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A taxonomic revision of geoemydid turtles from Siwalik-age of India and Pakistan

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Abstract. Neogene (Siwalik-aged) deposits from India and Pakistan have yielded many vertebrate fossils, of which most were named during the 19th century, including numerous geoemydid turtles. In contrast to many other faunal components from the Siwaliks, geoemydids have not undergone taxonomic revision for more than a century and most fossils have therefore been believed to correspond to recent taxa. In this study, we conduct a taxonomic revision of all previously described geoemydid material from the Siwalik-age. We propose that all specimens of '*Clemmys*' from the Siwaliks of Punjab, Pakistan should be identified as *Melanochelys sivalensis* comb. nov.; that *Melanochelys tricarinata* var. *sivalensis* represents a valid species, for which we propose the replacement name *Melanochelys tapani* to avoid homonymy; that specimens originally identified as *Batagur cautleyi* and *Pangshura flaviventer* cannot be identified beyond the generic level; and that many fragmentary palatochelydians cannot be identified to any particular species or genus due to the lack of preserved diagnostic osteological characters. With a few exceptions, the Siwalik fauna mostly corresponds in its distribution to that of the recent fauna, indicating a certain amount of geographic stasis. However, as the stratigraphic provenance of most material is poor, it is not possible to discern meaningful temporal patterns.

Keywords. Paleontology, Neogene, taxonomy, Siwaliks, turtles.

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Introduction

The Siwalik Group (Miocene–Pleistocene) is a fossil-bearing deposit that is situated in the Himalayan foreland basin along the north of the Indian subcontinent extending from the Indus river (Pakistan) in the west to the Irrawady river in the east (Myanmar) (Barry *et al.* 2013; Nanda *et al.* 2018) and south to the central portions of the subcontinent (e.g., Piram Island in the Gulf of Cambay in India and Trans-Indus, Sind and Baluchistan regions of Pakistan). The fossil vertebrate fauna of the Siwaliks has been studied in the course of the past 150 years, especially its mammalian component (e.g., Falconer & Cautley 1837, 1844, 1846; Lydekker 1885a, 1885b, 1885c, 1886a, 1886b, 1886c, 1887; Pilgrim 1910). The ape *Sivapithecus* Pilgrim, 1910, the giraffid *Sivatherium giganteum* Falconer & Cautley, 1836, the equid *Equus sivalensis* Falconer & Cautley, 1849*,* and the mammoth *Elephas hysudricus* Falconer & Cautley, 1845 are some of the better-known mammals that inhabited this region at some point during the Miocene–Pleistocene periods (Nanda 2013; Nanda *et al.* 2018).

In contrast to the mammals, other groups of vertebrates that inhabited this region are understudied, particularly reptiles (Nanda *et al.* 2016). Although the extinct turtle fauna from this region is well described (e.g., Theobald 1877; Lydekker 1885a, 1886a, 1889a, 1889b), the available material is poorly understood in terms of taxonomy and biogeographic implications. This is unfortunate, as most

Siwalik turtles are closely related to recent taxa (Turtle Extinction Working Group (TEWG) 2015; Turtle Taxonomy Working Group (TTWG) 2017) and thus provide a tool for understanding their Neogene and Quaternary history.

A great number of geoemydid turtle taxa was described from Siwalik aged sediments towards the end of the 19th century, in particular *Batagur bakeri* Lydekker, 1885a, *Batagur cautleyi* Lydekker, 1885a, *Batagur durandi* Lydekker, 1885a, *Batagur falconeri* Lydekker, 1885a, *Bellia sivalensis* Theobald, 1877, *Clemmys palaeindica* Lydekker, 1885a, *Clemmys punjabiensis* Lydekker, 1885a, *Clemmys theobaldi* Lydekker, 1885a, *Clemmys watsoni* Lydekker, 1886a, *Clemmys hydaspica* Lydekker, 1885a and *Nicoria tricarinata sivalensis* Lydekker, 1889b. Lydekker (1889a) soon after concluded, however, that most of these taxa are synonymous with each other or with extant species (e.g., *Geoclemys hamiltonii* (Gray, 1830), *Hardella thurjii* (Gray, 1831), *Batagur dhongoka* (Gray, 1832), a conclusion broadly followed by Smith (1931).

Four additional species of geoemydid species were described in the course of the 20th and 21st centuries: *Geoclemys sivalensis* Tewari & Badam, 1969, *Geoemyda pilgrimi* Prasad & Satsangi, 1967, *Pangshura tatrotia* Joyce & Lyson, 2010 and *Piramys auffenbergi* Prasad 1974. Das (1991, 1994) later synonymized *Geoclemys sivalensis* and *Geoemyda pilgrimi* with the extant *Geoclemys hamiltonii* and *Hardella thurjii*, respectively, while Ferreira *et al.* (2018) concluded that *Piramys auffenbergi* is a pleurodire, not a geoemydid. The taxonomy of Siwalik geoemydids was recently summarized by TEWG (2015), but as the vast majority of available material has not been evaluated directly in more than 100 years, many conclusions are based on outdated concepts of morphology and taxonomy.

The goal of this study is to conduct an up-to-date revision of the fossil geoemydid specimens from the Siwalik Group by providing detailed illustrations in combination with concise descriptions of most specimens. As the majority of fossil geoemydid material is represented by shells only, we compare the shell morphology of these fossils with those of recent geoemydid taxa. We also highlight valid taxa and discuss the biogeographic implications of our findings.

Geological setting

Geographically, the main Siwalik belt extends from the Potwar Plateau in the Punjab of Pakistan in the west to Kathmandu, Nepal in the east, just south of the Himalayan mountain range. However, the Himalayan Foreland basin has a much larger extent, from the Indus river basin and the Gulf of Cambay in the west, passing through the Ganges and Yamuna River basins, to the Brahmaputra River basin to Irrawady River basin in Indo-Myanmar-Andaman terrane in the east (Fig. 1) (Yin 2006; Chirouze *et al.* 2012; Valdiya 2010; Chakraborty *et al.* 2020). This explains why Siwalik age fossils are recovered far to the south of the main Siwalik belts (Nanda *et al.* 2018).

The Siwalik Group is commonly divided into three time intervals (Barry *et al.* 2013; Flynn *et al.* 2013): the Lower Siwaliks, Middle Miocene (between 18 and 11.6 Ma); the Middle Siwaliks, from the Middle to Late Miocene (between 11.6 and 5 Ma); and the Upper Siwaliks, from the Pliocene to mid-Pleistocene (around 5 to 1.6 Ma).

The material described herein was mostly collected by H. Falconer and P.T. Cautley during the early 19th century and later deposited at the Indian Museum in Kolkata, India and the British Museum of Natural History (now Natural History Museum) in London, UK. Although the precise provenance of the material of Falconer and Cautley was not provided for most specimens, it is very likely they were collected from the Potwar Plateau in the Punjab of current day Pakistan, from the Siwalik belt range between the cities of Saharanpur and Dehradun, and from the Doon Valley in the same area, as these collectors traveled throughout these areas during their journeys (Fig. 1; Falconer & Cautley 1846;

Murchinson 1868; Lydekker 1885a). At least five Siwalik formations are currently recognized from the Potwar Plateau (Barry *et al.* 2013; Nanda *et al.* 2018): the Kamlial formation, Lower Siwalik (18 to 14 Ma); the Chinji formation, Lower Siwalik (14 to 11.4 Ma); the Nagri formation, Middle Siwalik (11.5 to 9 Ma); the Dhok Pathan formation, Middle Siwalik (9.8 to 3.5 Ma); and the Tatrot formation, Upper Siwalik (3.5 to 3.3 Ma). The material collected by Falconer and Cautley from the Potwar Plateau can therefore only be identified as Middle Miocene to mid-Pleistocene in age.

Some material described herein came from localities south of the main Siwalik belt, in particular from Piram Island in the Gulf of Cambay and the Narmada River valley (Fig. 1). Recent studies suggest that the sediments exposed on Piram Island belong to the Middle Siwalik group, possibly the same age as the Nagri formation (11.6 – 9 Ma; Prasad 1974). However, Nanda *et al.* (2018) concluded that the fossils from Piram Island are also in agreement with the Dhok Pathan formation (9.8 – 3.5 Ma).

Quaternary alluvial sediments are broadly exposed along the Central Narmada Valley, from Harda in the west to Jabalpur in the east (Madhya Pradesh, India; Sonakia & Biswas 2011). In addition to many fossil ruminants, Theobald (1860) described *Emys namadicus* from the villages of Muwar and Doomar (his Moar Domar), which are located in the Central Narmada Valley between the Narmada and Tendori Rivers (Fig. 1). According to Tiwari & Bhai (1997), the deposits exposed in this area belong to the latest Pleistocene flood plain facies of the Hirdepur formation (25–13 Ka; Tiwari 2007), but Sonakia & Biswas (2011) note that Hirdepur sediments may contain redeposited fossil material from older units.

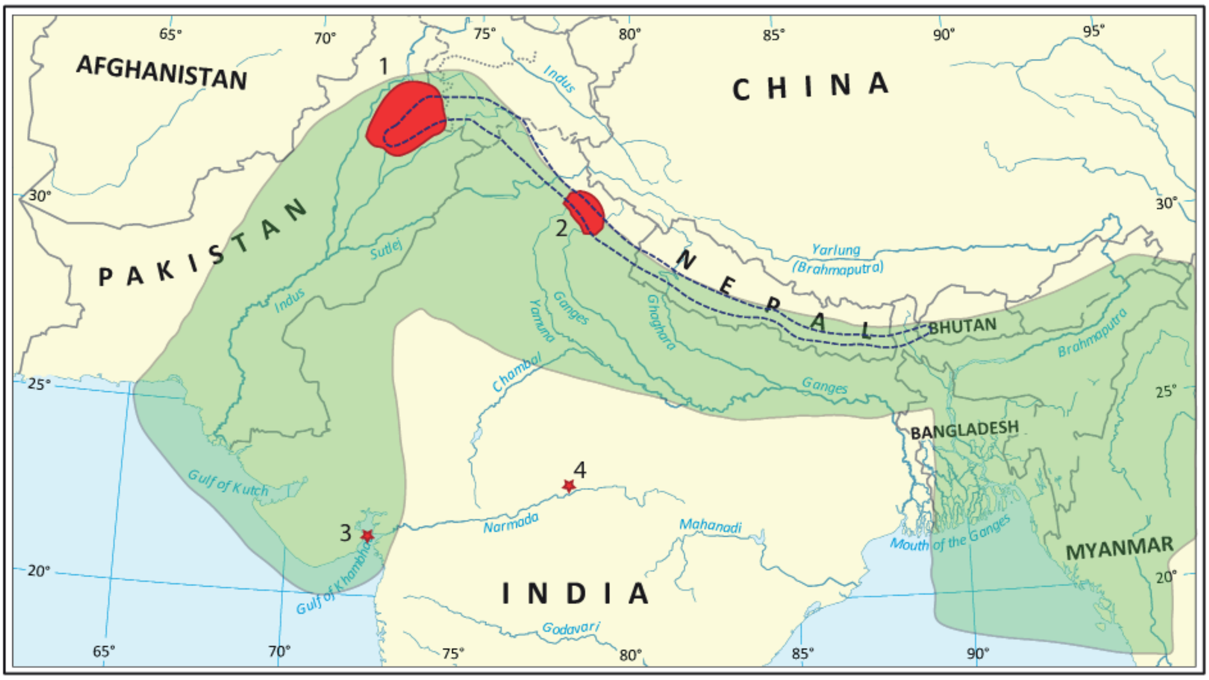

Fig. 1. Extent of the Himalayan foreland basin (green) on the Indian subcontinent, distribution of the Siwalik belt mountain range (dashed line), and the main localities that yielded geoemydid fossils. The main Siwalik-age localities here studied are marked with a red star. **1**. Potwar Plateau, Punjab, Pakistan. **2**. 'Typical' Siwalik Hills of India. **3**. Piram Island, Gulf of Cambay, India. **4**. Villages of Muwar and Doomar, Narmada Valley, India. Map modified from the United Nations, database of points from Flynn *et al.* (2013), range base from Valdiya (2010).

Material and methods

Material repository

The fossil material discussed herein is housed at the Indian Museum (Kolkata, India), under the protection of the Geological Survey of India, the British Museum of Natural History (Natural History Museum, London, United Kingdom), the Yale Peabody Museum of Natural History (New Haven, USA) and the Museum of the Center of Advanced Studies in Geology (Punjab University, Chandigarh, India). All material was studied in person, with the exception of the material held at Punjab University, which was accessed via the published literature.

Repository abbreviations

BMNH	=	British Museum of Natural History, London, United Kingdom
FMNH	=	Fiel Museum of Natural History, Chicago, USA
IM	=	Indian Museum, Kolkata, India
GSI	=	Geological Survey of India, Kolkata, India
MCASG	=	Museum of the Center of Advanced Studies in Geology, Punjab University, Chandigarh, India
NMW	=	Naturhistorisches Museum Wien, Vienna, Austria
YPM	=	Yale Peabody Museum, New Haven, USA

Anatomical abbreviations

Anatomical terms in the text follow Zangerl (1969) and are abbreviated in the figures as:

Ab	=	abdominal scute
An	=	anal scute
Ce	=	cervical scute
co	=	costal bone
ento	=	entoplastron
epi	=	epiplastron
Fe	=	femoral scute
fo	=	fontanelle
Gu	=	gular scute
Hum	=	humeral scute
hyo	=	hyoplastron
hypo	=	hypoplastron
lg	=	inguinal scute
Ma	=	marginal scute
mdf	=	musk duct foramina
ne	=	neural bone
nu	=	nuchal bone
Pe	=	pectoral scute
per	=	peripheral bone
Pl	=	pleural scute
py	=	pygal bone
spy	=	suprapygal bone
Ve	=	vertebral scute
xi	=	xiphiplastron

Comparative material

All examined material was compared with extant geoemydid species that occur today on the Indian subcontinent (Figs 2–3), in particular *Batagur baska* (Gray, 1830), *Batagur dhongoka* (Gray, 1832), *Batagur kachuga* (Gray, 1831), *Cuora amboinensis* (Riche *in* Daudin, 1801), *Cuora mouhotti* (Gray, 1862), *Cyclemys gemeli* Fritz *et al*., 2008, *Cyclemys fusca* Fritz *et al*., 2008, *Geoclemys hamiltonii*

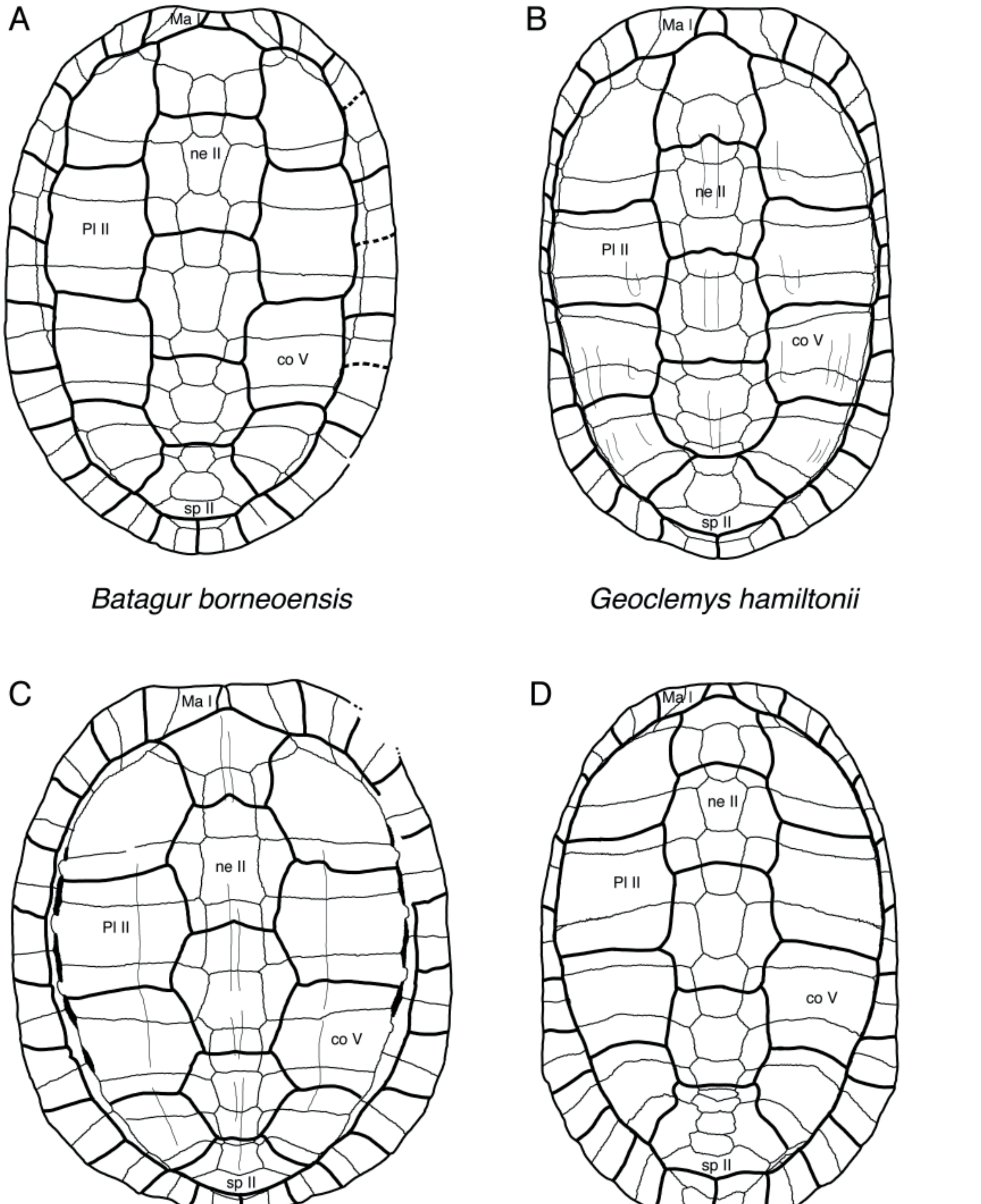

Fig. 2. Illustration of the carapace of four extant geoemydid species that were used for morphological comparison with Siwalik specimens. **A**. Carapace of *Batagur borneoensis* (Schlegel & Müller, 1845) (FMNH 251499), a geoemydid from Borneo that here illustrates the general shape of species of *Batagur* Gray, 1856. **B**. *Geoclemys hamiltonii* (Gray, 1830) (NMW 39986), a geoemydid from the Indian subcontinent. **C**. *Melanochelys trijuga* (Schweigger, 1812) (NMW 37159), a geoemydid from the Indian subcontinent. **D**. Carapace of *Hardella thurjii* (Gray, 1831) (FMNH 224153), a geoemydid from India and Pakistan.

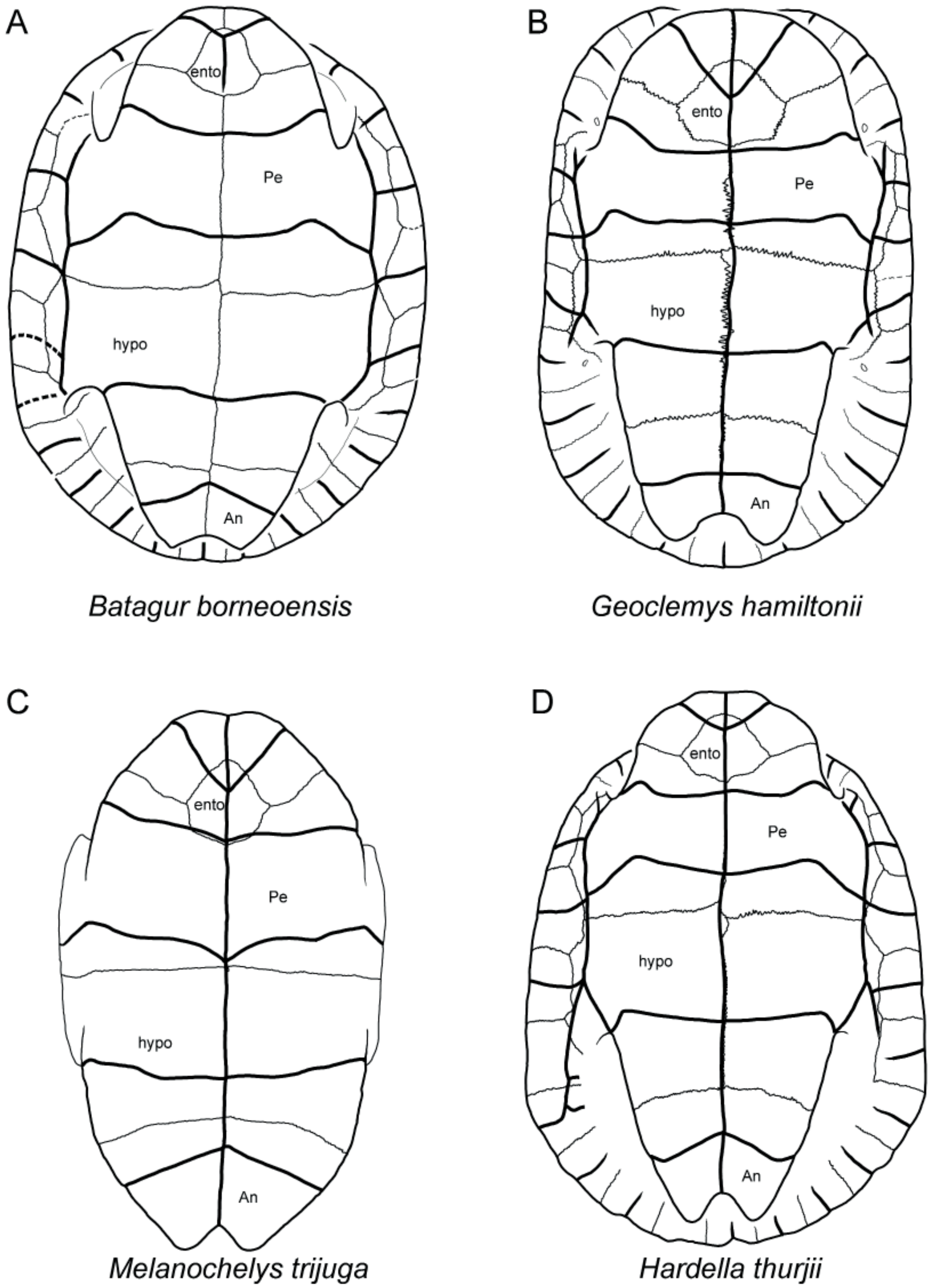

Fig. 3. Illustration of the plastron of four extant geoemydid species that were used for morphological comparison with Siwalik specimens. **A**. Plastron of *Batagur borneoensis* (Schlegel & Müller, 1845) (FMNH 251499), a geoemydid from Borneo that here illustrates the general shape of species of *Batagur* Gray, 1856. **B**. *Geoclemys hamiltonii* (Gray, 1830) (NMW 39986), a geoemydid from the Indian subcontinent **C**. *Melanochelys trijuga* (Schweigger, 1812) (NMW 37159), a geoemydid from the Indian subcontinent. **D**. Plastron of *Hardella thurjii* (Gray, 1831) (FMNH 224153).

(Gray, 1830), *Hardella thurjii* (Gray, 1831), *Melanochelys trijuga* (Schweigger, 1812), *Melanochelys tricarinata* (Blyth, 1856), *Morenia petersi* Anderson, 1879, *Pangshura smithii* (Gray, 1863), *Pangshura tecta* (Gray, 1830), *Pangshura tentoria* (Gray, 1834), *Pangshura sylhentensis* Jerdon, 1870 and *Vijayachelys silvatica* (Henderson, 1912) (TTWG 2017). The full list of specimens used is provided in the supplementary file S1 of Garbin *et al.* (2018).

Methods

We here document 29 fossil turtle specimens based exclusively on shells from the Siwalik-age of India and Pakistan that were described over the course of the 19th century. All specimens were photographed with a Nikon D750 camera and illustrated by tracing the digital photographs in Adobe Photoshop CC 2017 using Wacom drawing tablets. Larger specimens with highly domed carapaces were focus stacked using Helicon Focus ver. 7.0.2 Pro to yield images that are fully in focus. The illustrations and photographs of each specimen were then compiled in plates using Adobe Illustrator CC 2017 (Figs 4–32).

All examined material was scored in the morphological matrix of 96 shell characters for geoemydid species from Garbin *et al.* (2019) that extensively covers the use of polymorphic characters for this group (see Supplementary File). The fossils were then compared with material of extant Indian geoemydid species through photographs and based on the scoring of the characters in the matrix. Some notable characters used herein for description and comparison with extant groups are the presence of carapace keels, the position of anterior short sides on hexagonal neural bones and the intersection of the entoplastron by the humeropectoral sulcus. To simplify the identification of turtle shells and comparison with scoring data for extant species from a matrix of 96 characters, we created a taxonomic key for the extant geoemydids of the Indian subcontinent (see Appendix).

Results

As the present authors refrain from following higher Linnean hierarchies, the editors have decided to respect this position.

Testudines Batsch, 1788
Cryptodira Cope, 1868
Testudinoidea Fitzinger, 1826
Testuguria Joyce *et al.*, 2004
Geoemydidae Theobald, 1868

Palatochelydia sensu Joyce & Lyson, 2010
Figs 4–9

Differential osteological diagnosis

Palatochelydians can be diagnosed by the presence of a well-developed secondary palate (Joyce & Lyson 2010), as well as the presence of a well-developed bridge, strong axillary and inguinal buttress, the latter in clear contact with both the fifth and sixth costals, anteriorly short sided second to sixth neural bones, and the universal presence of a triangular or rounded anal notch (Garbin *et al.* 2018).

Material examined

INDIA • 3 specimens; Siwalik Hills; Miocene–Pliocene; BMNH R.329, BMNH R.959, BMNH 16204 • 2 specimens; Piram Island, Gulf of Cambay, Gujarat; late Miocene–Pliocene; BMNH R.603, BMNH R.958.

PAKISTAN • 1 specimen; Punjab, Hassnot; Miocene–Pliocene; IM E.94.

Description

BMNH R.329 (Fig. 4) – This is an incomplete specimen from the Miocene–Pliocene Siwalik Hills, likely of India, that was transferred to BMNH from the Indian Museum in 1880 (Lydekker 1889b). It was originally referred to *Damonia hamiltoni* (Gray 1831) by Lydekker (1889b), but remained unfigured. It consists of an articulated right lateral portion of a carapace formed by right peripherals III–VI, right costal I, and a part of the hyo- and hypoplastron (Fig. 4). All sutures and almost all sulci are visible. Growth annuli marks are preserved over costal I and peripherals IV–VI. Marginal V and VI overlap a portion of the hyoplastron, the second only covering a small portion of it. An inguinal scute likely present.

BMNH R.603 (Fig. 5) – This is an incomplete specimen from the Late Miocene–Pliocene of Piram Island, Gulf of Cambay, Gujarat, India that was presented to BMNH by Diwan Wajeshanker Gowreeshanker in 1885 and that was originally referred to *Hardella thurgi* (Gray, 1831) by Lydekker (1889b). No figure

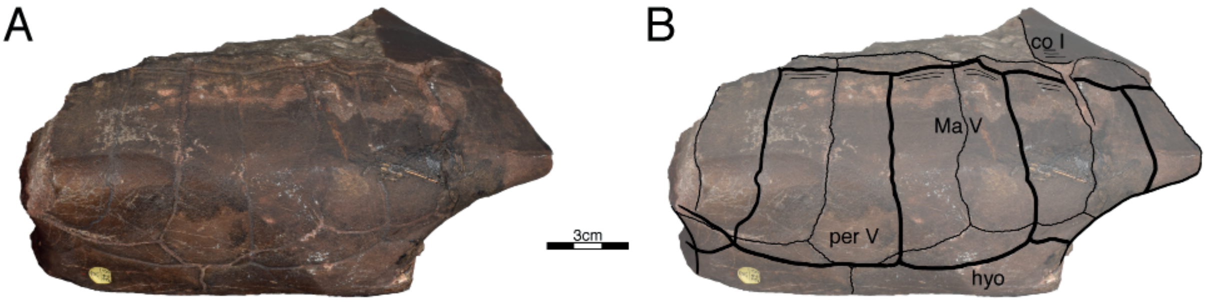

Fig. 4. BMNH R.329, referred to *Damonia hamiltoni* (Gray, 1830) by Lydekker (1889b), here identified as Palatochelydia indet. **A**. Photograph of carapace in lateral view. **B**. Illustration of carapace in lateral view. Scale bar: 3 cm.

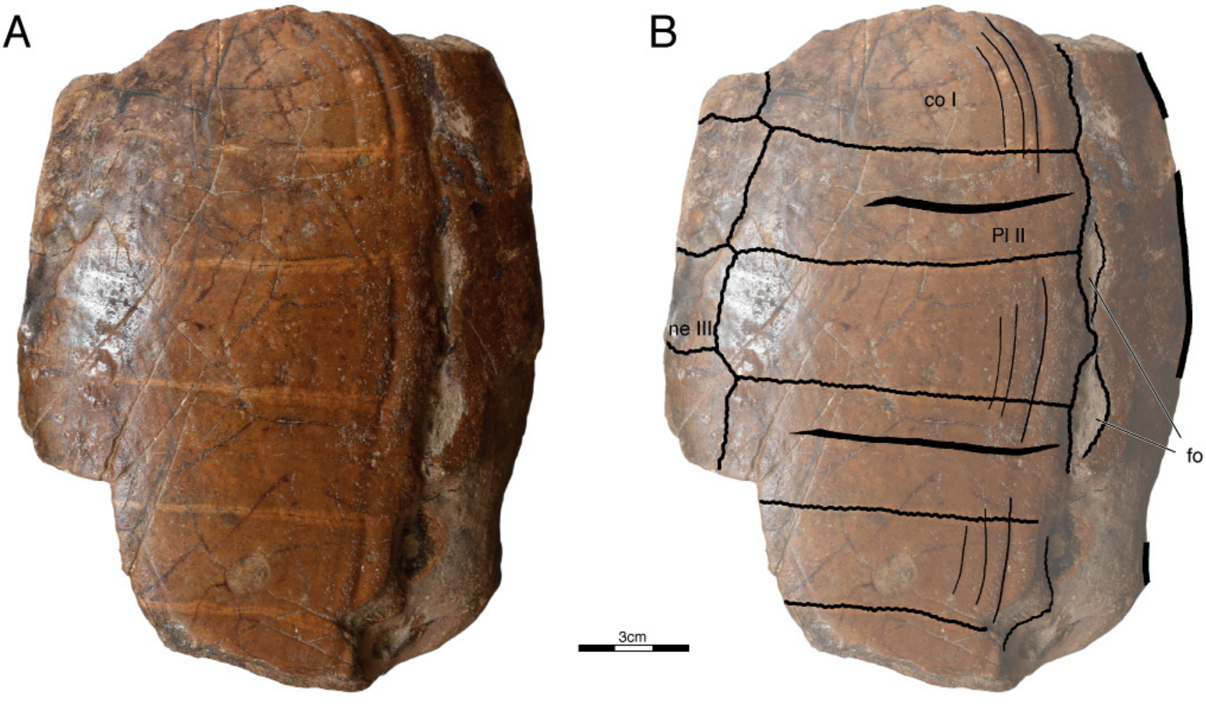

Fig. 5. BMNH R.603, referred to *Hardella thurgi* (Gray, 1831) by Lydekker (1889b), here identified as Palatochelydia indet. **A**. Photograph of right carapace side. **B**. Illustration of right carapace side. Scale bar: 3 cm.

Fig. 6. BMNH R.958, referred to *Hardella thurgi* (Gray, 1831) by Lydekker (1889b, under the number BMNH R.954), here identified as Palatochelydia indet. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of carapace in lateral view. **D**. Illustration of carapace in lateral view. **E**. Photograph of plastron. **F**. Illustration of plastron. Scale bar: 3 cm.

was associated. It consists of the right side of the carapace, with preserves parts of neurals I–IV, right costals I–VI and some right lateral peripherals, which are not clearly identifiable. It is clearly an adult specimen due to its large size and probably a male specimen due to the presence of two fontanelles adjacent to right costal III. Growth annuli marks are preserved on costals I, III and V. Neurals II–IV are likely hexagonal, with short sides faced anteriorly. The carapace is smooth and lacks signs of keels.

BMNH R.958 (Fig. 6) – This is an incomplete specimen from the Late Miocene–Pliocene of Piram Island, Gulf of Cambay, Gujarat, India that was transferred to BMNH from the East Indian Company Museum in 1880. Lydekker (1889b) originally referred this specimen to *Hardella thurgi*, but wrongly under the catalog number BMNH R.954. No figure was associated. Almost all sutures are obscured and this specimen therefore likely represents an adult, with a highly fused carapace. The only evident bones are right costals I–III, right peripherals IV–VI, and the right hyo- and hypoplastron. No signs of carapacial keels or growth annuli marks are present. Three fontanelles are apparent, adjacent to costal bones II and III, that suggesting that it is probable a male specimen. A strong axillary buttress is present. The hyo-hypoplastral suture contacts peripheral V, and an inguinal scute is present, over the right hypoplastron.

BMNH R.959 (Fig. 7) – This specimen from the Pliocene of the Siwalik Hills, likely of India, was presented to BMNH by P.T. Cautley in 1840. It was referred to *Hardella thurgi* by Lydekker (1889b), but without a figure. This is an almost complete specimen and clearly an adult (plastron length about 52 cm). The plastron is well preserved, but the carapace lacks visible sutures. Both the anterior and posterior plastral margins are missing, as well as the posterior peripheral bones. The entoplastron is large, intersected anteriorly by the gularohumeral sulcus, but not by the humeropectoral sulcus. The anterior portion of the entoplastron is larger than the posterior portion, at least as marked by the epi-hyoplastral

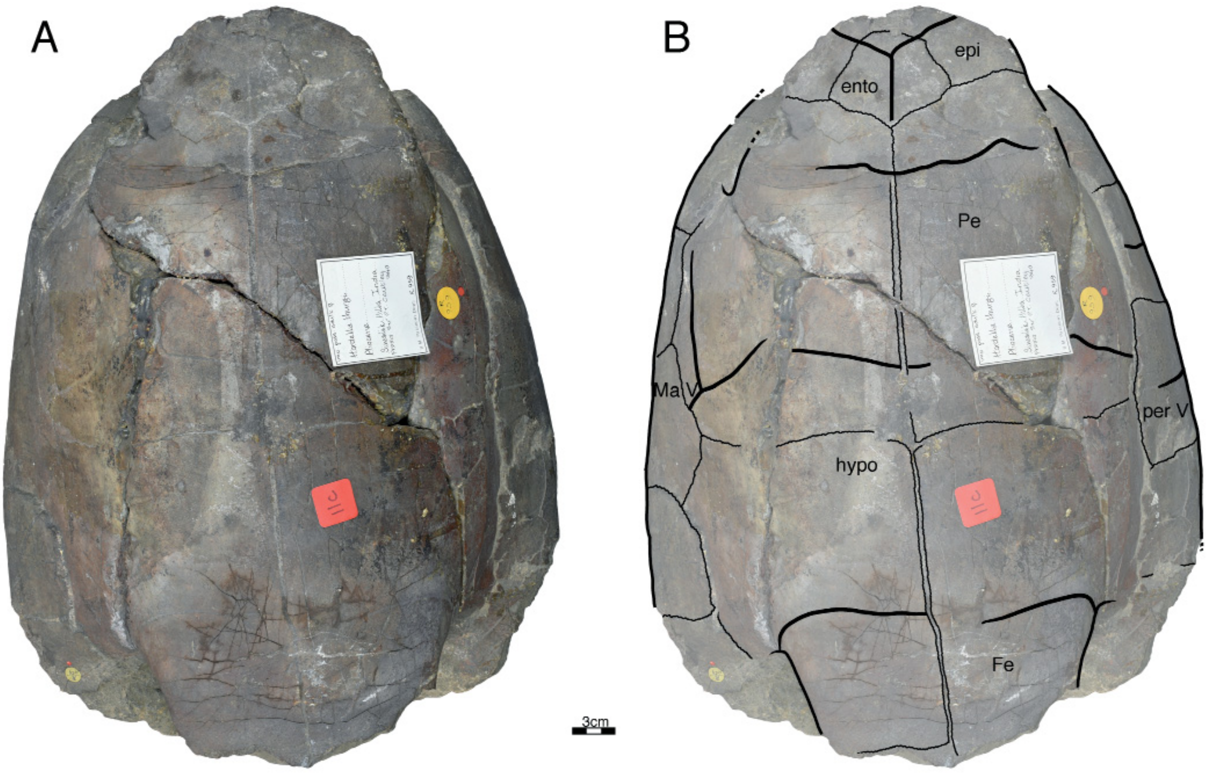

Fig. 7. BMNH R.959, referred to *Hardella thurgi* (Gray, 1831) by Lydekker (1889b), here identified as Palatochelydia indet. **A**. Photograph of plastron. **B**. Illustration of plastron. Scale bar: 3 cm.

suture. The hyo-hypoplastral suture contacts peripheral V and does not overlap the pectoroabdominal sulcus. The fifth marginal scute overlaps part of the hyoplastron.

BMNH 16204 (Fig. 8) – This specimen originates from the Pliocene of the Siwalik Hills, likely of India, and was presented to the BMNH by P.T. Cautley in 1840. It was originally referred to *Hardella thurgi* (Gray, 1831) by Lydekker (1889b), but not accompanied by a figure. This is an incomplete specimen consisting of the anterior half of a shell. The plastron is well preserved, but the carapace is crushed in the center. No carapacial keels, growth annuli, or intercostal fontanelles are preserved or present. The right lateral margin of the first vertebral scute is straight, suggesting the presence of square-shaped vertebrals. Both the anterior and posterior plastral margins are missing, as well as the posterior peripheral bones and posterior half of the plastron. The entoplastron is not preserved, but the posterior position of the humeropectoral sulcus suggests that it was not intersected by it. The hyo-hypoplastral suture does not overlap the pectoroabdominal sulcus and contacts peripheral V. The fifth marginal scute forms the bridge and overlaps part of the hyoplastron.

IM E.94 (Fig. 9) – This specimen from the Miocene–Pliocene of Hassnot, Punjab, Pakistan (Lydekker 1885a) consists of the central portion of a carapace that clearly documents all sutures and some sulci. It

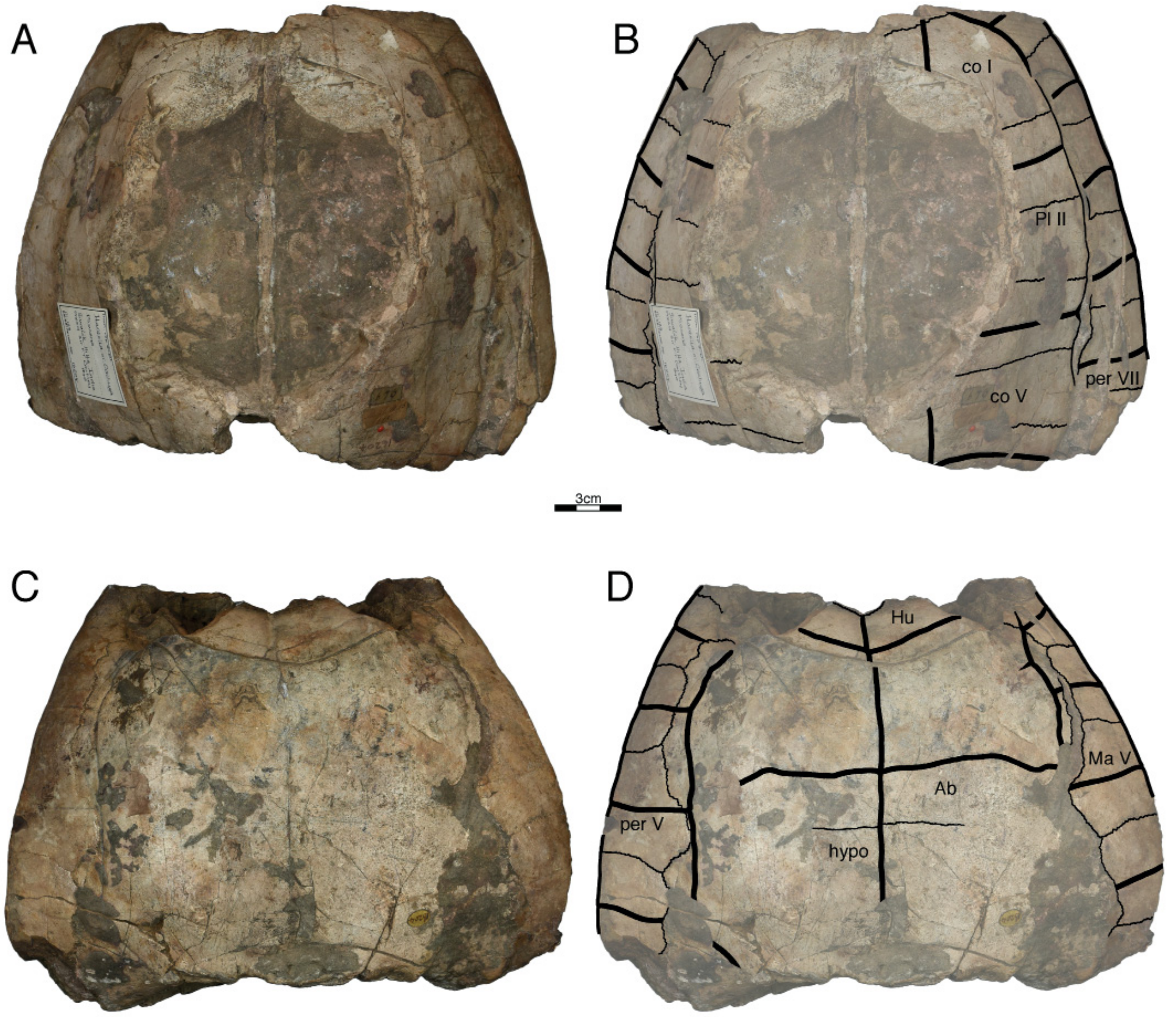

Fig. 8. BMNH 16204, referred to *Hardella thurgi* (Gray, 1831) by Lydekker (1889b), here identified as Palatochelydia indet. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

was originally figured and referred to *Batagur falconeri* Lydekker, 1885 by Lydekker (1885a: pl. 25.1). The first to fourth neurals are present and show anterior short-sides. A small midline knob can be seen on neural IV. Growth annuli marks are visible on the right anterior peripherals and on costals I, II and IV.

Comments

The six specimens herein referred to Palatochelydia indet. were initially either referred to the extinct *Batagur falconeri* or the extant *Damonia hamiltoni* (i.e., *Geoclemys hamiltonii*) and *Hardella thurgi* (i.e., *Hardella thurjii*) (Lydekker 1885a, 1889b), though not always with high confidence (see Lydekker 1889b for BMNH 16204). Although all historical attributions are consistent with the available data, the referred specimens lack diagnostic osteological characters that positively confirm these or any other species-level identifications. Thus, we here refer these specimens to 'Palatochelydia' indet., due to the presence of a well-developed bridge and large size. See Discussion (Indeterminate specimens) for more details.

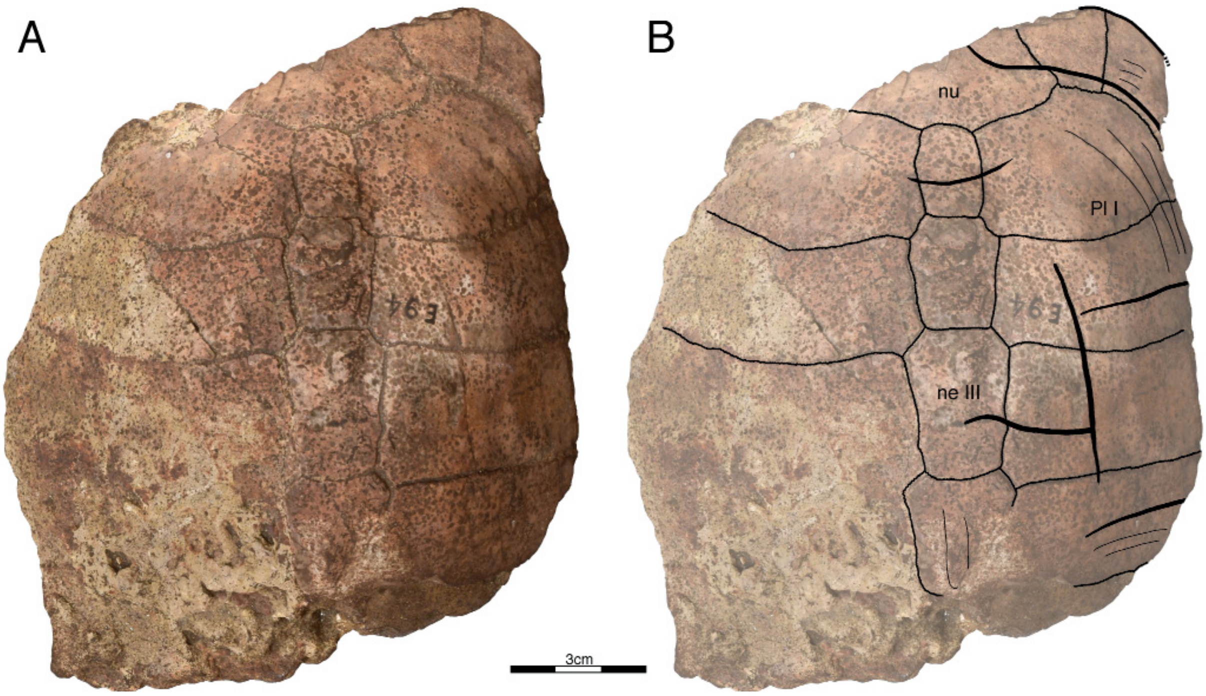

Fig. 9. IM E.94, referred to *Batagur falconeri* Lydekker, 1885, here identified as Palatochelydia indet. **A**. Photograph of carapace. **B**. Illustration of carapace. Scale bar: 3 cm.

Genus ***Batagur*** Gray, 1856
Figs 10–11

Type species

Batagur baska (Gray, 1830).

Differential osteological diagnosis using shell characters

A representative of *Batagur* can be diagnosed by the presence of a large carapace size (median carapace length of more than 40 cm in adults), a well-developed bridge, well-developed axillary and inguinal buttresses, neural scutes with anterior short sides, a long third neural bone, a short, anteriorly truncated gular scute, an entoplastron that is not intersected by the humeropectoral sulcus and a short anal notch.

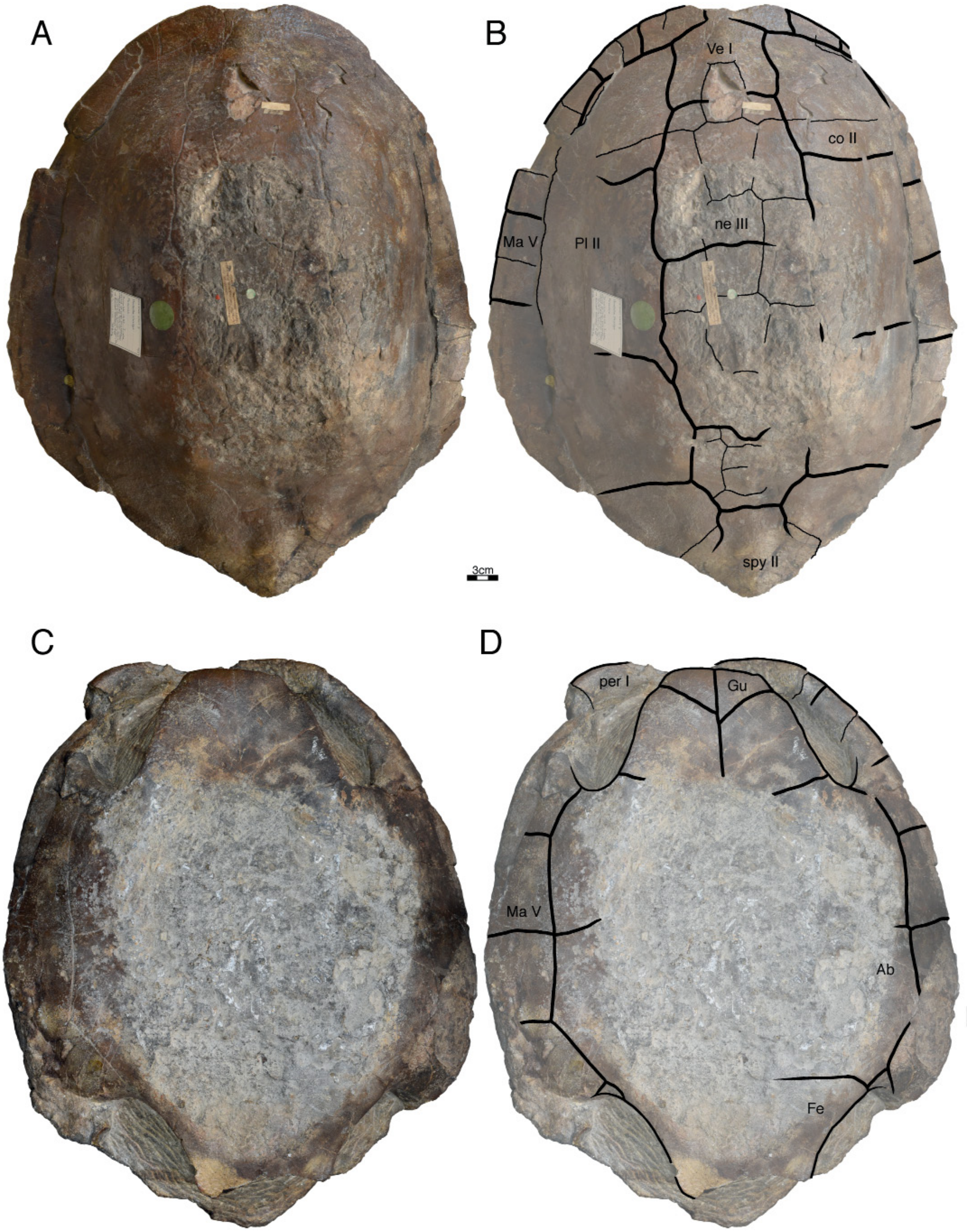

Fig. 10. BMNH 39834, holotype of *Batagur cautleyi* Lydekker 1885, here identified as *Batagur* sp. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

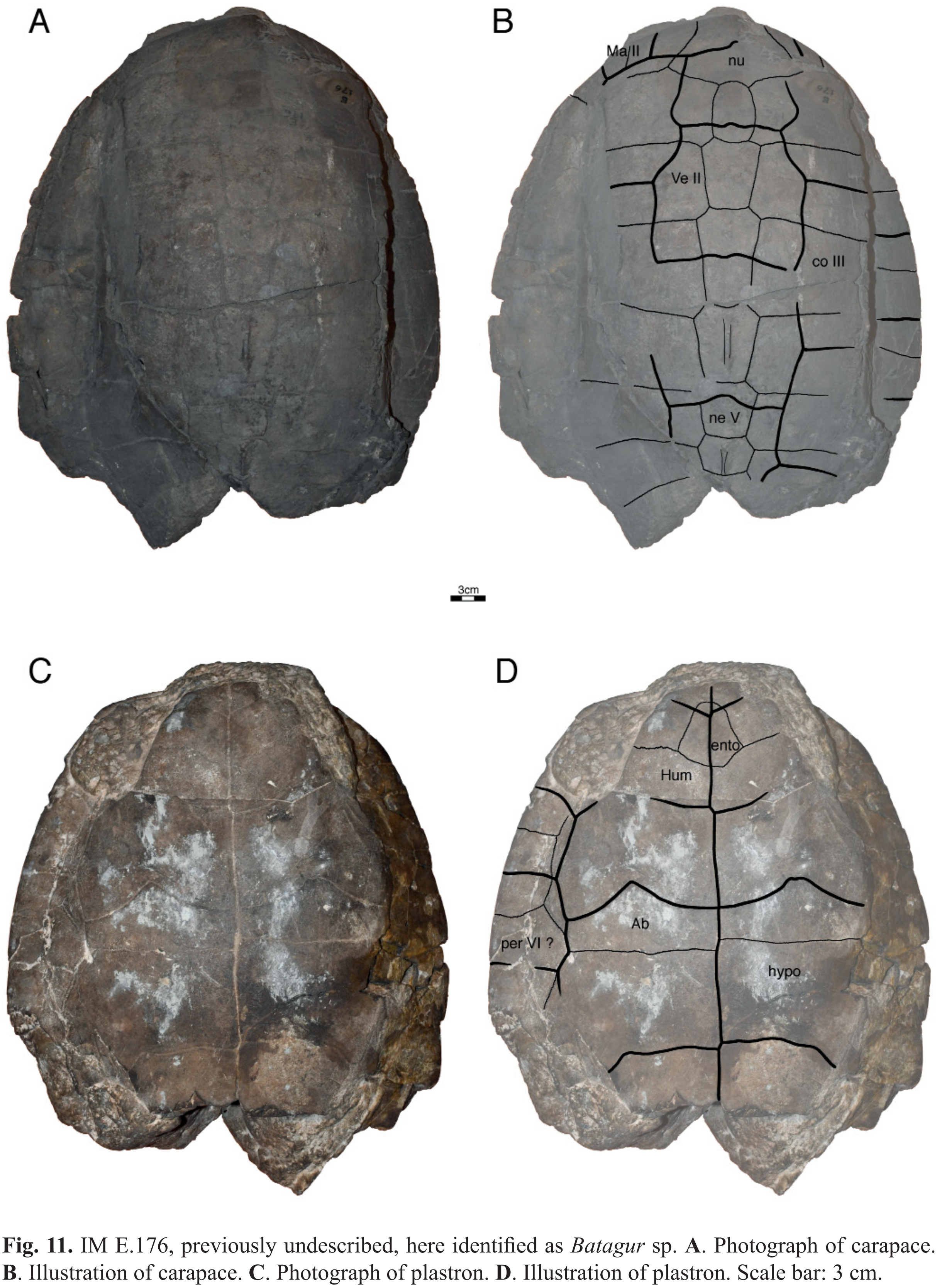

Fig. 11. IM E.176, previously undescribed, here identified as *Batagur* sp. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

Material examined

INDIA • 1 specimen, holotype of *Batagur cautleyi* Lydekker, 1885; Siwalik Hills; Miocene–Pliocene; BMNH 39834.

COUNTRY UNKNOWN • 1 specimen; IM E.176.

Description

BMNH 39834 (Fig. 10), holotype of *Batagur cautleyi* – This an almost complete shell from the Miocene/Pliocene of the Siwalik Hills, likely of India, showing the majority of sulci and of the sutures along the center of the carapace. It was originally figured by Lydekker (1885a: pl. 24.1), but our observations reveal many additional sutures. There are no signs of growth annuli. The specimen likely is an adult female due to its large size (carapace length greater than 54 cm). A small protuberance on neural IV suggests the previous presence of a median keel. A cervical scute is present. The first vertebral scute is longer than wide and shows a lateral constriction. Neurals II–IV have anteriorly short sides, but neural V has a short left posterior side, which is probably abnormal. The sulcus between the second pleural and the third vertebral is almost straight. The anterior plastral margin is straight and lacks an inflection on the contact of the gularohumeral sulcus. The pectoroabdominal sulcus contacts the sulcus between fifth and sixth marginal scutes. The anal notch is not preserved in this specimen. No plastral sutures can be seen.

IM E.176 (Fig. 11) – This is a well-preserved specimen that lacks provenance data and appears to be unpublished. The majority of sutures and sulci are clearly visible. This is an adult specimen due to its large size (carapace length greater than 35 cm), but its gender is unknown. A median carapacial keel is present on the posterior parts of the carapace and is strongly marked over neurals IV and VI. The carapace is rather domed at its center, with no signs of growth annuli. Vertebral scutes are subrectangular and have equally sized anterior and posterior margins. Neurals II to VI are anteriorly short-sided. Gular scutes appear to be wider than long and overlap part of the entoplastron. The humeropectoral sulcus is located posterior to the entoplastron. The pectoroabdominal sulcus does not intersect the hyo-hypoplastron suture and has two lateral notches, suggesting the former presence of parasagital plastral keels at the bridge.

Comments

We attributed BMNH 39834 and IM E.176, the type series of *Batagur cautleyi*, to *Batagur* indet. based on their massive size, highly domed carapace, and presence of an axillary notch and rather straight anterior plastral margin. However, we cannot identify these specimens to species level even though they display unique character combinations. See Discussion (*Batagur cautleyi* from the Siwalik Hills) for additional details.

Batagur kachuga (Gray, 1831)
Figs 12–13

Emys lineata Gray, 1831c: 9.
Emys kachuga Gray, 1831b: pl. 74.
Batagur ellioti Gray, 1862: 264.
Kachuga fusca Gray, 1870: 56 (part).
Batagur bakeri Lydekker, 1885a: 190.

Clemmys (Clemmys) *lineata* – Fitzinger 1835: 123.
Batagur lineata – Gray 1856 (“1855”): 35.
Batagur lineatus – Günther 1864: 39.

Batagur elliotti – Günther 1864: 40.
Clemmys ellioti – Strauch 1865: 88.
Kachuga lineata – Gray 1870: 56.
Batagur kachuga – Theobald 1876: 19. — Praschag *et al.* 2007: 439.
Kachuga kachuga – Smith 1931: 131.

Type

Unknown (Iverson 1992).

Material examined

INDIA • 1 specimen, holotype of *Batagur bakeri*; Siwalik Hills, Yamuna-Ganges River basin; Miocene–Pliocene; BMNH 39835a • 1 specimen; Siwalik Hills; Miocene–Pliocene; BMNH R.891.

Type locality

"India", restricted by Smith (1931) to "N. India" (Iverson 1992).

Occurrence

Miocene/Pliocene–Recent.

Differential osteological diagnosis using shell characters

Batagur kachuga can be differentiated from other species of *Batagur* by the presence of an elongated fourth vertebral scute that covers the fourth to eighth neural bones and second and third vertebral scutes with straight lateral margins.

Description of material examined

BMNH 39835a (Fig. 12), holotype of *Batagur bakeri* – This specimen is from Miocene/Pliocene of the Siwalik Hills of India (Yamuna or Ganges River basins) and was presented to BMNH by General W.E. Baker. It was initially figured and described by Lydekker (1885a: pl. 23.2). Our observations mostly agree with those of Lydekker (1885a), although we note an irregularity on the right side of the neural II/III contact and damage that must have incurred over the course of the last century to the anterior margin of the plastron. This is an almost complete specimen, with a well-preserved shell, and perhaps represents an adult female considering its large size (carapace length greater than 50 cm) compared with extant specimens. Most sulci and sutures are visible on the carapace, but only the sulci are apparent on the plastron. The specimen shows no signs of growth annuli or carapacial keels. The cervical scute is present and broader than long. The vertebral scutes are square shaped and with equidimensional anterior and posterior margins. The first vertebral scute has straight lateral margins, but lacks constrictions. The third vertebral scute is broader than long. All available neurals have anteriorly short sides, with exception of the left side of neural II, which displays an abnormality consisting of a supernumerary bone. The anterior margin of the fourth vertebral runs over neural IV. The bony bridge is well developed. The anterior plastron margin is not preserved anymore, but its original configuration is documented in Lydekker (1885a). The pectoroabdominal sulcus with lateral notches suggests the former presence of longitudinal keels that did not intersected the hyo-hypoplastral suture. The anal portion of the plastron not preserved.

BMNH R.891 (Fig. 13) – This specimen is from the Miocene/Pliocene of the Siwalik Hills, likely of India, and was presented to the British Museum by P.T. Cautley in 1840. It has not been figured previously. This specimen has an incomplete carapace and an almost complete plastron. The carapace consists only of neurals I–IV, a part of costals I–IV and some peripherals. There are no signs of carapacial keels or growth annuli, indicating that this is probably an adult specimen. Two large fontanelles are present,

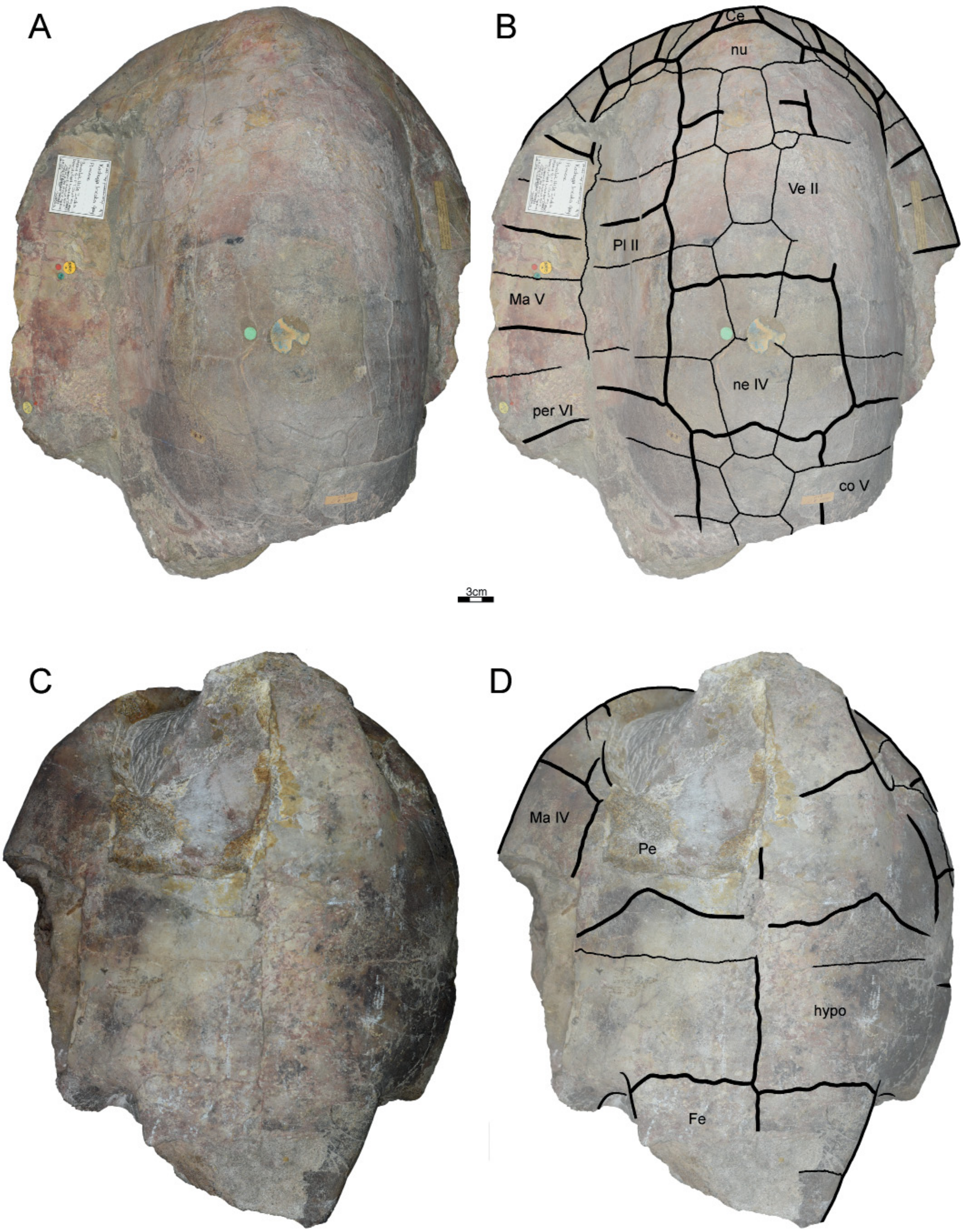

Fig. 12. BMNH 39835a, holotype of *Batagur bakeri* Lydekker, 1885, here identified as synonym of *Batagur kachuga* (Gray, 1831). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

which suggests that this is perhaps a male individual. Neurals II and III are hexagonal with anteriorly short sides. The second and third vertebral scutes have straight lateral sides. The posterior margins of the first and second pleural scutes are straight and cross over costals II and IV, respectively. The anterior and posterior plastral margins are not preserved. A strong axillary notch is present. The entoplastron is not crossed by the humeropectoral sulcus. The hyo-hypoplastral suture contacts peripheral V and does not overlap the pectoroabdominal sulcus. Inguinal scutes are present that contact the femoral scutes.

Comments

We confirm the previously established identification of these two specimens as *Batagur kachuga*, due to their large carapace size (greater than 50 cm), highly domed carapace (for BMNH 39835a), presence of a second vertebral that is as long as wide with straight lateral margins, a third vertebral that is hexagonal with short posterolateral sides (visible in BMNH 39835a), and a large plastron with medially converging humeropectoral sulci. This confirms the synonym of *Batagur bakeri* with *Kachuga lineata*, as originally proposed by Boulenger (1889) and supported by Lydekker (1889a), TEWG (2015) and TTWG (2017).

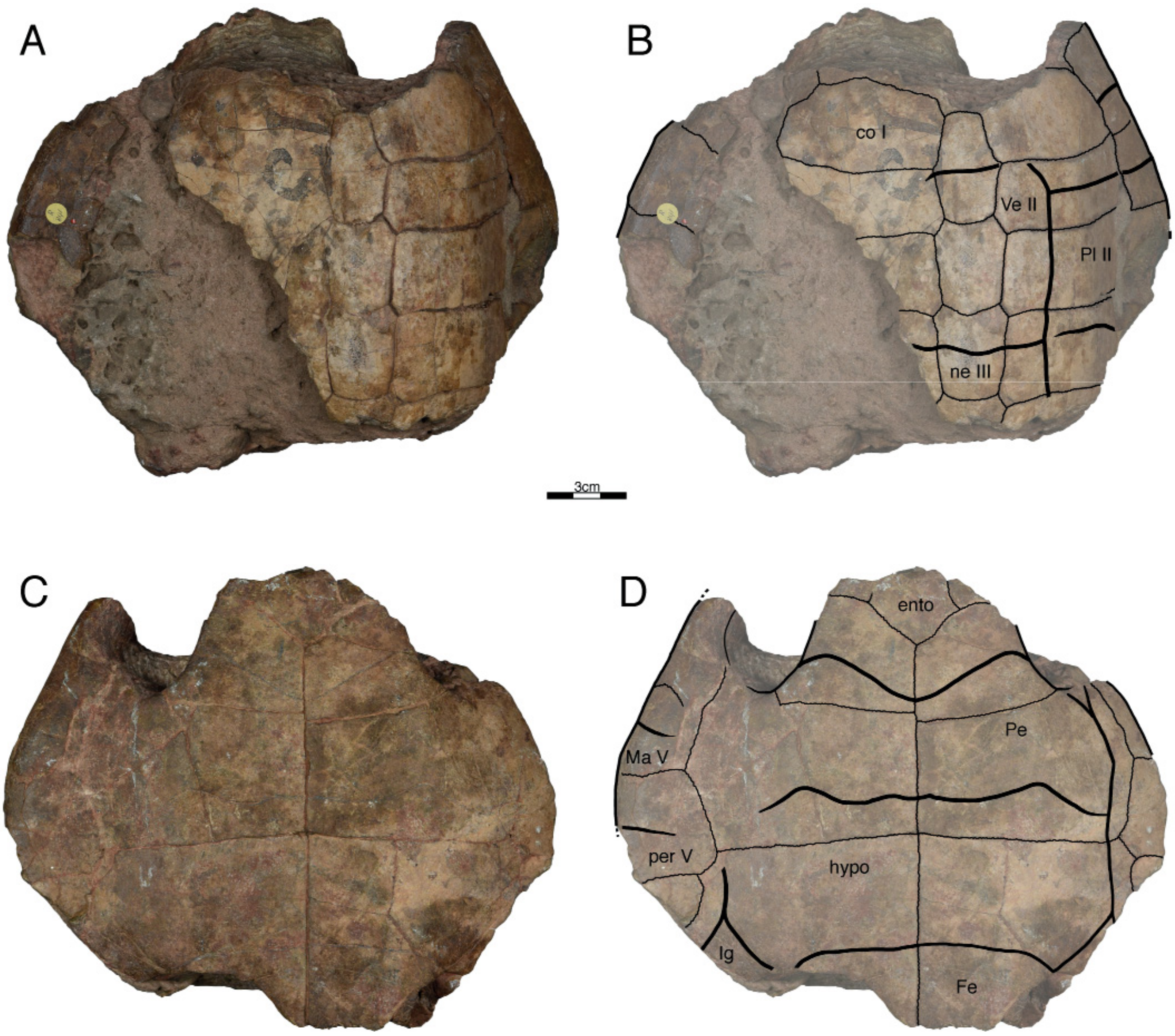

Fig. 13. BMNH R.891, referred to *Cachuga lineata* (Gray, 1831) by Lydekker (1889b), here identified as *Batagur kachuga* (Gray, 1831). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

Batagur dhongoka (Gray, 1832)
Figs 14–15

Emys dhongoka Gray, 1832: pl. 60.
Emys duvaucelli Duméril & Bibron, 1835: 334.
Kachuga hardwickii Gray, 1869: 202.
Batagur durandi Lydekker, 1885a: 192.

Batagur dhongoka – Gray 1855 (1856): 36. — Praschag *et al.* 2007: 439.
Clemmys dhongoka – Strauch 1862: 33.
Dhongoka hardwickii – Gray 1870: 56.
Batagur duvaucelli – Anderson 1879: 738.
Kachuga dhongoka – Boulenger 1889: 56.

Type

Unknown (Iverson 1992).

Material examined

INDIA • 1 specimen, holotype of *Batagur durandi*; Siwalik Hills; Miocene–Pliocene; BMNH 39841.

COUNTRY UNKNOWN • 1 specimen; IM W19/173.

Type locality

Not stated originally, restricted by Smith (1931) to "N. India" (Iverson 1992).

Occurrence

Miocene/Pliocene – Recent.

Differential osteological diagnosis using shell characters

Batagur dhongoka can be differentiated from other *Batagur* species by the presence of an elongated fourth vertebral scute that overlaps four neural bones, a second vertebral scute with a posterior protrusion into the third vertebral, a straight humeropectoral sulcus, and a gulohumeral sulcus that forms a right angle.

Description of material examined

BMNH 39841 (Fig. 14), holotype of *Batagur durandi* – This is an almost complete, well-preserved specimen from Miocene/Pliocene of the Siwalik Hills, probably of India, that was presented to BMNH by P.T. Cautley. The original figure by Lydekker (1885a: pl. 24.2) overall compares well to our observations, but we note differences in the shape of vertebrals III and IV and the presence of peripherals, and we document the plastron for the first time (Fig. 14C–D). A portion of the anterior margin of the carapace and some posterior left peripheral bones are missing. The specimen clearly represents an adult female due to its large size (carapace length greater than 40 cm). A median longitudinal carapacial keel is present, which is elevated in the posterior region of the second vertebral scute. All neural bones are hexagonal and anteriorly short-sided. The first to fourth neural bones are about the same size and longer than wide. The fifth to eighth neural bones are wider than long. The seventh neural is anomalously divided into two elements. The first vertebral scute is bell-shaped and has a small anterolateral constriction. The second vertebral scute has a deep protrusion along its posterior margin into the third vertebral.

The third vertebral scute has a smaller protrusion into the fourth vertebral scute. The fourth vertebral is twice as long than wide and its anterior margin intersects the fourth neural. The sulcus between the first and second pleural forms a deep anterolateral projection onto the first costal bone. The fifth and sixth marginal scutes overlap part of the costal bones. The anterior plastral margin is not completely preserved. The entoplastron is not intersected by the humeropectoral sulcus. the pectoroabdominal sulcus contacts the fifth marginal scute on one side of the specimen, but the sixth marginal on the other. Both the fifth

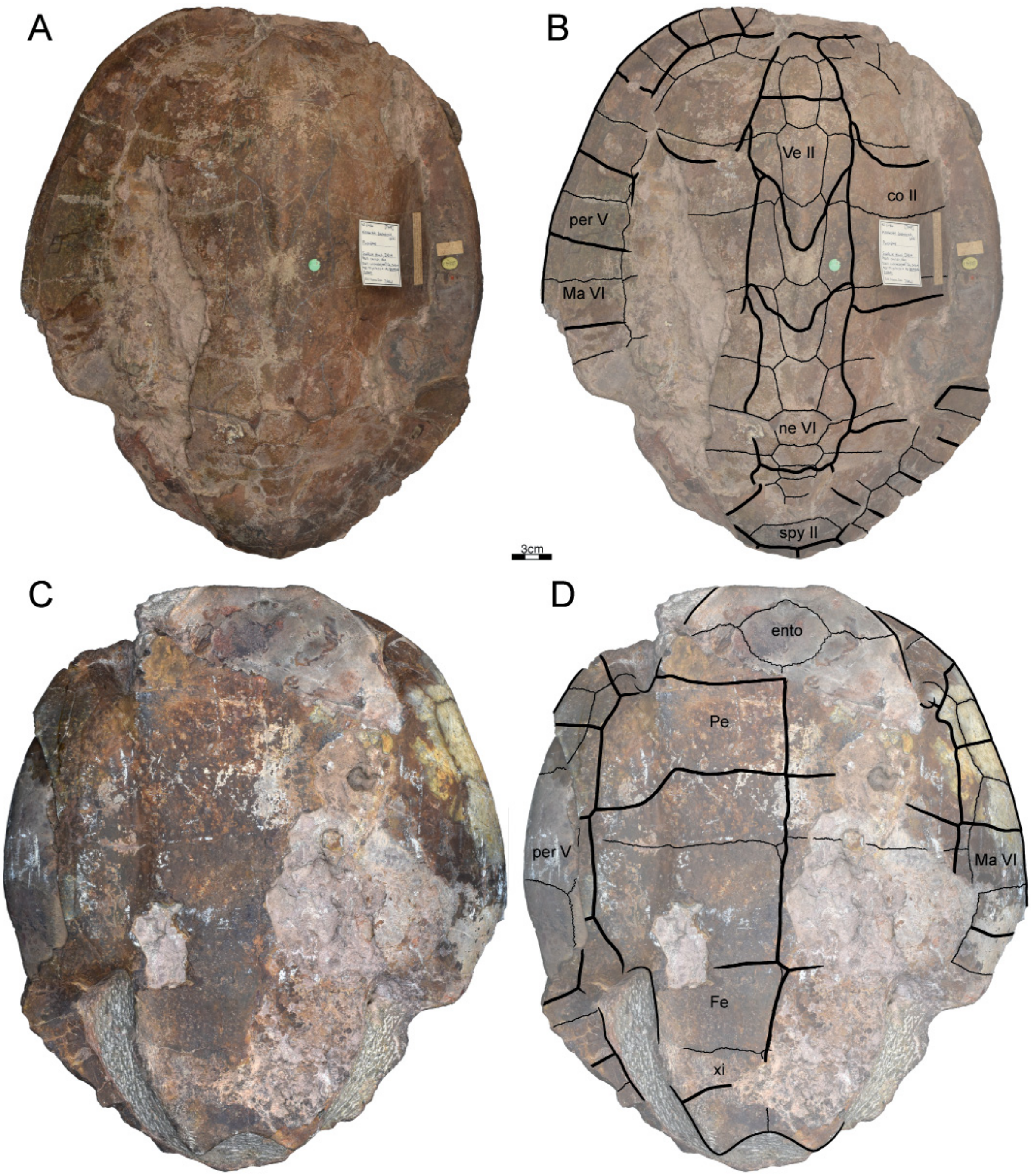

Fig. 14. BMNH 39841, holotype of *Batagur durandi* Lydekker, 1885, here identified as synonym of *Batagur dhongoka* (Gray, 1832). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

and sixth marginal scutes overlap the hyoplastron. The hyo-hypoplastral suture and pectoroabdominal sulcus do not overlap or coincide. The xiphiplastra have a small, rounded anal notch.

IM W19/173 (Fig. 15) – This is a well-preserved specimen that lacks provenance data and that appears to be unpublished. The majority of sutures and sulci of the carapace are clearly visible. The specimen likely represents an adult female due to its large size (carapace length greater than 40 cm). The carapace is highly domed at its center. A median carapacial keel is present, with protrusions at the posterior margins of the second and third vertebral scutes. The neural bones, likely the sixth to eighth, are anteriorly short-sided. The sulcus between the first and the second pleurals and the second and third pleurals are positioned over the second and fourth costal bones, respectively. The plastron is damaged and thus not shown here.

Comments

Here, we attribute these two specimens to *Batagur dhongoka* based on the protrusion of the second vertebral into the third, a medially short third vertebral scute, a fourth vertebral scute that is much longer than wide, and a large plastron with straight humeropectoral sulci that do not cross the entoplastron (noticeable on BMNH 39841). This confirms the synonym of *B. durandi* with *Batagur dhongoka*, as first suggested by Boulenger (1889) and later supported by Lydekker (1889a), TEWG (2015) and TTWG (2017).

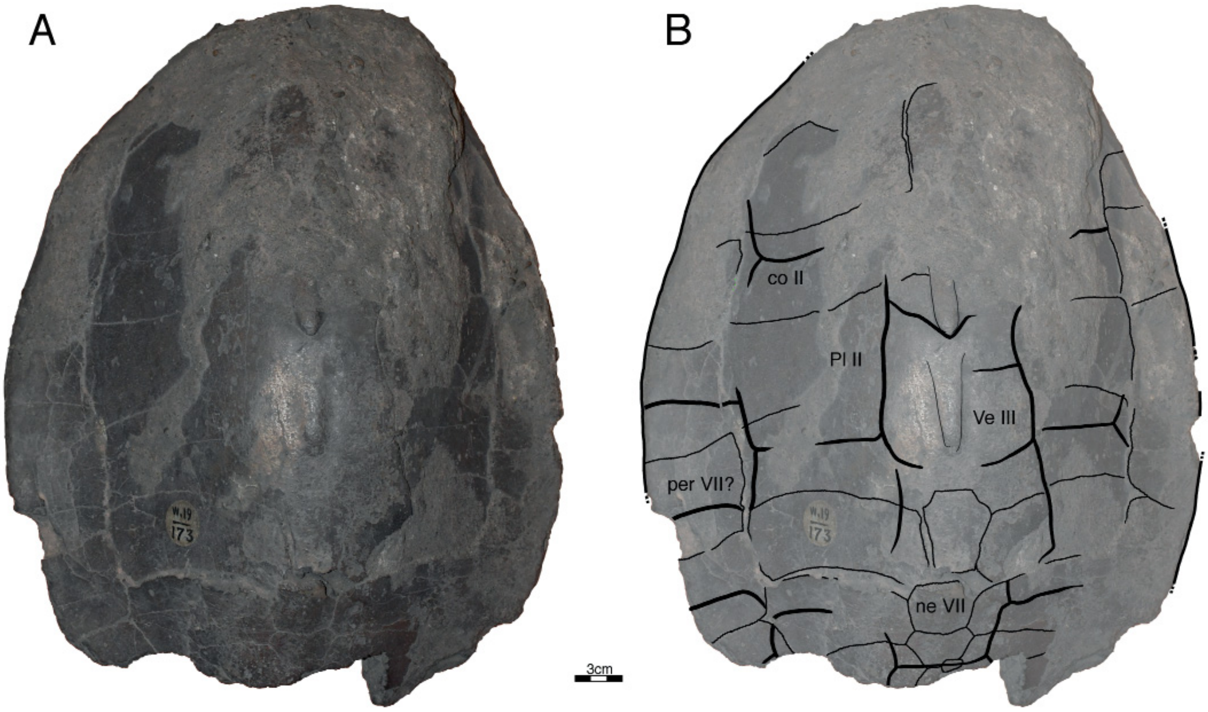

Fig. 15. IM W19/173, previously undescribed, here identified as *Batagur dhongoka* (Gray, 1832). **A**. Photograph of carapace. **B**. Illustration of carapace. Scale bar: 3 cm.

Genus ***Pangshura*** Gray, 1856
Figs 16–18

Type species

Pangshura tecta (Gray, 1830).

Differential osteological diagnosis using shell characters

A member of *Pangshura* can be diagnosed by the presence of a tectiform carapace, strong median carapacial keel, a pleural I/II sulcus with an anteromedial process, a pleural IV/vertebral V sulcus contacting the tenth marginal, a fourth vertebral scute that is much longer than wide and that is strongly constricted anteriorly, and an octagonal fourth neural (Garbin *et al.* 2018).

Material examined

INDIA • 1 specimen; Yamuna-Ganges River basin, Siwalik Hills; Miocene–Pliocene; BMNH 39837 • 1 incomplete specimen; Siwalik Hills; Miocene–Pliocene; BMNH 17435 • 1 specimen, original of "*Emys namadicus*"; Madhya Pradesh, Central Narmada Valley, Muwar and Doomar Villages; Late Pleistocene; IM E.110.

Description of material examined

BMNH 39837 (Fig. 16) – This is an almost complete shell from the Miocene/Pliocene of the Yamuna or Ganges River basins in the Siwalik Hills of India originally figured and described in dorsal view by Lydekker (1885a: pl. 22.3). The specimen is not particularly well preserved, but many more sutures are visible than apparent from the figure of Lydekker. The size (carapace length greater than 15 cm) indicates that it represents an adult female. A small keel is present between neural II and suprapygal II. There are no signs of growth annuli. Neural bones II, III, and VII are hexagonal with anterior short sides. Neural IV is octagonal. The third vertebral scute has a strong posterior keel, but no midline prominence. The posterior margin of the first and second pleural scutes have long finger-like anterior projections that intersect costal I and III, respectively. The fifth marginal scute contacts costal bones III and IV. The anterior and posterior plastral margins are not completely preserved. The entoplastron is not intersected by the humeropectoral sulcus. The pectoroabdominal sulcus has lateral notches, which suggest the former presence of longitudinal keels, does not intersect the hyo-hypoplastral suture, and contacts the fifth marginal scute. Axillary and inguinal scutes were likely present. The anal notch is deep.

BMNH 17435 (Fig. 17) – This is a small incomplete specimen (total length of 9 cm) from the Miocene/Pliocene of the Siwalik Hills, likely of India, that was presented to BMNH by P.T. Cautley in 1840 and figured and described in dorsal view by Lydekker (1885a: pl. 22.1). The specimen probably represents an adult male based on its small size and consists of the center of the shell, missing the anterior, posterior as well as part of lateral carapace margins. Some additional sutures are apparent relative to the original figure of Lydekker (1885a). A strong median keel is present, running from the most anterior to the most posterior region of the specimen. The carapace has a tectiform shape in anterior view (not illustrated). There are no signs of growth annuli or intercostal fontanelles. A cervical scute is present. The first vertebral scute is small, with straight lateral margins. The second vertebral scute is hexagonal, with shorter posterolateral margins, and a straight sulcus between the second and third vertebral. The third vertebral scute is pentagonal, has straight lateral margins and a small posterior projection into the fourth vertebral. The fourth vertebral scute is only partially preserved, but constricted anteriorly as strongly as other representatives of *Pangshura*. The interpleural sulcus I–II lies over the suture between costal I and II, and intersects it anteriorly, without a finger-like projection. The interpleural sulcus II–III has a small anterior projection that almost intersects the suture between costal III and IV. The anterior and posterior plastral margins are not preserved. The entoplastron is not intersected by the humeropectoral sulcus.

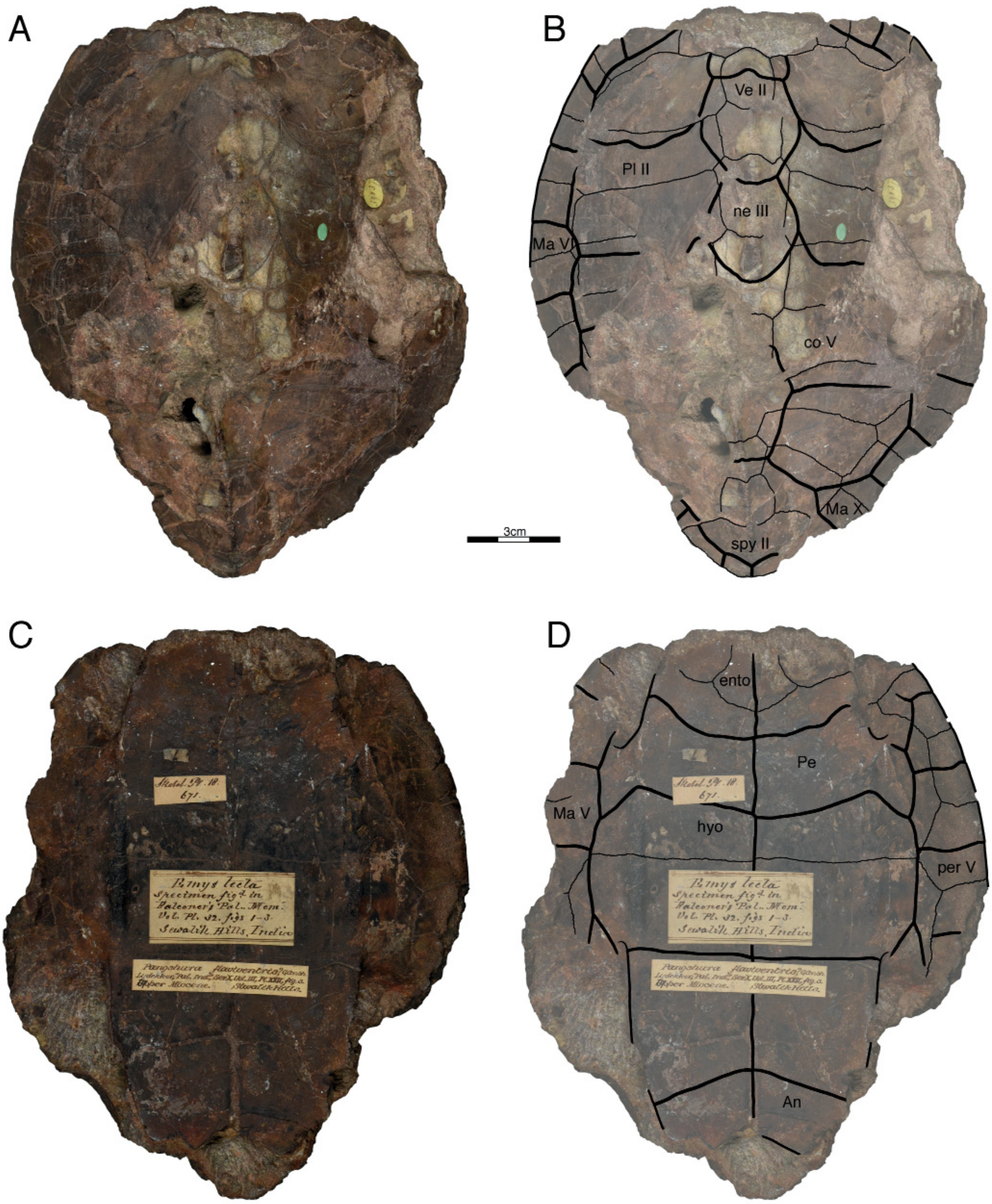

Fig. 16. BMNH 39837, referred to *Pangshura flaviventer* Günther, 1864 by Lydekker (1885a), here identified as *Pangshura* sp. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

The hyo-hypoplastral suture does not overlap the pectoroabdominal sulcus and contacts peripheral V laterally. The axillary and inguinal scutes are likely present. The fourth, fifth, and sixth marginals form the well-developed bridge.

IM E.110 (Fig. 18), original of “*Emys namadicus*” Theobald, 1860 (*nomen nudum*) – This specimen is a well-preserved shell of a small individual (total length of 8 cm) from the latest Pleistocene of Muwar-Doomar, Central Narmada Valley, India, originally named by Theobald (1860) but only later figured in dorsal view and described by Lydekker (1885a: pl. 22.2). Although we observe fewer sulci and sutures than originally documented by Lydekker, most are well preserved. The presence of a hyo-

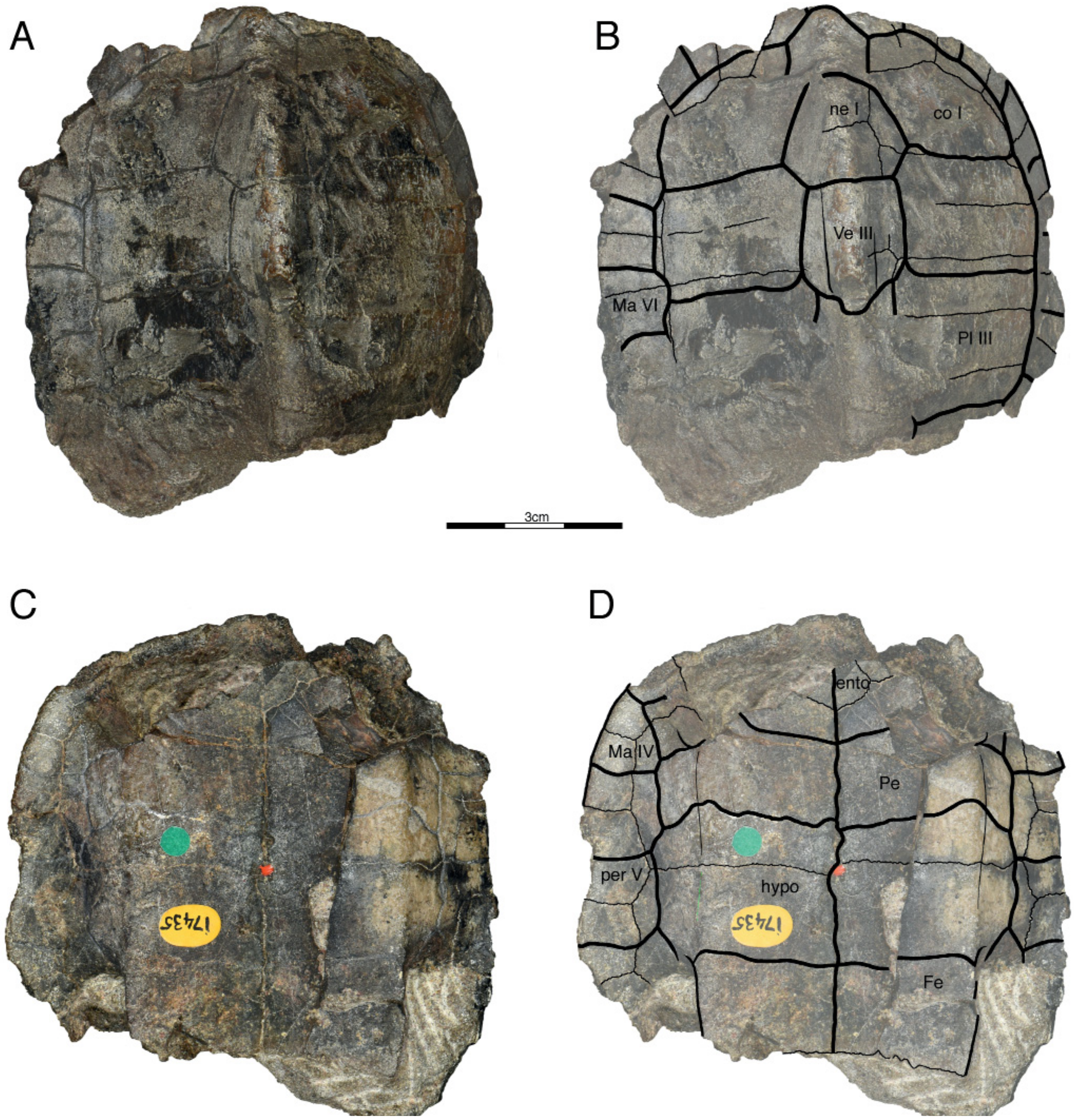

Fig. 17. BMNH 17435, referred to *Pangshura* sp. by Lydekker (1885a), herein confirmed. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

hypoplastral fontanelle suggests that this is likely a juvenile specimen. A strong median carapacial keel is present, which is at its highest at the posterior region of the third vertebral scute. There are no signs of growth annuli marks. The first vertebral scute has a wide anterior margin followed by a constriction of the lateral margins. The second vertebral scute is hexagonal, subquadrangular, and as long as broad. The third vertebral scute is pentagonal and pointed posteriorly. The fourth vertebral scute is rhomboid, with a slight anterior constriction, and its posterior margin overlaps the suture between the eighth neural bone and the first suprapygal. The sulcus between the first and second pleural scutes is almost straight, overlapping the suture between costal I and II. The sulcus between the second and third pleurals is directed anteriorly in the dorsal portion, without an anterior projection or finger-like process. The anterior and posterior plastral margins are missing. The bridge is well developed with the fourth,

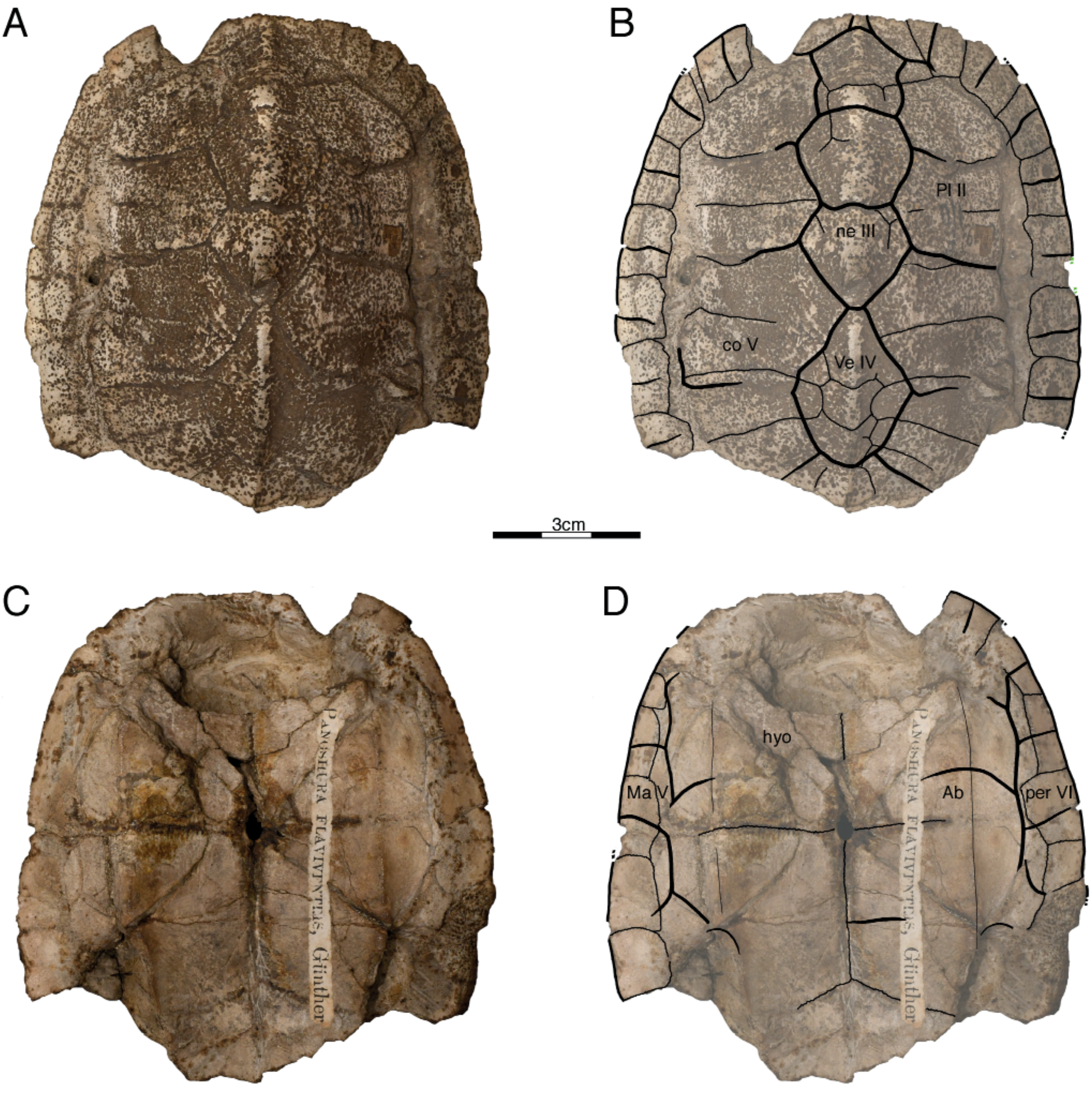

Fig. 18. IM E.110, referred to *Pangshura flaviventer* Günther, 1864 by Lydekker (1885a), here identified as *Pangshura* sp. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

fifth, and sixth marginals overlapping the hyo- and hypoplastra. The pectoroabdominal sulcus does not intersect the hyo-hypoplastral suture. The inguinal scute is likely present.

Comments

The three herein referred specimens in our opinion lack characters that would allow identifying them to species level. This contradicts in part the original assessments of Lydekker (1885a). See Discussion (*Pangshura* specimens section) for further details.

Pangshura tatrotia Joyce & Lyson, 2010

Type

YPM 4127, a near complete fossil shell.

Material examined

Holotype

PAKISTAN • Punjab, Potwar Plateau, 2 miles north-east of Padhri; Tatrot Formation; Late Pliocene; YPM 4127.

Type locality

Yale North India Expedition locality 99, about two miles north-east of Padhri, Potwar Plateau, Punjab, Pakistan.

Occurrence

Tatrot Formation, Late Pliocene (3.6 to 2.6 Ma, possibly Plio–Pleistocene boundary).

Differential osteological diagnosis using shell characters

Pangshura tatrotia can be differentiated from other species of *Pangshura* by the presence of a strong median keel projection on both the second and third vertebral, and a first vertebral scute that is constricted anteriorly.

Description of the type

YPM 4127, holotype of *Pangshura tatrotia* – This is an almost complete, well-preserved specimen, with a tectiform carapace from the Early Pliocene Tatrot Formation of the Potwar Plateau of Punjab, Pakistan. The posterior peripheral bones and left peripheral bones IV–VI are missing. A median, well-pronounced carapacial keel is present from neurals II to VIII. Neural bones II, III, VI–VIII are hexagonal with anterior short sides. Neural IV is octagonal, with both anterior and posterior sides short. Neural V is quadrangular, without short sides. The fourth vertebral scute runs from neural IV to VIII and has a strong anterior bottle-neck-shaped constriction. The posterior margins of the first and second pleural scutes run over costals II and IV, respectively, and have a strong anterior projection that crosses to the anterior costal bone. The pygal bone is completely divided by the twelfth intermarginal sulcus. Parts of the anterior and posterior plastral margins are missing. The entoplastron is intersected anteriorly by the gularohumeral sulcus, but not by the humeropectoral sulcus. The hyo-hypoplastral suture contacts peripheral V and does not overlap with the pectoroabdominal sulcus. The fifth and sixth marginal scutes form the bridge and overlap onto the hyoplastra. Only the sixth marginal scute overlaps with the hypoplastron. A large inguinal scute is present, likely contacting the femoral scute. For a more comprehensive description of this specimen, refer to Joyce & Lyson (2010).

Comments

Pangshura tatrotia was only recently named based on a well-preserved shell that documents with confidence a morphotype different from all extant representatives of *Pangshura*. The specimen is furthermore associated with quality locality data. We therefore here find the validity of this species to be unproblematic.

Genus ***Hardella*** Gray, 1870

Type species

Hardella thurjii (Gray, 1831a).

Differential osteological diagnosis using shell characters

See *Hardella thurjii* below.

Hardella thurjii (Gray, 1831)
Figs 19–21

Emys thurjii Gray, 1831a: 22 (*nomen novum*).
Emys thuryi Gray, 1831c: 8 (*nomen oblitum*).
Emys thuji Gray, 1831b (ex errore): pl. 73.
Emys flavonigra Lesson, 1831: 120.
Emys thugi Gray, 1832 (ex errore): Directions.
Clemmys (Clemmys) thurgii Fitzinger, 1835: 123 (*nomen novum*).
Kachuga oldhami Gray, 1869: 200.
Batagur falconeri Lydekker, 1885a: 187
Clemmys watsoni Lydekker, 1886a: 541
Hardella indi Gray, 1870: 58.
Geoemyda pilgrimi Prasad & Satsangi, 1967.

Emys thurgii – Gray 1844: 17.
Emys thurgi – Gray 1856 (“1855”): 21.
Clemmys thurgii – Strauch 1862: 32.
Batagur thurgii – Theobald 1868: 12.
Hardella thurgi – Gray 1870: 58.
Batagur (Hardella) thurgi – Anderson 1879: 764.
Hardella thurjii – Siebenrock 1909: 456.
Hardella thurgi – Smith 1931: 50.
Hardella thurjii thurjii – Wermuth & Mertens 1977: 40.
Hardella thurjii indi – Wermuth & Mertens 1977: 40.
Hardella thurji – Pritchard 1979 (ex errore): 193.
Hardella thurji thurji – Obst 1985: 221.

Type

Unknown (Iverson 1992).

Material examined

INDIA • 1 specimen, holotype of *Batagur falconeri*; Siwalik Hills; Miocene–Pliocene; BMNH 39835 • 1 specimen; Siwalik Hills; Miocene–Pliocene; BMNH R.890 • 1 specimen, holotype of *Clemmys watsoni*; Gulf of Cambay, Gujarat, Piram Island; Late Miocene–Pliocene; BMNH R.748.

Type locality

"India" (Iverson 1992).

Occurrence

Miocene/Pliocene – Recent.

Differential osteological diagnosis using shell characters

Hardella thurjii can be differentiated from other geoemydids by large carapace size (up to 60 cm in females), presence of hexagonal, nearly square second to fourth vertebrals, a first vertebral scute that is wider posteriorly, presence of an inflection at the margin of the gulohumeral sulcus, and an entoplastron that is not intersected by the humeropectoral sulcus.

Description of material examined

BMNH 39835 (Fig. 19), holotype of *Batagur falconeri* – This is an almost complete shell, exceptionally well preserved, from the Miocene/Pliocene of the Siwalik Hills, likely of India, originally figured and described in three views by Lydekker (1885a: pls 23.1, 24.4). Our figures are overall comparable to those of Lydekker, although we see more details to the peripherals (Fig. 19). The specimen clearly represents an adult female specimen based on overall size (carapace length greater than 40 cm). A small keel is present on neurals IV and VI. There are no signs of growth annuli. All neural bones have short anterior sides. The third neural is half one and a half time longer than the other neural bones. The cervical scute is present, longer than wide. The first vertebral scute is broader posteriorly and narrows anteriorly. The second and third vertebrals are much broader than the other vertebral scutes. The fifth vertebral has an anterolateral constriction. Marginal scutes IV–X overlap the adjacent costal bones. The anterior and posterior plastral margins are not preserved. The pectoroabdominal sulcus has lateral notches, suggesting the former presence of longitudinal keels as a juvenile. The pectoroabdominal sulcus does not intersect the hyo-hypoplastron suture and contacts the fifth marginal scute. Axillary and inguinal scutes are likely present.

BMNH R.748 (Fig. 20), holotype of *Clemmys watsoni* – This specimen originates from the Late Miocene–Pliocene of Piram Island, Gulf of Cambay, Gujarat, India, was presented to the BMNH in 1886 by Col. J.W. Watson and figured and described in a small contribution from Lydekker (1886a: pl. 1). Our illustrations in three views overall confirm most of Lydekker's observations, but we see fewer details along the neural column and the damaged portions of the costals and peripherals. The specimen is almost complete, full size, and misses some lateral peripheral bones (right and left), the anterior plastral margin, the posterior plastral lobe, and the right bridge (Fig. 20). The specimen is likely an adult considering its size (carapace length greater than 15 cm) and perhaps a male specimen, as modern male individuals of *H. thurjii* reach up to 18 cm and lack intercostal fontanelles (Das & Bhupathy 2009a). Most sulci and sutures of the carapace are visible, as well as a knob on neurals IV and VIII, indicating the presence of a median keel. Growth annuli are present. The cervical scute is as wide as long and lacks a posterior notch. The first vertebral scute is wider than long, its lateral sides converge anteriorly and lack an anterolateral constriction, and it contacts the first marginal scute. The neural bones are hexagonal and anteriorly short-sided. The third vertebral has straight lateral sides and the posterior margin has an anteriorly oriented inflection that crosses the suture between neural bones III–IV. The fifth vertebral scute has an anterolateral constriction. The pygal bone is completely intersected by the twelfth intermarginal sulcus. The humeropectoral sulcus is located posterior to the entoplastron. The pectoral scute contacts the fifth marginal. For a more extensive description of this specimen, we refer to Lydekker (1886a).

BMNH R.890 (Fig. 21) – This specimen is from the Miocene/Pliocene of the Siwalik Hills, likely of India, was purchased by P.T. Cautley in 1840, but remained unfigured to date. It is a crushed, partial specimen, that probably represents an adult female considering its large size (carapace length greater

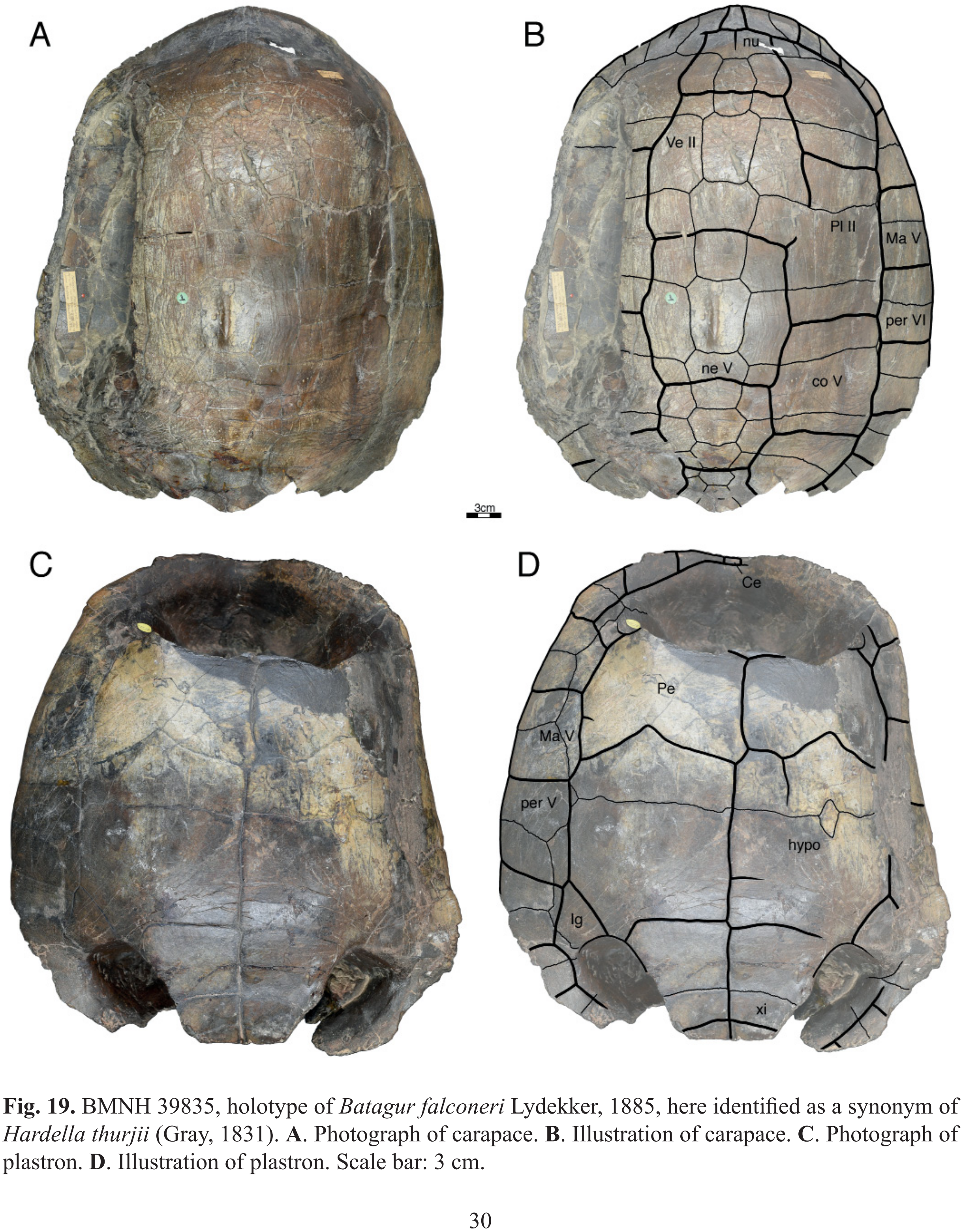

Fig. 19. BMNH 39835, holotype of *Batagur falconeri* Lydekker, 1885, here identified as a synonym of *Hardella thurjii* (Gray, 1831). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

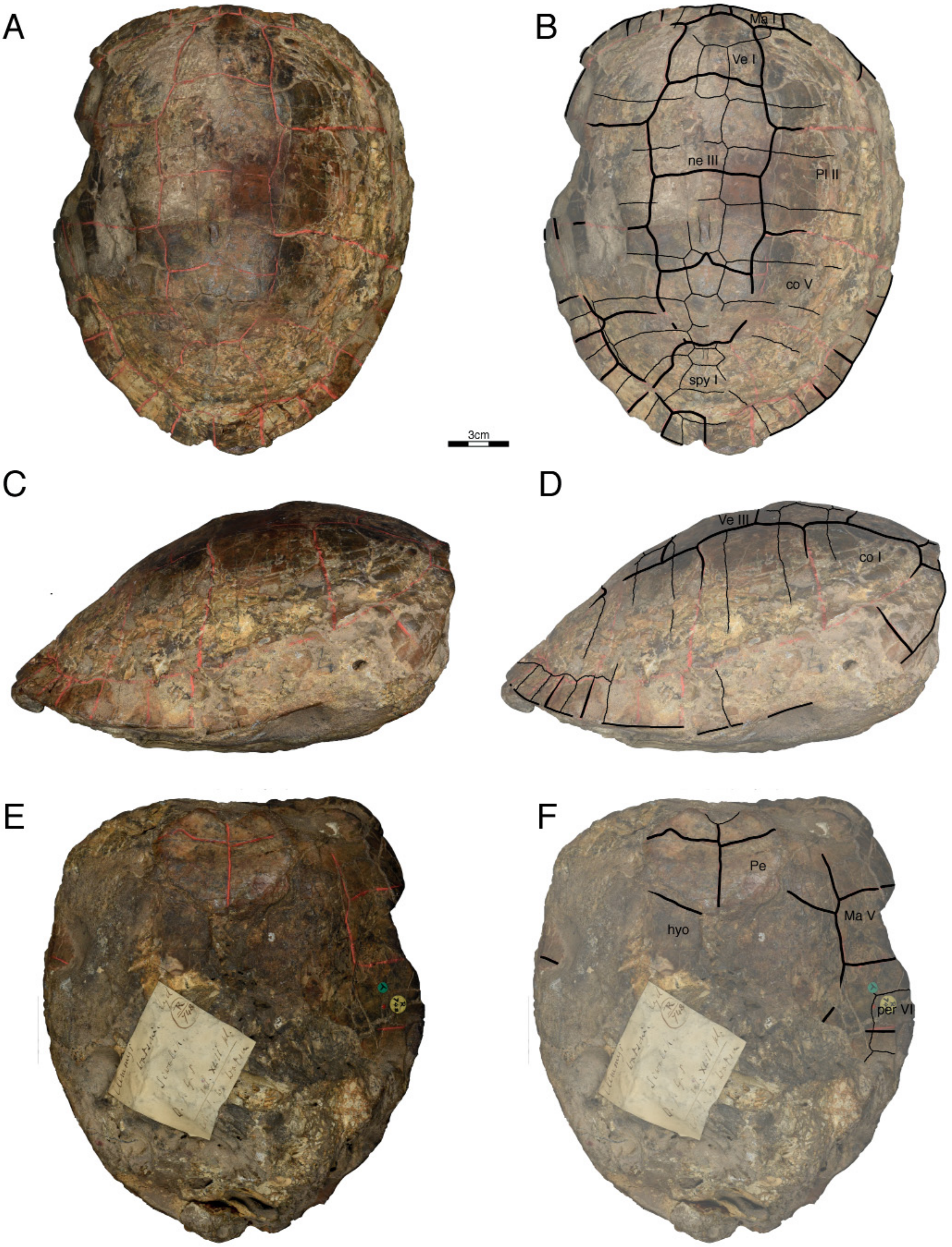

Fig. 20. BMNH R.748, holotype of *Clemmys watsoni* Lydekker, 1886a, here identified as synonym of *Hardella thurjii* (Gray, 1831). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of carapace in lateral view. **D**. Illustration of carapace in lateral view. **E**. Photograph of plastron. **F**. Illustration of plastron. Scale bar: 3 cm.

than 20 cm). Both the anterior and posterior margins of the carapace are missing. Neural bones III and IV have a knob, indicating the presence of a median carapacial keel. Neural bones II–IV are hexagonal with anterior short sides. The first vertebral scute has anteriorly converging lateral sides. The third vertebral scute has straight lateral sulci. The posterior margins of the first and second pleurals are straight, placed over costals II and IV, respectively, and lack an anterior projection. Both the anterior and posterior plastral margins are not preserved. The plastron has two lateral longitudinal keels, which cross the

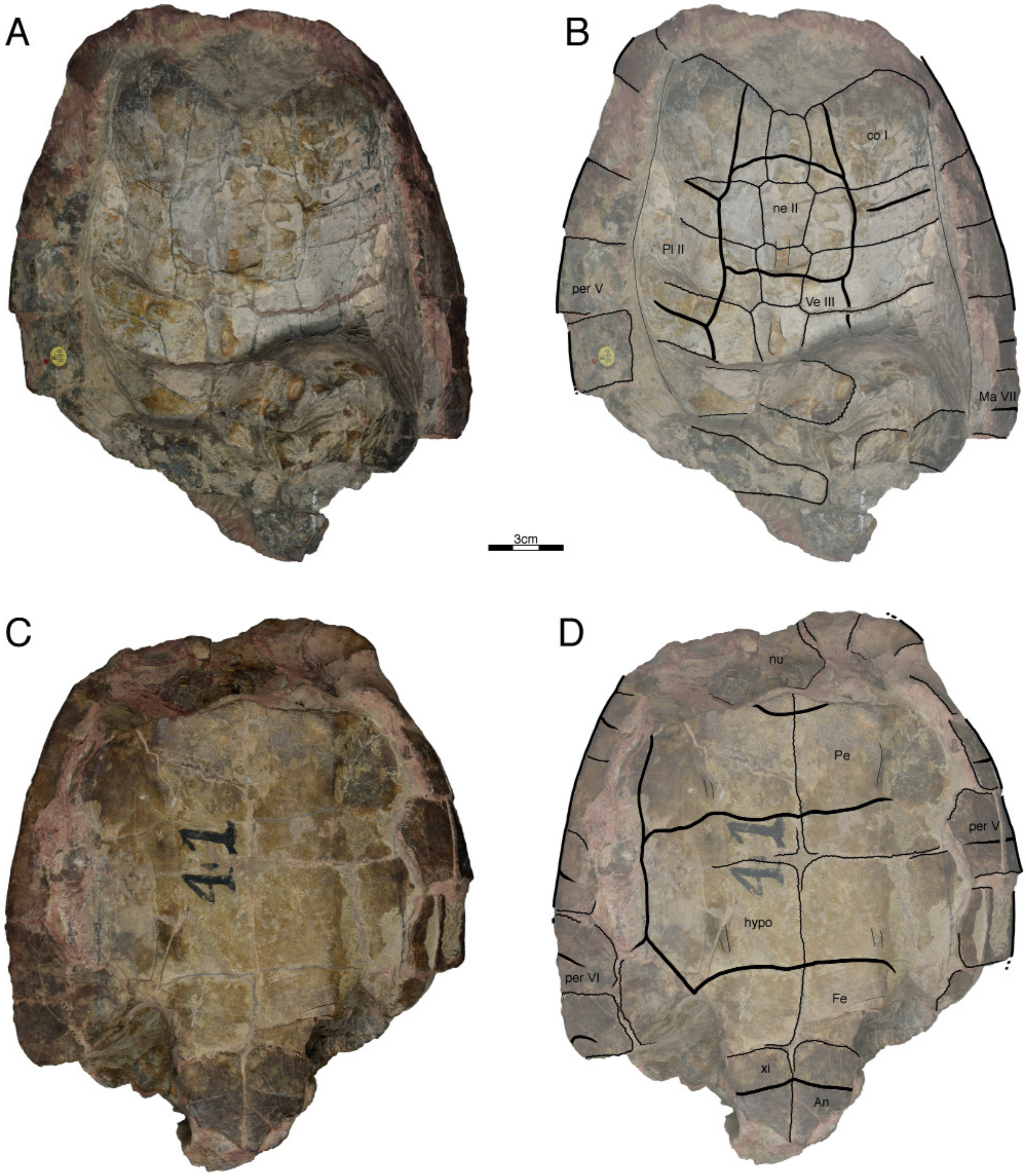

Fig. 21. BMNH R.890, referred to *Hardella thurgi* (Gray, 1831) by Lydekker (1889b), here identified as *Hardella thurjii* (Gray, 1831). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

lateral sides of the hyo- and hyoplastra. The humeropectoral sulcus is apparently located posterior to the entoplastron, which is not preserved. Inguinal scutes are likely present that contact the femoral scute.

Comments

We here attribute these specimens to *Hardella thurjii* based on the presence of a short median keel, large and square second and third vertebrals that are about the same width as the fourth vertebral scute, large inguinal scute, and an entoplastron that is not intersected by the humeropectoral sulcus. This confirms the synonymy of *B. falconeri* and *C. watsoni* with *H. thurjii*, as first suggested by Boulenger (1889) and later supported by Lydekker (1889a), TEWG (2015) and TTWG (2017). We furthermore follow Das (1994) by recognizing the synonymy of *Geoemyda pilgrimi* with *H. thurjii* (followed by TEWG 2015 and TTWG 2017) although we did not study the holotype of this species firsthand.

Genus ***Geoclemys*** Gray, 1856

Type species

Geoclemys hamiltonii (Gray, 1830).

Differential osteological diagnosis using shell characters

See *Geoclemys hamiltonii* below.

Geoclemys hamiltonii (Gray, 1830)

Figs 22–26

Emys hamiltonii Gray, 1830: 9.
Emys guttata Gray, 1832: pl. 76.
Emys picquotii Lesson, 1831: 120.
Emys picquotii Lesson *in* Duméril & Bibron, 1835: 316.
Emys hamiltonii Duméril & Bibron, 1835: 315.
Emys hamiltonoides Falconer & Cautley *in* Lydekker, 1880: 21.
Melanochelys pictus Murray, 1884a: 107.
Clemmys palaeindica Lydekker, 1885a: 178.
Geoclemys sivalensis Tewari & Badam, 1969: 555.
Geoclemys sivalensis Badam, 1979: 99.

Clemmys (Clemmys) hamiltonii – Fitzinger 1835: 123.
Geoclemys hamiltonii – Gray 1856 (“1855”): 17.
Clemmys hamiltonii – Strauch 1862: 32.
Damonia hamiltonii – Gray 1869: 195. — Boulenger 1889: 93.
Damonia hamiltonoides – Lydekker 1880: 37.
Damonia hamiltoni – Lydekker 1889b (ex errore): 105.
Geoclemys hamoltoni – Tewari & Badam 1969 (ex errore): 1.

Type

BMNH 1947.3.4.41 (Iverson 1992).

Material examined

INDIA • 1 specimen, holotype of *Clemmys palaeindica*; Siwalik Hills; Miocene–Pliocene; BMNH 39838 • 4 specimens; Siwalik Hills; Miocene–Pliocene; BMNH 39840, BMNH 39842, BMNH R.887, BMNH R.892 • 1 specimen, holotype of *Geoclemys sivalensis*; Punjab, Pinjore stage, 1 km southeast of Quranwalla; Early Pleistocene; MCASG A/665.

Type locality

"India" (Iverson 1992).

Occurrence

Miocene/Pliocene – Recent.

Differential osteological diagnosis using shell characters

Geoclemys hamiltonii can be differentiated from other geoemydids by the presence of three strong longitudinal carapace keels, neurals III-VI with anterior short sides, and an entoplastron that is intersected by the humeropectoral sulcus.

Description of material examined

BMNH 39838 (Fig. 22), holotype of *Clemmys palaeindica* – This is an almost complete, exceptionally well-preserved specimen from the Miocene/Pliocene of the Siwalik Hills, likely of India, originally figured and described by Lydekker (1885a: pl. 21.3). Our observations mostly compare with those of Lydekker, although we see more details in the plastron. The specimen appears to represent an adult due to its large size (carapace length greater than 30 cm). All sulci and sutures on the carapace and most sulci of the plastron are visible. Three longitudinal carapacial keels are present, with varying height throughout the keel. The lateral keels are closer to the neural series than to the peripheral bones. No signs of growth annuli are visible. The cervical scute is present and as long as wide. All vertebral scutes are about the same width. The first vertebral scute is longer than wide and has straight lateral margins. The second and third vertebral scutes are as long as wide. The sulcus between the second pleural and third vertebral is almost straight. Marginal scutes IV–VIII do not contact any costal bones. The eighth marginal scute is slightly serrated at the carapace margin. All neural bones are hexagonal, anteriorly short-sided, and about the same size. The second suprapygal is intersected by the sulcus between the fifth vertebral and twelfth marginal scutes. The anterior plastral margin is straight. The entoplastron is intersected by the gularohumeral sulcus anteriorly and likely by the humeropectoral sulcus posteriorly. A deep and rounded anal notch is present at the posterior plastral margin.

BMNH 39840 (Fig. 23) – This is a well-preserved subadult specimen (carapace length greater than 11 cm) from the Miocene/Pliocene of the Siwalik Hills, likely of India, originally figured and described by Lydekker (1885a: pl. 1). Our observations greatly compare with those of Lydekker. The specimen is missing the posterior half of the carapace and the xiphiplastra. Almost all carapacial sulci and sutures are visible. Three longitudinal keels are present on the carapace, with discontinuous height. The median keel starts at the posterior part of vertebral I. The lateral keels start on the posterior region of costal I and are positioned closer to the neural series than to the peripheral bones. No signs of growth annuli are visible. The cervical scute is present and wider than long. The first vertebral scute is as long as wide, has straight lateral margins, and contacts the second marginal scute. The second and third vertebral scutes are about the same width and are as long as wide. The sulcus between the second pleural and the third vertebral is almost straight. All neural bones are hexagonal, anteriorly short-sided, and about the same size. Peripheral bones III–VII do not have recurved margins that would form a longitudinal gutter. The anterior plastral margin is straight, without a median notch, and has small lateral tuberosities. A small inflection on the gular scute margin is present at the edge of the gularohumeral sulcus. The entoplastron is intersected anteriorly by the gularohumeral sulcus, but not by the humeropectoral sulcus. The pectoroabdominal sulcus and hyo-hyoplastron suture do not overlap. The posterior plastral margin is not preserved.

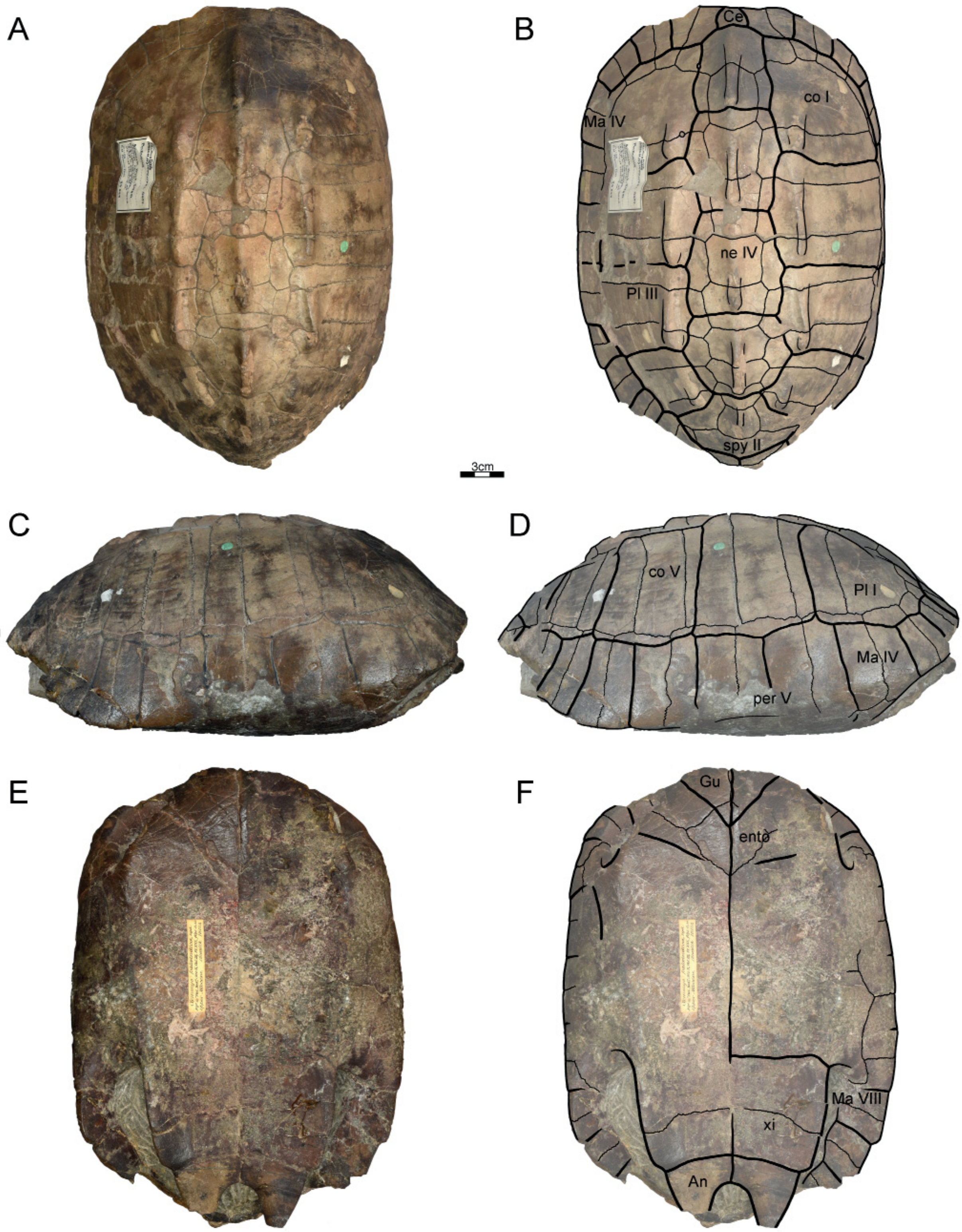

Fig. 22. BMNH 39838, holotype of *Clemmys palaeindica* Lydekker, 1885, here identified as synonym of *Geoclemys hamiltonii* (Gray, 1830). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of carapace in lateral view. **D**. Illustration of carapace in lateral view. **E**. Photograph of plastron. **F**. Illustration of plastron. Scale bar: 3 cm.

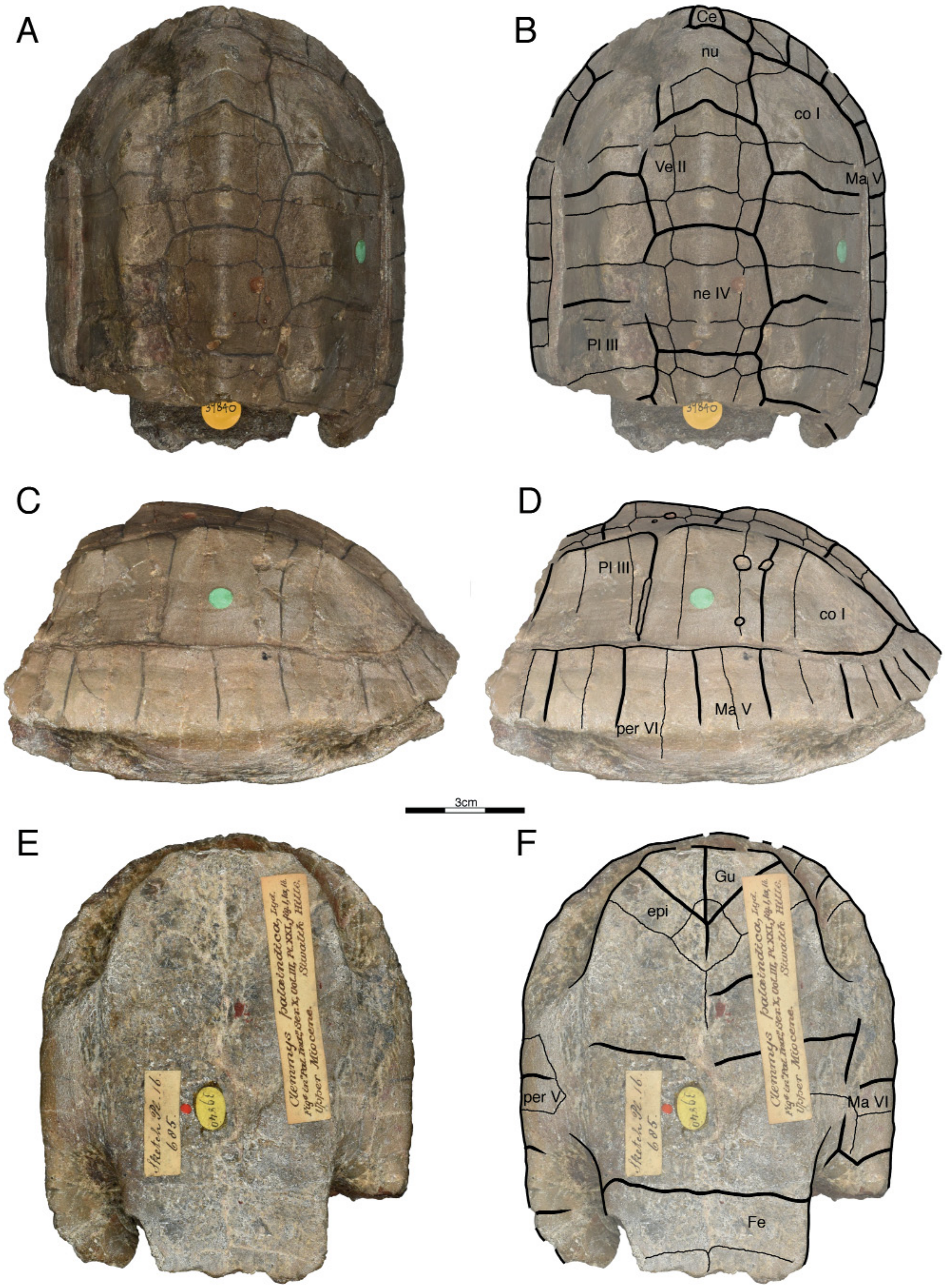

Fig. 23. BMNH 39840, referred to *Clemmys palaeindica* Lydekker, 1885, here identified as *Geoclemys hamiltonii* (Gray, 1830). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of carapace in lateral view. **D**. Illustration of carapace in lateral view. **E**. Photograph of plastron. **F**. Illustration of plastron. Scale bar: 3 cm.

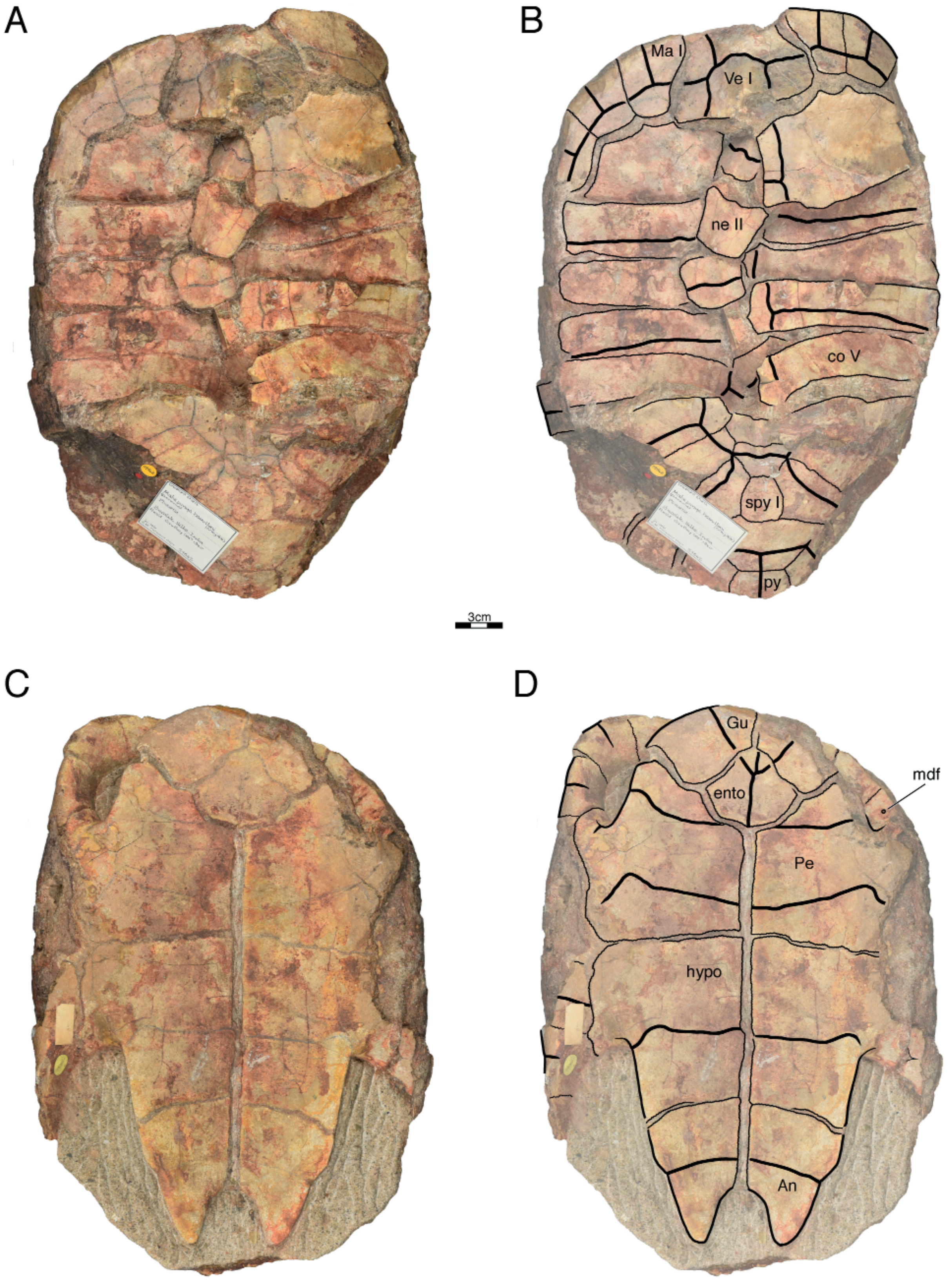

Fig. 24. BMNH 39842, referred to *Damonia hamiltonii* Gray, 1869 by Lydekker (1889b), here identified as synonym of *Geoclemys hamiltonii* (Gray, 1830). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

BMNH 39842 (Fig. 24) – This specimen originates from the Miocene/Pliocene of the Siwalik Hills, likely of India. It was presented to BMNH by Col. P.T. Cautley, but remains unfigured to date. It is an almost complete specimen that is missing the lateral peripheral bones and part of the anterior margin of the plastron. This is clearly an adult specimen due to large size (carapace length greater than 35 cm). The carapace surface is crushed, preventing observation of most sutures and sulci. At least the median longitudinal keel is present, crossing the first, seventh and eighth neural bones. The first vertebral scute has straight lateral margins, without any constriction, contacting the first marginal scute. The neural bones are hexagonal and anteriorly short-sided. The pygal bone is completely intersected by the intermarginal sulcus. The gular scute is longer than wide, overlapping part of entoplastron. The entoplastron is intersected posteriorly by the humeropectoral sulcus. The pectoroabdominal and abdominofemoral sulcus have two anterolateral notches, indicating the former presence of lateral longitudinal keels. The pectoroabdominal and hyo-hypoplastral suture do not overlap. The xiphiplastra have a deep anal notch.

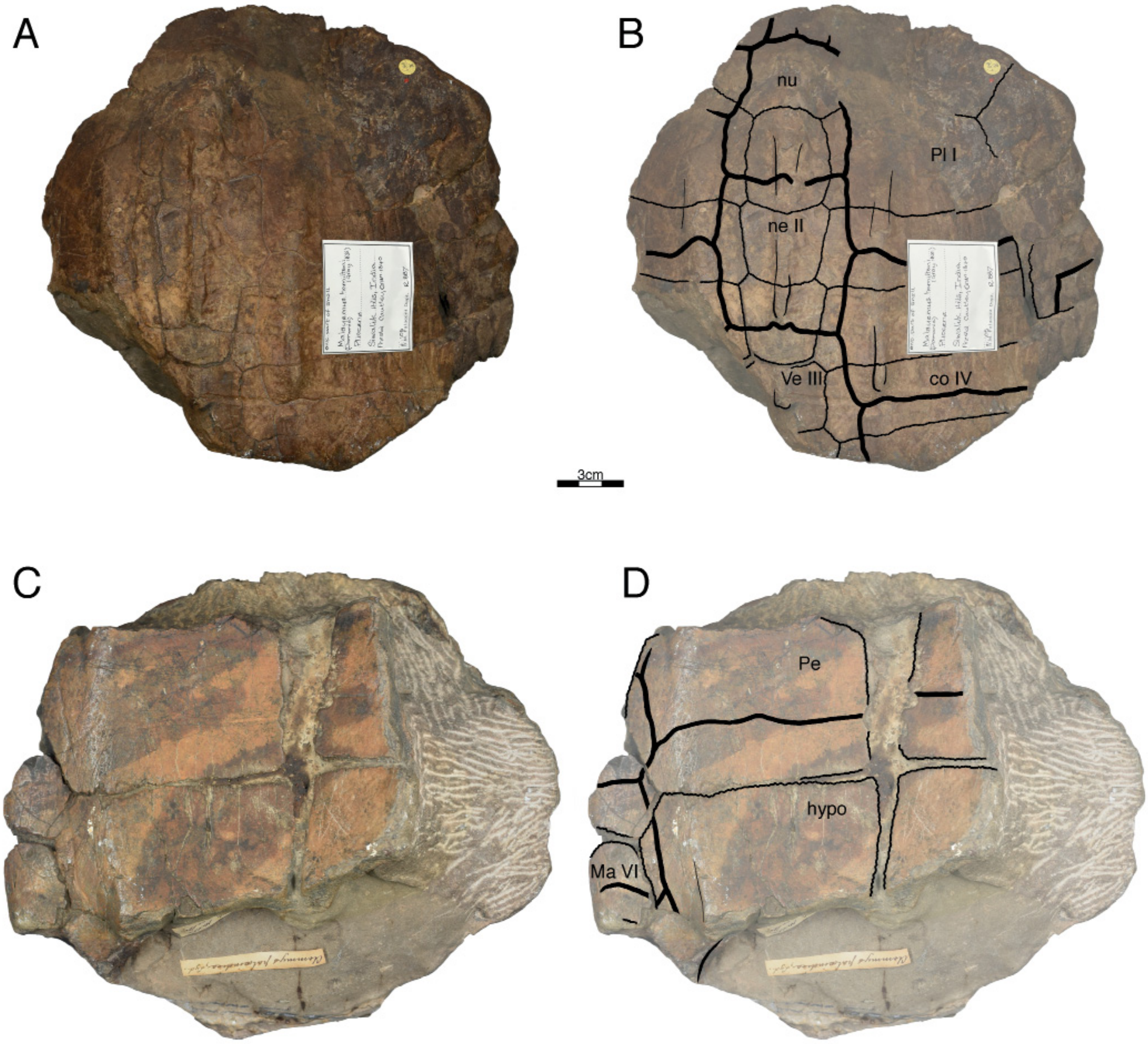

Fig. 25. BMNH R.887, referred to *Damonia hamiltonii* Gray, 1869 by Lydekker (1889b), here identified as *Geoclemys hamiltonii* (Gray, 1830). **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

BMNH R.887 (Fig. 25) – This specimen is from the Miocene/Pliocene of the Siwalik Hills, likely of India. It was presented by Col. P.T. Cautley in 1840 to BMNH, but remains unfigured until now. This is an incomplete specimen, consisting of the anterior part of the carapace and the middle part of the plastron. This is clearly an adult specimen with a total carapace length of approximately 15 cm. The nuchal, costals I–V, neural bones I–V, as well as some peripherals are preserved. A large part of the right hyo- and hypoplastron, the right bridge, and a small part of left hyo- and hypoplastron are preserved as well. A median carapacial keel and two lateral keels are clearly present. Neural bones II–V are hexagonal with anterior short sides. The first vertebral scute is longer than wide, with a small anterolateral constriction. The third vertebral has a straight lateral sulcus. The pectoroabdominal sulcus and the hyo-hypoplastral suture do not overlap. An inguinal scute is likely present.

BMNH R.892 (Fig. 26) – This specimen was collected from the Miocene/Pliocene of the Siwalik Hills, likely of India, was donated to BMNH by Col. P.T. Cautley in 1840, but remained unfigured to date. Lydekker (1889b) wrongly referred to this specimen as BMNH R.829. This is an incomplete adult specimen that only consists of the plastron (plastral length greater than 25 cm). Both the anterior and posterior plastral margins are missing, as well as the right bridge and a part of the left bridge. The entoplastron is intersected by the gularohumeral sulcus anteriorly and by the humeropectoral sulcus posteriorly. The fifth marginal scute covers a part of the left bridge and overlaps onto the hyoplastron. The sixth marginal scute does not overlap the hyoplastron. The hyo-hypoplastral suture contacts peripheral V and does not overlap the pectoroabdominal sulcus. The inguinal scute is likely present.

MCASG A/665, holotype of *Geoclemys sivalensis* – This specimen was collected from the Early Pleistocene Pinjore stage, 1 km south-east of Quranwalla, Punjab, India. It was preliminarily figured in Tewari & Badam (1969: figs 1–2) and in Badam (1979: fig. 36A–B, pl. 27), but could not be refigured herein due to logistic constraints. The specimen consists of the anterior half portion of the carapace as well as some plastral bones. Three longitudinal carapacial keels are clearly present, the lateral ones closer to the neurals than the peripherals. Growth annuli marks are present on the pleurals and first vertebral. The first vertebral scute is longer than wide and has slight anterolateral constrictions. Neural I

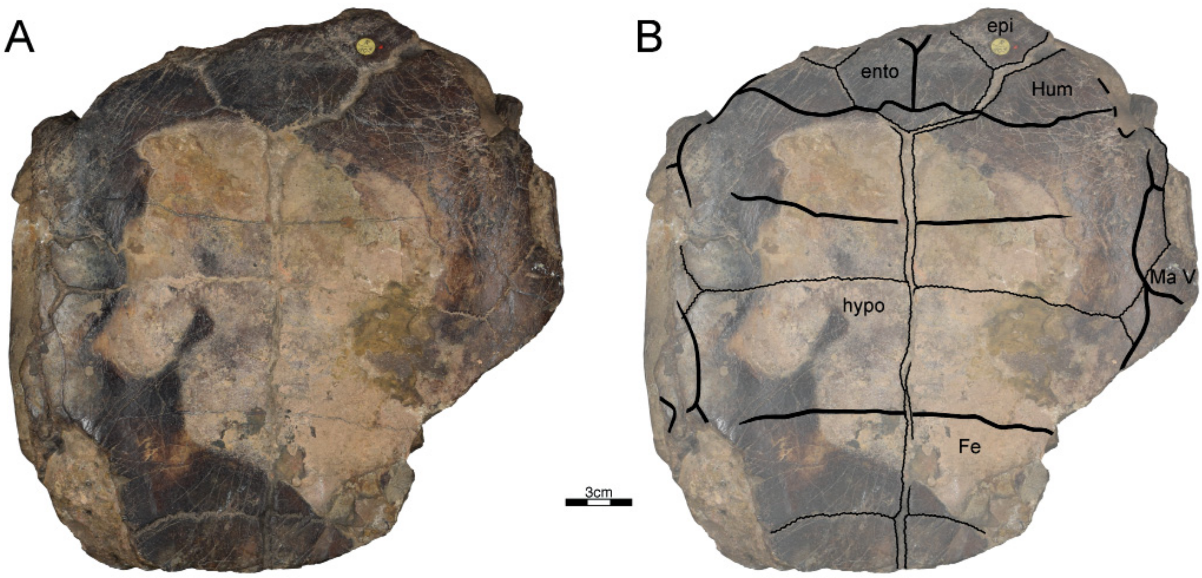

Fig. 26. BMNH R.892, referred to *Damonia hamiltonii* Gray, 1869 by Lydekker (1889b, under the number BMNH R.829), here identified as *Geoclemys hamiltonii* (Gray, 1830). **A**. Photograph of plastron. **B**. Illustration of plastron. Scale bar: 3 cm.

is oval in shape and neurals II and III are anterior short-sided. A large cervical scute is present, almost as long as wide. One hypoplastron and a bony part of the bridge are supposedly preserved, but not figured. Tewari & Badam (1969) state that mesoplastra are present, but Das (1991) indicated this to be an error.

Comments

We here attribute these specimens to *Geoclemys hamiltonii* based on, among other characteristics, the presence of a tricarinate carapace with interrupted median and lateral keels decorated by many prominent processes, and a cervical scute that is wider posteriorly. This confirms the synonymy of *Clemmys palaeindica* with *G. hamiltonii*, as initially suggested by both Boulenger (1889) and Lydekker (1889a), and of *Geoclemys sivalensis* with *G. hamiltonii*, as first recognized by Das (1991). These synonymies have been further supported by TEWG (2015) and TTWG (2017).

Geoemydinae Theobald, 1868

Genus ***Melanochelys*** Gray, 1869

Type species

Melanochelys trijuga (Schweigger, 1812).

Differential osteological diagnosis using shell characters

A member of *Melanochelys* can be diagnosed by having a small to medium sized, oval carapace (up to 30 cm in length), presence of three longitudinal keels, an octagonal second neural, neural III–VI with posterior short sides, a large first vertebral with lateral constriction, hexagonal second to fourth vertebral scutes, gular scutes that are longer than wide and an entoplastron that is intersected by the humeropectoral sulcus.

Melanochelys sivalensis (Theobald, 1877) comb. nov.
Figs 27–31

Bellia sivalensis Theobald, 1877: 44.
Clemmys hydaspica Lydekker, 1885a: 172.
Clemmys theobaldi Lydekker, 1885a: 173.
Clemmys punjabiensis Lydekker, 1885a: 175.
Geoemyda trijuga Smith, 1931: 97 (part).
Geoemyda sivalensis Smith, 1931: 89.
Melanochelys trijuga indopeninsularis TEWG, 2015: e.46.

Bellia theobaldi – Lydekker 1889a: 58.
Clemmys sivalensis – Lydekker 1885a: 171.
Bellia sivalensis – Lydekker 1889a: 58.

Type

IM E.88, the anterior half of a fossil shell (Fig. 27).

Material examined

PAKISTAN • 1 specimen, holotype of *Bellia sivalensis*; Punjab, south of Jhand; Middle to Upper Siwalik group of Potwar Plateau; Miocene–Pliocene; IM E.88 • 1 specimen, holotype of *Clemmys theobaldi*; Punjab, Jhand; Middle to Upper Siwalik group of Potwar Plateau; Miocene–Pliocene; IM E.89 • 1 specimen; Punjab, Potwar Plateau; Middle to Upper Siwalik group of Potwar Plateau; Miocene–

Pliocene; IM E.90 • 1 specimen, holotype of *Clemmys punjabiensis*; Punjab; Middle to Upper Siwalik group of Potwar Plateau; Miocene–Pliocene; IM E.92 • 1 specimen, holotype of *Clemmys hydaspica*; Punjab, Jhelum district; Middle to Upper Siwalik group of Potwar Plateau; Miocene–Pliocene; IM E.93.

Type locality and horizon

Miocene/Pliocene, Middle to Upper Siwaliks of Potwar Plateau, south of Jhand, Punjab, Pakistan (see Comments below).

Range

Miocene/Pliocene, Middle to Upper Siwaliks of Potwar Plateau, Punjab, Pakistan.

Differential osteological diagnosis using shell characters

Melanochelys sivalensis can be differentiated from other species of *Melanochelys* by the lack of longitudinal carapacial keels, the presence of hexagonal second to fourth vertebral scutes with concave posterolateral margins that are broader than long and a denser and more rounded shell.

Description of material examined

IM E.88 (Fig. 27), holotype of *Bellia sivalensis* – This is the anterior half of a shell from the Miocene/Pliocene, Middle to Upper Siwaliks of Potwar Plateau, south of Jhand, Punjab, Pakistan (see Comments below), initially figured and described by Lydekker (1885a: pl. 20.1). Our observations of the specimen mostly agree with those of Lydekker, although we document more details in the plastron. Most scutes are clearly visible, but only a few bony sutures are apparent. There are no signs of carapacial keels, but notches on the intervertebral sulci indicate the former presence of keels as a juvenile. This is clearly an adult specimen due to its large size (carapace length greater than 20 cm). Growth annuli marks are present on the anterior marginal scutes. The cervical scute is extremely reduced and clasped between the first marginals. First vertebral scute is longer than wide. The second and third vertebrals have rounded lateral margins. The plastron not well preserved, with few visible sutures. The anterior margin of the plastron is straight and the gular scutes are much longer than wide.

IM E.89 (Fig. 28), holotype of *Clemmys theobaldi* – This is the anterior half of a shell from the Miocene/Pliocene, Middle to Upper Siwaliks of Potwar Plateau, Jhand, Punjab, Pakistan (see Comments below) originally figured by Lydekker (1885a: pl. 20.2). Our illustrations mostly agree with those of Lydekker, but we disagree in the presence of a cervical and document the plastron for the first time. Most scutes are clearly visible, but only a few bones are apparent. It is clearly an adult specimen due to its large size (carapace length greater than 20 cm). There are no signs of carapacial keels or growth annuli marks. The cervical scute is present and as long as wide. The first vertebral scute is wider than long and exhibits an anterolateral constriction. The second and third vertebrals have rounded lateral margins. The anterior margin of the plastron is straight and lacks a median notch. The gular scutes are much longer than wide and completely intersect the entoplastron. The humeropectoral sulcus completely crosses the entoplastron posteriorly. The pectoro-abdominal sulcus does not intersect the hyo-hypoplastral suture.

IM E.90 (Fig. 29) – This is a nearly complete, previously unfigured shell from the Miocene/Pliocene, Middle to Upper Siwaliks of Potwar Plateau, Punjab, Pakistan. Old ontogenetic age combined with poor preservation of the surface makes it near impossible to discern most scutes and sutures. There are no signs of carapacial keels or growth annuli marks. The cervical scute is extremely reduced and placed between the first marginals. The gular scutes are much longer than wide.

IM E.92 (Fig. 30), holotype of *Clemmys punjabiensis* – This specimen was collected from the Miocene/Pliocene, Middle to Upper Siwaliks of Potwar Plateau, Punjab, Pakistan, and was initially figured and

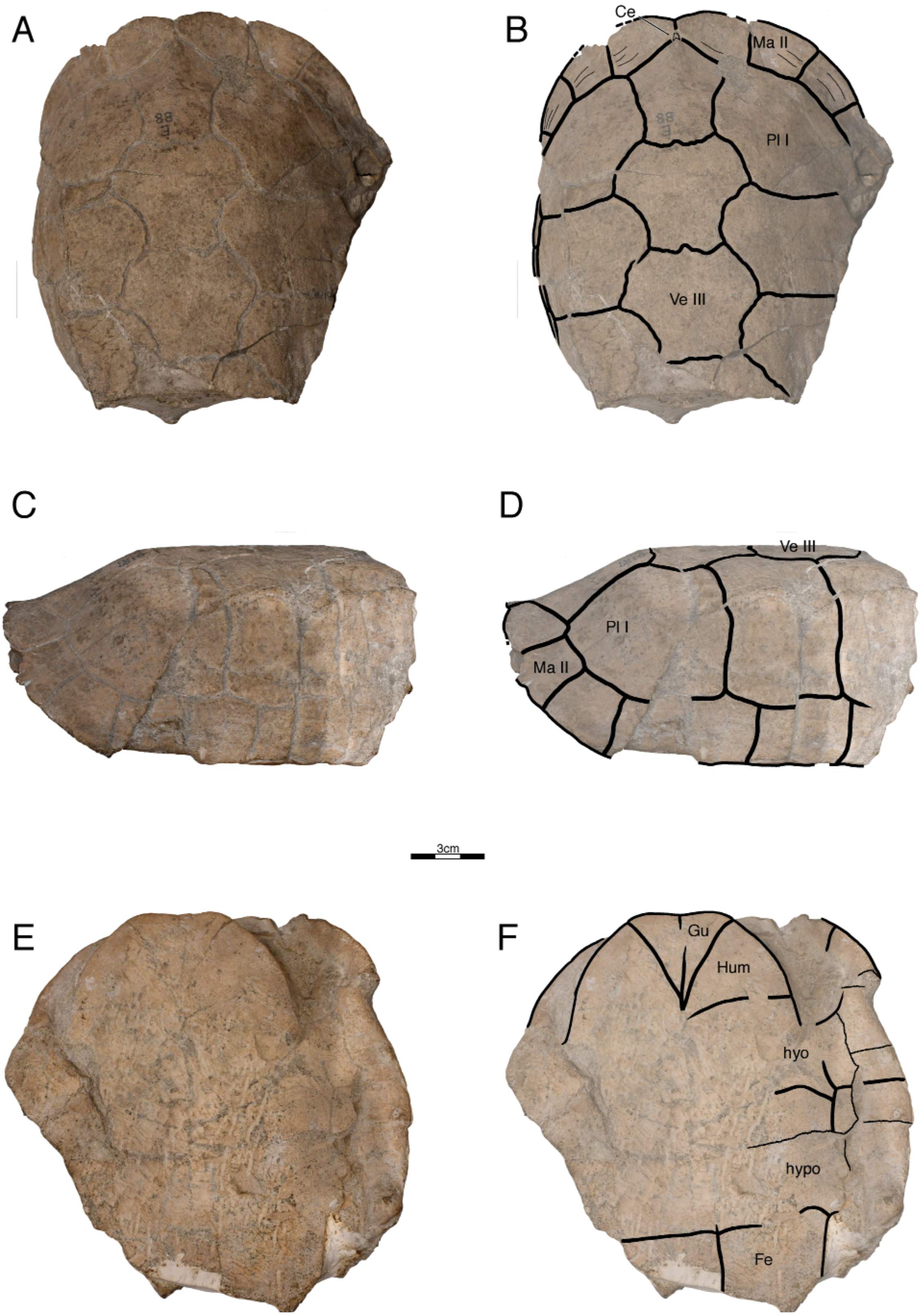

Fig. 27. IM E.88, holotype of *Bellia sivalensis* Theobald, 1877, here identified as *Melanochelys sivalensis* (Theobald, 1877) comb. nov. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of carapace in lateral view. **D**. Illustration of carapace in lateral view. **E**. Photograph of plastron. **F**. Illustration of plastron. Scale bar: 3 cm.

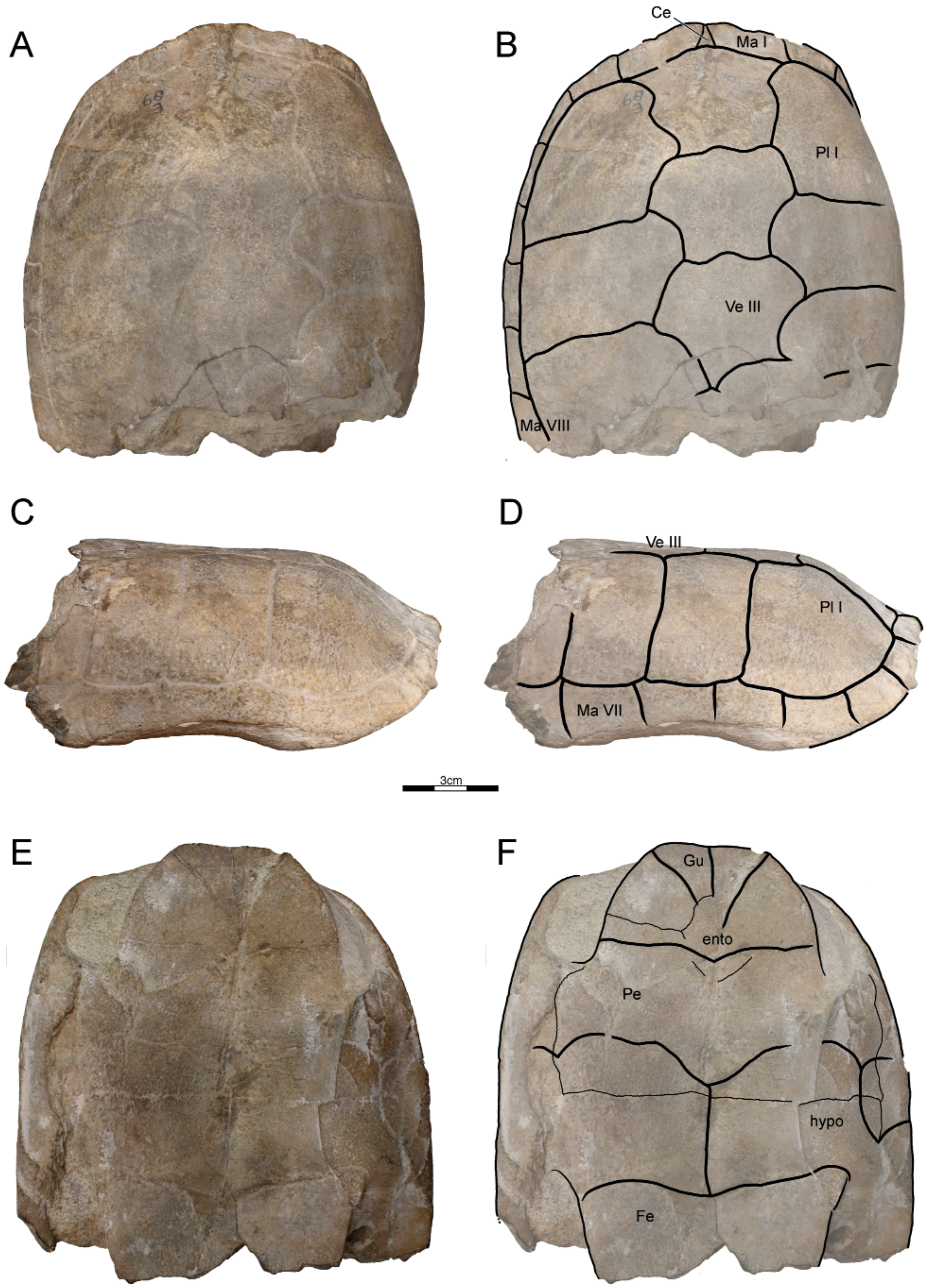

Fig. 28. IM E.89, holotype of *Clemmys theobaldi* Lydekker, 1885, here identified as *Melanochelys sivalensis* (Theobald, 1877) comb. nov. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of carapace in lateral view. **D**. Illustration of carapace in lateral view. **E**. Photograph of plastron. **F**. Illustration of plastron. Scale bar: 3 cm.

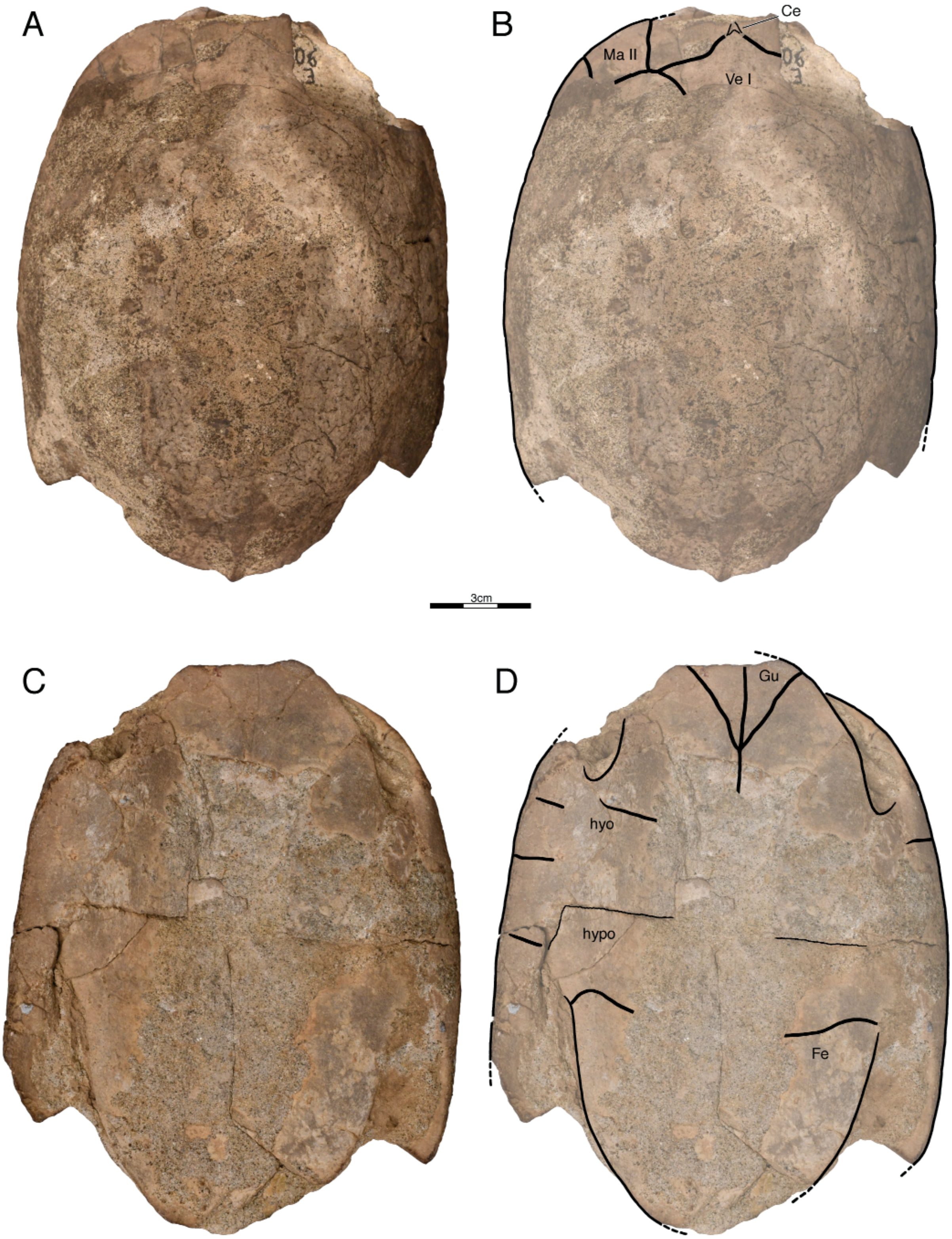

Fig. 29. IM E.90, referred to *Clemmys sivalensis* (Theobald, 1877) by Lydekker (1885a), here identified *Melanochelys sivalensis* (Theobald, 1877) comb. nov. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

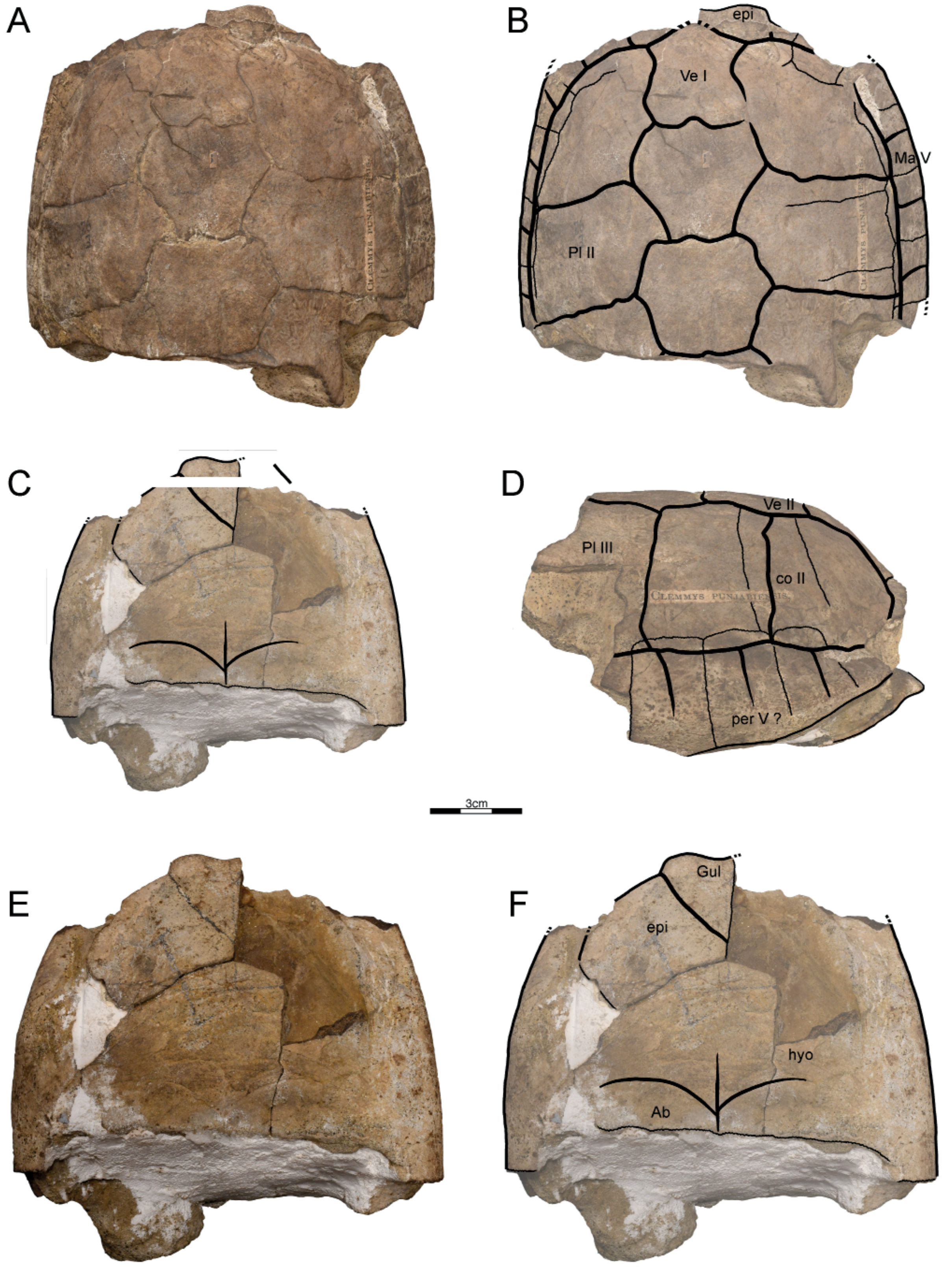

Fig. 30. IM E.92, holotype of *Clemmys punjabiensis* Lydekker, 1885, here identified *Melanochelys sivalensis* (Theobald, 1877) comb. nov. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of carapace in lateral view. **D**. Illustration of carapace in lateral view. **E**. Photograph of plastron. **F**. Illustration of plastron. Scale bar: 3 cm.

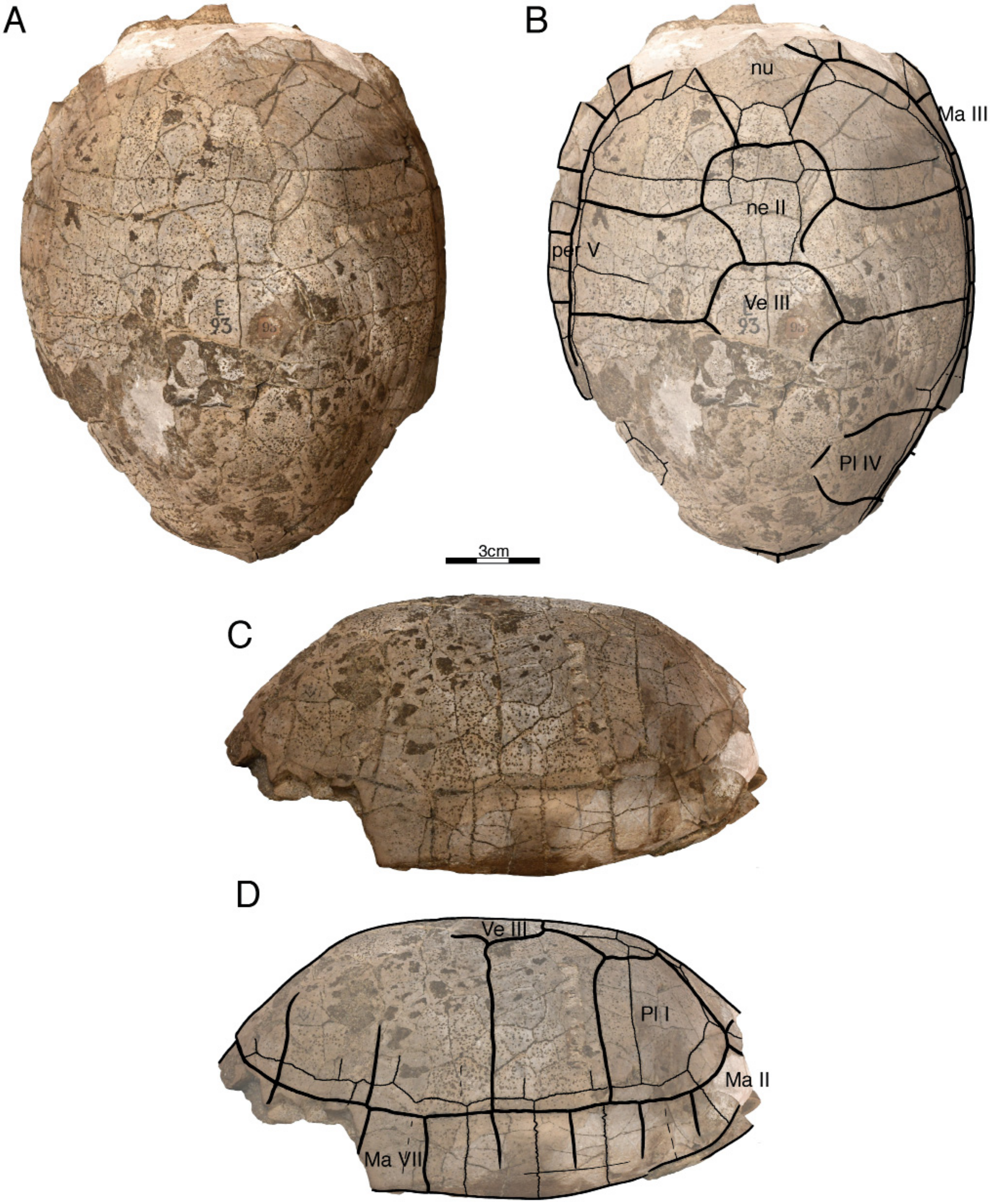

Fig. 31. IM E.93, holotype of *Clemmys hydaspica* Lydekker, 1885, here identified as *Melanochelys sivalensis* (Theobald, 1877) comb. nov. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of carapace in lateral view. **D**. Illustration of carapace in lateral view. Scale bar: 3 cm.

described by Lydekker (1885a: pl. 20.3). Our observations of this specimen overall confirm those of Lydekker, although we document some addition sutures. The specimen represents the anterior half of a carapace and articulated fragments of the plastron, and likely represents an adult specimen due to its larger size (carapace length greater than 15 cm). Scutes are clearly discernable, but sutures are restricted to the periphery of the specimen. No carapacial keels or growth annuli marks are visible. The first vertebral scute is as long as wide and has an anterolateral constriction. The second and third vertebral scutes have semi-sinuous lateral margins. The anterior plastral margin is concave. The gular scute is longer than wide. The pectoro-abdominal sulcus does not intersect the hyo-hyoplastral suture.

IM E.93 (Fig. 31), holotype of *Clemmys hydaspica* – This specimen consists of a nearly complete carapace and an articulated partial plastron from the Miocene/Pliocene, Middle to Upper Siwaliks of Potwar Plateau, Jhelum district, Punjab, Pakistan. The figures provided by Lydekker (1885a: pl. 20.4) overall agree with our figure, although we see more details in some areas, but less in others. This is a well-preserved specimen that clearly documents most sulci, but only some sutures. It is likely an adult specimen due to its large size (carapace length greater than 15 cm). The plastron is highly damaged and provides no information and we therefore do not figure it. There are no signs of carapacial keels or growth annuli marks. The first vertebral scute is wider than long and has straight lateral margins. The second and third vertebral scute have convex anterolateral and concave posterolateral sides. The sulcus between the first and second pleural, and the second and third pleural contact the fourth and sixth marginal scutes, respectively. The first neural bone only contacts the second costal on the right side, which is probably an anomaly.

Comments

Two of five specimens listed in this section originate from "south of Jhand" (Lydekker 1885a). We were able to locate three places called J(h)and in the Punjab of Pakistan and India: the large town of J(h)and in Attock District, Pakistan, the village of J(h)and in Chakwal District, Pakistan and the village of J(h)and in Jalandhar District, India. The two locations in Pakistan are surrounded by sedimentary exposures that have yielded fossils of Siwaliks age, while the Indian location is located in a flood plain lacking such exposures. We therefore are highly confident that the type locality is positioned in the Punjab of Pakistan. See Discussion for further details regarding the referral of this material to *Melanochelys sivalensis*.

Melanochelys tapani nom. nov.
Fig. 32

Nicoria tricarinata var. *sivalensis* Lydekker, 1889b: 100.
Geoemyda tricarinata Smith, 1931: 95.
Melanochelys tricarinata TEWG, 2015: e.46.

Type

BMNH 39839, a near complete fossil shell (Fig. 32).

Differential osteological diagnosis using shell characters

Melanochelys tapani can be differentiated from other *Melanochelys* species by the following combination of characters: presence of three carapacial keels, a highly domed shell, hexagonal second to fourth vertebrals that are wider than long, and a large cervical scute.

Etymology

The specific name is in honour of the late Prof. Tapan Roy Chowdhury of the Indian Statistical Institute, the distinguished teacher and researcher of Indian fossils, who established a school of vertebrate palaeontologists in India.

Material examined

Holotype

INDIA • Siwalik Hills; Miocene–Pliocene; BMNH 39839.

Type locality and horizon

Miocene/Pliocene of the Siwalik Hills, likely of India.

Description of type

BMNH 39839 (Fig. 32), holotype of *Melanochelys tapani* nom. nov. and subsequent holotype of *Nicoria tricarinata sivalensis* – This is an almost complete carapace associated with a partial plastron from the Miocene/Pliocene Siwalik Hills, likely of India, originally figured and described by Lydekker (1885a: pl. 21.4; 1889b: fig. 21). Our observation of this specimen overall confirms the observations of Lydekker (1889b), but we also illustrate the plastron and a less idealized carapace that lacks sutures (Fig. 32). A part of the anterior margin of the carapace and all posterior peripherals are missing. Total carapace length is approximately 17 cm. Most sulci are preserved on the carapace, but only very few on the plastron. Three longitudinal carapacial keels are present. The lateral keels are closer to the center of the carapace than to the borders. A cervical scute is present. The first vertebral scute is wider than long and contacts the first marginal scutes. The second to fifth vertebral scutes are about the same size and wider than long. The sulcus between the second pleural and third vertebral is straight. The sulcus between the second and third pleural contacts the fifth marginal scute. Most of the plastral surface is not preserved. The anterior plastron margin straight and lacks a median notch. The gular scutes are longer than wide. The pectoroabdominal sulcus contacts the sixth marginal scute.

Comments

See Discussion for further details.

Discussion

The vertebrate faunas from the Siwalik Group were first described over the course of the 19th century (see Lydekker 1885b, 1885c, 1886b, 1886c, 1887, 1889b for summary).

Turtles were initially believed to represent countless species that are closely related to, although different from, extant turtles that currently inhabit the region (e.g., Falconer & Cautley 1837, 1844; Lydekker 1885b, 1885c, 1886b, 1886c, 1887), but then mostly thought to represent fossil representatives of extant taxa (Boulenger 1889; Lydekker 1889b; Smith 1931; Das 1991, 1994). The resulting synonymies are recognized until today in taxonomic lists (e.g., TEWG 2015; TTWG 2017) and are in broad agreement with molecular studies that suggest that most geoemydids species from the Indian subcontinent originated before or during the Middle Miocene–Pliocene (i.e., Middle Siwaliks age; Pereira *et al.* 2017).

In contrast to many other groups of vertebrates, however, the geoemydids from the Siwalik Group have not been thoroughly revised from a taxonomic and morphologically perspective in at least a century (e.g., Boulenger 1889; Lydekker 1889a, 1889b) and their identification is therefore in need of a review that addresses recent updates in turtle taxonomy and paleontology (e.g., McDowell 1964; Gaffney 1975; Gaffney & Meylan 1988; Joyce *et al.* 2004). Such a review is especially needed, as the vast majority of specimens has not yet been documented using modern standards of photography and illustrating

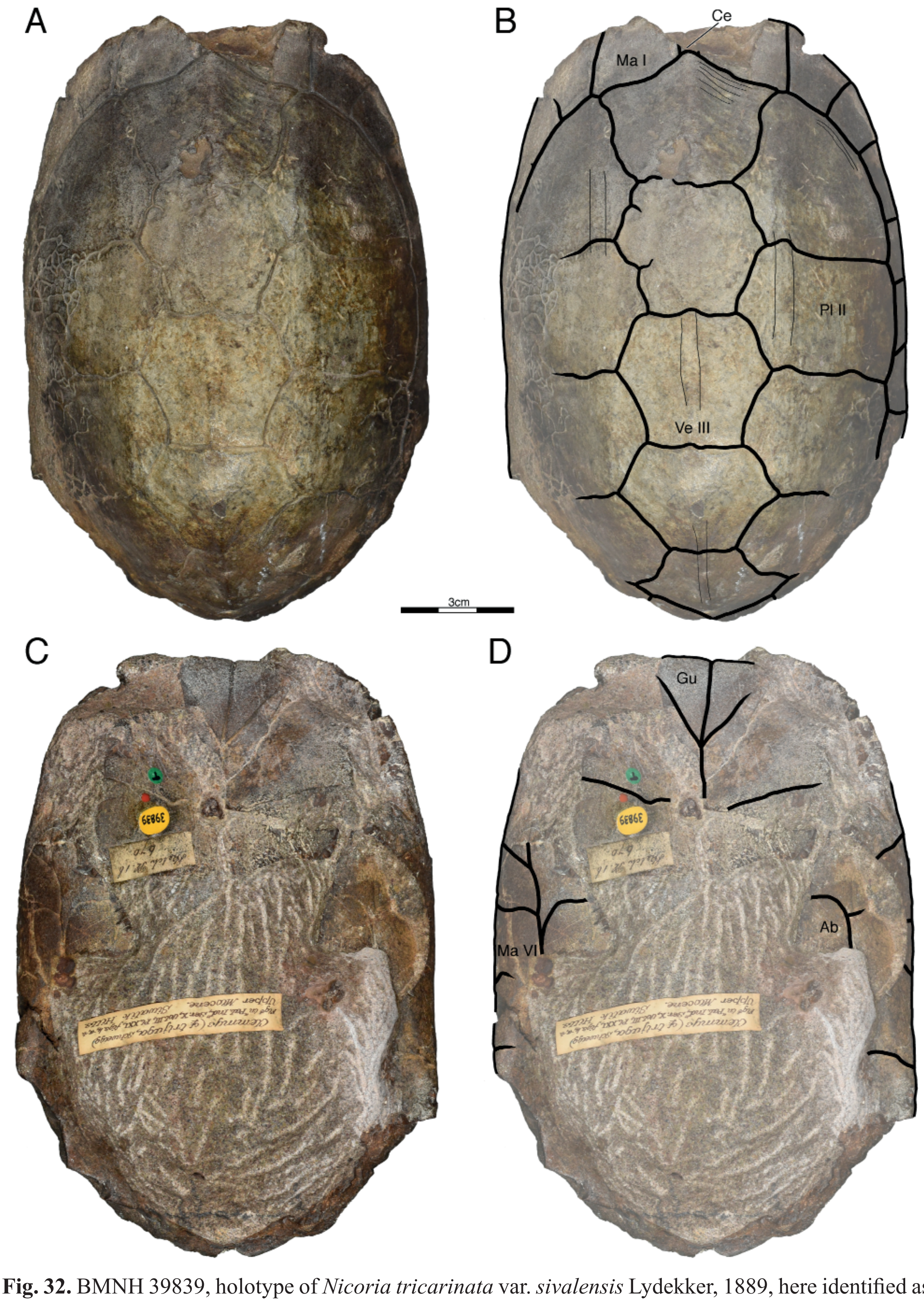

Fig. 32. BMNH 39839, holotype of *Nicoria tricarinata* var. *sivalensis* Lydekker, 1889, here identified as *Melanochelys tapani* nom. nov. **A**. Photograph of carapace. **B**. Illustration of carapace. **C**. Photograph of plastron. **D**. Illustration of plastron. Scale bar: 3 cm.

techniques. Instead, only some specimens are documented in the form of often idealized lithographic drawings that were likely produced by artists, not morphologists, as was common in the course of the 19th century (e.g., Anquetin & Joyce 2014 for other examples). From a palaeontological point of view, this review is challenging because there is a lack of precise information on the origin and age of nearly all material (e.g., “Siwalik Hills”).

Today, 17 species of geoemydids occur in India and Pakistan (TTWG 2017), the two countries that yielded the fossil material being discussed herein: 10 palatochelydian species (e.g., *Batagur baska*, *B. dhongoka* and *B. kachuga*, *Pangshura smithii*, *P. sylhetensis*, *P. tentoria* and *P. tecta*, *Geoclemys hamiltonii*, *Hardella thurjii* and *Morenia petersi*), two species of *Cuora* Gray, 1856 (*C. amboinensis* and *C. mouhotii*), two species of *Cyclemys* (*C. fusca* and *C. gemeli*), two species of *Melanochelys* (*M. tricarinata* and *M. trijuga*), and *Vijayachelys silvatica*. With the notable exception of *Pangshura tatrotia*, all fossil geoemydid specimens from the Siwalik-age were previously assigned to extant Indian species. We here suggest instead that 10 of 29 revised specimens can only be diagnosed to the generic or higher levels and that the remainder can be assigned to a mix of extinct and extant lineages. We for simplicity discuss groups of fossils below by taxon.

Indeterminate specimens

The lack of diagnostic osteological characters, the identification of specimens based on their provenance, the description of turtle species based solely on external morphology, and high amounts of shell polymorphism in geoemydids are some of the reasons for the previous misidentification of fossil turtles of Siwalik-age by naturalists. Here, we discuss why many of the fossils previously referred to species should instead be regarded in indeterminate.

Lydekker (1889b) refers BMNH R.329 (Fig. 4) to *Damonia hamiltonii* (= *Geoclemys hamiltonii*), but this right shell fragment does not possess the specific diagnostic characters of *G. hamiltonii*, in particular three longitudinal carapacial keels, neural bones with anterior short sides, an entoplastron intersected by the humeropectoral sulcus (Das & Bhupathy 2010). However, the presence of a large inguinal scute, a large bridge, a well-developed axillary buttress, and contact of the fifth marginal scute with the margin of the peripherals allows the attribution of BMNH R.329 to the clade Palatochelydia (Garbin *et al.* 2018). We therefore here identify this specimen as ‘Palatochelydia indet.’

Many incomplete shell fragments that exhibit small intercostal fontanelles were previously identified as *Hardella thurjii*, in particular BMNH R.603 (Fig. 5), BMNH R.958 (Fig. 6) and BMNH 16204 (Fig. 8). However, these specimens do not preserve any diagnostic characteristics of *H. thurjii*, such as a median carapacial keel, a strong gular inflection, and a large fourth vertebral scute. The attribution to this species is therefore not possible. The presence of a large bridge, a large inguinal scute, a well-developed axillary buttress and small intercostal fontanelles instead only allow us to refer these specimens to the clade Palatochelydia.

BMNH R.959 is a large specimen that only preserves the plastron (Fig. 7) and some associated peripherals (not shown). This specimen has previously been identified as *H. thurjii*, probably due to its enormous size (about 50 cm). BMNH R.959 clearly presents a large bridge, well-developed buttress, and an entoplastron that is not intersected by the humeropectoral sulcus. These characters are only sufficient, however, to identify it to the level of Palatochelydia indet.

Lydekker (1885a) discussed IM E.94 (Fig. 9) as possibly belonging to *Batagur falconeri*, a taxon that is now accepted as a synonym to *Hardella thurjii*, based on the presence of a short median keel and large second to fourth vertebral scutes, among other characteristics (see above). This carapace fragment shows only few bones, including a long neural III, a small protuberance on neural IV (probably a short median keel), a probably large second vertebral scute, and straight interpleural sulcus I and II. As these characters are not diagnostic for any geoemydid species in particular, we therefore identify this specimen as 'Palatochelydia indet.' based on the presence of neural bones with anterior short sides and a long neural III.

***Batagur cautleyi* from the Siwalik Hills**

Lydekker (1885a) described *Batagur cautleyi* based on two large specimens from the Siwalik Hills, likely of India (i.e., BMNH 39834 and IM E.178). Although IM E.178 preserves no sutures or sulci, both specimens resemble each other in the general shape of the carapace and may therefore reasonably represent the same species.

As noted by Lydekker (1885a), the holotype (BMNH 39834; Fig. 10) has a unique vertebral arrangement. The first vertebral is small, longer than wide, and has a slight lateral constriction (much wider in *Batagur baska* and larger in *Hardella thurjii*). The second vertebral of *Batagur cautleyi* is large, longer than wide, covers the first to third neural and has a straight posterior margin. This scute is as long as wide in *H. thurjii*, broader than long in *Batagur affinis* and *B. baska*, and has a long posterior process in *B. dhongoka*. The third vertebral of *Batagur cautleyi* is much longer than wide, covers the third to fifth neural, and has a small process on the posterior margin. This element is as wide as long in *H. thurjii*, broader than long in *B. affinis* and *B. baska*, and covers the third to fourth neural in *B. trivittata, B. kachuga* and *B. dhongoka*. The fourth vertebral is much shorter than all other vertebrals and almost as long as wide. This element is the same size as other vertebrals in *H. thurjii*, but shorter in *B. baska* and *B. affinis*. The fifth vertebral of *Batagur cautleyi* is not fully preserved, but it shows an anterior constriction, which is variable in *B. affinis* and *B. baska,* and present in *H. thurjii*.

These comparisons suggest that *Batagur cautleyi* is distinct from recent species of *Batagur* and *Hardella thurjii*. Nevertheless, Boulenger (1889) suggested synonymy of *B. cautleyi* with *Hardella thurjii*, a synonymy that was followed by Lydekker (1889a) and that is accepted until today (TEWG 2015; TTWG 2017). Here, we conclude that *B. cautleyi* (Fig. 10) differs substantially from *H. thurjii* (Figs 2D, 3D) not only in the shape of the vertebrals, but also by having a straight, not notched, anterior plastral margin, by lacking a strong inflection at the gulohumeral sulcus, by having much wider gular scutes, and much shorter anterior and posterior plastral lobes. We, therefore, find a relationship more likely with extant representatives of *Batagur*, in particular *Batagur affinis* and *Batagur baska*.

A few factors hinder us from resolving the alpha taxonomy of *Batagur cautleyi* with confidence. First, our sample of extant geoemydids does not include representatives of *Batagur baska*, but rather only *Batagur affinis*. We are, therefore, not able to differentiate *Batagur cautleyi* from *Batagur baska* with rigor. Second, although the two specimens that make up the type series of *Batagur cautleyi* resemble each other in most general aspects, both show enough variation to cast doubt if they represent the same taxon, a fact that is underlined by their poorly resolved temporal provenance. At the same time, however, the morphology of both specimens is greatly obscured by lacking preparation, fusion, and damage. We therefore here cautiously regard *Batagur cautleyi* as a *nomen dubium*, but note that future finds may well re-establish the validity of this taxon.

The potential presence of a close fossil relative of *Batagur baska* or *Batagur affinis* ('*Batagur* sensu stricto') in the central range of the Siwaliks has interesting biogeographic consequences, as *Batagur baska* is today distributed much further to the east in eastern India and Bangladesh (Ganges-Brahmaputra delta region) and south Myanmar (Irrawaddy delta region; TTWG 2017) and *Batagur affinis* even further eastward in Southeast Asia (Cambodia, Indonesia, Malaysia and Thailand; TTWG 2017). This may therefore imply that this lineage was formerly present much further to the west (see Biogeographical Implications section).

A third specimen, IM E.176 (Fig. 11), which has never been reported in the literature before, is quite distinct in its morphology. IM E.176 has an arrangement of vertebral scutes similar to BMNH 39834, in particular by having large second and third vertebral scutes, and a fourth vertebral scute that is much shorter than the others. This specimen was herein identified as belonging to the genus *Batagur*, but we could not confirm its identification to species level due to its unique variation. Perhaps, this specimen could belong to same species as BMNH 39834 and IM E.178, but due to the complete lack of information on its provenance and previous identification, we do not propose further actions.

Pangshura specimens

Pangshura is represented by four extant species (i.e., *Pangshura smithii*, *P. tentoria*, *P. tecta* and *P. sylhetensis*) and *Pangshura tatrotia*, an extinct species described from a single specimen from the Tatrot formation in the Upper Siwaliks (Le *et al.* 2007; Joyce & Lyson 2010; TTWG 2017). The extant species of *Pangshura* are distributed today across areas where Siwalik-age sediments were deposited in the past (Fig. 1; Valdiya 2010; Nanda *et al.* 2018).

Lydekker (1885a) recognized three Siwalik-age specimens as *Pangshura*, of which he referred two, IM E.110 and BMNH 39837, to *Pangshura flaviventer* Günther, 1864 (= *Pangshura tentoria flaviventer*), but the third, BMNH 17435, only to *Pangshura* sp., as he could not identify this specimen beyond generic level. He soon after referred both specimens to *Pangshura tecta* (Lydekker 1889b). In this study we encountered many challenges while revising the identification of these three specimens and we reiterated Lydekker (1885a: 185–186) about the *Pangshura* of the Siwaliks: "In a group like the present whose existing members exhibit a large amount of variation, it is extremely difficult to come to a conclusion as to what characters in a fossil should be regarded as of specific and what merely of individual value." We here nevertheless explain our decision to identify all *Pangshura* specimens to the exception of the holotype of *P. tatrotia* as *Pangshura* sp.

Lydekker (1885a) referred IM E.110 (Fig. 18) from the Narmada valley (Fig. 1) and BMNH 39837 (Fig. 16) from the Siwaliks Hills to *Pangshura flaviventer* based on the general contour of the shell and the shape of the second and third vertebral scutes, and by comparing the fossils with Recent specimens in the collections of BMNH. In the course of the last century, *Pangshura flaviventer* has been synonymized with many species (Boulenger 1889, 1890; Smith 1931; Mertens 1969), but today is considered a subspecies of *Pangshura tentoria* distributed across northeastern India (TTWG 2017). Nevertheless, IM E.110 and BMNH 39837 can be differentiated from *Pangshura tentoria flaviventer* by the shape of the first vertebral (bell-shaped, constricted anterolaterally, but larger posteriorly in *P. t. flaviventer* (Günther 1864), and the shape of the second vertebral that is hexagonal but much narrower behind in *P. t. flaviventer* (hexagonal, as broad as long in IM E.110 and hexagonal, longer than broad in BMNH 39837).

IM E.110 and BMNH 39837 furthermore cannot be attributed to the closely related species as *Pangshura tecta*, *Pangshura smithii*, *Pangshura sylhetensis* or the newly described Siwalik species, *Pangshura tatrotia*. *Pangshura tecta*, despite polymorphism, can be diagnosed by to the presence of a first vertebral that is constricted posterolaterally (character not preserved in BMNH 39837, the first vertebral is constricted anterolaterally in IM E.110), a posteriorly strongly constricted second vertebral that is longer than the third vertebral (absent in both fossil), and a fourth vertebral scute that is strongly bottlenecked anteriorly (likely present in BMNH 39837, but absent in IM E.110). *Pangshura tatrotia* shares the shape of the second and fourth vertebral scute with *P. tecta* (Joyce & Lyson 2010), but has a first vertebral scute that is constricted anterolaterally (not preserved in BMNH 39837, present in IM E.110) and a much wider third vertebral scute (absent in both specimens; Smith 1931; Ernst & Barbour 1989; Joyce & Lyson 2010). *Pangshura smithii* and *Pangshura sylhetensis*, finally, have a second vertebral that is short, hexagonal and overlaps only two neurals and a third vertebral that is sub-rectangular with parallel lateral margins, which differs significantly from the long hexagonal second vertebral of both IM E.110 and BMNH 39837 and the posterior convergent third vertebral of IM E.110.

BMNH 17435 (Fig. 17) was referred by Lydekker (1885a) to *Pangshura* sp., as the author could not identify this specimen to species level due to the distinctness of the specimen. This specimen from the Siwalik Hills of India indeed has a very particular arrangement of vertebral scutes: the first vertebral scute has straight lateral margins and lacks constriction (constricted anteriorly/posteriorly in *P. tecta*, *P. tentoria* and *P. tatrotia*); the second vertebral scute hexagonal, constricted anteriorly, as long as broad, and has short posterior sides (the lateral sides are of equal length and never with anterior constriction in any other *Pangshura* species; broader than long in *P. smithii*); the third vertebral scute is pentagonal, has straight parallel lateral margins and a posterior projection into the fourth vertebral (not posteriorly constricted as *P. tecta*, *P. tatrotia* and *P. tentoria*, but rather subrectangular as in *P. smithii*); the fourth vertebral scute has a broad anterior margin and lacks an anterior constriction (always with some degree of constriction in *P. tecta*, *P. tatrotia* and *P. tentoria*; anterior margin as broad as *Batagur kachuga*).

IM E.110 differs from the other two specimens by having been collected from the late Late Pleistocene deposits of the Central Narmada Valley. This part of India is currently inhabited by *Pangshura tecta* only (TTWG 2017). Although we note differences with this species above, IM E.110 is nevertheless broadly consistent with this taxon. Using temporal and spatial considerations, we therefore here speculate that IM E.110 probably represents a slightly deviant polymorphic subfossil of *Pangshura tecta*.

The other two specimens, BMNH 17435 and BMNH 39837, originate from the Miocene/Pliocene Siwalik Hills of India. The majority of extant *Pangshura* inhabit this region until today and it is therefore likely that the Siwalik Hills document the diversification of this lineage, which is predicted to have taken place over the course of the Neogene (Pereira *et al.* 2017). Although both specimens can be differentiated from all other named species, we here refrain from naming new fossil taxa, because 1) they are incomplete, 2) their age is poorly constrained, 3) extant *Pangshura* are known to be highly variable, and 4) because the taxa they may represent is only known from a single specimen. We find this approach preferable to the naming of poorly diagnosed species of uncertain age.

Melanochelys sivalensis **from the Siwaliks of Punjab, Pakistan**

Theobald (1877) and Lydekker (1885a) combined named four fossil species of "*Clemmys*" based on specimens from the Siwaliks of Punjab, Pakistan, in particular *Clemmys* (= *Bellia*) *sivalensis*, *Clemmys theobaldi*, *Clemmys punjabiensis* and *Clemmys hydaspica*. Lydekker (1889a) synonymized *Clemmys punjabiensis* with *Clemmys theobaldi* and *Clemmys hydaspica* with *Clemmys sivalensis*, and assigned then the two valid species to *Bellia*, as *Bellia theobaldi* Lydekker, 1889 and *Bellia sivalensis* (Table 1). Smith (1931) recognized the synonymy of the *Clemmys* from Lydekker with *Geoemyda*, but only specifically synonymized *Clemmys theobaldi* with the extant *Geoemyda trijuga* (now *Melanochelys trijuga*). These acts of synonymy were interpreted in the literature as if all species of *Clemmys* from Lydekker had been synonymized with *Melanochelys trijuga* (Das & Bhupathy 2009b; TEWG 2015), which were furthermore synonymized to *Melanochelys trijuga indopeninsularis* based on their provenance (TEWG 2015).

We agree with Smith (1931) that the five specimens discussed by Theobald (1877) and Lydekker (1889a) from the Siwaliks of Punjab can be assigned to *Melanochelys* (his *Geoemyda*) based on the shape of the vertebral scutes, presence of an entoplastron intersected by the humeropectoral sulcus, gular scutes that are longer than wide, and the general size and shape of the carapace (Figs 27–31). We also agree with Smith (1931) and TEWG (2015) that the Punjab fossils resemble the extant *Melanochelys trijuga* in having a small cervical scute, long triangular shaped gular scutes, and a first vertebral scute with a lateral constriction. However, the fossils clearly differ from *Melanochelys trijuga* by lacking longitudinal

Table 1 (continued on next three pages)**.** Species identification of Siwalik-age specimens through time.

Specimen	Figure	Theobald (1877)	Lydekker (1885a)	Lydekker (1886a)	Lydekker (1889a)
BMNH 16204	8				
BMNH 17435	17		referred to *Pangshura* sp.		
BMNH 39834	10		*Batagur cautleyi*, holotype		*Hardella thusgi*
BMNH 39835	19		*Batagur falconeri*, holotype		*Hardella thusgi*
BMNH 39835a	12		*Batagur bakeri*, holotype		*Kachuga lineata*
BMNH 39837	16		referred to *Pangshura flaviventer* Günther, 1864		*Kachuga teetum*
BMNH 39838	22		*Clemmys palaeindica*, holotype		*Damonia hamiltoni*
BMNH 39839	32				
BMNH 39840	23		referred to *Clemmys palaeindica*		*Damonia hamiltoni*
BMNH 39841	14		*Batagur durandi,* holotype		*Kachuga dhongoka*
BMNH 39842	24				
BMNH R.329	4				
BMNH R.603	5				
BMNH R.748	20			*Clemmys watsoni*, holotype	*Hardella thusgi*
BMNH R.887	25				
BMNH R.890	21				
BMNH R.891	13				
BMNH R.892	26				
BMNH R.958	6				
BMNH R.959	7				
IM E.88	27	*Bellia sivalensis*, holotype	*Clemmys sivalensis*		*Bellia sivalensis*
IM E.89	28		*Clemmys theobaldi*, holotype		*Bellia theobaldi*
IM E.90	29		referred to *Clemmys sivalensis*		*Bellia sivalensis*
IM E.92	30		*Clemmys punjabiensis*, holotype		*Bellia theobaldi* (Lydekker, 1885)
IM E.93	31		*Clemmys hydaspica*, holotype		*Bellia sivalensis* (Theobald, 1877)
IM E.94	9		referred to *Batagur falconeri*		*Hardella thusgi*
IM E.110	18		referred to as *Pangshura flaviventer* Günther		*Kachuga teetum*
IM E.176	11				
IM W19/173	15				
MCASG A/665	–				
GSI 18091	–				
YPM 4127	–				

Table 1 (continued)**.** Species identification of Siwalik-age specimens through time.

Specimen	Lydekker (1889b)	Smith (1931)	Prasad & Satsangi (1967)	Tewari & Badam (1969)
BMNH 16204	referred to *Hardella thurgi* (Gray, 1831)			
BMNH 17435	referred to *Kachuga* sp.			
BMNH 39834	referred to *Hardella thurgi* (Gray, 1831a)	*Hardella thurgi*		
BMNH 39835	referred to *Hardella thurgi* (Gray, 1831a)	*Hardella thurgi*		
BMNH 39835a	referred to *Kachuga lineata* (Gray, 1831a)			
BMNH 39837	referred to *Kachuga tectum* (Gray, 1831a)			
BMNH 39838	referred to *Damonia hamiltoni* (Gray 1830)	*Geoclemys hamiltoni*		
BMNH 39839	*Nicoria tricarinata sivalensis*, holotype	*Geoemyda tricarinata*		
BMNH 39840	referred to *Damonia hamiltoni* (Gray 1830)			
BMNH 39841	referred to *Kachuga dhongoka* (Gray, 1832)	*Kachuga dhongoka*		
BMNH 39842	referred to *Damonia hamiltoni* (Gray 1830)			
BMNH R.329	referred to *Damonia hamiltoni* (Gray 1830)			
BMNH R.603	referred to *Hardella thurgi* (Gray, 1831a)			
BMNH R.748	referred to *Hardella thurgi* (Gray, 1831a)	*Hardella thurgi*		
BMNH R.887	referred to *Damonia hamiltoni* (Gray 1830)			
BMNH R.890	referred to *Hardella thurgi* (Gray, 1831a)			
BMNH R.891	referred to *Kachuga lineata* (Gray, 1831a)			
BMNH R.892	referred to *Damonia hamiltoni* (Gray 1830)			
BMNH R.958	referred to *Hardella thurgi* (Gray, 1831a)			
BMNH R.959	referred to *Hardella thurgi* (Gray, 1831a)			
IM E.88		*Geoemyda sivalensis*		
IM E.89		*Geoemyda trijuga*		
IM E.90		*Geoemyda sivalensis*		
IM E.92		*Geoemyda trijuga*		
IM E.93		*Geoemyda sivalensis*		
IM E.94				
IM E.110				
IM E.176				
IM W19/173				
MCASG A/665				*Geoclemys sivalensis*, holotype
GSI 18091			*Geoemyda pilgrimi*, holotype	
YPM 4127				

Table 1 (continued)**.** Species identification of Siwalik-age specimens through time.

Specimen	Das (1991)	Das (1994)	Joyce & Lyson (2010)	TEWG (2015)
BMNH 16204				
BMNH 17435				
BMNH 39834				*Hardella thurjii*
BMNH 39835				*Hardella thurjii*
BMNH 39835a				*Batagur kachuga*
BMNH 39837				
BMNH 39838				*Geoclemys hamiltonii*
BMNH 39839				*Melanochelys tricarinata*
BMNH 39840				
BMNH 39841				*Batagur dhongoka*
BMNH 39842				
BMNH R.329				
BMNH R.603				
BMNH R.748				*Hardella thurjii*
BMNH R.887				
BMNH R.890				
BMNH R.891				
BMNH R.892				
BMNH R.958				
BMNH R.959				
IM E.88				*Melanochelys trijuga indopeninsularis* (Annandale, 1913)
IM E.89				*Melanochelys trijuga indopeninsularis* (Annandale, 1913)
IM E.90				
IM E.92				*Melanochelys trijuga indopeninsularis* (Annandale, 1913)
IM E.93				*Melanochelys trijuga indopeninsularis* (Annandale, 1913)
IM E.94				
IM E.110				
IM E.176				
IM W19/173				
MCASG A/665	*Geoclemys hamiltonii*			*Geoclemys hamiltonii*
GSI 18091		*Hardella thurjii*		*Hardella thurjii*
YPM 4127			*Pangshura tatrotia*, holotype	*Pangshura tatrotia*

Table 1 (continued)**.** Species identification of Siwalik-age specimens through time.

Specimen	TTWG (2017)	This study
BMNH 16204		Palatochelydia indet.
BMNH 17435		*Pangshura* sp.
BMNH 39834	*Hardella thurjii*	*Batagur* sp.
BMNH 39835	*Hardella thurjii*	*Hardella thurjii*
BMNH 39835a	*Batagur kachuga*	*Batagur kachuga*
BMNH 39837		*Pangshura* sp.
BMNH 39838	*Geoclemys hamiltonii*	*Geoclemys hamiltonii*
BMNH 39839	*Melanochelys tricarinata*	*Melanochelys puri*
BMNH 39840		*Geoclemys hamiltonii*
BMNH 39841	*Batagur dhongoka*	*Batagur dhongoka*
BMNH 39842		*Geoclemys hamiltonii*
BMNH R.329		Palatochelydia indet.
BMNH R.603		Palatochelydia indet.
BMNH R.748	*Hardella thurjii*	*Hardella thurjii*
BMNH R.887		*Geoclemys hamiltonii*
BMNH R.890		*Hardella thurjii*
BMNH R.891		*Batagur kachuga*
BMNH R.892		*Geoclemys hamiltonii*
BMNH R.958		Palatochelydia indet.
BMNH R.959		Palatochelydia indet.
IM E.88	*Melanochelys trijuga indopeninsularis* (Annandale, 1913)	*Melanochelys sivalensis*
IM E.89	*Melanochelys trijuga indopeninsularis* (Annandale, 1913)	*Melanochelys sivalensis*
IM E.90		*Melanochelys sivalensis*
IM E.92	*Melanochelys trijuga indopeninsularis* (Annandale, 1913)	*Melanochelys sivalensis*
IM E.93	*Melanochelys trijuga indopeninsularis* (Annandale, 1913)	*Melanochelys sivalensis*
IM E.94		Palatochelydia indet.
IM E.110		*Pangshura* sp.
IM E.176		*Batagur* sp.
IM W19/173		*Batagur dhongoka*
MCASG A/665	*Geoclemys hamiltonii*	*Geoclemys hamiltonii*
GSI 18091	*Hardella thurjii*	*Hardella thurjii*
YPM 4127	-	*Pangshura tatrotia*

carapacial keels, having a dense and round ‘boxy’ shell structure, and by exhibiting broader vertebral scutes that have concave anterolateral margins. We therefore feel justified in recognizing a separate, extinct taxon in the Mio/Pliocene of the Siwaliks of Punjab, *Melanochelys sivalensis* (Theobald, 1877), through synonymizing the four original *Clemmys* species of Lydekker.

Among the material we refer to *Melanochelys sivalensis*, we note that IM E.93 (Fig. 31), the holotype of *Clemmys hydaspica*, differs from the others by lacking a constriction on the lateral margin of the first vertebral, having more rounded ‘mushroom-shaped’ second and third vertebrals and an oval carapace shape. This specimen originates from the eastern part of the Potwar Plateau and may therefore reasonably sample a different time interval with the Siwalik Group. However, without additional material that confirms the persistent presence of this morphotype, we refer all of these specimens to *Melanochelys sivalensis*.

The molecular calibration analysis of Pereira *et al.* (2017) suggests that the divergence between the extant *Melanochelys tricarinata* and *Melanochelys trijuga* may have occurred during the Late Miocene (i.e., during Middle Siwalik-age). *Melanochelys sivalensis* may therefore either represent the stem lineage of the two recent species or the stem lineage of the genus. We are unfortunately not able to further explore these hypotheses, as *Melanochelys tricarinata* is not sampled in the most recent phylogenetic analysis of geoemydids (Garbin *et al.*, 2018) due to the unavailability of skeletal material.

Today, species of *Melanochelys* occur neither on the Potwar Plateau nor within the greater Indus River basin. Indeed, there is only one single, dubious record of an occurrence of *M. trijuga* in all of Pakistan (TTWG 2017). The large number of fossils of *Melanochelys* from the Potwar Plateau therefore firmly document the former presence of this lineage in this region and suggest that the range of *Melanochelys* expired there and contracted to the east over the course of the last one or two million years.

***Melanochelys tapani* nom. nov. from the Siwaliks Hills of India**

Lydekker (1885a) first reported the type specimen of *Melanochelys tapani* nom. nov. (Fig. 32) under the name *Clemmys cf. trijuga* and indicated that it might represent a fifth species of *Clemmys* from the Siwaliks. Later, Lydekker (1889b) described this specimen as a variation of the recent species *Melanochelys tricarinata* (Blyth, 1856), *Nicoria tricarinata* var. *sivalensis*, which must be considered to be an available subspecies name, even if it was initially phrased as a variety (ICZN 1999: Art. 10.2). We here agree with Lydekker (1889b) that the fossil specimen shows many similarities with the extant *Melanochelys tricarinata*, by exhibiting a more box-shaped shell, large cervical scute and wider than long vertebral scutes. However, we also note that the fossil differs from Recent material in the development of broad hexagonal second to fourth vertebrals. These elements are hexagonal but longer than wide in *M. trijuga* and broad, but with almost parallel lateral margins in *M. tricarinata*. We therefore feel justified in recognizing a separate, extinct taxon. Following the rule of coordination (ICZN 1999: Art. 46), the correct name for this taxon should be *Melanochelys sivalensis* (Lydekker, 1889), as Lydekker (1889b) established an available subspecies name. However, as this name is a secondary junior homonym with the herein recognized *Melanochelys sivalensis* Theobald, 1877, we here suggest the replacement name (ICZN 1999: Art. 60.3) *Melanochelys tapani* nom. nov. As noted above, we were not able to explore the phylogenetic relationships of fossil species of *Melanochelys* in a meaningful way, as even the most extensive available matrices (e.g., Garbin *et al.* 2018) lack *Melanochelys tricarinata* due to an overall lack of specimens. The overall tortoise-like shape of the shell of *Melanochelys tapani* nom. nov., a set of derived characters within geoemydids shared with *Melanochelys tricarinata*, combined with the presence of broad hexagonal vertebrals, a plesiomorphic character not shared with *Melanochelys trijuga*, allow us to hypothesize that *Melanochelys tapani* nom. nov. represents the stem lineage of *Melanochelys tricarinata*. However, the imprecise stratigraphic provenance does not allow us to propose a meaningful calibration data for the divergence of *Melanochelys*.

Melanochelys tricarinata today inhabits the forests that cover the Siwaliks of India and Nepal (TTWG 2017). The sediments exposed in the Siwalik Hills, however, were deposited in the Himalayan foreland basin before being uplifted to their current position (Nanda *et al.* 2018). This either suggests that *Melanochelys tapani* nom. nov. inhabited a different biotope, or, more likely, that the range of the extant *Melanochelys tricarinata* recently contracted to the Siwalik Hills through the human-induced deforestation of the current foreland basin.

Biogeographic implications

The 17 extant species of geoemydids that today occur in India and Pakistan have an uneven distribution across the Indian subcontinent (TTWG 2017), but little is known about the biogeographic evolution of the group. We, therefore, here provide brief comments.

The area just south of the central Siwalik belt of India and Nepal (Fig. 1) today hosts nine species of geoemydids, in particular *Batagur dhongoka*, *B. kachuga*, *Geoclemys hamiltonii*, *Hardella thurjii*, *Melanochelys tricarinata*, *M. trijuga*, *Morenia petersi*, *Pangshura smithii*, *P. tecta* and *P. tentoria* (TTWG 2017). We here refer fossils from the Siwalik Hills of India to the lineages of *Batagur dhongoka*, *B. kachuga*, *Geoclemys hamiltonii* and *Hardella thurjii* in particular as well as *Batagur* and *Pangshura* in general. The lack of detailed stratigraphic information, however, precludes making precise statements when these lineages first became established. *Melanochelys tapani* nom. nov. likely represents the stem lineage of the extant *Melanochelys tricarinata*. The two specimens of *Pangshura* from this region, BMNH 17435 (Fig. 17) and BMNH 39837 (Fig. 16), are too incomplete to allow detailed identification, but nevertheless document the lineage with confidence.

The great outlier we note in our sample of fossils from this region is the type series of *Batagur cautleyi* (BMNH 39834, Fig. 10 and IM E.176, Fig. 11), which suggests the former presence of a near relative of *Batagur baska* in northwestern India. We are only aware of two dubious records that mention the presence of *B. baska* in western India and Pakistan. In his description of *B. baska*, Murray (1884b) notes that this species occurs both along the Indus and Ganges Rivers. However, as this author does not list specimens or locaties, and as the species is not known to occur along the Indus River today (TTWG 2017), this 'record' must be regarded as doubtful. Praschag *et al.* (2008) recently confirmed using mtDNA that a specimen of *Batagur baska* reportedly collected from the Indus Delta of Sindh, Pakistan indeed is referrable to that species, but concluded as well that the provenience of this specimens is dubious, as the locality data of this historic specimen may reasonably have been swapped prior to its arrival at NMW. We agree with this assessment. A western distribution of the *Batagur baska* lineage should not be discarded entirely, however, but need to be confirmed by zooarchaeological specimens found along the Indus river valley. Until then, the type series of *Batagur cautleyi* can be considered the most western unambiguous documentation of the *Batagur* lineage.

The region around the Potwar Plateau of Pakistan, the most western part of the Siwaliks, is today inhabited by four species of geoemydid turtles, in particular *Geoclemys hamiltonii*, *Hardella thurjii*, *Pangshura tecta* and *Pangshura smithii* (TTWG 2017). The available sample of fossil turtles can only confirm the former presence of the *Pangshura* lineage in this region in the form of *Pangshura tatrotia*. The remaining two lineages, by contrast, have not yet been documented, but the absence of specimens should not be taken as evidence of absence. The vast majority of fossils from the Potwar Plateau document a single species, *Melanochelys sivalensis*, with unclear relationships with the two extant species of *Melanochelys*. Its occurrence nevertheless documents the former presence of the *Melanochelys* lineages in this region.

The southern Indus River valley and its delta in Pakistan are inhabited today by *Geoclemys hamiltonii*, *Hardella thurjii*, *Pangshura tecta* and *Pangshura smithii* (TTWG 2017), with dubious records registered from the Sind region for *Melanochelys trijuga* (TTWG 2017), *Batagur dhongoka* (Murray 1884b), *Batagur baska* (Praschag *et al.* 2008) and *Pangshura tentoria* (Murray 1884b, although the author here was probably referring to *Pangshura tecta* sensu strictu). As none of the fossil material analysed in this study is coming from southern Pakistan, we cannot confirm the presence of geoemydid species in the Sind region during Siwalik-age.

The tiny island of Piram is currently located in the Gulf of Cambay and is not inhabited by geoemydid turtles, but the rivers that drain into the Gulf are inhabited by *Melanochelys trijuga* and *Pangshura tecta* (TTWG 2017). There is no fossil evidence for either species on Piram Island. The former presence of *Hardella thurjii*, by contrast, is documented by at least one well-preserved shell (BMNH R.748) (Fig. 20) and further supported by larger fragments that lack the specific characteristics of *H. thurjii*, but that are nevertheless consistent with this taxon (i.e., BMNH R.958, Fig. 6 and BMNH R.603, Fig. 5). These finds therefore imply a significant range extension of *H. thurjii* from the Indus and Ganges drainage systems to the south.

Only two geoemydids currently occur in the central Narmada Valley of India, in particular *Pangshura tecta* and *Melanochelys trijuga* (TTWG 2017). The only fossil documented here from this region represents a subfossil from the latest Pleistocene, and likely documents the former presence of *P. tecta* in this region, but the fragmentary nature of this find precludes a more affirmative statement.

A number of turtles that currently inhabit the most eastern extremes of the Siwaliks are absent from our list of fossils, in particular *Cuora amboinensis, Cuora mouhotii, Cyclemys gemeli, Cyclemys fusca* and *Pangshura sylhentensis* (TTWG 2017). The same is true for *Vijayachelys sylvatica*, which today inhabits southern India (TTWG 2017). On the other hand, *Melanochelys trijuga*, *Pangshura smithii* and *Morenia petersi* do inhabit the central Siwalik today (TTWG 2015), but nevertheless are lacking in our sample of fossils. As the collection of fossil turtles in Siwalik age sediments has not occurred systematically, sampling of fossil turtles is certainly not complete. These summaries of negative evidence therefore do not provide biogeographic insights for the moment.

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Appendix

Key for the identification of adult Indian geoemydid turtles with regard of their shell

We created this key to simplify the identification of geoemydid shell specimens that occur since Miocene and as of today at the Indian subcontinent, belonging to the following species: *Batagur kachuga*, *Batagur dhongoka*, *Batagur baska*, *Cuora amboinensis*, *Cuora mouhotti*, *Cyclemys gemeli*, *Cyclemys fusca*, *Geoclemys hamiltonii*, *Hardella thurjii*, *Melanochelys trijuga*, *Melanochelys tricarinata*, *Morenia petersi*, *Pangshura tatrotia*, *Pangshura sylhetensis*, *Pangshura tecta*, *Pangshura smithii*, *Pangshura tentoria* and *Vijayachelys sylvatica*.

This key was created based on the scoring of characters from our matrix and should be used together with descriptions and illustrations from the literature (Boulenger 1889; Ernst & Barbour 1989; Das 1991, 1994) for correct identification. This key can only be used for adult shells deprived of horny scutes.

1. Carapace with three longitudinal keels 2
– Carapace without longitudinal keels or with a median keel only; carapace median length more than 150 mm 7

2. Neural bones III-VI hexagonal, with anterior short sides........... ***Geoclemys hamiltonii*** (Gray, 1830)
– Neural bones III–VI hexagonal, with posterior short sides 3

3. Presence of a plastral hinge 6
– Absence of a plastral hinge; pectoroabdominal sulcus and hyo-hypoplastron suture do not contact 4

4. Neural bone II hexagonal; pygal bone overlapped by fifth vertebral scute ....***Vijayachelys sylvatica*** (Henderson, 1912)
– Neural bone II octagonal; pygal bone not overlapped by fifth vertebral scute................................. 5

5. Second to fourth vertebral scutes longer than wide or as long as wide; cervical scute very small; longitudinal gutter on the lateral of the carapace formed by the uplift of peripherals ....***Melanochelys trijuga*** (Schweigger, 1812)
– Second to fourth vertebral scutes broader than long; first vertebral scute anteriorly wider; cervical scute large, carapace with straight lateral sides .... ***Melanochelys tricarinata*** Blyth, 1856

6. Carapace ovoid rounded on top; median vertebral keel weakly developed; posterior margin of the carapace not serrated .... ***Cuora amboinensis*** (Riche *in* Daudin, 1801)
– Carapace flattened between second and fourth vertebral scutes; anterior margin of the carapace slightly serrated; posterior margin of the carapace slightly serrated ....***Cuora mouhotii*** (Gray, 1862)

7. Entoplastron intersected by humeropectoral sulcus; plastral buttresses absent or very reduced.. ***Cyclemys*** Bell, 1834

– Entoplastron not intersected by humeropectoral sulcus; presence of well developed plastral buttresses.. 8

8. Presence of intercostal fontanelle in adults (sexually dimorphic); fourth to sixth marginal scutes can overlap adjacent costal bones 9
– Absence of intercostal fontanelle in adults; fourth to sixth marginal scutes never overlap costal bones ....***Morenia petersi*** Anderson, 1879

9. Long fourth vertebral scute, with its anterior margin over neural IV 10
– Short fourth vertebral scute, anterior margin crossing neural V.. 12

10. Fourth vertebral bottleneck anteriorly; neural IV octagonal .... ***Pangshura*** Gray, 1856
– Fourth vertebral straight laterally; neural IV hexagonal with anterior short-sides..........................11

11. Second vertebral scute with a strong process on posterior margin with invagination into third vertebral; gulohumeral sulcus forming a right angle; humeropectoral sulcus straight....................... ....***Batagur dhongoka*** (Gray, 1832)
– Second vertebral scute large, as long as wide, with straight lateral margins; third vertebral scute with lateral margin with posterior shorter side .... ***Batagur kachuga*** (Gray, 1831)

12. Fourth vertebral scute shorter than second and third vertebrals; anterior plastral margin straight; anal notch absent, or if present, in a wide angle...***Batagur baska*** (Gray, 1830)
– Carapace median keel present; fourth vertebral scute about the same length and width as second and third vertebrals; first vertebral wider posteriorly; strong gular inflection; anal notch rounded ....***Hardella thurjii*** (Gray, 1831)

13. Second vertebral scute much shorter than third vertebral, embracing two neural bones; posterior margin of carapace strongly serrated...***Pangshura sylhetensis*** Jerdon, 1870
– Second vertebral scute as long as broad, embracing three neural bones; posterior margin of fourth vertebral over neural VIII or posterior.. 14

14. Third vertebral scute much longer than wide, with almost parallel lateral margins........................... .... ***Pangshura smithii*** (Gray, 1863)
– Third vertebral scute pentagonal, pointed behind... 15

15. Second vertebral scute hexagonal to square/rectangular............***Pangshura tentoria*** (Murray, 1884)
– Second vertebral scute hexagonal, greatly constricted posteriorly... 16

16. First vertebral scute significantly constricted posteriorly....................***Pangshura tecta*** (Gray, 1830)
– First vertebral scute rectangular or anteriorly constricted .... ***Pangshura tatrotia*** Joyce & Lyson, 2010

17. Carapace elongated to rectangular; crown of the head brown, but not lighter than temporal region.. ....***Cyclemys gemeli*** Fritz, Guicking, Auer, Sommer, Wink & Hundsdorfer, 2008
– Carapace ovoid when viewed from above; crown of the head lighter than temporal region ....***Cyclemys fusca*** Fritz, Guicking, Auer, Sommer, Wink & Hundsdorfer, 2008