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Pangshura tatrotia, a new species of pond turtle (Testudinoidea) from the Pliocene Siwaliks of Pakistan

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We describe a new species of fossil testudinoid from the Indian subcontinent, *Pangshura tatrotia* sp. nov., and suggest a new clade name, Palatochelydia, for the monophyletic assemblage of South Asian turtles to which it belongs. A combined analysis using recent molecular data and an updated morphological dataset confidently places *P. tatrotia* as sister to the extant turtle *P. tecta.* The holotype specimen is unique relative to most previously described palatochelydian material in that it is associated with good quality locality information. We therefore can conclude that this specimen comes from the Pliocene Tatrot Formation of north-eastern Pakistan, which corresponds to an interval of 2.59 to 3.59 Ma. This can now serve as a minimum divergence date for the *P. tecta* clade. However, given that no other palatochelydian fossils are associated with good quality locality information, this date must also serve as the minimum for all other, more inclusive palatochelydian clades.

Keywords: *Pangshura tatrotia*; Testudinoidea; Palatochelydia; Siwaliks; Pliocene; Bayesian analysis

Introduction

Although the fossils of testudinoid pond turtles are ubiquitous in the Neogene of the Indian subcontinent, their taxonomy and evolutionary history remain poorly understood. Many specimens from this region were described during the second half of the 19th century and were variously interpreted as either new species or as fossil representatives of extant species (see Lydekker 1885 for summary). Although a modern cladistic review of these specimens is still outstanding, it appears clear that the vast majority of fossils described are representatives of a mostly south Asian group that was recognized on morphological grounds by Gray (1870) as the Bataguridae (*non sensu* McDowell 1964; Joyce *et al.* 2004) and recently confirmed to be monophyletic based on molecular evidence (Spinks *et al.* 2004; Le *et al.* 2007).

Identifying fossil testudinoids to the species level based on shells only is often hampered by a lack of unique and diagnostic characters (Joyce & Bell 2004) and due to a lack of understanding of variation (Bever 2007). However, the batagurid (*sensu* Joyce *et al.* 2004) clade *Pangshura* is somewhat unique in that it displays a variety of characters that rarely or never occur in other turtles (Hirayama 1985). In particular, representatives of this clade have highly domed carapaces that are tent- or bell-shaped

in anterior view and a strong median keel that often displays fin-like protrusions. These Asiatic turtles thus greatly resemble the shells of the North American map turtle clade *Graptemys* (Joyce & Bell 2004). More importantly, instead of the usual hexagonal vertebral scutes seen in most other turtles, representatives of *Pangshura* have a unique arrangement of compressed and elongated vertebral scutes, often with strange finger-like projections. Due to the presence of these unique features, a number of fossils from the Plio/Pleistocene of the Indian subcontinent were confidently assigned to this clade, but all were referred to recent species, in particular *Pangshura tecta* (Gray, 1831) and *Pangshura flaviventris*, which is now synonymous with *Pangshura tentoria* (Gray, 1834) (Lydekker 1885).

In 1932 a specimen of *Pangshura* was collected by one of the Yale North India expeditions in what is now Pakistan, but the specimen was never formally described. This specimen is arguably the oldest and best-preserved representative of *Pangshura* and also one among few testudinoids from the Indian subcontinent with detailed locality data. The purpose of this paper is to describe formally this specimen as a new species of testudinoid turtle, and to assess its phylogenetic position using a combined molecular and morphological dataset analysed in a Bayesian framework.

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Institutional abbreviations

BMNH: Natural History Museum, London, UK; **CRI**: Chelonian Research Institute, Oviedo, Florida, USA; **FMNH**: Field Museum of Natural History, Chicago, Illinois, USA; **YPM**: Yale Peabody Museum Vertebrate Paleontology Collections, New Haven, Connecticut, USA; **YPM R**: Yale Peabody Museum Herpetology Collections, New Haven, Connecticut, USA.

Terminology

Anatomical terms of the shell follow those of Zangerl (1969). The generic assignment of recent batagurid species follows Spinks *et al.* (2004), but clade definitions follow Joyce *et al.* (2004).

Material and methods

All anatomical systems were systematically scrutinized for phylogenetically informative characters, but the majority was recognized in Hirayama's (1985) phylogenetic analysis of the Bataguridae, or Joyce & Bell's (2004) review of testudinoid characters. As an initial step, all characters were scored for all ingroup and outgroup taxa, but only those characters that were parsimony informative or autapomorphic for representatives of *Pangshura* were ultimately used. The final data matrix includes 26 osteological characters with 34 derived character states for 10 extant representatives of Palatochelydia (see definition below) and the new fossil taxon. The list of morphological characters used is presented in Appendix 1 and their distribution is provided in Table 1. *Geoclemys hamiltonii* (Gray, 1831) was selected as the outgroup for this analysis because all recent molecular phylogenies place it as the immediate sister to a clade consisting of *Batagur baska* (Gray, 1831), *Callagur borneoensis* (Schlegel & Müller, 1844), *Hardella thurjii* (Gray 1831), *Kachuga kachuga* (Gray 1831), and *Pangshura tecta* (Gray, 1831) (Spinks *et al.* 2004; Diesmos *et al.*

2005; Le *et al.* 2007). A complete list of comparative specimens used in the analysis is provided in Appendix 2.

The morphological dataset was combined with the aligned molecular sequences of Le *et al.* (2007) consisting of 4015 mitochondrial and nuclear base pairs. However, given that we did not have access to specimens of *Morenia ocellata* (Duméril & Bibron, 1835) but the closely related *Morenia petersi* (Anderson, 1879) instead, we combine the molecular data of the former taxon with the morphological observations of the latter taxon and refer to this combination as *Morenia*. Data were analysed using Bayesian analysis as implemented in MrBayes v3.1 (Huelsenbeck & Ronquist 2001). We divided the data into 21 partitions, including morphology and each gene, which were each further broken into two partitions: 1st/2nd codon and 3rd codon position. The optimal model for each partition was determined using Modeltest with parameters estimated by MrBayes v3.1. All characters were considered reversible and of equal weight and those morphological multistate characters were ordered that form morphoclines (morphological characters 23, 24 and 25, see Appendix 1). Analyses were conducted with a random starting tree and run for 5×10^6 generations. Two simultaneous runs and four Markov Chains, one cold and three heated (using default heating values), were sampled every 100 generations. Convergence between the two simultaneous runs was determined by the stabilization of the standard deviation of the split frequencies below 0.01. The first 25% of samples (12 500 total) were eliminated in the burn-in. The topology and posterior probability (PP) for all clades in the final majority rule consensus tree are reported (Fig. 1). The Nexus file resulting from this analysis is provided with the Supplementary Material.
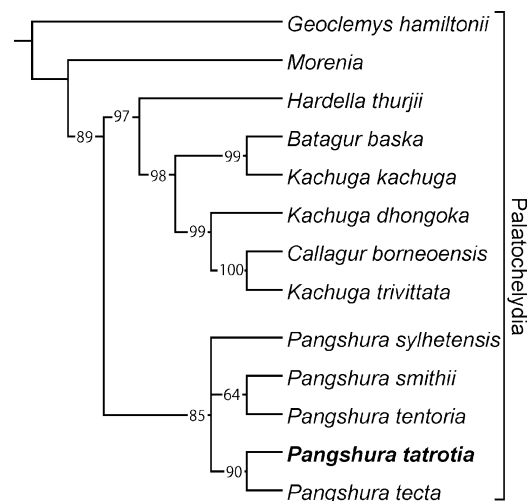
Table 1. Data matrix of 26 morphological characters for one outgroup taxon (*Geoclemys hamiltonii*) and 11 ingroup taxa. a = 0/1; b = 0/2; c = 1/2.

Geoclemys hamiltonii	0000000000	0000000000	010000
Batagur baska	0000000003	0003001101	112121
Callagur borneoensis	00000000a1	0000000101	101111
Morenia petersi	000b000001	0000000000	121220
Hardella thurjii	0000000001	0000000101	101120
Kachuga kachuga	000000001a	0000000100	102121
Kachuga dhongoka	100000001a	0100c0a101	101121
Pangshura smithii	0000011110	00a1111001	101010
Pangshura tecta	0100011012	1212211001	101010
Pangshura tentoria	0100011a10	00ac211001	111010
Pangshura tatrotia	1100011010	021221100?	?????0
Pangshura sylhetensis	011111111b	001200–01?	?????0

Figure 1. The strict consensus topology resulting from the phylogenetic analysis presented herein. Numbers below nodes are Bayesian posterior probabilities.

Geological settings

The new specimen, YPM 4127, was collected at fossil locality #99 during the 1932/33 Yale North India Expedition in what is now Pakistan. Locality #99 can be confidently assigned stratigraphically to the Tatrot Formation of the Upper Siwaliks (Barry *et al.* 1982). Unfortunately, it has been difficult to determine the exact age of the Tatrot, mostly because this formation consists of only a single, normal magnetic polarity and because it is unclear whether the underlying formational contact with older sediments is continuous. Barry *et al.* (1982) originally postulated that a significant hiatus existed below the Tatrot Formation and attributed the Tatrot to the upper normal interval of the Gauss Chron based on the thickness of the sedimentary package and faunal elements. Using the revised geomagnetic calibrations of Ogg & Smith (2004), this would correspond to an interval between 2.58 and 3.03 Ma. However, given that it is plausible to refer to the Tatrot Formation to the lower normal interval of the Gauss Chron instead (personal communication WGJ with John Barry), it appears more conservative to refer the Tatrot Formation to the entire Gauss Chron. YPM 4127 should thus be estimated as having an age anywhere between 2.59 and 3.59 Ma (Ogg & Smith 2004).

Systematic descriptions

Testudines Batsch, 1788
Cryptodira Cope, 1868
Testudinoidea Fitzinger, 1826
Palatochelydia new clade

Etymology. In reference to the well-developed secondary palate that is diagnostic for this group.

Definition. 'Palatochelydia' refers to the most inclusive clade containing *Batagur baska, Callagur borneoensis, Hardella thurjii, Kachuga kachuga, Morenia ocellata* and *Pangshura tecta*.

Comments. In his revision of the turtles of the world, Gray (1870) was the first to note that various broad-headed turtles from Asia form a natural group to which he applied the name Bataguridae. After years of disuse, McDowell (1964) used this term again, however, this time to unite Asian pond turtles and representatives of *Rhinoclemmys*. This name/clade association was later co-opted by Joyce *et al.* (2004) because it predominated in the literature for the second half of the 20th century. As a result, however, Gray's original grouping is now unnamed, even though recently compiled molecular data support its monophyly (Spinks *et al.* 2004; Le *et al.* 2007). To alleviate this situation, we here name this clade Palatochelydia in reference to the well-developed secondary palate that diagnoses representatives of this group.

Pangshura tatrotia sp. nov.
(Figs 2, 3)

Etymology. In reference to the Tatrot Formation, from which the holotype was recovered.

Holotype. YPM 4127, an all but complete shell that documents nearly all portions of the carapace and plastron.

Type locality. Yale North India Expedition locality #99, Tatrot Formation, Early Pliocene, about two miles northeast of Padhri, Pakistan.

Diagnosis. *Pangshura tatrotia* is a testudinoid turtle diagnosed by the following combination of characters: tectiform carapace, posterior constriction of third vertebral, anterior constriction of the first vertebral, pleural I/II sulcus with long anteromedial process, vertebral IV with anteromedial projection, contact of marginal X with vertebral V, wavy pleural/marginal sulcus pattern.

Description of YPM 4127

Preservation. The specimen is generally well preserved in a fine-grained carbonate-cemented conglomerate and is only slightly crushed. Significant portions of both sides of the carapace are missing, but with exception of the posterior rim, most of the right side complements what is missing on the left, and vice versa. The plastron is mostly complete as well, with the exception of the right epiplastron and much of the xiphiplastra. Sutures and sulci are clearly preserved over much of the surface of the specimen (Figs 2, 3).

Carapace. In dorsal view the carapace is oval and lacks a distinct nuchal notch. The exact shape of the pygal area is unclear due to damage of the peripheral series. In anterior view, the carapace is notably high-domed and exhibits a pronounced median keel. Although this shell shape may well be termed tectate (i.e. roof shaped) it is important to note that the sides are distinctly rounded, and not flat. The keel runs down the entire dorsal side of the carapace and is thus formed by the nuchal, neurals and pygal series. At its highest point, the midline ridge is raised approximately 0.5 cm above the level of the surrounding costal bones.

Neurals. All eight neurals are preserved. The keel is strongly developed along the first to fourth neural, dwindles at the fifth neural, but rises prominently along the rest of the neural series. The first neural is subrectangular, longer than wide, and the anterior and lateral sides are slightly convex. The second neural is approximately as long as the first but is hexagonal with short anterior sides. The third neural is
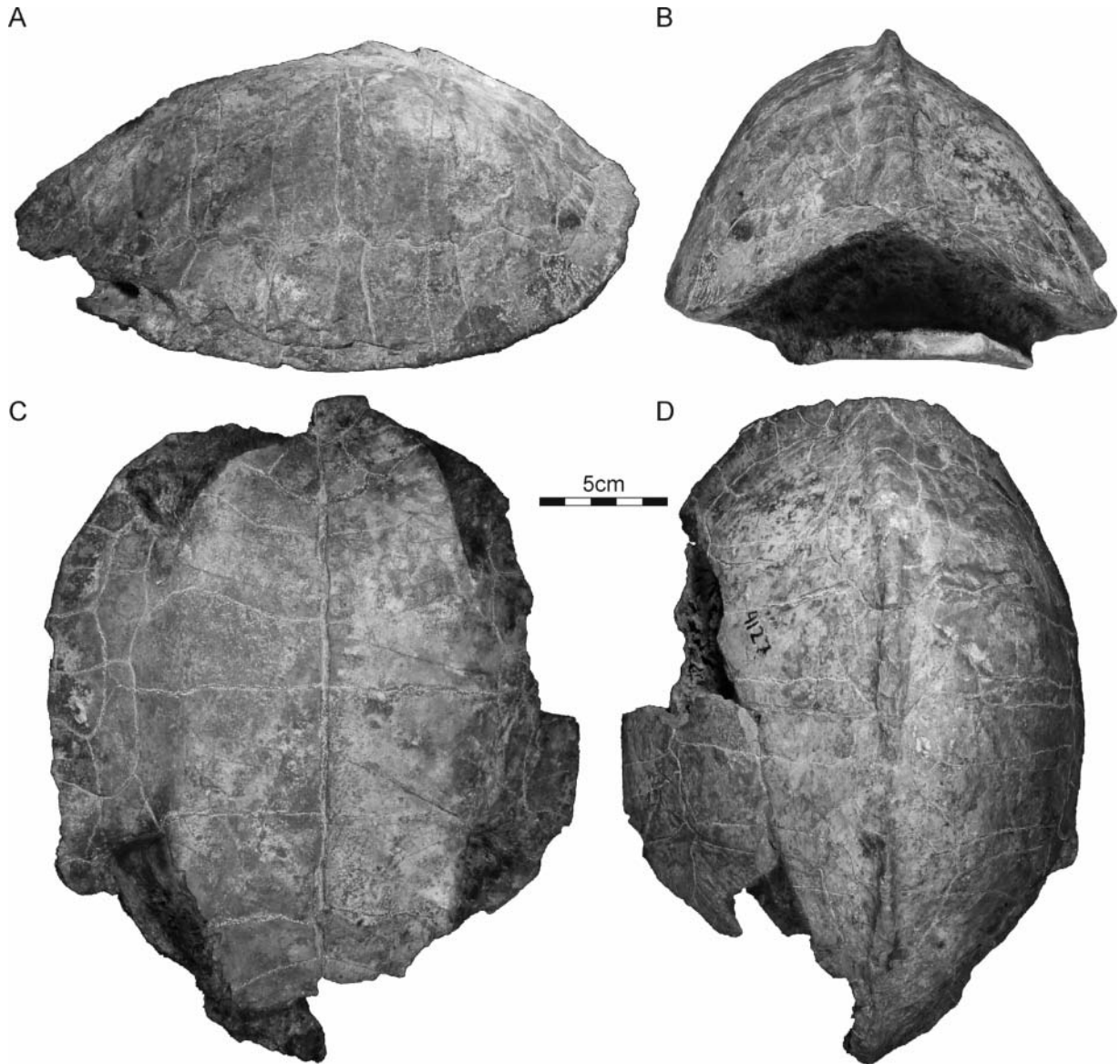
Figure 2. Photographs of YPM 4127, holotype of *Pangshura tatrotia* sp. nov, from the early Pliocene Tatrot Formation of Pakistan. **A,** lateral view of shell; **B,** anterior view of shell; **C,** ventral view of shell; **D,** dorsal view of shell.

significantly larger than the second, but is hexagonal as well with short anterior sides. The fourth neural is the longest of the neural series and has a clear octagonal outline. All following neural elements decrease in size posteriorly. The fifth is a stretched rectangle, like the first, and all sides are convex. The sixth to eighth neurals are hexagonal like the second and third, but the anterior sides are only a little shorter than the posterior ones.

Costals. The costals are best preserved on the right side. Whereas the first seven are distinctly rounded to form the domed shape of the carapace, the eighth pair is somewhat flatter. Also, whereas the first six pairs of costals are positioned perpendicular to the neural column, the seventh and

eighth are somewhat rounded posteriorly. The first costal is the longest element (i.e. from front to back), but is distinctly narrower than the second. It contacts the nuchal antero-medially, peripherals I–III anterolaterally, costal II posteriorly, and neurals I and II medially. The second to fifth costals have about the same dimensions. Medially, costal II contacts neurals II and III; costal III contacts neurals III and IV; costal IV contacts neural IV only; and costal V contacts neurals IV–VI. Laterally, costal II contacts periph-eral IV and a little of peripheral III; costal III contacts peripheral V only; costal IV contacts peripherals V and VI; and costal V contacts peripherals VI and VII. The poste-rior three costals incrementally decrease in size and rotate posteriorly. Medially, costal VI contacts neurals VI and
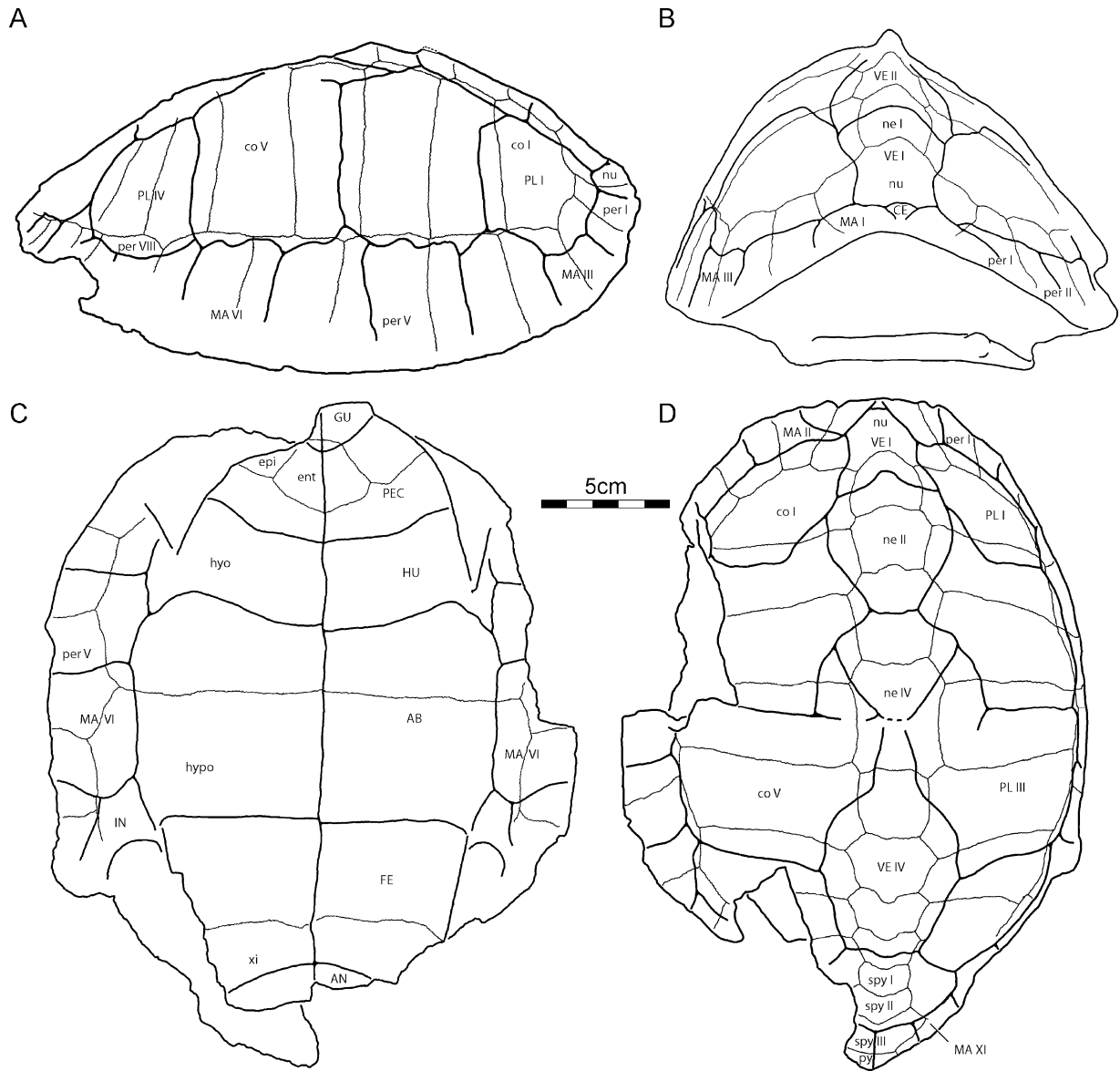
Figure 3. Line drawings of YPM 4127, holotype of *Pangshura tatrotia* sp. nov, from the early Pliocene Tatrot Formation of Pakistan. **A,** lateral view of shell; **B,** anterior view of shell; **C,** ventral view of shell; **D,** dorsal view of shell. Abbreviations: AB, abdominal scute; AN, anal scute; CE, cervical scute; co, costal; ent, entoplastron; epi, epiplastron; FE, femoral scute; GU, gulars scute; HU, humeral scute; hyo, hyoplastron; hypo, hypoplastron; IN, inguinal scute; MA, marginal scute; ne, neural; nu, nuchal; PEC, pectoral scute; PL, pleural scute; py, pygal; spy, suprapygal; VE, vertebral scute; xi, xiphiplastron.

VII; costal VII contacts neurals VII and VIII; and costal VIII contacts neural VIII and all three suprapygal elements. Laterally, costal VI contacts peripheral VII and VIII; costal VII contacts peripheral VIII and IX; and costal VIII contacts peripherals IX and X.

Nuchal. The nuchal is trapezoidal with a distinct notch midway through the posterior contact with neural I. The nuchal narrows in width anteriorly. It contacts peripheral I laterally along a slightly convex suture, and costals I and

neural I along a wavy posterior suture. The keel of the carapace originates at the anterior end of the nuchal and is notably blunt.

Peripherals. Eleven pairs of peripherals are present. The left side preserves most of peripherals I–III and peripherals VI and VII. The right side preserves most of peripherals I–IV, significant portions of peripherals V–VII, as well as the medial portions of peripherals IX–XI. The anterior margin of the shell is rather smooth, but the posterior rim is

not preserved at all. Whereas peripherals III–VII have clear contacts with the plastron, it is unclear if peripheral II did so as well. All peripherals are similar in size and have more or less square outlines in dorsal view, with the exception of the first, which is more wedge-shaped. The contacts of the peripherals are described above. The presence of musk duct foramina is uncertain.

Suprapygals. All three suprapygals are present, although the posterior two are missing parts of the left side. The first suprapygal is rectangular, wider than long, and as large as the eighth neural. The second suprapygal is larger than the first and retains a rectangular shape. Laterally, the first two suprapygals contact the eighth costal only. The third suprapygal is much larger, almost twice as wide and one and a half time as long as the second. It has a distinct hexagonal shape. This element contacts the second suprapygal anteriorly along a concave line, the eight costal anterolaterally, peripherals X and XI posterolaterally, and the pygal posteriorly.

Pygal. The exact side of the pygal is uncertain, given that its posterior edge is missing. However, from what is preserved it is apparent that it contacted the third suprapygal anteriorly and the 11th peripheral laterally.

Vertebrals. Five vertebral scutes are present and each one has a unique shape. Vertebral I is bell shaped, the anterior half being about 70% the width of the posterior half. It anteriorly contacts the cervical, anterolaterally contacts marginal I, laterally contacts pleural I along a concave line, and posteriorly contacts vertebral II. The vertebral I–II sulcus displays a small, anterior protrusion and is positioned over neural I. Vertebral II has a concave anterior contact with vertebral I and constricts posteriorly significantly to a blunt apex where it contacts vertebral III over neural III. It is heptagonal in shape. Laterally it contacts pleurals I and II. The keel below this element comes to an abrupt drop at its posterior margin, indicating that it has a sharp conical shape in life. Vertebral III has a distinct pentagonal, vase-like shape. Its anterior contact with vertebral II is rather blunt, but its posterior contact with vertebral IV over neural IV is obscured due to some damage to the keel. This damage also obscures the original shape of this element, although it is apparent from the shape of what remains that this element also formed a distinct posterior protrusion that was much larger than the one formed by vertebral II. Vertebral IV forms a somewhat stretched hexagon, although its anterior side forms a finger-like protrusion that reaches anterior to contact vertebral III. The posterior contact with vertebral V is over neural VIII. The greatest width of the first four vertebrals is about the same. The fifth vertebral forms an irregular, multisided element. It anteriorly contacts verte-

bral VI, anterolaterally contacts pleural IV, and laterally and posteriorly contacts marginals X–XII.

Pleurals. Four pairs of pleurals are present and their shapes are rather unique as well. In lateral view, pleural I is a mostly square element, but its medial contact with the vertebral is constricted due to the anterior process of the second pleural. The anterior contacts with marginals I–III and is clearly situated on top of the peripherals, but the lateral contact with peripheral IV closely follows the costoperipheral suture. The second pleural is about as long as the first but exhibits an increased medial contact with vertebral II due to an anteriorly projecting process next to this element. However, its lateral contact with vertebral III is reduced due to a similar process of pleural III. The lateral contact with marginals IV–VI is wavy, but closely approximates the costoperipheral suture. Pleural III is the largest pleural and it broadly contacts vertebrals III and IV medially due to the development of its anterior process. Its lateral contact with marginals VI–VIII is also wavy and is clearly situated along the costoperipheral suture. In lateral view, pleural IV is a square element that contacts marginals VIII–X in a convex line mostly lateral to the costoperipheral suture.

Cervical. A single cervical scute is present that is somewhat unusual in that it forms a triangle and barely contacts the anterior margin of the shell. However, given that the anterior margin of the shell is somewhat damaged, it is possible that this is an artefact of preservation.

Marginals. Twelve pairs of marginal scutes are present. As described above, their medial contacts with the pleural scutes and the fifth vertebral is rather wavy, especially along marginals IV–VIII. The marginal I–III sulcus with the first pleural is mostly placed over the peripherals, as is the sulcus between marginals VIII–X and pleural IV. However, the sulcus between marginals IV–VII and pleurals II and III and between marginals X–XII and vertebral V closely approximates the costoperipheral suture. Although the full size of the 12th marginals is unclear, it is apparent that the marginals were much taller than the pygal and thus partially subdivide the third suprapygal.

Plastron. The plastron is generally well preserved and only the lateral tips of the plastral lobes are not represented. Significant portions of the anterior and posterior plastral buttresses have not been prepared, making it impossible to assess their extent.

Plastral bones. The entoplastron is a relatively large element with a bell-like shape. Laterally it contacts the epiplastra, which form much of the anterior plastral margin. Although the anterior plastral margin is generally smooth, the gulars form a squarish anterior projection. Much of this anterior morphology and the internal extent of the skin

sulcus generally resemble that seen in extant representatives of the group. The hyoplastra and hypoplastra form the vast majority of the plastron. Well-developed axillary and inguinal buttresses are present, but their full extent is unclear. The bridge articulates with peripherals III–VII and perhaps with peripheral II as well. The hypoplastra contact the xiphiplastra along a rather straight suture, at least externally. The size of the latter is uncertain, as is the development of an anal notch.

Plastral scutes. As in all testudinoids, YPM 4127 has one pair each of gular, humeral, pectoral, abdominal, humeral and anal scutes. The midline sulcus that separates all pairs coincides fully with the midline suture. The plastral formula, based on midline length and excluding the anal, is gul < hum < pec < fem < ab. The gulars are triangular, have a long medial contact with one another, but are mostly positioned over the epiplastra and only slightly come to lie over the entoplastron. The humeropectoral sulcus is slightly curved and clearly does not encroach onto the entoplastron. The abdominals are large plastral scutes and only barely contribute to the posterior plastral lobe in the deepest portion of the inguinal notch. Axillary scutes were likely present but cannot be observed due to a lack of preparation. Inguinal scutes are present as well, and they substantially contribute to the bridge and articulate broadly with marginal VII laterally and marginal VI anteriorly.

Discussion

Over the course of the second half of the 19th century, a number of fossil testudinoid turtles were described from the Indian subcontinent, but little has been added to the subject since the comprehensive review of Lydekker (1885). A remarkable aspect of the testudinoid fauna from the Siwaliks is that specimens are often rather complete and most can be attributed comfortably to extant species lineages. For instance, fossils are available that clearly represent (stem)-representatives of *Kachuga dhongoka* (Gray, 1834) (BMNH 39841, holotype of *Batagur durandi* Lydekker, 1885), *Hardella thurjii* (BMNH R748, holotype of *Clemmys watsoni* Lydekker, 1886), or *Geoclemys hamiltonii* (BMNH 39838, BMNH 39840, both originally referred to *Clemmys palaeindica* Lydekker, 1885). As a consequence, it should be possible to reconstruct the Miocene to Pleistocene evolution of Indian testudinoids. However, given that fossils were typically collected during the 19th century with only little locality information (e.g. 'Siwalik Hills'), these turtles may originate from sediments dating anywhere from early Miocene (*c*.25 Ma) to Pleistocene (*c*.11 000 a) and most evolutionary questions can thus not be addressed with any confidence. The holotype specimen of *Pangshura tatrotia* described herein is unique in that it is rather complete and the first to be associated with detailed locality data.

The topology of the phylogeny presented here is identical to the one published by Le *et al.* (2007) for all taxa for which molecular data is available. This is not surprising, given that this analysis is based on the Le *et al.* (2007) molecular dataset and given that similar methods of analysis were used. Using the morphological data only, *Pangshura tatrotia* is placed as sister to *P. tecta* deep within the clade Palatochelydia (Fig. 1). This arrangement received rather high posterior probability values, even though *P. tatrotia* lacks all molecular data, which comprises more than 99% of the dataset. In contrast, morphological data alone are not able to resolve the phylogenetic position of *P. sylhetensis* (Jerdon, 1870) and place it in a polytomy at the base of the *Pangshura* clade. *P. sylhetensis* clearly exhibits a number of characteristics of the *Pangshura* clade, in particular the tectiform carapace and the unique shape of the vertebral scutes, but in other regards this taxon is highly autapomorphic. Furthermore, the rather unique development of 13 pairs of marginal scutes seen in this taxon, as opposed to the usual 12, renders much of its morphology non-comparable to other representatives of the clade. We therefore conclude that molecular data will be necessary to resolve better the placement of this taxon.

In overall gestalt, *P. tatrotia* greatly resembles the extant turtles *P. tentoria* and *P. tecta*. *Pangshura tatrotia* is a plesiomorphic relative of *P. tecta* in the placement of the vertebral IV/V sulcus over the eighth neural and the presence of an anteriorly constricted first vertebral. However, the autapomorphic development of a medial keel formed by vertebral II indicates that this taxon is not ancestral relative to *P. tecta*, but rather forms an autonomous side lineage. *P. tecta* still occurs today in the general area where the holotype specimen of *P. tentoria* was found, in contrast to *P. tentoria* which is found further to the east (Iverson 1992). At the very least, this specimen implies that the minimum divergence time of the *P. tecta* lineage occurred 2.59 Ma. Until further fossil evidence is available, this date will also have to suffice as the minimum for all other, more inclusive clades of palatochelydians.

Unlike various other groups of testudinoid turtles, palatochelydians are ideal for molecular calibration studies because every extant taxon exhibits highly unique morphological features that allow confident diagnosis of lineages to species level. It is therefore quite lamentable that the beautiful material collected during the 19th century lacks the temporal data that is necessary for a rigorous analysis. We see two primary ways to alleviate the situation. Although the various fossil turtles collected during the 19th century lack detailed locality information, most are not prepared internally and may thus contain sufficient quantities of sediment to warrant dating them with palaeontological techniques (palynology, geochemical signatures, etc.). However, considering that fossil turtles are generally common and do not appear to be rare on the Indian subcontinent as well, we suggest that the collection of

additional material may be a more efficient way to gain further insights into the morphological and temporal evolution of this group.

Acknowledgements

Note

Supplementary Material can be viewed online.

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Appendix 1

Characters

1. Pronounced midline projection formed by vertebral II (new character): 0 = absent; 1 = present.
2. Pronounced midline projection formed by vertebral III (see Hirayama 1985, character N; Joyce & Bell 2004, character 36): 0 = absent; 1 = present.
3. Pronounced midline projection formed by vertebral IV (new character): 0 = absent; 1 = present.

Comments regarding characters 1–3: The carapacial midline of testudinoids is either smoothly domed or decorated by a keel. In various representatives of the ingroup, the second, third and fourth vertebrals may form pronounced

projections that rise well above the remaining carapace. Although less pronounced, these projections are clearly visible in osteological and fossil specimens that lack their scutes.

4. Shape of the second neural (see Hirayama 1985, G; Joyce & Bell 2004, 37): 0 = hexagonal, short sides anteriorly; 1 = octagonal; 2 = square.
5. Shape of the third neural (see Hirayama 1985, G; Joyce & Bell 2004, 38): 0 = hexagonal, short sides anteriorly; 1 = rectangular.
6. Shape of the fourth neural (new character): 0 = hexagonal, short sides anteriorly; 1 = octagonal.
7. Shape of the fifth neural (new character): 0 = hexagonal, short sides anteriorly; 1 = rectangular.

Comments regarding characters 4–7: The shape and orientation of the neurals of testudinoids has commonly been utilized to characterize various groups, especially the shape and orientation of the anterior three (e.g. Auffenberg 1974; Hirayama 1985; Stephens & Wiens 2003). Within the ingroup, variation occurs in the second to fifth neurals. In particular, instead of being hexagonal with short anterior sides, the second is occasionally octagonal, the third occasionally rectangular, the fourth occasionally octagonal, and the fifth rectangular. Although the distribution of characters 4 and 5 and characters 6 and 7 score redundant within this study, both character pairs are left separate, because they are not logically redundant.

8. Location of vertebral II–III sulcus (new character): 0 = neural III; 1 = neural II.
9. Location of vertebral III–IV sulcus (see Hirayama 1985, L+M; Joyce & Bell 2004, 42): 0 = neural V; 1 = neural IV.
10. Location of vertebral IV–V sulcus (see Hirayama 1985, L+M; Joyce & Bell 2004, 42): 0 = neural VIII; 1 = neural VII; 2 = over suprapygals; 3 = posterior neurals absent and sulcus runs over costals only.
11. Shape of vertebral I (new character): 0 = rectangular or constricted anteriorly (typically variable through ontogeny); 1 = significantly constricted posteriorly.
12. Shape of vertebral II (new character): 0 = hexagonal to rectangular; 1 = hexagonal to rectangular, with a fingerlike posterior process that protrudes deeply into vertebral III; 2 = hexagonal, but greatly constricted posteriorly to a blunt tip that may protrude slightly into vertebral III.
13. Shape of vertebral III (new character): 0 = hexagonal to rectangular, may accommodate for the posterior process of vertebral II; 1 = hexagonal, but greatly constricted posteriorly to a blunt tip, may accommodate for the posterior process of vertebral II.

14. Shape of vertebral IV (new character): 0 = hexagonal to rectangular; 1 = hexagonal, but with a broad fingerlike anterior process that is framed by the pleural scutes; 2 = hexagonal, but with a narrow fingerlike anterior process that is framed by the pleural scutes; 3 = hexagonal, but with a small anterior process that protrudes into vertebral III.

Comments regarding characters 11–14: The vertebral series of most turtles consists of a fan shaped first vertebral, three hexagonal vertebrals and a posterior, fan-shaped fifth vertebral. Variation is typically restricted to the shape of the first vertebral. Within the ingroup, the shapes vary significantly and capturing this variation is somewhat challenging, in part because the effect of one vertebral may affect the shape of the next. The three characters listed above were developed specifically to avoid any problems that arise from logically correlated character complexes.

15. Placement of pleural I–II sulcus (new character): 0 = sulcus straight, only positioned over costal II or near costal I+II suture; 1 = sulcus curved to form an anteromedial projection, that does not cross the costal I+II suture; 2 = sulcus curved to form a distinct anteromedial project that crosses the costal I+II suture. This character forms a morphocline.
16. Placement of pleural II–III sulcus (new character): 0 = sulcus straight, only positioned over costal II or near the costal III+IV suture; 1 = sulcus curved to form an anteromedial projection, that crosses the costal III+IV suture.

Comments regarding characters 15–16: The interpleural sulci of most turtles are relatively straight and positioned on costals II, IV, VI and VIII. The pleural scutes consequently have parallel anterior and posterior margins. In various representatives of the ingroup, the anteromedial corner of pleural II and III form finger-like projections that squeeze between the anterior pleural and vertebral. The relative width and depth of these projections varies and not all projections necessarily cross the anterior intercostals suture. However, to establish an easily reproducible character, we here use the crossing of the interpleural sulcus and intercostals suture as a discrete character. The interpleural sulci of *Pangshura sylhetensis* closely approximate the intercostals suture and even appear to cross it, but this taxon is scored primitive, because the finger-like projections are lacking.

17. Lateral contact vertebral V with marginals (see Hirayama 1985, K; Joyce & Bell 2004, 46): 0 = contact with marginals XI and XII only; 1 = contact with marginals X–XII. *Pangshura sylhetensis* is scored inapplicable for this character, given that

it possesses 13 pairs of peripherals and thus does not exhibit a homologous morphology to the posterior region of the carapace of other batagurids.

18. Anterior plastral buttresses (see Hirayama 1985, Q; Joyce & Bell 2004, 51): 0 = anterior buttresses well developed and in clear contact with the first costal bones; 1 = anterior buttresses well developed and in direct contact with the first dorsal rib.

19. Number of marginal scutes (new character): 0 = 12 pairs; 1 = 13 pairs.

20. Frontal contribution to the orbital rim (see Hirayama 1985; 3; Joyce & Bell 2004, 3): 0 = absent; 1 = present.

21. Canalis praepalatinum (see Hirayama 1985, 24; Joyce & Bell 2004; 20): 0 = absent; 1 = present.

22. Participation of palatine in the triturating surface of the upper jaw (see Hirayama 1985, 26; Joyce & Bell 2004, 28): 0 = absent; 1 = present, but small; 2 = present and substantial. This character forms a morphocline.

23. Number of lingual ridges of the triturating surfaces of the upper jaw (see Hirayama 1985, 29, 44; Joyce & Bell 2004, 30): 0 = no lingual ridges present; 1 = one lingual ridge present; 2 = two lingual ridges present. This character forms a morphocline.

24. Median ridge or sulcus on the triturating surface of the upper jaw (see Hirayama 1985, 30; Joyce & Bell 2004, 32): 0 = both structures absent; 1 = median ridge present; 2 = median sulcus present.

25. Posterior extension of the lower triturating surface behind the symphysis of the dentary (see Hirayama 1985, 42; modified from Joyce & Bell 2004, 33): 0

= absent; 1 = equal to the symphysis; 2 = clearly present. This character forms a morphocline.

26. Carapacial fontanelles in adults (new character, see Le *et al.* 2007): 0 = fontanelles absent, even in subadult individuals; 1 = fontanelles present even in fully adult males.

Appendix 2

Specimens used

Batagur baska (Gray, 1831): FMNH 224124, FMNH 224097.

Callagur borneoensis (Schlegel & Müller, 1844): FMNH 224099, FMNH 224109, FMNH 224096, FMNH 224121, FMNH 224098, FMNH 224130, FMNH 224123, FMNH 224129, FMNH 224148, FMNH 224122, FMNH 224107.

Geoclemys hamiltonii (Gray, 1831): YPM R 10399.

Morenia petersi (Anderson, 1879): FMNH 260390, FMNH 224150, FMNH 260378, FMNH 260377.

Hardella thurjii (Gray, 1831): FMNH 224153.

Kachuga kachuga (Gray, 1831): FMNH 224152, FMNH 224127.

Kachuga dhongoka (Gray, 1834): FMNH 224108, FMNH 224154, FMNH 223678.

Pangshura smithii (Gray, 1863): FMNH 260384, FMNH 260444.

Pangshura tecta (Gray, 1831): FMNH 260413, FMNH 260416, FMNH 260386.

Pangshura tentoria (Gray, 1834): FMNH 224185, FMNH 259433, FMNH 224105, FMNH 259431, FMNH 259430, FMNH 260379.

Pangshura sylhetensis Jerdon, 1870: CRI 11880.