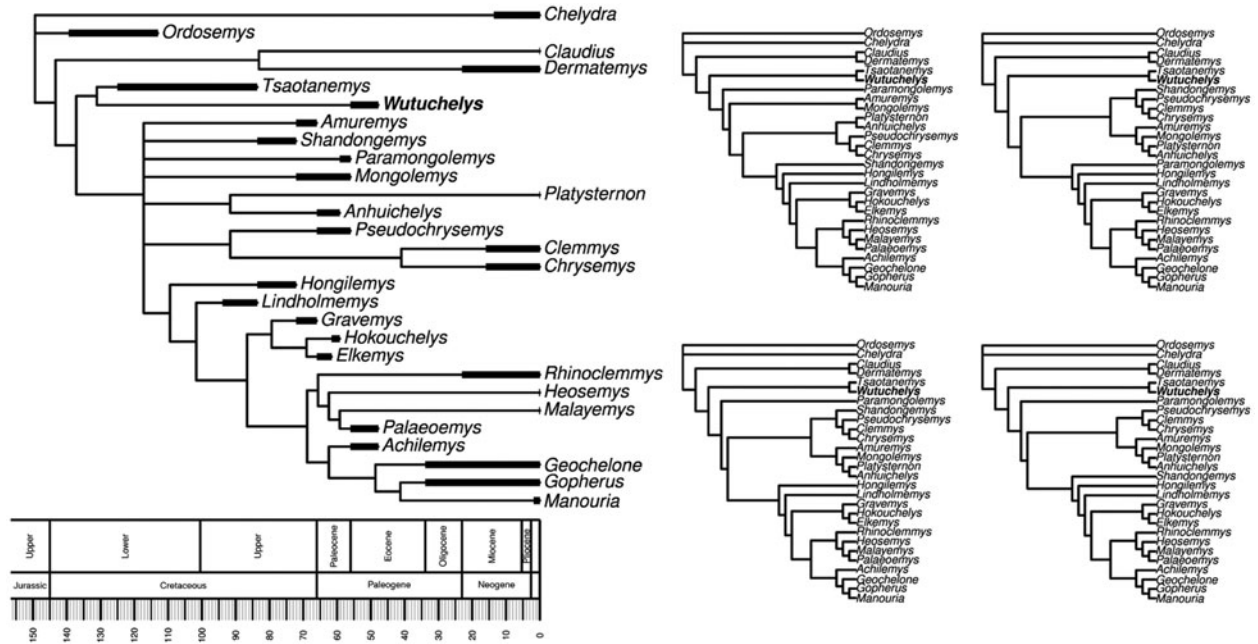
Figure 8. Strict consensus on the left and the four trees obtained for the constrained phylogenetic analysis.

Elkemys, *Gravemys* and *Hokouchelys* form a clade in the constrained analysis as recognized by Danilov *et al*. (2012), although in the unconstrained analysis *Gravemys* is closer to Geoemydidae + Testudinidae than the *Elkemys* + *Hokouchelys* clade. Second, in all our phylogenetic hypotheses, *Wutuchelys* and *Tsaotanemys* form a basal monophyletic clade. This clade is not supported by any exclusive synapomorphy but shares two characters that evolved independently in the clade formed by *Elkemys*, *Gravemys*, *Hokouchelys*, Geoemydidae and Testudinidae: the presence of four inframarginals and a well-developed anal notch. But unlike the *Elkemys*, *Gravemys*, *Hokouchelys*, Geoemydidae and Testudinidae clade, the bridge of *Wutuchelys* and *Tsaotanemys* is short. The larger number of inframarginals in this clade seems not to have evolved, as a consequence of bridge lengthening. In addition, in *Wutuchelys* and *Tsaotanemys*, the inframarginals do not overlap the peripherals to a great extent as is the case in *Elkemys*, *Hokouchelys* and *Gravemys*. This further suggests that the evolution of the number of inframarginals is convergent in these two groups. The *Wutuchelys*/*Tsaotanemys* clade demonstrates that there is an important gap in the fossil record for this clade, spanning from the Cretaceous to the Palaeocene. For both taxa, one-quarter to one-third of the characters are missing in the matrix because of the incompleteness of the material. On the other hand, because fossil testudinoids are poorly documented at present in terms of skull morphology, most conclusions regarding skull evolution within the superfamily have not really been challenged since the work of McDowell (1964). Further material, notably skull remains, would allow us to test whether this relationship is robust.

6. Conclusion

Wutuchelys eocenica n. gen n. sp. is part of an ancient lineage of Testudinoidea that split from other groups before the Turonian and is characterized by a short bridge. It represents a relict taxon of stem testudinoids which survived after the Palaeocene/Eocene boundary, as some mammals from the same locality. The apparent close relationships between *Wutuchelys* and *Tsaotanemys* support the hypothesis that ghost lineages are present in testudinoids and that the fossil record in the late Cretaceous should be investigated to better understand the early radiation of testudinoids.

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Appendix 1. Character states

1. Alternating costal plates: 0 no, 1 polymorphic or intermediate, 2 yes.

2. Inguinal and axillary buttresses contacting costals: 0 no, 1 yes.

3. Second suprapygal larger than first: 0 no, 1 polymorphic or equally larger, 2 yes.

4. Longer than wide pygal plate: 0 no, 1 polymorphic or as long as wide, 2 yes.

5. Marginal 12 relative to pygal: 0 marginals 12 higher than pygal, 1 marginals 12 = pygal, 2 marginals 12 lower than pygal.

6. Neurals: all hexagonal with shortest sides facing antero-laterally: 0 yes, 1 no.

7. Costal 1 reaching peripheral 4: 0 yes, 1 polymorphic, 2 no.

8. Lateral epiplastral lip present: 0 yes, 1 no.

9. Epiplastral lip present in the middle: 0 yes, forming an elevated bulge or a pocket, 1 yes but flat, 2 no.

10. Gular reaching entoplastron: 0 no, 1 polymorhic, 2 yes.

11. Humeropectoral sulcus behind entoplastron: 0 yes, 1 polymorphic, 2 no.

12. Presence of a central carina at least in juvenile, and sometimes persistent in adults: 0 no, 1 yes.

13. Cervical scute: 0 as long as wide as or wider than long, 1 longer than wide, 2 absent.

14. Coalescent trochanters of the femur: 0 no, 1 yes.

15. Bony bridge: 0 no, 1 yes.

16. Anal midline length relative to that of femoral: 0 anal longer than femoral, 1 anal equal to femoral, 2 anal shorter than femoral.

17. Midline length of xiphiplastron greater than the one of the hypoplastron: 0 no, 1 yes.

18. Anal notch: 0 absent, 1 small, 2 clearly present.

19. Inframarginal row: 0 complete and wide, 1 complete and narrow, 2 polymorphic, 3 incomplete.

20. Wide entoplastron: 0 yes, 1 polymorphic or intermediate, 2 no.

21. Three carinae in juveniles, sometimes persistent in adults: 0 no, 1 yes.

22. Pairs of anterior and posterior musk ducts: 0 no, 1 yes.

23. Nuchal emargination: 0 absent, 1 small or variable, 2 well developed.

24. Vertebrals 2–3: 0 wider than long, 1 longer than wide.

25. Vertebral 1: 0 wide, 1 narrow (anterior end included in nuchal plate).

26. Contact between nuchal plate and first peripheral: 0 nearly parallel to body axis, 1 convergent forward.

27. Gular notch: 0 absent, 1 present.

28. Inguinal buttresses: 0 does not reach costal, 1 reaches costal 5 only, 2 reaches costals 5 and 6.

29. Suture between epiplastron and hyoplastron: 0 nearly perpendicular to body axis or backward laterally, 1 forward laterally.

30. Pectoral scutes: 0 present, 1 absent.

31. Number of inframarginal scutes when the row is complete: 0 three, 1 four.

32. Inframarginal scutes on plastron: only on plastron 0, extending slightly on peripheral 1, extending strongly on peripheral 2.

33. Bridge length / plastron width ratio: 0 less than 55 %, 1 above 55 %.

34. Pleural 3 reaching marginal 6: 0 no, 1 yes.

35. Contribution of hyoplastron and hypoplastron to minimal bridge length: 0 almost equal, 1 greater in hyoplastron.

36. Flange of the prearticular longer than anterior extension of angular in lingual view: 0 no, 1 yes.

Appendix 2. Taxon/character matrix

Achilemys   21000 10010 0?011 10230 ?0011 10{12}00 ??101 ?

Amuremys   01012 01??2 0?0?1 ???11 ?0010 1?100 ?0?0? ?

Anhuichelys   1111{12} 00021 100?1 01{01}31 00111 11100 ??100 ?

Chelydra   00002 {01}2120 01000 01002 10200 00000 00000 0

Chrysemys   01022 01012 21101 00130 00000 10110 ?1000 0

Claudius   00001 02122 01000 11030 10000 10001 ??000 0

Clemmys   01022 02012 21101 00130 00000 10110 ?1000 0

Dermatemys   00022 02122 01001 10200 00110 10011 11100 0

Elkemys   01002 01012 210?1 10200 ?0111 11{12}10 12101 ?

Geochelone   21221 12001 00{12}11 20230 00000 10210 ? 1111 1

Gopherus   21121 12002 00011 20230 00000 10110 ?1111 1

Gravemys   01000 00022 0?0?1 20200 ?0111 10110 12101 ?

Heosemys   01000 10012 21001 20230 11101 10110 ?1011 1

Hokouchelys   01??? 01022 010?1 20200 ?0111 11110 12101 ?

Hongilemys   01??? 02??1 0?0?1 20?11 ?0111 10?10 01100 ?

Lindholmemys   01002 01022 0?0?1 20110 ?0011 10210 01100 ?

Malayemys   01000 00012 21001 20230 11101 10210 ?1101 1

Manouria   2102{01} 12011 00011 20230 00100 10110 ?1101 1

Mongolemys   01022 01021 0?001 10101 00010 00{12}00 00000 0

Ordosemys   00000 1212? 0?000 10002 ?0200 10000 10000 ?

Palaeoemys   01000 00012 01001 20230 11111 10210 ?1101 ?

Paramongolemys   01002 02122 0?1?1 10111 ?0010 10110 00100 ?

Platysternon   00002 {01}2021 11000 11210 0020{01} 10000 00001 0

Pseudochrysemys   01002 02012 0?1?1 10120 ?0111 10110 01001 ?

Rhinoclemmys   01000 11012 21001 20230 0100{01} 10110 ?1101 1

Shandongemys   01??? 02??2 0???1 20?00 ?001? ?1?10 00000 ?

Tsaotanemys   01?02 0???2 0?0?1 20211 ?0100 11110 100?0 ?

Wutuchelys   0101? 0???? 0???1 10201 ?0?0? ??110 11000 ?