FOSSIL TURTLES AND CROCODILES FROM THE CAENOZOIC OF S-ASIA

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Editor's note

Preliminary words, explanations and excuses for the present publication seem to me unavoidable to find some understanding. And we are just publishing this monography for its unique character of a first comprehensive collection of material and data being dispersed widely even over continents. The history about all is that I myself was granted by Volkswagen foundation and DAAD (German Academic Exchange Service), also by Goethe Institut to lecture in Kathmandu and Chandigarh. It was late Dr. Gudrun Corvinus who requested help for study of fossil reptiles she had collected from the Siwaliks of Nepal and also for a technical workshop for the preservation of those fossils. Big confusion arouse with all the amount of fossil reptiles described from India and often locality or stratification was lacking in those publications from the 19th century. As my main subject was to study and describe the herpetofauna of Nepal also interesting was to compare the prehistoric till young fossil situation and development of preceding forms. In the beginning of the nineties I drafted some notes on fossils seen at the Wadia Institute of Himalayan geology and left this draft unpublished. Surprisingly, in 2015 two colleagues, Dr. Avinash Nanda and Dr. Bahadur Kotlia brought this drafted ms to publication, simply adding my name. But I did not see this presented manuscript before its publication and of course, clear enough as it only was drafted – it contained some errors. After its publication we had some issue about it and I can confess that I am still alive and being active. My addresses and fields of interests changed slightly, but having looked up at Google it would have been easy to find out about my latest activities and life. Ok, things happen but it was still worth confirmation. After my time as director at Fuhlrott Museum & Research Institute, the museum became demolished till no clues of its former existence remained. Material were destroyed, fossils lost or even stolen and also the original photographs were lost. The original version of this manuscript dates back to 15 years, and both Dr. Srivastava and myself changed ways of life and activities. But we felt all the information and previous works those investigations contained offered great wealth to science and would be a loss if not published. It took us more than a year to update the manuscripts as much as possible – each one of us lacking special institutional background (lab, libraries, access to material, etc.) and we dare now to present it to the public in the hope that it serves its aim – to deliver information on what is available and what it might and could be.

Respectfully,

Hermann Schleich

Review of Neogene-Quaternary Turtles from the Indian Subcontinent

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Abstract

A revision of the taxonomic status of Siwalik turtles with the systematic description of new material from Plio-Pleistocene horizons of India and Nepal is presented. The material described by previous authors, especially by the 19th century workers has been restudied in view of detailed diagnostic features. In the present work, the studies were made mainly on the turtle shells (the carapace and the plastron) as only a very few cranial and post-cranial remains of the fossil chelonians have so far been recovered from the Siwaliks. The only skull material reported from the Siwaliks belongs to *Megalochelys sivalensis* FALCONER & CAUTLEY (Testudinidae), *Hardella thurjii* GRAY, *Geoclemys hamiltonii* GRAY (Emydidae) and *Nilssonia gangetica* CUVIER (Trionychidae).

The comparison of the fossil material with the extant chelonians revealed that most of the Siwalik turtle fauna is still living, except the giant land tortoise *Megalochelys sivalensis* which apparently lived up to Early Pleistocene and then disappeared. However, more researches would prove, if this giant tortoise lived after early Pleistocene and had any impact by ancient men.

Introduction

The turtles and tortoises, though ecologically very significant, are poorly studied and draw insignificant attention to scientists and the common people. The turtles, terrapins and tortoises (usually termed simply, 'turtles') belong to the reptilian order Chelonia and are distinguished by their shell comprising carapace (upper shell) and plastron (lower shell). Modern turtles are generally classified into two subgroups: Pleurodirans (side neck turtles) which bend their necks sideway, and Cryptodirans (generally called hidden necked turtles and tortoises) which bend their neck into a vertical sigmoid curve (ROMER, 1956; DAS, 1995). The typical turtles and tortoises found in northern latitudes belong to the Suborder Cryptodira divided into eleven families of which five *viz.,* Dermochelyidae (leatherback sea turtle), Cheloniidae (sea turtles), Testudinidae (land tortoises), Trionychidae (softshell turtles) and Geoemydidae (pond turtles) are found in South Asia especially in the Indian Subcontinent. The evolutionary trends of turtle shells and abnormalities in their carapace has been noticed and described showing the variation within a single species of turtle and is possible due to individual

abonormalities or within the range of variability. (LYSON et. al., 2013 and FARKE & DISTLER, 2015).
If we talk about the fossil turtles of South Asia, the chelonian record of the South Asian turtles is mostly limited to the discovery and description of Siwaliks from India that was published a way back in the 19th century (FALCONER & CAUTLEY, 1837, 1844; FALCONER, 1868 and LYDEKKER, 1885, 1886, 1887, 1889).
The fossil material from the Siwaliks forming the basis of the present paper is mainly represented by elements of the carapace and the plastron. However, a few turtle skulls referable to *Megalochelys sivalensis*, *Hardella thurjii, Geoclemys hamiltonii* and *Nilssonia* (ex. *Aspideretes) gangetica* were also described from the Siwaliks of India (LYDEKKER, 1885, GRIGORESCU & VERMA, 1976; SRIVASTAVA & PATNAIK, 2002).

The taxonomic status and diagnostic characters of the fossil testudines, both, trionychids and geoemydids from the Indian subcontinent need a thorough revision as it seems very unrealistic and artificial that all the fossil species described by the 19th century workers and also by many 20th century workers *viz.*, PRASHAD & SATSANGI (1967), TEWARI & BADAM (1969), PRASHAD (1974), BADAM (1979) WEST (1984), WEST & MUNTHE (1983), WEST *et al.* (1978, 1991), CORVINUS (1988), CORVINUS & SCHLEICH (1994) are different from the extant ones, having only a very few common members.

An attempt in this direction was taken by DAS (1991a, 1995), when he restudied many specimens of LYDEKKER (1885, 1886), TEWARI & BADAM (1969) and PRASHAD & SATSANGI (1967). Das (1991a, 1995) confirmed that none of the geoemydine (ex. batagurine) species from the Siwaliks are extinct.

Most of the material described by FALCONER & CAUTLEY (1937, 1844) as well as by LYDEKKER (1885, 1886, 1887, 1889) does not have evidence of precise locality or stratification. The only available identification is 'Siwalik Hills' (Ganges-Jamuna basin) and Siwalik Hills (Indus basin) of Punjab (vide LYDEKKER, 1885), that ranges from Pakistan, via India and Nepal to Bhutan (fig. 1, 2) and stratigraphically from Miocene to Pleistocene (Table 1). This incomplete information is the main hurdle in the study of character evolution and phylogenetic relationships of the Siwalik turtles; we can not state even to which extent relations among different specimen exist.

The different shapes and type of epiplasta of *Megalochelys* earlier described under different genera and species could be interpreted as of the individuals of different ages or as sexual dimorphism. This suggestion does not rule out the possibility of different taxonomical units, if there is more material available from different horizons and different localities. Moreover, most of the material described by 19th century worker is suspected by many recent scientists that the fossils were taken or purchased from local people and therefore no full reference of the locality and stratification is available. From these unfortunate circumstances we suggest treating all this unstratified material of uncertain locality as belonging provisionally to the collective genus *Megalochelys*.

One might easily suggest different taxonomical species or even genera just by the morphological details of the fossil turtle material but due to lack of locality and age data we do not believe in such artificial grouping and would logically keep these fossils taxonomically together until new findings prove their whereabouts.

The material described and discussed in the present work comes from the Plio-Pleistocene rocks exposed in Perim Island (Gujarat) and Siwaliks near Chandigarh, Saketi, Nahan, Quranwalla (Punjab) in India; near Rawalpindi, Jhelum and Dhok Pathan in Pakistan; Kathmandu Valley, Siwaliks of Surai Khola, Rato Khola, Gidhnia, Binai Khola, Tinau Khola and Babai Khola localities in Nepal (Text fig. 2). The stratigraphic status of these exposures remains debated and have been described as Upper Pleistocene (TEWARI & BADAM, 1969) to Pre-Pinjor beds (=Saketi Formation, = Tatrot Formation, = Dharamsala Formation) and only Pre-Pinjor and Pinjor beds have been considered to be richly fossiliferous (PILGRIM, 1932, 1938; VERMA, 1989; NANDA, 2002 & 2015).

Fig. 1. Extension of Siwalik group of rocks in the Indian Subcontinent

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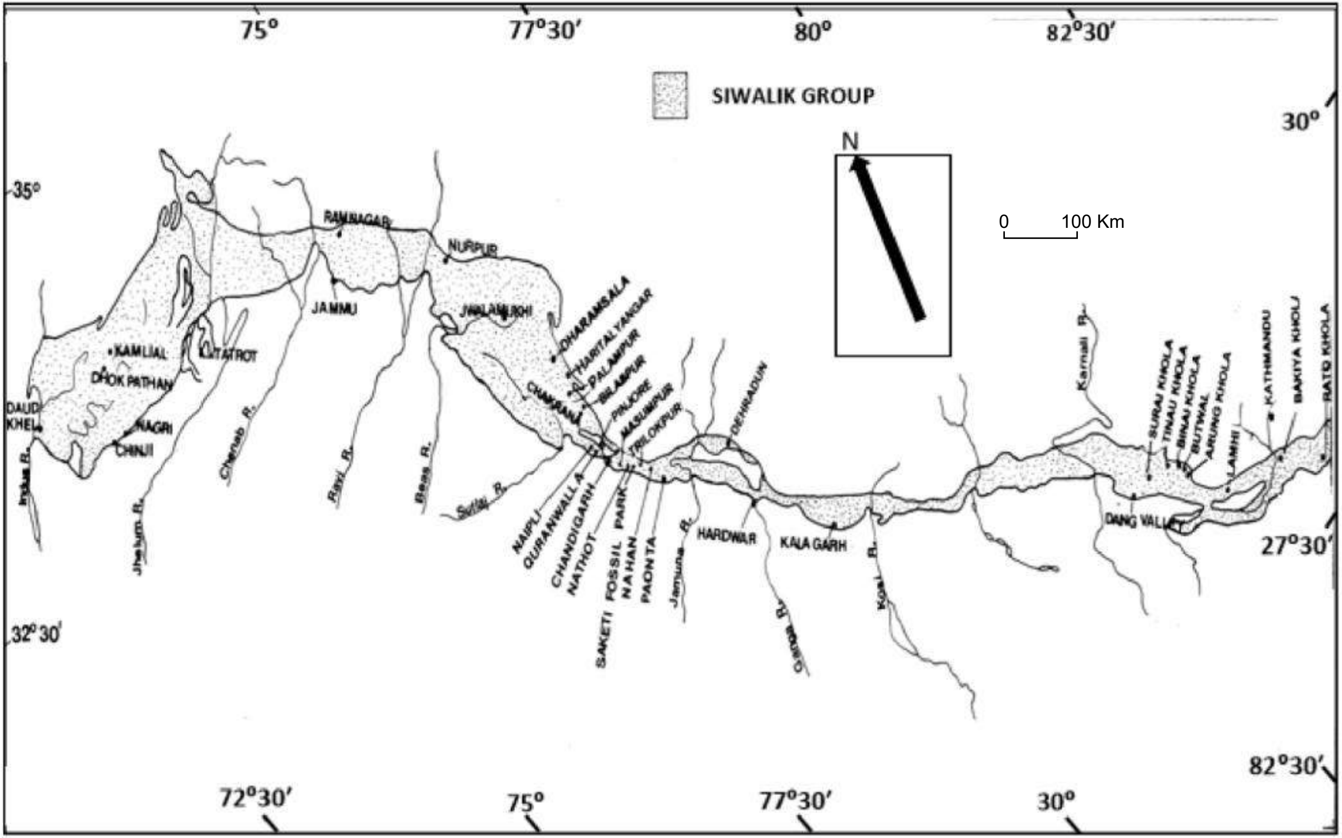
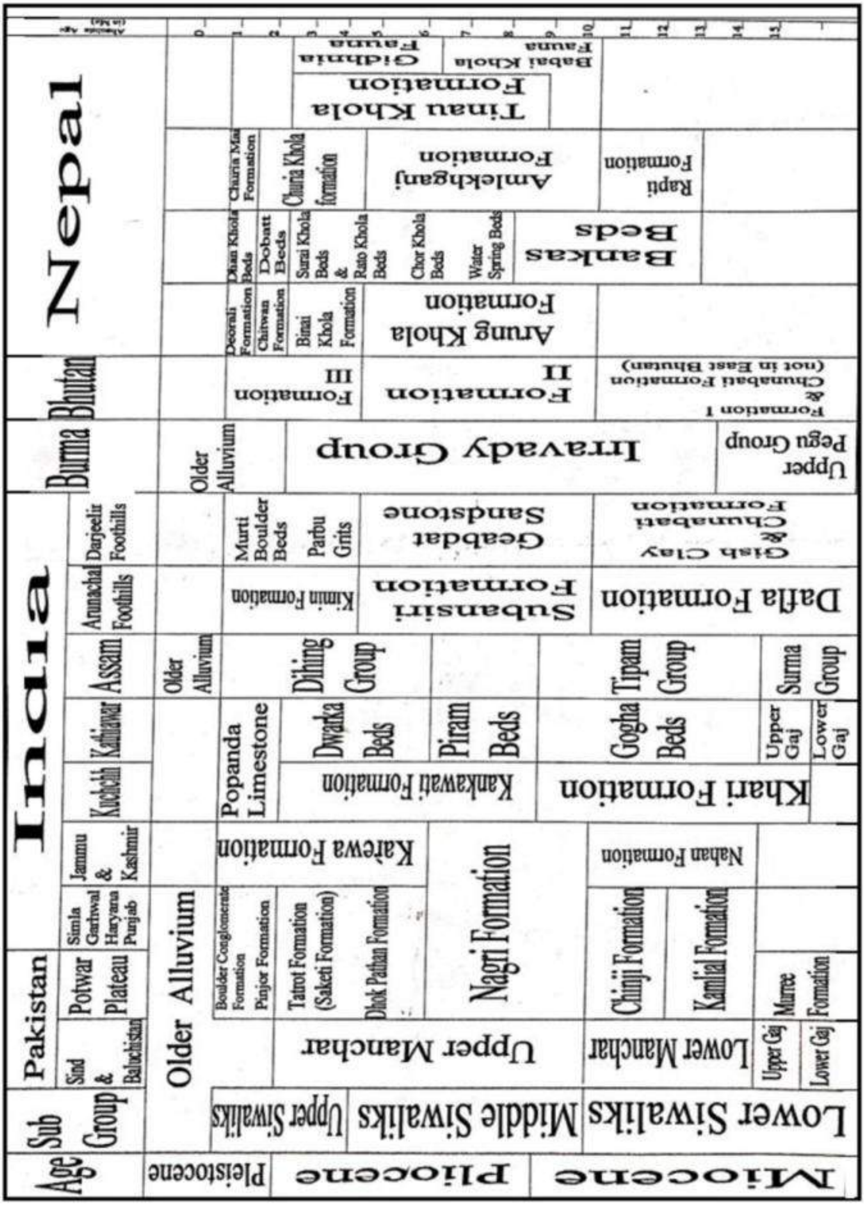
Fig. 2. (next page). Siwalik belt of Northwestern Himalaya showing principle fossil turtle localities (modified after NANDA & SEHGAL, 1993).



75°
77°30′
80°
82°30′
SIWALIK GROUP
N
0
100 Km
30°
35°
27°30′
32° 30′
82°30′
72°30′
75°
77°30′
30°
RAMNAGAR
NURPUR
JAMMU
JWALAMUKHI
KAMLIAL
KHATATROT
DHOK PATHAN
DAUD KHEL
NAGRI
CHINJI
Indus R.
Jhelum R.
Chenab R.
Ravi R.
Beas R.
Sutlej R.
DHARAMSALA
HARITALYANGAR
PALAMPUR
BILASPUR
PINJORE
MASUMPUR
TRILOKPUR
CHAMBA
NAIPLI
GURANWALLA
CHANDIGARH
NATHOT
SAKETI FOSSIL PARK
NAHAN
PAONTA
Jamuna R.
DEHRADUN
HARDWAR
KALA GARH
Ganga R.
Kosi R.
Karnali R.
DANG VALLEY
SURAI KHOLA
TINAU KHOLA
BINAI KHOLA
BUTWAL
ARUNG KHOLA
LAMHI
KATHMANDU
BAKIYA KHOLA
RATO KHOLA



Tab. 1. Siwalik formations correlated to stratigraphy.

Material and Methods

The present work is based mainly on the undescribed shell material (carapace and plastron remains) of testudinid and geoemydine turtles from the Siwaliks of India and Nepal. The material was casted by one of the co-authors (HS) during his various lecture programs in India and Nepal. The original material is catalogued in the Field Museum of the Saketi Fossil Park, Saketi; (India) and in the Natural History Museum of the Kathmandu University, Kathmandu (Nepal). Besides, the already reported material (comprising of either complete shells or carapace or plastron) catalogued in the Museums of CAS in Geology, Panjab University Chandigarh, Indian Museum Kolkata, Wadia Institute of Himalayan Geology Dehradun, Natural History Museum, London was also studied and revised. The material which was not available for the study was either photographed in the respective museums and/or sketched from the literature for the revision and taxonomic identification/confirmation.

The morphological details of the carapace and the plastron of various fossil turtles were studied and compared with the extant turtle species from the Indian Subcontinent considering the researches on phylogeny and evolutionary trends amongst the turtles especially among cryptodirans (GAFFNEY, 1975; GAFFNEY & MEYLAN, 1988; MEYLAN, 1987; MEYLAN & GAFFNEY, 1989 and CRUMLEY, 1982, 1984).

Measurements of the carapace were taken following DAS (1991a):
Straight Carapace Length (SCL) = Distance between cervical at restored carapace midline to posterior-most point of postcentral.
Straight Carapace Width (SCW) = Distance across widest part of restored carapace, perpendicular to the longitudinal body axis.
Plastron Length (PL) = Distance between the anterior-most tip of the gulars and the posterior-most tip of the anals.
Plastron Width (PW) = Distance across widest part of plastron perpendicular to the longitudinal body axis.
Straight Height (SH) = Distance across highest part of shell perpendicular to the longitudinal body axis.

Abbreviations

AMNH: American Museum of Natural History, New York, USA
BMNH: British Museum (Natural History), London, England
CAS: Centre of Advanced Study in Geology, Panjab University, Chandigarh, India
MCASG: Museum of Centre of Advanced Study in Geology, Panjab University, Chandigarh, India.
MNHN: Museum National d'Histoire Naturelle, Paris, France
OUM: Oxford University Museum, England
PU: Panjab University, Chandigarh, India
SFP: Saketi Fossil Park, Saketi, India
NHM/TU: Natural History Museum/ Tribhuvan University, Kathmandu, Nepal
WIHG: Wadia Institute of Himalayan Geology, Dehradun, India
WIF: Wadia Institute Museum Fossil, Wadia Institute of Himalayan Geology, Dehradun, India.

Terminology

The terms for describing the carapace and plastron characters were used following SCHLEICH (1980). The term scutes has been used for the protecting horny shields on the carapace and plastron; and bones has been used for the underlying ossified plates. A detailed terminology of the various scutes and bones is given in fig. 3.

Carapace: Unpaired **scutes** in the central row are: Cervical (Cerv), Centrals 1 – 5 (C 1 – 5), Postcentral (Pc). Paired scutes in the lateral row: laterals 1 – 5 (L 1 – 5), Marginals 1 – 11 (M 1 – 11) and two Postcentrals (Pc).
Plastron: Paired scutes along the median seam are: Gulars (G = Gul), Humerals (Hum), Pectorals (Pec), Abdominals (Abd), Femorals (Fem) and Anals (An).
Axillary and Inguinal scutes.

Carapace: Unpaired **bones** in the central row are: Nuchal (Nu), Neurals 1 – 8 (N 1 – 8), Metaneurals 1 – 3 (Mn 1 – 3), Pygal (Pyg). Paired bones in the lateral row: Pleurals 1 – 8 (Pl 1 – 8), Peripherals 1 – 11 (Per 1 – 11).
Plastron: Unpaired bone on the median suture: Entoplastron (E = Ento).
Paired bones along the median suture: Preplastra (in Trionychids), Epiplastra (Epi), Hyoplastra (Hyo), Hypoplastra (Hypo), Xiphiplastra (X = Xiphi).

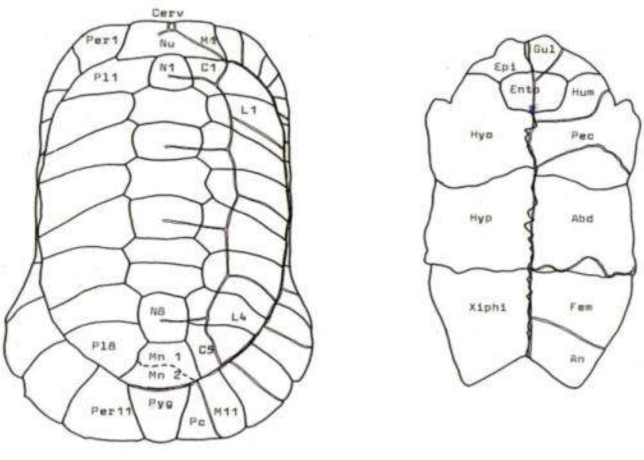


Fig. 3. General morphology and terminology of turtle shell used in the present work (after SCHLEICH, 1981).

Right half: epidermal scutes on carapace and on plastron;

Left half: underlying bones (plates) on carapace and on plastron. In all the text figures thick lines indicate epidermal scute seams and thin lines indicate bony sutures. The restoration of bony sutures and scute seams in all the figures is marked by broken lines.

Revised Taxonomy

Family Testudinidae GRAY, 1822

The shell is convex; the feet are club shaped and adapted for walking (the hind feet are partially webbed in *Manouria*).

The plastron and highly arched carapace is unreduced (an exception to this rule is found in the genus *Malacocherus* in which the shell is reduced); the carapace and plastron are hingeless (in adult *Kinixys* a posterior carapacial hinge is present between the femoral and abdominal scutes,); a medial keel may be present in juveniles but disappears with age in all the species. Axillary and inguinal glands are absent (AUFFENBERG, 1974; CRUMLY, 1984). A plastral bridge is well developed.

The skull is short to moderate in length which is different from those in emydid turtles (GAFFNEY, 1979). The temporal region primitively and generally emarginates from behind; the temporal roof is reduced; the post-orbital is reduced than that in emydids (ERNST & BARBOUR, 1989); the squamosal does not meet the parietal. Frequently, one or more ridges on the alveolar surface of the upper jaw. The pubis and the ischium usually meet their mates ventrally. There are five claws in the front and four in the hind feet; The phalanges are not more than two in number. The trochanteric fossa of the femur is tending to be reduced.

The family Testudinidae is a typically terrestrial group of chelonians. They are small to very large tortoises, largely herbivorous, only occasionally taking animal matter (DAS, 1991a).

Today, members are found in the tropical portion of Africa, Madagascar, South and South-East Asia, South America, Aldabara Atoll, and the Galapagos Archipelago. The fossil tortoises date from the Early Eocene and extend upto recent.

Megalochelys sivalensis FALCONER & CAUTLEY, 1837

Holotype: An epiplastron (BMNH-40630) catalogued in the British Museum (Natural History), London.

Type Locality: Siwalik Hills, Punjab, India, Early Pleistocene.

Synonymy:
1844: *Colossochelys atlas* Falconer & Cautley
1869: *Colossochelys (Megalochelys) atlas* Maack
1879: *Cautleya annulieger* Theobald
1880: *Testudo (Colossochelys) atlas* Lydekker)
1885 & 1886: *Colossochelys atlas* (Lydekker)
1885 & 1886: Gen. *et* sp. indet. 1 Lydekker
1885 & 1886: Gen. *et* sp. indet. 2 Lydekker

1885 & 1886: Gen. *et* sp. indet. 3 Lydekker
1885 & 1886: Gen. *et* sp. indet. 4 Lydekker
1885: *Cautleya annulieger* (Lydekker)
1889 a: *Testudo (Megalochelys) atlas* Lydekker
1889 a: *Testudo cautleyi* Lydekker
1889 a: *Testudo punjabiensis* Lydekker
1889 b: *Manuria emys* Lydekker
1915: *Testudo cauthley* Riabinin
1931: *Testudo atlas* (Brown)
1948: *Testudo margae* Hooijer
1954: *Testudo margae* Hooijer
1974: *Geochelone (Megalochelys) atlas* Auffenberg
1974: *Geochelone (Megalochelys) cautleyi* Auffenberg
1974: *Geochelone (Manouria) punjabiensis* Auffenberg
1981: *Colossochelys atlas* (Badam)
1994: *Colossochelys atlas* (Corvinus & Schleich)

Palaeontological History:

The first fossil remains of this giant tortoise were discovered in 1835 by FALCONER & CAUTLEY from the "Tertiary strata of the Siwalik hills, or Sub-Himalayas skirting the southern foot of the great Himalayah chain" (FALCONER & CAUTLEY, 1837). These remains were found associated with the 'four extinct species of *Mastodon* and Elephant, species of Rhinoceros, *Hippopotamus*, Horse, *Anoplotherium*, Camel, Giraffe, *Sivatherium* and a vast number of other Lower Pleistocene mammals. After the year 1835 many other remains of the *Megalochelys* were collected during a period of eight or nine years "along a range of eighty miles of hilly country" (FALCONER, 1868) belonging to different individuals varying in size and age. The age consideration of the fossil remains was not given much significance as FALCONER (1868) states "this is not the place to enter upon the geological question of the age of the Sewalik strata; suffice it to say, that the general bearing of the evidence is that they belong to the newer tertiary period".

The relationship of this large tortoise with the ancient man is not clear; it is questionable until proved, whether these giant tortoises descended to the human period and ancient man which subsequently became the cause of the extinction of this animal. There are traditions connected with the cosmogenic speculations of almost all eastern countries having reference to a tortoise of such gigantic size; also in the pythagorean cosmogony the infant world is represented as having been placed on the back of an elephant, which was sustained on a huge tortoise. Besides, there are many stories and poetries in the Indian Mythology in which reference of a large tortoise comparable in size with the elephant has been given. Was this large tortoise a mere creature of the imagination, or was the idea of it drawn from a reality, like the *Megalochelys* (*sensu* FALCONER, 1868)?

In this work, the name *Megalochelys sivalensis* FALCONER & CAUTLEY has been retained for the species. This name was first, given to the large sized tortoise from the Siwalik hills (FALCONER & CAUTLEY, 1837, p. 358) but was later withdrawn by FALCONER & CAUTLEY (1844). They thought the generic name *Megalochelys* is not sufficient to convey the large size of the animal. Therefore, to express the colossal size of the animal the name *Colossochelys* was given (FALCONER, 1868 and FALCONER & CAUTLEY, 1844). The specific name *sivalensis* was changed to *atlas* as the fossil was a fit to represent the mythological tortoise of the Hindus that sustained the world according to the systems of Indian cosmogony (FALCONER & CAUTLEY, 1837 and FALCONER, 1868). Having said that, *Colossochelys atlas* is merely another name *of Megalochelys sivalensis*.

The largest land tortoises referable to the genus *Megalochelys* have so far been recovered from the Upper Pliocene rocks of Siwaliks (BADAM, 1981), Perim Island in Gujarat (Pliocene) and Pleistocene deposits of Punjab in India; Lower to (?) Middle Pleistocene deposits of Potwar (LYDEKKER, 1889) and Upper Myanmar, Java, Celebes and Timor in Indonesia (AUFFENBERG, 1974, MLYNARSKI, 1976 and DAS, 1991, WALTER & LYSON, 2010) and from Upper Siwaliks of Nepal (CORVINUS & SCHLEICH, 1994).

Distinguishing features:

Gigantic size; a short and narrow cervical is present only in young individuals (absent in adults); the centrals are hexagonal and large, occupying maximum central region of the carapace so that the laterals are short; the laterals alternately are wide and narrow on their proximal and distal extremities. The postcentral is divided but only in young individuals. The buttresses are short, never extending beyond the edge of the laterals. The carapace is flattened at the top and steeply inclined (nearly vertical) at the sides.
The plastron is broad. A median cuneiform keel on the inferior surface of its plastron is one of the principal features in this fossil (FALCONER, 1868); the keel terminates at the point where the entoplastron starts; it is feeble in young individuals. In grown up individuals, the epiplastron is largely extended anteriorly beyond the carapacial rim; its width gradually increases anteriorly with age, and on the anterior most margin it is bifurcated along the median seam (Growth Stage IV in Text fig. 4) which is a characteristic feature of this species. The only use of such a structure could be the protection or combate against other animals and individuals. The entoplastron and xiphiplastron are similar to as in *Testudo* s.l.. The anal margin is thickened and downturned. The postcentral and adjacent marginals are incurved inferiorly and situated nearly vertical, so that when the shell is viewed directly from above very little of the postcentral is visible.
It is distinguishable from other testudinids by its characteristic large size, a strong triangular keel on the plastron on which the gulars are borne and also by the thickening and anterior extension of the epiplastron.

Material: Restored large shell, displayed in the British Museum (Natural History) London, and the cast is displayed in the Indian Museum Kolkata.
(Plate 1, fig. 1 & Text fig. 5)

Locality: Various fragments of different individuals used in the restoration of the specimen were collected from the Siwaliks of the Punjab; Lower Pleistocene.

Description

Carapace: We studied the cast of the shell displayed in the Indian Museum, Kolkata. The shell is extremely large and is vertically compressed (diagenetic compression is very high). The centrals are very large covering maximum part of the carapace. The bony sutures are completely reduced indicating a mature individual.

Cervical: The cervical is absent.

Centrals: The 1st central is nearly pentagonal having straight posterior and lateral margins. The anterior margin of the 1st central is slightly concave; centrals 2 & 3 are sub-hexagonal. The anterio-lateral margins of the 2nd and 3rd centrals are concave and posterio-lateral margins are nearly straight. The 4th central is hexagonal having its posterior margin shorter than anterior. The 5th central is the smallest among all having arcuade posterior margin. The postcentral is undivided having posterior width more than the anterior width. The post-central is incurved inferior and situated nearly vertically.

Laterals: The laterals are small due to large centrals covering maximum portion of the carapace. The 1st lateral has convex proximal and nearly straight distal margin. The proximal ends of the 1st, 2nd and the 4th laterals are smaller than the distal end; whereas, the proximal end of the 3rd lateral is larger than its distal end. The 4th lateral is wedge shaped and smallest amongst all. The 1st lateral is the largest followed by 2nd and 3rd.

Marginals: The marginals 1- 3 are upturned and forming nearly a horizontal lip on the anterior margin of the carapace. The 1st pair of marginals are extremely large in comparison to other posterior marginals. The 1st marginal is contacting the 1st central. The 2nd marginal is reaching upto the 1st lateral and the 3rd marginal is contacting the 1st lateral. The 4th is reaching upto the 2nd lateral and 5th is contacting the 2nd lateral. The 6th marginal is in contact of the 2nd lateral. The 7th marginal is reaching upto the 3rd and 8th marginal is reaching upto the 4th lateral. The 9th marginal is contacting the 4th lateral. The 10th marginal is reaching upto the 5th central and 11th marginal is contacting the 5th central. The 11th pair of the marginals is incurved towards the inferior surface.

Plastron: The shell is displayed in the Indian Museum (Kolkata) and it is not possible to turn over the specimen for the study of its plastron. From the visible portion it can be noticed that the anterior portion of the plastron is considerably thick, having an extremely exaggerated anterior portion of epiplastron which is bifurcated anteriorly along the median seam (a characteristic feature of *Megalochelys sivalensis*). A median cuneiform keel on the visceral surface of the plastron is also distinct. A small portion of the anals is also visible clearly showing a deep posterior notch. The plastron is reduced posterior not reaching upto the marginals of the carapace.

The dimensions taken on the carapace are as follows:
Straight Carapace Length (SCL) = 293 cm
Straight Carapace Width (SCW) = 270 cm
Straight Height (SH) = 82.5 cm

Remarks: The original material was not available to us for a detailed study. The description is based on the cast of the shell displayed in the Indian Museum and on the photographs of the specimen taken by one of the authors (HS).
The specimen was restored and described originally by FALCONER & CAUTLEY (1844, 1868). The material was collected along with other mammalian fossils (Rhinoceros, Hippopotamus, Horse, *Anoplotherium*, Camel, Giraffe, *Sivatherium*) recovered from a horizon above the last appearance of *Mastodon*. On this basis a Lower Pleistocene age has been given to this large tortoise. The precise locality information of the specimen is not available and was originally described to be collected from the "Tertiary strata of the Sewalik hills in the north of India – a tertiary chain apparently formed by the detritus of the himalayah mountains" (FALCONER, 1868).

Fig. 4. (next page). Development of Epiplastra in *Megalochelys sivalensis*. We suggest that the anterior extension of the epiplastra is a result of ontogenic development in male *Megalochelys*. The specimen E-80 shows the epiplastra in a juvenile individual in which no anterior extension is visible; the final stage of ontogenic development is visible in the holotype specimen (BMNH-40630) in which the anterior extremity is deeply bifurcated. Various intermediate stages between E-80 and BMNH-40620 are illustrated in the figures and are evident in the specimens PU A/702, E-82, E-84 and E-82a respectively.

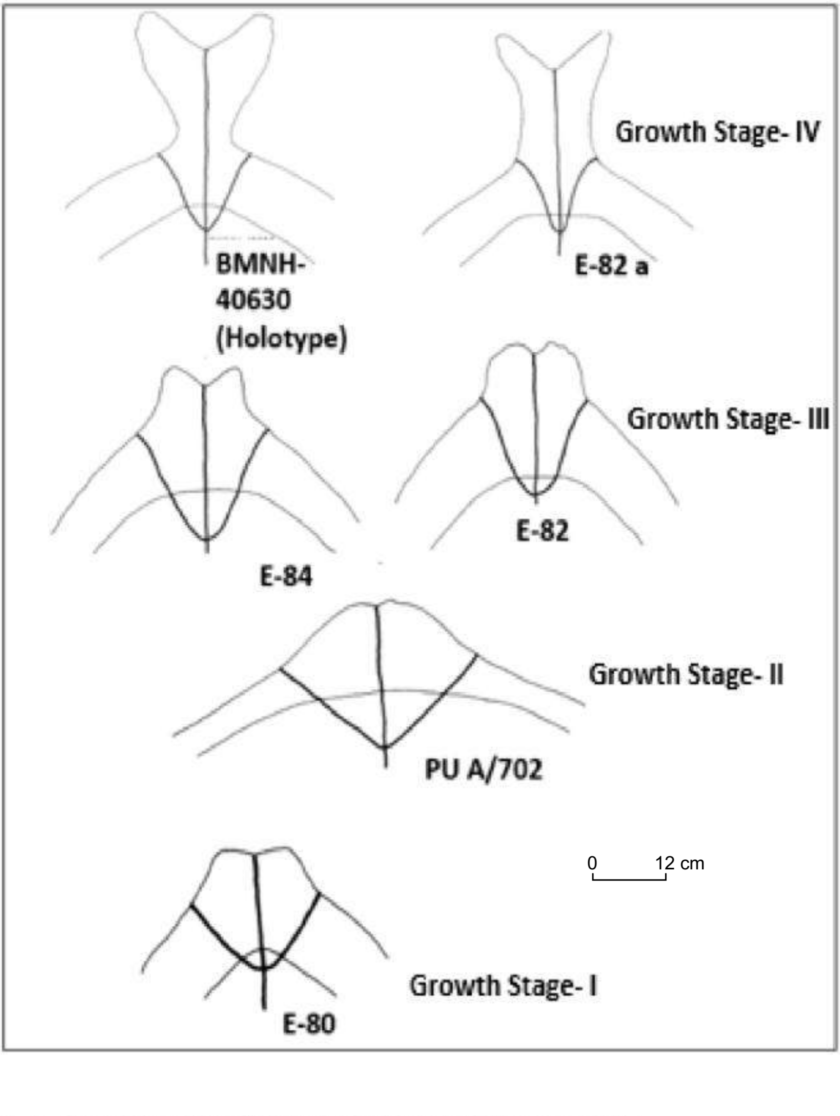


Fig. 4. Development of Epiplastra in *Megalochelys sivalensis*.

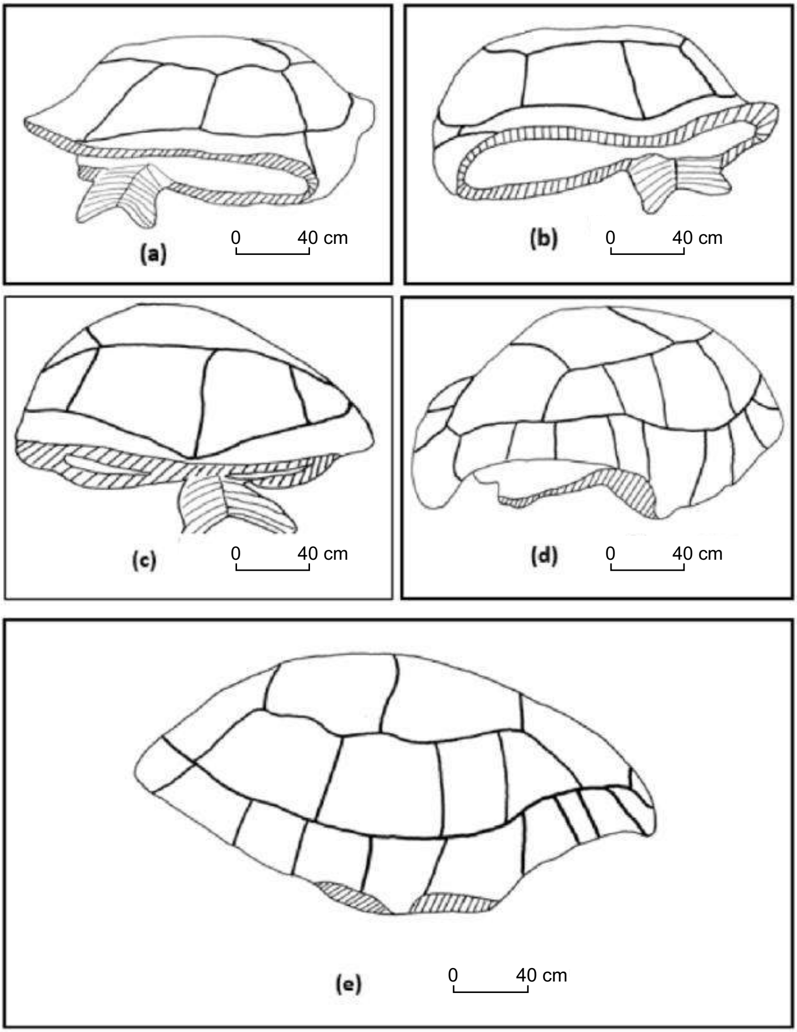
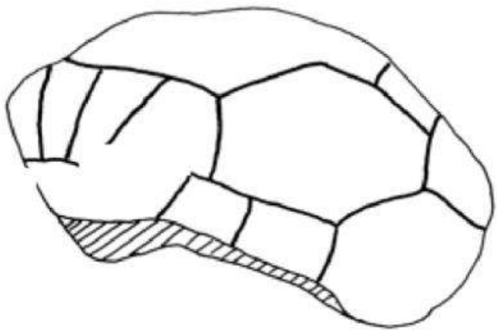
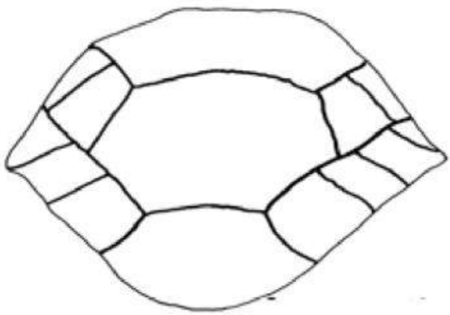


Fig 5. Large shell of *Megalochelys sivalensis* displayed in the Indian Museum, Kolkata. The figures show various views of the carapace. The bony sutures are not distinguishable on the carapace whereas epidermal scutes are distinct having very large centrals and narrow laterals. The fig. (a), (b) and (c) show anterior deeply bifurcated epiplastra. Fig. (d) very small anal portion of a posterior notched plastron. Fig. (e) lateral view of same specimen.



(f) 0 40 cm



(g) 0 40 cm

Fig 5, continued. Large shell of *Megalochelys sivalensis* displayed in the Indian Museum, Kolkata; same specimen from before.
f) posteriolateral view,
g) posterior view

Considering the size of the *Megalochelys* shell, the space between the carapace and plastron in the above specimen is very small to accommodate such a large animal. Also, the shell seems dorsally compressed. It is very likely that the shell has passed through a vertical diagenetic compression.

The bony sutures are not distinct on the carapace which suggests that this large carapace represents a grown-up individual in which the epiplastron extends beyond the carapacial rim.

Material: Detached right and left epiplastron (E-80), catalogued in the Indian Museum, Kolkata. The material was collected by THEOBALD in 1879 and was previously described by LYDEKKER (1885) as Genus *non- det.* species 4 and then as *Testudo punjabiensis* (LYDEKKER, 1889a).
(Plate 2, fig. 1 & Text fig. 6)

Locality: Siwaliks of Punjab

Description

Epiplastra: The material is comprising of a detached right and left epiplastron. The anterior part of the epiplastron does not show any kind of development like in other epiplastra of the species. However, a hypothetical extension of the anterior most part of the epiplastron suggests that the material belongs to the same species. The straight anterior margin and smaller size (in comparison to the type material) of the specimen suggest that it probably belongs to a young individual or a female, in which the anterior extension of epiplastron did not start (hypothetical reconstruction shows a tendency of anterior extension). It is very interesting to note here that the seam between gular and post-gulars in *Megalochelys sivalensis* is laterally convex in this (young) individual (as seen in the present specimen) but it tends to become concave laterally with age (as seen in other epiplastra decribed in the following sections.

The plastron is broken posterior to the suture between epiplastron and hyoplastron. The epiplastron is pentagonal; its anterio-lateral margins are slightly concave; the anterior margin of the epiplastron is nearly straight. The gular is separated from the post-gular by a seam making an acute angle with the median line. The gulars are nearly pentagonal. The gular portion is produced in advance of the post-gular. The specimen is considerably larger than adult extant *Manouria emys*.

The dimensions taken on the specimen are as follows:
The mid-seam length of the epiplastron = 8.2 cm
The anterior width of the epiplastron = 3.8 cm
The straight length of the suture between gular and post-gular = 6.5 cm

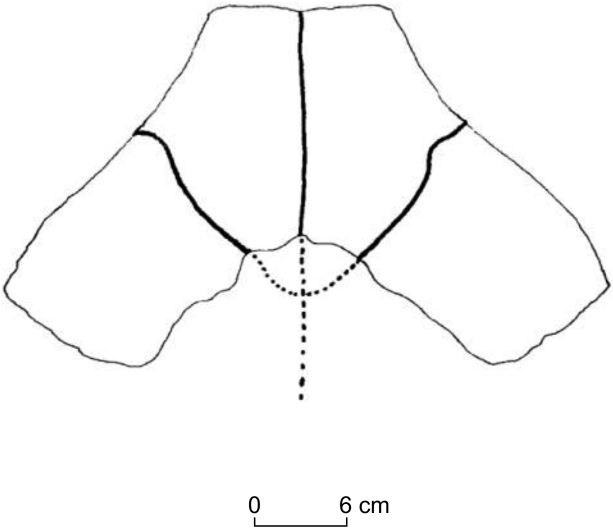


Fig. 6. Restored Epiplastra (E-80) of *Megalochelys sivalensis* displayed in the Indian Museum, Kolkata. The specimen represents an early stage in ontogenic development of epiplastra in *Megalochelys sivalensis*.

Remarks:
The age consideration of the material is doubtful. The material was originally collected by THEOBALD (1879) and described by LYDEKKER (1885, 1889a). They have not described the horizon or precise locality from where the material was collected.

Material: Shell of a giant tortoise (PU A/702) stored and catalogued in the museum of CAS in Geology, Panjab University, Chandigarh. The shell was restored from about hundred fragments of the carapace and plastron and described by BADAM (1981) as *Colossochelys atlas*.
(Plate 2, fig. 2 & Plate 3, fig. 1 & Text fig. 7)

Locality: 0.6 km Northwest of Naipli, near Chandigarh, Tatrot Formation, Upper Pliocene.

Description

Carapace: The straight carapace length (SCL) of the restored shell is about 180 cm and straight carapace width (SCW) is about 151 cm. The straight height of the shell is about 50 cm. The carapace is oblong; it is longer than broad and strongly arched transverse. The anterior edge of the carapace is in the form of an arc. The seams between the scutes are occasionally traceable. The seams between the centrals and laterals are not discernible. The postcentral is distinctly seen which is divided and curved towards the inferior surface and is nearly vertical.

Plastron: It was not possible to study the plastron part of the shell as the plastron is cemented for the display in the Museum. Only the visceral surface of the epiplastron was visible which was casted (Plate 3, fig.1 and Text fig. 7) by the second author (HS).

The middle portion of the plastron is concave. The plastron is quite thick in middle. The anteriormost portion of the epiplastron is bifurcated. The gular portion is strongly convex with distinct intergular seam. The portion covered by the gulars forms a very distinct triangular keel, projecting beneath the portion covered by the postgulars. The median seam is also keeled and sharply ridged. In the specimen the seam between gulars and humerals is nearly straight. A small bifurcation of the anterior margin of the epiplastron is distinct indicating a specimen which is older in age in comparison to the previously described speicmen (E-80) in which the anterior extension of the epiplastron had started.

Dimensions of the restored plastron are as follows:
Maximum length of the plastron (based on the reconstruction) = 130 cm
Maximum width of the plastron (based on the reconstruction) = 105 cm

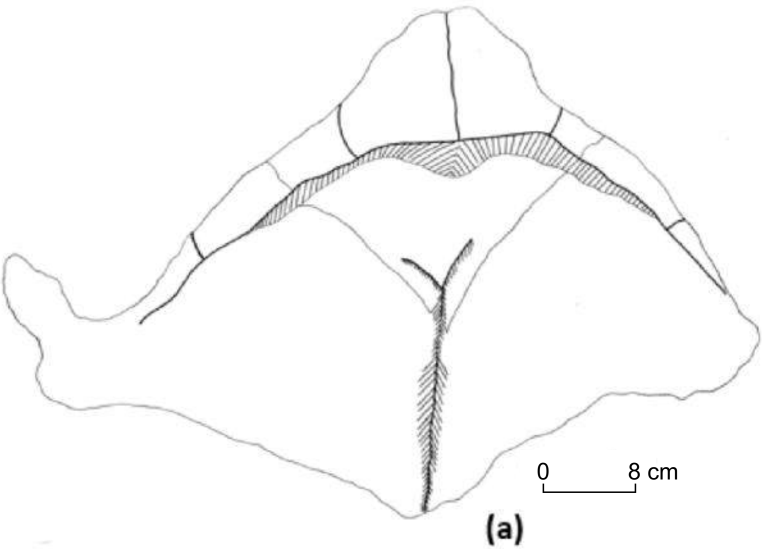


Fig. 7a. Anterior plastron lobe of a giant tortoise (PU A/702); reconstructed visceral plastron side.

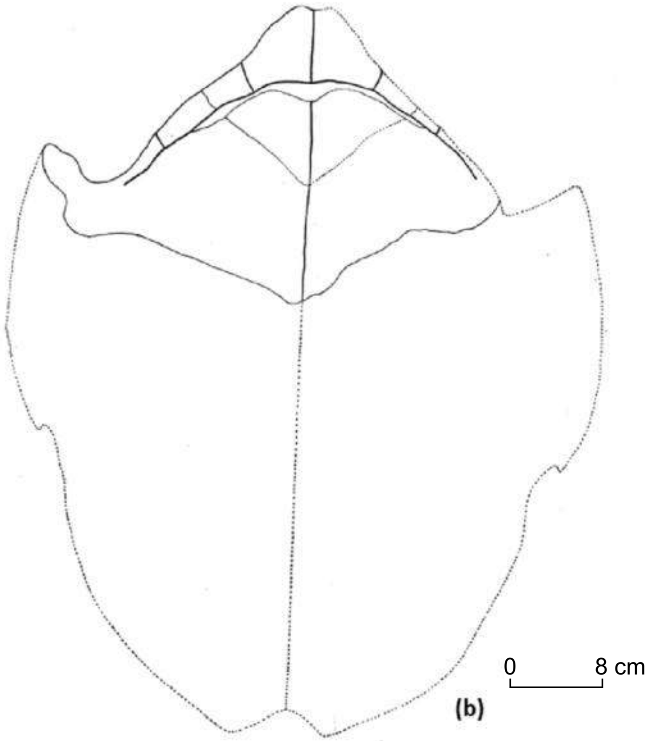


Fig. 7b. Reconstructed visceral plastron of a giant tortoise (PU A/702);
Visceral surface of the epiplastra is shown. The ventral surface of the plastron is cemented for the display purpose and therefore not possible for the study. A slight anterior bifurcation of the epiplastra is distinguisbale. A reconstruction of the epiplastra is based on the observable characters on the visceral surface.

Remarks: The divided postcentral and weak bifurcation of anterior margin of the epiplastron indicate that the speicmen is still an adolescent. The complete shell was earlier described by BADAM (1981) however, he did not take an attempt to describe the epiplastra in detail which bears the most important features (described above) of *Megaloschelys sivalensis*. This material is important because of its age (Upper Pliocene). The earlier material designated to the genus, *Megalochelys* comes from Early Pleistocene (LYDEKKER, 1885, 1886).

Material: Epiplastra (E – 82). The material is catalogued in the Indian Museum, Kolkata. The material was collected BYTHEOBALD in 1879 described as *Cautleya annuliger* and was described later by LYDEKKER (1885) as Genus *non- det.* species 2 (? *Cautleya annuliger*).
(Plate 3, fig. 2, Text fig. 8)

Locality: Siwaliks, of Punjab

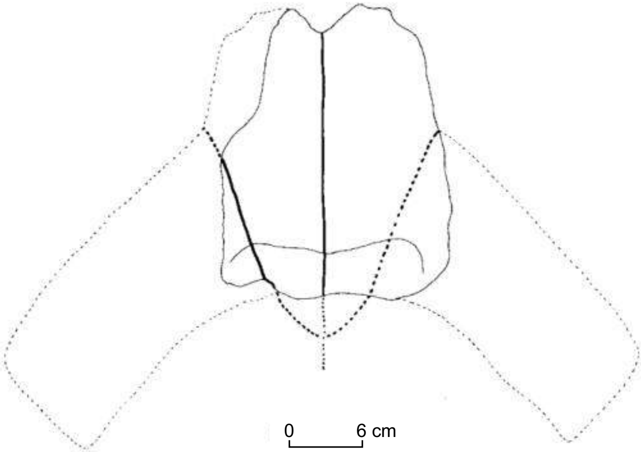


Fig. 8. Reconstructed Epiplastron of *Megalochelys sivalensis* (E-82). A small anterior bifurcation of the epiplastra indicates towards an adolescent individual and represents the third stage in ontogenic development of epiplastra in *Megalochelys sivalensis*.

Description

The left epiplastron is broken and is corroded ventral. The intergular seam and the gular-humeral seam is well marked. The growth lines on the epiplastron indicate towards an anterior and anterio-lateral growth of the epiplastra. The specimen is larger than the two previously described epiplastra (E- 80 & PU A/702). The seam between the gulars and the humerals is rather straight and the two seams meet on the median seam (based on reconstruction) forming an angle which is more acute than in the two previously described epiplastra (E- 80 & PU A/702). The ventral surface of the plastron is convex. The gular portion of the plastron is distinctly raised above the postgulars.

The anterior margin of the epiplastron is bifurcated; the bifurcation is deeper in comparison to that in the specimen PU A/702. The size and the anterior bifurcation of the epiplastron suggests that the speicmen is older to the previously described epiplastra and representing the growth stage III (see text fig. 4 for suggested ontogenic developmental stages in *Megalochelys*).

Material: Epiplastra (E-76). The material is catalogued in the Indian Museum, Kolkata. It was collected and described by FALCONER (1859) and recorded by LYDEKKER (1886) as *Colossochelys atlas.*
(Plate 3, fig. 3 & Text fig. 9)

Locality: Siwalik hills, India (FALCONER, 1859)

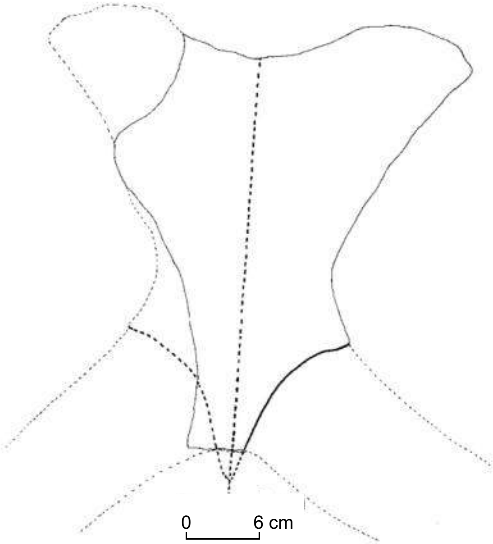


Fig. 9. Reconstructed epiplastra of *Megalochelys sivalensis* (E-76). The anterior bifurcation of the epiplastron is more pronounced representing the 4th stage in ontogenic development of epiplastra in *Megalochelysis sivalensis.*

Description

The material consists of the anterior portion of the epiplastron, so called epiplastral beak. It is bifurcated at the apex similar to the type specimen. Behind the apex, the epiplastron is contracted and supplied underneath on the visceral surface with a thick cuneiform keel. The region of the left bifurcation is broken. The epiplastron is posterior broken from the suture between the gulars and humerals. The anterior extremity shows that the width of bifurcation of the epiplastron is smaller than in the holotype. The specimen is larger than the reconstructed specimen -E-84, earlier described by LYDEKKER as Genus *non det* Sp. 3 (Text fig. 10); the specimen is precisely comparable to the reconstructed specimen E-82a (Text fig. 11) earlier described by FALCONER (1859) as female of *Colossochelys atlas* and then by LYDEKKER (1885) as Genus *non det.* Sp. 1. The specimen is considerably smaller than the holotype (BMNH-40630, see Plate 4, fig. 1 and Text fig. 12). We consider that the specimen's ontogenetic stage lies between specimen E-84 and the holotype (BMNH-40630) and represents growth stage 5 (Text fig. 4) similar to specimen E-82a. The seam between the gulars and humerals is not preserved on the specimen. The growth lines on the visceral surface of the plastron indicate an anterior development of the epiplastron. The dorsal surface of the epiplastron is convex.

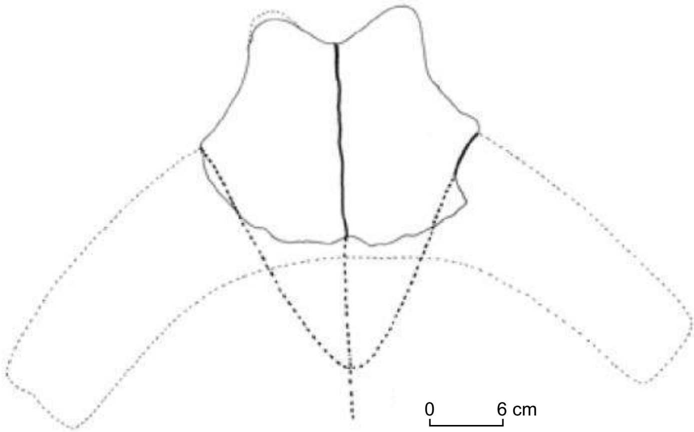


Fig. 10. Reconstructed epiplastra of a young *Megalochelys sivalensis* (E-84). The specimen represents an intermediate stage of development that lies between the specimen E-76 and E-82.

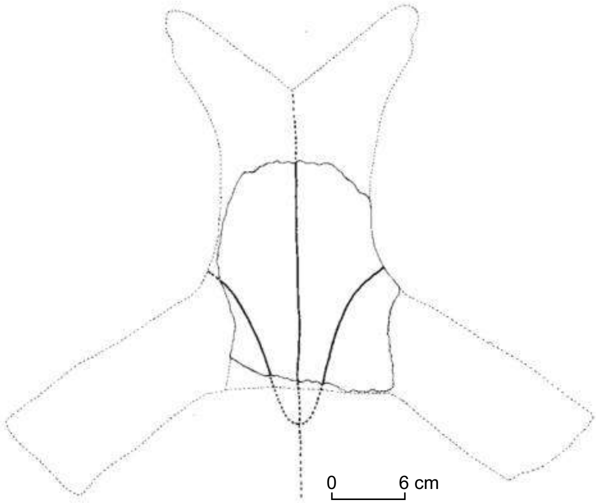


Fig. 11. Reconstructed epiplastra of *Megalochelys sivalensis* (E-82A). The specimen is similar to E-76 (Fig. 9). Note the narrow angle between the humero-gular seam. This angle is wider in juvenile and young individuals; also, the humero-gular seam is laterally more concave in grown individuals.

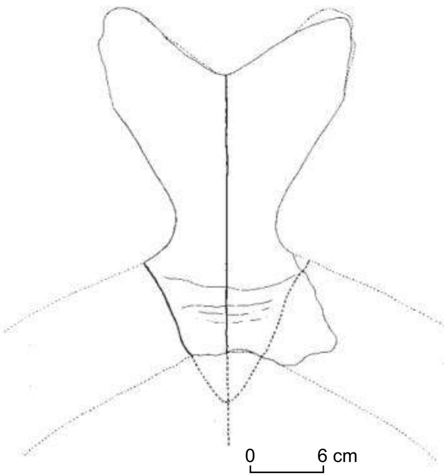


Fig. 12. Reconstructed epiplstra of *Megalochelysis sivalensis* (BMNH 46030). This is the holotype specimen first described by FALCONER & CAUTLEY (1837).

Material: Right peripheral 11 (E-86). The material is catalogued in the Indian Museum, Kolkata and was earlier described by THEOBALD (1879) and LYDEKKER (1885) as *Cautleya annuliger*.
(Plate 4, fig. 2 & Text fig. 13)

Locality: Middle Siwaliks of Nila, Punjab, Rawal Pindi, ?Middle Pliocene (THEOBALD, 1879).

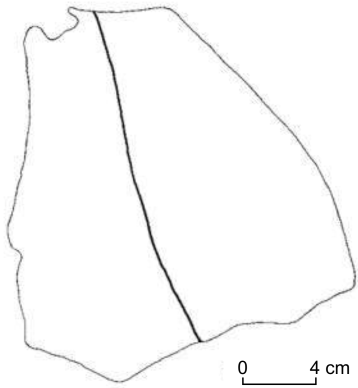


Fig. 13. Reconstructed right peripherial of *Megalochelys sivalensis* (E-86). The concave outer rim exhibits probably the contacts with the last pleural and metaneural (THEOBALD, 1879; LYDEKKER, 1885).

Description

The specimen has narrow proximal and wide distal margins. It is furrowed with the anterior margin of the postcentral. The maximum length of the peripheral (along the anterior margin of the postcentral) is approx. 12.7 cm. The maximum width of the peripheral is approx. 12.3 cm and the width at the proximal end is approx. 5.5 cm. The size of the specimen indicates an animal having the size of epiplastron E-82, i.e. an adolescent.

The specimen is peculiar in having the situation (concave outer surface) exhibiting its contacts with the last pleural and metaneural (THEOBALD, 1879 & LYDEKKER, 1885). If this is the situation, is it very likely that the posterior peripherals had a similar connection -indicating towards palustrine habits of adolescent *Megalochelys*- as shown by the living *Manouria* (*sensu* LYDEKKER, 1885)? *Megalochelys* is known from the Indian Subcontinent by very poor bone material (mainly nuchal). For the affirmation of a possibility of the above hypothesis, more material is needed to approach to a comparative analysis.

Material: Cast of a skull (E-77), catalogued in the Indian Museum, Kolkata. The original (BMNH-39819) is catalogued in the British Museum (Natural History), London and was earlier illustrated by FALCONER (1868) and LYDEKKER (1885) as *Colossochelys atlas.*
(Plate 4, fig. 3 & Text fig. 14).

Locality: Siwalik hills, North of India (FALCONER, 1868, LYDEKKER, 1885).

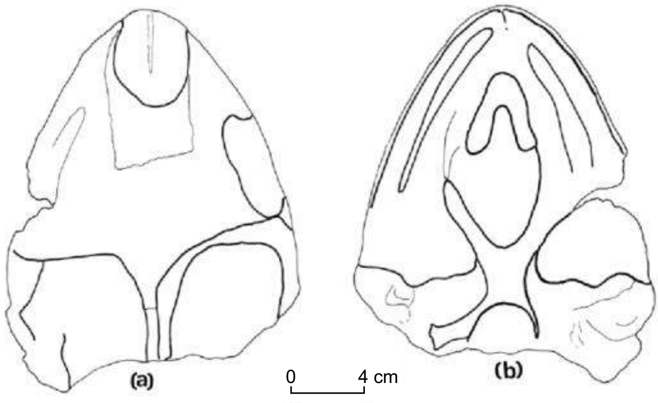


Fig. 14. Cranium of *Megalochelys sivalensis;* skull of specimen E-77 which is a cast of the original specimen (BMNH-39819). (a)- Dorsal view, (b) ventral view.

Description

The skull is broken posterior behind the quadrates and basisphenoid. The anterior part of the prefrontal is also broken. On the skull, no traces of the bony sutures can be detected indicating that the specimen belongs to an adult.

On the dorsal surface, the suture between the prefrontal and the frontal is indistinct. The characteristic prefrontal is broken; but enough remains to indicate that the nasal opening was probably higher than wide and that the front margin of the premaxillary projected far in advance of the prefrontals as to cause the nasal opening to slope downwards. The prefrontals and frontal are characteristically wide and convex (maximum width of the prefrontals is approx. 7.8 cm and that of the frontal is approx. 11.1 cm). The frontal region is elevated in front of the orbits. The suture between the right frontal and postorbital is distinct. The postorbital bar is characteristically broad (1.6 cm). The width of the parietal at the level of the anterior margin of the ootic is approx. 4 cm. The suture between the frontal and the parietal and also between the postorbital and parietal is indistinguishable. The parietal is posteriorly incomplete. The quadrate is distinct but the suture between the quadrate and the squamosal (incomplete on the specimen) is indistinct.

On the ventral surface of the skull, a feeble premaxillary process is seen on both the sides; its contact with the maxillary is indistinct. The palate is deeply concave. The vomer is wide and deeper than the palatine. The suture between the right palatine and the pterygoid is faintly seen. The pterygoid is large but posteriorly incomplete. A horse-shoe shaped basisphenoid is distinct. The anterio-posterior diameter of the basisphenoid is approx. 2.2 cm. Posterior to the basisphenoid, the skull is broken. The total length of the skull from premaxillary to basisphenoid is approx. 19 cm and its width across the orbits is 15.6 cm. Such a large size of the skull is not comparable to any of the living turtles, however, in general morphological features it is similar to the skulls of living *Manouria* and *Testudo.*

Discussion

Megalochelys, the largest extinct land tortoise very interestingly possesses both primitive and evolved characters. Amongst the primitive characters of testudinids it has a hingeless carapace and plastron, presence of a cervical and divided postcentral (only in young individuals), thickened gular area and long but somewhat narrow and elongated gulars; whereas, among the derived characters it possesses absence of a cervical and undivided postcentral in adults and an entoplastron which is anterior to the humero-pectoral seam. The gulars overlapping the entoplastron (a derived condition possessed by *Megalochelys*) was probably related to the enormous increase in size and might be weakly associated with the plastral mobility (CRUMLEY, 1984).
The immature specimens of testudinids have relatively shorter and broader cervical which becomes narrow very quick as size increases (CRUMLY, 1984) but in Megalochelys *sivalensis*, the cervical is completely lost in the adult individuals and at the place of the cervical, the first marginals join narrowly each other in front of the first central.

The small testudinid individuals generally have short and broad non- overlapping gulars. As growth continues the gulars acquire a long, less broad shape (CRUMLY, 1984). This change is probably associated with the selective growth axes. In large testudinid individuals such as *Megalochelys,* the growth is predominantly along the anterio-posterior axis (growth rings directed mostly transversely) and therefore the gulars are not very broad but are rather elongated and overlapping the entoplastron.
CRUMLEY (1984a) discussed the primitive and evolved features of the testudinids; he mentioned that the equal mid-seam length of the gulars and femoral is a primitive character. This statement may not be true for *Megalochelys*, as it has a tendency of anterior extension of the epiplastron region (specimen PU A/702 shows equal mid-seam length of gulars and femorals, BADAM, 1981). This unique character of *Megalochelys* is not shared by other testudinids, therefore, the mid-seam length of the gular can not be compared with that of the femorals.
The above discussion suggests that *Megalochelys* possessed primitive characters but only in young individuals, as the growth continued the more derived characters appeared on the shell of *Megalochelys*. In light of these facts, more ecological and climatic data would be needed to understand the reason of extinction of this large, evolved and successful testudinid.

Indotestudo LINDHOLM, 1929

Synonymy
1974: *Geochelone* (*Indotestudo*) Auffenberg

Distinguishing features
Indotestudo was elevated to full generic rank by ERNST & BARBOUR (1989). It is a medium-sized Asiatic tortoise found in southern peninsular India, northern India, Nepal, Bangladesh, southward to Vietnam and Thailand and on Celebes and Halmahera, Indonesia. It has a hingeless, low carapace which is usually elongated. The cervical is narrow; it is absent in *I. forstenii*; the posterior marginals may be serrated; undivided postcentral. The hingeless plastron has a posterior deep notch which completely separates the anal scutes. The humero-pectoral seam intersects the entoplastron (it is posterior to entoplastron in *Geochelone* s.l.). In *Geochelone* s.l. only two marginals (rarely three) contact the first lateral whereas in *Indotestudo* three marginals contact the first lateral.

Indotestudo forstenii SCHLEGEL & MÜLLER (1844)

Holotype: Not defined (IVERSON, 1992)

Type Locality: Gilolo (Halmahera Island, Moluccas, Indonesia)

Habitat and Distribution
It is found in evergreen and semi-evergreen forests. The species is found within rock clefts along rivers and streams and under boulders inside forests. It is primarily a herbivorous species, eating mostly grass, fungi, fallen fruits, flowers etc., but occsasionally feed on insects, frogs, fishes also. The species is restricted to the Western Ghats of south-western India, though a population in Indonesian islands, believed to be introduced, also exists (DAS, 1995).

Synonymy
1907: *Geochelone travancorica* Boulenger
1982: *Geochelone travancorica* Groombridge
1982: *Geochelone forstenii* Groombridge
1984: *Geochelone travancorica* Hoogmoed & Crumly
1985: *Geochelone travancorica* Tikader & Sharma
1991: *Indotestudo forstenii* (Das)
1992: *Indotestudo forstenii* (Iverson)
1995: *Indotestudo forstenii* (Das)

Distinguishing features

The shell is elongated and somewhat depressed; the nuchal is absent; the centrals are broader than long; the postcentral is joined; the humero-pectoral seam is transverse and crosses the entoplastron (in *Geochelone* s.l. the entoplastron is anterior to the humero-pectoral seam). The interpectoral seam is shorter than the interhumeral seam (in *Indotestudo elongata* the interpectoral seam is as long or longer than the interhumeral seam); the upper jaw is slightly hooked, trachea short (DAS, 1995).

It can be distinguished from *Geochelone* s.l. and *Indotestudo elongata* on the basis of the absence of a cervical.

Material: Complete shell (SFP 213), catalogued in the Field Museum of the Saketi Fossil park, Saketi. The material was collected by R. L. GARG.
(Plate 4, fig. 4 & Text fig. 15).

Locality: Johran Village, Nahan, Tatrot Formation, Upper Pliocene.

Description

Carapace:
The shell is small, domed and highly arched. There is no trace of depression on the centre of the carapace. No trace of central or lateral keels are found on the carapace. The marginals and peripherals are almost vertical.

On the carapace, neurals 2-5, peripherals 6 & 7, and marginals 7 & 8 are not distinct. The cervical and nuchal are incomplete.

Cervical: The cervical is not perserved (probably absent?).

Centrals: The 1st central is pentagonal, having angular anterior margin. It overlies the nuchal and the 1st neural. The 2nd central is larger than the 1st and is hexagonal; it is broader than long. The 3rd central is larger than the previous two centrals and is also broader than long. The 4th central is slightly broader than long; it is smaller than the 3rd central but longer than the 1st and 2nd. The 4th central is overlying the 3 neurals. The 5th central has arcuade posterior margin; it is as long as the 1st central. A single undivided postcentral is also seen on the carapace.

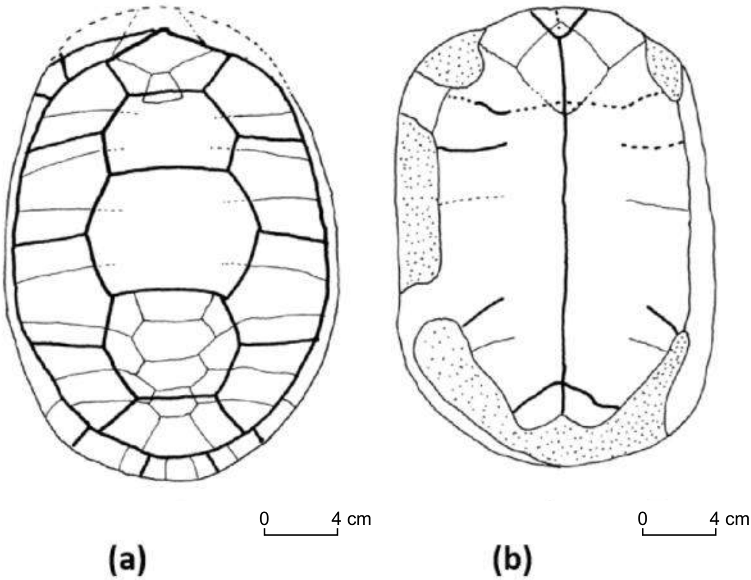


Fig. 15. Shell of *Indotestudo* cf. *forstenii* (SFP-213). (a) restored carapace in dorsal view; (b) ventral view showing plastral surface.

Laterals: The 1st lateral is quadrilateral with arcuade outer margin. The 2nd and 3rd laterals are pentagonal. The 4th lateral having posterior margin is smaller than the anterior. The margins of the laterals are straight.

Marginals: The shell has distinctly preserved 2nd – 11th marginals; 1st marginal is completely broken whereas the 2nd marginal is partly broken at the distal margin. All the marginals are quadrilateral. The 2nd marginal is reaching upto the 1st lateral. The 3rd, 4th and 5th marginals are contacting the 1st lateral. The 6th marginal is reaching upto the 2nd lateral. The 7th marginal is contacting the 2nd lateral and the 8th is reaching upto the 3rd lateral. The 9th marginal is reaching upto the 4th lateral and 10th is contacting the 4th lateral. The 11th marginal is reaching upto the 5th central.

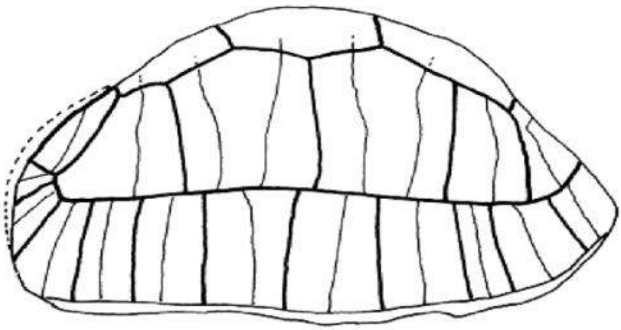


Fig. 15 (c). Left lateral view of *Indotestudo* cf. *forstenii* (SFP-213).

Nuchal: The restoration of the anterior portion suggests that the nuchal is hexagonal having wider anterior margin. It has nearly straight lateral margins. It is furrowed with the anterior margin of the 1st central.

Neurals: The 1st neural is narrow anterior and wide posterior; it is rectangular. The 2nd – 5th neurals are not distinct due to erosion of the dorsal surface (5th is partly preserved). The 6th neural is hexagonal and is broader than long. The 7th neural is also hexagonal so is the 8th neural. The 7th neural is smaller than the 6th but also broader than long. The 8th neural is smaller than both the previous neurals but also hexagonal and broader than long. A metaneural and the pygal are also distinct. The metaneural has slightly concave lateral margins; its anterior margin is shorter than the posterior. The posterior termination of the pygal is not clear due to broken nature of the carapace.

Pleurals: The proximal end of 1st - 5th pleurals are broken; however, the posterior suture of 5th pleural is complete. The 5th and 7th pleurals are proximal wider, whereas, 6th and 8th are distal wider. The 5th, 6th and 7th pleurals are pentagonal; the 8th neural is quadrilateral with arcuade distal margin.

Peripherals: The peripherals 1 – 3 are contacting the 1st pleural; The 4th is reaching upto the 2nd pleural and 5th is reaching upto the 3rd pleural. The 6th peripheral is contacting half of the 3rd and almost complete 4th pleural. The 7th peripheral contacts partially 4th, complete 5th and half of the 6th pleural. The 8th peripheral is contacting the 6th pleural and 9th peripheral is reaching upto the 7th pleural. The 10th peripheral shares the 7th and 8th pleural. The 11th peripheral reaching upto the metaneural. The peripherals are rectangular; the sutures between peripherals are straight.

The dimensions of the species based on the restored carapace are as follows:
The straight carapace length (SCL) = 17.6 cm
The straight carapace width (SCW) = 11.7 cm
The straight carapace height (SH) = 10.8 cm

Plastron: The preserved parts of the plastron include traces of the seams between gular-humeral, humero-pectoral, pectoral-abdominal, abdominal-femoral, and femoro-anal. The traces of the suture between epi-hyoplastron, hyo-hypoplaston, and hypo-xiphiplastron are also present.

Gulars: On a restored carapace, the gulars appear triangular with arcuade anterior margin; the lateral margins of the gulars are meeting on the midline and intersecting the anterio-lateral sutures of the entoplastron. The mid–seam length of the gulars is considerably lesser than that of femorals.

Humerals: The humeral is quadrilateral with arcuade distal margin. The proximal margin of the humeral is narrower than the distal margin. The humero-pectoral seam is sinuated and intersects the entoplastron.

Pectorals: The pectoral is considerably narrower than the abdominal (almost one-fourth of the abdominal); it is rectangular; its mid – seam length is similar to that of gulars and anals.

Abdominals: The abdominal is rectangular. The posterior margin of the abdominal is dipping downwards meeting the lateral margins of the plastron just above the suture between hypoplastron and xiphiplastron. Its mid - seam length is much more than that of other scutes.

Femorals: The posterior margin of the femoral is sloping downward and sinuated distal; its proximal and distal width is nearly equal; however, its anterior width is more than the posterior width.

Anals: The anal has arcuade posterio-lateral margin; the anal is notched posterior and is nearly triangular.

Epiplastra: The epiplastron is quadrilateral; its distal width is more than the proximal width. It has nearly straight anterior margin.

Entoplastron: The entoplastron is rhombiform; it is intersected by the humero-pectoral seam.

Hyoplastra: The hyoplastron is pentagonal with arcuade distal margin; it is anterior narrower and posterior wider. The suture between hyoplastron and hypoplastron is nearly straight.

Hypoplastra: The hypoplastron is rectangular and is almost as long as the hyoplastron. The suture between hypoplastron and xiphiplastron is shallow dipping downward.

Xiphiplastra: The xiphiplastron is wider anterior and narrower posterior; it has arcuade posterio-lateral margin.

The maximum length of the restored plastron is approx. 15.5 cm and maximum width is approx. 10.5 cm.

Testudinidae indet.

Synonymy
1991: *Geochelone* (? *Hesperotestudo*) sp. indet. West *et al.*
1994: Testudines indet. Corvinus & Schleich

Material: Peripheral fragment (NHM/TU 1989/c) **and distal part of 1st pleural** (NHM/TU 1989/d). The material is catalogued in the Natural History Museum of Tribhuvan University, Kathmandu, Nepal.
(Plate 5, fig. 1).

Locality: Surai Khola, Upper Siwaliks

Description

A fragment of the peripheral (NHM/TU 1989/c) of a testudinid is illustrated in CORVINUS & SCHLEICH (1994). The distal surface of the peripheral is smooth and rectangular. The two sides of the peripheral are complete and the other two sides are broken thus a precise measurement of the peripheral is not possible. However, a large size of the peripheral indicates towards a large animal comparable to *Geochelone* (70 – 80 cm straight carapace length).
Another specimen NHM/TU 1989/d is probably a distal end of the 1st pleural. The proximal and posterior margins of the pleural are broken and therefore, its size measurement is also not possible. The distal margin of the pleural is arcuade. From its visceral morphology and more comparative material, a generic identifcation of the specimen might be possible.

Family Trionychidae BELL, 1828

The shell is much depressed and covered with a cartilageous layer and no horny shields. The shape of the ossified part of the carapace of trionychids varies from a highly arched rectangle to a nearly flat circular disc. The genus *Lissemys* is mostly like other freshwater cryptodires, having bony carapace that is longer than wide; most *Aspideretes/Nilssonia* have an oblong to circular ossified carapace; whereas, genus *Chitra* has a rather flat and actually wider than long carapace (MEYLAN, 1984). As the disc becomes flatter and wider, it constitutes a smaller portion of the total carapace, which is a derived condition in trionychids (MEYLAN, 1984).

Horny scutes are absent; the reduction of the 8th pleural is common which is a derived condition however, cyclanorbines and old world trionychines have a large 8th pleural. There is a trend toward the loss of the 8th pleurals in new world forms (MEYLAN, 1984). The most posterior pair of the pleurals may meet at midline; no pygals or metaneurals. The peripherals are absent (except for vestigial ones in *Lissemys*). The distal end of the ribs is projecting freely; a plastral brigde is absent.

The plastron is somewhat reduced with a central lacuna in modern forms and the lateral fontanelles; the plates in the plastron are reduced and so are the sutures between them. Thus, the presence of plates in the plastron is considered a primitive condition. MEYLAN (1984) considered seven plates as a primitive condition and an increase or decrease in the number a derived condition. The anterior portion of the plastron is highly modified; there are paired crecentric structures present apparently being neomorphs; a median V-shaped fused epiplastron, an entoplastron is absent (an entoplastron is present in *Lissemys).*

The temporal region is widely open with a loss of the contact of the parietal and the postorbital with the squamosal. The snout is usually a long proboscis. The premaxillary is fused. The postorbital is small, the jugal is relatively large, in contact with parietal except on some *Nilssonia/Aspideretes*. A small palatine fenestra is present. The pterygoid is broad, in contact with the maxillary, separated by the basisphenoid which is in contact with the palatines. The dentary reaches lateral upto the posterior end of the jaw; the neck is long and retractile; there are no biconvex centra in the neck vertebrae. The limbs are paddle like; there are three claws only; the feet are elongated (ROMER, 1956). The 'soft shell turtles' are seldom found far from water and feed on both plant and animal matter; many are aggressive capable of inflicting severe injury.

Subfamily Cyclanorbinae LYDEKKER, 1889

The subfamily is characterised by seven or more plastron plates; the hyo- and the hypoplastra are fused; a xiphiplastron surrounding the middle prong of the posterio-medial process of the hypoplastron is present; The presence of a hypoplastron lateral to the xiphiplastron at their junction is a derived condition unique to cyclanorbine trionychids (MEYLAN, 1984). The nuchal bone of the carapace has a conspicuous ventral ridge on each side which extends under the 1st pleural. The members of this subfamily are restricted to Africa, India and Burma (ERNST & BARBOUR, 1989).

Lissemys SMITH, 1931

Formerly regarded as a monotypic genus containing only the Asiatic softshell *Lissemys punctata* LACÉPÈDE (1788), three species are now listed.

Lissemys punctata (LACÉPÉDE, 1788)

Holotype: MNHN-7978.

Type Locality: "des grandes Indes" restricted by WEBB (1980) to Pondicherry, Coromandel Coast, India.

Habitat and Distribution

Three species are listed: *Lissemys punctata* (BONNATERRE. 1789)*; Lissemys ceylonensis* (GRAY, 1856) and *Lissemys scutata* (PETERS, 1868). The first two occur on the Indian subcontinent and the third is restricted to Thailand and Irawaddy, Sittan and Salween rivers in Myanmar (Burma). The typical coloration is olive brown, grey-green or pale green above and pale yellow, cream or pink yellow. The Indian flapshell turtle (*Lissemys punctata)* is widely distributed on the Indian subcontinent and in peninsular India, South of Ganga and Indus, as well as the Andaman Islands where it has probably been introduced. The subspecies *andersoni* is found in northern India, Pakistan, Bangladesh and Nepal, near the areas of the rivers Indus, Ganga, Brahmaputra and their tributaries. This heavily exploited species is still abundant in many areas in the region, as it adopts to a variety of environments (DAS, 1991, 1995) from salt marshes, river, ponds, ox-bow lakes, streams, rice field and aquatic burial sites to even gutters and canals in metropolitan cities. The temperament of individuals varies; some refuse to bite, while others plunge with open mouths and withdraw their heads into the shell to tear pieces out of the object seized. It is largely carnivorous but also herbivorous (DAS, 1995), feeds on frogs, fishes, tadpoles, snails, insects, earthworms and water plants.

Synonymy

1788: *Testudo punctata* Lacépède
1795: *Emyda granosa* Schoepff
1854: *Emyda vittata* Peters
1855: *Emyda ceylonensis* Gray
1885: *Emyda vittata* Lydekker
1886: *Emyda vittata* (Lydekker)
1885: *Emyda sivalensis*, Lydekker
1886: *Emyda sivalensis*, (Lydekker)
1885: *Emyda lineata* Lydekker
1886: *Emyda lineata* (Lydekker)
1885: *Emyda palaeindica* Lydekker
1886: *Emyda palaeindica* (Lydekker)
1885: *Trionyx* sp. (Lydekker)
1886: *Trionyx* sp. (Lydekker)
1991: *Lissemys punctata* (Das)
1991: *Lissemys punctata* (West *et. al.*)
1992: *Lissemys punctata* (Iverson)
1994: *Lissemys punctata* (Corvinus & Schleich)
1994: *Lissemys* cf. *punctata* (Corvinus & Schleich)
1995: *Lissemys punctata* (Das)

Distinguishing features

The carapace is oval and domed; it is unique among the trionychids in having a series of peripheral bones along the posterior rim (primitive character; MEYLAN, 1984) which are not homologous with the peripherals of hard-shelled turtles (ERNST & BARBOUR, 1989). These peripherals are not present in any other members of the family. It is different from *Chitra* by the presence of a prenuchal bone (derived condition; MEYLAN, 1984); in *Lissemys punctata* two neural bones separate the first pair of pleural, whereas in *Chitra* a single neural separates the first pair of pleurals and in *Nilssonia/Aspideretes* a preneural and a neural or one or two pairs of the neurals separate the first pair of the pleurals. In *Lissemys* 7th and 8th pairs of the pleurals touch medially; in *Chitra* and *Nilssonia* only 8th pair of the neural touches medially. Seven plastral plates occur in *Lissemys*; five occur in *Nilssonia*; and four (rarely five) plastral plates occur in *Chitra*. In *Lissemys* two xiphiplastral plates may be fused mesially, reducing the total to six. *Lissemys* is differentiated from *Chitra* and *Nilssonia* by the presence of an entoplastral plate. In *Chitra* and *Nilssonia/Aspideretes* the hyo- and the hypoplastra are not fused and a preplastron and an epiplastron are not in contact whereas in *Lissemys* the hyo- and the hypoplastra are fused and the epiplastra is in contact with the preplastra; also, there is a hinge at the point of attachment of the preplastra to the epiplastra (SRIVASTAVA & PATNAIK, 2002). The plates are much smaller and easy to distinguish from other Trionychids.

Material: Nearly complete shell (E-163). The specimen is catalogued in the Indian Museum, Kolkata. The specimen was obtained in exchange with the Museum of Comparative Anatomy at Cambridge and was earlier described by LYDEKKER (1885) as *Trionyx* sp. 2.
(Plate 5, fig. 2).

Locality: Siwaliks of India.

Description

On the dorsal aspect the carapace of the specimen is considerably damaged, leaving no traces of neurals. However, the sutures between the pleurals are distinguishable occasionally on the carapace. On the rim of the carapace peripherals are also distinct. Based on typical callosities and characteristic peripherals, it can easily be identified as *Lissemys punctata* s.l.

On the ventral side, the plastron is well preserved excepting the epiplastra which are anterior broken. The hyo- and hypoplastra are fused having concave anterior and posterior margins. The anterior margin is less concave than the posterior one; these margins tend to become convex near the mid-line. The lateral margins of the hyo-hypoplastral plates are nearly straight. There is a well marked entoplastral plate which is characteristic of *Lissemys*. The entoplastron is large and is in contact with hyo-hypoplastral plates. In *Lissemys punctata* the entoplastron is of moderate size and does not touch the hyo-hypoplastral plates (as in specimen 39618 catalogued in the British Museum, described as *Emyda vittata,* LYDEKKER, 1885, 1886).

Remarks:
The age consideration of the material is questionable as the material was obtained by the Indian Museum in exchange from the Museum of Comparative Anatomy, Cambridge. It was purchased by the latter institution amongst a small collection of Siwalik fossils. Rest of the material has been described by LYDEKKER (1885, 1886) as from Siwaliks of Punjab without giving any precise age and locality information.

The anterior peripherals and other associated material recovered by THEOBALD (1879) from the Siwaliks of Punjab and described by LYDEKKER (1885, 1886) also belong to *Lissemys punctata* s.l.. The material classified as *Emyda sivalensis* and *Emyda lineata (*LYDEKKER, 1885, 1886) is very close to *Lissemys punctata punctata*; whereas *Emyda palaeindica* is close to *Lissemys (punctata) scutata.*

cf. *Lissemys* SMITH, 1931

Material: Left epiplastron (NHM/TU 1989/37, cast: BSP 1989 XVIII 21), catalagued in the Natural History Museum of Tribhuan University, Kathmandu, Nepal.
(Plate 5, fig. 3).

Locality: Surai Khola, Upper Siwaliks

Description

The specimen NHM/TU 1989/37 was casted by the second author and was illustrated in CORVINUS & SCHLEICH, 1989 (as BSP 1989 XVIII 21). It is probably a left epiplastron with broken anterior margin. The specimen measures 8.8 X 4.8 cm. Its surface shows pustulate rugosity of isolated approximately 1 mm big tubercles. The specimen was compared with the left epiplastron of *Lissemys*; the length of the fossil as well as the living specimen was found to be identical whereas the width of the fossil specimen is 1 cm more than that of the living specimen. The general shape of both the specimens are rather identical.

Trionychidae indet.

Synonymy:
1978: Trionychidae indet. West *et al.*
1991: Trionychinae indet. West *et al.*
1994: Trionychidae indet. Corvinus & Schleich

Material: Fragmentary part of a large neural bone (NHM/TU 1989), **fragmentary neural** (NHM/TU 1989/44), **distal pleural fragment** (NHM/TU 1989/40, cast: BSP 1989 XVIII 23), **proximal pleural fragment** (NHM/TU 1989, cast: BSP 1989 XVIII 20). The material is catalagued in the Natural History Museum of Tribhuan University, Kathmandu, Nepal.
(Plate 5, figs. 4 – 6 & Plate 6, fig. 1).

Locality: Surai Khola (BSP 1989 XVIII 20, NHM/TU 1989), Dang Valley (NHM/TU 1989/40), Rato Khola (NHM/TU 1989/44).

Description

A large fragmentary neural (NHM/TU 1989/, Plate 5, fig. 4) was first described by CORVINUS & SCHLEICH (1994). The bad preservation and highly fragmentary nature of the specimen led authors (op. cit.) to speculate that the material might be a crocodile. We examined the material with care and could conclude that the specimen is a large neural of a trionychid similar to the genus *Chitra*. On the visceral surface of the neural, groove for the vertebral column and on the dorsal surface callosities are also distinct.

Another specimen NHM/TU 1989/44 (Plate 5, fig. 5) is comprising fragmentary neural bones from Rato Khola and was casted by the second author and described in CORVINUS & SCHLEICH (1994). The callosities on the neurals (probably neurals 2 & 3) are distinct. The neurals are hexagonal; the maximum width of the neurals is more than their maximum length. The shape and size of the neurals is comparable to that of the living *Lissemys*.

A distal pleural fragment (NHM/TU 1989/40, Plate 5 fig. 6) from Dang Valley, (cast: BSP 1989 XVIII 23) was described by CORVINUS & SCHLEICH (1994) as Trionychidae indet. As suggested by them, it is very difficult to assign the material to a genus due to its fragmentary nature. The callosities clearly designate the material under the family Trionychidae. The proximal end of the pleural is broken. On the visceral surface, the rib impression is distinct. The large size of the pleural relates it to Nilssonia/*Aspideretes* and *Chitra*.

The specimen NHM/TU 1989/ (cast: BSP 1989 XVIII 20) from Surai Khola is a proximal fragment of a left pleural (Plate 6, fig. 1). The specimen is distally broken. The surface callosities are dintinct. The specimen belongs to a large trionychid comparable in size to *Nilssonia*/*Aspideretes* and *Chitra*.

Family Geoemydidae (GAFFNEY & MEYLAN, 1988)

The shell is somehow convex, apparently depressed and covered with horny plates; the feet are webbed and adapted for swimming.

The skull is relatively small and smaller to those of testudines. The temporal region is widely emarginated from behind, so that the squamosal does not touch

the parietal; there are four to five claws. The carapace is usually low arched but may be considerably domed in some species. A central keel may be present or absent; some species also have a pair of the lateral keels. The carapace and the plastron are usually united by a broad bridge. The plastron is well developed; a mesoplastral bone is absent. The dentary occupies nearly complete outer surface of the jaw. The maxilla and the quadratojugal are separated and are rarely in contact. The frontal often enters the orbital margin. The quadrate usually opens behind. The feet are not markedly shortened; commonly more than 2 phalanges in the digits 2 and 3 (ROMER, 1956; ERNST & BARBOUR, 1989). The batagurids may be herbivorous or carnivorous but the majority are omnivorous.
Today, the family is represented on all continents but Australia (and Antarctica); the fossil record indicates that the family was more widely spread in Europe and Asia than at present and ranges in age from Upper Cretaceous to recent.

Subfamily Batagurinae GRAY, 1870

The turtles with the well-developed axillary and inguinal buttresses contacting the pleurals and biconvex eighth cervical vertebra (HIRAYAMA, 1985; GAFFNEY & MEYLAN, 1988); the limbs and the forehand are scaled; the limbs are with or without webs. The 'Asian pond turtles' may be herbivorous or carnivorous, though the majority are omnivorous. The batagurines range in age from Palaeocene – Recent. Presently Asian pond turtles are found in Southern Europe, Northern Africa, Southeast Asia, Indonesia, The Philippines and Japan.

Omegachelys sahnii gen. et sp. nov.

Etymology: The name of the genus has been taken from the Greek word "Omega" (Ω) representing the shell outline of the turtle. The species name has been given in honour of Prof. Ashok Sahni an eminent vertebrate palaeontologist from India.

Holotype: SFP – 24, a carapace, catalogued in the field museum of the Saketi Fossil Park, Saketi.

Type locality: Pipal Wala Village (Nahan), Saketi Formation, Upper Siwaliks, H.P., India.

Distinguishing Features

Very large batagurine characterised by its typical shape. The shell outline is like the symbol of "omega" (Ω); the shell is highly convex, domed and antero-posteriorly much elongated. It forms an elongated hump in the central region. The centrals occupy a larger portion of the carapace and therefore the laterals are short. The 1st central is larger than that of any other batagurid turtles. It contacts the posterior border of the 1st marginal. The laterals are steeply inclined and the marginals are upturned and nearly horizontal. The nuchal is small and it is enclosed by the 1st central. The neurals are hexagonal and have their short-side towards posterior.

Material & Holotype: Anterior broken Carapace (SFP – 24). The material is catalogued in the Field Museum of Saketi Fossil Park, Saketi.
(Plate 6, fig. 2 & Text fig. 16)

Type Locality: Pipal Wala Village (Nahan), Saketi Formation, Upper Siwaliks.

Description

Carapace: The carapace is highly convex, elevated and arched, steeply sloping on sides (nearly vertical). It is slightly depressed in the centre and diagenetically deformed. The carapace outline is in the shape of "omega" (Ω) mostly, the carapace is smooth, specially the right portion where no bones or scutes are traceable.

On the left side of the carapace, traces of centrals 2-5 (2nd central is anterior broken), paired postcentrals, laterals 2-4, marginals 5-10, 4th neural, 4th pleural and peripherals 4-9 (4th peripheral is anterior broken) are noticed.

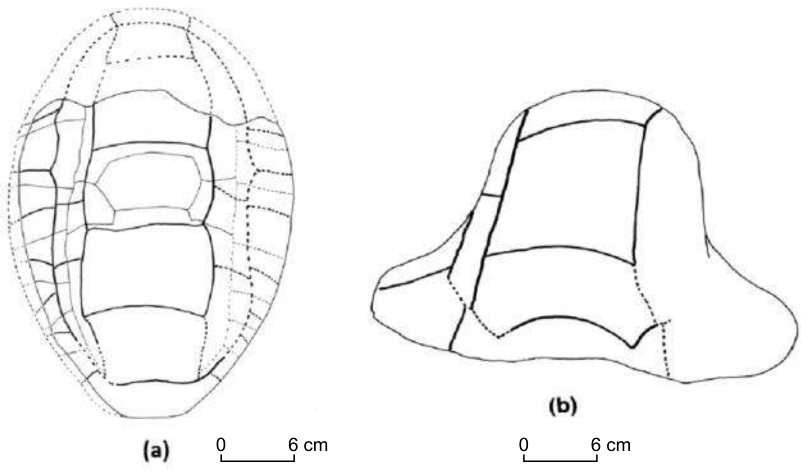
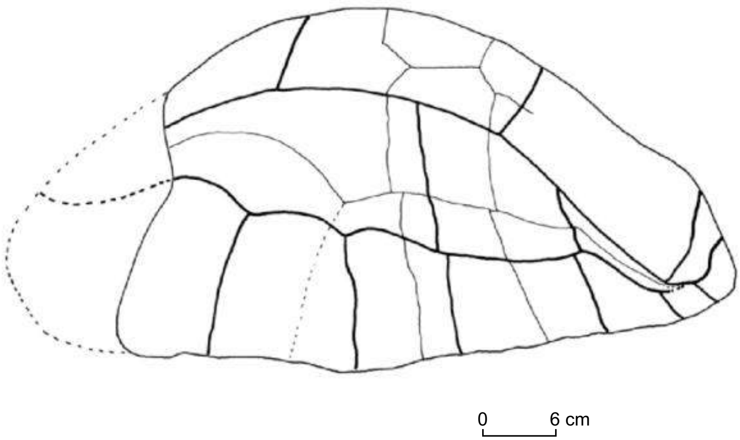


Fig. 16. Holotype of *Omegachelys sahnii* n. gen. et n. spec. (SFP-24).
a. Dorsal view of the carapace,
b. anterior view of the carapace

Centrals: The 2nd central is anterior broken, however, reconstruction of the carapace suggests that the 2nd central is sub-hexagonal and is broader than long. It is larger than the 3rd central, which is hexagonal and is also broader than long. The anterior margin of the 2nd central is convex. The 4th central is larger than the

3rd and like previous two centrals, it is also broader than long. The 4th central is as long as the 2nd but is broader than the 2nd and 3rd centrals. The carapace is posterior sloping from the margin between 3rd and 4th centrals. The 5th central is smaller than the preceding three centrals; it is also wider than long. A broad and paired postcentral is also traceable.

Laterals: The carapace is sloping lateral at a very steep angle, upto the proximal end of the marginals. The laterals are short and nearly vertical. The 2nd lateral is nearly pentagonal and is larger than the 3rd lateral. The 3rd lateral is rectangular and the 4th lateral is larger than the previous two laterals.



(c)

Fig. 16 c. Lateral view of the holotype of *Omegachelys sahnii* (SFP-24).

Marginals: The marginal portion of the carapace is so upturned that it tends to become horizontal. The 4th marginal is contacting 2nd lateral whereas the 6th marginal is contacting the 3rd lateral. The 10th marginal is contacting the 4th lateral. The marginals 5th 7th and 9th are proximally broader whereas, marginals 6th, 8th and 10th distally wider. The 5th marginal is nearly pentagonal. The marginals 6-10 are rectangular.

Neurals: On the carapace only one neural 4 is traceable. It is hexagonal and is broader than long. The remaining neurals are not distinct on the carapace.

Pleurals: The 4th is the only traceable pleural which has convex anterior and concave posterior margins (the margins are little sinuated). The lateral suture between pleurals and peripherals is highly sinuated.

Peripherals: The 4th, 6th and 8th peripherals are proximally broader, whereas, 5th, 7th and 9th are distally broader. The 4th peripheral is larger than the latter peripherals and is contacting the 2nd lateral.

The dimension of the restored carapace is as follows:
The straight carapace length (SCL) = 51 cm
The straight carapace width (SCW) = 34.5 cm
The straight carapace height (SH) = 26.5 cm

Material: Terminally broken large carapace (WIF/A-451), catalogued in the Museum of the Wadia Institute of Himalayan Geology, Dehradun. The material was earlier described by Nanda et al., (2016) as *Batagur* sp.
(Plate 6, fig. 3 & Text fig. 17)

Locality: 1 km ENE of Masumpur Village (Ambala), Basal part of the Pinjor Formation.

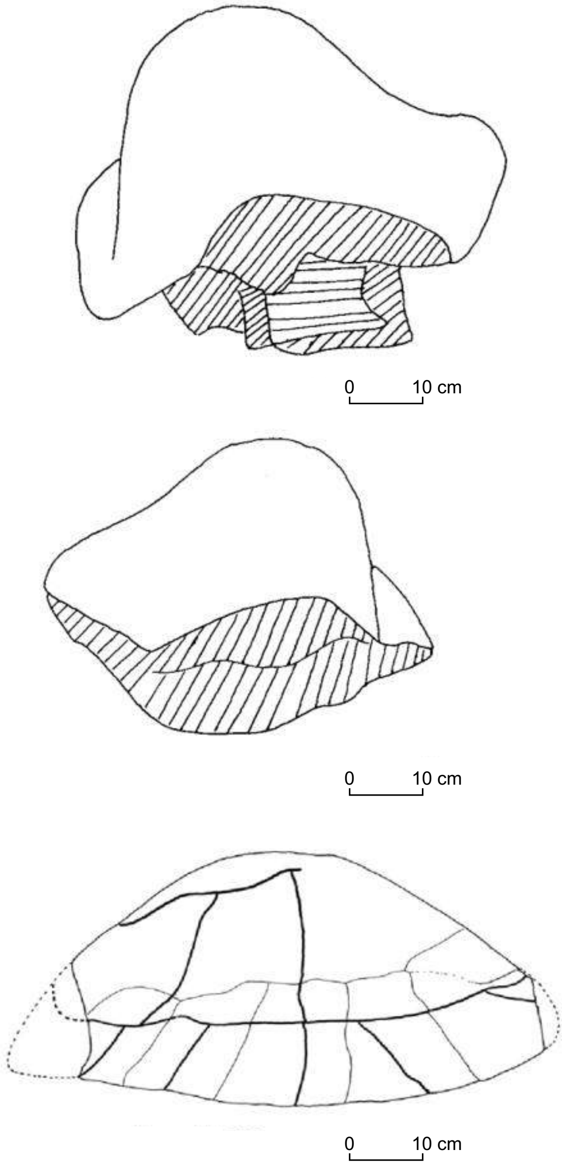
Description

Carapace: The shell is large, convex, depressed in the centre of the carapace, the shell outline is oval and is broken anterior and posterior. The shell is highly elevated and arched and is almost vertical on the lateral margins. The scute seams and bony sutures are mostly indistinct on the specimen which is a fully-grown adult; however, lateral 3, marginals 5-9 and peripherals 4-9 are distinguishable.

Laterals: The laterals are more or less vertical. The 3rd lateral is narrow proximal and wide distal; it has nearly straight anterior and posterior margins.

Marginals: The marginals are so upturned that they tend to become nearly horizontal. The seam between the marginals is either faintly seen or indistinct. The 5th marginal is narrow proximally and wide distally. The marginal 6 is nearly pentagonal; it is also wider distally than proximally. The 7th marginal is rectangular and is narrower proximal. The 8th marginal is pentagonal.

Peripherals: The anterior margin of the 4th peripheral is not distinct. The 5th peripheral is wider distal than proximal; its rectangular anterior and posterior margins are slightly sinuated and concave; The 6th peripheral is larger than the 5th and is also distal wider. It is also rectangular and has nearly straight posterior margin. The 7th peripheral is pentagonal; it is nearly as large as the 6th peripheral; it has distal sinuated posterior margin. The 8th peripheral is nearly rectangular and is smaller than the 7th peripheral. The posterior margin of 9th peripheral is not clearly seen.



a

b

c

Fig. 17. Carapace of *Omegachelys sahnii* (WIF/A – 451)
(a) anterior view; (b) posterior view; (c) reconstructed left lateral view.

The dimension of the carapace is as follow:
SCL (straight carapace length) = 94 cm
SCW (straight carapace width) = 50 cm
SH (straight height) = 42 cm

Material: Nearly complete shell (SFP 245) comprising of marginal and anterior broken carapace and broken plastron. The material was collected by B. C. VERMA. (Plate 6, fig. 4, Text fig. 18)

Locality: Moginand, Tatrot Formation, Late Pliocene.

Description

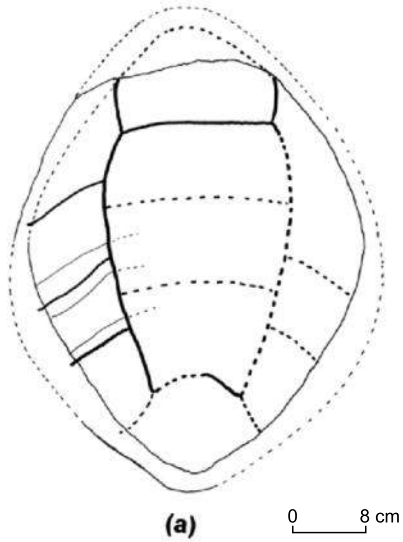


Fig. 18 a. Reconsctructed dorsal view of the shell of *Omegachelys sahnii* (SFP 245).

Carapace: The shell is domed, highly arched, diagenetically deformed and broken on the anterior and lateral margins. The shell outline is of "Omega" shape. There is no trace of central or lateral keels on the carapace. On the surface, scutes and bones are not traceable. However, a close examination reveals the traces of posterior margin of 1st central; 2nd, 3rd and 4th laterals and pleural 5. The carapace is depressed in the middle of the surface; besides in the central portion of the carapace many depression pits are present. The carapace is sloping on the laterals and then becomes nearly horizontal on the marginals; it is nearly in the shape of saddleback (narrower and elevated anteriorly, wider and lower posterior).

Centrals: The 1st central is much wider anterior reaching upto the posterior border of the 1st marginal. The posterior margin of the 1st central is nearly straight. The margins of the 2nd, 3rd and 4th laterals are also straight. A restoration of the centrals reveals that the centrals are broader than long.

Marginals: The seam between the marginals is not distinct. The anterior marginals of the carapace are nearly horizontal (upturned).

Pleurals: The 5th pleural is wider proximal and narrower distal.

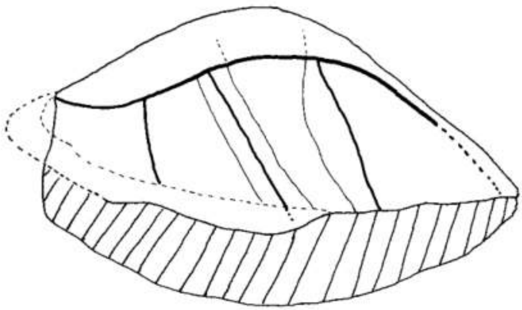


Fig. 18 b. Reconsctructed left lateral view of the shell of *Omegachelys sahnii* (SFP 245).

Plastron: On the plastral surface only the trace of median suture is distinguishable and remaining parts of the plastron are indistinguishable.

The dimension taken on the restored carapace is as follows:

The straight carapace length (SCL) = 50.5 cm
The straight carapace width (SCW) = 35.5 cm
The straight carapace height (SH) = 25.5 cm

Material: Anterior broken large shell (SFP-225), consisting of deformed carapace and plastron; catalogued in the Field Museum of the Saketi Fossil Park, Saketi.
(Plate 7, fig. 2)

Locality: Dewni ridge (Nahan), Saketi Formation, Upper Siwaliks

Description

Saddlebacked carapace which is narrower and elevated anteriorly, wider and lower posterior; shell outline is typical "Omega" shaped.
The carapace is large, domed, highly arched and slightly depressed on the centre. The surface of the carapace is smooth, the carapace scutes and bones are not traceable, indicating towards an adult animal. The carapace is anterior broken; posterior marginal part is also broken. It is lateral and anterio-posterior sloping. The lateral slope is steeper than the anterio-posterior slope. The marginals of the carapace are upturned tending to become horizontal.

The plastron part is also smooth on which no bones or scutes are traceable. The shell is diagenetically deformed lateral.

The dimensions taken on the restored carapace are as follow:
The straight carapace length (SCL) = 51.2 cm
The straight carapace width (SCW) = 37 cm
The straight carapace height (SH) = 27 cm

Material: Lateral half of the carapace (TU/NHM 1989/36). The material is catalogued in the Natural History Museum of Tribhuan University, Kathmandu, Nepal.
(Plate 7, fig. 3 & Text fig. 19)

Locality: Surai Khola, Upper Siwaliks, Late Pliocene.

Description

Carapace: The carapace seems to be highly diagenetically compressed; the size of the preserved part of the carapace is about 60 x 26 cm. There is a longitudinal hump on the discus part of the carapace; on the carapace no bony sutures or scute seams are distinguishable excepting the marginals and peripherals which are also highly fractured and broken. A very close observation reveals a seam between the laterals and between the laterals and centrals.

Centrals:
A restoration of the carapace suggests that the centrals are nearly hexagonal. The 1st central has wide anterior margin contacting the posterior border of the 1st marginal. The 4th central is nearly as wide as long. The 5th is wider posteriorly.

Laterals: The laterals are not clearly distinguishable. They are short and steeply inclined (nearly vertical). The seam between the laterals is nearly straight (based on restoration).

Marginals: The marginal part is highly fractured and therefore it is very difficult to dsecribe the precise shape and size of the marginals; however, on the basis of the restoration of the carapace it is observed that the 1st marginal is contacting

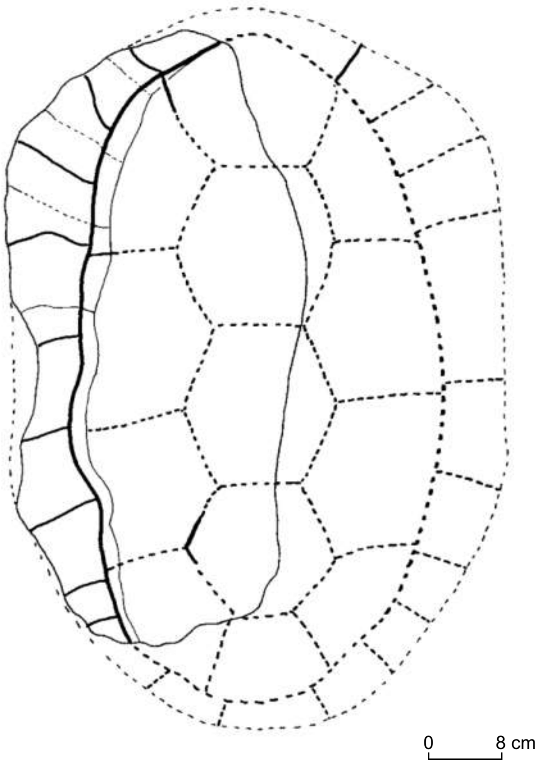


Fig. 19. Reconstructed dorsal view of a carapace of *Omegachelys sahnii* (TU/NHM 1989/36).

the 1st central. The 2nd marginal is reaching up to the 1st lateral. The marginal 3 and 4 are contacting the 1st lateral. The marginal 5 and 6 are contacting the 2nd lateral. The 7th is contacting the 3rd lateral and the 8th marginal is reaching up to the 4th lateral. The marginal 9 and 10 are contacting the 4th lateral. The marginal 11 is reaching upto the 5th central. The marginals are rather flat and horizontal. In general appearance the marginals are mostly rectangular. The anterior marginals are larger than the posterior ones.

Peripherals: The peripherals are not distinguishable on the specimen. A restoration suggests that the peripheral 4 is reaching up to the 2nd lateral.

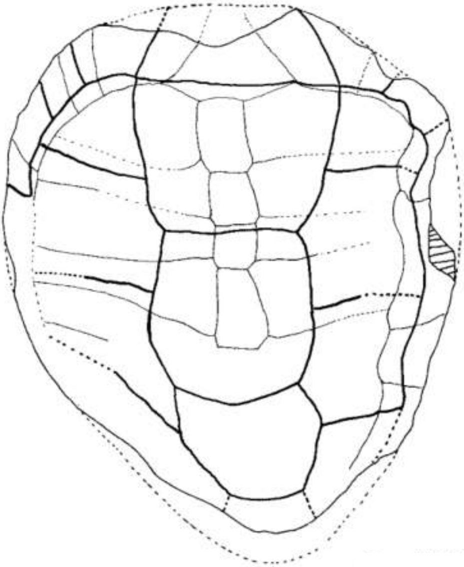
The length of the restored carapace is approx. 62 cm at a width of approx. 44 cm. The original height of the carapace is very difficult to calculate as the diagenetic compression is very high.

Material: Nearly complete carapace (H 18/1)
(Plate 7, fig. 4 & Plate 8, fig. 1 & Text fig. 20 a, b)

Locality: Upper Siwaliks of Himachal Pradesh (Precise locality information not available).

Description

Carapace: The carapace is large, domed, highly arched forming an elongated hump in the centre. The scutes are distinct but the bony sutures are traceable only here and there on the carapace. The restoration makes 1-4 neurals distinguishable. The right anterior and posterior marginals are not preserved. The carapace is terminally broken; cervical part is also broken.



(a)

0 5 cm

Fig. 20 a. Nearly complete carapace of *Omegachelys sahnii* (H18/1). The specimen is stored in the Indian Museum, Kolkata; dorsal view.

The carapace is lateral and anterio-posterior sloping. The lateral slope is steeper than the anterio-posterior slope. The marginals of the carapace are upturned and they tend to become horizontal. The cervical is not distinct on the carapace.

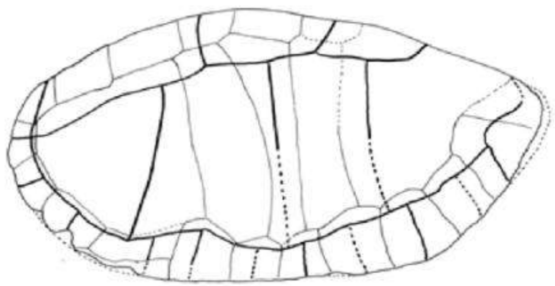


Fig. 20 b. Nearly complete carapace of *Omegachelys sahnii* (H18/1). The specimen is stored in the Indian Museum, Kolkata; lateral view of the specimen.

Centrals: Only anterior three centrals are traceable. All the centrals are broader than long. In the 1st central, the anterior margin is broader than posterior. It contacts the posterior border of the 1st marginal. The 2nd central is sub-hexagonal, it is larger but narrower than the 1st entral. The 3rd central is hexagonal; it is broader than the 2nd central. The centrals occupy most of the central part of the carapace.

Laterals: The laterals are steeply inclined on the carapace. The laterals are short due to wide centrals. The seams between the laterals are not clearly distinguishable. The restoration suggests that the 2nd lateral is pentagonal.

Marginals: Only anterior marginals (2nd – 5th) are distinguishable. The 2nd marginal reaches upto the 1st lateral. The 3rd, 4th and 5th marginals contact the 1st lateral.

Nuchal: An anterior broken nuchal is present. It is hexagonal and is enclosed by the 1st central.

Neurals: Only 4 anterior neurals (1st – 4th) were restorable on the carapace. The neurals are longer than broad. They are hexagonal having short sides towards posterior. The 3rd neural is larger than the 1st and 2nd . The 4th is slightly smaller than the 3rd neural.

Pleurals: Only 3rd, 4th and 5th pleurals are traceable. The pleural 4th is narrower than the 3rd and 5th. The 3rd and 5th pleurals have wider distal margin, the alternate pleurals are wider distally.

Peripherals: The anterior peripherals are smaller than the posterior peripherals. The restoration of 1st –10th peripherals is possible on the carapace. The 4th peripheral reaches upto the 2nd pleural. The 5th peripheral reaches upto the 3rd pleural. The 6th peripheral reaches upto the 4th pleural. The 7th peripheral is reaching upto the 5th pleural and the 8th peripheral reaches upto the 6th pleural. The 1st – 4th peripherals are smaller and nearly rectangular. The 5th peripheral is pentagonal. The anterior peripherals are wider than long whereas posterior peripherals are longer than wide.

The dimensions of the restored carapace are as follow:
SCL (straight carapace length) = 64 cm
SCW (straight carapace width) = 40 cm
SH (straight height) = 34 cm

Material: broken carapace (SFP-226). The material is catalogued in the Field Museum of Saketi Fossil Park, Saketi.
(Plate 8, fig. 2)

Locality: Saketi Fossil Park Ridge (Nahan), Saketi Formation, Upper Siwaliks

Description

The partly preserved carapace is very large; the length of the specimen is approx. 54 cm and the width is approx. 43 cm. The scute boundaries and bony sutures are not clearly distinct on the carapace. A reconstructed length of the carapace is approx. 80 cm and the width should be approx. 55 cm at a height of approx. 23 cm. The central portion of the carapace is humped and the marginal portion is nearly horizontal (characteristic feature of *Omegachelys sahnii*). The central portion is very large, so that the laterals are small; they are steeply inclined (nearly vertical).

Discussion

Omegaochelys sahnii has been found very different and does not resemble any of the living batagurid turtles. The typical shape of the turtle seems to represent a habitat of swimming in high energy streams. On the basis of its shape only it can be concluded that the turtle was probably inhabiting an area along the large streams and channels.

Geoclemys GRAY 1855

This is a monotypic genus represented by only one species *Geoclemys hamiltonii* GRAY (1831).

Geoclemys hamiltonii (GRAY 1831)

Holotype: BMNH 1947.3.4.41, Natural History Museum, London (presumably the specimen illustrated by GRAY, 1831 "1830-35"": plate 76 as *Emys guttata,* according to SMITH, 1931 :111; IVERSON, 1992).

Type Locality: India

Habitat and Distribution

Geoclemys hamiltonii the 'spotted pond turtle' is a rare species living in sloughs, preferably shallow limpid waters, rich in aquatic vegetation. It attains the carapace length of approximately 36 cm, whereas, fossil forms may be as large as 45 cm. It is a widely distributed but critically endangered batagurine species in South Asia today, extending from Pakistan eastward through the plains of northern India and Bangladesh to Asam and Meghalaya in north-eastern India. Its range encompasses the Indus-Ganga-Brahmaputra river systems (DAS, 1985; 1991). It is entirely carnivorous, feeding on snails and other invertebrates and probably also fishes and amphibian larvae (ERNST & BARBOUR, 1989).

Synonymy

1831: *Emys hamiltonii* Gray
1855: *Geoclemys hamiltonii* Gray
1859: *Emys hamiltonoides* Falconer & Cautley
1885: *Clemmys palaeindica* Lydekker
1886: *Clemmys palaeindica* Lydekker
1889: *Damonia hamiltonii* Lydekker
1931: *Geoclemys hamiltonii* Smith
1936: *Geoclemys hamiltonii* Prashard
1964: *Geoclemys hamiltonii* Mcdowell
1969: *Geoclemys sivalensis* Tewari & Badam
1976: *Geoclemys* cf. *hamiltonii* Grigorescu & Verma
1991: *Geoclemys hamiltonii* Das
1991a: *Geoclemys hamiltonii* Das
1992: *Geoclemys hamiltonii* Iverson
1995: *Geoclemys hamiltonii* Das
2016: Geoclemys hamiltnii Nanda *et al.*

Distinguishing Features

The skull is broad, rather rhombic with a short rhombic snout exceeding the orbital diameter; the orbits are large, flat and short; the frontals are having rather triangular shape; the parietals are convex; the prefrontals are greatly expanded, taking the place of the nasals; a parietal crest is long and narrow; the postorbital forms the largest part of the anterior margin of the temporal fossa. The maxillaries are largely extended meeting the jugals posteriorly; a palatine foramen is situated laterally; an elongated pterygoid meeting on the mid line; posteriorly it meets the quadrate; a basiosphenoid is large and elongate (GRIGORESCU & VERMA, 1976); the narial opening is large.
The shell is convex, moderately elevated, elongate and arched transversely; the central and the lateral keels are interrupted with a series of nodose projection on each central and lateral; a cervical is broadest posterior. The plastron is

hingeless; an entoplastron lies anterior to the humero-pectoral seam. A deep posterior notch between the anals is present.

Material: Cast of a complete shell (E-95), catalogued in the Indian Museum, Kolkata. The original (BMNH-39838) is catalogued in the British Museum (Natural History), London and was earlier described by LYDEKKER (1885) as *Clemmys palaeindica.*
(Plate 8, fig. 3 & Text fig. 21)

Locality: Pliocene of Siwalik hills (LYDEKKER, 1888)

Description

Carapace: The shell is convex, and arched transversely. The interuppted central and lateral keels are greately developed. The keels are interrupted with a series of nodose projections on each centrals and laterals.

The preserved part of carapace includes cervical, centrals 1-5, divided postcentral, laterals 1-4, marginal 1-11, nuchal, neurals 1-8, metaneurals 1 and 2, pygal, pleurals 1-8 peripherals 1-11. A very small area of 1st and 11th pair of marginals is broken.
The condition of the bony sutures and posterior serrated margins of the carapace suggest that the shell belongs to an individual which was still not completely grown up.

Cervical: The cervical is short but rather broad and convex lateral. It is broader posterior than anterior.

Centrals: The 1st central is narrow anterior and broader posterior. It is longer than broad; the posterio-lateral margins of the 1st central are convex and anterio-lateral margins are concave. The anterior half of the 1st central is enclosed with the nuchal and contacting the 1st marginals. The 2nd central has a straight anterior margin. It gives off a small process in the middle of the anterior border which projects into the 1st central; it is larger than the 1st central and still longer than braod. It is hexagonal. The 3rd central is also hexagonal and is as large as the 2nd central; it is slightly longer than broad. The anterior margin of the 3rd central is straight and that of the 4th central is slightly concave. The 4th central is almost as broad as long; it is slightly smaller than the 3rd central and is also hexagonal. The 5th central is smaller than the previous 4 centrals; its posterior margin is broader than the anterior margin.
The postcentral is distinct, it is divided; the seam dividing the postcentral is distinctly seen.

Laterals: The 1st lateral is almost triangular with arcuade distal margin. Its distal width is more than the proximal width. The anterior margin of 2nd lateral is concave; it is pentagonal. The distal width of the 2nd lateral is less than its proximal width. its distal margin is almost straight. The 3rd lateral is also pentagonal; its distal width is more than the proximal width. The 4th lateral is smaller than the previous 3 laterals. Its width is slightly lesser than than that of the 3rd lateral.

Marginals: The 1st marginal is larger than the posterior ones; it is nearly rectangular; however, its distal width is more than their proximal width. The marginals 1-4 are contacting the 1st lateral. The 5th is reaching upto the middle of the 2nd lateral. The 6th is contacting the posterior margin of the 2nd lateral. The 7th and the 8th marginals are contacting the 3rd lateral (the 8th marginal is very close to the posterior margin of the 3rd lateral) and 9th and 10th marginals are contacting the 4th lateral. The 11th is reaching upto the 5th central (based on the restoration). The anterior marginals are entire while the posterior marginals are distally serrated.

Nuchal: The nuchal is narrower anterior and broader posterior; it is very characteristic having concave anterio-lateral and convex posterio-lateral margins; The nuchal is furrowed with the cervical and anterior and lateral margins of the 1st central.

Neurals: The 1st neural is convex anterior and is longer than broad; it is quadrilateral, and furrowed with the anterior margin of the 2nd central. The 2nd neural is hexagonal and has concave anterior margin; it is smaller than the 1st neural and is nearly as broad as long. The 3rd neural is concave anterior and is hexagonal is shape; it is larger than the 2nd neural but slightly smaller than the 1st neural. It is furrowed with the anterior margin of the 3rd central. The 4th neural is broader than the 3rd; its anterior margin is concave; it is as broad as long and hexagonal. The 5th neural is broader than long and is also hexagonal; its anterior margin is also concave. It is furrowed with the anterior margin of the 4th central. The 6th neural is smaller than the 5th and is also broader than long with concave anterior margin. Its posterior margin is protruded into the 7th neural. The 7th neural is smaller than than the 6th having straight posterior margin. It is also broader than long. The 8th neural is less broad than the 7th but still broader than long; it is almost as large as the 7th; it is furrowed with the anterior margin of the 5th central. The neurals are short-sided anteriorly. The metaneural 1 is nearly rectangular; it is broader than long. It is nearly as long as the neural 8th. The metaneural 2 has arcuade posterior margin and is much broader than long. It is smaller than the metaneural 1.

Pleurals: The 1st pleural is the largest in comparison to the other pleurals; it is nearly in the shape of an elongated pentagon; it is arched anterio-lateral; its posterior margin is sinuated. It is furrowed with the lateral margins of 1st and 2nd centrals. The 2nd pleural is narrower than the 1st; it is furrowed with the anterior margin of the 2nd lateral and the lateral margin of the 2nd central. The anterio-posterior dimension of 2nd– 6th pleurals is more or less equal and all are almost like an elongated pentagon. The 3rd pleural is furrowed with the lateral margins of the 2nd and 3rd centrals. The 4th pleural is furrowed with the lateral margin of the 3rd central and the anterior margin of the 3rd lateral. The 5th pleural is furrowed with the lateral margins of the 3rd and 4th centrals. The 6th pleural is furrowed with the lateral margin of the 4th central and the anterior margin of the 4th lateral. The

7th pleural is furrowed with the lateral margin of th 4th central and the 8th is furrowed with the posterior margin of the 4th lateral.
The proximal margins of the 1st, 3rd and 5th and 7th pleurals are wider than those of the 2nd, 4th, 6th and 8th pleurals whereas, the distal margins of 1st, 3rd and 5th and 7th pleurals are narrower than those of 2nd, 4th, 6th and 8th pleurals.

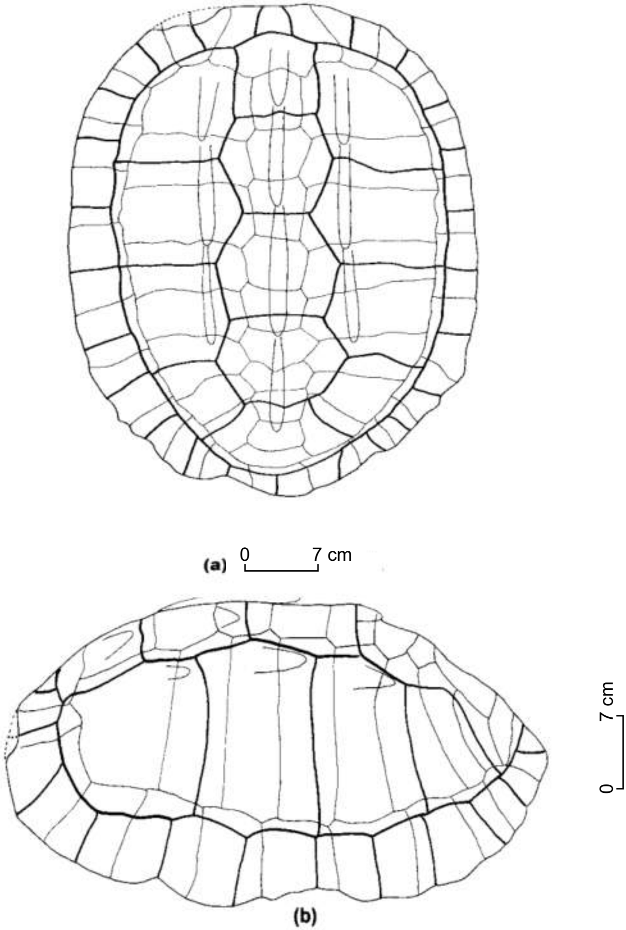


Fig. 21. Complete shell of *Geoclemys hamiltonii* (E-95). (a) dorsal view; (b) beft lateral view.

Peripherals: The 1st peripheral is very characteristic, almost in the shape of a holster; its outer margin is much broader than the inner margin. It is furrowed with the posterior margin of the 1st marginal and proximal margins of the 1st and 2nd marginals. The 2nd peripheral is also broader on outer margin but is quadrilateral. It is furrowed with the posterior margin of the 2nd marginal and proximal margin of the 2nd and 3rd marginals. The 3rd peripheral is furrowed with the posterior margin of the 3rd marginal and proximal margins of the 3rd and 4th marginals. The peripherals 3–8 are all almost rectangular. The 1st–3rd peripheral are reaching the 1st pleural. The 4th peripheral is contacting the 2nd pleural and the 2nd lateral. It is furrowed with the posterior margin of the 4th marginal and proximal margins of the 4th and 5th marginals. 5th and 6th peripherals are contacting the 3rd and 4th pleurals respectively. The 5th is furrowed with the posterior margin of the 5th marginal and proximal margins of the 5th and 6th marginals whereas the 6th peripheral is furrowed with the posterior margin of the 6th marginal and proximal margins of the 6th and 7th marginals. The 7th peripheral is reaching upto the 6th pleural and is furrowed with the posterior margin of the 7th marginal and proximal margin of the 7th and 8th marginals. The 8th peripheral is contacting the 6th pleural and is furrowed with the posterior margin of 8th marginal and proximal margin of the 8th and 9th marginals and 9th peripheral is contacting the 7th pleural; It is furrowed with the posterior margin of the 9th marginal and proximal margins of 9th and 10th marginals. The 10th peripheral is contacting the 8th pleural and is furrowed with the posterior margin of the 10th marginal and proximal margin of the 10th and 11th marginal and the 11th is contacting the metaneural 2 and 5th central (based on the restoration). It is furrowed with the posterior and proximal margin of the 11th marginal and proximal margin of the postcentral.

On the basis of the restoration the shell dimensions are as follows:
SCL (straight carapace length) = 28 cm
SCW (straight carapace width) = 18.5 cm
SH (straight height) = 14 cm

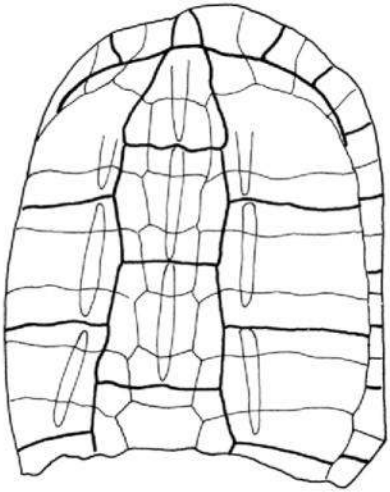
Material: Shell (WIF/A-452) **including posterior broken carapace and partly preserved plastron**. The material is catalogued in the Museum of Wadia Institute of Himalayan Geology, Dehradun and was earlier described by NANDA et. al. (2016).
(Plate 8, fig. 4 & Plate 9, fig. 1 & Text fig. 22).

Locality: 0.7 km east Charanwala Village (Sirmur), pre-Pinjor beds (= Tatrot Formation).

Description

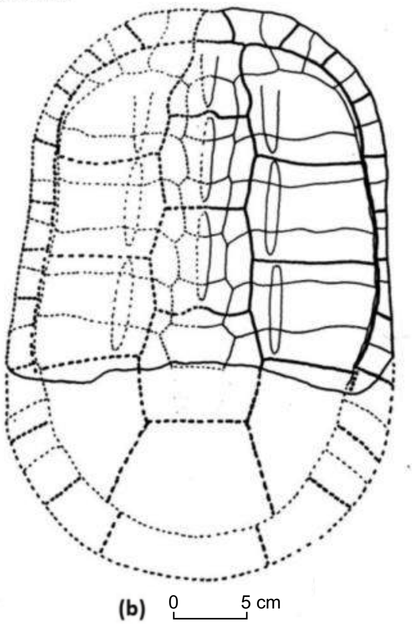
Carapace: The preserved parts of carapace include cervical, centrals 1-4 (4th central is partly preserved), laterals 1-4 (only anterior 1/6th of 4th lateral is preserved), marginal 1-9 (9th lateral is partly preserved), nuchal, neurals 1-6, pleurals 1-6 (carapace is broken from the suture between 6th and 7th pleurals) and peripherals 1-8.

The shell is convex and arched transversely. The interupted central and lateral keels are well developed.



(a) 0 5 cm

Fig. 22. Posterior broken shell of *Geoclemys hamiltonii* (WIF/A-452).
(a) Dorsal view.



(b) 0 5 cm

Fig. 22. Posterior broken shell of *Geoclemys hamiltonii* (WIF/A-452).
(b) Restored dorsal view.

Cervical: The cervical is convex lateral and broader posterior.

Centrals: The 1st central is narrow anterior and broadest posterior and is nearly in the shape of a bell and reaches upto the 1st marginals. It's anterio-lateral margins are concave and posterio-lateral margins are convex. The 2nd central is concave anterior. It gives off a small process in the middle of the anterior border which projects into the 1st central; it is longer than the 1st central and almost as broad as long. It is sub-hexagonal; the 3rd central is hexagonal; it is as broad as long; it is almost equal to the size of 2nd central. The anterior margin of 3rd central is straight and that of the 4th central is undulated. The 4th central is almost as long as the 3rd; it is broader than long, overlying 3 neurals; it is also hexagonal.

Laterals: The 1st lateral has arcuade outer margin; it is broader than long. The anterior margin of the 2nd lateral is concave; it is nearly rectangular. The posterior margin of the 3rd lateral is narrower than the anterior margin which is almost straight. The anterio-posterior dimensions of 2nd and 3rd lateral is identical.

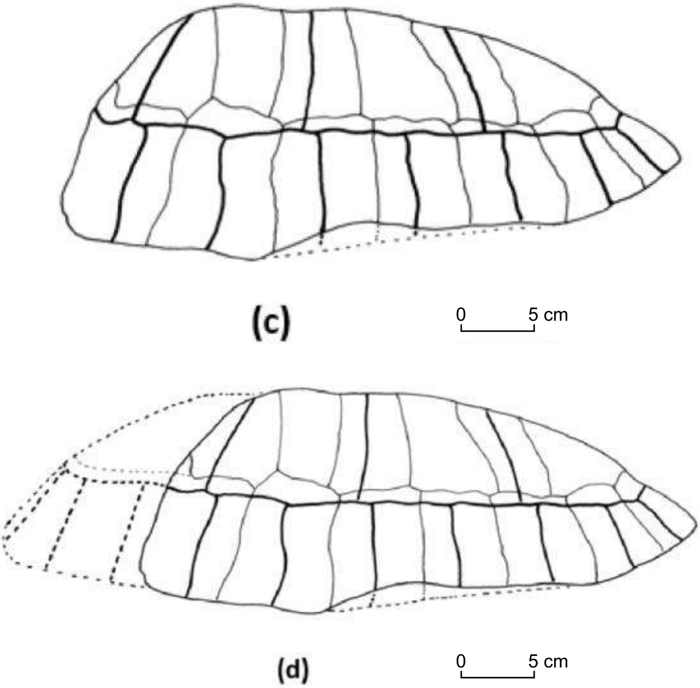


Fig. 22. Posterior broken shell of *Geoclemys hamiltonii* (WIF/A-452).
(c) Lateral view, (d) restored right lateral view.

Marginals: The 1st is the broadest marginal, approximately in the shape of a rectangle. Its posterior margin is narrower than the anterior. The following marginals are smaller and rectangular. The marginals 1-4 are contacting the 1st lateral. The 5th is reaching upto the middle of the 2nd lateral. The 6th is contacting the 2nd lateral. The 7th and the 8th marginals are contacting the 3rd lateral.

Nuchal: The nuchal is narrow anterior and broad posterior; it is very characteristic in having concave anterio-lateral and convex posterio-lateral margins. The nuchal is furrowed by the cervical and anterior and lateral margins of the 1st central.

Neurals: The 1st neural is convex anterior and is longer than broad; it is quadrilateral. The 2nd neural is concave anterior and is hexagonal; it is smaller than the 1st neural but still longer than broad. The 3rd neural is concave anterior and is hexagonal is shape; it is larger than the 2nd neural but smaller than the 1st. The 4th neural is broader than the 3rd; its anterior margin is concave; it is as broad as long and hexagonal. The 5th neural is broader than long and is also hexagonal; its anterior margin is also concave. The 6th neural is also broader than long with concave anterior margin. The neurals are short-sided anterior.

Pleurals: The 1st pleural is the largest in comparison to the following pleurals; it is in the shape of an elongated hexagon; it is arched anterio-lateral; its posterior margin is undulated. The anterio-posterior dimension of 2nd– 6th pleurals is more or less almost equal and elongated pentagonal. The proximal margins of the 1st, 3rd and 5th pleurals are wider than the 2nd, 4th and 6th pleurals; the distal margins of 1st, 3rd and 5th pleurals are narrower than 2nd, 4th and 6th pleural.

Peripherals: The 1st peripheral is very characteristic, almost in the shape of a holster; its outer margin is much broader than the inner margin. The 2nd peripheral is also broader at outer margin but is quadrilateral. The peripherals 3 and 4 are almost rectangular. The 1st–3rd peripheral are contacting the 1st pleural. The 4th peripheral is contacting the 3rd pleural and the 2nd lateral. The 5th, 6th and the7th peripherals are contacting the 3rd, 4th and the 6th pleural respectively.

Based on the restored shell the dimensions are as follows:
SCL (straight carapace length) = 44.8 cm
SCW (straight carapace width) = 29.3 cm
SH (straight height) = 16.5 cm

Plastron: A very small portion of the plastron is preserved comprising both almost complete femorals. The posterior part of the right hypoplastron and anterior part of the right xiphiplastron is also preserved; the suture between the hypoplastron and xiphiplastron is nearly straight. Posterior to the femoral-anal seam the plastron is broken.
The median seam is straight and clearly marked. Due to the erosion a substantial portion of the shields and plates is not distinct.

Femorals (based on the restoration)**:** The femorals are wedge shaped broader anterior and narrower posterior. The seam between femoral and anal is convex anterior (based on restoration). The maximum length of each femoral is approx. 10 cm at a maximum width of approx. 6.5 cm.

Entoplastron (based on the restoration)**:** A trace of entoplastron is distinct. The entoplastron lies just anterior to the humero-pectoral seam. On the basis of restoration, the maximum length of the plastron is approx. 39 cm and width is approx. 15 cm.

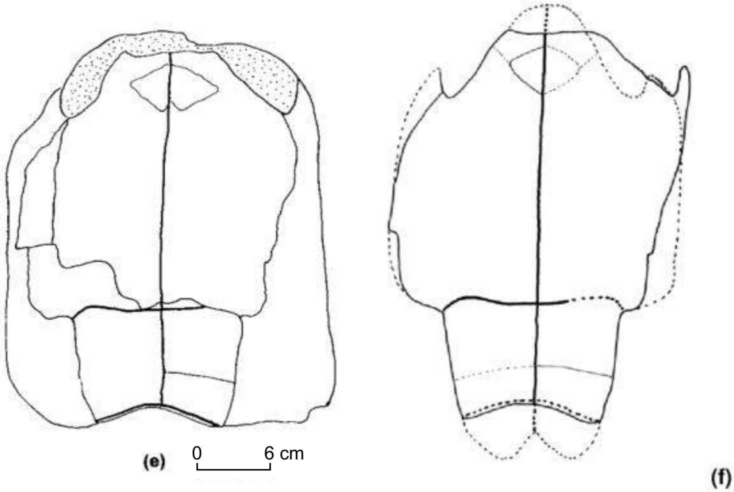


Fig. 22 e. Ventral view of broken plastron of *Geoclemys hamiltonii* (WIF/A-452)
22 f. Restored ventral view of the plastron of *Geoclemys hamiltonii* (WIF/A-452).

Comment on the (type) specimen MCASG A/665

The material was originally described as *G. sivalensis* by TEWARI & BADAM in 1969 (description republished by BADAM in 1979), based on an incomplete shell from the Pinjor Formation of the Upper Siwaliks (Basal Pleistocene), 1 km southeast of Quranwalla, Punjab, India.
The (type) specimen MCASG A/665 is an incomplete shell. The preserved part of carapace includes centrals 1 and 2 (both complete), central 3 (partial), pleural 1 (both left and right entire), pleural 1 and 2 (left and right partial), four left and three right anterior marginals (mostly damaged on the free ends) and a cervical (partially damaged anterior).

The estimated shell measurements are as follows:

SCL (straight carapace length) = 34 cm
SCW (straight carapace width) = 24 cm
SH (straight height) = 9.0 cm

TEWARI & BADAM (1969) remarked that their new species is comparable to the extant *Geoclemys hamiltonii* in the shape and morphology of the neurals.

DAS (1991) reviewed the material and suggested the material as junior synonym of living *G. hamiltonii*. He noted that neural bones are not visible. We, on the basis of the reconstruction of the carapace, could note at least 4 neural bones. Besides, DAS (1991) observed that the 1st central is concave anterio-lateral and second central is longer than broad, whereas, in our observation, the 1st central is concave lateral and contacting the 1st marginal (which is in the shape of an elongated hexagon), and the 2nd central is almost as broad as long (Plate 9, fig. 2 & Text fig. 23). The 3rd central is nearly as broad as the 2nd and is hexagonal. The width of the 3rd central is more than its length. The material described by TEWARI & BADAM (1969) as *G. sivalensis* is indistinguishable from *G. hamiltonii* GRAY 1831 in major taxonomic characters and therefore may be classified under *G. hamiltonii*.

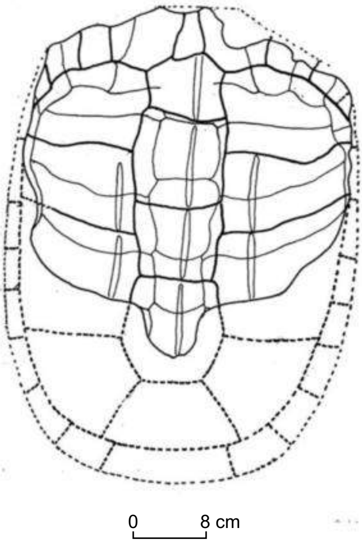


Fig 23. Restored dorsal view of carapace of *Geoclemys hamiltonii*, MCASG A/665 (type specimen of *Geoclemys sivalensis*, TEWARI & BADAM, 1969).

cf. *Geoclemys hamiltonii* (GRAY, 1831)

Material: Shell (WIF/A-454) **consisting of partly preserved carapace and anterio-posterior broken plastron.** The material is catalogued in the Museum of Wadia Institute of Himalayan Geology, Dehradun described as *Geoclemys hamiltonii* by NANDA et al., (2016).
(Plate 9, fig. 3 & Text fig. 24)

Locality: 2.5 km NE of Rampur Village (Ambala), Pinjor Formation.

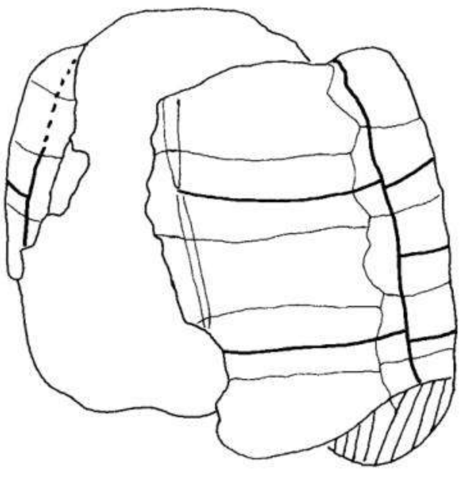
Description

Carapace: The carapace is consisting of partly preserved 1st lateral, complete 2nd lateral, partly preserved 3rd lateral, partly preserved 4th marginal, complete 5th and 6th marginal, partly preserved 7th marginal; complete 2-5 pleurals, complete 4-6 peripherals and partly preserved 7th peripheral.

The shell is convex, and slightly depressed in the middle. A trace of lateral keel is distinct; however, it is difficult to say whether the keel is continuous or interrupted.

Laterals: The proximal termination of laterals is not seen owing to the broken central part. The posterior margin of 1st lateral is slightly concave. The 2nd lateral has nearly straight posterior margin; based on the extension of the margins of 2nd lateral it can be noted that its proximal width is less than its distal width.

Marginals: The anterior margin of 4th marginal is not preserved. The 4th marginal is contacting the 1st lateral. The 5th and 6th marginals are nearly rectangular. The 6th marginal is reaching the 2nd lateral. The 10th marginal is contacting the 4th lateral (based on the restoration).



(a) 0 8 cm

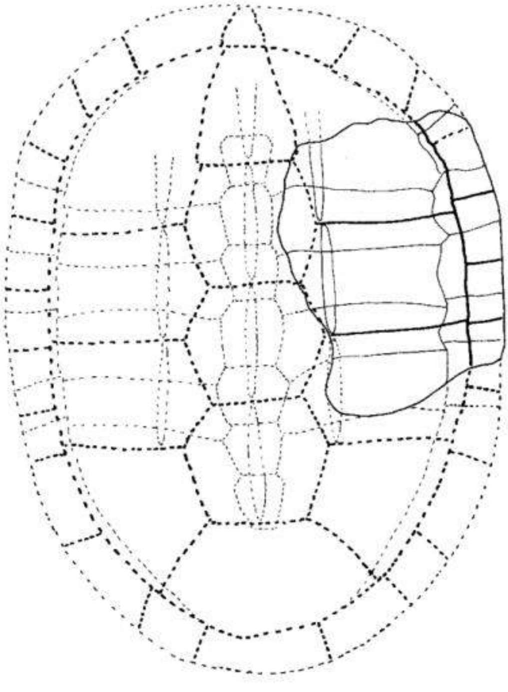
Fig. 24 a. Dorsal view of partial carapace of *Geoclemys hamiltonii* (WIF/A-454).

Pleurals: The proximal termination of pleurals is not seen due to a broken central part. The carapace is broken from the anterior margin of 2nd pleural. The anterior and posterior margins of 2nd pleural are nearly straight. The posterior margin of

3rd – 5th pleurals is concave. Based on the proximal extension of the 2nd – 5th pleural, it is inferred that the proximal width of 2nd and 4th pleural is more than their distal width, whereas, in pleural 3 and 5, the distal width is more than the proximal width.

Peripherals: The 4th, 5th and 6th peripherals are nearly pentagonal; peripheral 7 is nearly rectangular. The peripheral 5 is larger than peripherals 4, 6 and 7. The peripheral 4 is larger than 6 and 7 and is reaching upto the 2nd lateral; the peripheral 7 is larger than the 6th.

On the restored carapace the dimensions taken are as follows:
SCL (straight carapace length) = 41.5 cm
SCW (straight carapace width) = 31 cm
SH (straight height) = 11 cm



(b)

Fig. 24 b. Restored dorsal view of *Geoclemys hamiltonii* (WIF/A-454).

Plastron: The plastron is concave and probably belongs to a male specimen. The preserved part of the plastron includes a part of epiplastron, complete entoplastron, hyoplastron and posterior broken hypoplastron; partly preserved humeral, pectoral and abdominal. The plastron is broken from the anterio-lateral margin of epiplastron and from the seam between abdominal and femoral. The plastron is connected to the carapace between pectoral and abdominal with the ossified bridge. The median seam is very prominent.

Humerals: The humerals are larger than the pectorals in mid-seam length (based on restoration)

Pectorals: The anterior and posterior margins of the pectorals are slightly concave. It is much narrower in comparison to the abdominal.

Abdominals: The posterior margin of the abdominals is nearly straight. It is the largest plastral scute and is rectangular.

Epiplastra: The epiplastron has straight anterior margin; no anterior notch is seen.

Entoplastron: The angle between anterio-lateral margins of the entoplastron is nearly equal to the angle between its posterio-lateral margins. The entoplastron lies anterior to the humero-pectoral seam.

Hyoplastra: The hypoplastron is distal broader than medial. The suture between hyo- and hypoplastron is nearly straight.

Hypoplastra: It is much broader than the hyoplastron. The distal and the medial width of the hypoplastron are nearly equal. The suture between the hypo- and xhiphiplastron is slightly concave posterior.
The maximum length of the restored plastron is about 30.5 cm and the maximum width is about 16 cm.

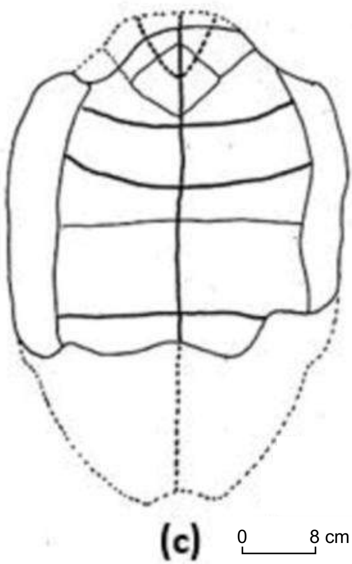


Fig. 24 c. Restored ventral view of *Geoclemys hamiltonii* (WIF/A-454).

Hardella GRAY, 1870

It is a monotypic genus represented by only one species *Hardella thurjii* GRAY (1831).

Hardella thurjii GRAY, 1831

Holotype: IVERSON (1992) assumed that it sould be in Natural History Museum, London, since it is illustrated in GRAY, 1831 "1830-35": plate 73 as *Emys thuji*, although no specimen is listed in their catalogue or in Boulenger's (1889:66); however, OUM 8433-34 are listed in their catalogue as syntypes (IVERSON, 1992).

Type Locality: India

Habitat and Distribution

The turtle is found mainly in pools, ponds, canals, slow moving rivers and estuaries. The strong axillary and inguinal buttresses suggest a highly aquatic nature. It is a non- aggressive species; when threatened, the animal retracts its head and limbs into the shell and does not attempt to bite. It is generally herbivorous although some eat frog, fishes etc. It is distributed over the flood plains of the northern parts of the Indian subcontinent, including the drainages of the Indus, Ganga and Brahmaputra in Bangladesh, India, Nepal and Pakistan.

Synonymy

1831: *Emys thurjii* Gray
1868: *Batagur thurgi* Theobald
1870: *Hardella indi* Gray
1885: *Batagur cautleyi* Lydekker
1885: *Batagur falconeri* Lydekker
1886: *Clemmys watsoni* Lydekker
1886: *Batagur watsonii* Lydekker
1889: *Hardella thurgi* Boulenger
1931: *Hardella thurgi* Smith
1967: *Geoemyda pilgrimi* Prasad & Satsangi
1985: *Hardella thurgi* Tikader & Sharma
1991: *Hardella thurjii* Das
1992: *Hardella thurjii* Iverson
1995: *Hardella thurjii* Das
2016: *Hardella cf. thurjii* Nanda *et al.*, 2016

Distinguishing features

The carapace is fairly depressed with an interrupted central keel. The marginals are unserrated in adults; the centrals are broader than long; the carapace is extensively sutured with the plastron with strong buttresses. The posterior lobe of the plastron is narrow, notched terminal and truncate anterior.

It is different from *Geoclemys, Cuora, Cyclemys, Geoemyda, Melanochelys* and *Pyxidea* by the presence of only one central keel and ellipsoidal moderately domed carapace. It is different from *Geoemyda. Cyclemys, Cuora* and *Melanochelys* by the presence of the hexagonal neurals which are short sided anterior. It is much larger than *Geoclemys*.

Material: Laterally crushed and fractured large shell (E-176), catalogued in the Indian Museum, Kolkata and is noted in LYDEKKER (1886).
(Plate 9, fig. 4 & Plate 10, fig. 1 & Text fig. 25)

Locality: Siwalik hills, India

Description

Carapace: The shell is large, convex and domed. A central intrrupted keel is prominent. The shell is lateral crushed and broken and transverse fractured.

The preserved part of the carapace includes cervical, centrals 1-4 (4th is posterior broken), laterals 1-4 (4th is incomplete), marginal 1-8 (8th is income-plete), nuchal, neurals 1-6 (6th incomplete), pleurals 1-6 (6th incomplete) and peripherals 1-7.

Cervical: The cervical is broad having convex anterio-lateral margins; it is broader posterior than anterior. The straight posterio-lateral margins join sharply the anterio-lateral margins.

Centrals: The 1st central is narrow anterior and broader posterior. It is longer than broad; The anterior half of the 1st central is enclosed with the nuchal and its lateral margins are contacting the cervical. The 2nd central has straight anterior margin having a small process in the middle of the anterior border which projects into the 1st central; it is larger than the 1st central and longer than braod. It is sub-hexagonal. The 3rd central is also sub-hexagonal and slightly larger than the 2nd central, also slightly broader than long. The anterior margin of 3rd and 4th central is straight. The 4th central is almost as broad as long (based on restoration); it is smaller than the 3rd central and is also hexagonal.

Laterals: The 1st lateral is almost triangular with arcuade distal margin. Its distal width is more than the proximal width. The anterior margin of 2nd lateral is straight; it is nearly rectangular. The distal width of the 2nd lateral is slightly lesser than its proximal width. its distal margin is almost straight. The 3rd lateral is sub-pentagonal; its distal width is more than its proximal width. The 4th lateral is smaller than the previous 3 laterals. Its proximal width is less than than the distal width.

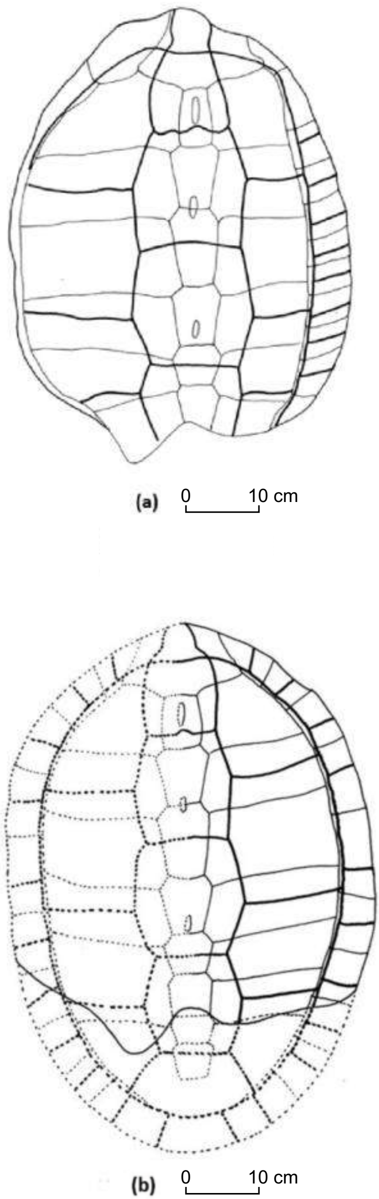


Fig. 25. Posterior broken shell of *Hardella thurjii* (E-176).
(a) Dorsal view; (b) reconstructed dorsal view.

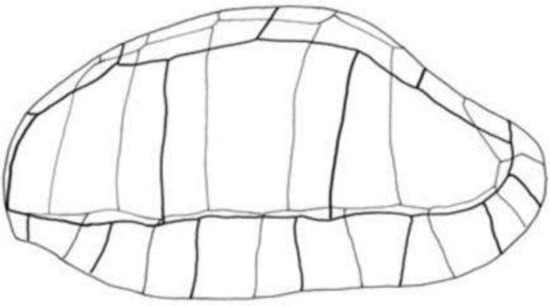


Fig. 25 c. Lateral view of *Hardella thurjii* specimen E-176

Marginals: The first pair of the marginals is larger than the 2nd and 3rd pair; it is nearly pentagonal. The 2nd and 3rd pairs are rectangular; their distal width is more than their proximal width. The marginals 1-3 are contacting the 1st lateral. The 4th is reaching upto the 2nd lateral. The 5th is contacting the 2nd lateral. The 6th is reaching the 3rd lateral, and the 7th marginals contacting the 3rd lateral. The 8th marginal is reaching upto the 4th lateral. A restoration on the similar pattern suggests that the 10th marginal contacts the 5th central.

Nuchal: The nuchal is narrower anterior and broader posterior; it is hexagonal having concave anterio-lateral and posterio-lateral margins; The nuchal is furrowed with the cervical and anterior and lateral margins of the 1st central.

Neurals: The 1st neural has straight anterior margin; it is longer than broad and rectangular. It is furrowed with the anterior margin of the 2nd central. The 2nd neural is hexagonal and has straight anterior margin; it is larger as the 1st neural and longer than broad. The 3rd neural has straight anterior margin being hexagonal is shape; it is larger than the 1st and the 2nd neural. It is furrowed with the anterior margin of the 3rd central. The 4th neural is broader and smaller than the 3rd; its anterior margin is concave; it is also longer than broad hexagonal. It is as large as the 2nd neural. The 5th neural is broader than long and is also hexagonal; its anterior margin is straight. It is furrowed with the anterior margin of the 4th central. It is smaller than the previous 4 neurals. The 6th neural is nearly as large as the 5th; it is nearly as braod as long (based on restoration).

Pleurals: The 1st pleural is the largest compared to the other pleurals; it is nearly of an elongated pentagon; it is arched distally; its posterior margin is straight. It is furrowed with the lateral margins of 1st and 2nd centrals and very small part of anterior margin of 2nd central. The 2nd pleural is narrower than the 1st. It is furrowed with the anterior margin of the 2nd lateral and the lateral margin of the 2nd central. The 3rd pleural is furrowed with the lateral margins of the 2nd and 3rd centrals. The 4th pleural is furrowed with the lateral margin of the 3rd central and the anterior margin of the 3rd lateral. The 5th pleural is furrowed with the lateral margins of the 3rd and 4th centrals. The 6th pleural is furrowed with the lateral margin of the 4th central and the anterior margin of the 4th lateral (based on restoration).

The proximal margins of the 1st, 3rd and 5th pleurals are narrower than those of the 2nd, 4th and 6th pleurals whereas, the distal margins of 1st, 3rd and 5th pleurals are wider than those of 2nd, 4th and 6th pleurals.

Peripherals: The 1st peripheral is very characteristic, almost in the shape of a holster; their outer margins are much broader than the inner margins. It is furrowed with the posterior margin of the 1st marginal and proximal margins of the 1st and 2nd marginals. The 2nd peripheral is also broader on outer margins but is quadrilateral. It is furrowed with the posterior margin of the 2nd marginal and proximal margin of the 2nd and 3rd marginals. The 1st and 2nd peripherals are contacting the 1st pleural. The 3rd peripheral is furrowed with the posterior margin of the 3rd marginal and proximal margins of the 3rd and 4th marginals; it is contacting the 2nd pleural but the 1st lateral. The 4th peripheral is reaching the 3rd pleural and 2nd lateral. It is furrowed with the posterior margin of the 4th marginal and proximal margins of the 4th and 5th marginals. 5th peripheral is reaching the 4th pleural and 3rd lateral; it is furrowed with the posterior margin of the 5th marginal and proximal margins of the 5th and 6th marginals. The 6th peripherals is reaching upto 5th pleural; it is furrowed with the posterior margin of the 6th marginal and proximal margins of the 6th and 7th marginals. The 7th peripheral is reaching upto the 6th pleural and 4th central; it is furrowed with the posterior margin of the 7th marginal and proximal margin of the 7th and 8th marginals (based on restoration).

On the basis of the restoration the shell dimensions are as follows:
SCL (straight carapace length) = 54 cm
SCW (straight carapace width) = 36 cm
SH (straight height) = 28 cm

Plastron: The preserved parts of the plastron include gulars, humerals, pectorals, abdominals and anterior half of the femorals. On the plastron, faintly preserved entoplastron, epiplastra, hyoplastra and a large proportion of hypoplastra are distinct. The plastron is wide and elongated.

Gulars: The gular is reduced; it is smaller than the femoral in mid-seam length. The gular has straight anterior margin; no anterior notch is seen.

Humerals: The mid-seam length of the humeral is nearly equal to mid-seam length of the pectoral. In overall size it is smaller than the pectoral. The seam between humeral and pectoral is undulated

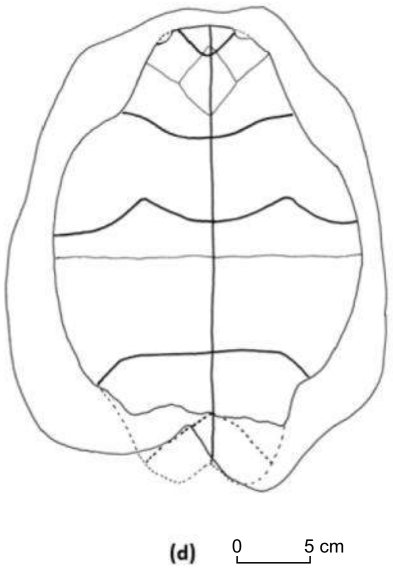


Fig. 25 d. Restored ventral view of *Hardella thurjii* specimen E-176

Pectorals: The pectoral is larger than the femoral and smaller than abdominal in mid-seam length. The seam between pectoral and abdominal is concave up to mid way and then suddenly dropping downwards toward the distal margins.

Abdominals: The abdominal is the largest amongst the all plastral scutes in mid-seam length. The seam between abdominal and femoral is nearly straight, it drops down on the distal margins. The length of abdomino-femoral seam is less than the abdomino-pectoral seam.

Femorals: The femoral is wedge shaped having anterior width more than its posterior width. The seam between femoral and anal is dropping downward (based on restoration).

Epiplastra: The epiplastra are faintly distinct. Based on restoration, the epiplastron is small having straight anterior margin.

Entoplastron: The entoplastron is also faintly seen. Based on the reconstruction, the entoplastron is intersected by the gulars, at a very short distance from their anterior end. It lies anterior to the humero-pectoral seam.

Hyoplastra: The hyoplastron is as large as the hypoplastron in mid-seam length (based on restoration). The suture between the hyo- and the hypoplastron is nearly straight. Its posterior width is nearly twice the anterior width.

Hypoplastra: The posterior width of the hypoplastron is nearly half of its anterior width (based on restoration).

The maximum length of the restored plastron is about 37 cm and the maximum width is about 26 cm.

Material: Marginal and anterio-posterior broken carapace (E-94). The material is catalogued in the Indian Museum, Kolkata and was earlier described by LYDEKKER (1885) as *Batagur falconeri*.
(Plate 10, fig. 2 & Text fig. 26).

Locality: Siwaliks of Asnot, Punjab

Description

The carapace is arched and slightly depressed. The central keel is developed. The preserved parts of the carapace include partly preserved cervical, faintly visible 1st, 2nd and 3rd centrals, 1st and 2nd laterals, partly preserved 1st marginal, anteriorly broken nuchal, 1st-4th neurals and 1st -4th pleurals. The disunited condition of the bony sutures indicates towards an immature individual.

Cervical: The anterior marginal part of the carapace is broken so that the cervical is not complete. The restoration suggests that the cervical is broad posterior and narrow anterior, having slightly convex lateral margins.

Centrals: The 1st central is small; narrow anterior and broader posterior. It is broader than long; the anterior half of the 1st central is covered by the nuchal and its lateral margins are contacting the cervical. The 2nd central has a straight anterior margin having a small process in the middle of the anterior border which projects into the 1st central; it is larger than the 1st central is longer than braod and sub-hexagonal. Its posterior margin is much broader than the anterior margin. The 3rd central is also sub-hexagonal. It is slightly smaller than the 2nd central and broader than long (based on restoration).

Laterals: The 1st lateral is almost triangular with arcuade distal margin. Its distal width is more than the proximal width. It is wider than long. The anterior margin of 2nd lateral is straight; it is nearly rectangular. The distal width of the 2nd lateral is slightly more than its proximal width; its distal margin is slightly convex. The 3rd lateral is sub-pentagonal; its distal width is nearly equal to its proximal width (based on restoration).

Marginals: Only 1st marginal is distinguishable on the specimen. It is larger than the 2nd and 3rd marginals (based on restoration). The distal width of 1st marginal is more than the proximal width. On the basis of restoration, it is noticed that the marginals 1-3 are contacting the 1st lateral. The 4th is reaching upto the 2nd lateral. The 5th marginal is contacting the 2nd lateral. The 6th is reaching the 3rd lateral, and the 7th marginals are contacting the 3rd lateral (based on restoration).

The restoration on the similar pattern suggests that the 10th marginal contacts the 4th lateral.

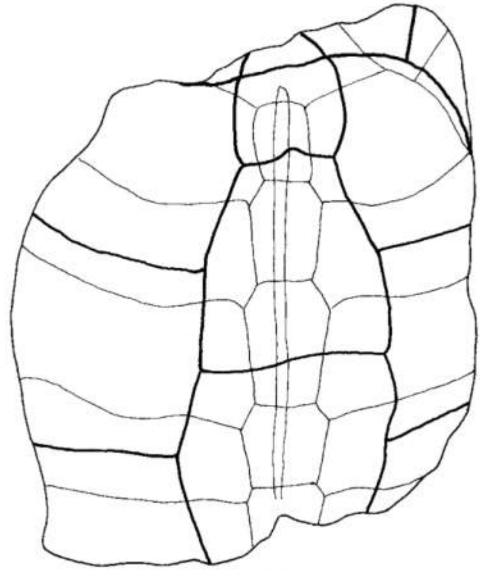


Fig. 26 a. Dorsal view of broken carapace of *Hardella thurjii* specimen E-94

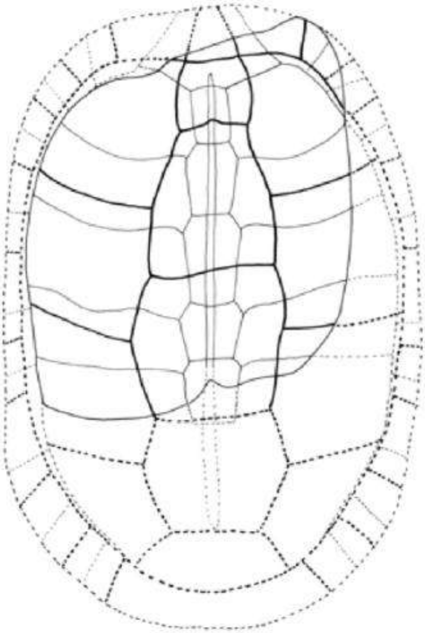
Nuchal: The nuchal is anterior broken, narrower anterior and broader posterior (based on restoration); it is hexagonal having nearly straight lateral margins; The nuchal is furrowed with the cervical and anterior and lateral margins of the 1st central.

Neurals: The 1st neural has slightly convex anterior margin; it is longer than broad and rectangular. It is furrowed with the anterior margin of the 2nd central. The 2nd is hexagonal and has straight anterior margin; it is little longer than 1st neural and is also longer than broad. The 3rd neural has straight anterior margin and is also hexagonal in shape; it is larger than the 1st and the 2nd neural and longer than broad. It is furrowed with the anterior margin of the 3rd central. The 4th neural is broader and smaller than the 3rd; its anterior margin is concave; it is broader than long and also hexagonal. The 5th neural is incomplete posterior. It is nearly as broad as long, and is also hexagonal (based on restoration). It is furrowed with the anterior margin of the 4th central (based on restoration). It is smaller than the previous 4 neurals (based on restoration). All the hexagonal neurals are short-sided anterior.

Pleurals: The 1st pleural is the broadest compared to the other pleurals; it is nearly in the shape of an elongated pentagon; it is distally arched; its posterior margin is convex. It is furrowed with the lateral margins of 1st and 2nd centrals and very small part of anterior margin of 2nd central. The 2nd pleural is narrower than the 1^{st}. It is furrowed with the anterior margin of the 2^{nd} lateral and the lateral margin of the 2^{nd} central. It has slightly convex posterior margin. The 3^{rd} pleural is furrowed with the lateral margins of the 2^{nd} and 3^{rd} centrals. The 4^{th} pleural is furrowed with the lateral margin of the 3^{rd} central and the anterior margin of the 3^{rd} lateral. The 5^{th} pleural is furrowed with the lateral margins of the 3^{rd} and 4^{th} centrals (based on restoration).

Peripherals: The 1^{st} peripheral is very characteristic, almost in the shape of a holster; their outer margins are much broader than the inner margins (based on restoration). It is furrowed with the posterior margin of the 1^{st} marginal and proximal margins of the 1^{st} and 2^{nd} marginals. The 2^{nd} peripheral is also broader on outer margins but is quadrilateral (based on restoration). It is furrowed with the posterior margin of the 2^{nd} marginal and proximal margin of the 2^{nd} and 3^{rd} marginals. The 1^{st} and 2^{nd} peripherals are contacting the 1^{st} pleural.

Based on the restoration the shell dimensions are as follows:
SCL (straight carapace length) = 23 cm
SCW (straight carapace width) = 15.5 cm



(b) 0 4 cm

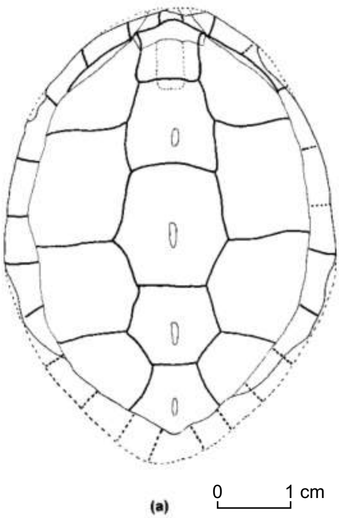
Fig. 26 b. Restored dorsal view of broken carapace of *Hardella thurjii* specimen E-94

Material: Cast of a complete shell (E-179) catalogued in the Indian Museum, Kolkata. The original (BMNH-39834) catalogued in the Natural History Museum, London, was collected by FALCONER and earlier described by LYDEKKER (1885) as *Batagur cautleyi*.
(Plate 10, fig. 3 & Text fig. 27)

Locality: Siwalik hills, India (LYDEKKER, 1885).

Description

Carapace: The shell is large, depressed vertical. A central interrupted keel is prominent. The anterior part of the carapace has gentle ascent, and posterior is slightly concave. The scutes are distinguishable but underlying bony sutures are reduced and not distinguishable. A small anterior and complete posterior marginal part is broken on the specimen.



(a)

Fig. 27 a. Restored dorsal view of nearly complete (cast E-179) shell of specimen BMNH-39834. The specimen E-179 is housed in Indian Museum and the original specimen is catalogued in British Museum, London.

Cervical: A very small posterior part of the cervical is distinguishable. The restoration of the cervical suggests that it is short and broad. The cervical is posterior broad and narrow anterior having convex lateral margins.

Centrals: The 1st central is rectangular. It is nearly as broad as long; the anterior half of the 1st central is enclosed with the nuchal. The 2nd central has straight anterior margin; it is larger than the 1st central and braoder than long. It is sub-hexagonal with convex lateral margins. The 3rd central is hexagonal and is larger than the 2nd central. It is slightly longer than broad. The lateral margins of the 3rd central are slightly concave. The anterior margin of 3rd and 4th central is straight.

The 4th central is broader than long; it is smaller than the 3rd central and is also hexagonal. The lateral margins of the 4th central are nearly straight. The 5th central has curved lateral margins. Its posterior margin is broader than the anterior margin.

Laterals: The 1st lateral is almost triangular with arcuade distal margin. Its distal width is more than the proximal width. It is wider than long. The anterior margin of 2nd lateral is slightly concave; it is nearly rectangular. The distal width of the 2nd lateral is nearly equal to its proximal width. Its distal margin is curved. The 3rd lateral is pentagonal; its distal width is more than its proximal width. The 4th lateral is smaller than the previous 3 laterals. Its proximal width is less than the distal width.

Marginals: On the specimen only 7 anterior marginals are distinguishable. The first pair of the marginals is smaller than the 2nd and 3rd pair; they are rectangular; their distal width is more than their proximal width. The marginals 1-3 are contacting the 1st lateral. The 4th is reaching upto the 2nd lateral. The 5th is contacting the 2nd, the 6th is reaching the 3rd lateral, and the 7th marginals are contacting the 3rd lateral. The 8th marginal is reaching upto the 4th lateral (based on restoration). A restoration on the similar pattern would suggest that the 10th marginal contacts the 5th central.

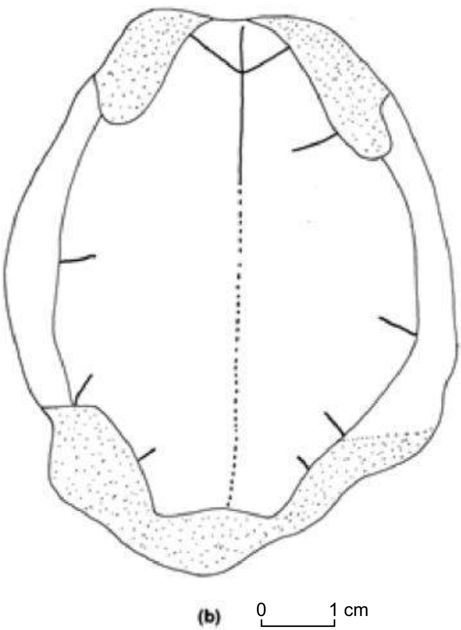


Fig. 27 b. Restored ventral view (plastron view) of nearly complete cast (E-179) of shell of specimen BMNH-39834

Nuchal: Only slightly concave lateral borders of the nuchal are seen. A restoration suggests that the nuchal is narrower anterior and broader posterior; it is hexagonal having concave anterio-lateral and posterio-lateral margins (based on restoration). The nuchal is furrowed with the cervical and anterior and lateral margins of the 1st central.

On the basis of the restoration the shell dimensions are as follows:
SCL (straight carapace length) = 62 cm
SCW (straight carapace width) = 45 cm
SH (straight height) = 18 cm

Plastron: The plastron is large and relatively wide. The preserved parts of the plastron show gulars, traces of distal end of humero-pectoral seam, distal end of abdomino-pectoral seam, distal end of abdomino-femoral seam, and femoral-anal seam.

Gulars: The gular is reduced; it is slightly smaller than the femoral in mid-seam length (based on restoration). The gular has straight anterior margin; no anterior notch is seen.

The length of restored plastron is 50.5 cm and width is 37.3 cm.

Material: A cranium (E-103), catalogued in the Indian Museum, Kolkata. The material was collected by THEOBALD (1879) and earlier described by LYDEKKER (1885) as *Batagur falconeri.*
(Plate 11, fig. 1, Text fig. 28)

Locality: Siwalik of Asnot, Punjab (LYDEKKER, 1885)

Description

The cranium is nearly in perfect condition. It is broken posterior after the supraoccipital (supraoccipital spine is broken) and alveolar border of the right maxilla. Several fractures are distinct on the fronto-parietal region. The bony sutures are faintly distinguishable indicating towards a mature individual. The snout is blunt and only slightly projecting. The specimen is rather similar with the cranium of the living *Hardella thurjii*, but, the orbits of the fossil form are more elliptical than those in the living form. The anterio-posterior diameter of the orbits is approx. 2.6 cm.

On the dorsal surface, the straight length from the anterior edge of the cranium to the posterior end of the occipital condyle is approx. 10.5 cm and the width posterior to orbits is approx. 7.0 cm and between the external surface of the quadrates approx. 10 cm. The prefrontal is flat, whereas, the frontal region is slightly elevated. The suture between the prefrontal and frontal is faintly distinct.

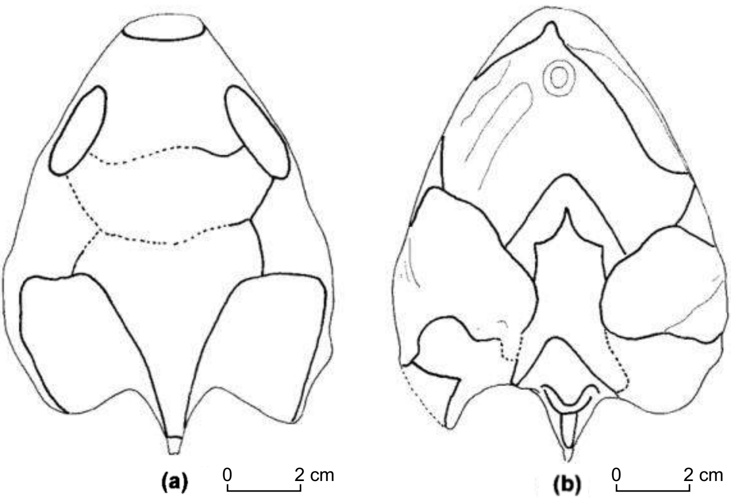


Fig. 28. Restored complete cranium of *Hardella thurjii* specimen E-103.
(a) Dorsal view, (b) ventral view.

The length of the prefrontal along the median suture from the posterior margin of the external narial aperture to the suture between prefrontal and frontal is approx. 2.8 cm. The maximum width of the interorbital along the prefrontal-frontal suture is approx. 3.8 cm. Excepting for a small part on the right side, the suture between the frontal and parietal is indistinct. The maximum width of the parietal is approx. 4.6 cm. On the right side, the suture between the frontal and postorbital is distinct. On the restored cranium, the length of the frontal along the median line is approx. 2.4 cm and the maximum width at the posterior border of the orbits is approx. 2.6 cm. The length of the postorbital is approx. 2.4 cm. The suture between the postorbital and jugal is indistinct. On the right side, a small part of the suture between the prootic and quadrate is faintly visible.

On the ventral surface, the lateral borders of both the jaws are serrated (well exhibited on the left side). The prominent premaxillary processes on anterior most side of each jaw is seen with the intervening median notch. The palatal ridge is distinct; the median pit is distinguishable. The suture between the palatine and the pterygoid is distinct. The pterygoid is characteristically small (maxium length along the median line is approx. 1.4 cm) and basisphenoid is characteristically large (maxium length along the median line is approx. 3.3 cm). The suture between basisphenoid and basioccipital is convex anterior inclined towards the median suture. The occipital and supraoccipital are also distinct. On the right side, the suture between the quadrate and squamosal is distinct; it is very characteristic moves anterior from the outer margin of squamosal forms a great arc and then turns backwards and then joins posterio-lateral margin of the basisphenoid. The suture between the right squamosal and opisthotic is also faintly distinct (restored on the cranium).

Material: Complete shell (WIF/A-453), comprising of a nearly complete carapace and plastron. The material is catalogued in the Museum of Wadia Institute of Himalayan Geology, Dehradun and was earlier described by NANDA et al (2016).
(Plate 11, fig. 2 & Text fig. 29).

Locality: 1.75 km NE of Rampur Village (Ambala), pre-Pinjor beds (= Tatrot Formation).

Description

Carapace: The shell is convex with only one interrupted central keel The preserved parts of the carapace includes centrals 1-5 (5th central is posterior broken), laterals 1-4 (4th lateral is posteriorly incomplete), marginals 1-9 (9th marginal is incomplete), broken nuchal, neurals 1-7 (7th neural is posterior incomplete); 1-6 pleurals and peripherals 1-9 (9th peripheral is incomplete).

Centrals: The 1st central is very small in comparison to 2nd, 3rd and 4th; it is contacting the 1st marginal and broader than long. Lateral margins are convex, also anterior one and enclosed with the nuchal. The 2nd central is nearly as long as broad; It has nearly straight anterior margin. it is rectangular but has a tendency towards hexagonal. The 3rd central is smaller than the 2nd but it is as broad as the 2nd central. It is broader than long and also has a tendency toward hexagonal; it has straight anterior margin and convex lateral margins. The 4th central is smaller than the 2nd and 3rd but longer than the 1st central, and overlying 3 neurals. It is also broader than long having convex lateral margins and is sub-hexagonal. It gives off a small process in the middle of the anterior border which projects into the 3rd central.

Laterals: The 1st lateral is nearly triangular with arcuade outer margin. The 2nd lateral is rectangular. Its anterior margin is nearly straight. The 3rd lateral has nearly equal anterio-posterior margins; it is rectangular. The 4th lateral has smaller posterior and arcuade distal margin.

Marginals: The 1st marginal is rectangular and so as the other marginals. The 1st marginal is reaching upto the 1st lateral. The 2nd and the 3rd marginals are contacting the 1st lateral. The 4th marginal is reaching upto the 2nd lateral. The 5th marginal is contacting the 2nd lateral and the 6th is reaching to the 3rd lateral. The 7th and the 8th are contacting the 3rd lateral and the 9th is reaching upto the 4th lateral. The 10th marginal is contacting the 4th lateral and 11th marginal is reaching the 5th central (based on the restoration).

Nuchal: The nuchal is concave lateral and convex and wider posterior; it is hexagonal. It is furrowed with the cervical, anterior seam of the 1st central and very small part of the lateral seams of the 1st central.

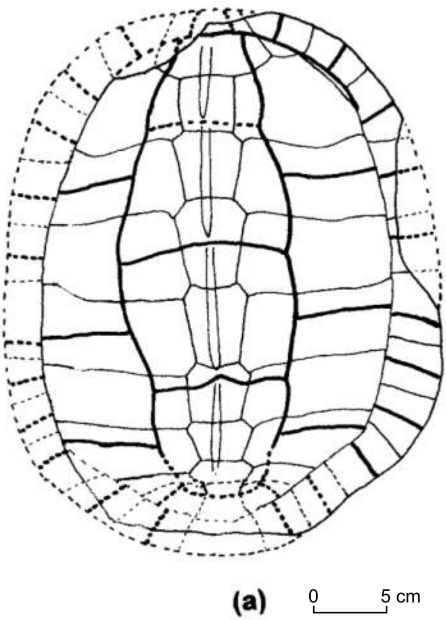


Fig. 29 a. Restored dorsal view of marginal broken shell of *Hardella thurjii* specimen WIF/A 453.

Neurals: The 1st neural is rectangular and is longer than broad. The 2nd neural is larger than the 1st and also longer than broad; it is hexagonal. The 3rd neural is convex anterior slightly larger than the second and is also hexagonal. The 4th neural is concave anterior and is as large as the 2nd neural but slightly broader than the 2nd and 3rd neurals, however, the length is more than the width. The 5th neural is smaller than the previous 4 neurals. It is also hexagonal, and concave anterior; it is almost as broad as long. The 6th neural is concave anterior, wider than long, hexagonal. The 7th neural is also wider than long and is smaller than the 6th neural, and is hexagonal. The neurals are short-sided anterior. The posterior neurals after the 6th are not seen owing to the erosion. However, the restoration suggests absence of the metaneural 1 and 2, though, the pygal is present.

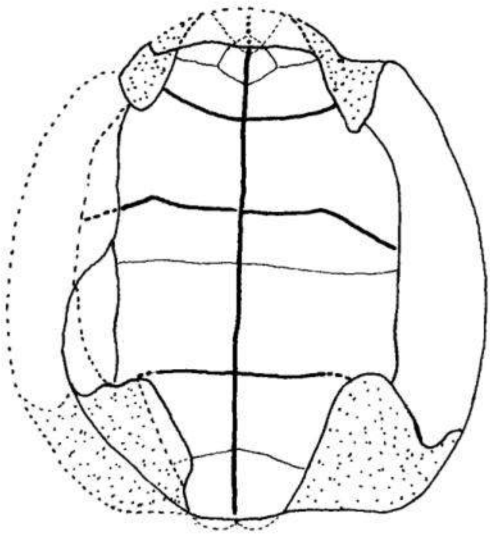
Pleurals: The 1st – 6th pleurals are pentagonal. The 1st pleural has arcuade distal end. In the pleurals 2nd, 4th and 6th, the distal end is wider than the proximal and in the pleurals 1st, 3rd and 5th the proximal end is wider than the distal. The anterior margin of 2nd pleural is concave and that of 3rd and 4th pleural is wavy. The anterior margin of 5th and 6th pleural is slightly convex near the proximal end and then straight. The restoration suggests that the 8th pleural is probably reduced.

Perihperals: The 1st peripheral has broader distal end and is quadrilateral. The peripherals 2 – 8 are nearly rectangular. The peripheral 6th is larger than the neighbouring peripherals. The peripheral 1 and 2 are contacting the pleural 1. The peripheral 3 is reaching upto the 2nd pleural. The peripheral 4 is reaching upto the 3rd pleural and 2nd lateral. The 5th peripheral is contacting the 3rd pleural. The 6th peripheral is contacting the 4th pleural. The 7th peripheral is reaching upto the 5th pleural and 8th peripheral is reaching upto the 6th pleural; 9th is contacting the 6th pleural and 10th peripheral is reaching upto 7th pleural. The 11th peripheral is reaching upto the 8th pleural.

The measurement taken on the restored carapace are as follows:
SCL (straight carapace length) = 32.5 cm
SCW (straight carapace width) = 25.5cm
SH (straight height) = 17.5 cm

Plastron: The perserved parts of nearly complete plastron include, anterior broken entoplastron, the suture between right epiplastron and hyoplastron (epiplastron is not preserved), hyoplastron, hypoplastron, xiphiplastron, anterior incomplete humerals, pectorals, abdominals, femorals and posterior incomplete anals. A median suture is clearly distinct.

Humerals: The mid-seam length of the humeral is nearly equal to mid-seam length of the pectoral. In overall size it is smaller than the pectoral. The seam between humeral and pectoral is posterior convex.



(b)

Fig. 29 b. Restored ventral view of marginal broken shell of *Hardella thurjii* specimen WIF/A 453.

Pectorals: The pectoral is larger than the femoral and smaller than the abdominal in mid-seam length. The seam between pectoral and abdominal is straight up to mid way and then dropping downwards distal.

Abdominals: The abdominal is the largest amongst the plastral scutes in mid-seam length. The seam between abdominal and femoral is nearly straight. The length of abdomino-femoral seam is less than the abdomino-pectoral seam.

Femorals: The femoral is wedge shaped having anterior width more than its posterior width. The seam between femoral and anal is dropping downwards.

Anals: The anal is having unnotched complete posterior margin. The inter-pygal seam is distinct. The anal is smaller than the gular in mid-seam length.

Epiplastra: The epiplastra are not distinct, only a very small portion of the right epiplastron is distinct. Based on restoration, the epiplastron is small having straight anterior margin.

Entoplastron: Only the posterior margin of the entoplastron is visible. Based on the reconstruction, the entoplastron is intersected by the seam between the gulars and the humerals and is anterior to the humero-pectoral seam.

Hyoplastra: The hyoplastron is as large as the hypoplastron in mid-seam length. The suture between the hyo- and the hypoplastron is nearly straight.

Hypoplastra: The posterior width of the hypoplastron is much smaller than the anterior width. The suture between the hypoplastra and the xiphiplastra is dropping downwards.

Xiphiplastra: The xiphiplastron is posterior complete, unnotched and nearly as large as the epiplastron in mid-seam length.

The maximum length of the restored plastron is approx. 30 cm and the maximum width is approx. 18.5 cm.

Material: Complete shell (W19/178) includes broken but complete carapace and complete plastron. The material is catalogued in the Indian Museum, Kolkata. (Plate 12, fig. 1 & Text fig. 30)

Locality: Siwalik of Himachal Pradesh (precise locality information not available).

Description

Carapace: The shell is convex having one interrupted central keel; there is no trace of lateral keels. The carapace is serrated posterior.

Cervical: The cervical is posterior broader and anterior narrow having rather straight lateral margins.

Centrals: The 1st central is rather bell shaped, it is broader posterior; It is constricting anterior enclosed with the nuchal. The 1st central is contacting the 1st pair of marginals. The 2nd central is hexagonal and is larger than the 1st. The 2nd central is nearly as broader as long. The 3rd central is little larger and less broad than the 2nd and is sub-hexagonal. The 4th central is smaller than the 2nd and the 3rd and is broader than long. It is overlying the 3 neurals. The central 5th is as long as the 4th, but it is broader posterior having a nearly straight posterior margin. The paired post-central is pentagonal. Both post-centrals are separated posterior.

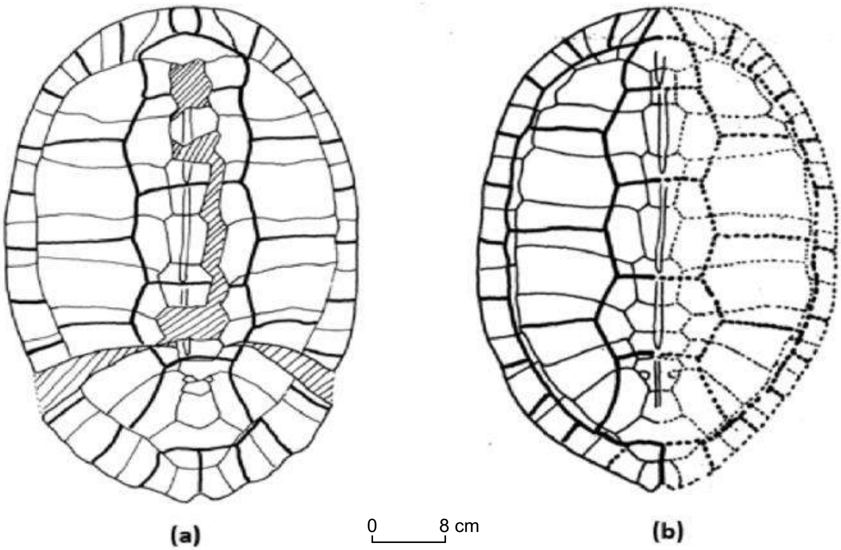


Fig. 30. Complete shell of *Hardella thurjii* specimen W 19/178;
(a) dorsal view, (b) restored dorsal view.

Laterals: The laterals are steeply inclined. Lateral 1 is nearly triangular; it has arcuade distal margin. The anterio-posterior width of the 2nd lateral is more than its transverse length. The 2nd and 3rd laterals are pentagonal. The anterio-posterior dimension of the 3rd lateral is nearly equal to its dimension in transverse direction. The proximal end of the 3rd lateral is slightly wider than its distal end. The distal end of the 4th lateral is wider than its proximal end.

Marginals: The 1st marginal is quadrilateral and larger than the 2nd and 3rd rectangular marginals but smaller than the 4th; however, the 1st marginal is wider than the other marginals. The 4th and 6th marginals are pentagonal; the 5th, 6th and 7th marginals are largest; the 6th marginal is slightly larger than the 5th and 7th.

The marginals 8 – 11 have distal more wider ends than proximal and than other marginals. The growth lines on the laterals and marginals are prominent which are parallel to the lateral margin. The marginal 1–3 are reaching upto the 1st lateral. The 4th marginal is reaching upto the 2nd lateral. The 5th marginal is contacting the 2nd lateral and the 6th is reaching upto the 3rd lateral. The 7th is contacting the 3rd lateral and the 8th is reaching upto the 4th lateral. The 9th and the 10th marginal are contacting the 4th lateral and the 11th marginal is reaching upto the 5th central.

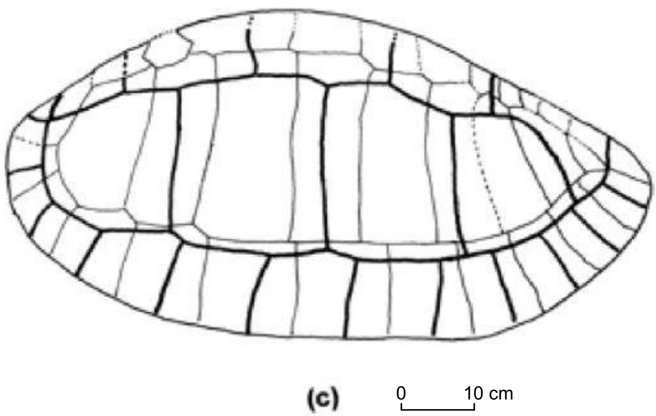


Fig. 30 c. Lateral view of a complete shell of *Hardella thurjii,* specimen W19/178.

Nuchal: The nuchal is identifiable due to its typical characters as seen in most of the species i.e. concave anterio-lateral and is convex posterio-lateral; it is broader posterior and nearly hexagonal. The nuchal is furrowed with the cervical and anterior and lateral margins of the 1st central.

Neurals: The neural 1 is rectangular and all remaining neurals are hexagonal. The 1st neural is anterior convex. The 2nd neural is larger than the 1st and is also anterior convex. The 3rd and 4th neurals are slightly broader than the 2nd but are longer than broad; they are anterior concave. 5th neural is broader than previous 4 neurals, but, still longer than broad. 6th and 7th neurals are smaller and broader than the 5th and are broader than long. The 8th neural is longer than broad and is less broad than the previous 3 neurals. Metaneural 1 is rectangular with curved sutures. Metaneural 2 is again hexagonal with nearly straight posterior margin and concave anterior margin. The pygal is notched posterior.

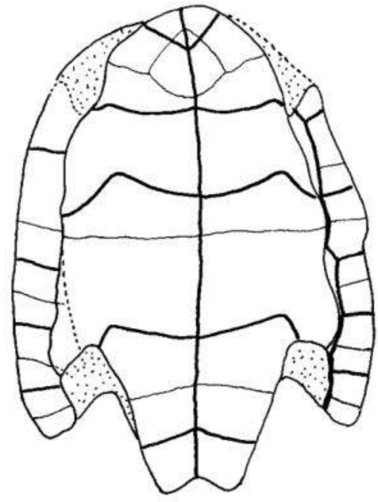
Pleurals: The pleural 1 is pentagonal with arcuade distal end. The 2nd and 3rd pleurals are hexagonal. The sutures between the pleurals are nearly straight. The proximal and distal width of the 2nd pleural is nearly equal. The distal width of 1st, 3rd, 5th, 6th, and 7th pleural is more than the proximal width; whereas, in plerual 4, the proximal width is more than the distal width.

Peripherals: The peripherals 1, 2 and 8 are distal wider than proximal. The peripherals are rectangular excepting the peripherals 3 and 4, which are pentagonal. The peripheral 1 and 2 are contacting the 1st pleural. The 3rd is reaching upto the 2nd pleural. The 4th peripheral is reaching upto the 3rd pleural and the 2nd lateral. The 5th peripheral is reaching upto the 4th pleural and the 6th peripheral is reaching upto the 5th pleural and contacting the 3rd lateral. The 7th and the 8th peripheral is reaching upto the 6th pleural and 9th is contacting the 7th pleural. The 10 peripheral is contacting the 8th pleural and the 11th pair of peripheral is in contact with the metaneural 2.

The dimensions of the carapace are as follows:
SCL (straight carapace length) = 43.6 cm
SCW (straight carapace width) = 27.6 cm
SH (straight height) = 24 cm

Plastron: All parts of the plastron are clearly visible. A median seam is well marked.

Gulars: The triangular gulars cover the anterior portion of the entoplastron. Their length is much shorter than from the femorals in mid-seam length.



(d) 0 10 cm

Fig. 30 d. Ventral view of a complete plastron of *Hardella thurjii* specimen W19/178.

Humerals: The humeral is quadrilateral and wider distal. The seam between humeral and pectoral is slightly below the entoplastron and is nearly straight but becomes slightly sinuated on the distal margins.

Pectorals: The pectoral is rectangular. The seam between pectoral and abdominal is concave anterior but distal it drops sharply joining the lateral margins of the plastron. The mid-seam length of the pectoral is less than that of the abdominal, more than that of the humeral and is equal to that of the femoral.

Abdominals: The abdominal is also rectangular but is larger than the pectoral. The seam between abdominal and femoral is concave anterior but sharply dropping distal just like the seam between pectorals and abdominals.

Femorals: The femoral is quadrilateral; it is broader anterior. It is much larger than the anal and gular in mid-seam length. The seam between femorals and anals is dropping towards the distal margin.

Anals: The anals are almost equilateral; they are notched posterior. The mid-seam between the two anals is clearly distinct. It is slightly larger than or equal to the gulars in mid-seam length.

Entoplastron: The angle between anterio-lateral sutures of the entoplastron is more acute than the angle between its posterio-lateral sutures which are reaching upto the lateral margins of the plastron. The entoplastron lies anterior to the humero-pectoral seam.

Epiplastra: The epiplastron is rectangular. The anterior margin of the epiplastra is complete showing no trace of any notch or bifurcation.

Hyoplastra: The hyoplastron is a large rectangular plate laterally connected with the carapace. It is slightly smaller than or equal to the hypoplastron. It is distally wider than medial. The suture between the hyoplastron and epiplastron is pointing upwards.

Hypoplastra: The hypoplastra are large rectangular plates. The suture between the hypoplastron and hyoplastron is nearly straight. It is the largest suture on the plastron.

Xiphiplastra: The xiphiplastron is quadrilateral, anterior wider than posterior. It is larger than the epiplastron and entoplastron.

The maximum length of the plastron is about 39 cm and maximum width is about 21 cm.

Batagur GRAY, 1855

Batagur is a genus of large turtles found in South and Southeast Asia. The specimen described here are very close to *B. baska* and so are the earlier described material of GRAY (1831), DAS (1991, 1995) and IVERSON (1992). Basis on its proximity with *B. baska* in features (described below) we collectively describe all the reported specimens as *Batagur cf. baska.*

Batagur cf. *baska* (GRAY, 1831 "1830-35")

Holotype: Not located; specimen illustrated in GRAY'S original paper (IVERSON, 1992).

Type Locality: Not stated; India according to GRAY, 1831 (IVERSON, 1992).

Habitat and Distribution

It is found in the mouths of rivers that are under tidal influence and mangrove-dominated. It is a non-agressive species feeding on fruits of *Sonneratia* a mangrove plant (DAS, 1995). It also consumes leaves, stems and other fruits besides molluscs, crustaceans and fishes. It is restricted to the estuary of the rivers Ganga and Brahmaputra, known as Sunderbans in India also in Myanmar (Burma), through Thailand and west Malaysia to Sumatra (Indonesia), Cambodia and Vietnam.

Synonymy

1831: *Emys baska* Gray
1991: *Batagur baska* Das
1992: *Batagur baska* Iverson
1995: *Batagur baska* Das

Distinguishing features

The carapace is domed and heavily buttressed; in adults, the marginals are modified into spine-like projections, and the shell is comparatively flatter (DAS, 1995). There is only one central keel (in young individuals) which is low and disappears with the age. The centrals are broader than long; a cervical is small, broader than long. The plastron is long truncated anteriorly and notched posteriorly. The head is small and the snout is upturned; the forehead is covered with the small scales; the upper jaw is notched. It can be distinguished from other batagurines on the basis the absence of the keels in adult; the large size of the animal is comparable to only *Hardella* and large species of ex. *Kachuga* now *Batagur.*

Material: **Posterior broken shell** (W19/174). The material is catalogued in the Indian Museum, Kolkata.
(Plate 13, fig. 1 & Test fig. 31).

Locality: Not known

Description

Carapace: The carapace is high and domed. No traces of any keels on the carapace. The underlying bony sutures are reduced indicating that the animal was an adult. The anterior profile of the carapace is slightly concave. The cervical is not distinct on the carapace.

Centrals: The seams between the centrals are traceable here and there on the carapace. A restoration suggests that the centrals are mostly longer than broad (2nd central is nearly as broad as long). The 1st central is nearly in the shape of an inverted bell; it has broader anterior margin and narrower posterior margin. The 2nd central has broader posterior margin. The 3rd central is larger than the previous 2 centrals. The 4th central is larger than the 3rd central. The 5th central is incomplete showing only 1/4th anterior portion. The restoration suggests that the 5th central is smaller than the 4th central but larger than the 1st central.

Laterals: The laterals are steeply inclined on the carapace. They are small due to large marginals. The width of the 1st lateral is nearly equal to the length.

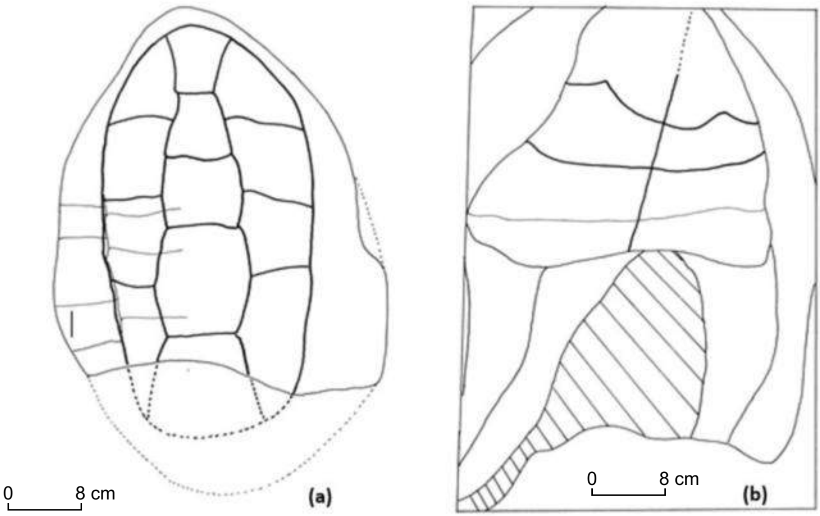


Fig. 31. Posterior broken shell of *Batagur* cf. *baska* specimen W19/174.
(a) Restored dorsal view; (b) ventral view of plastron.

Marginals: The marginal reagion of the carapace is characteristically wide. The marginals are steeply inclined (nearly vertical) on the carapace. The seams between the marginals are not distinguishable.

Pleurals: The 5th and 6th pleurals are traceable. The proximal width of the 5th pleural is less than distal, whereas, the proximal width of the 6th pleural is more than its distal width. The 5th pleural is furrowed with the lateral margin of the 3rd and 4th centrals. The 6th pleural is furrowed with the lateral margin of the 4th central and the anterior margin of the 4th lateral.

Peripherals: On the left margin of the carapace, only 3 peripherals (7th –9th) are traceable. The 7th and 8th peripheral are pentagonal; the 9th peripheral is rectangular. The peripherals are much longer than wide. The 7th peripheral contacts the 3rd lateral and 5th pleural. The 8th peripheral reaches upto the 6th pleural and 4th lateral. The 9th peripheral reaches upto 7th pleural but contacts 4th lateral.

The dimensions taken on a restored carapace are as follow:
SCL (straight carapace length) = 49.5 cm
SCW (straight carapace width) = 30 cm
SH (straight height) = 26 cm

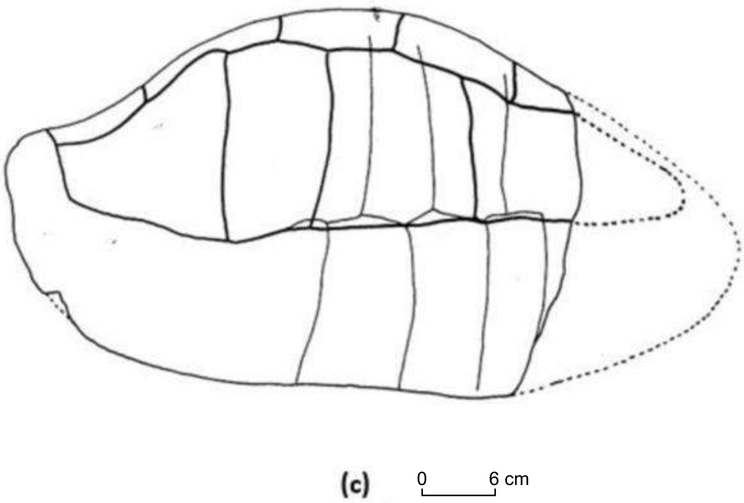


Fig. 31 c. Restored lateral view of *Batagur* cf. *baska* specimen W19/174.

Plastron: The plastron is posterior incomplete. It is broken beyond the suture between hyo-and hypoplastron. On the plastron gulars are indistinct. The seam between humerals pectorals and pectorals abdominals is present. The postition of the humero-pectoral seam suggests that it is posterior to the entoplastron. It is concave and rises upwardly upto the middle of the plastrron, and then it takes a sharp bend downwards towards the distal margin of the plastron. The mid-seam length of the pectoral is less than that of the abdominals. The seam between pectorals and abdominals is slightly concave.

The only bony suture distinct on the plastron is between the hyo-and hypoplastron. It is nearly straight.

cf. *Batagur baska* (GRAY, 1831 "1830-35")

Material: Complete Nuchal (E- 104). The material is catalogued in the Indian Museum, Kolkata and was earlier described by LYDEKKER (1885) as Genus *non-det.* (? cf. *Geomyda* sp.).
(Plate 13, fig. 2 & Text fig. 32)

Locality: Siwaliks of the Punjab.

Description

A large nuchal comparable to that of extant *Batagur,* having a maximum length of about 11.5 cm and maximum width about 14 cm. The nuchal is slightly depressed in the posterio-central margin indicating towards a depressed carapace. The anterior and anterio-lateral margins of the nuchal are concave and the posterio-lateral margins are convex. The posterior margin of the nuchal is sinuated.

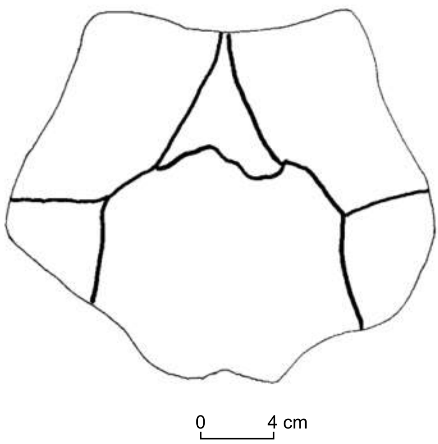


Fig. 32. Nuchal of *Batagur baska* (E-104).

The cervical is very prominent in the shape of an isosceles triangle; it is broader posterior; it tapers to a point on the anterior margin. The lateral margins of the cervical are slightly concave. The maximum length of the cervical (along the median suture) is about 4 cm. The 1st central is distinguishable with the anterior and the anterio-lateral margins. The anterior margin of the 1st central is indented by a blunt projection into the cervical. The 1st central has concave anterio-lateral margin and it is apparently sub-hexagonal: it is certainly longer than broad. The 1st pair of marginal is partly seen which should be pentagonal. The anterio-proximal part of 1st lateral is also distinct.

Material: A posterior peripheral (E-108). The material is catalogued in the Indian Museum, Kolkata.
(Plate 13, fig. 3 & Text fig. 33)

Locality: Siwaliks of the Punjab.

Description

The specimen is comparable to the right 7th peripheral of extant *Batagur*. The proximal width of the peripheral is less than the distal width. The suture between 7th and 8th marginal is distinct. On the 7th peripheral completion of the connecting bridge between carapace and plastron takes place which is evident towards the distal end of the anterio-lateral margin of the peripheral. On the ventral surface of the peripheral, a small depression is visible (probably a place for the muscle connection). The dimensions of the specimen are as follows:
Proximal width of the peripheral = 5.6 cm
Distal width of the peripheral = 8.0 cm
Length of the peripheral = 11.6 cm

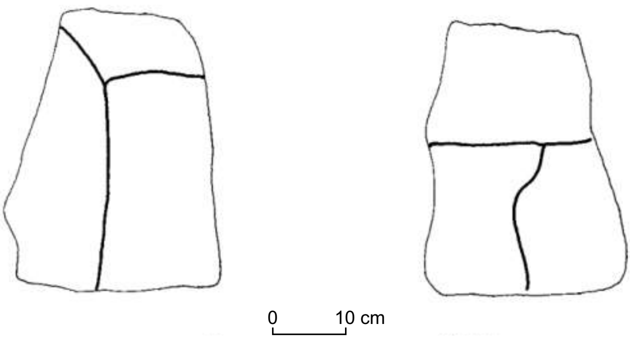


Fig. 33. Right 7th peripherial of cf. *Batagur baska* (E-108).

Melanochelys GRAY, 1869

Distinguishing features

It is a genus of terrestrial and semi-aquatic turtles restricted to Assam, Nepal, Bangladesh, Sri Lanka and Burma. It has moderate to high domed carapace; the posterior marginal serration is present only in juveniles (in *Melanochelys* posterior marginal serration is very strong). It bears three low keels, which are sometimes absent (in *Geoclemys* the keels are prominent and ridged), hexagonal and posterior shorter neurals (in *Geoclemys* the hexagonal neurals are short sided anterior). The plastron is hingeless; the entoplastron is intersected by the humero-pectoral seam (the entoplastron is anterior to humero-pectoral seam in

Geoclemys, Batagur, Geoemyda, Hardella, Kachuga and *Morenia*). The three-keeled genus can easily be differentiated from *Batagur* (very large genus with one central keel only in juvenile), *Hardella* (larger genus with one central keel), *Pangshura* (single central keel with no marginal serration).

Melanochelys trijuga SCHWEIGGER, 1812

Holotype: possibly in MNHN (IVERSON, 1992)

Type Locality: "Insula Java", Indonesia (in error) (IVERSON, 1992)

Habitat and Distribution

Melanochelys trijuga the 'Indian black turtle' prefers still water bodies with aquatic vegetation, although it may be found in rivers and another lotic habitat. It has also been located away from water (DAS, 1995). The turtle is found searching for food in dark on the edges of waterbodies. It is a non-aggressive species which defaecates when picked up. It is an omnivorous species which feeds upon prawn, fishes, insect larvae, molluscs, water hyacinth, grass, fruits etc. It is a widely distributed species (excluding the arid north-west and north-central region of Indian subcontinent) found in India (Assam, Meghalaya, West Bengal, Bihar, Uttar Pradesh, Tamil Nadu, Maharashtra, Andhra Pradesh, Karnataka and Gujarat), Nepal, Sri Lanka, Maldives (Hulule, Male) and Bangladesh.

Synonymy:
1758: *Testudo scabra* Linnaeus
1812: *Emys trijuga* Schweigger
1830: *Clemmys trijuga* wagler
1885: *Clemmys sivalensis* Lydekker
1885: *Clemmys theobaldi* Lydekker
1885: *Clemmys punjabiensis* Lydekker
1885: *Clemmys hydaspica* Lydekker
1886: *Clemmys sivalensis* (Lydekker)
1886: *Clemmys theobaldi* (Lydekker)
1886: *Clemmys punjabiensis* (Lydekker)
1886: *Clemmys hydaspica* (Lydekker)
1889: *Melanochelys trijuga* Boulenger
1931: *Geoemyda trijuga* Smith
1941: *Geoemyda trijuga* Bourret
1985: *Melanochelys trijuga* Tikader & Sharma
1991: *Melanochelys trijuga* Das
1992: *Melanochelys trijuga* Iverson
1995: *Melanochelys trijuga* Das

Distinghishing features:

The carapace is elongated; it is elevated in adults and depressed in juveniles. The central and lateral keels are developed (absent in subspecies *Melanochelys* *trijuga coronata, Melanochelys trijuga parkeri* and in *Melanochelys trijuga indopeninsularis*); *the* lateral keels are found only along the first three laterals (lateral keels go up to the fourth lateral in *Melanochelys tricarinata*); the posterior marginals are feebly serrated. The cervical is small and triangular; the centrals are typically as long as wide or longer than wide (central 5 is wider than long). It can be differentiated from *Melanochelys tricarinata* in which the centrals are broader than long. The plastron is truncated anterior and notched posterior, the head is moderate with a short snout; the upper jaw is notched and the toes are fully webbed (foretoes only half webbed in *Melanochelys tricarinata*).

Material: Nearly complete shell (E-89) catalogued in the Indian Museum, Kolkata. The material was collected by THEOBALD in 1879 and was previously described by LYDEKKER (1885) as *Clemmys theobaldi*.
(Plate 14, fig. 1 & Text fig. 34)

Locality: Jhand, Punjab, Siwalik Hills.

Description

Carapace: The carapace is complete upto the 3rd central; the 4th central is visible only by its anterior most part. The carapace is dorsal depressed (diagenetic compression). The bony sutures on the carapace are reduced (excepting a part of the nuchal), suggesting that the animal was an adult. The carapace is depressed and the central region of the carapace is flat.

Cervical: The cervical is small, narrow anterior and triangular. It is posterior much broader than anterior. The posterior margin of the cervical is not clearly seen and thus LYDEKKER (1885) concluded that there is no cervical; 1st central is pentagonal.

Centrals: The specimen is preserved by three anterior centrals. A very small part of 4th central is seen. The 1st central is as broad as long; it has convex posterio-lateral and concave anterio-lateral margins. The anterior margin of the 1st central is convex and it is much wider than the posterior margin. The 1st central reaches upto the 1st marginal. The 2nd and 3rd centrals are mostly as broad as long. The width of the 2nd and 3rd centrals is more than their length at the junction of the anterio-lateral and posterio-lateral borders. They are nearly as large as the 1st central. The anterior margins of the 2nd and 3rd centrals are sinuated; the posterior margin of the 2nd central is sinuated but that of 3rd central is concave. The anterior margins of the 2nd and 3rd centrals are slightly wider than the posterior ones. The 2nd and 3rd centrals are hexagonal; their anterio-lateral margins are slightly convex and posterio-lateral margins are concave. The anterio-lateral and posterio-lateral margins meet each other at an acute angle.

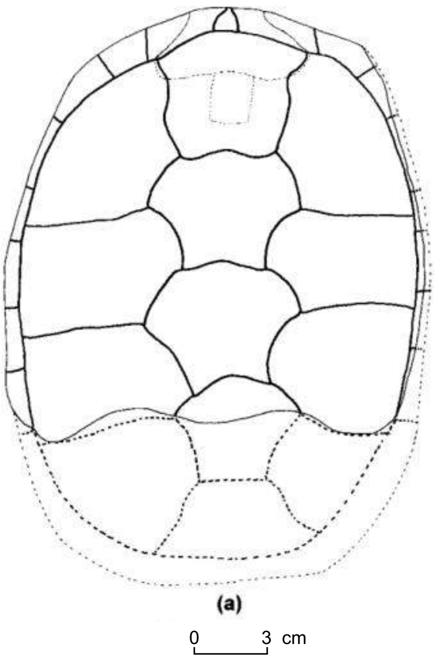


Fig. 34 a. Reconstructed dorsal view of a posterior broken shell of *Melanochelys trijuga* (E-89).

Laterals: The 1st lateral is wedge shaped; it has wider and arcuade distal margin; the proximal margin is sinuated and the posterior one is straight. The distal width of the 1st lateral is more than the proximal width. The 2nd lateral has nearly straight distal margin; its distal width is less than the proximal width. The 3rd lateral has only anterior margin preserved; a restoration of the carapace suggests that the distal width of the 3rd lateral is more than its proximal width. The 2nd and 3rd laterals are pentagonal.

Marginals: Only marginals 1-7 are preserved. The marginals especially the anterior ones are narrow. The 1st marginal is reaching upto the 1st lateral; it is remarkably narrow in anterio-posterior direction in comparison to transverse direction. The 2nd and the 3rd marginals are contacting the 1st lateral. The 4th marginal is reaching upto the 2nd lateral. The 5th marginal is contacting the 2nd lateral and the 6th is reaching upto the 3rd lateral. The 7th marginal is contacting the 3rd lateral and restoration suggests that the 8th marginal reaches upto the 4th lateral.

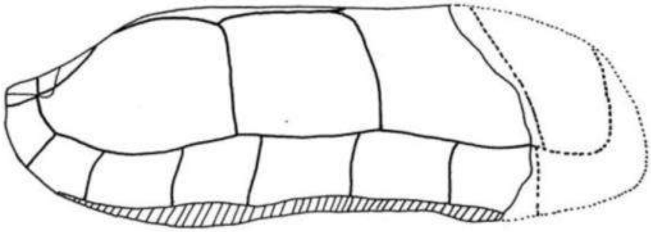


Fig. 34 b. Reconstructed lateral view of a posterior broken shell of *Melanochelys trijuga* (E-89).

Nuchal (based on restoration)**:** The nuchal is lateral concave and posterior convex and wider; it is furrowed with the cervical and the anterior seam of the 1st central. The nuchal contacts the anterio-lateral margins of the 1st central on the proximal margins of the 1st pair of the marginals. The maximum length of the nuchal is about 2.0 cm.

The measurements taken on the restored carapace are as follows:
SCL (straight carapace length) = 19.5 cm
SCW (straight carapace width) = 13.4 cm
SH (straight height) = 4.5 cm

Plastron: The preserved parts of a posterior broken plastron includes gulars, humerals, pectorals, abdominals and anterior part of femorals. The suture between the hyo-and hypoplastron is feebly and has been completed on the restored plastron.

Gulars: The gular is large; its mid-seam length is nearly equal to that between the pectorals. The gular has straight anterior margin; no anterior notch is seen.

Humerals: The mid-seam length of the humeral is much less than that between pectorals. The seam between humeral and pectoral is sinuated. The more anterior position of the humero-pectoral seam indictes that it intersects the entoplastron which is not distinct on the specimen.

Pectorals: The pectoral is larger than the humeral. It is smaller than the abdominal in mid-seam length. The seam between pectoral and abdominal is sinuated; on the middle it takes a small upward curve; on the distal ends the seam drops downwards.

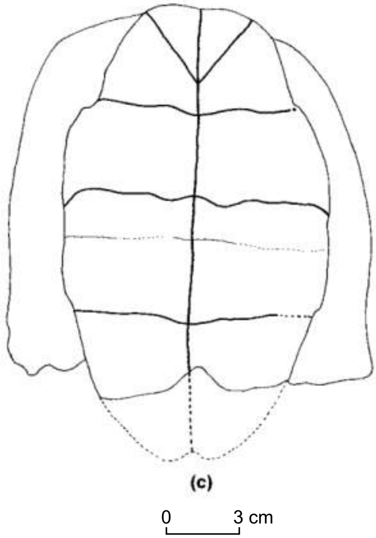


Fig. 34 c. Reconstructed ventral view of plastron of *Melanochelys trijuga* (E-89).

Abdominals: The abdominal is the largest amongst all the plastral scutes in mid-seam length. The seam between abdominal and femoral is nearly straight. Shortly posterior to the abdomino-femoral seam the carapace is broken.

The maximum length of the restored plastron is about 16.8 cm and the maximum width is about 9.8 cm.

Material: Nearly complete shell (E-90) catalogued in the Indian Museum, Kolkata. The material was collected by Mr. THEOBALD in 1879 and was described by LYDEKKER (1885) as *Clemmys sivalensis.*
(Plate 14, fig. 2 & Text fig. 35).

Locality: Siwalik hills of Punjab (LYDEKKER, 1885)

Description

Carapace: The carapace is complete keelless and flattened at its central region. Except the faintly distinguishable cervical, 1st and 5th centrals, anterior two marginals and nuchal, the scute seams and bony sutures are not distinct on the carapace.

Cervical: The cervical is small, narrow anterior and triangular being much broader posterior. The posterior margin of the cervical is not clearly distinguishable.

Centrals: On the specimen only 1st and 5th centrals are distinguishable. The 1st central is identical to specimen E-89 in shape. The anterior margin of the 1st central is broader than the posterior. It has convex posterio-lateral and concave anterio-lateral margins, being slightly broader than long. The 5th central is broader posterior. A small posterior part of 4th central is seen. A reconstruction of the 4th central suggests that it has slightly concave posterio-lateral and convex anterio-lateral margins. It is also wider than long. No other centrals are traceable on the specimen.

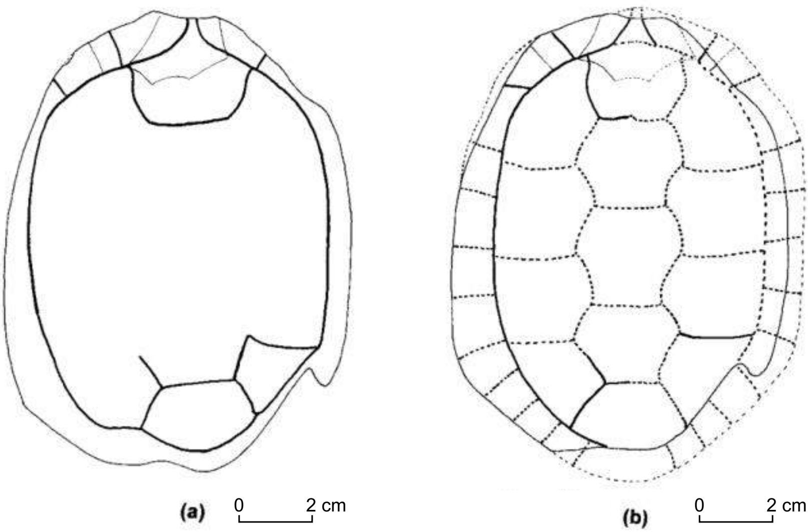


Fig. 35. *Melanochelys trijuga* (E-90). (a) Dorsal view, (b) restored dorsal view.

Marginals: Only marginal 1 and 2 are distinguishable on the specimen. The 1st central is wider than the 2nd. The proximal width of 1st and 2nd marginals is less than the distal width.

Nuchal (based on restoration)**:** The nuchal is concave lateral and convex and wider anterior; it is furrowed with the cervical and the anterior seam of the 1st central. The nuchal contacts the anterio-lateral margins of the 1st central on the proximal margins of the 1st pair of marginals.

The measurements taken on the restored carapace are as follows:

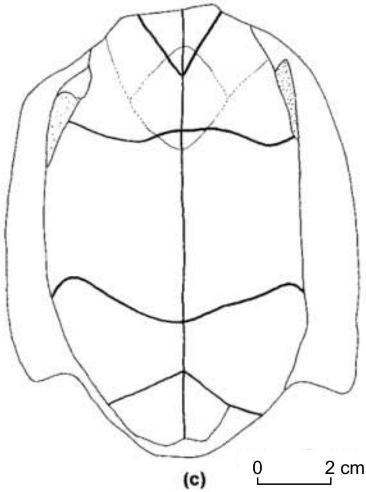
SCL (straight carapace length) = 15.5 cm
SCW (straight carapace width) = 11.6 cm
SH (straight height) = 4.9 cm

Plastron: The preserved parts of the plastron include gulars, humerals, pectorals, abdominals, femorals and anals. The bony sutures are not distinguishable excepting a trace of entoplastron and epiplastron.

Gulars: The gular is large; its mid-seam length is more than that of humerals. The gular has straight anterior margin; no anterior notch is seen.

Humerals: The mid-seam length of the humeral is nearly equal to that between the femorals. The seam between humeral and pectoral is sinuated. It intersects the entoplastron.

Pectorals: The seam between pectoral and abdominal is not distinguishable due to eroded surface of the specimen. The size of the pectorals and abdominals also can not be distinguished for the same reason. However, a combined mid-seam length of the pectorals and abdominals is about three times that between the anals. A restoration suggests that the mid-seam length of the pectorals is equal to that between the abdominals.



(c)

Fig. 35 c. Ventral view of plastron of *Melanochelys trijuga* (E-90).

Femorals: The seam between abdominals and femorals is concave upto the middle of the plastron and then on distal margins it drops downward. The mid-seam length of the femorals is less than that between the anals.

Anals: The seam between anals and femorals drops gently downwards from the mid-seam. A posterior notch is seen in the anals.

Epiplastra: The anterior margin of the epiplastron is truncated and shows no sign of notch. Its distal width is more than the proximal width.

Entoplastron: The entoplastron is large; it is intersected by the humero-pectoral seam.
The maximum length of the restored plastron is approx. 14 cm and the maximum width approx. 8.5 cm.

Material: Posterior broken shell (E-92) catalogued in the Indian Museum, Kolkata. The material was collected by THEOBALD in 1879 and was previously described by LYDEKKER (1885) as *Clemmys punjabiensis*.
(Plate 15, fig. 1 & Text fig. 36)

Locality: Siwalik hills, Punjab (LYDEKKER, 1885).

Description

Carapace: The carapace is highly vaulted, complete upto the 3rd central. The bony gomphosis on the carapace is reduced, suggesting that the animal was an adult. The cervical region, part of right anterior marginals and posterior marginals after the 7th are broken.

Centrals: The specimen shows three anterior centrals. Central 1 is little longer than broad; it has convex posterio-lateral and concave anterio-lateral margins. The anterior margin of the 1st central is convex and it is much wider than the posterior margin. The 1st central reaches up to the 1st marginal. The 1st central is nearly in the shape of an inverted bell. In the middle of the posterior border, the 1st central is notched to receive a corresponding projection from the 2nd central. The 2nd central is as broad as long. The width of the 2nd central is more than its length at the junction of its anterio-lateral and posterio-lateral borders. It is larger than the 1st central. The anterior margin of the 2nd central is slightly wider than the posterior. The 2nd central is hexagonal. The anterio-lateral margin of the 2nd central is slightly convex and the posterio-lateral margin concave. The 3rd central is wider than long. It has straight anterior margin which is narrower than its posterior margin. It is also hexagonal; its anterio-lateral margins are nearly straight and posterio-lateral margins are concave. The anterio-lateral and posterio-lateral margins of the 2nd and 3rd centrals meet each other at an acute angle.

Laterals: The 1st lateral is wedge shaped; it has wider and arcuade distal margin; the proximal margin is sinuated and the posterior one is little convex. The distal width of the 1st lateral is more than the proximal width. The 2nd lateral is nearly straight distal and its distal width is less than the proximal width. The 3rd lateral has only anterior margin preserved; a restoration of the carapace suggests that the distal width of the 3rd lateral is more than its proximal width. The 2nd and 3rd laterals are pentagonal (based on restoration).

Marginals: Only anterior marginals 1 – 7 are preserved. The marginals especially the anterior ones are narrow. The 1st marginal is reaching upto the 1st lateral; it is remarkably narrow in anterio-posterior direction in comparison to transverse direction. The 2nd and the 3rd marginals are contacting the 1st lateral. The 4th marginal is reaching upto the 2nd lateral. The 5th marginal is contacting the 2nd lateral and the 6th is reaching upto the 3rd lateral. The 7th marginal is contacting the 3rd lateral (based on restoration).

Measurements taken on the restored carapace are as follows:
SCL (straight carapace length) = 17 cm
SCW (straight carapace width) = 12.7cm
SH (straight height) = 6.6 cm

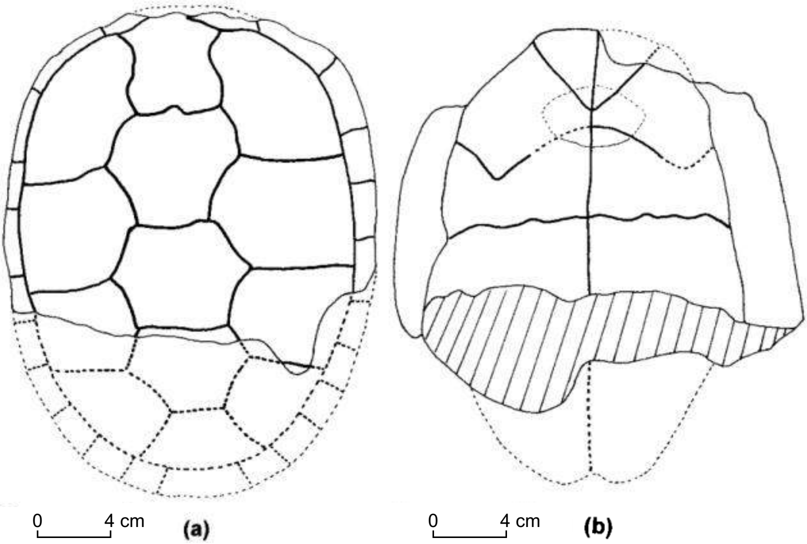


Fig. 36. Reconstructed view of a posterior broken carapace of *Melanochelys trijuga* (E-92). a) Dorsal, b) ventral view.

Plastron: The preserved parts of a posterior broken plastron include gulars, left humeral, and pectoral and posterior broken abdominals and anterior part of femorals. A very small posterior part of the entoplastron is also preserved, which has been completed on the restored plastron.

Gulars: The gular is large; its mid-seam length is slightly less than that of the pectorals. The gular has straight anterior margin; no anterior notch is seen.

Humerals: The mid-seam length of the humeral is much less than that between pectorals. In overall size it is smaller than the pectoral. The seam between humeral and pectoral is directed downwards from the mid-seam; close to distal end it turns sharply upwards. A restoration suggests that it intersects the entoplastron.

Pectorals: The pectoral is larger than the humeral. It is smaller than the abdominal in mid-seam length (based on restoration). The seam between pectoral and abdominal is sinuated; on the middle it takes a small upward curve; on the distal ends the seam drops downward at a gentle angle.

Abdominals: The abdominal is posterior broken. It is the largest amongst all plastral scutes in mid-seam length (based on restoration).

The maximum length of the restored plastron is approx. 14.8 cm and the maximum width is approx. 9.6 cm.

Material: Complete shell (E-93), consisting of a partly broken carapace and plastron. The material is catalogued in the Indian Museum, Kolkata. The material was collected by THEOBALD in 1879 and was previously described by LYDEKKER (1885) as *Clemmys hydaspica*.
(Plate 15, fig. 2 & Text fig. 37).

Locality: Jhelum, Punjab, Siwalik Hills.

Description

Carapace: The specimen lacks parts of anterior and posterior peripherals. The specimen is very perfect preserved. The carapace is more vaulted and oval. The lateral surface of the carapace is highly arcuade and the sides of the anterior portion instead of shelving rapidly are full and convex. The cervical portion of the carapace is not preserved.

Centrals: The region of centrals is highly convex, having no trace of a depressed carapace. There is no trace of any central or lateral keels. The 1st central is pentagonal reaching up to the 1st marginal; it is wider anterior than posterior, but enclosed by the nuchal. The anterio-lateral margins of 1st central make an acute angle with each other. The 2nd central is little longer than the 1st; its width is more than the length. The 2nd, 3rd and 4th centrals are hexagonal and their posterio-lateral borders are slightly concave. The 3rd and 4th centrals are almost equal in length; the 3rd central is almost as wide as long. The width of the 4th central is more than its length. The anterio-posterior margins of the centrals are nearly straight. The 5th central is much wider than long. Its posterior border equals the width of post-central. The post-central is divided, the seam between the two post-centals is clearly distinct.

Laterals: The 1st lateral is quadrilateral; its outer margin is arcuade. The 2nd and 3rd laterals are pentagonal and are transverse wider than anterio-posterior. The 4th lateral is quadrilateral; its dimension in transverse and anterio-posterior direction is nearly equal.

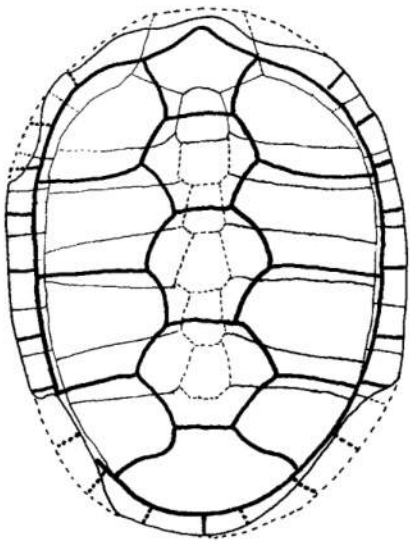


Fig. 37 a. Reconstructed dorsal view of a marginal broken carapace of Melanochelys *trijuga* (E-93).

Marginals: 2-8 marginals are preserved and distinct. The anterior margin of the 2nd marginal is not distinct. 3rd and 4th marginals are contacting the 1st lateral. The 5th marginal is reaching upto the middle of 2nd lateral. The 6th marginal is contacting the 2nd lateral. The 7th marginal is reaching upto the middle of the 3rd lateral. The 8th marginal is contacting the 3rd lateral.

Nuchal: The nuchal is distinguishable with nearly straight lateral margins; it is nearly pentagonal which is wider posterior (based on restoration). It is furrowed with the anterior and lateral margins of 1st central.

Neurals: The 1st neural is wider posterior; its anterior margin is convex whereas the posterior margin is straight. The remaining neurals are not traceable. The posterior border of the 1st pleural contacts posterior border of the 1st neural and thus indicates that the neurals are short-sided anterior.

Pleurals: The distal part of pleural 1 is broken. Owing to the indistinct neurals it is not possible to demarcate the proximal end of pleurals.
The pleurals 1, 4, 6 and 7 are wider than pleurals 2, 3, 5 and 8. The sutures between all the pleurals are nearly straight. The proximal width in 1st, 3rd, 5th and 7th pleurals is less than the distal width; whereas, in pleurals 2nd, 4th, 6th and 8th, the distal width is less than the proximal width.

Peripherals: 22nd – 8th peripherals are distinct; anterior border of the 2nd and posterior border of the 8th peripheral is broken. The peripherals are generally quadrilateral (excepting 8th peripheral which is pentagonal). The 3rd peripheral is wider than the 4th. The 4th and the 7th are the smallest among all the distinct peripherals. The 3rd peripheral reaches upto the 2nd pleural and th 4th contacts the 2nd pleural. The 5th peripheral contacts the 3rd pleural and the 6th peripheral reaches upto the 5th pleural. The 7th peripheral contacts the 5th pleural. The 8th peripheral contacts the 6th pleural (based on restoration).

The dimensions of the restored carapace are as follow:
SCL (straight carapace length) = 18.2 cm
SCW (straight carapace width) = 13.5 cm
SH (straight height) = 7.5 cm

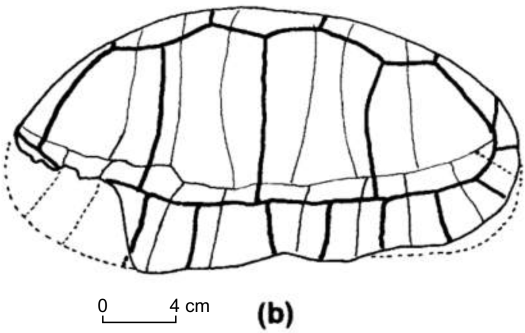


Fig. 37 b) Reconstructed lateral view of a marginal broken carapace of *Melanochelys trijuga* (E-93).

Material: Complete shell (K-53/222). The material is catalogued in the Indian Museum, Kolkata.
(Plate 15, fig. 3 & Text fig. 38).

Locality: Siwalik hills

Description

Carapace: The carapace is convex with moderately domed surface. The carapace is complete excepting the left marginal and right anterior marginal part. The cervical portion is also broken. The ossified sutures on the carapace are completely reduced suggesting that the animal was an adult.

Centrals: The 1st central is as broad as long; it has convex posterio-lateral and concave anterio-lateral margins. The anterior margin of the 1st central is convex and is wider than posterior. The 1st central reaches upto the 1st marginal. The 2nd and 3rd centrals are longer than broad. They are larger than the 1st central. The anterior margins of the 2nd and 3rd centrals are sinuated; the posterior margin of the 2nd and 3rd central is straight. The 2nd and the 3rd centrals are hexagonal. The 4th central is broader than long; it is smaller than the first three centrals. In centrals 2-4, the anterio-lateral margins are slightly convex and the posterio-lateral margins are concave. Their anterio-lateral and posterio-lateral margins meet each other at an acute angle and anterior margins are wider than the posterior margins. The 5th central is the smallest having wider posterior margin.

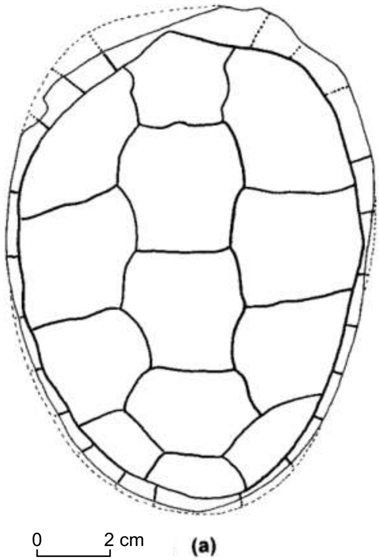


Fig. 38 a. Restored dorsal view of a marginal broken shell of *Melanochelys trijuga* (K53/222).

Laterals: The 1st lateral is wedge shaped and the largest; it has wider and arcuade distal margin; the proximal margin is sinuated and the posterior one is straight. The distal width of the 1st lateral is more than the proximal width. The 2nd lateral has nearly straight distal margin; its distal width is less than the proximal width. The anterior margins of the 2nd and 3rd laterals are wavy. In 3rd lateral, distal width is more than the proximal width. The 2nd and 3rd laterals are pentagonal. The 4th lateral is the smallest; its distal width is also greater than the proximal width. It is quadrilateral.

Marginals: The marginals especially the anterior ones are narrow. The 1st marginal is reaching upto the 1st lateral. The 2nd, 3rd and 4th marginals are contacting the 1st lateral. The 5th marginal is reaching upto the 2nd lateral. The 6th marginal is contacting the 2nd lateral and the 7th is reaching upto the 3rd lateral. The 8th marginal is contacting the 3rd lateral and 9th is reaching upto the 4th lateral. The 10th is contacting the 4th lateral and the 11th marginal is reaching upto the 5th central.

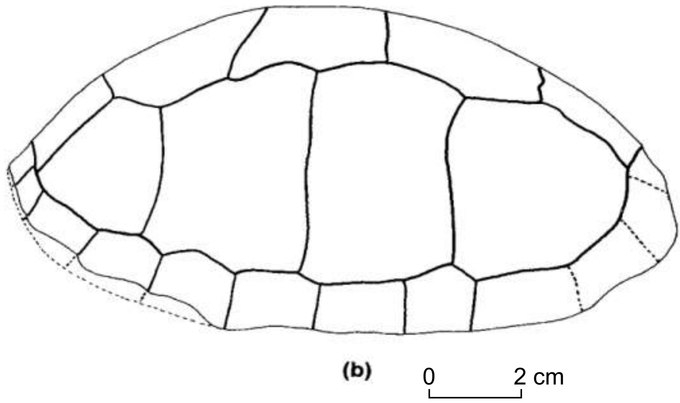


Fig. 38 b. Restored lateral view of a marginal broken shell of *Melanochelys trijuga* (K53/222).

The measurements taken on the restored carapace are as follows:

SCL (straight carapace length) = 19.5 cm
SCW (straight carapace width) = 13.5 cm
SH (straight height) = 10 cm

Plastron: The preserved parts of the plastron include humerals, pectorals, abdominals, femorals and anals. The sutures between underlying bones are completely reduced. The gular portion is broken.

Humerals: The humerals are not complete. The seam between humeral and pectoral is sinuated. The more anterior position of the humero-pectoral seam indicates that it intersects the entoplastron which is not distinct on the specimen.

Pectorals: The pectoral is larger than the humeral. It is smaller than the abdominal in mid-seam length. The seam between pectoral and abdominal is sinuated; at the middle it takes a small upward curve; on the distal ends the seam drops downward.

Abdominals: The abdominal is the largest amongst all plastral scutes in mid-seam length. The seam between abdominal and femoral is concave, it drops downward on the distal margins.

Femorals: The femoral is smaller than humerals and anals in mid-seam length. It has wider anterior and narrower posterior margin.

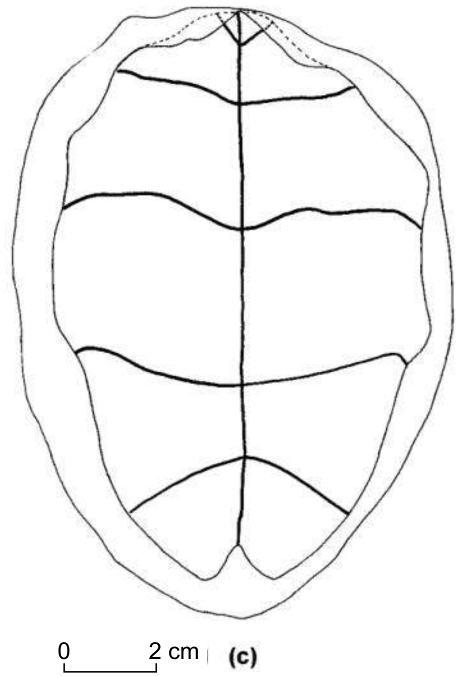


Fig. 38 c. Restored ventral plastron view of *Melanochelys trijuga* (K53/222).

Anals: The seam between the femorals and anals drops downward. The mid-seam length of the anal is smaller than that of humerals. A posterior notch is present in the anals.

Pangshura GRAY, 1855

Distinguishing features

This genus of batagurine turtles was earlier described as *Kachuga* (GRAY, 1855) that contains several species of Asian turtles, viz, *P.flaviventer*, *P. smithii, P. sylhetensis, P. tecta* and *P. tentoria.* All the species of this genus are aquatic. The carapace is elongated and oval (20-50 cm long), without marginal serration; It has a single median keel (central keel) which has posterior pointing projection in several species. It is distinguishable from *Geoclemys, Cuora, Cyclemys, Geoemyda, Melanochelys* and *Pyxidea* which are three keeled. *Pangshura* is much smaller than *Hardella* and *Batagur*. The neurals are hexagonal and short sided anterior. The 4th central is much longer than broad and covers parts of four or five neurals. The plastron is rigid with large buttresses. The entoplastron lies anterior to the humero-pectoral seam. The recent species of *Pangshura* are distinguishable from others by their colour pattern on the body. They are reported from Pakistan, India, Bangladesh, Burma and Nepal. In view of these generic condensation based on morphological similarities and habitat, we consider that all *Kachuga tatrotia* described earlier are *Pangshura tatrotia* (JOYCE & TYLER, 2010).

Pangshura flaviventer GÜNTHER, 1864

Holotype: BMNH 1947.3.4.82 (IVERSON, 1992)

Type Locality: none designated (IVERSON, 1992)

Habitat and Distribution

*Pangshura (*ex. *Kachuga) flaviventer* the 'yellow bellied tent turtle' is basically a riverine species; it is found both in small and large rivers. They like to bask on shorelines, rocks and on tree trunks. They are non-aggressive, only sometimes attempting to bite. They prefer a herbivorous diet including leaves and stems of green plants, however, they can be carnivorous as well. They are found in Ganga, its northern tributaries and Brahmaputra river from Behar, India eastward to Bangladesh and Nepal.

Synonymy

1860: *Emys namadica* Theobald
1864: *Pangshura flaviventer* Günther
1864: *Kachuga tentoria flaviventer* (Günther)
1870: *Cuchoa flaviventris* Gray
1885: *Pangshura flaviventris* (Lydekker)
1886: *Pangshura flaviventris* (Lydekker)
1991: *Kachuga tentoria flaviventer* Das
1992: *Kachuga tentoria flaviventer* Iverson
1995: *Kachuga tentoria flaviventer* Das

Distinguishing features

The carapace is oval, elevated with a distinct central keel which is spiked on the third central. The carapace grows upto 21 cm in length. The cervical is narrow; it is larger and wider than in *P. tentoria* and smaller and narrower than in *P. tecta.* The 1st central is bell-shaped (it is subquadrangular in *P. tentoria;* pentagonal in *P. tecta* and *P. sylhetensis*). The 1st & 2nd central are either longer than broad or as broad as long, and can be distinguished from that of *P. tentoria* and *P. tecta* in which it is broader than long. The 2nd central of *P. flaviventer* is distinguishable from that of *Batagur dhongoka* in which the posterior border of the 2nd central is pointed backward. The 3rd central has pointed posterior end; It can be distinguished from *P. smithii* in which the posterior border of the 3rd central is straight. It can be differentiated from *P. sylhetensis* which has strongly serrated carapace and 26 marginals instead of normal 24 (an extra pair is formed by subdivision of the two postcentrals. The recent members of *Pangshura flaviventer* can be distinguished from other *Pangshura* by their carapace which is brownish olive with a light-coloured stripe on the first three centrals; the yellow plastron, brownish olive with a pink patch behind the eyes. It is very closely related to *P. tecta, P. tentoria* and *P. smithii.* An intensive study is needed to explore the relationships of *P. flaviventer* with the above three.

Material: Posterior incomplete shell (F-110), described by LYDEKKER (1885) as *Pangshura flaviventris*. The material is catalogued in the Indian Museum, Kolkata under the wrong catalogue number (E-110).
(Plate 16, fig. 1 & Text fig. 39).

Locality: Pleisctocene of Moar Domar in the Narmada Valley (LYDEKKER, 1885, 1886).

Description

Carapace: The shell is elongated oval, convex having a strongly developed central keel which is spiked on 3rd vertebral. A small part of left anterior marginals (1st and 2nd marginals) is broken. The carapace is complete upto 4th central. A small anterior part of 5th central is also preserved. The 4th lateral is posterior incomplete; 1-7 marginals are complete and the carapace is broken posterior to 7th marginal; the 8th marginal is partially preserved. The nuchal is anterior broken; neurals 1-7, pleurals 1-7 and peripherals 1-7 are distinct on the carapace.

Cervical: The cervical is very narrow and small (based on restoration); its anterior width is slightly less than the posterior width.

Centrals: The 1st central is nearly as broad as long; the anterior half of the 1st central is enclosed with the nuchal. The anterior margin of the 1st central is deeply convex projecting into the marginal region. The 1st central is almost in the shape of an inverted bell. Its posterio-lateral margins are convex and anterio-lateral margins are concave. The 2nd central has convex anterior margin; it is larger than the 1st central and is broader than long. It is hexagonal. The 3rd central is also hexagonal and is nearly as large as the 2nd central and nearly as broad as long. Its posterior margin is characterstically narrow and so is the anterior margin of 4th central which is much longer than braod. The contact of 3rd central with the 4th is very narrow. The anterior margin of 3rd and 4th central is slightly concave. The 4th is the largest central which overlies 5 neurals; it is hexagonal like the 2nd and 3rd centrals. The 5th central is also longer than broad. Its posterior margin is broader than the anterior margin (based on restoration).

Laterals: The 1st lateral is almost triangular with arcuade distal margin. Its distal width is more than the proximal width. The anterior margin of 2nd lateral is concave; it is pentagonal. The distal width of the 2nd lateral is slightly more than its proximal width. its distal margin is almost straight. The 3rd lateral is also pentagonal; its distal width is nearly equal to its proximal width. The 4th lateral is incomplete. Its proximal width is less than than the distal width (based on restoration).

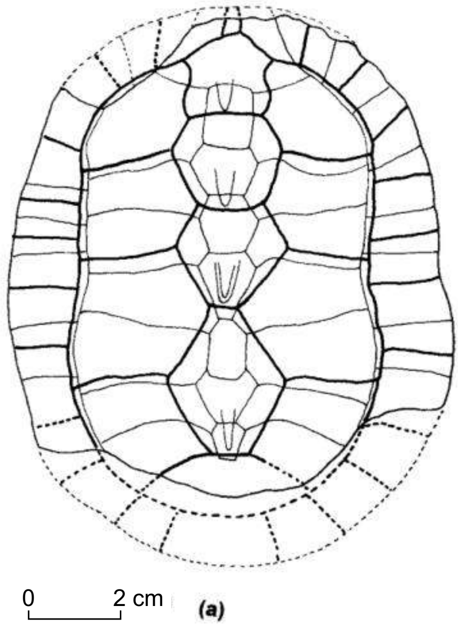


Fig. 39 a. Posterior broken shell of *Pangshura flaviventer*, specimen F-110. Restored dorsal view.

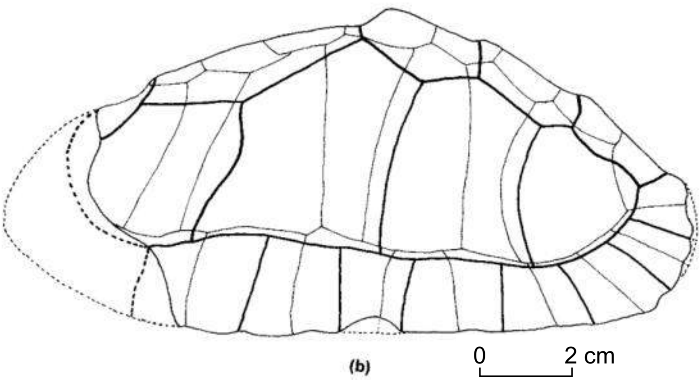


Fig. 39 b. Restored lateral view of carapace of *Pangshura flaviventer*, specimen F-110.

Marginals: The first pair of the marginals is larger than the 2nd and 3rd pair; it is nearly pentagonal. The 2nd and 3rd pairs are rectangular; their distal width is more than their proximal width. The marginals 1-3 are contacting the 1st lateral. The 4th is reaching up to the 2nd lateral. The 5th is contacting the 2nd lateral. The 6th is reaching the 3rd lateral, and the 7th marginals are contacting the 3rd lateral. The 8th marginal is reaching upto the 4th lateral. A restoration on the similar pattern suggests that the 10th marginal contacts the 5th central.

Nuchal: The nuchal is narrower anterior and broader posterior; it is hexagonal having concave anterior margins and being furrowed with the cervical and anterior and lateral margins of the 1st central.

Neurals: The 1st neural has straight anterior margin; it is longer than broad and rectangular. It is furrowed with the anterior margin of the 2nd central. The 2nd neural is hexagonal and has straight anterior margin; it is smaller than the 1st neural and is broader than long. The 3rd neural has straight anterior margin and is also hexagonal is shape; it is larger than the 2nd neural. It is furrowed with the anterior margin of the 3rd central. It is nearly as broad as long. The 4th neural is larger than the previous 3 neurals; its anterior margin is straight and is much larger than the posterior margin; it is longer than broad and hexagonal. It is furrowed with the anterior margin of the 4th central. The 5th neural is also longer than broad and hexagonal; its anterior margin is straight and the posterior margin is projected into the 6th neural. It is as long as the 1st neural. The contact between 4th and 5th neural is very narrow. The 6th neural is smaller than the 5th; it is braoder than long and hexagonal. The 7th neural is smaller than all the previous neurals; it is nearly as broad as long. All the hexagonal neurals are short-sided anterior.

Pleurals: The 1st pleural is the largest in comparison to the other pleurals; it is nearly in the shape of an elongated pentagon; it is arched distally; its posterior margin is convex. It is furrowed with the lateral margins of the 1st and the 2nd centrals and anterior margin of the 2nd lateral. The 2nd pleural is narrower than the 1st. It is furrowed with the lateral margins of the 2nd and the 3rd centrals. The 3rd pleural is furrowed with the lateral margin of the 3rd central and anterior margin of the 3rd lateral. The 4th pleural is furrowed with the lateral margin of the 3rd and 4th central. The 5th pleural is furrowed with the lateral margin 4th central and anterior margin of the 4th lateral. The 6th pleural is furrowed with the lateral margin of the 4th central (based on restoration).
The proximal margins of the 1st, 3rd and 5th pleurals are narrower than those of the 2nd, 4th and 6th pleurals whereas, The distal margins of 1st, 3rd and 5th pleurals are wider than those of 2nd, 4th and 6th pleurals.

Peripherals: The 1st peripheral has broader outer margin compared to the inner margin. It is furrowed with the posterior margin of the 1st marginal. The 2nd peripheral is also broader on outer margins but is quadrilateral. It is furrowed with the posterior margin of the 2nd marginal and proximal margin of the 2nd and 3rd marginals. The 1st and 2nd peripherals are contacting the 1st pleural. The 3rd peripheral is furrowed with the posterior margin of the 3rd marginal and proximal margins of the 3rd and 4th marginals; it is reaching upto the 2nd pleural and 2nd lateral. The 4^{th} peripheral is reaching the 3^{rd} pleural and 2^{nd} lateral. It is furrowed with the posterior margin of the 4^{th} marginal and proximal margins of the 4^{th} and 5^{th} marginals. The 5^{th} peripheral is contacting the 3^{rd} pleural and 2^{nd} lateral; it is furrowed with the posterior margin of the 5^{th} marginal and proximal margins of the 5^{th} and 6^{th} marginals. The 6^{th} peripheral is reaching upto 5^{th} pleural and 3^{rd} lateral; it is furrowed with the posterior margin of the 6^{th} marginal and proximal margins of the 6^{th} and 7^{th} marginals. The 7^{th} peripheral is contacting the 5^{th} pleural and 3^{rd} lateral; it is furrowed with the posterior margin of the 7^{th} marginal and proximal margin of the 7^{th} and 8^{th} marginals. The 8^{th} peripheral is reaching upto the 6^{th} pleural and 4^{th} lateral (based on restoration).

On the basis of the restoration the shell dimensions are as follows:

SCL (straight carapace length) = 11.2 cm
SCW (straight carapace width) = 8.6 cm
SH (straight height) = 4.8 cm

Plastron: The preserved parts of the plastron include anterior incomplete humerals, pectorals, abdominals, femorals and posterior broken anals. On the plastron, the hypoplastra, posterior incomplete xiphiplastra and the suture between hyo-and hypoplastron, are also distinct.

Humerals: The mid-seam length of the humeral is more than the mid-seam length of the pectorals (based on restoration). The seam between humeral and pectoral is projecting upward to the middle and on the distal margin it drops downward.

Pectorals: The pectoral is smaller than the femoral and abdominal in mid-seam length. The seam between pectoral and abdominal is straight, droping downward on the distal margins.

Abdominals: The abdominal is the largest amongst all plastral scutes in mid-seam length. The seam between abdominal and femoral is nearly straight it drops down on the distal margins. The length of the abdomino-femoral seam is less than the abdomino-pectoral seam.

Femorals: The femoral is wedge shaped having anterior width more than its posterior width. The seam between femoral and anal drops downward.

Hypoplastra: The posterior width of the hypoplastron is nearly half of its anterior width. The suture between hyo- and hypoplastron is straight and drops gently downward on the distal margins. The suture between hypo-and xiphiplastron is straight and drops gently downward from mid-seam to the distal margins.

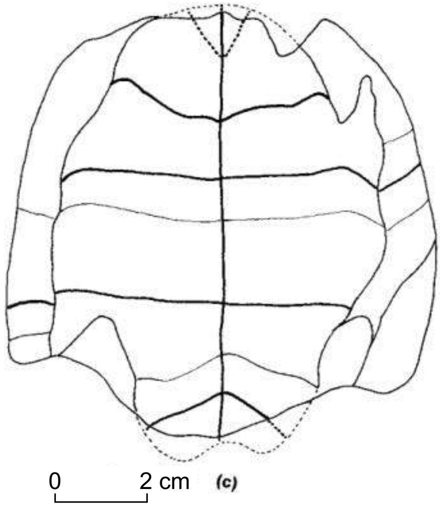


Fig. 39 c. Restored ventral view of plastron of *Pangshura flaviventer* specimen F-110.

The maximum length of the restored plastron is about 8.5 cm and the maximum width is about 6.7 cm.

Pangshura sp.

Material: broken carapace (F-111), catalogued in the Indian Museum, Kolkata. The material was noted by LYDEKKER (1886).
(Plate 16, fig. 2).

Locality: Pleistocene of Narmada basin (LYDEKKER, 1886).

Description

The preservation of the shell is very poor, the carapace is badly crushed and broken. The anterior part is not preserved. It is very difficult to trace the scutes and bony sutures on the carapace. However, one can notice the seam between the 3rd and 4th central that is very narrow so that a very small part of 3rd and 4th central are in contact. This feature helps describing the specimen under the present genus. The specific identification of the specimen is not possible due to its bad state of preservation. It could be either *P. flaviventer* or *P. tecta*. The features differentiating the two species are not distinct on the carapace.

Material: Left hypoplastron (F-108), catalogued in the Indian Museum, Kolkata. The material was noted by LYDEKKER (1886).
(Plate 16, fig. 3).

Locality: Pleistocene of Narmada basin (LYDEKKER, 1886).

Description

The maximum length of the hypoplastron is approximately 13.5 cm and the maximum width is approximately 13 cm. The mid-seam length of the specimen is approximately 7 cm. On the ventral surface a very characteristic inguinal is similar to that in the living *Pangshura.*

Pangshura tatrotia JOYCE & TYLER (2010).

Material: Rather complete and well-preserved shell. YPM 4127, BMNH.
Text Fig. 39.

Locality: Siwaliks of Pakistan; Early Pliocene Tatrot formation (approx. 2.59-3.59 yrs.)

Description

A detailed description is presented in the original publication by JOYCE & TYLER.

The diagnose given by JOYCE & TYLER is as follows:

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

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

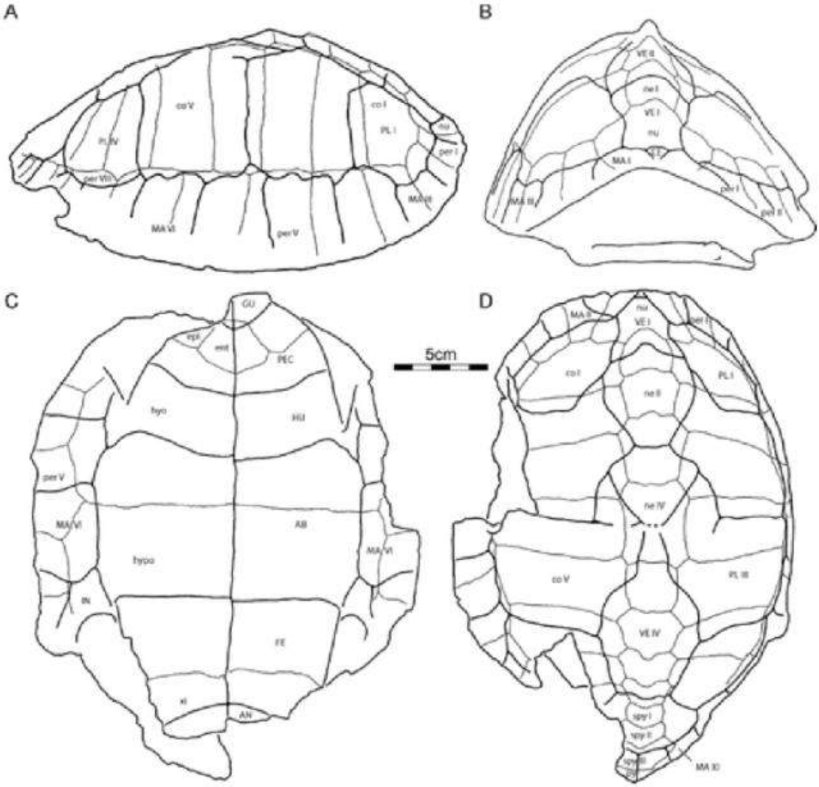


Fig. 39. Drawing from the original description by JOYCE & TYLER, 2010.

JOYCE & TYLER provide a thorough discussion of the extant and fossil species and the Asian Batagurids.

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

Bataguridae indet.

Synonymy:
1991: Batagurinae indet. West *et al.*
1994: Batagurini indet. Corvinus & Schleich
1994: Geoemydini indet. Corvinus & Schleich
1994: Emydoidea indet. Corvinus & Schleich

Material: Pleural (NHM/TU 1989/40 & NHM/TU 1989), **nuchal fragment** (NHM/TU 1989/). The material is catalogued in the Natural History Museum of Tribhuvan University, Kathmandu.
(Plate 16, Fig. 4 & Plate 17, figs. 3, 4 & 5)

Locality: Surai Khola, Upper Siwalik

Description

The specimen NHM/TU 1989/a (Plate 16, fig. 4) is a broken nuchal of a batagurid turtle. The nuchal is furrowed with the anterior borrder of the 1st central. The generic identification of the fragmentary nuchal is difficult until more comparative material is available. The maximum width of the nuchal is about 6.8 cm. Due to fragmentary nature, it is difficult to decipher its length.

Another specimen, a fragment of pleural of a batagurid turtle (NHM/TU 1989/b) was casted by the second author (cast: BSP 1989 XVIII 19). The pleural is furrowed with the lateral margin of the central. It may either belong to the anterior left or posterior right part of the carapace. The maximum length of the pleural is about 3.8 cm and the width is indeterminable due to its fragmentary nature. The visceral surface of the fragment shows a groove probably for the muscle connection, this visceral part was earlier described by CORVINUS & SCHLEICH (1994) as hypo- (hyo) plastron fragment of an emydid turtle (Plate 17, fig. 1).

The third specimen, a pleural (NHM/TU 1989/40) was earlier described by CORVINUS & SCHLEICH (1994) as a pleural belonging to Geoemydini indet. The pleural is curved indicating towards a carapace which is steeply inclined laterally; on proximal margin it is furrowed with the lateral margin of a central and along the length it is furrowed with the margin of a lateral (Plate 17, fig. 2). The size of the pleural (proximal width 3.7 cm, distal width 3.5 cm & length 15.8 cm) indicates towards a turtle which is rather larger (approximately 40 – 50 cm straight carapace length). It is difficult to assign a generic status to the specimen, however, it resembles the pleurals of *Omegachelys sahnii* (gen et sp. nov., this publication).

Material: A right hypoplastron (E-105). The material is catalogued in the Indian Museum, Kolkata. The material was noted by LYDEKKER (1886).
(Plate 17, fig. 3 & Text fig. 40).

Locality: Siwaliks of the Punjab (LYDEKKER, 1886).

Description

The maximum length and width of the specimen is 9 cm. The mid-seam length of the specimen is about 11 cm. The hypoplastron is furrowed by the abdomino-femoral seam. The seam is very characteristic; it rises upward from the median seam upto the middle of middle and then it drops downward towards distal end.

The size of the hypoplastron indicates that the plastron should be around 45 cm long.

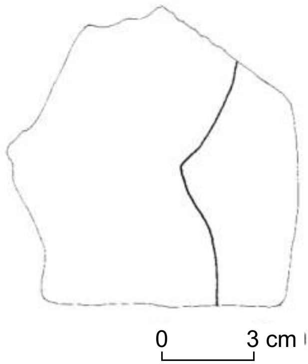


Fig. 40. Right hypoplastron of Bataguridae indet.; specimen F-105.

Material: A left hyoplastron (E-106). The material is catalogued in the Indian Museum, Kolkata. The material was noted by LYDEKKER (1886).
(Plate 17, fig. 4 & Text fig. 41).

Locality: Siwaliks of the Punjab (LYDEKKER, 1886).

Fig. 41. Left hyoplastron of Bataguridae indet.; specimen F-106.

Description

The specimen is very large. The maximum length of the specimen is 19.6 cm and the maximum width 17.6 cm. The mid-seam length of the specimen is 12.1 cm. The hyoplastron is furrowed by the abdomino-pectoral seam which is much posterior to the entoplastron; the distance between the posterio-lateral margin of entoplastron and abdomino-pectoral seam is 7.7 cm. The abdomino-pectoral seam rises upward from the mid-seam upto the middle and then drops downward towards the distal margin of the plastron. The humero-pectoral seam is not discernible on the specimen.

Additional material:

The material listed in the following table (2) was neither found catalogued nor locality information was available.

Reference of the specimen as marked on its surface and repository	Locality Information	Identification	Taxonomic Status
Number : 53; Field Museum, Saketi Fossil Park, Saketi	Not available	Turtle plate fragment (14 X 16 cm) has a smooth surface with a keel in the middle.	Bataguridae indet.
Number : 59; Field Museum, Saketi Fossil Park, Saketi	Not available	Marginal plate fragment (11 X 6.7) with a 'M' type shield furrow.	cf. *Megalochelys*
Number : 77; Field Museum, Saketi Fossil Park, Saketi	Not available	Two left pleural fragments sticking together 13 X 7.5 cm) having callosities. Margins of the plates are broken.	*Trionychidae* indet
Number : 78; Field Museum, Saketi Fossil Park, Saketi	Not available	Right pleural fragment (14.3 X 8 cm) having callosities. On the visceral surface rib is exposed proximal and posterior margin of the plate is broken.	*Trionychidae* indet.
Number : 79; Field Museum, Saketi Fossil Park, Saketi	Not available	Left pleural fragment (8.7 X 7.5 cm) having callosities. Proximal end of the plate is broken.	*Trionychidae* indet.
Number : 132; Field Museum, Saketi Fossil Park, Saketi	Not available	Distal fragment of Hypo (Hyo) plastron (4.5 X 3.2 cm) having callosities.	*Trionychidae* indet.
Number : 235; Field Museum, Saketi Fossil Park, Saketi	Not available	Marginal plastral fragment (23 Xx 15 cm). The marginal thickness of the fragment is approx. 5 cm.	cf. *Megalochelys*
Number : 243; Field Museum, Saketi Fossil Park, Saketi	Not available	Right hyoplastral fragment with an extremeley prominent hypoplastral rim; sulcus demarcatus not developed	Bataguridae indet.
Number 332; Indian Museum, Calcutta	Not available	Large but broken carapace (42.5 X 32.5 cm) having humped central region and upturned marginal region (nearly horizontal). The shield margins and bony sutures are not traceable on the carapace.	*Omegachelys sahnii*
Number : W.19/173; Indian Museum, Calcutta	Not available	Posteriorly broken carapace (straight carapace length is 33.5 cm). No keels are traceable on the carapace. Bony sutures and shield margins are also not distinct due to sediment cover and also due to erosion. Nevertheless, one posterior pleural and two posterior peripherals are distinct.	cf. *Batagur*
Number : K 23/245; Indian Museum, Calcutta	Not available	Antero-posteriorly broken carapace (straight ength is 37.5 cm). No keels traceable on the carapace. Bony sutures not traceable and most of the shield margins are also not distinct due to erosion, but, right laterals are traceable. The 1st and 4th laterals are broken. Marginal region is characteristically wide.	cf. *Batagur*

Tab. 2. Aditional material neither being catalogued nor with locality reference

Palaeoecology and Palaeoclimate

The palaeoecological interpretation in this work is based on the principle of actualism as all of the fossil turtle species (excepting the *Megalochelys sivalensis and Omegachelys sahnii*) are extant in the Indian Subcontinent (DAS, 1991, 1995).

Most of the living testudinids, and few batagurines (*Geoemyda* and *Melanochelys*) from the Indian subcontinent are inhabitants of the semi-green to ever green tropical moist forests and sub-humid grassland near the rivers streams and ponds. However, all the trionychids and batagurines reported from the Indian subcontinent are found to be aquatic, dwelling in rivers, streams, small channels and lakes (DAS, 1995).

Rescent most data on the biology of the extant turtles from Nepal are presented in Schleich, H.H. & Kaestle, W. (2002), Schleich, H. (2012) and Kaestle, W., Rai, K.R. & H.H. Schleich (2013).

The presence of large testudinids like *Megalochelys sivalensis*, batagurines (*Batagur, Melanochelys, Hardella* and *Geoclemys*) and trionychids in the Plio-Pleistocene localities of the Siwaliks of India, Nepal and Pakistan, and in Perim Island (Gujarat) suggests a warm tropical rainy paratropical monsoon climate with well watered streams (sensu CORVINUS & SCHLEICH, 1994). The presence of the large *Megalochelys sivalensis* in Early Pleistocene of India, Pakistan and Nepal together with the large crocodile *Rhamphosuchus crassidens* in Late Pliocene (FALCONER & CAUTLEY, 1840; CORVINUS & SCHLEICH, 1994; SRIVASTAVA & SCHLEICH, 1999, NANDA et. al., 2016) suggests the presence of open grasslands and woodlands with perennial rivers and swamps (sensu BADAM, 1984; PATNAIK, 1991). The presence of *Rhamphosuchus crassidens* also in Late Miocene rocks of Siwaliks (LYDEKKER, 1886; SRIVASTAVA & SCHLEICH, 1999, NANDA et al., 2016) along with the other large mammals suggests that there was not much variation in the ecological conditions from Miocene to Pleistocene time of the Siwaliks.

The shape of the carapace of the new species *Omegachelys sahnii* which is streamline suggests that the animal was most probably of aquatic habit inhabiting fast flowing streams.

The presence of associated riverine shore areas ranging from rocks, sand banks and grassbanks were best for many batagurines and trionychids feeding on many molluscs, crabs, grass, algae and weeds (DAS, 1995). These data coincide with the palaeoenvironmental conditions drawn from the geological and sedimentological studies (PATNAIK, 1991; 1995; PATNAIK & SCHLEICH, 1993).

Towards the end of early Pleistocene as the climate became cooler, the distribution of tortoises was obviously affected (HIBBARD, 1960; BRATTSTROM, 1961). Quaternary tortoises in the middle and northern latitudes were subjected to at least four major periods of colder climate, often moister. Drier, warmer climates characterised parts of the three interglacial ages. Each of the glacial and interglacial periodes may have been cooler than the preceding corresponding periodes. Though the evidence is meagre, tortoises seem to have expanded northward during each interglacial (AUFFENBERG, 1974). During and after the last glacial, severe drought and cold in the northern latitudes played important complementary roles in extinction of large tortoises (AUFFENBERG, 1974) and unlike their large contemporaries, smaller species of tortoises survived these major temperature changes by retreating into a burrow. It is inconceivable on mechanical grounds alone that the giant tortoises of Plio-Pleistocene (like *Megalochelys sivalensis*) tunnelled and therefore could not survive. However, few living testudinids of any size burrow in the earth (AUFFENBERG, 1974; ERNST & BARBOUR, 1989).

Not all tortoise extinction can be explained solely on late Quaternary climatic changes. For example, it does not fully explain the extinction of truly gigantic land species in tropical continental areas (sensu AUFFENBERG, 1974). However, a single sex dominance due to slight change in temperature may be possible in view of the fact that sex determination in many reptiles is correlated to minor temperature changes during incubation.

The extinction of giant land tortoises in all parts of the world probably cannot be explained by a single theory. The man may have played a role in it, though only near the culmination of series of climatic changes that had already greatly reduced the ranges of the giant species of many different animals (WEBB, 1969, AUFFENBERG, 1974), man's repeated visits to those Pacific and Indian Ocean islands formerly harbouring innumerable individuals of gigantic land tortoises has certainly caused near or complete extinction in several species. It is also true that in several continental areas the disappearance of some tortoise species can be roughly correlated with the presence of early man. In the case of *Megalochelys sivalensis* it is very difficult to say if these giant tortoises extended to the time of early man and there existed any relationships between the both, however, a possibility can not be ignored as in many Indian mythological stories a reference of a large tortoise is given as mentioned in the preceding section of the paper. It would be premature to comment on the cause of extinction of *Megalochelys sivalensis* until new investigations and discoveries are made in Middle and Late Pleistocene localities of the Indian Subcontinent.

Acknowledgements

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PLATES

PLATE 1

Megalochelys sivalensis FALCONER & CAUTLEY, 1837

Fig. 1. Large shell displayed in the Indian Museum, Kolkata.
a - anterior view showing large epiplastra,
b – latero-posterior view showing posterior notched plastron,
c – posterior view showing inferior incurved postcentral which is nearly vertical.

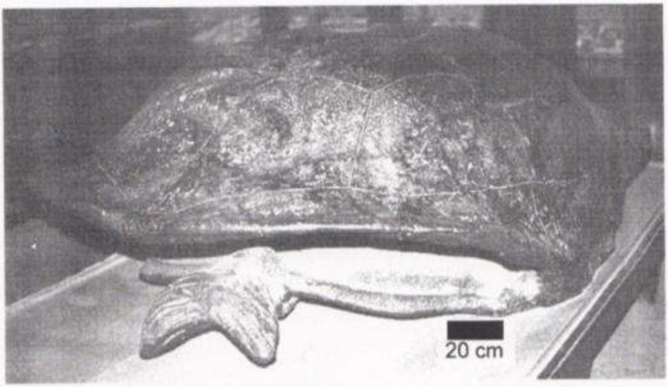


Fig.1a

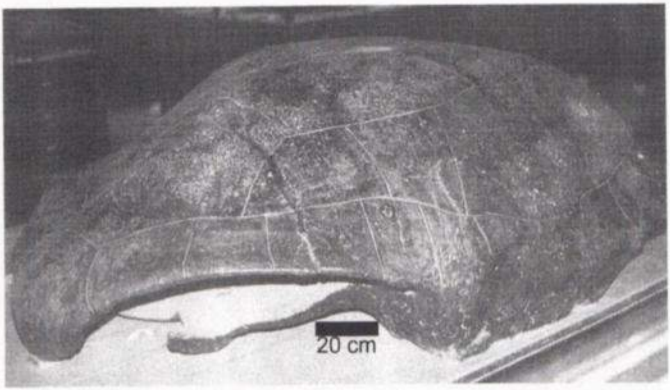


Fig.1b

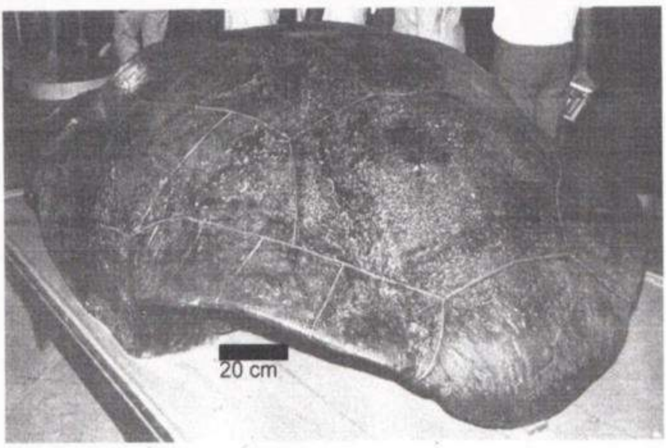


Fig. 1c

PLATE 2

Megalochelys sivalensis **FALCONER & CAUTLEY, 1837**

Fig. 1. Specimen E – 80. Visceral view of detached epiplastra.

Fig. 2. Specimen PU A/702. A large shell displayed in the Museum of CAS in Geology, Panjab University, Chandigarh,
a – anterior view showing slightly extended and bifurcated epiplastra,
b– right lateral view showing inferior incurved postcentral which is nearly vertical.

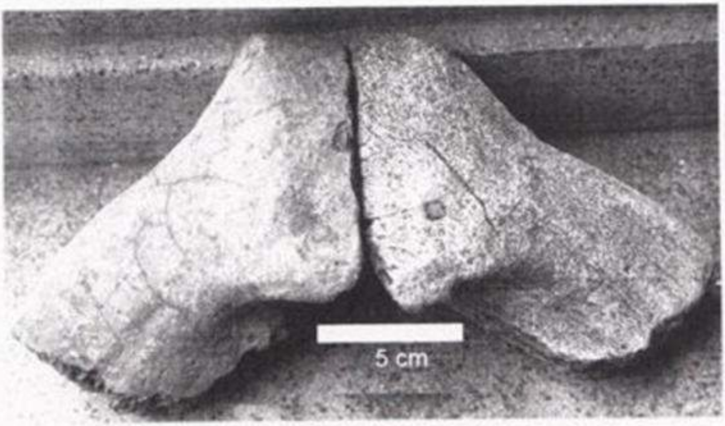


Fig. 1

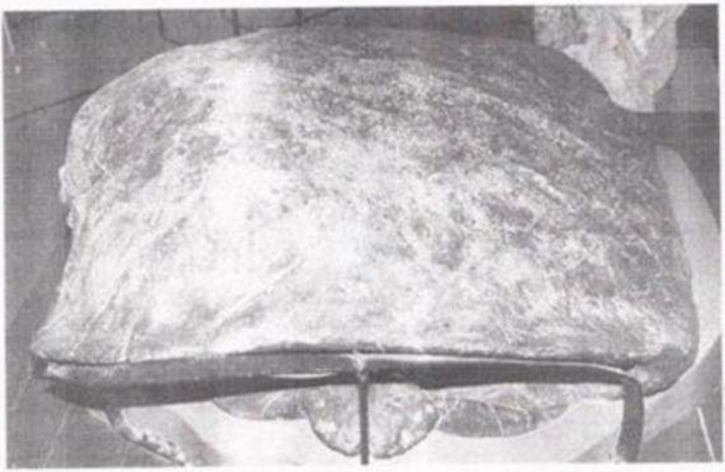


Fig. 2a

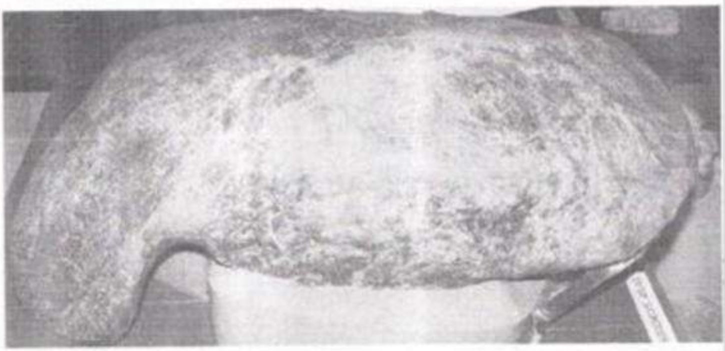


Fig. 2b

PLATE 3

Megalochelys sivalensis FALCONER & CAUTLEY, 1837

Fig. 1. Specimen PU A/702. Cast of the visceral surface of partial anterior plastron lobe.

Fig. 2. Specimen E – 82. Anterior broken epiplastra,
a – visceral view,
b – ventral view.

Fig. 3. Specimen E – 76. Anterior incomplete epiplastra,
a – visceral view,
b – ventral view.

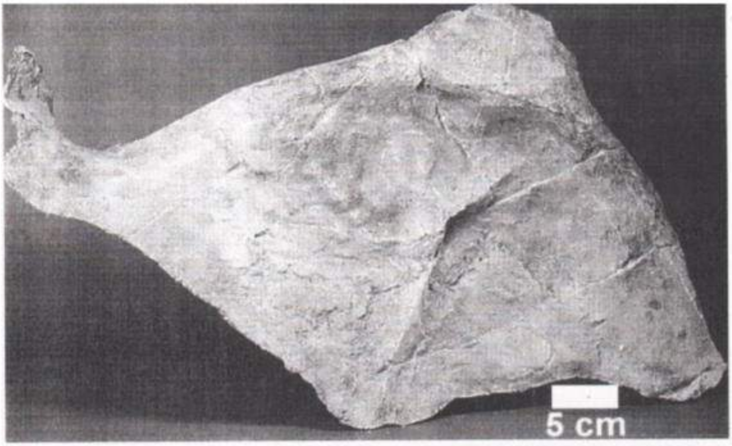


Fig. 1

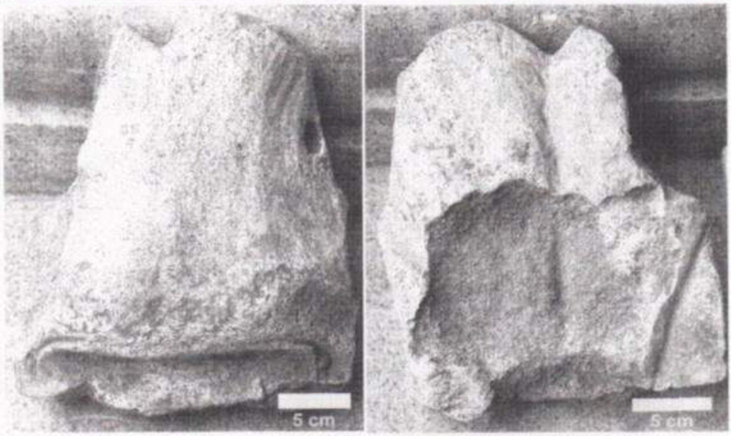


Fig. 2a,b

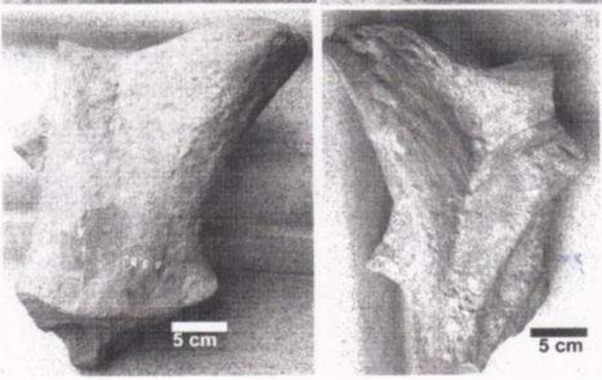


Fig. 3a,b

PLATE 4

Megalochelys sivalensis FALCONER & CAUTLEY, 1837

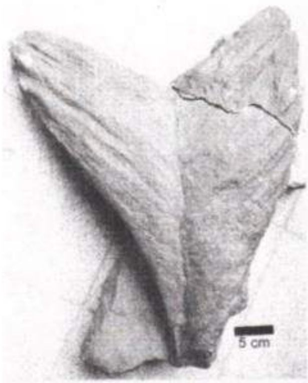
Fig. 1. Holotype specimen BMNH – 40630. Ventral view of complete epiplastra.

Fig. 2. Specimen E – 86. Dorsal view of right 11th peripheral.

Fig. 3. BMNH – 39819 (cast : E – 77). Partially broken cranium,
a – dorsal view,
b – ventral view.

Indotestudo forstenii SCHLEGEL & MÜLLER (1844)

Fig. 4. Specimen SFP – 213. Complete shell,
a – dorsal view and,
b – right lateral view of carapace.



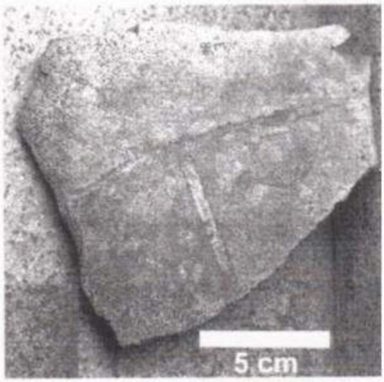


Fig.1,2

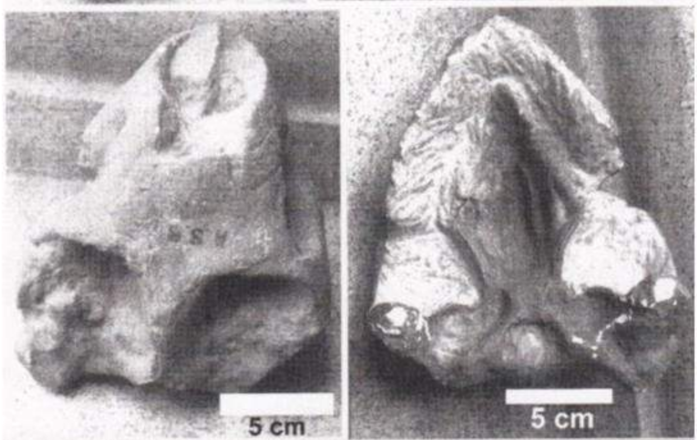


Fig.3a,b

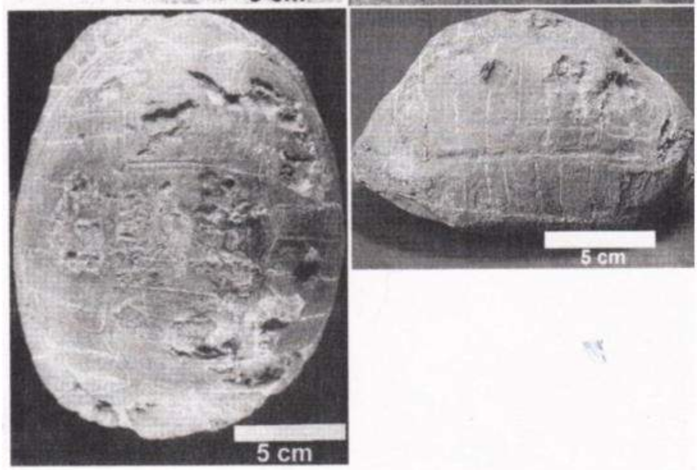


Fig.4a,b

PLATE 5

Testudinidae indet.

Fig. 1. Specimen NHM/TU 1989.
(a) Dorsal view of fragmentary peripheral NHM/TU 1989/c.
(b) Dorsal view of distal part of 1st pleural NHM/TU 1989/d.

Lissemys punctata LACÉPÉDE, 1788

Fig. 2. Specimen E – 163. Ventral view of plastron.

cf. *Lissemys* SMITH, 1931

Fig. 3. Specimen NHM/TU 1989/37 (cast: BSP 1989 XVIII 21). Ventral view of left epiplastron.

Trionychidae indet.

Fig. 4. Specimen NHM/TU 1989/. Dorsal view of large fragmentary neurals.

Fig. 5. Specimen NHM/TU 1989/44. Dorsal view of fragmentary neurals (? 2nd and 3rd neurals).

Fig. 6. Specimen NHM/TU 1989/40. Dorsal view of distal part of a pleural.

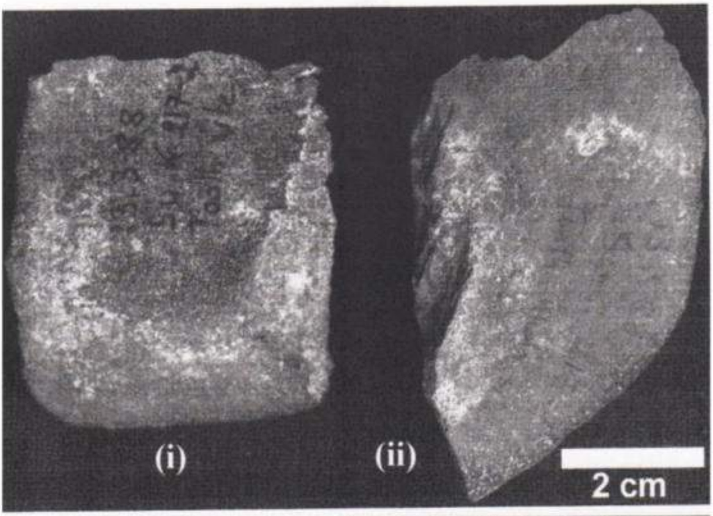
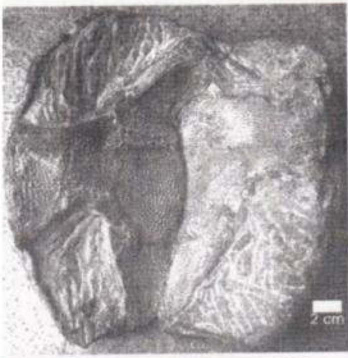


Fig. 1a,b



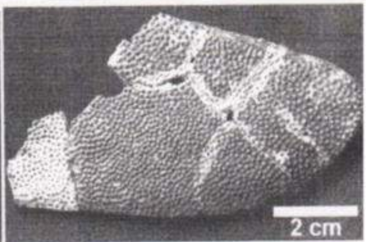
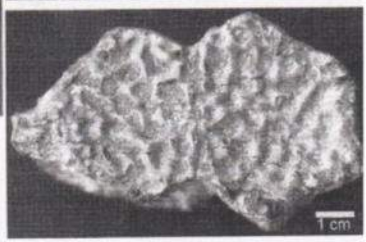
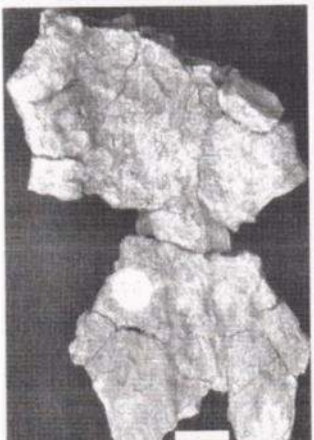


Fig.2,3





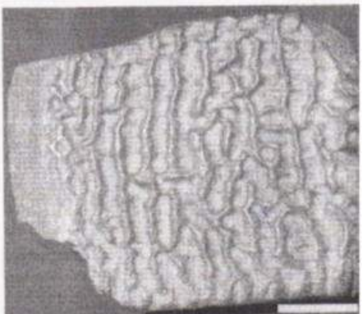


Fig. 4,5,6

PLATE 6

Trionychidae indet.

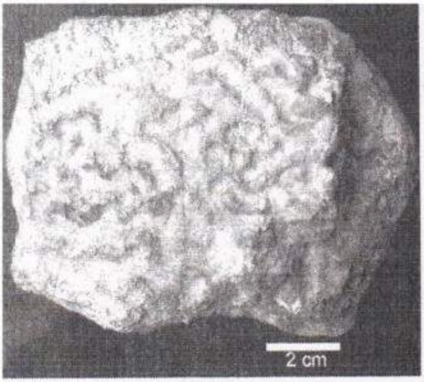
Fig. 1. Specimen NHM/TU 1989/. Dorsal view of proximal part of a pleural.

Omegachelys sahnii gen. et sp. nov.

Fig. 2. Holotype specimen SFP – 24. Anteriorly broken large shell,
a – dorsal view
b – right lateral view of carapace.

Fig. 3. WIF/A 451. Terminally broken large shell,
a – posterior view
b – dorsal view of carapace.

Fig. 4. Specimen SFP – 245. Dorsal view of carapace of a large terminally broken shell.



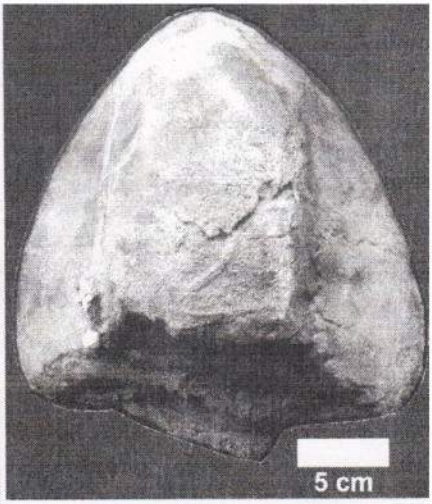
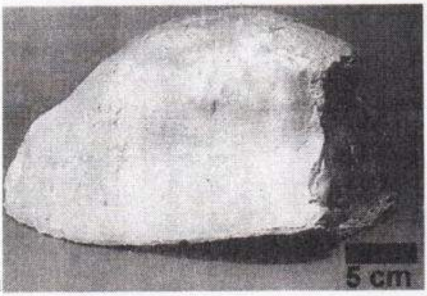


Fig. 1, 2a



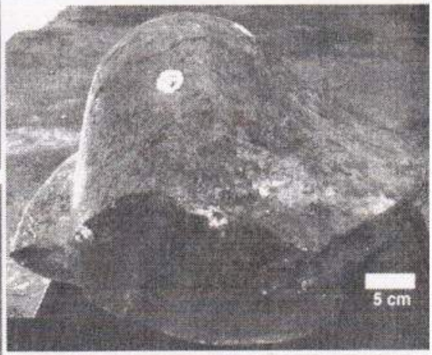


Fig.2b, 3a

Fig. 3b, 4

PLATE 7

Omegachelys sahnii gen. et sp. nov.

Fig. 1. Specimen SFP – 245. Right lateral view of carapace of a large terminally broken shell.

Fig. 2. Specimen SFP – 225. Complete large shell,
a – dorsal view
b – posterior view of carapace.

Fig. 3. Specimen NHM/TU 1989/36. Dorsal view of left part of large carapace.

Fig. 4. Specimen H 18/1. Left lateral view of carapace of a posteriorly broken large shell.

Fig. 1

Fig. 2a,b

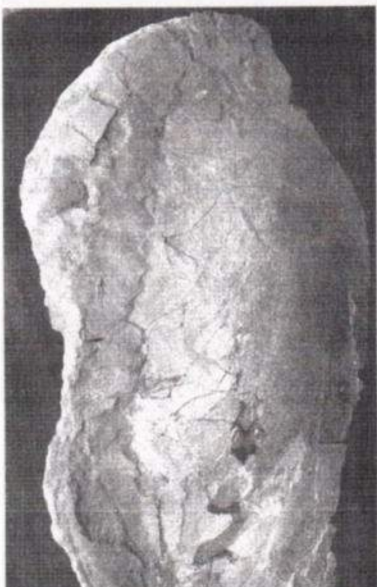


Fig. 3,4

PLATE 8

Omegachelys sahnii gen. et sp. Nov

Fig. 1. Specimen H 18/1. Antero-dorsal view of carapace.

Fig. 2. Specimen SFP – 226. Dorsal view of marginally broken incomplete carapace.

Geoclemys hamiltonii GRAY, 1831

Fig. 3. Specimen BMNH – 39838 (cast: E –95). Complete shell,
a – dorsal view
b – left lateral view of carapace.

Fig. 4. Specimen WIF/A 452. Posteriorly broken shell,
a – dorsal view of carapace,
b – ventral view of plastron.

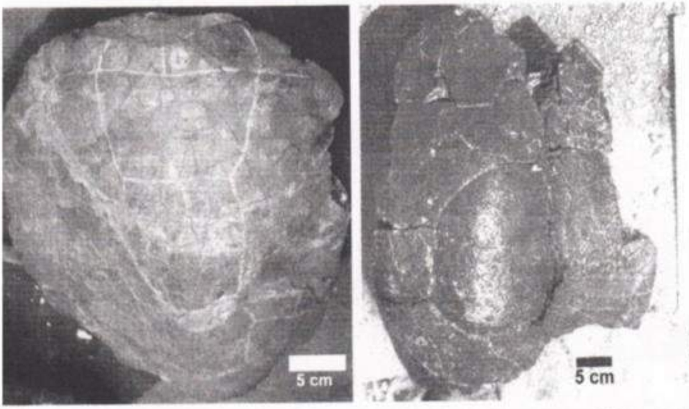


Fig. 1,2

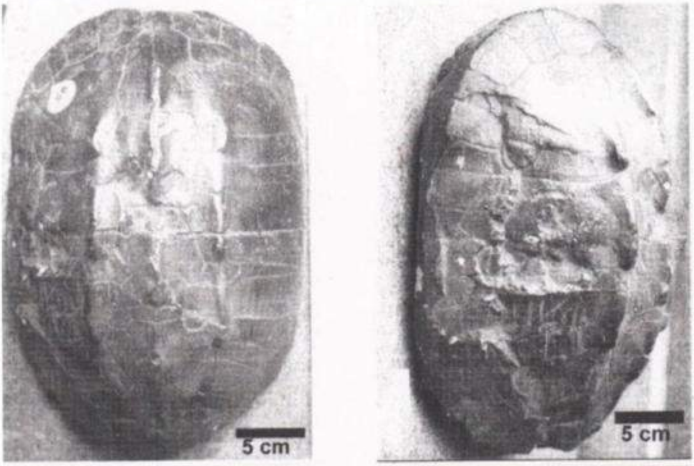


Fig.3a,b

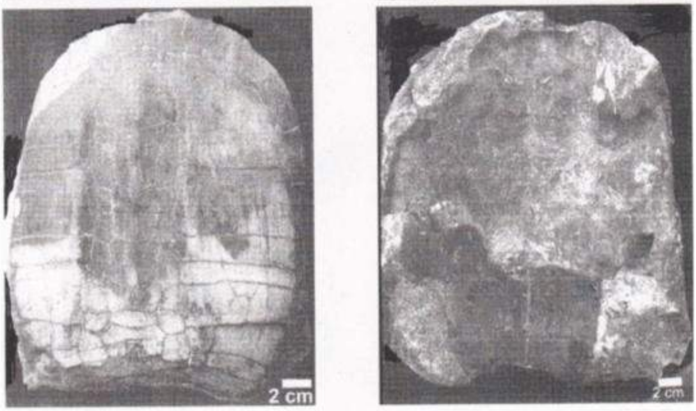


Fig.4a,b

PLATE 9

Geoclemys hamiltonii GRAY, 1831

Fig. 1. Specimen WIF/A 452. Right lateral view of posteriorly broken shell.

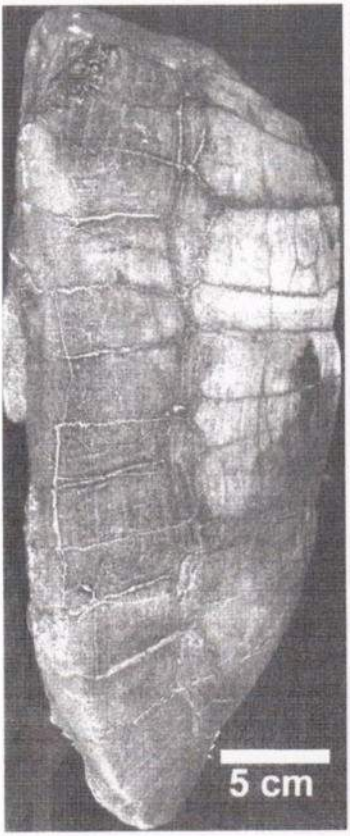
Fig. 2. Specimen MCASG A/665. Dorsal view of marginally broken shell. The specimen was earlier described by TEWARI & BADAM (1969) as type specimen of *Geoclemys sivalensis*.

cf. *Geoclemys hamiltonii* GRAY, 1831

Fig. 3. Specimen WIF/A 454. Incomplete shell with partially preserved carapace and posteriorly broken plastron.
a – dorsal view of carapace,
b – ventral view of plastron.

Hardella thurjii GRAY, 1831

Fig. 4. Specimen E – 176. Dorsal view of carapace of a laterally crushed and posteriorly broken shell.



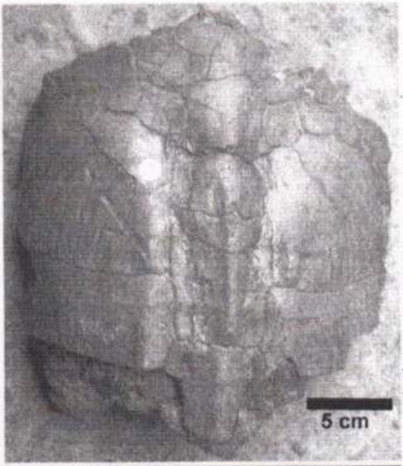


Fig.1, 2

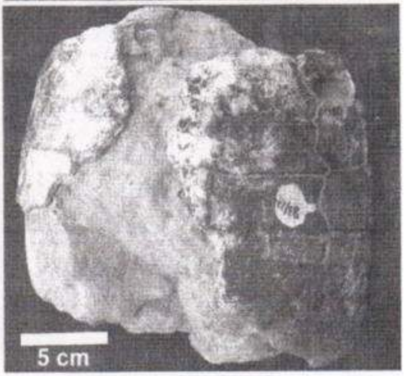
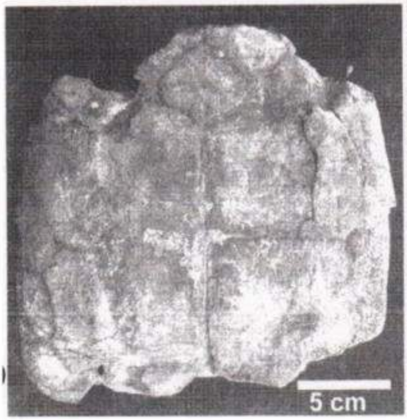


Fig. 3a



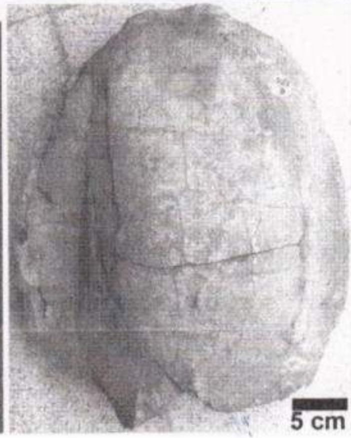


Fig. 3b, 4

PLATE 10

Hardella thurjii GRAY, 1831

Fig. 1. Specimen E – 176. Lateral crushed and posterior broken shell,
a – right lateral view of carapace,
b – ventral view of plastron.

Fig. 2. Specimen E – 94. Dorsal view of marginal broken carapace.

Fig. 3. Specimen BMNH – 39834 (cast: E – 179). Posterior marginal broken shell,
a – dorsal view of carapace,
b – ventral view of plastron.

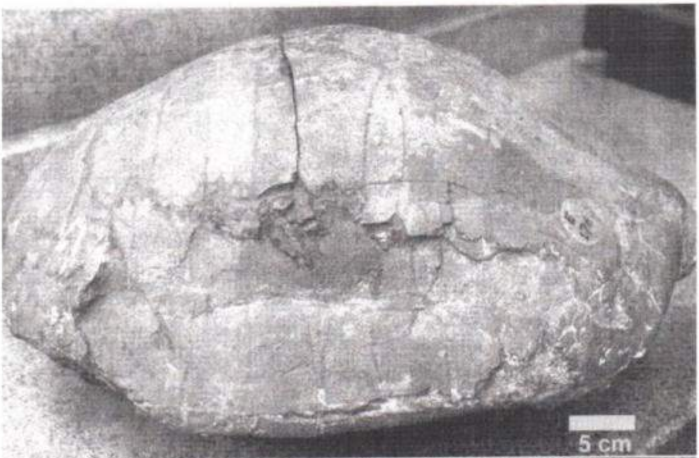


Fig. 1a

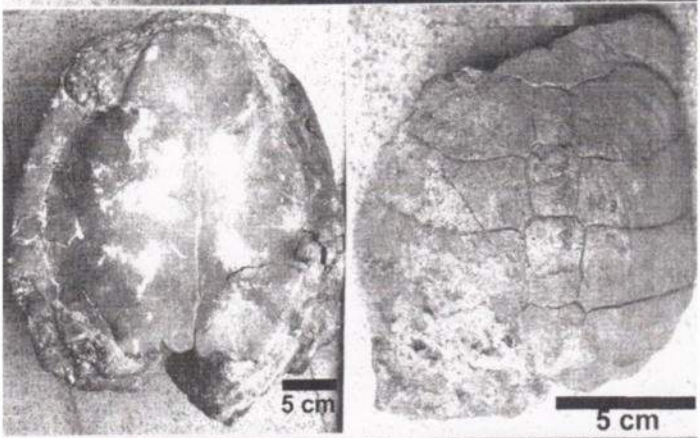


Fig. 1b, 2

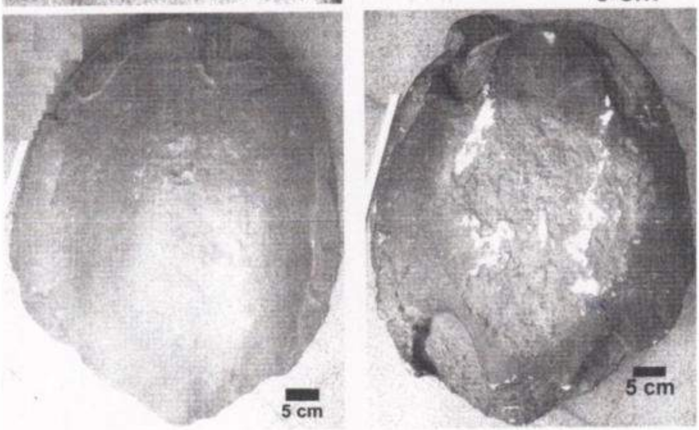


Fig. 3a,b

PLATE 11

***Hardella thurjii* GRAY, 1831**

Fig. 1. Specimen E – 103. Nearly complete cranium,
a – left lateral view,
b – dorsal view
c – ventral view.

Fig. 2. Specimen WIF/A 453. Nearly complete shell,
a – dorsal view
b – left lateral view of carapace,
c - ventral view of plastron.

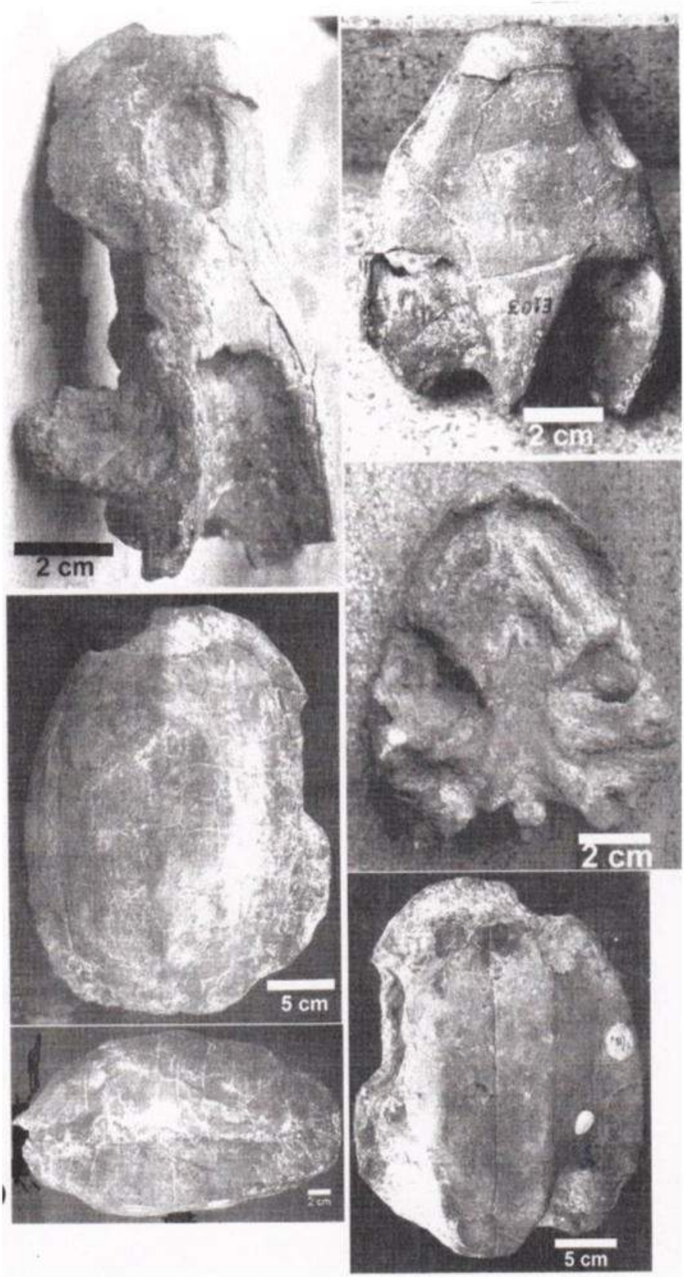


Fig.1a,b

Fig. 1c

Fig. 2a

Fig. 2b,c

PLATE 12

***Hardella thurjii* GRAY, 1831**

Fig. 1. Specimen W 19/178. Complete shell having detached neurals and pleurals on the carapace.

a – dorsal view
b – left lateral view of carapace,
c- ventral view of plastron.

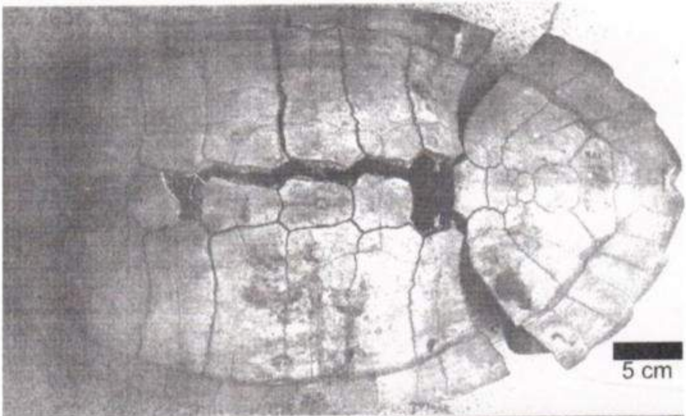


Fig. 1a

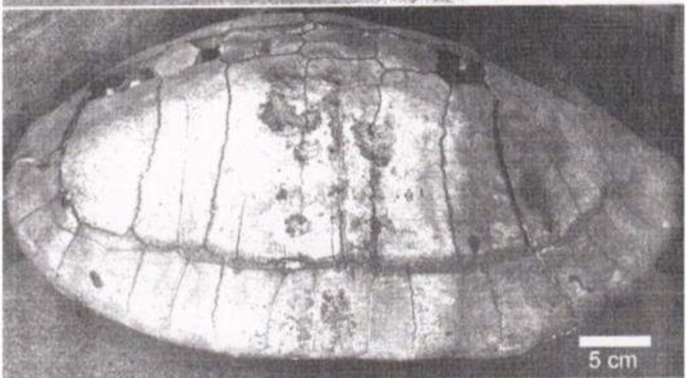


Fig. 1b

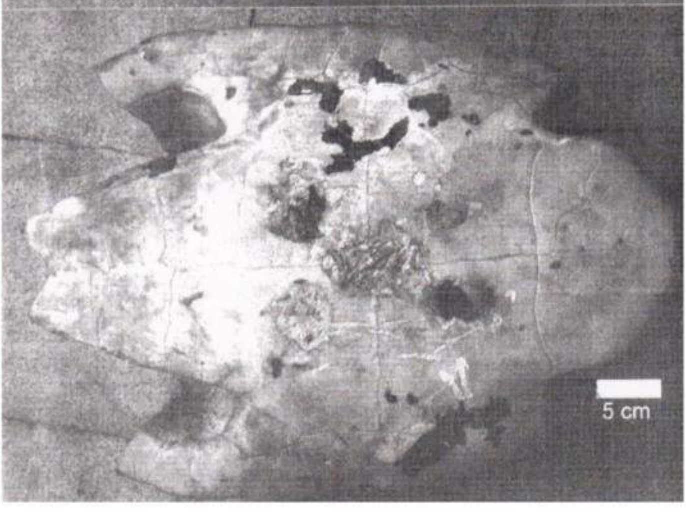


Fig.1c

PLATE 13

Batagur baska **GRAY, 1831**

Fig. 1. Specimen W 19/174. Posteriorly incomplete shell,
a – dorsal view
b – left lateral view of carapace,
c – ventral view of plastron.

cf. ***Batagur baska*** **GRAY, 1831**

Fig. 2. Specimen E – 104. Compete nuchal,
a – visceral view
b – dorsal view.

Fig. 3. Specimen E – 108. Dorsal view of right 7^{th} peripheral.

Fig. 1a,b

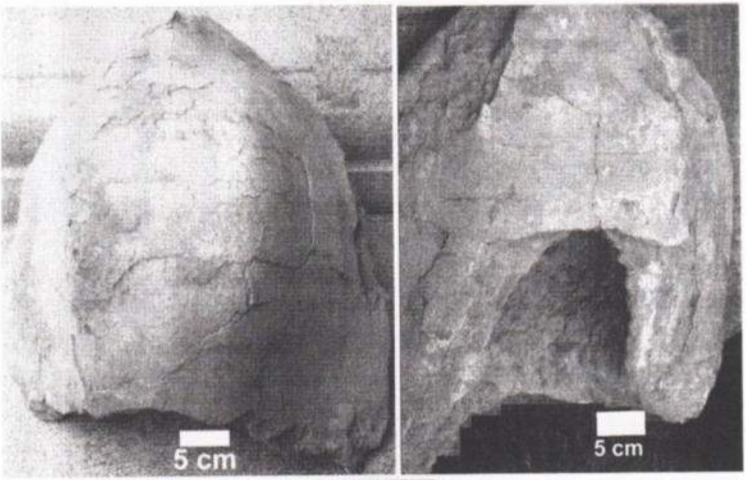


Fig.1c, 2a

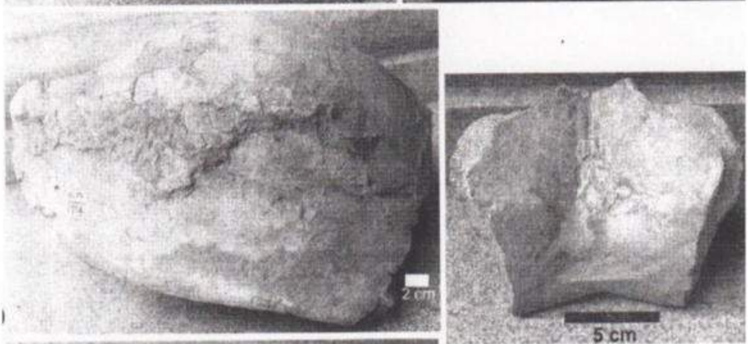


Fig. 2b, 3

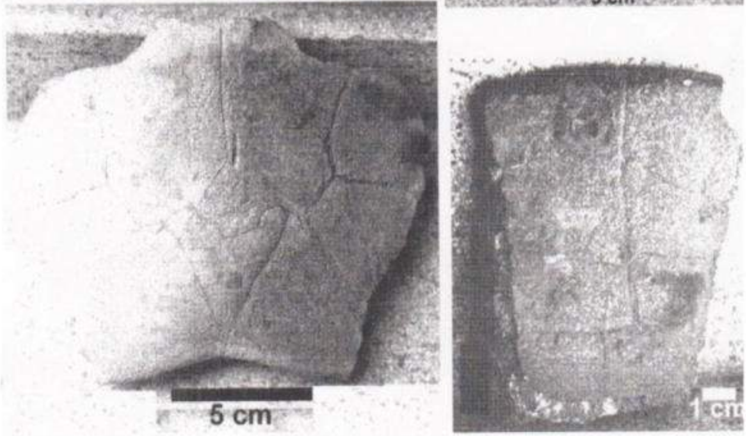


PLATE 14

Melanochelys trijuga SCHWEIGGER, 1812

Fig. 1. Specimen E – 89. Posteriorly broken shell,
a – dorsal view
b – left lateral view of carapace,
c – ventral view of plastron.

Fig. 2. Specimen E – 90. Partially broken shell,
a – dorsal view
b – left lateral view of carapace,
c – ventral view of plastron.

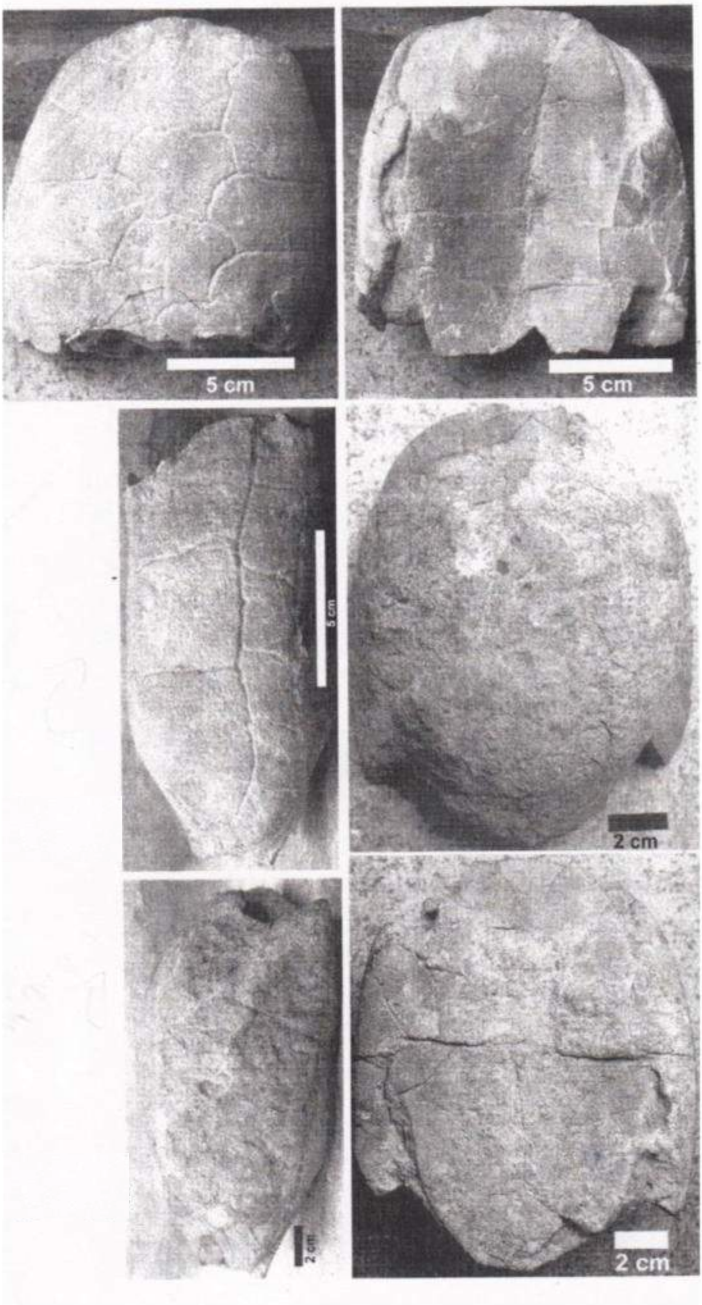


Fig. 1a,b

Fig. 1c

Fig. 2a

Fig. 2 b,c

PLATE 15

Melanochelys trijuga SCHWEIGGER, 1812

Fig. 1. Specimen E – 92. Posterior incomplete shell,
a – dorsal view of carapace,
b – ventral view of plastron.

Fig. 2. Specimen E – 93. Posterior marginal broken shell,
a – right lateral view of carapace,
b – dorsal view.

Fig. 3. Specimen K 53/222. Nearly complete shell,
a – dorsal view
b – right lateral view of carapace.

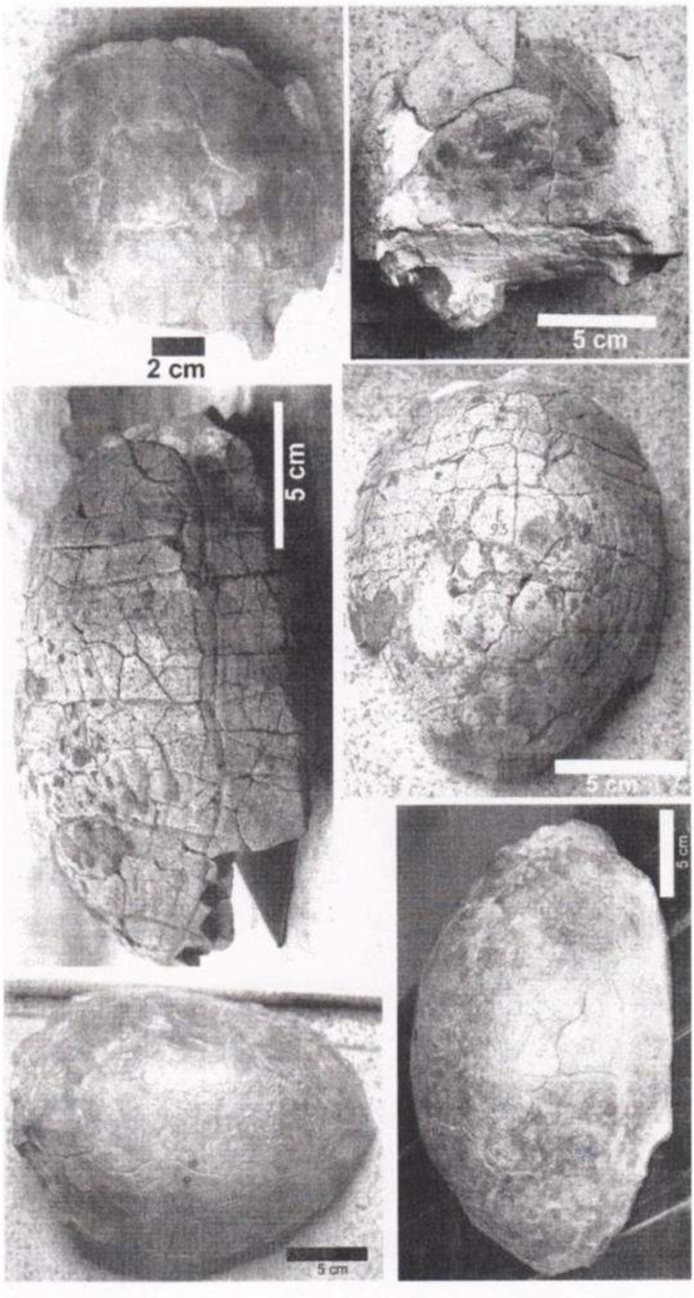


Fig.1a,b

Fig.2a,b

Fig.3a,b

PLATE 16

Pangshura flaviventer GÜNTHER, 1864

Fig. 1. Specimen F –110. Posteriorly broken shell. The specimen was described by LYDEKKER (1885) under the wrong catalogue number E – 110.

a – dorsal view
b – right lateral view of carapace,
c – ventral view of carapace.

Pangshura sp. GRAY, 1855

Fig. 2. Specimen F – 111. Lateral view of highly crushed and marginal incomplete carapace.

Fig. 3. Specimen F – 108. Visceral view of left hypoplastron.

Bataguridae indet.

Fig. 4. Specimen NHM/TU 1989/a. dorsal view of marginal broken nuchal.

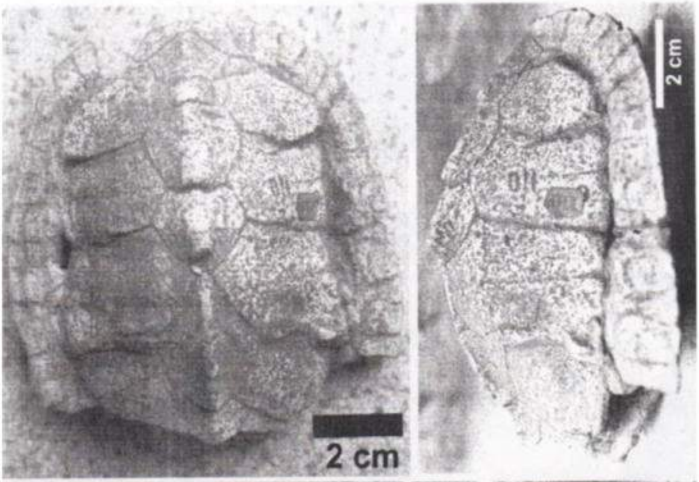


Fig.1a,b

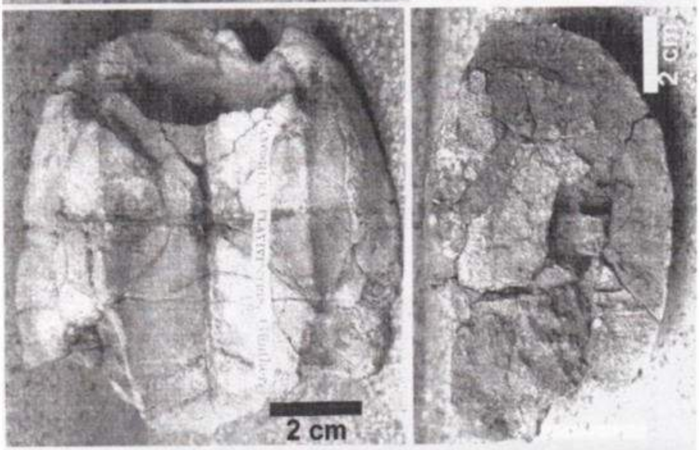


Fig. 1c, 2

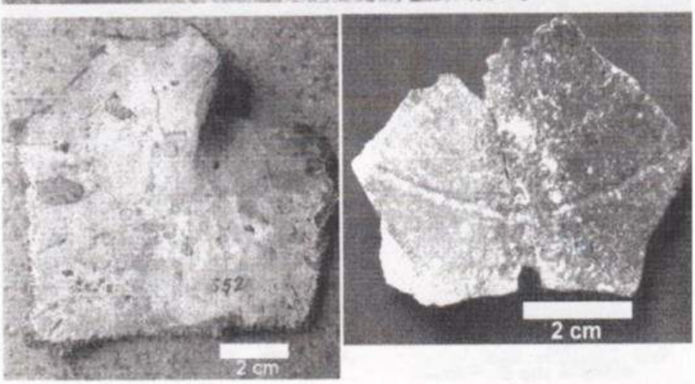


Fig.3, 4

PLATE 17

Bataguridae indet.

Fig. 1. Specimen NHM/TU 1989/b. A fragmentary pleural. The ventral view of the specimen was earlier described by CORVINUS & SCHLEICH (1994) as hypo- (hyo) plastron fragment of an emydid turtle.
a – dorsal view,
b – visceral view.

Fig. 2. Specimen NHM/TU 1989/40. Broken pleural,
a – visceral view,
b – dorsal view.

Fig. 3. Specimen E – 105. Dorsal view of a right hypoplastron.

Fig. 4. Specimen F – 106. Visceral view of a left hyoplastron.

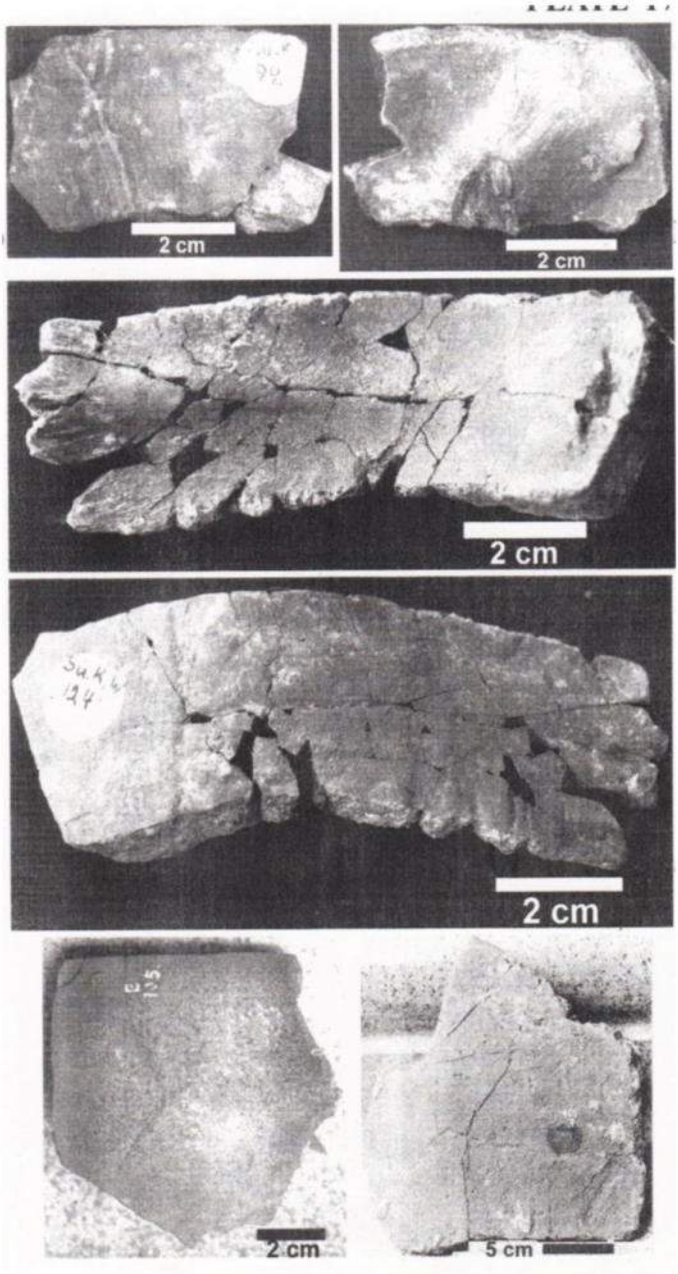


Fig. 1a,b

Fig. 2a,b

Fig.3, 4

Review of Neogene-Quarternary Crocodiles from the Siwaliks of India and Nepal

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Abstract

The present work deals with the revision of the Caenozoic crocodiles from the Indian Subcontinent in the light of the new findings from the Siwaliks of India and Nepal. The taxonomic status of multiple species of *Crocodylus* and *Gavialis* as established by 19th century and early 20th century workers, appears to be doubtful. A detailed study of these *Crocodylus* and *Gavialis* species reveals that the fossil record of genus *Crocodylus* in S-Asia may be restricted to only three species i.e. *C. palustris, C. palaeindicus* and *C. biporcatus* (= *porosus*) and that of the genus *Gavialis* may be restricted to only four species i.e., *G. gangeticus, G. browni, G. curvirostris* (along with the sub species *gajensis*), and *G. breviceps*. The giant tomistomid *Rhamphosuchus crassidens*, found from Nepal and India Siwaliks, retains its systematic position and is proved by the new material.

Introduction

A large number of Upper Siwalik fauna including various reptilian fossils has been described from the Siwalik sequences in Nepal and India, ranging in age from Miocene to Pleistocene. Amongst these reptiles, the living species of crocodiles (*Crocodylus palustris, Crocodylus porosus* and *Gavialis gangeticus*) have been found from the Siwaliks, Indo-gangetic plain and west coast of India.

Systematic studies of fossil crocodilian remains from the Siwaliks have been carried out by many workers since the nineteenth century (FALCONER & CAUTLEY, 1836, 1840; LYDEKKER, 1886; 1888; PILGRIM, 1908; MOOK, 1933; BADAM, 1973, 1974; CORVINUS, 1988; WEST et al., 1991; CORVINUS & SCHLEICH, 1994; SCHLEICH, 1993; PATNAIK & SCHLEICH, 1993 and NANDA & SCHLEICH, 2002) and the material is catalogued in various museums of the world.

In this work, an attempt has been made to restudy all the previously described crocodile material along with the taxonomic description of some new material. As more and more comparative material is available and a lot of work on evolutionary trends and phylogeny of caenozoic crocodiles is done (lately by BUFFETAUT, 1985; ANTUNES, 1987; NORELL, 1989 and

TARSITANO, et al., 1989), it becomes quite necessary to evaluate the validity of various previously described taxa and to correctly place the Siwalik crocodile material in the evolutionary history of the crocodiles.

The Siwalik foothills are the southernmost and youngest mountain ranges along the Himalaya, extending from the Salt Range in Pakistan in the West, via India and Nepal, to Bhutan in the East. They were formed during the last phase of the Himalayan orogeny in geologically very recent times, in the Early Pleistocene (CORVINUS & SCHLEICH, 1994). The Siwalik sediments were deposited as molasse deposits from the rising Himalayas into the foredeep to the south from Middle Miocene times onwards into the Early Pleistocene. They contain terrestrial sediments of claystones, shales and siltstones, thick sequences of sandstones, and of conglomerates at the very end.

Most of the crocodilian fauna so far recovered from the Siwaliks comes mostly from the Upper Siwalik sequences belonging to the Tatrot-Pinjor faunal zone. The crocodilian fauna studied and revised here is housed in the Indian Museum, Kolkata; Museum of Centre of Advanced Study in Geology (CASG), Panjab University, Chandigarh; Museum of Wadia Institute of Himalayan Geology (WIHG), Dehradun; Natural History Museum of Tribhuvan University, Kathmandu (NHM/TU) and British Museum of Natural History (BMNH), London. The casts of several specimens were made by one of the authors (HS) during his several visits to India and Nepal between the years 1989 and 1993.

The crocodilian fauna so far described from the Upper Siwaliks of India and Nepal is listed below:

N E P A L

Crocodylus palustris (SHAH & SHRESHTA, 1992)	anterior part of lower jaw (snout)	Rato Khola (Upp. Siwaliks)
Crocodylus aff. *palustris* (CORVINUS & SCHLEICH, 1994)	fragmentary osteoscute	Surai Khola (Upp. Siwaliks)
Crocodylus sp. indet. (WEST et al., 1991)	osteoderm, tooth (posterior)	Tinau Khola
	lower mandible fragment	Thui Khola, Surai Khola Lamhi (Rapti River Valley) (Lower Siwaliks)
Crocodylus sp. (MUNTHE et al., 1983) (CORVINUS, 1988) (SAH, 1992)	isolated teeth	Tinau Khola (Lower Siwaliks) Surai Khola (Upp. Siwaliks)

(DONGOL, 1987)		Rato Khola (Upp. Siwaliks) Kathmandu Basin (Lukundol lacustrine sediments)
Gavialidae gen. indet. (SAH, 1992) (WEST & MUNTHE, 1983)	isolated teeth	Tinau Khola (Lower Siwaliks)
Gavialis sp. (SAH, 1992)	occipital condyle, dermal bone	Rato Khola
(CORVINUS, 1988) (SHAH & SHRESHTA, 1992) (MUNTHE et al., 1983)	tooth, anterior maxillary part	Surai Khola (Upp. Siwaliks)
Gavialis sp. indet. (WEST et al., 1991)	osteoderm fragment, isolated teeth incomplete exoccipital osteoderm, short series of vertebrae	Thui Khola (Lower Siwaliks)
Gavialis cf. *gangeticus* (CORVINUS & SCHLEICH, 1994)	snout fragment, basioccipital part of Skull	Rato Khola (Upp. Siwaliks)
Rhamphosuchus (syn. *Crocodylus crassidens*) (CORVINUS & SCHLEICH, 1994)	premaxillar part of snout teeth gigantic gavialid ranging in length from 15-20 metres	Rato Khola Surai Khola (Upp. Siwaliks)

I N D I A

Crocodylus palustris (LYDEKKER, 1888)	isolated teeth, skull	Narbada Valley (Pleistocene)
(MÜLLER, 1923)		Siwaliks
(TRIVEDY, 1966)		Upp. Miocene of Tripura
Crocodylus cf. *palustris* (PATNAIK & SCHLEICH, 1993)	fragmentary mandible,	Moginand, H.P. Upp. Siwaliks
(GARG, 1988)	Maxillary, isolated teeth, partly broken vertebrae,	Plio-Pleistocene Saketi, F. P

	osteoscutes and a complete skull.	
Crocodylidae indet. (GAUR & CHOPRA,1984)	isolated teeth	Near Chandigarh Tatrot-Pinjor; Upp. Siwalik, Late Pliocene – Early Pleistocene
Crocodylus sp. (TIWARI, 1990)	isolated teeth	Midd. Siwalik, (late Miocene) Palampur (H.P.) & Mohargarh Fm.
(GUPTA & VERMA, 1988) Labli Member		Midd. Siwaliks, (= Tatrot Fm of Upp. Pliocene) Midd. Pliocene Jammu & Kashmir (J&K)
Crocodylus biporcatus *(= porosus)* (BADAM, 1973)	skull	Naipli, Pinjor Fm. Lower Pleistocene
Crocodylidae . (THEOBALD, 1858)	vertebra	Narbada beds (Upp. Pleistocene)
Gen. et. sp. indet (LYDEKKER, 1886)		Upp. Pleistocene
Crocodylus sivalensis (LYDEKKER, 1886) (MOOK, 1933)	skull	Saketi, Himachal Pradesh Pinjor Fm, Early Pleistocene and Tatrot Fm - Late Pliocene
Crocodylus cf. *sivalensis* (GARG, 1988)	skull	Saketi, Himachal Pradesh. (Upp. Siwaliks, Late Pliocene)
Crocodylus palaeindicus (FALCONER, 1859)	partial skull (cranium)	Perim Island Lower-Middle Siwaliks
(LYDEKKER, 1879) (PRASAD, 1974) (BADAM, 1979)		Early Pliocene – Early Pliocene Naipli (Pinjor Fm., Lower Pleistocene)

(BADAM, 1998)		Devakachar (Upp. Group, Late Pleistocene)
Crocodylus bombifrons (FALCONER, 1868) (included in *C. palustris*)	part of skull	Siwaliks (Pliocene)
Crocodylus bugtiensis (PILGRIM, 1908)	skull	Bugti Hills, Baluchistan (Lower Miocene)
Crocodylus sinhaleyus (DERANIYAGALA, 1958)	only one tooth	Ceylon (Pleistocene)
Gavialis cf. *gangeticus* (PATNAIK & SCHLEICH, 1993)	mandibular & cranial fragments isolated, broken teeth	Moginand, Himachal Pradesh (Upp. Siwaliks,
(NANDA & SCHLEICH, 2005)		Upp. Pliocene)
(PATNAIK, 1995)		Devakachar (Upp. Narmada Group, Upp. Pleistocene)
Gavialis sp. (GUPTA & VERMA, 1988)	isolated teeth	Labli Member Upp Pliocene, (J & K)
Gavialis browni (BADAM, 1974) (MOOK, 1932)	part of skull	Chandigarh Fm (Lower Pleistoc.)
Gavialis gangeticus (LYDEKKER, 1888) (GMELIN, 1789)	imperfect crania and other body parts	Siwalik Hills, Perim Island,Kangra Dist. Punjab, Upp. Miocene
(TRIVEDY, 1966)		Tripura, Burma
Gavialis hysudricus (CAUTLEY, 1868) (LYDEKKER, 1886)	imperfect cranial rostrum lower jaw, post. portion of mandibular symphysis, post. region of adult cranium and of an immature cranium	Perim Island Siwalik Hills (Upp. Pliocene)
Gavialis curvirostris (LYDEKKER, 1886)	cranium maxillary	Siwalik Hills (Lower Pliocene)
Gavialis curvirostris (PILGRIM, 1912)	cranium rostrum	Bugti Hills, Baluchistan

var. *gajensis*	posterior portion of rostrum mandibular symphysis	(Lower Miocene)
Gavialis breviceps (PILGRIM, 1912)	mandibular symphysis and cranial rostra	Bugti Hills, Baluchistan (Lower Miocene)
Gavialis leptodus (CAUTLEY & FALCONER, 1836) (syn. *Crocodylus*) (CAUTLEY, 1868) (*Leptorhynchus leptodus*)	maxillary rostrum	Siwalik Hills from Punjab (Upp. Pliocene)
Gavialis pachyrhynchus (LYDEKKER, 1886)	cranial rostrum, fragments of cranium rostrum and tooth	Siwalik Hills (Upp. Miocene)
Gavialis lewisi (LULL, 1944)	skull (lacking rostrum) with referable rostral fragment	Siwalik Hills (Middle Pliocene)
Rhamphosuchus (FALCONER & CAUTLEY, 1840) (*Leptorhynchus*)	rostrum, mandibular symphysis part, lower tooth	Siwalik Hills (Upp. Pliocene)

(syn. *Crocodylus crassidens*) gigantic gavialid ranging in length from 15-20 metres

Geology and Stratigraphy

The Siwalik foothills (altitude rarely exceeds 1000 m) are the southernmost and youngest mountain ranges along the Himalaya. The Siwalik sequence extends from the Indus River in the West to the Brahmaputra River in the East with a small gap that occurs near Sikkim (text fig. 1). The sequence is about 7 km thick and ranges in age from 18.3 Ma to 0.22 Ma. The origin of the Siwaliks is related to the last phase of the Himalayan orogeny in the Early Pleistocene; and the sediments of the Siwaliks were deposited as molasse from the rising Himalayas into the foredeep to the south from Middle Miocene times onwards into the Early Pleistocene (CORVINUS & SCHLEICH, 1994). The Siwalik sediments are terrestrial sediments comprising claystones, shales, siltstones, thick sequence of sandstones and conglomerates on the top. A number of volcanic ash horizons and tuffaceous mudstone beds were also identified in the Upper Siwaliks of India and Pakistan and have been dated to be around 2.5 Ma in age (OPDYKE et al., 1979; JOHNSON et al., 1982; TANDON et al., 1984; RANGA RAO et al., 1988; PATNAIK & SCHLEICH, 1993).
The threefold classification of the Siwaliks given by PILGRIM (in 1910; 1913 and 1934) was further subdivided by COLBERT (1934; 1942) into the Kamlial, Chinji, Dhok Pathan, Nagri, Tatrot, Pinjor and Boulder Conglomerate Zones.

Fig. 1. Extension of Siwalik Group of rocks in Indian Subcontinent.

This classification is still widely used however faunal zones are now called as Formations: Kamlial and Chinji Formations (comprising Lower Siwalik Subgroup); Nagri and Dhok Pathan Formations (Middle Siwalik Subgroup) and Tatrot, Pinjor and Boulder Conglomerate Formations (Upper Siwalik Subgroup). The biostratigraphy established by PILGRIM was highly confusing because to recognize his faunal zones in field he widely used lithology instead of fauna (most of the fauna were also not in situ fossils). To overcome this confusion the lithology was replaced by magnetostratigraphy (BARRY et al., 1982) and four biostratigraphic interval zones came into existence (equivalent to the Middle and the Upper Siwalik subgroups). These are: (1) *Elephas planifrons* interval – Zone (2.9 Ma to 1.5 Ma), (2) *Hexaprotodon sivalensis* Interval – Zone (5.3 Ma to 2.9 Ma), (3) *Selenoportax lydekkeri* Interval – Zone (7.4 Ma to 5.3 Ma), and „*Hipparion* S. 1." Interval – Zone (9.5 Ma to 7.4 Ma). Each of these zones is marked by the first and the last appearance along with the relative abundance and extinction of the various taxa in various standard sections. The upper and lower limits of the zones are dated by magnetostratigraphy.

In the Siwaliks of India the biostratigraphy proposed by BARRY et al. (1982) is not fully useful as its upper limitation is 1.5 Ma whereas youngest rocks of the Indian Siwaliks are dated to be 0.22 Ma, and Indian Siwaliks are comparatively poor in fossils and they are found mainly in pockets (NANDA & SEHGAL, 1993). However, NANDA (1995) modified the lower and the upper limit of *Elephas planifrons* Interval – Zone (3.6 Ma – 2.7 Ma) and identified another new zone i.e. *Elephas hysudricus* Interval – Zone (2.7 Ma – 0.6 Ma) in India. The older zone includes fauna of the pre-Pinjor beds exposed near Chandigarh and younger zone includes fauna recovered from the Pinjor Formation. In the Lower Siwalik Subgroup exposed at Ramnagar, Jammu & Kashmir (J & K), Nurpur (Kangra) and Kalagarh (Uttar Pradesh) the taxa have been found to represent Chinji Fauna (GAUR & CHOPRA, 1983; NANDA & SEHGAL, 1993) however, Kalagarh local fauna represent both Lower and Middle Siwalik elements and thus it is transitional between Lower and Middle Siwaliks.

The Middle Siwalik Subgroup exposed near Haritalyangar area of Bilaspur and Nurpur, Himachal Pradesh (H. P.) represent typical Middle Siwalik, Nagri and Dhok Pathan fauna (PRASAD, 1970; VASISHAT, 1985 and NANDA & SEHGAL, 1993).

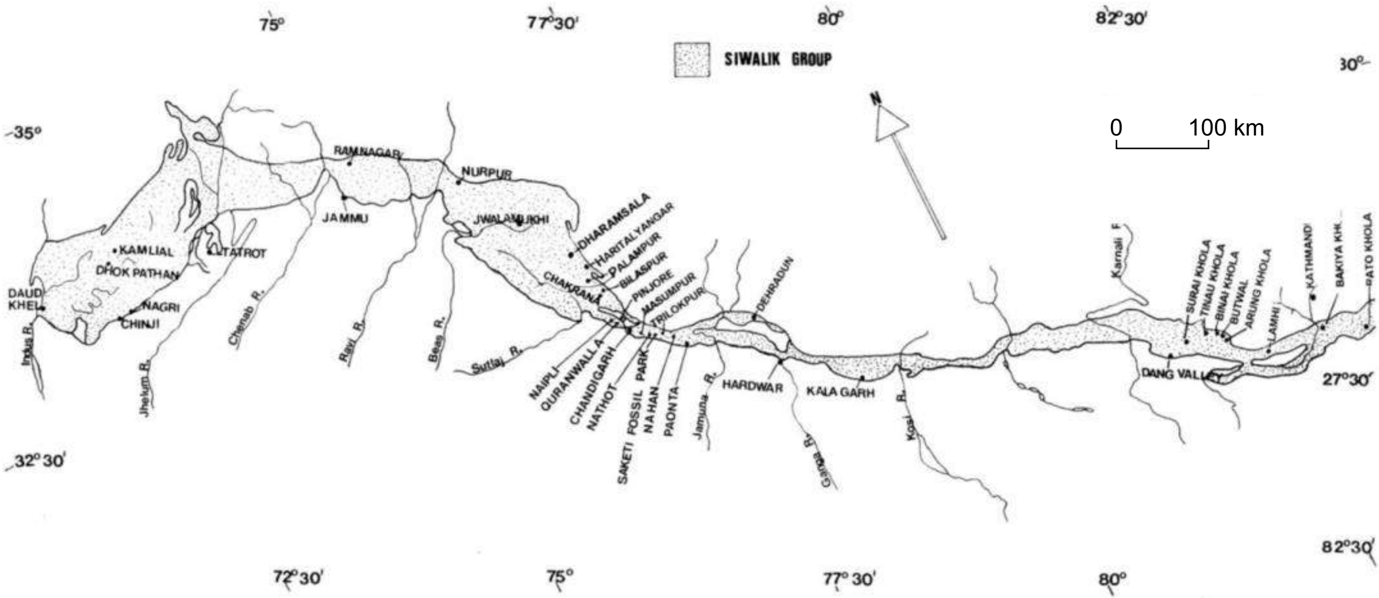
The Middle and Upper Siwalik units exposed near Chandigarh, Jammu and Saketi Fossil Park (H. P.) are around 780 m in thick sequence. The contact between the Middle and the Upper Siwalik rocks is of tectonic origin. The Middle Siwalik sediments are represented by massive grey sandstones and underlying orange, red, yellow and grey mudstones. The overlying Tatrot Formation (also known as Saketi Formation, approximately 260 m thick) represents alternating bands of grey friable and occasionally pebbly sandstone/siltstone and variegated mudstones (approximately 40 sequences from Kala Amb to Saketi, PATNAIK & SCHLEICH, 1993).
SAHNI & KHAN (1964) were the first to indentify Tatrot beds in the type section of Pinjor Formation. This identification was based on the lithology (grey clays, the characteristic of Tatrot Formation) and fauna (*Hipparion* and *Proamphibos*). Typical Pinjor fauna includes *Cervus, Equus, Rhinoceros, Bos* etc. and typical Tatrot Fauna includes *Stegodon bombifrons, Hipparion* and Carmohipparion. In Nepal Siwaliks (Churia Group) very little stratigraphical and biostratigraphical research has been carried out. A magnetic stratigraphic study of a Lower Siwalik section near Butwal was done by an American team where they recorded the first molar of a Ramapithecine (WEST et al., 1978; WEST & MUNTHE, 1983; MUNTHE et al., 1983; WEST, 1984; WEST et al., 1991). In 1997, SCHLEICH presented a faunal and stratigraphic correlation of various siwalik profile sections of Nepal (SCHLEICH, 1997). This study was based on extensive field work that he carried out with R. B. Sah from West to East of Nepal. The litho – and biostratigraphical studies of several Siwalik sequences in Nepal (CORVINUS, 1988; 1988a; 1991 and CORVINUS & NANDA, 1994, APPEL

et al. 1989,1991) suggest that vertebrate fauna from Lower Siwalik Bankas beds (contain very few vertebrate fossils), Babai Khola, Balim Khola and Tinau Khola are equivalent to the Chinji Fauna (WEST & MUNTHE, 1983).

A rich assemblage of Middle Siwalik vertebrate fauna has been recorded from the Rapti River Valley between Lamhi and Bhalubang and also from Tinau Khola area of Nepal which includes *Hipparion* sp., *Merycopotamus* sp., cf. *Giraffokeryx* sp., etc (WEST & MUNTHE, 1985). Dang Valley, along Babai and Thui Khola area and also Tinau Khola area yield a Lower Siwalik fauna which includes *Conohyus sindiensis, Ramapithecus punjabicus* etc. (MUNTHE et al., 1983 and WEST, 1984).

The Surai Khola and Dobatta Beds, Rato Khola and Gidhnia areas yield vertebrate fossils of Tatrot and Pinjor Faunal Zone and it includes Upper Siwalik species such as *Archidiskodon planifrons, Stegodon insignis, Hexaprotodon sivalensis, Hippohyus tatroti, Cervus* sp., *Elephas planifrons* etc (WEST & MUNTHE, 1981). The Chor khola beds at Surai Khola yield almost no vertebrate fossils except a few fragments of turtles, but, a very rich plant fossil material is recorded from the area (CORVINUS & SCHLEICH, 1994). The Binai Khola area yields almost no fossils except for some crocodile teeth (TOKUOKA et al., 1986). The relationship of Churia Group with the classic biostratigraphic divisions of type Siwaliks (Table 1) in Pakistan (BARRY et al., 1982) suggests that the Binai Khola rocks yield fossils which are representative of Dhok Pathan and Tatrot Zones; the Chitwan Formation corresponds to the Pinjor Zone.
A detailed listing of the palaeontological record from various localities from Nepal is given by SCHLEICH (1997).
The crocodilian fauna described and reviewed in this work, comes from various horizons of the Siwaliks and ranges in age from Lower Miocene to Lower Pleistocene (Table 1 & 2; Text fig. 2). Out of all the crocodilian *fauna Crocodylus palustris, Crocodylus porosus* and *Gavialis gangeticus* extend upto recent.

Fig. 2, next page. Siwalik belt of Northwestern Himalaya showing principal fossil crocodile localities (modified after NANDA & SEHGAL, 1993).


SIWALIK GROUP
N
0 100 km
75°
77°30′
80°
82°30′
30°
35°
32°30′
27°30′
72°30′
75°
77°30′
80°
82°30′
RAMNAGAR
NURPUR
JAMMU
JWALAMUKHI
DHARAMSALA
HARITALYANGAR
PALAMPUR
BILASPUR
CHAKRANA
PINJORE
MASUMPUR
TRILOKPUR
DEHRADUN
KAMLIAL
TATROT
DHOK PATHAN
DAUD KHEL
NAGRI
CHINJI
Indus R.
Jhelum R.
Chenab R.
Ravi R.
Beas R.
Sutlaj R.
NAIPLI
QURANWALL A
CHANDIGARH
NATHOT
SAKETI FOSSIL PARK
NAHAN
PAONTA
Jamuna R.
HARDWAR
KALA GARH
Ganga R.
Kosi R.
Karnali F.
SURAI KHOLA
TINAU KHOLA
BINAI KHOLA
BUTWAL
ARUNG KHOLA
LAMHI
KATHMANDU
BAKIYA KH.
PATO KHOLA
DANG VALLEY

Stratigraphic distribution of *Crocodylus* from the Indian Subcontinent

Recent	*C. palustris*	*C. porosus*	
Pleistocene	*C. palustris*		
	C. palustris	*C. biporcatus*	*C. palaeindicus*
Pliocene	*C. palustris* *C.* aff. *palaeindicus*	*C.* aff. *palustris* *C. palaeindicus*	
Miocene	*C. palustris*	*C. palaeindicus*	
Oligocene			
Eocene	Pristichampsine crocodiles		

Tab 1. Fossil representatives of *Crocodylus* from the Caenozoic of S-Asia

Stratigraphic distribution of *Gavialis* and *Rhamphosuchus* from the Indian Subcontinent.

Recent	*G. gangeticus*		
Pleistocene	*G. gangeticus* *G.gangeticus*	*G. aff. gangeticus*	*G. browni*
Pliocene	*G. gangeticus*	*R. crassidens* *G. curvirostris*	*G.* aff. *gangeticus* *G. browni*
Miocene	*G. gangeticus* *G. breviceps*	cf. *R. crassidens* *G. curvirostris* var. *gajensis*	*G.* aff. *browni*
Oligocene			
Eocene	*Gavialis dixoni* (from England)		

Tab. 2. Fossil representatives of *Gavialis* and *Rhamphosuchus* from the Caenozoic of S-Asia

Previous work on Siwalik Crocodiles

CAUTLEY & FALCONER (1836) were the first to study the fossil crocodiles from the Siwaliks when they described some cranial fragments of *Gavialis leptodus* form the Upper Pliocene of the Siwalik Hills. Later, FALCONER & CAUTLEY (1840), described a giant crocodile *Leptorhynchus crassidens* from the Tertiary Strata of the Siwalik hills, this was subsequently referred to as *Gharialis crassidens*. LYDEKKER (1886a; and 1888) figured the distal portion of a rostrum and lower jaw, together with part of a mandibular symphysis, cranial ad lower jaw material, teeth etc. and assigned all the material of *Leptorhynchus* (*Gharialis*) *crassidens* under a new genus *Rhamphosuchus crassidens*.

FALCONER in 1859 and then in 1868, described *Crocodylus palaeindicus* and *Crocodylus bombifrons* from the Pliocene of the Siwalik hills. This was followed by the descriptions of *Crocodylus sivalensis* from the Pliocene, *Gavialis hysudricus* from the Upper Pliocene, *Gavialis pachyrhynchus* from the Upper Miocene, and *Gavialis curvirostris* from the Lower Pliocene of the Siwaliks from India (LYDEKKER, 1886a, 1886b). In the early 20th century, PILGRIM (1912) reported *Gavialis curvirostris* var. *gajensis* and *Gavialis breviceps* from the Lower Miocene deposits of Bugthi hills, Baluchistan. In the year 1932, in an important work, MOOK described a very sifnificant gavial, *Gavialis browni* from the Lower Pliocene bed of the Siwaliks of India; later in 1973, *Gavialis browni* was reported from Lower Pleistocene beds of Siwalik hills, too (BADAM, 1973). Another Gavial *Gavialis lewisi* from the Upper Pliocene Dhok Pathan Formation was described by LULL (1944), this material was collected by G. E. LEWIS during his Yale North India expedition on 24th April, 1932.

Most recent listings of fossil crocodiles from the Siwaliks of Nepal are reported in SCHLEICH & MASKEY (1992), STEEL (1973) and WEST et al., (1991) and CORVINUS & SCHLEICH (1994) and represent following taxa: *Crocodylus, Gavialis, Rhamphosuchus,* and ?*Tomistoma*.

Methods

For the review, the crocodile material studied was catalogued in the Indian Museum, Kolkata; Museum of Wadia Institute of Himalayan Geology, Dehradun; Museum of Centre of Advanced Study in Geology, Panjab University, Chandigarh; Field Museum, Saketi Fossil Park, Saketi (India); Natural History Museum and Central Department of Geology, Tribhuvan University, Kathmandu (Nepal); British Museum Natural History, London (England). Several casts were made by the authors during various research trips, by one of the authors (HS: acknowledgements for grants to DAAD and VW-foundation) to India and Nepal during the years 1989-96. The material which was not available for study was analyzed from photographs/sketches and descriptions given in the literature.

For comparative analysis four recent specimens of *Gavialis gangeticus* (ZSM 2528/0,62/1959, 29/1912 and 521/1911) and three specimens of *Crocodylus palustris* (ZSM 34/1912, 517/1911 and 231/0) from the Zoological State Collection, Munich were used.

For the reconstructions of various crocodilian skulls, first, the recovered skull elements were compared with the recent specimens and then its ratio with the complete skull was noticed. Finally, the skulls were reconstructed taking the same ratios.

Abbreviations

ZSM: Zoologische Staatssammlung München; BSP: Bayerische Staatssammlung für Paläontologie; VPL: Vertebrate Palaeontology Laboratory, CAS / CASG: Centre of Advanced Study in Geology, Panjab University, Chandigarh; SFP: Saketi Fossil Park; F: Fossil; WIF: Wadia Institute Fossil / Wadia Institute of Himalayan Geology, Dehradun; IM: Indian Museum, Kolkata; BMNH: British Museum Natural History, London; NHM/TU: Natural History Museum, Tribhuvan University, Kathmandu.

Measurements of crocodylid skull elements used in the present study

Straight Teeth Length (TL)
Teeth Width A (compressed) (TWA)
Teeth Width B (extended) (TWB)
Alveolar Diameter A (along the median suture) (ADA)
Alveolar Diameter B (across the median suture) (ADB)
Interalveolar Length (IAL)
Mandibular Width (MW)
Maxillar Width (MXW)
Right Premaxillar tooth (RPM)
Left Premaxillar tooth (LPM)
Right Maxillar tooth (RM)
Left Maxillar tooth (LM)
Right Mandibular tooth (RMD)
Left Mandibular tooth (LMD)

Alveole

Alveole with only tooth base preserved

Alveole with tooth preserved

Terminology

The skull terminology is given in text figure 3 & 4.

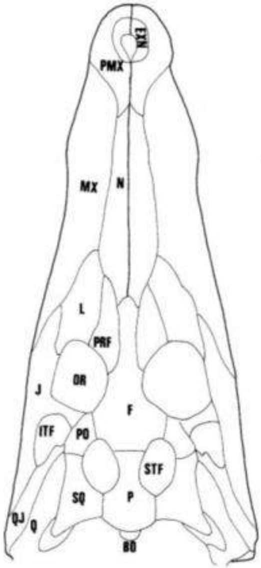


Fig. 3 c

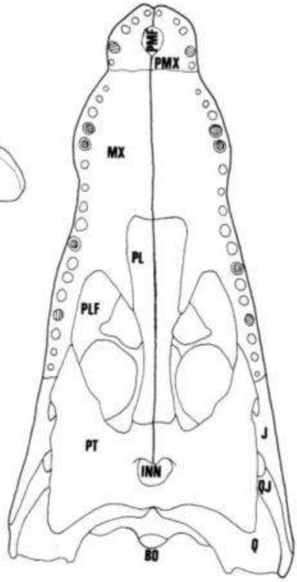


Fig. 3 a

Fig. 3 b

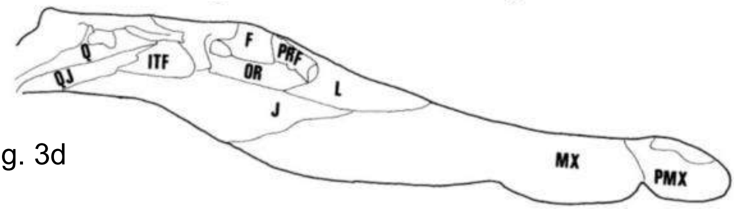


Fig. 3d

Fig. 4 a

Fig. 4 b

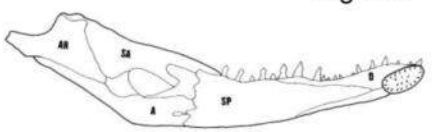


Fig. 3. Morphology and terminology of cranium and upper jaw of crocodile used in the present work. (a) dorsal view, (b) ventral view, (c) occipital view and (d) right lateral view of skull.

Fig. 4. Morphology and terminology of mandibles of crocodile used in the present work. (a) Lateral view and (b) lingual view of left mandible. The preserved part of the fossil crocodiles in all the figures is illustrated by continuous lines and reconstructed part is illustrated by broken lines.
The terms used in the figures (3, 4) are:

A = Alveole; a = Angular; ar = Articular; bo = Basiooccipitale; bs = Basisphenoid; d = Dentary; eo = Exoccipital; ec = Ectopterygoid; ExN = External Narial Aperture; f = Frontal; FA = Foramen Aerum; FM = Foramen Magnum; itf = Infratemporal Fenestra; InN = Internal Narial Aperture; j = Jugal; l = Lacrymal; mx = Maxillary; n = Nasal; or = Orbit; p = Parietal; pl = Palatine; plf = Palatine Fenestra; pmx = Premaxillary; prf = Prefrontal; po = Postorbital; pt = Pterygoid; q = Quadrate; qj = Quadratojugal; sa = Surangular; so = Supraoccipital; sp = Splenial; sq = Squamosal; stf = Supratemporal Fenestra.

Revised Taxonomy

Family Crocodylidae CUVIER, 1807

The snout is generally rather long and slender, but not sharply demarcated from posterior region of the skull. The nasal bones extend forward to meet the premaxillae and frequently reaching the external nares. The supratemporal fenestrae are proportionately small but an antorbital opening is sometimes present. The mandibular symphysis is relatively long; the dentition is powerfully developed with caniniform elements and sometimes with blunt cheek teeth. The lower teeth are generally accommodated in pits between the upper teeth, the caniniform 4th mandibular element being typically received in an upper jaw notch or a foramen. The scutes on dorsal surface are in two or more rows, a ventral armour is absent.
Lower Cretaceous - Miocene of Europe, Eocene - Recent of Africa, Paleocene - Eocene and Miocene - Recent of Asia, Upper Cretaceous - Eocene and Miocene - Recent of North America, Paleocene - Miocene and Recent of South America, Upper Miocene or Pliocene - Recent of Australasia.
The early representatives of this family appeared during the Cretaceous and by Eocene times. *Crocodylus* had taken advantage of the prevailing warm climate to establish themselves in Europe, Asia, Africa and the Americas, whilst by the Pliocene they were also present in Australasia. The onset of colder conditions as the Tertiary drew to a close resulted in a withdrawal of the *Crocodylus* towards the existing tropical regions, but they remain a widespread and successful group whose future is threatened only through the destruction of wild habitats by modern technology and agriculture.
In South America the *Crocodylus* never seem to have occupied a prominent position, although they are now the dominant crocodilians of Central America and Caribbean: all of the known fossil *Crocodylus* from the neo-tropical region are of the slender-snouted adaptive type that failed to evolve among the indigenous caimans and thus left vacant the longirostrine, piscivorous ecological niche (also exploited by the gavials, which were present in south America from the Oligocene to the Pliocene). More recently *Crocodylus acutus* has, however extended its range southwards into northern South America with apparent success (STEEL, 1973).

Crocodylus LAURENTI, 1768 (type species: *C. niloticus*)

The prefrontal lacks any contact with the maxilla; the external nares are unpaired; a fronto-parietal suture is excluded from the supratemporal fenestra; the premaxilla is notched or perforated for the reception of the 1st mandibular tooth. The palatines are produced anteriorly considerably beyond the pterygoid vacuities; the symphysis is without a splenial inclusion and is extending no further back than the 8th member of the inferior dental series. Normal premaxillary teeth count 5, although one of these may be lost in adult animals (e.g. *C. porosus, C intermedius, C. cataphractus*). The upper jaw contains 16-19 teeth in each ramus and the lower jaw contains 14-15 teeth; 5th maxillary tooth is enlarged. The stratigraphic distribution of the genus *Crocodylus* in different continents is given in table 3.

Age	**Europe**	**N, America**	**Asia**	**Africa**	**Australia**
Recent	-	+	+ *C. palustris* *C. porosus*	+	+
Pleistocene	-	-	*C. palustris*	*C. illoidi*	*C.porosus*
Pliocene	-	-	*C.* aff. *palustris* *C. palustris* *C. palaeindicus* *C.* aff. *palaeindicus*		
Miocene	C. bambolii C.sp. ind.		*C. palustris* *C. palaeindicus*	*C. pigotti*	
Oligocene	? *C. indet*			*C. megarhinus*	
Eocene		*C. sulcifer*	Pristichampsine crocodiles		

Tab. 3. Stratigraphic distribution of *Crocodylus* in various continents (modified after WINDOLF, unpub. work, 1996).

Crocodylus palaeindicus FALCONER, 1859

Holotype: E-31 a cranium, catalogued in the Indian Museum Kolkata

Type Locality: Lower Siwaliks, Perim Island, Gujarat, India, Middle Miocene

Synonymy:
Crocodilus palaeindicus Falconer, 1859
Crocodilus palaeindicus (Lydekker 1879)
Crocodilus palaeindicus (Lydekker, 1886)
Crocodilus palaeindicus (Lydekker, 1888)
Crocodylus palaeindicus (Steel, 1973)
Crocodylus palaeindicus (Prasad, 1974)
Crocodylus palaeindicus (Badam, 1979)
Crocodylus palaeindicus (Badam, 1998)

Distinguishing Features

Maximum length is approx. 6-8 meter. The skull is short and broad. The snout is broad. The upper cranial profile is flat. A maxillao-premaxillary constriction in most of the cases is deep; it may be moderate also. The external narial aperture is rounded. The palatine fenestrae are rhomboidal; The orbits are large and oval (Plate 1, fig. 1). There are 4 pairs of premaxillary teeth (3rd largest) and 14 pairs of maxillary teeth (4th largest). The alveolies for the teeth attachment are deep; the lacrymals are stout and broad. The lateral margins of interorbital plate are flat. The proportion of the breadth of the preorbital region to its length is 1:1.2.

Material: **Anterior part of cranium** (E-32), catalogued in the Indian Museum, Kolkata.
(Plate 1, fig. 2 & Text fig. 5)

Locality: Lower Siwaliks of Perim Island, Gujarat (LYDEKKER, 1886), Middle – Upper Miocene

Description

The specimen is comprising anterior maxillary part of the cranium. The specimen is broken anterior to the maxillo-premaxillary suture and posterior to the 7th maxillary tooth. On the ventral side, the alveolies for the 5 left maxillary teeth (3rd – 7th) and 5 right maxillary teeth (2nd – 6th) are present. The alveole for the 6th tooth in the right maxillary is broken. The alveoles for the attachment of the teeth are deep. A reconstruction suggests that the total length of the cranium is approx. 460 mm which is nearly same as that of the type specimen. The width of the snout at the level of the 4th maxillary teeth is lesser than in the type specimen. The maxillary bones at the level of the 4th maxillary teeth are, larger and stouter than in living C. *palustris*. The anterior margin of the palatine fenestrae is distinct on the specimen which tapers at the posterior level of the 6th maxillary teeth. A reconstruction of the palatine fenestrae suggests a rhomboidal shape similar to that in the type specimen. The suture between the palatine and maxillaries is not distinct. Based on the reconstruction it is evident that the maxillo-premaxillary constriction is deep. There are only 4 premaxillary (3rd largest) and 14 maxillary teeth (4th largest).

The alveolar dimensions taken on the specimen are comparable to that in the type specimen of *C. palaeindicus*, however, interalveolar distance is slightly more than that in the type specimen.

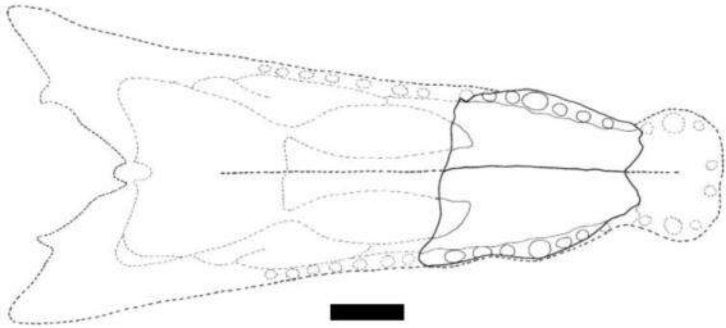


Fig. 5. Reconstructed ventral view of cranial rostrum of *Crocodylus palaeindicus*, E-32 (Scale = 5cm).

Position of tooth (based on reconstruction)

	ADA (in mm)	ADB (in mm)	IAL (in mm)
RM2	09	07	07 (2nd – 3rd RM)
RM3	09	09	06 (3rd – 4th RM)
RM4	17	14	04 (4th – 5th RM)
RM5	07	09	06 (5th – 6th RM)
RM6	09	09	
LM3	09	07	04 (3rd – 4th LM)
LM4	17	14	06 (4th – 5th LM)
LM5	07	09	10 (5th – 6th LM)
LM6	11	09	06 (6th – 7th LM)
LM7	14	11	

Remarks: For the fossil age consideration, LYDEKKER (1886) did not mention the precise locality and horizon for the specimen. The only information available is Lower Siwaliks of Perim Island. On this basis we consider the stratigraphic age of the specimen from Middle to Upper Miocene.

Material: **Cranium**, A/683, catalogued in the Museum of Centre of Advanced Study in Geology, Panjab University, Chandigarh. The material was originally
described by BADAM (1979). (Plate 2, fig. 1 & Text fig. 6)

Locality: 8 km North of Naipli; Pinjor Formation, Lower Pleistocene

Description

In general form the skull is broad and long. The posterior portion of the skull is broken. The constriction at the side of snout after the 4th premaxillary teeth is very deep and sharp. The premaxillo-maxillary suture extends forward, curves inwards on the lateral margins and then curves backward and inward to reach the median line at about the level of first maxillary teeth. The medial suture is very thick and heavy.
The snout is broad and deeply pitted. The proportion of the breadth of the snout at the level of the anterior ends of the orbits to its length anterior to the orbits is nearly 1:1.2. The snout occupies a greater portion of the length of the skull. It expands very rapidly back to the level of the 4th maxillary teeth. From the level of the 6th to the 7th maxillary teeth, there is a constriction followed by an expansion from the 8th maxillary teeth to the back. The right marginal border after the 7th maxillary tooth, is broken.

The external narial aperture is more or less rounded; it is broadest in the middle. The posterior part of the aperture tapers to a point in the median line.

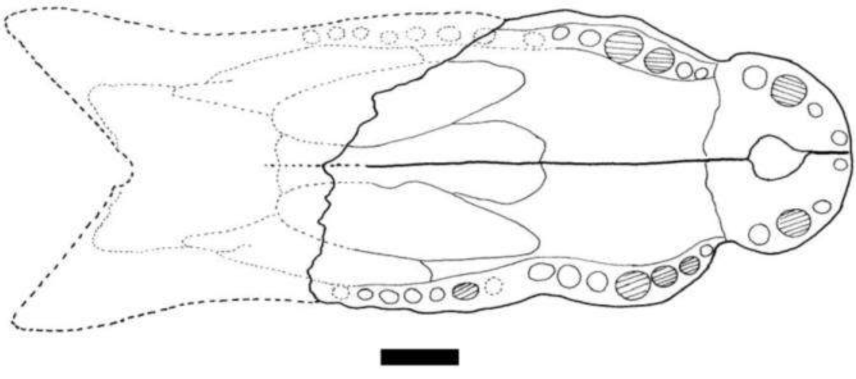


Fig. 6. Reconstructed ventral view of cranial rostrum of *Crocodylus palaeindicus*, A/683 (Scale = 5cm).

Only the anterior part of the left orbit is preserved which tapers sharply joining the lacrymals. The cavities of palatine fenestrae are large and are probably rhomboidal. Both the fenestrae have tapering anterior end reaching up to the anterior border of 7th maxillary teeth. The outer part of right fenestra and posterior part of both the fenestrae are incomplete. The fenestrae are broadest near the 11th maxillary teeth. The maximum width of the fenestrae is approx. 66 mm. The maximum length of the fenestrae cannot be determined due to broken posterior end of the skull. The minimum distance between the fenestrae is at the level of the 11th maxillary teeth (45 mm). The borders of the fenestrae are converging forward. The anterior end of the fenestrae is pointed. The distance from the anterior ends of the palatine fenestrae forward to the junction of the two maxillo-palatine sutures at the median line, measured along the median line is 4 mm.
The premaxillary bones are broad and short. The premaxillary foramen has a diameter of approx. 39 mm. The maximum breadth of the snout across the two premaxillaries is at its centre, near 3rd tooth. The length of the premaxillaries along the median line is approx. 100 mm. The suture along the median line is undulated.

On the ventral side, each premaxillary contains alveolies for 4 teeth. The teeth are however, broken. The first pair of alveolies are sub-rounded. They are quite close to each other. On each side the 1st tooth is widely separated from the 2nd. The distance beween the 1st and the 2nd premaxillary teeth is about 17 mm. The 2nd alveoli on each side is as large as the 1st.

The 2nd, 3rd and 4th alveolies are quite close to one another, the 3rd being the largest in the series; the 4th again is small but larger than 1st and 2nd and smaller than 3rd. The space between 2nd and 3rd premaxillary teeth is 2 mm and between 3rd and 4th is 5 mm.

The re-eruption of left 2nd premaxillary tooth is distinctly seen. The maxillaries are broad and large. The maxillo-palatine suture extends obliquely forward and inward from the inner border of the palatine fenestrae at the anterior margin of 10th maxillary teeth upto the anterior border of 9th maxillary teeth, then they join each other on the median line with a suture curved backward on the median line at the level of anterior margin of 7th maxillary teeth.

Each maxillary contains alveoles for fourteen teeth. The teeth are mostly broken. The 4th pair of the maxillary teeth is the largest in the series. The teeth are moderately spaced; anterior teeth are somewhat irregularly and posterior ones are regularly spaced. The space between the 7th and the 8th maxillary teeth is however, the largest (15 mm). In general, the spacing between maxillary teeth varies between 1-2 mm, but space between 4th and 5th and 5th and 6th varies between 4-5 mm. The maxillo-nasal suture is uncertain. The nasals are narrow; the maximum width of nasal is near the prefrontal and it is approx. 78 mm. Most of the area of the snout is occupied by the maxillaries; the maximum width of maxillaries is 110 mm. The lacrymals are broad and long. Their contact with the jugals is distinct. They have no direct contact with the frontal.

Only the anterior part of left ectopterygoid is preserved reaching upto the anterior border of the 12th maxillary tooth. The prefrontals are not clearly distinct and the frontal is broken. Similarly, postorbital, squamosal, and parietal are also broken. The jugal is partly preserved, thinning out at the anterior end and seems to be broad and stout. The supraoccipital, the pterygoid and the ectopterygoid are not preserved. An internal narial aperture is distinct; it has a diameter of approx. 11 mm. The Interdental pits are present.

MW (taken across the medial suture on the junction of the two maxillo - palatine sutures): 235 mm.

Position of tooth (based on reconstruction)

	ADA (in mm)	ADB (in mm)	IAL (in mm)
Distance between 1st and 2nd RPM			17 (1st – 2nd RPM)
RPM1	11	11	2 (2nd – 3rd RPM)
RPM2	11	09	5 (3rd – 4th RPM)
RPM3	30	30	1 (1st – 2nd RM)
RPM4	16	15	2 (2nd –3rd RM)
RM1	12	09	3 (3rd – 4th RM)
RM2	17	15	5 (4th – 5th RM)
RM3	15	19	4 (5th – 6th RM)
RM4	28	30	??
RM5	17	16	4 (8th – 9th LM)
RM6	14	13	3 (9th – 10th LM)
LM7	21	19	3 (10th – 11th LM)
LM9	21	18	2 (11th – 12th LM)
LM10			
	21	18	1 (12th – 13th LM)
LM11	16	13	2 (13th – 14th LM)
LM12	17	13	
LM13	15	12	
LM14	16	13	

Material: Posterior broken cranium (18136) catalogued in the Indian Museum, Kolkata. The specimen was originally described by PRASAD (1974). (Plate 2, fig. 2 & Text fig. 7)

Locality: Perim Conglomerate (= Dhok Pathan Stage), Perim Island, Gujarat, Lower Pliocene.

Description

The skull is broad; the orbital and post orbital region of the skull is broken. The specimen is dorsally pitted. The external narial aperture is rounded. The maxillaries are broad. In comparison to the type specimen of *C. palaeindicus*, the maxillo-premaxillary constriction is moderate. The upper cranial profile is nearly flat. The portion surrounding the external narial aperture is more convex in comparison to the type specimen. Two pits anterior to external narial aperture are distinct which accomodate the first pair of mandibular teeth. The specimen is diagenetically deformed and is considerably damaged ventral, lateral and posterior. An approximated length of the reconstructed cranium is 500 mm. The traces of nasals are clearly distinct on the dorsal surface of the rostrum. The width of the nasal is biggest near the external narial aperture (approx. 60 mm) and is smallest near the orbits (35 mm, based on reconstruction).

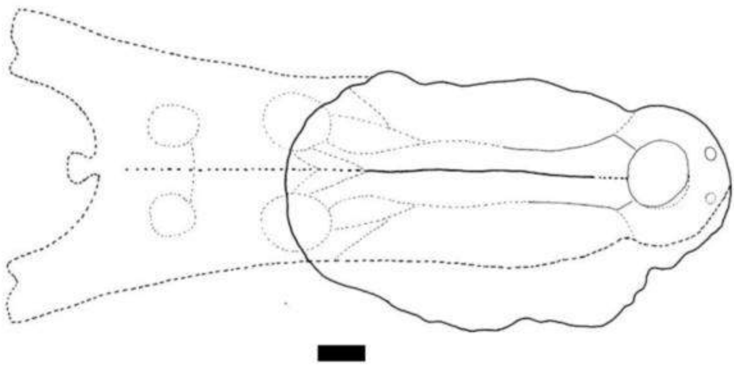


Fig. 7. Reconstructed dorsal view of cranium of *Crocodylus palaeindicus*, 18136 (Scale = 5cm).

Crocodylus cf. *palaeindicus* FALCONER, 1859

Synonymy:
Crocodilus bugtiensis Pilgrim, 1908
Crocodylus bugtiensis (Steel, 1973)
Crocodylus bugtiensis (Prasad, 1974)

Material: **Anterior part of maxillary**, KN/751 (E-281), collected by K. N. PRASAD and catalogued in the Indian Museum, Kolkata as *Crocodylus bugtiensis*. (Plate 3, fig. 1 & Text fig. 8)

Locality: Perim Conglomerate (Dhokpathan Stage), Perim Island, Lower Pliocene

Description

Crushed anterior part of maxillary is preserved with distinctly marked median suture. The alveoles for the left maxillary teeth are seen. Total 12 alveoles are seen; 1st, 2nd, 3rd, and 7th alveolies are not clearly distinct. 4th alveole is the largest in series, followed by 3rd and then 5th. The alveoles are very large in diameter when compared with the living *C. palustris*. Interdentnal space is moderate. The constriction of the jaw from 5th to 7th maxillary teeth and then expansion from 8th maxillary tooth to back is more pronounced in the specimen in comparison to that in *C. palustris*.

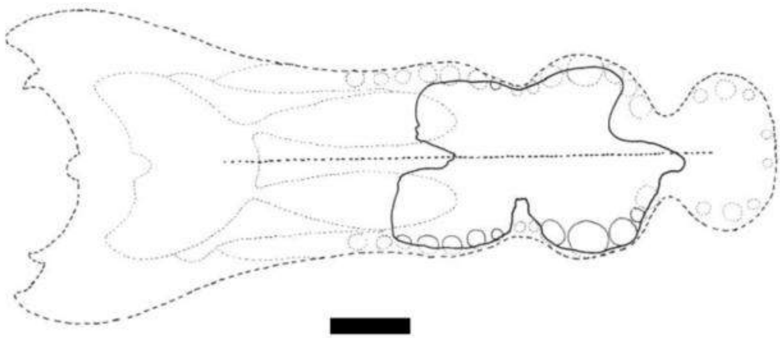


Fig. 8. Reconstructed ventral view of cranial rostrum of *Crocodylus* cf. *palaeindicus*, KN/751 (E-281). Scale = 10 cm

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
LM3	36	36	3 (3rd – 4th LM)
LM4	46	39	6 (4th – 5th LM)
LM5	30	27	
LM7	22	18	4 (7th – 8th LM)
LM8	33	22	6 (8th – 9th LM)
LM9	27	18	6 (9th – 10th LM)
LM10	27	19	6 (10th – 11th LM)

The alveoles are very large in diameter suggesting towards giant teeth size and therefore towards a large animal size. The reconstruction of the skull suggest an individual ranging in length between 11-13 metres. The large and stout maxillaries, and deep maxillo-premaxillary constriction is similar to *C. palaeindicus* but the specimen is larger than the type specimen of *C. palaeindicus.*

Remarks:
The species was widely distributed in the Siwaliks of Indian Subcontinent. The material is recorded from the Middle Miocene (LYDEKKER, 1886) and Lower Pliocene (PRASAD, 1974) rocks of Perim Island and from the Lower Pleistocene rocks (BADAM, 1979) of Naipli near Chandigarh. Very laterly, the species has been recorded from the Late Pleistocene rock of Upper Narmada Group also (BADAM, 1998).

Crocodylus biporcatus CUVIER 1807

Holotype: Not located, but illustrated in CUVIER, (1807), Ann. Mus. Nat. Hist., Paris, vol. 10, plate 1 & 2.

Type Locality: Indian Subcontinent

Synonymy:
Crocodilus nattans Meyer, 1795
Crocodilus oopholis Schneider, 1801
Crocodilus biporcatus Cuvier 1812
Crocodilus biporcatus raninus Schlegel & Müller, 1844
Oopholis porosus Gray, 1863
Oopholis pondicherianus Gray 1863
Crocodilus pondicherianus Günther, 1864
Champse porsa Werner, 1933
Oopholis porosus (Deraniyagala, 1939)
Crocodylus biporcatus (Badam, 1973)
Crocodylus biporcatus (Steel, 1973)

Distinguishing features

The maximum length is approx. 10 meters. The skull is long with triangular outline. The snout is moderately sharp. A maxillo-premaxillary constriction is moderate. The upper cranial profile is sloping; the palatine fenestrae are rhomboidal. The orbits are large and oval. Generally, 4 pairs of premaxillary teeth (3rd largest); rarely 5 pairs (4th largest); 14 - 15 pairs of maxillary teeth (5th largest). The maxillo-premaxillary suture is deep (W shaped). The alveoles for the teeth attachment are large and generally shallow. The lacrymals are slender and long; the lateral margins of the interorbital plate are elevated. The proportion of breadth of preorbital region to its length is 1:1.5.

Material: **Complete skull** A/684, catalogued in the Museum of Centre of Advanced Study in Geology, Panjab University, Chandigarh. The material is originally described by Badam (1973; 1979).
(Plate 3, fig. 2)

Locality: About 0.6 km north northwest of Naipli; Pinjor Formation, Lower Pleistocene.

Description

The skull is relatively long, narrow anterior and broader posterior in comparison to *C. palustris*. The dorsal surface of the skull is highly pitted like *C. palustris*.
The maxillo-premaxillary constriction is moderate (deep in *C. palustris*). The proportion of the breadth of the snout at the level of the anterior ends of the orbits to its length anterior to the orbits is nearly 1:1.5. The snout occupies a greater proportion of the total length of the skull. It expands rapidly back upto the level of 5th maxillary teeth. From the level of 6th to 7th maxillary teeth there is a constriction followed by an extension from 8th maxillary teeth. To the back of 8th maxillary teeth, the two lateral borders remain almost parallel (BADAM, 1973).

The external narial aperture has an auricular shape. The anterior part of the aperture is somewhat rounded and posterior part tapers at the median suture.

An auricular premaxillary foramen is present on the ventral surface. It tapers anterior and is rounded, posterior. The premaxillary foramen has a diameter of approx. 28 mm (in *C. palustris* the diameter is approx. 21 mm, and is at approx. 39 mm from the well defined maxillaropremaxillary suture. On the median line in *C. palustris* the distance is about 27 mm.

The orbits are large and oval and are similar to those of *C. palustris*. The internal borders of orbits are sharply curved in comparison to the external borders. The frontal is nearly flat and is relatively narrow having a width of approx. 56 mm; it is deeply pitted (BADAM, 1973). The lateral sides of the frontal (inter-orbital plate) are strongly elevated. (it is less elevated in *C. palustris*). The prefrontal is a wedge-shaped bone having a sharp contact posterior with the frontal.

The supratemporal fenestrae are rather small and are similar to those of *C. palustris*. The right fenestra is sub-oval and tapers posterior; the left fenestra is broken. The parietal between the two fenestrae has a width of approx. 22 mm (BADAM, 1973).

The palatine fenestrae are rhomboidal. They extend anterior up to the anterior border of the 8th maxillary teeth. The fenestrae are broadest at the 11th maxillary teeth. The maximum anterio-posterior length of each fenestra

is approx. 152 mm and the maximum width is approx. 66 mm; the minimum distance between the fenestrae is near the middle and is approx. 48 mm (BADAM, 1973). The posterior borders of the fenestrae converge sharply and join the suture between pterygoid and ectopterygoid. The ratio of the length of the fenestrae in proportion to the length of the skull from the premaxillaries to the supraoccipital is 1:3.4 (BADAM, 1973). The distance from the anterior ends of the palatine fenestrae forward to the junction of the two maxillo-palatine sutures at the median line, measured along the median line is 40 mm. The internal narial aperture (14 mm in diameter) is somewhat rounded and faces obliquely downwards and backwards.
The premaxillary bones are short and broad (52 mm) in comparison to *C. palustris* (45 mm). The length of the premaxillaries along the median line is 95 mm.

On the ventral side, the premaxillaries contain alveoles for 4 premaxillary teeth; The 1st pair of the alveoles is poorly distinct. The anteriormost portion of the snout, right premaxilla and anteriormost part of the maxillary is broken. The alveoles for the 4th premaxillary teeth are not complete, especially on the right maxilla. The 3rd premaxillar teeth are the largest. The dental pits for the mandibular teeth are preserved. The largest and deepest pit is at maxillo-premaxillary suture.
The maxillaries are relatively broad in comparison to *C. palustris*. The maximum width of each maxillary is approx. 100 mm (in *C. palustris*, the maximum width of each maxillary is approx. 70 mm). 13 alveoles for maxillary teeth are visible on left maxilla (BADAM, 1973 described only 12 alveoles). The remnants for the 3rd left premaxillary tooth, and 4th, 5th, 8th, 9th and 11th left maxillary teeth are present. The 5th maxillary tooth is the largest. The inter-dental space is the maximum between 7th and 8th maxillary teeth (BADAM, 1973, mentioned the maximum space between 4th and 5th maxillary teeth). The maxillo-palatine suture extends obliquely forward and inward from the inner border of the palatine fenestrae at the level of the 8th maxillary teeth and then it takes a turn transversely across the median line to a corresponding point on the opposite side and obliquely backward and outward to the opposite palatine fenestra (BADAM, 1973).

The maximum width of the nasal is near the prefrontals and it is relatively high (92 mm) in comparison to *C. palustris* (80 mm). The contact of the nasal with the lacrymal and the jugal is not distinct and its contact with the prefrontal is also not well defined. The lacrymal is long and slender (anterio-posterior length: 80 mm) but shorter than that in *C. palustris* (anterio-posterior length 90 mm); its contact with the jugal and the prefrontal is not well defined.
The postorbital is considerably smaller than the squamosal. In *C. palustris* the postorbital is similar to squamosal in size. The squamosal is triangular in outline. The parietal is broken in this specimen; both the jugals are present, but the right jugal is distorted by crushing. The quadratojugals, the quadrates and the supraoccipitals are not well preserved. On the posterior side a rounded foramen magnum is distinct.

The pterygoids are triangular bones separeted by a median ridge. The suture with the pterygoid and ectopterygoid is not distinct. The anterior ends of ectopterygoids reach up to the 11th maxillary teeth as in *C. palustris*. Posterior, the ectopterygoid reaches far over the pterygoid. In *C. palustris*, posterior, the ectopterygoid reaches two-third the length of the pterygoid. The interdental pits are visible. MW (taken across the median suture, on the junction of the two maxillo - palatine sutures): 200 mm

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
LPM2	14	18	3 (2nd – 3rd LPM)
LPM3	22	18	3 (3rd – 4th LPM)
RM1	17	15	1 (2nd – 3rd LM)
LM2	12	12	3 (3rd – 4th LM)
LM3	17	17	7 (4th – 5th LM)
LM4	20	20	8 (5th – 6th LM)
LM5	27	23	9 (6th – 7th LM)
LM6	16	16	17 (7th – 8th LM)
LM7	11	13	6 (8th – 9th LM)
LM8	12	09	9 (9th – 10th LM)
LM9	13	12	8 (10th – 11th LM)
LM10	13	12	7 (11th – 12th LM)
LM11	13	11	3 (12th – 13th LM)
LM12	12	12	
LM13	13	13	

Remarks:
The species shows most of the general characters similar to living *Crocodylus porosus* but the habitat of living *Crocodylus porosus* is estuarine and salt water and enters the rivers only during the breeding seasons. Whereas, *Crocodylus biporcatus* (Lower Pleistocene) has been recorded from the freshwater sediments of Siwaliks. The character similarities suggest a phylogenetic relationship between *Crocodylus biporcatus* and *Crocodylus porosus*.

Crocodylus palustris **LESSON, 1831**

Holotype: Not located

Type Locality: India

Habitat and distribution:
The Mugger (Magaar), Goa or Swamp crocodile is attaining a length of 5 m and ranging from Sind and Baluchistan through Assam (India) and south to Ceylon. LYDEKKER (1888) provisionally referred several teeth from the Pleistocene of the Narbada Valley, India to this species. MÜLLER (1923)

reported it from the Siwalik beds, and TRIVEDY (1966) identified *C. palustris* from the Upper Miocene of Tripura, India.
Snout broad and short, with no development of bony ridges; 13 -14 and 14-15 mandibular teeth. Usually 4 longitudinal rows of bony ridges along the back (STEEL, 1973).
An exclusively fresh-water form that frequents inland rivers and marshes but rarely if ever enters tidal estuaries. In the dry season this species may migrate overland by night to find lakes and streams that still contain water but NEILL (1971) considers reports of aestivation to be improbable. It is generally timid, feeding on birds and smaller mammals; the incubation period for the eggs is 17-18 weeks. WERMUTH (1953) recognized two subspecies:
C. palustris palustris LESSON, 1831 is the common form of the species, excluding only the Ceylonese race. It includes *Champse palustris palustris* RUST, 1937, *Crocodylus palustris palustris* DERANIYAGALA, 1936. *C. palustris brevirostris* (WERNER, 1933) is restricted to Ceylon and includes *Champse palustris kimbula* RUST, 1937 and *C. pallustris kimbula* DERANIYAGALA, 1936 (see MERTENS, 1960).

Synonymy:
Crocodilus palustris Lesson, 1831
Crocodilus vulgaris indicus Gray, 1831
Crocodilus bombifrons Gray, 1831
Crocodilus vulgaris Dumeril & Bibron, 1834 (in part)
Ccrocodilus trigonops Gray, 1844 (the wide-faced Crocodile)
Crocodylidae gen. et. sp. indet (Theobald, 1858)
Bombifrons trigonops Gray, 1862
Bombirons indicus Gray 1867
Crocodilus bombifrons (Falconer, 1868)
Crocodilidae gen. et. sp. indet (Lydekker, 1886)
Crocodilus sivalensis Lydekker, 1886
Crocodilus sivalensis (Lydekker, 1888)
Crocodilus palustris (Lydekker, 1888)
Crocodilus sivalensis or Crocodilus palaeindicus (Boule, 1910)
Crocodilus sivalensis (Mook, 1933)
Champse palustris Werner, 1933.
Crocodylus sinhaleyus Deraniyagala, 1958
Crocodylus sinhaleyus (Steel, 1973)
Crocodylus palustris (Steel, 1973)
Crocodylus sivalensis (Steel, 1973)
Crocodylus sp. (Munthe et al., 1983)
Crocodylidae indet. (Gaur & Chopra, 1984)
Crocodylus sp. (Gupta & Verma, 1988)
Crocodylus sivalensis or *Crocodylus palustris* (Garg, 1988)
Crocodylus sp. (Tewari, 1990)
Crocodylus sp. indet. (West et. al., 1991)
Crocodylus palustris (Sah & Shreshta, 1992)
Crocodylus cf. *palustris* (Patnaik & Schleich, 1993)
Crocodylus aff. *palustris* (Corvinus & Schleich, 1994)

Distinguishing features

The skull is moderately broad and short. The snout is also broad and short. The upper cranial profile is convex. The external narial aperture is auricular. The maxillo-premaxillary constriction is deep. The orbits are large and sub-oval. The palatine fenestrae are rhomboidal or oval. Four pairs of premaxillary teeth (3rd largest); 14 pairs of maxillary teeth (5th largest). The alveoles for the teeth attachment are deep. The lacrymals are broad. The lateral margins of the interorbital plate are slightly elevated. The proportion of the breadth of the preorbital region to its length is more than 1:1.3. The teeth are slender, large, and keeled with sharp apex. 4th and 10th maxillary teeth are caniniform. The osteoscutes are oval or subcircular, with deep grooves and well developed medial keel. (PATNAIK & SCHLEICH, 1993).

Material: **Cast of a complete skull** (E-186), catalogued in the Indian Museum, Kolkata. The original is catalogued in the British Museum (Natural History), London (BMNH-39798). The material is figured in FALCONER'S palaeontological memoir (1968) as *Crocodilus bombifrons*. Subsequently, the material was described by LYDEKKER (1886) as *Crocodilus sivalensis* (as number BMNH –39797).
(Plate 3, fig. 3)

Locality: Pliocene of the Siwalik hills (LYDEKKER, 1888).

Description

The skull is relatively small (380 mm) compared to the living *C. palustris* (500 mm). The dorsal surface of the skull is highly pitted like in the living *C. palustris*. The upper cranial profile is slightly convex. The maxillo-premaxillary constriction is deep like in the living *C. palustris*. The proportion of the breadth of the snout at the level of the anterior ends of the orbits to its length anterior to the orbits is nearly 1:1.3. The snout occupies a greater proportion of the total length of the skull. It expands rapidly back up to the level of the 5th maxillary tooth.

The external narial aperture is reniform. The anterior part of the aperture is somewhat rounded and posterior part tapers at the median line.

The orbits are large; the shape and size of the orbits is similar to those of the living *C. palustris*. The frontal is slightly concave having everted margins towards the orbits similar to that in the living *C. palustris*.

The supratemporal fenestrae are slightly smaller (anterioposterior diameter 35 mm) than those of the living *C. palustris* (42 mm). The shape of the supratemporal fenestrae is rounded whereas in the living species the shape of supratemporal fenestrae is anterioposterior elongated. The ratio of anterioposterior and transverse diameter of supratemporal fenestrae in the fossil form is approx. 1:1 whereas in the living form this ratio is approx. 1:1.7.

A parietal between the two fenestrae has a width of approx. 17 mm which is slightly smaller than that in the living form (23 mm), however, the width of the parietal posterior to the supratemporal fenestrae is similar to that of the recent *C. palustris.*

The width of the premaxillary bones anterior to the maxillo-premaxillary constriction at the level of the 3rd maxillary tooth is approx. 36 mm and it is quite smaller than that in the living species of *C. palustris* (55 mm). From the level of 6th to 7th maxillary teeth there is a constriction followed by an extension from 8th maxillary teeth.
The maxillaries are relatively narrow in comparison to the living *C. palustris.* Maximum width of each maxillary is approx. 55 mm (in the living *C. palustris,* the maximum width of each maxillary is approx. 70 mm).
The maximum width of the nasal is near the prefrontal (65 mm) and it is lesser than that in the living *C. palustris* (80 mm). The contact of the nasal with the prefrontal, the lacrymal and the jugal is not well defined. The lacrymals are broad and stout and similar to those in the living form. Their contact with the jugal and the prefrontal is not well defined. The jugals are less broad (width lateral to orbits is approx. 35 mm) compared to those in the living *C. palustris* (43 mm). The squamosals and the postorbitals are compared in size, similar to those in the recent form.
The ventral surface of the cranium is not visible as it is covered by the mandibular symphysis, however, the right lateral view of the skull shows 3 maxillary and 3 mandibular teeth alternating in closed position of the jaws. The teeth are stout and slender; the posterior teeth are smaller than the anterior teeth.

Remarks:
The specimen shows most of the general characters similar to the living *Crocodylus palustris.* Few dissimilarities in the size as discribed above might be related with the overall difference in size and ontogenetic alterations. The only difference we note is the shape of the supratemporal fenestrae. This difference might be related with the intraspecific variation. It could also be related with the evolutionary pattern but to reach such conclusion more comparative material is needed.

Material: Mandiblular part of the skull, SFP 201. Collection of R. L. GARG, catalogued in the Field Museum of the Saketi Fossil Park, Saketi.
Locality: Saketi Formation (Tatrot Fm); Khera Village, Distt. Nahan. Upp. Pliocene.
(Plate 4, fig. 1 & Text fig. 9)

Description

Well preserved right and left mandibles with alveoles for 10 teeth in left mandible and 12 teeth in right mandible. The front two teeth are partly broken on anterior margin. On the right mandible, 3rd, 4th, 5th, 8th alveoles are seen for the respective teeth; the 6th tooth is nearly complete and 11th and 12th

teeth bases are preserved. In 2nd, 7th, 9th and 10th alveoles, teeth bases are present. On the left mandible, teeth bases are present in 3rd, 4th, 5th, 7th, 9th, and 10th alveoles; for 6th and 8th teeth only alveoles are present. The interdental pits are distinct at some places. Vertical striations are seen on the teeth and the lateral keels are well developed. The teeth are laterally compressed rather than anterioposterior. On both mandibles the 4th is the largest tooth. 4th and 5th teeth are placed higher on the jaw, in relation to other teeth. The teeth are not of uniform size. 1st, 4th, 11th teeth are larger in than other teeth.
The width of the jaw at the level of the 4th mandibular tooth is approx. 145 mm.
The mandibular bones are slender, flat and laterally compressed.
The interdental space beween the two front teeth is approx. 7 mm (between the rims of the two alveoles), between 2nd and 3rd teeth it is 19 mm and between 8th and 9th teeth it is 21 mm.
The preserved specimen is approx. 280 mm long. The total length of the skull (estimated from the preserved part of mandibles) should be approx. 475 mm.
The shape of the mandible is triangular and it takes sharp curve anteriorly, from the 4th mandibular teeth.

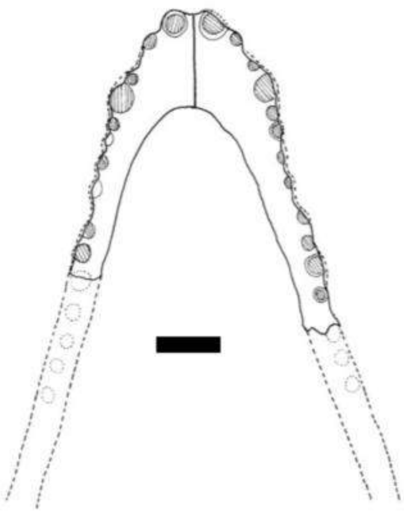


Fig. 9. Reconstructed occlusal view of posterior broken mandibles of *Crocodylus palustris*, SFP-201. Scale = 5 cm

Position of tooth (reconstructed

	ADA (in mm)	ADB (in mm)	IAL (in mm)
RMD1	25	23	10 (1st – 2nd RMD)
RMD2	14	12	14 (2nd – 3rd RMD)
RMD3	15	11	03 (3rd – 4th RMD)

RMD4	26	28	03 (4th – 5th RMD)
RMD5	13	16	02 (5th – 6th RMD)
RMD6	14	13	06 (6th – 7th RMD)
RMD7	13	13	04 (7th – 8th RMD)
RMD8	14	13	21 (8th – 9th RMD)
RMD9	15	13	06 (9th – 10th RMD)
RMD10	16	14	03 (10th – 11th RMD)
RMD11	19	14	06 (11th – 12th RMD)
RMD12	16	14	
LMD1	28	26	10 (1st – 2nd LMD)
LMD2	16	12	19 (2nd – 3rd LMD)
LMD3	14	14	03 (3rd – 4th LMD)
LMD4	23	24	02 (4th – 5th LMD)
LMD5	12	13	02 (5th – 6th LMD)
LMD6	13	12	05 (6th – 7th LMD)
LMD7	13	11	08 (7th – 8th LMD)
LMD8	14	12	21 (8th – 9th LMD)
LMD9	12	11	03 (9th –10th LMD)
LMD10	13	13	

Material: Fragmented part of cranium (WIF/A 463) with partly preserved pre-maxillary and maxillary. The material is catalogued in the Museum of Wadia Institute of Himalayan Geology, Dehradun and was earlier described by NANDA & SCHLEICH (2002)
(Plate 4, fig. 2 & 3 & Text fig. 10 & 11)

Locality: 0.5 km north of Khetpurali Village (Ambala), Pre-Pinjor beds (= Tatrot Formation)

Description

Two specimens are catalogued under the number WIF/A 463. For convenience we describe them as WIF/A 463 (a) and WIF/A 463 (b).

The specimen WIF/A 463 (a) is consiting of an anterior fragmented part of snout with a part of right premaxillary and maxillary. The total length of the preserved specimen is 185 mm. A deep constriction between the premaxillry and maxillary is clearly seen. The total length of the individual should be approx. 4-5 meter (based on the reconstruction of the cranium). The dorsal surface is highly pitted. Three alveoles for the premaxillary teeth and 7 alveoles for the maxillary teeth are preserved on the specimen. The alveoles are mostly rounded. On the basis of the reconstruction it is inferred that premaxillary contains 5 pairs of teeth (4th is the largest) and maxillary contains 14 pairs of teeth. The interdental pits are distinct.
The specimen WIF/A 463 (b) is consisting of alveoles for two premaxillary teeth (3rd and 4th) and 7 maxillary teeth (1st – 7th). The 3rd is the largest premaxillary and the 5th is the largest maxillary tooth. The teeth bases are present in all the alveoles excepting the 7th alveole. The alveoles are

rounded. A small part of maxillo-premaxillary suture is distinct which has been restored in the text fig. 11. The interdental distances ranges between 2 – 5 mm. The alveolar dimension suggest that the specimen is very close to the living *Crocodylus palustris*.

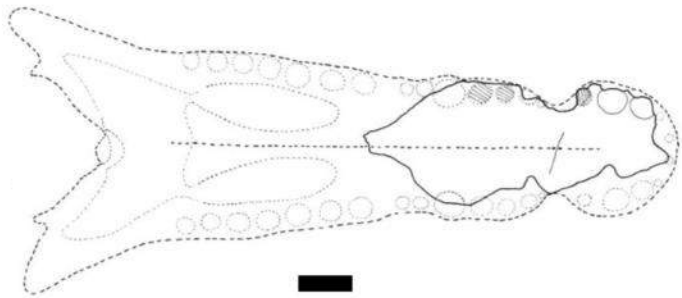


Fig. 10. Reconstructed ventral view of right rostrum of *Crocodylus palustris*, WIF/A 463 (Scale = 4 cm).

Position of tooth (reconstructed)

	ADA (in mm)	ADB (in mm)	IAL (in mm)
RPM3	15	12	05 (3rd – 4th RPM)
RPM4	18	15	05 (4th – 5th RPM)
RM3	11	07	04 (2nd – 3rd RM)
RM4	17	11	05 (3rd – 4th RM)
RM5	20	18	06 (4th – 5th RM)
RM6	12	09	05 (5th – 6th RM)
RM7	09	05	

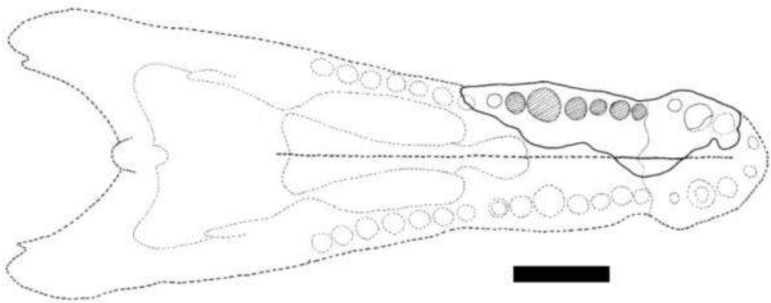


Fig. 11. Reconstructed ventral view of right maxillo-premaxillary part of rostrum of *Crocodylus palustris*, WIF/A 463 (Scale = 6 cm).

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
RPM3	13	11	4 (3rd – 4th RPM)
RPM4	17	17	5 (4th – 5th RPM)
RPM5	09	08	2 (1st – 2nd RM)
RRM1	08	08	3 (2nd – 3rd RM)
RM2	10	10	2 (3rd – 4th RM)
RM3	09	09	3 (4th – 5th RM)
RM4	15	15	2 (5th – 6th RM)
RM5	22	22	5 (6th – 7th RM)
RM6	11	11	10 (7th – 8th RM)
RM7	08	08	

Material: **Fragmentary osteoscutes** (NHM/TU 1989 & 1989/30). The material is catalogued in the Natural History Museum of Tribhuvan University, Kathmandu, Nepal.
(Plate 5, figs. 1 & 2)

Locality: Surai Khola, Upper Siwaliks.

Description

The osteoscute (NHM/TU 1989; cast: BSP 1989 XVIII 13) shows a grooved surface. The grooves are elongated. A median keel is indistinct probably due to the poor preservation. The length of the scute is approx. 6.4 cm and the width is approx. 4.6 cm.

Another osteoscute (NHM/TU 1989/30; cast: BSP 1989XVIII 12) shows the similar grooved surface, however, they are rather shallow. The osteoscute looks squarer with a prominent keel. The maximum length of the scute is about 8.0 cm.

Crocodylus cf. *palustris* LESSON, 1831

Material: Anterior portion of the snout (E-34), catalogued in the Indian Museum, Kolkata.
(Plate 5, fig. 3 & Text fig. 12)

Locality: Burma (LYDEKKER, 1886)

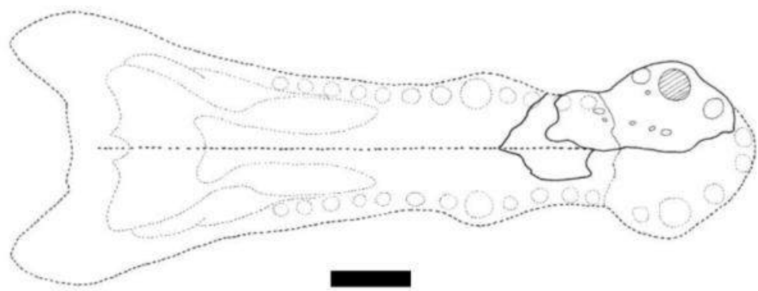


Fig. 12. Reconstructed ventral view of a right maxillo-premaxillary of *Crocodylus palustris*, E-34 (Scale = 5cm).

Description

The specimen is consisting of the right maxillo-premaxillary part of the snout. Anterior the specimen is broken beyond the 2nd premaxillary tooth and posterior it is broken beyond the 3rd maxillary tooth. On the specimen alveoles only for the three premaxillary teeth (2nd – 4th) are distinct; the tooth base is present in the 3rd tooth. The part containing 1-3 maxillary teeth is considerably damaged so that the alveoles are not distinct. A reconstruction suggests that premaxillary contains 4 teeth (3rd largest) and maxillary contains 14 teeth (5th largest). The alveoles for the attachment of the teeth are deep. The reconstructed length of the cranium is approx. 440 mm. The interdental pits are distinct.

The dimension taken on the alveoles are as follows:

Position of tooth (reconstructed; in mm)

	ADA	ADB	IAL
RPM2	13.5	12	10.5 (2nd – 3rd RPM)
RPM3	19.5	19.5	04.5 (3rd – 4th RPM)
RPM4	10.5	10.5	

Remarks:
The only locality information of the material available is 'Burma'. Precise age and horizon of the specimen is not known.

Material: Two specimens of the symphysial extremity of the mandible (E42). The material is catalogued in the Indian Museum, Kolkata. The larger specimen was described by LYDEKKER (1886).
(Plate 5, figs, 4 & 5, Text figs. 13 & 14)

Locality: Siwaliks of Punjab (LYDEKKER, 1886)

Description

In this work, for identification, the larger specimen is being mentioned as E-42 (a) and the smaller one as E-42 (b). Both the specimens represent left anterior part of the mandible.

In the smaller specimen E-42 (a), 7 alveoles are distinct for the attachment of 1st – 7th mandibular teeth. The 1st and 7th alveoles are incomplete. The alveoles are deep and rounded. In the 4th alveole the tooth base is distinct. The interdental pits are very prominent and deep. The median suture is well marked. A reconstruction suggests that the 4th is the largest alveole followed by the 1st. The dimensions of the alveoles and the interdental space is in accordance with those of the living *C. palustris*.
On the basis of reconstruction, the total width of the mandible at the level of the 4th mandibular tooth is approx. 82 mm.

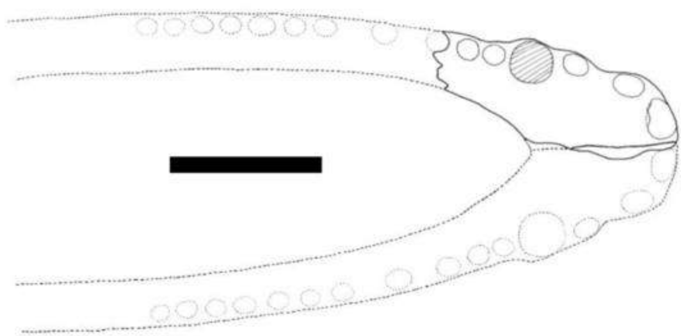


Fig. 13. Reconstructed occlusal view of left mandible, E-42 (a) (Scale = 5cm).

The dimension taken on the mandible are as follows:

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
LMD1	09.5	14.5	04.0 (1st – 2nd LMD)
LMD2	11.0	08.0	09.0 (2nd – 3rd LMD)
LMD3	08.0	07.5	03.5 (3rd – 4th LMD)
LMD4	14.5	15.0	02.0 (4th – 5th LMD)
LMD5	07.5	07.0	01.5 (5th – 6th LMD)
LMD6	07.5	07.5	02.0 (6th – 7th LMD)
LMD7	08.0	07.5	

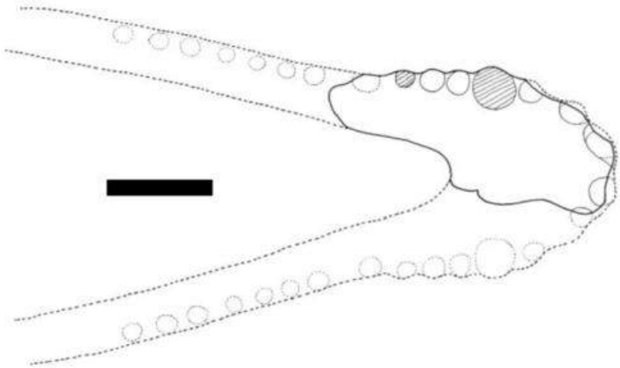


Fig. 14. Reconstructed occlusal view of left mandible, E-42 (b) (Scale = 5cm).

The specimen E-42 (b) is about 25% larger than the specimen E-42 (a). The specimen was figured and described by LYDEKKER (1886) as *Crocodilus sivalensis*. In our opinion, the specimen is very close to the living C. palustris in alveolar diameter and interalveolar distance. The specimen is consisting of 7 alveoles on left side for the attachment of 1- 7 left mandibular teeth, and two broken anterior most alveoles for the attachment of 1 – 2 right mandibular teeth. The alveoles are mostly rounded. The bases of the teeth are preserved for the left 4th and 7th mandibular teeth. The width of the mandible at the level of the 4th mandibular tooth is approx. 105 mm. The dimensions taken on the alveoles are as follows.

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
RMD1	11	12	04 (1st – 2nd RMD)
RMD2	10	09	10 (2nd – 3rd RMD)
LMD3	09	10	03 (3rd – 4th LMD)
LMD4	18	18	02 (4th – 5th LMD)
LMD5	10	10	02 (5th – 6th LMD)
LMD6	11	10	03 (6th – 7th LMD)
LMD7	08	07	

Remarks:
The stratigraphic age of the specimen is not clear as THEOBALD & LYDEKKER (1886) did not mention the precise location in their description. They reported the material as "recovered from the Siwalkis of Punjab".

Material: Complete skull with mandibles and maxillaries (SFP 200), catalogued in the field museum of the Siwalik Fossil Park, Saketi, described by GARG (1988), as *C. sivalensis* or *C. palustris*.
(Plate 6, fig. 1)

Locality: Mandpa Village, Northern extension of Saketi Fossil Park, Saketi, Tatrot Formation, Upper Pliocene.

Description

Complete skull with maxillaries and mandibles is preserved. In general form, the skull is relatively small and narrow. The snout is also narrow and small in comparison to the living *C. palustris*. The upper cranial profile is convex and the maxillo-premaxillary constriction is deep. The external narial aperture is rounded. Due to the intact mandibles, ventral part of the cranium is not visible therefore palatine fenestrae, premaxillary foramen, pterygoid, ecto-pterygoid, palatines etc. are not visible. The orbits are large and oval. The right orbit is larger than the left as seen in the present form of preservation. The occlusal view of the maxillary teeth is not possible. The mandibular teeth are not visible excepting the 4th one (seems to be the largest).
Dorsal surface of the cranium is smooth in comparison to the *living C. palustris* and therefore the lacrymals are faintly seen, they are long and slender (66 mm long) but broader posterior near the orbit. The suture between the right maxilla and the jugal is distinct. The proportion of breadth of the preorbital region to its length is 1:1.5. The snout occupies a greater proportion of the total length of the skull. It expands rapidly back to the level of the 5th maxillary teeth. From 6th - 7th maxillary teeth there is a constriction and then from 8th maxillary teeth to back an expansion of the skull is seen. The cranial table is moderate. The lateral borders of the external narial aperture are less curved than the anterioposterior borders.

The orbits are large and their external borders are nearly straight. The internal borders are however, sharply curved. The space between the orbits (parietal) is almost flat (feebly elevated); it is slightly inclined towards right orbit (probably distorted specimen). It is relatively narrow (27 mm) and deeply pitted.

The supratemporal fenestrae are rather small but the shape is indeterminable. The left supratemporal fenestra is shifted more towards right side. The median area of cranial table separating the two fenestrae, is relatively narrow (12 mm).

The internal narial aperture is somewhat oval with maximum diameter of 8 mm. It faces obliquely downward and backwards. The premaxillary bones are short and broad. Maximum breadth of the snout across the two premaxillaries is at its centre near the second teeth. The length of the premaxillaries along the median line is about 68 mm. The suture along the median line is not distinct. Observations from the lateral side of the skull suggest that each premaxillary on ventral side contains alveoles for five teeth. The 4th is the largest premaxillary tooth. The first pair of the alveoles is not clearly distinct. They are quite close to each other (interdental space is 1.5 mm). 2nd, 3rd, and 4th are at moderate distance from each other (3-4 mm). The distance between the 4th and the 5th premaxillary tooth is the maximum (8 mm). A constriction at the side of the snout after the 4th premaxillary teeth is moderately pronounced. The maxillopremaxillary suture is not very well marked in the present state of preservation. The maxillaries are relatively broad. The interdental space among maxillary teeth is approx. 5 – 7 mm. On viewing from lateral side, 14 pairs of maxillary teeth (5th is the largest one) are distinct. The space between the 7th and the 8th maxillary teeth is maximum (16 mm). The posterior teeth are relatively smaller than the anterior.

The maxillo-nasal suture is approx. 50 mm long. The exact outline of the nasals is uncertain. Nasals are narrow anterior and expand gradually, posterior.

The lacrymals touch anterior the nasal borders and posterior the orbital order. The prefrontal is not well defined. The frontal outline is pentagonal.

Width of the jugals, on the side of the orbits is 26 mm. They are broad in the middle and thinning out, anterior and posterior. A supraoccipital is auricular (diameter is 22 mm). The squamosals are relatively large and are nearly triangular.

Relative size of the skull, the snout, supratemporal fenestrae, orbits and teeth suggest that the preserved specimen most likely belongs to a juvenile individual. As only lateral the view of maxillary teeth is seen, hence correct dimensions of teeth, alveoles and interdental space are not possible.

Remarks:

The described specimen from the Upper Plicocene bed of the Siwalik rocks India, reflects characters similar to *Crocodylus sivalensis* described by LYDEKKER, 1886 and MOOK, 1933. It may be distinguished from the living form by 5 pairs of premaxillary and 14 pairs of maxillary teeth; its wider inter-orbital bar, the longer facial surface of the premaxilla, the greater posterior convexity of the maxillopremaxillary palatal suture, the more rugose facial sculpture, the smaller preorbital nodules, and the wider nasal bones (BADAM, 1973 and STEEL, 1973). As discussed earlier by LYDEKKER (1886) and MOOK (1933) the skull characters of *Crocodylus sivalensis* are very close to the living *Crocodylus palustris*; therefore all the material so far described under the species *Crocodylus sivalensis* may be regarded as Pliocene ancestor of the living *C. palustris*.

Family Gavialidae ADAMS, 1854

The snout is slender, rounded in section, and demarcated from the posterior region of the skull. The maxillaries meeting dorsal and preventing the nasals from reaching the premaxillae or external nares. The supratemporal fenestra is large, the mandibular symphysis is extensive. The teeth are essentially isodont and slender, the upper and lower series interlocking. The dorsal scutes are present but there is no ventral armour. Stratigraphic distribution is hown in Tab.4.

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Primarily piscivorous forms that comprise the living Indian gavial and its fossil relatives. The relatively long hind limbs and extensively webbed feet of *Gavialis* are indicative of its dependence upon water, and it is interesting to note that the Gangetic Dolphin *(Platanista gangetica*) which lives in the same rivers has evolved a similar rostrum containing slender teeth: this evidence of parallelism due to a similar environment and diet may be significant when considering the relationship of the superficially very similar teleosaurs.
LULL (1944) noted that the rostrum tended to become progressively more elongate (from the short muzzle of *G. breviceps* to the slender beak of *G. gangeticus*), with a greater depression in advance of the orbits and a corresponding abruptness of the eye socket's anterior border, while the upward curvature of the rostrum as a whole apparently diminishes during the course of gavialid evolution. The terminal swelling at the rostral extremity seems to be an old-established character, although not all the species display evidence of it.
The earliest recorded occurrence of a true gavial appears to be by the teeth of early Oligocene age from Colombia reported by LANGSTON (1965), but it does not necessarily follow that the subfamily is of neo-tropical origin.

Gavialis OPPEL 1811 (type species *Gavialis gangeticus)*

The snout is narrow and of varying length. The orbits are rounded and directed upwards and forwards, approximately equalling the supratemporal openings in size. The jugal but little sculptured below and behind the short, massive postorbital bar, which rises from the jugal's dorsal margin and is recessed below the skull table at its upper end (STEEL, 1973). The frontal is reaching but failing to enter the supratemporal fenestrae; an occipital plate inclined downwards with a huge nuchal prominence formed partly by the supraoccipital (which extends to the skull table). The palatomaxillary suture is inverted V- shaped with apex far in advance of palatal fenestrae.
Leptorhynchus (no specific name published) was proposed for portions of lower jaw and several vertebrae found on the banks of the Irrawady; MEYER (1832) published the designation *Leptorhynchus cliftii* for this taxon and PICTET (1844) referred to it as *Crocodilus cliftii*.
The snout is very long and slender, at least three times as long as broad at the base. Each side of the jaw bears 27 – 29 teeth. It appears, that *Gavialis* is a surviving member of an early eusuchian radiation and diverged from this lineage before complete verticalisation of the braincase was established (TARSITANO et al., 1989).
The gavialids are characterized by the presence of a bulbous narial and pterygoid bullae (stressed by HECHT & MALONE, 1972). In the living *G. gangeticus* and perhaps in fossil gavials as well, bullae are very developed in large males, but they may occur, if smaller, in females (ANTUNES, 1987). The stratigraphic distribution of gavials in different continents is given in table 4.

Age	Europe	Africa	Asia	North America
Recent - Holocene			*G. gangeticus* *T. schlegeli*	
Pleistocene			*G. gangeticus* *T. machikanense* *G. browni* *G.* aff *gangeticus* *G. gangeticus*	
Pliocene		*T. dowsoni*	cf. *Tomistoma* *G. gangeticus* *G.* aff. *gangeticus* *R. crassidens* *G. browni* *G. curvirostris*	*T. americanus*
Miocene	*T. lusitanica* *T. eggenburgensis* *T. champsoides* *T. calaritanus* *T.* sp.		cf. *R. crassidens* *G. gangeticus* *G.* aff. *browni* *G. curvirostris* var. *gajensis* *G. breviceps*	
Oligocene		*T. tenuirostre*	*T. borisovi*	
Eocene	*G.* cf. *macro-rhynchus dixoni*		*T. gavialoides* *T. cairense* *T. africanum* *T. kerunense*	*T. petrolica* *T. tandoni*

Tab. 4. Stratigraphic distribution of *Gavialis (G), Tomistoma (T), Rhamphosuchus (R)* in various continents (modified after WINDOLF, unpub. work, 1996).

Gavialis gangeticus GMELIN, 1789 *(Lacerta gangetica)*

Holotype: Not located

Type Locality: India

Habitat and Distribution:

The Indian gavial or Nakoo; the spellings gharial, gharrial and ghuryal all derive from the Indian Ghariyal, but modern usage favours the French

corruption gavial which dates from 1789. Generally considered to be the largest living crocodilian, attaining a reported length of over 9 m. Recent of the Indian subcontinent and Burma, frequenting the rivers Indus, Brahmaputra, Irrawaddy, Bhima, Ganges, Mahanadi (Orissa) and Kaladan (Arakan), together with their tributaries; also described from the Siwalik Hills and Perim Island (LYDEKKER, 1888) and questionably reported from the Upper Miocene of Tripura, India (TRIVEDY, 1966).
A timid reptile that is generally not dangerous to man or the larger mammals. Apparently some 40 eggs are deposited in the sand of river banks; the young are very active and possess disproportionately long snouts.

Synonymy:

Gavialis gangeticus Gmelin, 1789 (*Lacerta gangetica*)
Crocodilus gavial Bonnaterre, 1789,
Crocodilus longirostris Schneider, 1801,
Crocodilus arctirostris Daudin, 1803,
Crocodilus tenuirostris Cuvier, 1807,
Gavialis tenuirostris Guerin-Meneville, 1829,
Rhamphostoma tenuirostris Wagler, 1830
Leptorhynchus gangeticus Falconer, 1868
Garialis gangeticus Lydekker, 1888
Garialis gangeticus Dubois, 1892
Gavialis lewisi Lull, 1944
Gavialis gangeticus Trivedy, 1966
Gavialis gangeticus (Steel, 1973)
Gavialidae gen. indet (West & Munthe, 1983)
Gavialis sp. (Munthe et. al., 1983)
Gavialis sp. (Corvinus, 1988)
Gavialis sp. (Gupta & Verma, 1988)
Gavialis sp. indet. (West, et al., 1991)
Gavialidae gen. indet. (Sah, 1992)
Gavialis sp. (Sah, 1992)
Gavialis sp. (Sah & Shreshta, 1992)
Gavialis cf. *gangeticus* (Patnaik & Schleich, 1993)
Gavialis cf. *gangeticus* (Corvinus & Schleich, 1994)

Distinguishing features

The skull table is very wide, a transition from face to rostrum is sharply defined and this character alone distinguishes *Gavialis gangeticus* from other species. The snout shows a slight upward curvature and a distal expansion, a mandibular symphysis extending back to the 23rd or 25th tooth. The orbits are widely separated with prominently everted anterio-lateral rims and a deeply concave frontal bar. The supratemporal fenestrae are relatively large (approx. equal to the eye sockets in size), and broader than long with a narrow parietal bar averaging one-fifth to one-third the inter-orbital width. The palatal openings are wide and broadly rounded at each end; the internal nares without anterior parapet. The quadratojugal ramus of the jugal is

slender with a transversely ovate to square section; the quadratojugal spine exhibits a ridge-like rearward continuation (STEEL, 1973).
A basioccipital with pendulous tuberosities attaining their greatest width ventrally and extending to the level of the pterygoids posterior edge. The axis of the jaw articulation is inclined caudo-medial; the quadrate condyles are broad, flat, indistinctly divided and diagonal orientated. The teeth are weak, obtuse and lateral compressed, with differentiation occurring only anterior (the 2nd premaxillary tooth is relatively small); the teeth count 27-29 in upper jaw and 25-26 in mandible; the tooth diameter equaling or exceeding the interspace. The nuchal and dorsal plates forming a continuous shield consisting of 4 longitudinal rows and 21-22 transverse bands; along the back external to the shield, there is a row of soft plates that are either smooth or only slightly keeled. The toes are well webbed. The upper surface is dark olive in adults; young greyish-brown with irregular dark oblique bands on body and tail. No interdental pits in maxillary.

Material: Dorsal portion of skull, SFP-185. Collection of B. C. VERMA and S. S. GUPTA, catalogued in the Field Museum of the Saketi Fossil Park, Saketi.
(Plate 6, fig. 2 & Text fig. 15)

Locality: Masol village, Dist. Nahan, Saketi Formation (Tatrot Formation), Upper Pliocene

Description

The anterior part of the snout is broken. Total preserved length of the skull from anterior broken end to the posterior end of basioccipital is 317 mm. Snout occupies the greater proportion of the total length of the skull (based on restoration, Text fig. 15), it has slight upward curvature. The cranial table is small. A transition of the rostrum anterior to the orbits is sharply defined. The orbits are large and are sub-rounded. On the specimen the right orbit is complete whereas the left one is incomplete. Anterior and posterior borders of the orbits are more curved than the external borders. The frontal is approx. 50 mm wide having slightly concave and highly pitted surface.

The supratemporal fenestrae are as large as the shape of orbits is, are distorted and unclear. The anterio-lateral margins of supratemporal fenestrae are sharply curved; the posterior margins are nearly straight whereas the lateral margins are moderately curved. The lateral margins of the fenestrae meet sharply and forming diagonal sharp curved anterio-lateral margins. The space between the fenestrae is flat and deeply pitted.
The postorbital area is narrow (12 mm) and raised separating orbits from supratemporal fenestrae. The parietal bar is narrow and deeply pitted. The squamosal is also narrow (6 mm wide) and pitted; the right squamosal is not preserved.

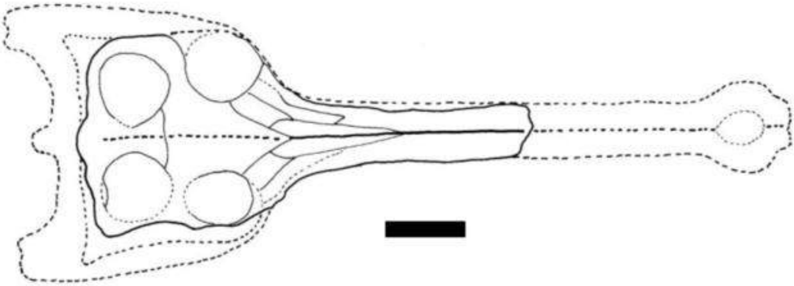


Fig. 15. Reconstructed dorsal view of cranium of *Gavialis gangeticus*, SFP-185 (Scale = 5cm).

The median suture is straight. Nasal outline is clearly distinguishable; the width of the nasals anterior to the prefrontal is approx. 22 mm. The nasals gradually narrow down anterior and join median suture at a distance of approx. 82 mm from the point of its contact with the prefrontal. The length of the prefrontal is approx. 34 mm and at a width of approx. 13 mm. Posterior, the nasals are wedged apart by the anterior process of the prefrontals. The suture between the nasals and the prefrontal is irregular and well marked. The lacrymals are long, slender and well defined and their contact with the nasals is irregular and sutured. The suture between the jugal and the lacrymal is not well defined. The jugals are not distinct. The prefrontal is a paired, irregularly wedge-shaped bone. It is narrow anterior and having maximum width posterior where it forms the anterior border of the orbits. The frontal is almost pentagonal.

The parietal is well marked. It occupies about one third of the posterior border of the cranial table. The supraoccipital is well defined.
The suture between the lacrymal and the maxillary is well marked. Anterior, the maxillary occupies the maximum portion of the snout (between 14 – 18 mm). The maximum width of the snout is near prefrontal (58 mm). On the broken anterior margin, the width of the snout is approx. 35 mm.

Material: Anterior mandibular fragment, SFP 137; catalogued in the Field Museum of the Saketi Fossil Park, Saketi.
(Plate 6, fig. 3 & Plate 7, fig. 1 & Text fig. 16)

Locality: Saketi Fossil Park, Saketi Formation (Tatrot Formation), Upper Pliocene

Description

Anterior part of the mandible is preserved. It is 105 mm long having alveoles for 5 pairs of teeth (3rd – 7th mandibular teeth). The terminal alveoles are incomplete, especially in the left jaw. The teeth bases are distinct in all the right alveoles and 3rd left alveole. The distance between the two successive teeth is approx. 9 mm. Teeth are placed on almost equal distance. From the shape of the alveoles, it can be deciphered that teeth are of nearly equal size; however, size of teeth increases anterior. The maximum diameter of the alveoles is 13 mm and minimum is 7.5 mm. The median suture is distinct. A reconstruction of the mandible suggests a total length of approx. 600 mm.

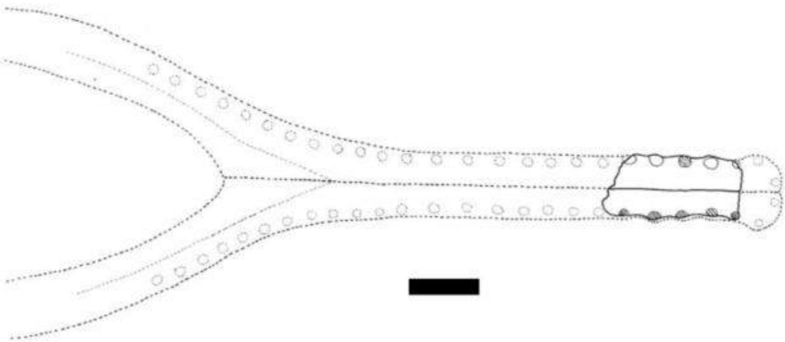


Fig.16. Reconstructed occlusal view of mandibular rostrum of *Gavialis gangeticus*, SFP-137 (Scale = 5cm).

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
RMD3	10.00	06.00	09.00 (3rd – 4th RMD)
RMD4	10.00	10.00	09.00 (4th – 5th RMD)
RMD5	12.00	09.00	09.00 (5th – 6th RMD)
RMD6	11.00	11.00	09.00 (6th – 7th RMD)
RMD7	13.00	12.00	08.00 (7th – 8th RMD)
LMD4	11.00	11.00	09.00 (3rd – 4th LMD)
LMD5	10.00	09.00	07.00 (4th – 5th LMD)
LMD6	09.00	08.00	10.00 (5th – 6th LMD)
Distance between 6th & 7th alveolae			09.00 (6th – 7th LMD)

Material: Posterior part of the mandibular rostrum (E-11), catalogued in the Indian Museum, Kolkata. The specimen was described by LYDEKKER (1886) as *Gharialis leptodus*.
(Plate 7, fig. 2 & Text fig. 17)

Locality: Siwalik Hills Punjab (Middle Siwaliks), Middle Pliocene (LYDEKKER, 1886)

Description

The specimen comprises a middle portion of a mandible containing 16 pair of teeth (8th to 23rd mandibular tooth). The specimen is approx. 318 mm long. In the right jaw, bases of 8th, 20th and 22nd teeth are distinct. In the left jaw, 9th, 11th and 12th teeth/alveoles are indistinct, whereas rest of the alveoles in the left jaw contain their teeth bases; three alveoles equal little less than one-half of the mandibular width. A reconstruction suggests an approximate length of the mandible with approx. 890 mm. The size and spacing of the alveoles are comparable to those of the living *Gavialis gangeticus*. Like the living gavial, the specimen contains 23 teeth in the mandibular symphysis. The median suture on the mandible is clearly distinct. The splenials are also distinctly seen. Anterior, they meet at the median suture at the level of the 18th mandibular teeth. In the living species of *Gavialis gangeticus*, the splenials meet at the median suture at the level of 14th mandibular teeth.

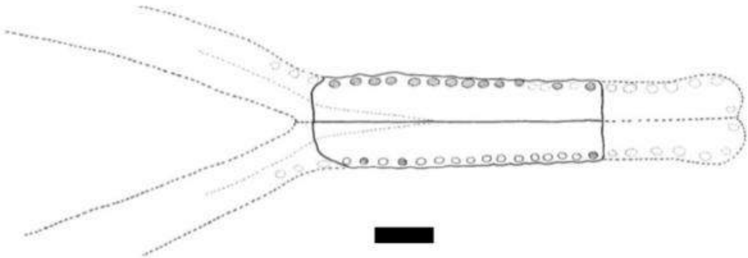


Fig. 17. Reconstructed occlusal view of mandibular rostrum of *Gavialis gangeticus*, E-11 (Scale = 6 cm).

The dimensions taken on the alveoles are as follows:

Position of tooth	ADA (in mm) (reconstructed)	ADB (in mm)	IAL (in mm)
RMD8	9.0	9.0	9.0 (8th – 9th RMD)
RMD9	10.5	9.0	7.0 (9th – 10th RMD)
RMD10	9.0	9.0	7.0 (10th – 11th RMD)
RMD11	8.5	8.5	7.0 (11th – 12th RMD)
RMD12	9.5	9.0	9.0 (12th – 13th RMD)
RMD13	9.0	9.5	7.0 (13th – 14th RMD)
RMD14	10.5	10	8.0 (14th – 15th RMD)
RMD15	9.5	9.0	9.0 (15th – 16th RMD)
RMD16	9.0	9.5	10 (16th – 17th RMD)

RMD17	10	10	8.0 (17th – 18th RMD)
RMD18	9.5	9.0	7.0 (18th – 19th RMD)
RMD19	9.5	9.0	8.0 (19th – 20th RMD)
RMD20	8.5	9.0	9.0 (20th – 21st RMD)
RMD21	9.0	9.5	10 (21st – 22nd RMD)
RMD22	10.5	10	12 (22nd – 23rd RMD)
RMD23	10	10	
LMD8	9.0	9.0	
LMD10	9.0	9.0	
LMD13	9.5	9.0	9.0 (13th – 14th LMD)
LMD14	9.0	9.5	7.0 (14th – 15th LMD)
LMD15	10.5	10	8.0 (15th – 16th LMD)
LMD16	9.5	9.0	8.0 (16th – 17th LMD)
LMD17	9.0	9.5	7.0 (17th – 18th LMD)
LMD18	10	10	9.0 (18th – 19th LMD)
LMD19	9.5	9.0	10 (19th – 20th LMD)
LMD20	8.5	9.0	11 (20th – 21st LMD)
LMD21	9.0	9.5	11 (21st – 22nd LMD)
LMD22	10.5	10	12 (22nd – 23rd LMD)
LMD23	10	10	

Remarks:
From the above it is clear that the specimen can easily be categorized as *Gavialis gangeticus*. Based on the position of splenials (meeting anterior at the level of 17th mandibular teeth in the present specimen and at the level of 14th mandibular teeth in the living gavial), the specimen cannot be classified under a different species as done earlier by LYDEKKER (1886).

Material: Cast of the posterior portion of a cranium (E-22) catalogued in the Indian Museum Kolkata. The original is catalogued in the British Museum (Natural History), London (BMNH-36727)
(Plate 7, fig. 3 & Plate 8 fig. 1 & Text fig. 18)

Locality: Pliocene of the Siwalik hills, India (LYDEKKER, 1888).

Description

The specimen (280 mm long) consists of a posterior region of the cranium of a young individual. A small portion of the splenials is also preserved on the ventral side of the cranium. On the dorsal side of the specimen, the suture between the frontal and the prefrontals is clearly distinct. The prefrontal is narrow and elongated; the length of the prefrontal is approx. 33 mm at a width of approx. 12 mm and similar to the living gavial. The suture between the nasal

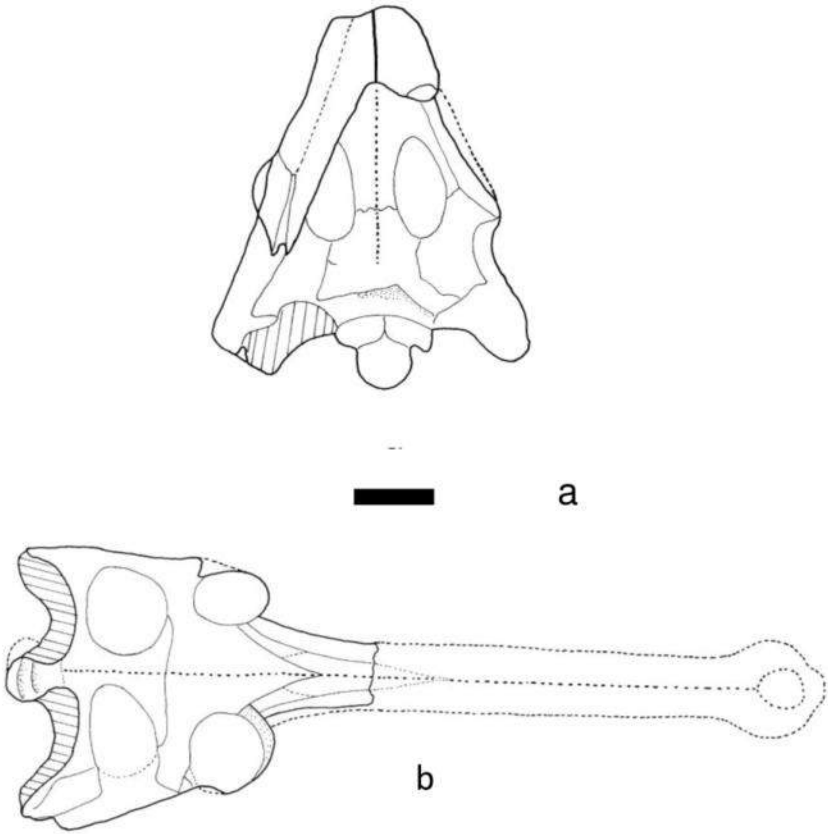


Fig. 18. *Gavialis gangeticus*, BMNH-36727. (a) ventral view and (b) reconstructed dorsal view of skull (scale = 5 cm).

and the prefrontal is very faintly seen; the width of the nasal anterior to the prefrontal is approx. 33 mm. The orbits are sub-rounded; they are widely separated with a concave frontal having everted lateral margins towards the orbits. The anterioposterior diameter of the orbits is approx. 57 mm. The frontal and parietal region is highly pitted. The width of the parietal bar between the supratemporal fenestrae is about 1/3 the width of the interorbital bar. The length of the parietal bar is approx. 78 mm. The supratemporal fenestrae are large (anterioposterior diameter 59 mm) and equal in size to the orbits. The transverse diameter of the fenestrae (70 mm) is more than their anterioposterior diameter. The skull table is wide and a transition from face to rostrum anterior to orbits is abrupt and sharply defined. The width of the rostrum anterior to orbits is about approx. 78 mm. The total reconstructed length of the cranium should be approx. 630 mm.

On the ventral surface of the specimen, the dental region of the maxillaries is not visible as the portion is covered with the posterior part of the splenials. The palatine fenestrae are distinctly seen. The fenestrae are anterioposterior elongated. Their anterior and posterior margins are rounded; the posterior margin is more rounded than the anterior one. The ratio of its maximum width and maxium length is about 1: 2.4. The pterygoid and the ectopterygoid are distinct. The length of the pterygoid is equal to the length of the palatine fenestrae. The posterior margin of the left and both the margins of the rigth ectopterygoid are not visible. The internal narial aperture is also distinct. The basioccipital is prominent; its transverse diameter is equal to its anterioposterior diameter (33 mm).

Material: Cast of posterior portion of cranium (E- 184) catalogued in the Indian Museum Kolkata. The original is catalogued in the British Museum (Natural History), London (BMNH-40695).
(Plate 8, fig. 2 & Text fig. 19)

Locality: Pliocene rocks of Perim Island, Gujarat (LYDEKKER, 1888).

Description

The specimen (38 mm long) is the posterior region of the cranium of a grown individual. A small portion of the splenials is also preserved on the ventral side of the cranium. On the dorsal side of the specimen, the suture between the frontal and prefrontal is clearly distinct, but between the prefrontal and lacrymal is not distinct. The prefrontal is partly seen which is narrow and elongated and is comparable to that of the living gavial. The nasal borders are distinct. The width of the nasal anterior to the prefrontal is approx. 60 mm. The orbits are subrounded; they are widely separated with a concave frontal having everted lateral margins at the orbital borders. The anterioposterior diameter of the orbits is approx. 98 mm.
The frontal and the parietal are highly pitted. The width of the parietal bar between the supratemporal fenestrae is about 1/5 the width of the interorbital bar. The length of the parietal bar is approx. 128 mm. The supratemporal fenestrae are large (anterioposterior diameter 88 mm) and equal the orbits in size. The transverse diameter of the fenestrae (104 mm) is more than their anterioposterior diameter. The skull table is wide and a transition from face to rostrum anterior to orbits is abrupt and sharply defined. The width of the rostrum anterior to orbits is approx. 140 mm. The total reconstructed length of the cranium should be approx. 960 mm.

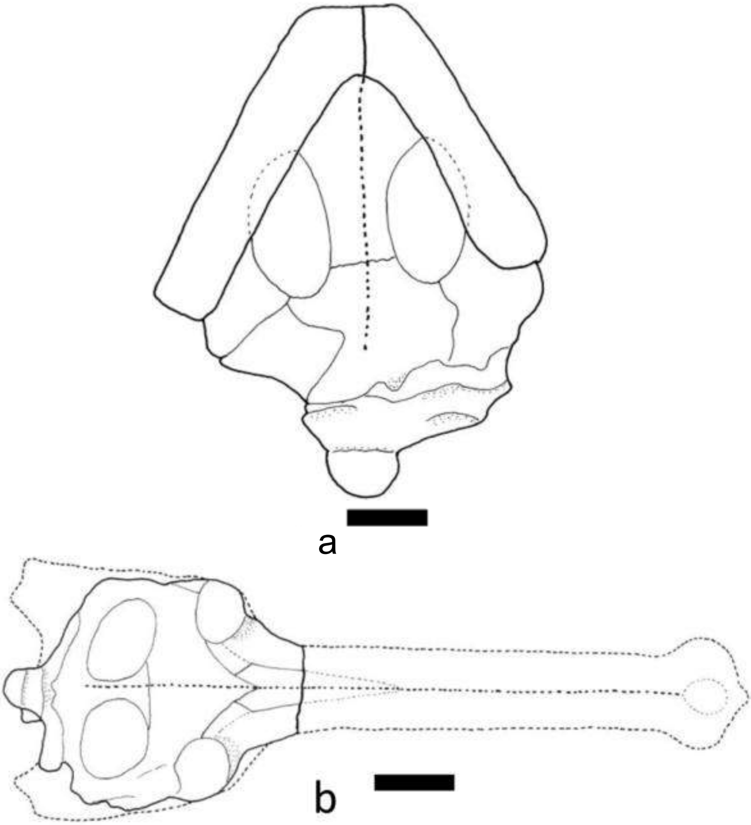


Fig. 19. *Gavialis gangeticus*, BMNH-40695.
(a) Ventral view,
(b) reconstructed dorsal view of skull (Scale = 10 cm).

On the visceral surface of the specimen, the dental region of the maxillaries is not visible. The palatine fenestrae are distinctly seen. The fenestrae are anterioposterior elongated. Their anterior and posterior margins are rounded; the posterior margin is more rounded than the anterior one (based on restoration). The ratio of its maximum width and maximum length is about 1:2. The pterygoid and the ectopterygoid are distinct, but the margins of the ectopterygoid are not distinct. The length of the pterygoid is equal to the length of the palatine fenestrae. The internal narial aperture is also distinct. The basioccipital is prominent; its transverse diameter is equal to its anterioposterior diameter (44 mm).

Material: Posterior portion of the cranium (E-25). The material is catalogued in the Indian Museum, Kolkata.
(Plate 8, fig. 3 & Text fig. 20)

Locality: Pliocene of the Siwalik hills (LYDEKKER, 1886).

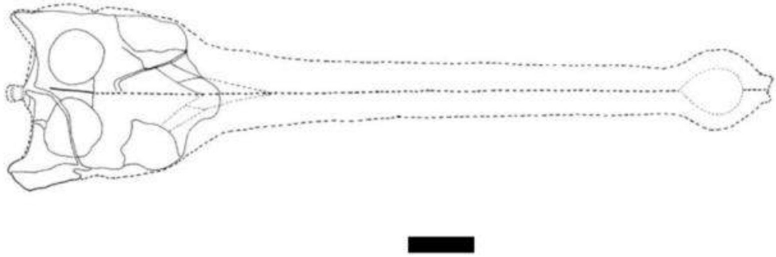


Fig. 20. *Gavialis gangeticus*, E-25, reconstructed dorsal view of cranium (Scale = 6 cm).

Description

The specimen comprises the posterior region of the cranium of an adolescent individual. The specimen is broken anterior to the orbits and posterior to the parietals. The orbits are sub-rounded; they are widely separated with a concave frontal having everted lateral margins at the orbital borders. The anterioposterior diameter of the orbits is approx. 55 mm. The frontal and the parietal region are highly pitted. The width of the parietal bar between the supratemporal fenestrae is about 1/4 the width of the interorbital bar. The length of the parietal bar is approx. 60 mm. The supratemporal fenestrae are large (anterioposterior diameter 57 mm) and equal the orbits in size. The transverse diameter of the fenestrae (62 mm) is more than their anterioposterior diameter. The skull table is wide and a transition from face to rostrum anterior to orbits is abrupt and sharply defined. On the left side margins of the prefrontal are distinct. The size and shape of the prefrontal (35 X 13 mm) is precisely comparable to that of the specimen E-22 and living *G. gangeticus*. The width of the rostrum anterior to orbits is approx. 80 mm (based on reconstruction). The total reconstructed length of the cranium should be approx. 700 mm.

Material: Anteriormost portion of snout (E-14) catalogued in the Indian Museum, Kolkata.
(Plate 9, fig. 1 & Text fig. 21)

Locality: Middle Siwaliks of Kangra District (LYDEKKER, 1886).

Description

The specimen comprises anterior most portion of the snout of a young individual. The specimen contains alveoles for the 6 teeth in the right and 5 teeth in the left jaw. The anterior expansion of the snout at the level of the 2nd tooth is prominent and it is similar to that in the living gavial. The teeth bases in all the alveolies of the right maxilla and 1st, 2nd, 3rd and 5th alveoles in left maxilla are present. A premaxillary foramen is distinct and it is probably very large.

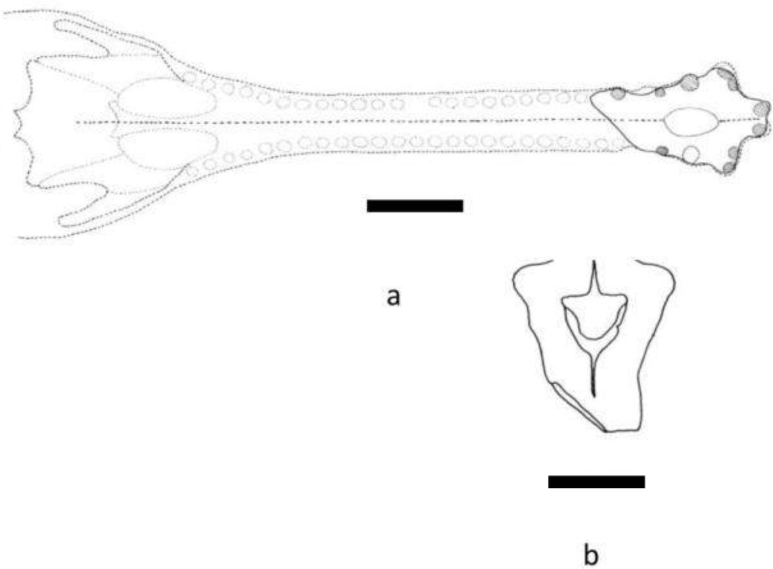


Fig. 21. *Gavialis gangeticus*, E-14. (a) Dorsal view and (b) reconstructed ventral view of cranial rostrum (Scale = 6 cm)

On the dorsal surface of the jaw an external narial aperture is distinct; it has broader and straight anterior margin and narrower but rounded posterior margin. The lateral margins of the external narial aperture are converging posterior.

The total reconstructed length of the cranium should be approx. 53 mm. The width of the snout at the level of the 2nd tooth is approx. 82 mm.

The alveoles are rounded; the 3rd and the 4th alveoles are larger than other alveoles. The dimension taken on the specimen are as follows:

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
RM1	10	10	18.8 (1st –2nd RM)
RM2	6.3	8.8	2.0 (2nd – 3rd RM)
RM3	11.3	10	16 (3rd – 4th RM)
RM4	11.3	11.3	12.5 (4th – 5th RM)
RM5	6.3	6.3	14.5 (5th – 6th RM)
RM6	8.8	8.8	
LM1	7.5	8.8	17.5 (1st – 2nd LM)
LM2	10	8.8	2.5 (2nd – 3rd LM)
LM3	12.5	8.8	18.5 (3rd – 4th LM)
LM4	10	13.8	12.5 (4th – 5th LM)
LM5	6.3	6.3	

Material: Complete mandibular rostrum catalogued in the Indian Museum, Kolkata. (tentative catalogue number IM- 5)
(Plate 9, fig. 2)

Locality: Middle Son Valley, M. P. (Upper Pleistocene)

Description

The preserved specimen is around 120 mm long, containing 26 alveoles; 15 out of these have their respective teeth preserved. The size of mandibles indicates for quite a large size of the animal (approx.11 meters). The length of the jaws is 570 mm. The width of the mandible at the second mandibular teeth is approx. 75 mm. The specimen is quite similar with the mandibles of the living *Gavialis gangeticus*. The splenials are distinctly seen which join at the median suture at the level of the 15th mandibular teeth. The mandibular symphysis extends back to the level of the 23rd mandibular tooth.

Right 7th and left 6th mandibular teeth are complete. The teeth have sharp apex and vertical striations. The posterior teeth are curved posterio- lingual and anterior teeth are curved lingual. Their dimensions fall very much within the range of those of the recent *G. gangeticus*.

Remarks:
We notice that in the present specimen (Upper Pleistocene) the splenials meet at the level of the 15th mandibular teeth; in the previous specimen (Middle Pliocene) they meet at the level of the 17th mandibular teeth and in the living gavial the splenials meet at the level of the 14th mandibular teeth. It might be possible that an increase in the length of the splenials is an evolutionary feature in *Gavialis gangeticus*.

Material: Anterior maxillary part of snout (NHM/TU 1989/28; cast: BSP 1989 XVIII 9). The material is catalogued in the Natural History Museum of Tribhuvan University, Kathmandu, Nepal.
(Plate 9, fig. 3 & Text fig. 22)

Locality: Rato Khola, Upper Siwaliks

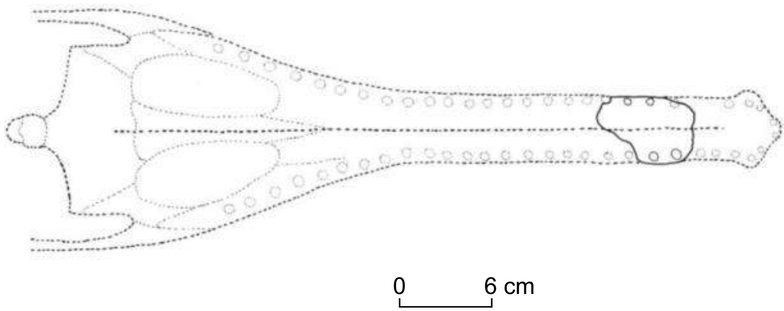


Fig. 22. *Gavialis gangeticus*, NHM/TU 1989/28. Reconstructed ventral view of cranial rostrum

Description

The specimen is represented by the broken anterior part of maxillary. The maximum length of the specimen is approx. 130 mm and the maximum width is about 84 mm. It is quite similar to the snout of the living *Gavialis gangeticus*. The alveolar dimensions taken on the specimen are also comparable to that in the living specimen (15 – 16 mm). The alveoles for 8th and 9th teeth are present (10th is incomplete) on right maxilla and on left maxilla only two alveoles for 7th & 8th teeth are preserved. The distance between two alveoles is about 11 mm and is similar to that in the recent specimen. A reconstructed length of the cranium should be approx. 950 mm.

Gavialis cf. *gangeticus* GMELIN, 1789

Material: Two specimens of the anterior extremities of the mandible (E-20). The material is catalogued in the Indian Museum, Kolkata.
(Plate 9, figs. 4 & Plate 10, fig. 1 & Text figs. 23 & 24)

Locality: Pliocene Siwaliks of Punjab (LYDEKKER, 1886).

Description

Here, we describe the two specimens as E-20 (a) and E-20 (b).

The specimen E-20 (a) consists of an anteriormost extremity of the mandibular symphysis. On the specimen, alveoles for the reception of left 1st –3rd and right 1st mandibular teeth are present. The alveoles are mostly rounded. The width of the mandible at the level of the 2nd mandibular tooth is approx. 114 mm and it is similar to that of the líving *Gavialis gangeticus*. The only clues for the taxonomical identification of the material is the size and shape of the alveoles and the interalveolar distance. The dorsal surface of the mandible is pitted and crenulated. The anterior most end of the mandible is bifurcated. A median suture is distinct. A total reconstructed length of the mandible should be approx. 730 mm.

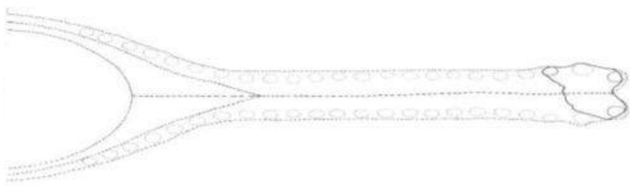


Fig. 23. *Gavialis* cf. *gangeticus*, E-20. Reconstructed occlusal view of mandibles (Scale = 10 cm).

The dimensions taken on the alveoles are:

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
LMD1	16.5	18	16.5 (1st –2nd LMD)
LMD2	20	18	16.5 (2nd – 3rd LMD)
LMD3	13.5	14	
RMD1	18	20	15 (1st – 2nd LMD)

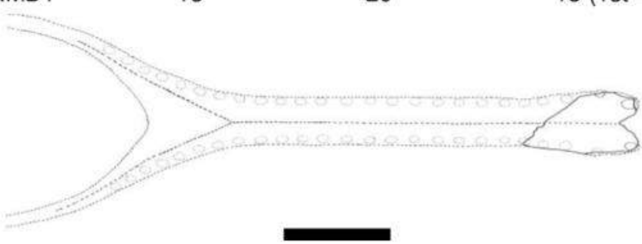


Fig. 24. *Gavialis* cf. *gangeticus*, E-20 (b). Reconstructed occlusal view of mandibles (Scale = 10 cm)

The specimen E-20 (b) shows the anteriormost part of a mandible having alveoles for the reception of right 1st – 4th and left 1st mandibular teeth. The alveoles for the 2nd left and 5th right mandibular teeth are partly preserved; they are rounded. Like the previous specimen, the anterior most end of the mandible is bifurcated. The width of the mandible at the level of the 2nd mandibular tooth is approx. 90 mm, it is little less than that of the living *Gavialis gangeticus*. The dorsal surface of the mandible is highly pitted.

The dimensions taken on the alveoles are:

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
RMD1	10.5	10.5	24 (1st – 2nd RMD)
RMD2	9.0	10.5	19.5 (2nd – 3rd RMD)
RMD3	10.5	10.5	10.5 (3rd – 4th RMD)
RMD4	9.0	10.5	7.5 (4th – 5th RMD)
RMD5	10.5	9.0	
LMD1	13.5	12	19.5 (1st-2nd LMD)
LMD2	10.5	9.0	

Material: Posterior portion of snout (WIF/A 461), catalogued in the Museum of Wadia Institute of Himalayan Geology, Dehradun.
(Plate 10, fig. 2 & Text fig. 25)

Locality: 2 km north of Taprian Village (Ambala), Basal part of Pinjor Formation.

Description

The preserved part of left maxilla contains alveoles for the 6 posterior teeth. The anterior most alveole is incomplete. The size of alveoles is almost equal. The alveoles are anterioposterior elongated. The nasal margins are clearly distinct; the width of the nasal anterior to prefrontal is approx. 32 mm; this width is similar to that of the living *G. gangeticus*. The margins of the prefrontals are also clearly marked; they are narrow and elongated; the length of the prefrontal is approx. 34 mm and width is approx. 13. 6 mm. The lacrymals are also distinct; they are also narrow and elongated, their width is approx. 13.5 mm.

On the ventral side, the anterior part of the left palatine fenestra is preserved. The reconstruction of the cranium suggests a length of the oval shaped palatine fenestrae being approx. 85 mm what is much less than that in the living *Gavialis gangeticus*. The medial suture is well marked. The anterior part of the ectopterygoid is preserved. The diameter of posterior most 4 alveoles ranges between 7 – 9 mm which is similar to the living *Gavialis* *gangeticus*. Dimensions for rest of the alveoles are not possible because of their incomplete margins.

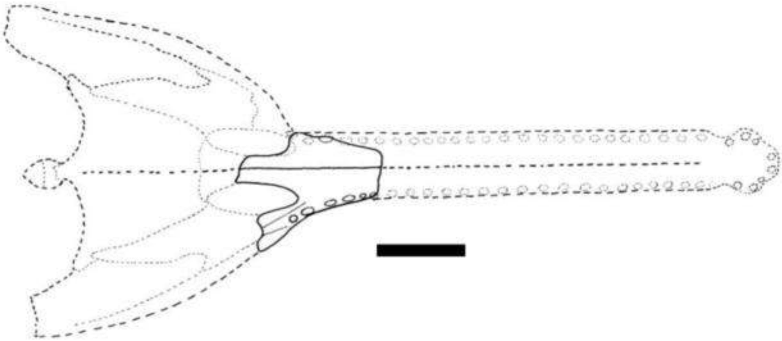


Fig. 25. *Gavialis* cf. *gangeticus*, WIF/A 461. Reconstructed ventral view of cranial rostrum (Scale = 10 cm).

Material: Part of upper cranium with posterior part of maxillary (WIF/A 460), catalogued in the Museum of Wadia Institute of Himalayan Geology, Dehradun. The material was earlier described by NANDA & SCHLEICH (2002). (Plate 10, fig. 3 & Text fig. 26)

Locality: Just north of Khetpurali Scarp (Ambala), pre-Pinjor beds (= Tatrot Formation).

Description

The specimen shows the posterior part of the nasal, its width is approx. 40 mm. Both orbits are preserved; their diameter (anterioposterior) is approx. 85 mm and it is similar to that in living *Gavialis gangeticus* (80 mm). The space between the two orbits is approx. 70 mm which is considerably less than that in living *Gavialis gangeticus* and is closer to that in *Gavialis browni* (75 mm). The interorbital space is slightly concave and its margins with the orbits are raised. The margins of the prefrontal are distinct; the prefrontal is approx. 42 mm long and 22 mm wide. The lacrymals are slightly stout and large; they are 113 mm long and 36 mm wide. The anterioposterior diameter of the supratemporal fenestrae is approx. 68 mm; in the living *Gavialis gangeticus* this is approx. 75 mm and in *Gavialis browni* it is approx. 55 mm. The alveoles for the 8 left maxillary teeth and 6 right maxillary teeth are preserved; they are almost of equal diameter. The diameter of all the alveoles ranges between 15 – 18 mm. The inter-alveoler space ranges between 4 – 10 mm. These dimensions are comparable to that of living

Gavialis gangeticus. The palatine fenestrae are oval; their anterioposterior diameter is approx. 100 mm. The space between the two supratemporal fenestrae is approx. 40 mm and is comparable to that in the living *Gavialis gangeticus*. The inter-orbital space and the space between the two supratemporal fenestrae is highly pitted.

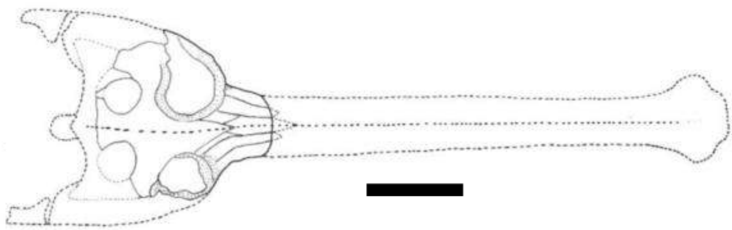


Fig. 26. *Gavialis* cf. *gangeticus*, WIF/A 460. Reconstructed dorsal view of cranium (Scale = 10 cm).

The anterior margin of the ectopterygoid reaches upto the last maxillary teeth. The posterior margin of the ectopterygoid reaches almost two-third the length of the pterygoid. This situation is comparable to that in the living *Gavialis gangeticus*. The suture between the pterygoid and the palatine and between the ectopterygoid and pterygoid is distinct. The anterioposterior length of the pterygoid is approx. 80 mm.

Material: Part of upper cranium, WIF/A 459. The specimen is catalogued in the Museum of Wadia Institute of Himalayan Geology, Dehradun.
(Plate 10, fig. 4 & Plate 11, fig. 1 & Text fig. 27)

Locality: About 2.5 km NE of Rampur Village (Ambala), Pinjor Formation.

Description

The specimen contains upper part of the cranium. The left supratemporal fenestra is well preserved; it is rounded and has a diameter of approx. 40 mm; the right fenestra is incomplete. The suture between the prefrontals and frontal is distinct; the anterior part of the prefrontals is broken. A large basioccipital is seen distinctly. A space between the two supratemporal fenestrae is approx. 23 mm (in living *Gavialis gangeticus* the space is approx. 35 mm). The suture between the parietal and the frontal is distinct. The width of the parietal bar is approx. 1/3 the width of the frontal bar. The foramen magnum is also distinct. A pterygoid comparable to that of *G. gangeticus* is present; the left ectopterygoid is distinct.

The orbits are not preserved but inner margins of the orbits and the frontal are preserved. The width of frontal between the two orbits is approx. 75 mm.

The anterio-posterior length of post-orbital is around 34 mm (in living *Gavialis gangeticus* the length is approx. 50 mm). The posterior part of palatine is seen.

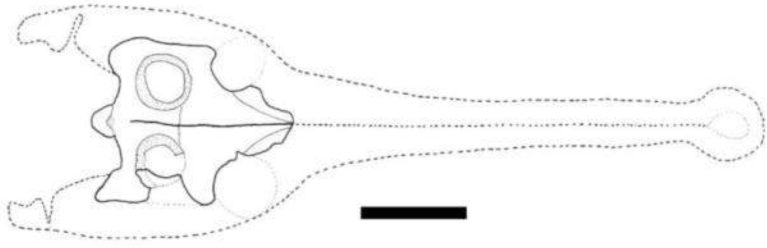


Fig. 27. *Gavialis* cf. *gangeticus*, WIF/A 459. Reconstructed dorsal view of cranium (Scale = 10 cm).

Comment on *Gavialis lewisi* (LULL, 1944) (= *Gavialis* cf. *gangeticus)*

The specimen described by LULL (1944) as *Gavialis lewisi* (Text fig. 28) is an advanced gavialid and shows characters very much close to *Gavialis gangeticus* (LANGSTON, 1965; BUFFETAUT, 1978; NORELL & STORRS, 1989) like large circular orbits with everted borders, maxillary lacking interdental pits, large supratemporal fenestrae etc; however, the interdental spacing in LULLS specimen is more than that in the living *Gavialis gangeticus*. A decrease in interdental spacing has been considered an evolutionary feature (MOOK, 1932 and BADAM, 1974) seen in the living *Gavialis gangeticus*. A greater interdental space in the LULL' s specimen may be regarded as a generalised feature. Therefore, we prefer to consider *Gavialis lewisii* LULL very close to *Gavialis gangeticus* and may be regarded as Pliocene ancestor of the living *Gavialis gangeticus*.

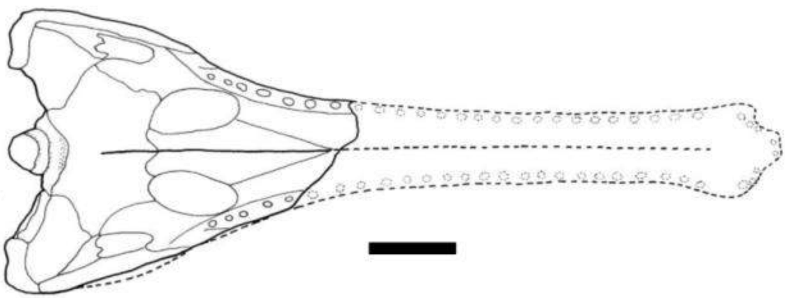


Fig. 28. Reconstructed ventral view of *Gavialis* cf. *gangeticus* (YPM-3226). The material was earlier described by LULL (1944) as *Gavialis lewisi*. Scale = 10 cm.

The consideration of the presence or absence of interdental pits in the maxillary for the reception of the mandibular teeth (LYDEKKER, 1886) seems to be valid to classify the gavials into two groups. Group A, in which the pits are absent includes *G. gangeticus* and *G. browni* Group B, in which pits are present includes *G. curvirostris, G. curvirostris gajensis* and *G. breviceps.*

The gavials from the Indian Subcontinent have a long geological history (Lower Miocene – Recent) and are represented by a number of species which give evidence of many changes in the Genus *Gavialis* through time. An elongation of the rostrum through time is of prime importance (LULL, 1944); gavials exhibit a short rostrum as evident in the species *G. curvirostris* and *G. breviceps* upto Lower Pliocene time; whereas, from Lower Pliocene to Recent an elongation of the rostrum is documented in the species *G. browni* and *G. gangeticus.*

The presence of the interdental pits for the reception of the apices of the mandibular teeth also seems to be a primitive feature (LULL, 1944) which gradually vanishes in the species after Lower Pliocene.

A decrease in the upward curvature of the rostrum may also be regarded as an evolutionary feature however, it is impossible to determine this for the species *G. breviceps* owing an incomplete rostrum. The curvature is prominently marked in the Miocene species of *G. curvirostris* especially in the subspecies *gajensis* (LULL, 1944). The curvature of rostrum was very less (almost flat) in Upper Pliocene species of gavials having close affinity with the living *Gavialis gangeticus* (probably the Upper Pliocene ancestors of the living *Gavialis gangeticus*). A detailed character comparison of various Siwalik species of *Crocodylus* and *Gavialis* is given in table 6 & 7.

Remarks:
Other referable material includes an imperfect cranial rostrum and lower jaw (lacking the distal extremities) what was figured by FALCONER & CAUTLEY (1868), and FALCONER (1868) as *Crocodilus leptodus* and by STEEL (1973) as *Gavialis leptodus* catalogued in the Natural History Museum, London (catalogue number 39806). Also referable are the posterior portion of a mandibular symphysis, the hinder region of an adult cranium, and the posterior of an immature cranium.
Described by FALCONER (1868) as *Crocodilus leptodus* and by LYDEKKER, (1886) and STEEL (1973) as *Gavialis* (= *Gharialis*) *hysudricus*, catalogued in the Indian Museum Kolkata and the Natural History Museum, London (catalogue number 39805, 39808, R-325 and R-326). This complete material has been recovered from the Pliocene of the Siwalik hills of India (LYDEKKER, 1888).
The upper teeth in the above referred material numbering 22 and agreeing in size and spacing with those of *G. gangeticus* (three alveoles ar equal one-third to one-half the rostral width). The interdental pits are absent. The rostrum is concave anterior to the orbits. The orbits are closely placed. The supratemporal fenestrae are relatively smaller and broader than long, with an

intervening parietal bar that is more than half the width of the inter-orbital frontal plate. The anterior border of the orbits is prominent and thickened and the jugal-quadratojugal region is greatly expanded.

The age consideration of the material described above is doubtful due to lack of precise locality information. The age Middle Pliocene to Upper Pliocene for all the material has been suggested by the associated mammalian faunal content described by LYDEKKER (FALCONER, 1868, FALCONER & CAUTLEY, 1868 and LYDEKKER, 1886, 1888)
The specimen described above and other referred specimens are very close to the living *Gavialis gangeticus*; however, the width of the parietal and the jugal-quadratojugal region (in specimen BMNH 39805) is much more and the width of frontal is much less than in the living *Gavialis gangeticus*. The number of the upper teeth is much less than that in the living *Gavialis gangeticus*. An increase in the number of teeth has been regarded as an evolutionary feature by MOOK (1932), LULL, (1944) and by BADAM (1974) in light of this the specimen may be regarded to be very close to an Upper Pliocene ancestor of the living *Gavialis gangeticus*. The specimen 39806 catalogued in the British Museum described as *Gharialis leptodus* possesses no interdental pits whereas STEEL (1973) described it possessing interdental pits.

Gavialis browni MOOK, 1932

Holotype: AM 6279, catalogued in the American Museum of Natural History, New York.

Type Locality: One mile south of Nathot, India; Lower part of the Middle Siwaliks; Lower Pliocene (MOOK, 1932)

Synonymy:
Garialis gangeticus (in part) Lydekker, 1885
Gavialis browni, Mook, 1932
Gavialis browni (Colbert, 1938)
Gavialis browni (Romer, 1956)
Gavialis browni (Steel, 1973)
Gavialis browni (Badam, 1974)
cf. *Tomistoma* (West, et al., 1991)

Distinguishing features
Skull massive, with no apparent abrupt depression in front of the eye sockets (although some post-mortem crushing may have obscured this feature in the type specimen). Teeth are strong and set relatively wide apart, 3 alveoli are equal about three-quarters of the rostral width; interdental pits absent, upper tooth count approximately 20. Orbits relatively close together, with no prominent eversion of the anterior border.

The supratemporal fenestrae are large (equal to the orbits in size) and wider than long, the frontal bar is almost twice the width of the parietal bar. The palatal vacuities are narrow and elongate, with parallel inner margins. The skull is gavialoid but more massive in construction than it is usual in *Gavialis gangeticus*; supraoccipital bone absent on the dorsal surface of the skull; the nasal bones are relatively long and narrow (after MOOK, 1932; STEEL, 1973 and BADAM, 1974).

G. browni differs from *G. leptodus*, *G. curvirostris*, and *G. breviceps* in having the teeth or their alveoli, farther apart in proportion to the breadth of the snout.

In the living gharial, *G. gangeticus*, the distance from the anterior ends of the palatine fenestrae forward to the junction of the two maxillo-palatine sutures at the median line, measured along the median line is considerably less than the breadth of the snout at this junction, whereas in *G. browni*, this distance along the median line is considerably greater than the breadth of the snout.

The palatine fenestrae of *G. browni* are much longer and relatively much narrower than in *G. gangeticus*. Further, in *G. browni*, the length of either fenestra is about one and one-third times the length of the pterygoids whereas in *G. gangeticus* the fenestrae are equal in length to the pterygoids.

Dimensions of *G. browni* (AM 6279, holotype) described by MOOK (1932).

MW (taken across the medial suture, on the junction of the two maxillae - palatine sutures): 82.50 mm

The dimensions are based on the reconstruction of the skull made by MOOK (1932).

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
RM3	11.00	10.00	09.00 (3rd – 4th RM)
RM4	11.00	10.00	15.00 (4th –5th RM)
RM5	11.50	10.50	15.00 (5th –6th RM)
RM6	10.00	09.50	12.50 (6th –7th RM)
RM7	12.50	11.50	11.50 (7th – 8th RM)
RM8	10.00	11.50	10.00 (8th – 9th RM)
RM9	10.00	10.00	10.50 (9th –10th RM)
RM10	10.00	10.00	13.50 (10th –11th RM)
RM11	10.00	10.00	12.50 (11th –12th RM)
RM12	10.00	09.50	12.50 (12th –13th RM)

Material: Part of a Maxillary. WIF/A 458, catalogued in the Museum of Wadia Institute of Himalayan Geology, Dehradun. The material was earlier described by NANDA & SCHLEICH (2005) as cf. *Gavialis gangeticus*.
(Plate 11, fig. 2 & Text fig. 29)

Locality: 2.5 km NE of Rampur Village (Ambala), Pinjor Formation (Lower Pleistocene).

Description

The preserved specimen belongs to the posterior part of the maxillary which is much more massive than in the living gavial. The maximum length of the preserved specimen is approx. 158 mm and maximum width is approx. 95 mm.

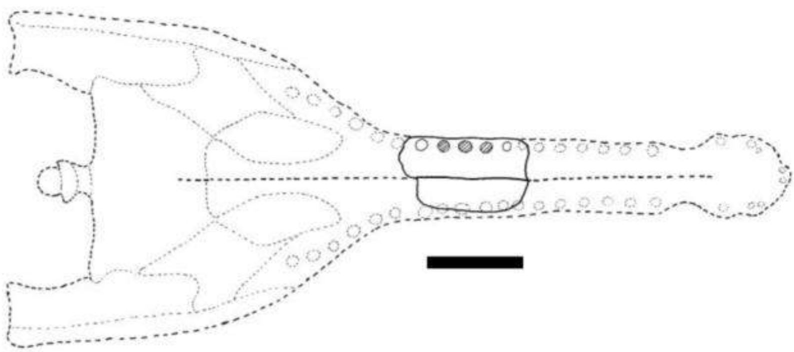


Fig. 29. Reconstructed ventral view of cranial rostrum of *Gavialis browni*, WIF/A 458 (Scale = 5 cm).

The snout of the specimen WIF/A 4 is thicker than *G. browni* described by MOOK (1932), but is closer to the specimen CASG A/647 (Text fig. 30) described by BADAM (1974). On the dorsal side, a median line is distinct with two maxillary bones. On the ventral surface of the specimen, five alveoles are distinct for the right maxillary teeth. The alveoles are of almost identical size. The alveoles are large and placed farther apart in proportion the breath of the snout and therefore the specimen differs from *G. gangeticus*, *G. leptodus*, *G. breviceps* and *G. curvirostris*. On the basis of the size of alveoles and interdental space, the specimen may be classified under the species *G. browni*.

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
RM8	12	15	17 (8th – 9th RM)
RM9	13	17	13 (9th – 10th RM)
RM10	14	18	15 (10th – 11th RM)
RM11	13	16	16 (11th – 12th RM)
RM12	14	17	

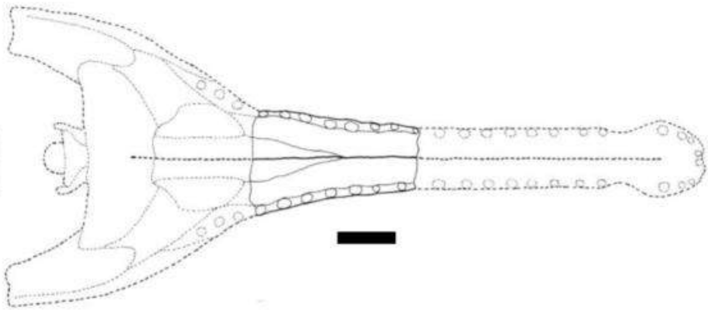


Fig. 30. Reconstructed ventral view of cranial rostrum of *Gavialis browni*, CASG A/647 described by BADAM (1974) (Scale = 6 cm).

Material: Palato-maxillary portion of the snout (E-13). The material is catalogued in the Indian Museum, Kolkata.
(Plate 11, fig. 3 & Text fig. 31)

Locality: Siwalik Hills (Middle Siwaliks).

Description

The specimen is consisting of the posterior part of a maxillary. The alveoles for the reception of 4 teeth (15th –18th maxillary teeth) on the left maxilla are distinct. The teeth bases are present in the anterior two alveoles on the left maxilla. The posterior expansion of the snout after the 15th maxillary teeth is pronounced. On the ventral side, traces of the maxillo-palatine sutures are distinct and they appear to extend to the level of the fifth pair of teeth from behind. Thus, these sutures extend farther forward than in *G. gangeticus*. The distance from the anterior ends of the palatine fenestrae forward to the junction of the two maxillo-palatine sutures measured along the median line, is more than the breadth of the snout at this junction. This distance is less than the breadth of the snout in the living gavial. The inter-alveolar distance in the present specimen is closely comparable to those in the type specimen described by MOOK (1932), however, the size of the alveoles is smaller than those in the type specimen. The palatine fenestrae are not distinct due to surface erosion; however, a reconstruction suggests fenestrae which are elongated with rounded anterior and tapering posterior margins.

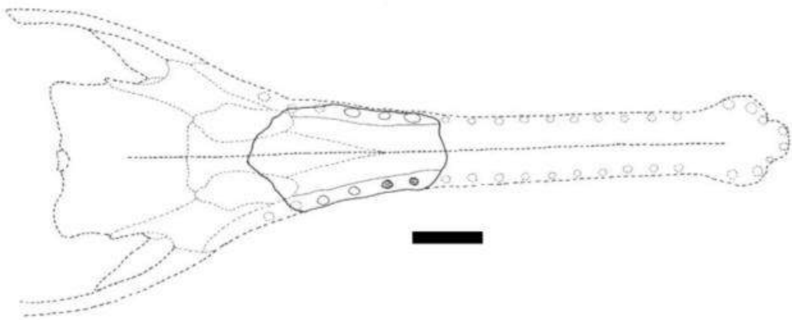


Fig. 31. Reconstructed ventral view of cranial rostrum of *Gavialis browni*, E-13 (Scale = 5 cm).

The dimensions taken on the alveoles are given below:

Position of tooth (reconstructed)

	ADA (in mm)	ADB (in mm)	IAL (in mm)
LM15	5.5	6.3	12.5 (15th – 16th LM)
LM16	7.8	7.0	17.2 (16th – 17th LM)
LM17	7.8	7.0	15.6 (17th – 18th LM)
LM18	7.8	7.0	12.5 (18th – 19th LM)
RM15	9.4	7.8	10.9(15th– 16th RM)
RM16	9.4	7.0	14.1 (16th – 17th RM)
RM17	9.4	7.8	17.2 (17th – 18th RM)

Remarks:

The material was obtained in exchange from Rurki Museum (LYDEKKER, 1886) and gives no precise locality information except its presence in the Middle Siwaliks. The Middle Siwalik ranges from Upper Miocene to Middle Pliocene which could be the range of the age of the present material.

Material: Anterior part of mandibular rostrum (E-24), catalogued in the Indian Museum, Kolkata. The material was earlier described by LYDEKKER (1886) as *Gharialis gangeticus*.
(Plate 11, fig. 4 & Plate 12, fig. 1 & Text fig. 32)

Locality: Perim Island, Gujarat (LYDEKKER, 1886).

Description

The specimen comprises anterior most part of the mandibular rostrum of a young individual. Four pairs of mandibular teeth are visible on the specimen (2nd –5th mandibular teeth). The portion of the 1st mandibular tooth and posterior portion after the 5th pair of mandibular teeth is broken. The median suture is clearly marked on the specimen. The anterior expansion of the mandible at the level of the 2nd mandibular tooth is negligible in comparison to that in the living gavials. In addition to these chracacters, the size of the alveoles and the interalveolar distance place the specimen closer to *Gavialis browni* rather than *Gavialis gangeticus*. The width of the rostrum at the level of the 5th mandibular tooth is approx. 48 mm and the total reconstructed length of the mandible is approx. 400 mm.

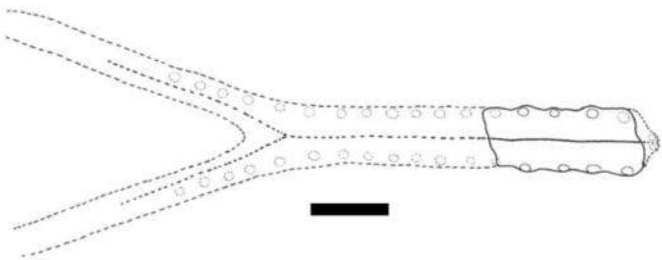


Fig. 32. Reconstructed occlusal view of fragmented mandibular rostrum of *Gavialis browni*, E-24 (Scale = 5 cm).

The dimensions taken on the alveoles are:

Position	of tooth (reconstructed)		
	ADA (in mm)	ADB (in mm)	IAL (in mm)
RMD2	7.5	5.8	13.2 (2nd – 3rd RMD)
RMD3	9.0	5.8	1.7 (3rd – 4th RMD)
RMD4	6.6	5.0	18.2 (4th – 5th RMD)
RMD5	8.3	8.3	
LMD2	8.3	6.0	13.2 (2nd – 3rd LMD)
LMD3	8.3	6.0	16.6 (3rd – 4th LMD)
LMD4	6.6	5.0	13.2 (4th – 5th LMD)
LMD5	6.6	5.0	

Gavialis curvirostris LYDEKKER, 1886

Holotype: E-26, An incomplete cranium (in two fragments), catalogued in the Indian Museum, Kolkata.

Type Locality: Laki Hills, Sind, Lower Pliocene (LYDEKKER, 1885).

Synonymy:
Garialis curvirostris Lydekker, 1886
Gavialis curvirostris (Steel, 1973)

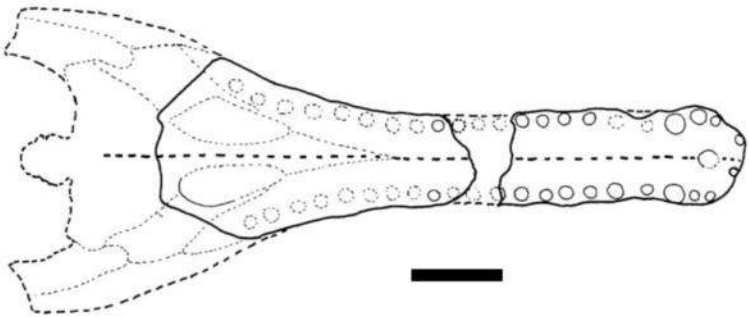


Fig. 33. Reconstructed cranial rostrum of holotype (E-26) of *Gavialis curvirostris*, described by LYDEKKER (1886). Scale = 8 cm.

Distinguishing features

The maximum length of the animal should be approx. 6-7 m. The size and spacing of the teeth is similar to *G. gangeticus*; three alveoli occupy more than half of the rostral width. The interdental pits are mesad of the tooth row. The aleveoles for the teeth are mostly shallow. Twenty-two maxillary teeth can be counted on the specimen (text fig. 33). The interalveolar spaces range between 5-14 mm. No depression of the profile anterior to the orbits is discernable; the rostrum is relatively short and upwards curved, with very little premaxillary expansion. An external narial aperture appears subrounded to rounded. The inter-orbital is highly pitted. The orbits are sub-rounded and have more anterioposterior elongation than lateral. The lacrymals are slender and smaller than that of *G. gangeticus*. The palatine fenestrae are narrow and elongate (based on the reconstruction of holotype, Text fig. 33).

Material: Anterior part of maxillary (E-16) catalogued in the Indian Museum, Kolkata.
(Plate 12, fig. 2 & Text fig. 34)

Locality: Laki, Siwalik Hill, Sind, Lower Pliocene

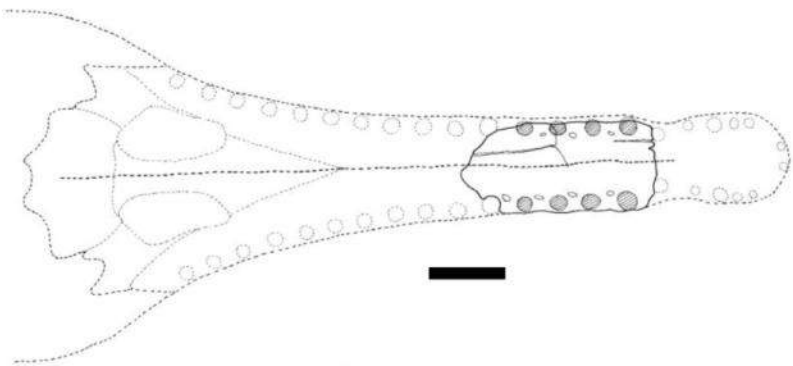


Fig. 34. Reconstructed cranial rostrum of *Gavialis curvirostris*, E-16. (Scale = 5 cm).

Description

The material is an anterior part of the maxillary. The width of the snout at the level of the 10th maxillary teeth is far less (67 mm) than that in the living *Gavialis gangeticus* (85 mm). On the specimen alveoles for the reception of 7th –11th maxillary teeth are preserved. The alveoles are rounded and are placed at a moderate distance from each other. The three alveoles are more than half the rostral width. The inter-alveolar space is not flat but slightly concave. The size of the alveoles and the inter-alveolar distance is larger than that in the living *Gavialis gangeticus*. On the left maxilla 5 alveoles (posterior most is incomplete) and on the right maxilla 4 alveoles are present. Except the posterior most alveole on the left maxilla, the teeth bases are present in all the alveoles. The interdental pits are present, mesad of the tooth row. A median suture is well preserved. A reconstruction suggests a very small premaxillary expansion compared to *Gavialis gangeticus* in which it is more pronounced. The suture between the palatine and maxillaries is faintly distinct.

The measurements taken on the alveoles are as follows:

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
LM7	13	13	13 (7th – 8th LM)
LM8	12.5	11	10 (8th – 9th LM)
LM9	11.7	10	13 (9th – 10th LM)
LM10	11.7	11	11.7 (10th – 11th LM)
LM11	13	13	

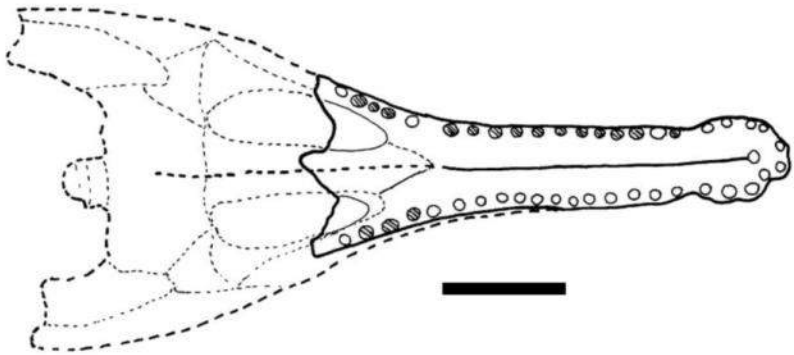
RM7	11.7	11.7	13 (7th – 8th RM)
RM8	10	10	13 (8th – 9th RM)
RM9	11.7	10	11.7 (9th – 10th RM)
RM10	11.7	10	

Gavialis curvirostris gajensis PILGRIM 1912

Holotype: Cranial rostrum (E-222) and mandibular rostrum (E-224) catalogued in the Indian Museum, Kolkata

Type Locality: Guj of Kumbhi, Bugti Hills, Baluchistan, Lower Miocene (PILGRIM, 1912).

Synonymy:
Gharialis curvirostris Lydekker, 1886 (in part)
Garialis curvirostris gajensis Pilgrim, 1908
Crocodilus naricus Pilgrim, 1908
Gavialis curvirostris gajensis (Steel, 1973)



a

Fig. 35 a. Reconstructed view of fragmented cranial rostrum (E-222)

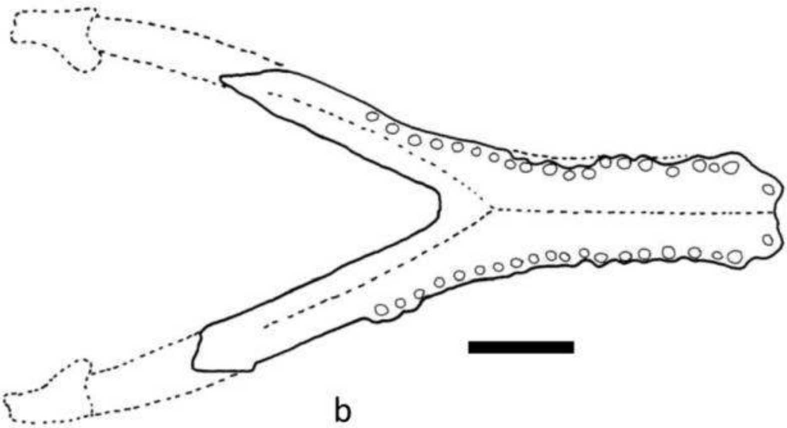


Fig 35 b. Reconstructed view of nearly complete mandibular rostrum (E-224). The material is the holotype, described by PILGRIM, 1912. (Scale = 12 cm).

Distinguishing features

The maxium length of the animal is around 7-8 m. The short cranial rostrum and the mandible are upwardly curved to a steep angle. Upper teeth count approximately 22; three alveoles measure about three quarters of the rostral width. There are 20 pair of mandibular teeth visible on the specimen ((Plate 12, fig. 3 & Text fig. 35a and 35b); orbits are wider transverse with no eversion of rims. The rostrum expands posterior; the parietal bar is approximately one and half times the width of the inter-orbital bar (narrower than in *G. curvirostris*). The lacrymals are smaller than those of *G. gangeticus* and slenderer than in *G. curvirostris.* Interdental pits are mesad of tooth row.

Material: A mandibular symphysis. E-223; the material is catalogued in the Indian Museum, Kolkata and has been originally described by PILGRIM (1912). (Plate 12, fig. 4 & Text fig. 36)

Locality: From Gaj of Kumbhi, Bugti Hills, Baluchistan, Lower Miocene.

Description

The mandible is curved upwards to a steep angle in comparison to the living *G. gangeticus* which has a shallow angle of upward curvature. The curvature is steeper than in *Gavialis curvirostris.* On the basis of the reconstruction, the length of the mandible is approx. 870 mm and it is comparable to the living *G. gangeticus.* Three alveoles equal approx. three-quarters of the mandibular width; in the living species of gavial it is about one-third to one-half of the rostral width. The specimen contains 14 widely spaced alveoli on each side. On the right mandible 4 posterior alveoles are indistinct. Except left 1-3 and right 1st, the tooth base is preserved in all the alveoles. The two anterior most teeth are pointing forward and not looking as occlusal as the rest of the teeth. The width of the mandible across the 2nd mandibular teeth is about 60 mm and this is lesser than that in the living *G. gangeticus* (about 92 mm).

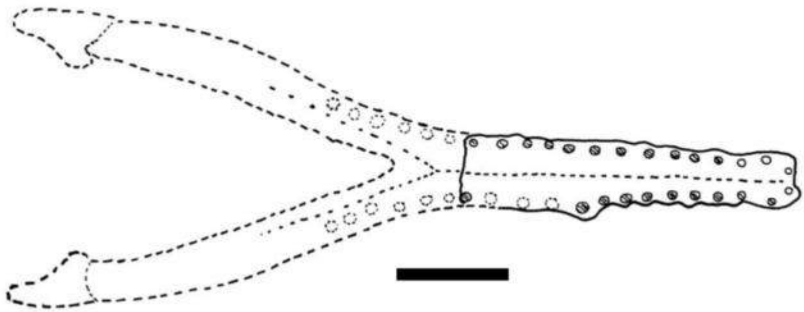


Fig. 36. Reconstructed mandibular rostrum of *Gavialis curvirostris gajensis*, E223 (Scale = 12 cm).

Position of tooth (reconstructed)	ADA (in mm)	ADB (in mm)	IAL (in mm)
RMD1	11	13	14 (1st – 2nd RMD)
RMD2	12	10	16 (2nd – 3rd RMD)
RMD3	11	09	10 (3rd – 4th RMD)
RMD4	12	12	18 (4th – 5th RMD)
RMD5	09	09	11 (5th – 6th RMD)
RMD6	07	07	18 (6th – 7th RMD)
RMD7	08	10	13 (7th – 8th RMD)
RMD8	10	11	10 (8th – 9th RMD)
RMD9	10	13	18 (9th – 10th RMD)
RMD10	12	12	
LMD1	11	13	14 (1st – 2nd LMD)
LMD2	12	10	16 (2nd – 3rd LMD)
LMD3	11	10	10 (3rd – 4th LMD)
LMD4	11	10	14 (4th – 5th LMD)
LMD5	07	08	15 (5th – 6th LMD)
LMD6	07	08	17 (6th – 7th LMD)

LMD7	08	08	12 (7th – 8th LMD)
LMD8	10	09	10 (8th – 9th LMD)
LMD9	09	10	10 (9th – 10th LMD)
LMD10	10	11	11 (10th – 11th LMD)
LMD11	11	09	11 (11th – 12th LMD)
LMD12	13	11	09 (12th – 13th LMD)
LMD13	13	12	12 (13th – 14th LMD)
LMD14	11	11	

Remarks:
The present species may be useful in establishing the relationships between the gavials and tomistomids, as its short cranial rostrum and small count of teeth is very similar to that in *Tomistoma* (PILGRIM, 1912). This shortness of the cranium is also evident in the cranial rostrum of the holotype (E-226) *Gavialis breviceps* (see Text fig. 37).

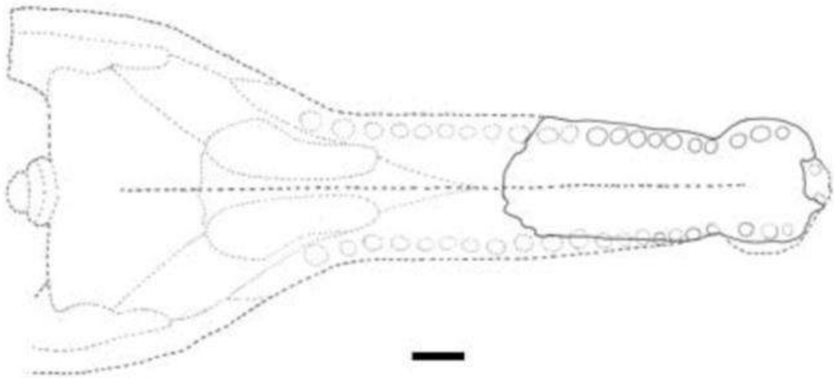


Fig. 37. Reconstructed cranial rostrum of the holotype of *Gavialis breviceps* (E-226). Scale = 6 cm.

Family Tomistomidae EASTMAN, 1902

Longirostrine eusuchians show anterior tapering of the skull with no sharp demarcation of the rostrum from the post-orbital region. The nasal bone is long and slender contacting the premaxillary. The prefrontal is smaller than the lacrymals. The orbits are oval and equal or larger than the supratemporal fenestrae. The mandibular symphysis is long with splenial inclusion. The distribution is:
Upper Cretaceous – Eocene and Miocene of Europe; Upper Cretaceous – Palaeocene and Upper Miocene-Lower Pliocene of North America; Upper Cretaceous and Eocene of Eastern Asia; Eocene-Pleistocene of Northern Africa;

Pliocene – Pleistocene of South America; Miocene, Pliocene and Recent of Southern Asia (Table 5).
By Upper Miocene times a decline of this group had set on with persistence of few forms in Africa and a giant form occurring in northern India and S-Nepal (perhaps indicating an eastward migration route through the Mediterranean). The Pleistocene witnessed the extinction of the family in Africa, Asia and South America, only *Tomistoma schlegelii* remaining to represent this once extensive and important group of crocodilians (STEEL, 1973).

***Rhamphosuchus* LYDEKKER, 1886**

Monotypic genus represented by only the species *Rhamphosuchus crassidens* FALCONER & CAUTLEY, 1840.

***Rhamphosuchus crassidens* (FALCONER & CAUTLEY, 1840)**

Holotype: BMNH-39802, catalogued in the Natural History Museum, London.

Type Locality: Pliocene of the Siwalik hills.

Synonymy:
Crocodilus Leptorhynchus crassidens Falconer & Cautley, 1840
Gharialis crassidens Lydekker in 1880
Crocodilus crassidens Falconer, 1868
Gharialis pachyrhynchus Lydekker, 1886
Rhamphosuchus crassidens Lydekker, 1886
Rhamphosuchus crassidens (Lydekker, 1888)
Rhamphosuchus crassidens (Steel, 1973)
Gavialis pachyrhynchus (Steel, 1973)
Rhamphosuchus crassidens (Corvinus & Schleich, 1994)

Distinguishing features
One of the largest known crocodilians, attaining an estimated length of 15-18 meters. The premaxillary is huge and apparently separated from nasals, facial profile straight. First lower tooth inserts into an upper jaw notch, whilst the enlarged 4th mandibular tooth is accepted into a pit.

Material: Complete snout (BMNH-39802), consisting of a posterior broken snout and intact mandibles (closed jaws) catalogued in the Natural History Museum, London. The cast of the specimen (E-183) is catalogued in the Indian Museum, Kolkata. The material was earlier described by CAUTLEY (1868) as *Crocodilus crassidens* and then by LYDEKKER (1886) *as Rhamphosuchus crassidens.*
(Plate 13, fig. 1 & Text fig. 38)

Locality: Pliocene of the Siwalik hills (LYDEKKER, 1888).

Description

The size of the preserved specimen is approx. 740 mm; a reconstruction indicates towards the large size of the cranium (2.5 m). The teeth are also very large in size indicating towards a large animal. The teeth are more inwardly curved (more than that in *Gavialis*). On the dorsal surface of the cranium, a large external narial aperture is distinct; it is oblong. Its diameter across the length of the snout is approx. 150 mm. The suture between the maxillaries and premaxillaries is very long extending back throughout the length of the specimen (Text fig. 38b). The width of the maxillaries is approx. 55 mm. The width of each maxillary is about 65 mm. The width of each nasal is about 55 mm. The specimen was found with intact upper and lower jaw and therefore it is not possible to study the ventral aspects of the maxillary and mandibles. The two anterior most teeth are pointing forward and not looking that occlusal as the following ones. In their middle a characteristic notch like incision is distinct. The following pair of teeth is separated by a much wider interdental gap than preceding ones.

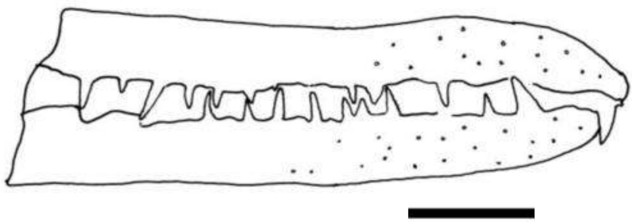


Fig. 38 a. Holotype specimen of *Rhamphosuchus crassidens* (BMNH-39802). Right lateral view of rostrum having anterior portion of occluded upper and lower jaw.

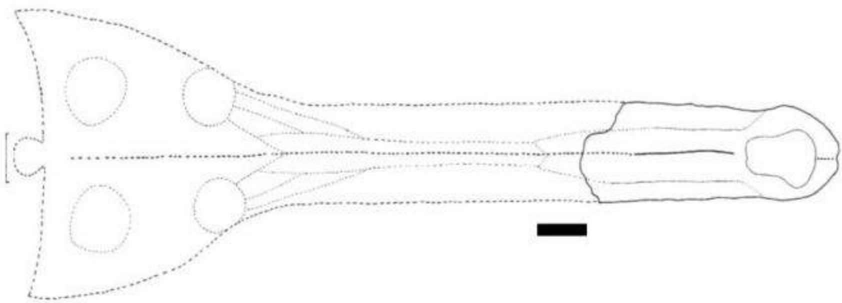


Fig. 38 b. Holotype specimen of *Rhamphosuchus crassidens* (BMNH-39802). Reconstructed dorsal view of cranial rostrum (Scale = 12 cm).

Position of tooth (reconstructed)	TL (in mm)	IAL (in mm)
RMD5	43	15 (3rd – 4th RPM)
RMD8	34	13 (1st – 2nd RM)
RPM4	37	13 (2nd – 3rd RM)
RM9	40	12 (3rd – 4th RM)
RM11	37	10 (4th – 5th RM)
		10 (5th – 6th RM)
		12 (6th – 7th RM)
		13 (7th – 8th RM)
		15 (8th – 9th RM)
		17 (9th – 10th RM)
		15 (10th – 11th RM)
		17 (2nd – 3rd RMD)
		15 (3rd – 4th RMD)
		15 (4th – 5th RMD)
		13 (5th – 6th RMD)
		13 (6th – 7th RMD)
		13 (7th – 8th RMD)
		15 (8th – 9th RMD)
		14 (9th –10th RMD)

Remarks:
The specimens described by LYDEKKER (1886) as *Gavialis* (= *Gharialis*) *pachyrhynchus* (LYDEKKER, 1886; STEEL, 1973) reflect most of the characters present in *Rhamphosuchus crassidens*. Broader premaxillaries and snout of *Gavialis pachyrhynchus* is very much evident in *Rhamphosuchus crassidens* recorded from the Upper Pliocene rocks of the Siwaliks of India and Nepal. We regard the material described as *Gavialis pachyrhynchus* synonymous to *Rhamphosuchus crassidens*. This eventually indicates towards a monotypic species of *Rhamphosuchus* having only the species of *Rhamphosuchus crassidens*.

Material: Maxillary fragment, WIF/A 464, catalogued in the Museum of Wadia Institute of Himalayan Geology, Dehradun.
(Plate 13, fig. 2 & Text fig. 39)

Locality: 1.75 km ENE of Jamni Village (Sirmur), pre-Pinjor beds (= Tatrot Formation).

Description

The preserved specimen shows six alveoles on the right and five alveoles on the left jaw. The anterior most alveole of the left maxilla and 7th anterior most alveole of the right maxilla is partly seen. The alveoles are very large and indicating by such large teeth size a giant animal. The reconstruction of the skull suggests a size of animal ranging between 15-17 meters. The diameter of all alveoles on the fragment do not vary much but is the width of the fragment is reducing anteriorly. It is not possible to decipher from the given specimen if the size of alveoles reduces or remain same anterior. A logical expression is that the size of alveole will also reduce with the reduction of the width of the snout. The alveoles for the teeth attachment are shallow. The interdental space is nearly negligible. Two teeth are separated by interdental space ranging between 1-3 mm. The maximum length of the preserved specimen is 260 mm. The median suture is well marked. The interdental pits are distinct.

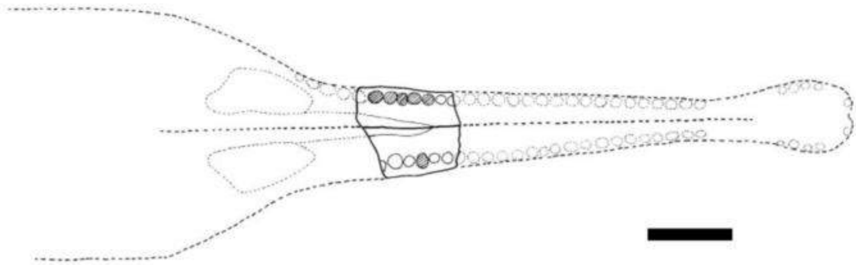


Fig. 39. Reconstructed ventral view of cranial rostrum of *Rhamphosuchus crassidens*, WIF/A 464 (Scale = 20 cm).

The maxillary bones are thick. The suture between the palatine and the maxillaries is clearly demarcated and it extends anterior joining median suture with a sharp termination at the anterior level of 9th maxillary teeth (based on the reconstruction of the skull). The posterior portion of the palatine is broken. The palatine fenestrae are not distinct.
On the dorsal surface of the skull, the maxillo-nasal sutures are distinctly seen and they join sharply the median line.
The size of the teeth and presence of maxillo-nasal sutures suggests that the specimen belongs to a posterior maxillary part of the skull of *Rhamphosuchus crassidens*.

Position of tooth (reconstructed)

	ADA (in mm)	ADB (in mm)	IAL (in mm)
RM8	30	38	3 (8th – 9th RM)
RM9	29	39	4 (9th – 10th RM)
RM10	29	40	4 (10th – 11th RM)
RM11	29	41	3 (11th - 12th RM)
RM12	29	42	4 (12 – 13th RM)
RM13	30	43	
LM8	32	37	2 (7th – 8th LM)
LM9	29	41	4 (8th – 9th LM)
LM10	31	38	3 (9th – 10th LM)
LM11	30	41	2 (10th 11th LM)
LM12	33	42	4 (11th – 12th LM)

Material: Premaxillary part of snout (original: NHM/TU 1989/27; cast: BSP 1989 XVIII 8); isolated teeth (original: NHM/TU 1989/32 - 33; cast: BSP 1989 XVIII 10 – 11). The material is catalogued in the Natural History Museum of Tribhuvan University, Kathmandu, Nepal.
(Plate 13, fig. 3 & 14, figs. 1 - 3 & Text fig. 40)

Locality: Rato Khola, Surai Khola, Upper Siwaliks

Description

The bone sutures are hardly visible on that specimen and it can only be interpreted as the anterior most part of the skull, showing probably a huge premaxillay part and just reaching the narial aperture. Its outer surface is characterized by elongated grooves, rather widely separated from each other and not arranged that densely as it is seen in a recent *Crocodylus palustris* or *Gavialis gangeticus* skull, but resembling slightly more than latter one. Viscerally eight broken but well-rounded teeth are seen and the most distal one measures 30 mm in its diameter at the height of the jaw's rim. The total size of that fossil measures 21x17 cm. The two anterior most teeth are pointing forward and not being oriented that occlusal as the following ones. In their middle a characteristic notch like incision is seen. The following pair of

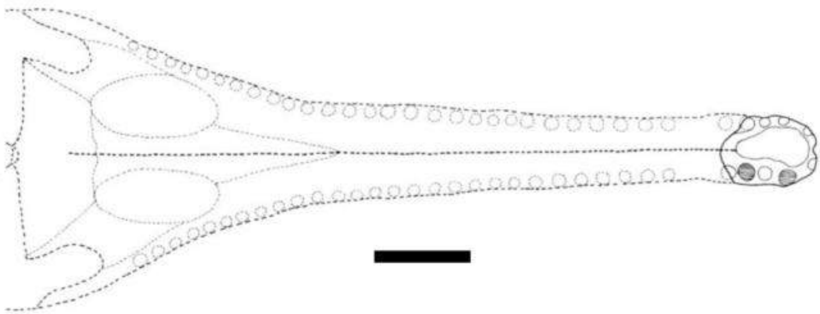


Fig. 40. Reconstructed ventral view of a cranial rostrum of *Rhamphosuchus crassidens*, NHM/TU 1989/27 (Scale = 20 cm).

teeth is separated by a much wider interdental gap than preceeding ones. All teeth are broken at the jaw surface, but a replacement tooth measures 33.5 mm in its broken cavity and shows lateral ridges like the hereafter described isolated teeth.
Viscerally the specimen looks rather similar to the one of *Rhamphosuchus* figured by LYDEKKER (1886). It exposes dorsally the midpremaxillar notch, also the second tooth looks prominent (CORVINUS & SCHLEICH, 1994).
The teeth show typical features as being present in the teeth of *Gavialis*, they are laterally keeled and slightly depressed (but comparatively large) and therefore one might relate to or even regard *Rhamphosuchus* as a tremendous gavialid crocodile.

The teeth are quite identical to those from a compared skull of a recent gharial and show a rather smooth surface and fine crenulations in the enamel's surface. One tooth is curved, labially wedged and slightly pointed (NHM/TU 1989/32, cast: BSP 1989 XVIII 10, Plate 14, fig. 3) while the other is more rounded, only slightly curved and rather blunt (NHM/TU 1989/33, cast: BSP 1989 XVIII 11, Plate 14, fig. 4). For their relation to the diameter they are rather short in comparison to the teeth from *Gavialis gangeticus* of the recent specimen (CORVINUS & SCHLEICH, 1994).

The dimensions taken (in mm) on the isolated teeth are as follow:

Catalogue number	Height of preserved crown	Maximum Diameter
TU/NHM 1989/32	39	19
TU/NHM 1989/33	39	15

The dimensions taken on the alveoles of the premaxillary part (CORVINUS & SCHLEICH, 1994) are:

Position of tooth (reconstructed)

	ADA (in mm)	ADB (in mm)	IAL (in mm)
RPM1	27	33	39 (1st – 2nd RPM)
RPM2	27	27	14 (2nd – 3rd RPM)
RPM3	25	27	09 (3rd – 4th RPM)
LPM1	27	28	29 (1st – 2nd LPM)
LPM2	27	28	19 (2nd – 3rd LPM)
LPM3	25	26	09 (3rd – 4th LPM)
LPM4	31	31	

Additional Crocodile Material

For the crocodile material listed below, locality information was not available. (FMS = Field Museum Saketi Fossil Park, Saketi)

Reference of the specimen as marked on its surface and repository

Crocodylus sp., No. 01; FMS/na: Fused tail vertebrae with the anterior part of pelvic

Crocodylus sp., No. 38; FMS/na: Caudal vertebra

Crocodylus sp., No. 78; FMS/na: Lateral half of osteoscute, viscerally showing cross striation similar to *Iberosuchus* from the Eocene of Spain. Reconstructed length and width should be approximately 9 cm and 14 cm respectively. Maximum height of the osteoscute at the dorsal crest is 2.8 cm.

? ***Crocodylus*** sp., No. 83, 91, 104(FMS) small osteoderms with slightly wedged margins and less prominent straight median keel probably latero-dorsally oriented

Crocodylus sp., No. 86(FMS): Diagonally broken ventral scute; the maximum length of the specimen is about 4.9 cm.

Crocodylus sp., No. 87-FR1 (FMS): Mandibular fragment with 4 alveoles. In two alveoles the tooth base is preserved.

Crocodylus sp., No 94 (FMS). Probably skull fragment with articulation facet. No. 95; FMS/na Mid-dorsally fragmented osteoscute with diagonally oriented dorsal ridge. Total scute length is approx. 9 cm and height is approx. 6 cm. The total reconstructed width of the scute should be approx. 14-15 cm.

Crocodylus sp. No. 119(FMS): Cervical vertebra

Crocodylus sp. No. 121;(FMS): Large caudal vertebra

Crocodylus sp., No. 134;(FMS): Mandibular fragment with 4 alveoles. The base of a tooth is present in the middle of two alveoles.

Crocodylus sp. No. 210;(FMS): Lateral half of osteoderm. Reconstructed width approx.16 cm. Thickness is approx. 2.7 cm.

Crocodylus sp. No. 87/FR14 (FMS): Single tooth having well developed lateral keels and vertical striations. Crown height approx. 5.6 cm.

Crocodylus sp., No. 30 (FMS): Isolated tooth with well developed vertical striations and lateral keels.

Gavialis sp. No 210 (FMS): Two caudal vertebrae

Gavialis sp., No. 250 (FMS): Caudal vertebra

Gavialis sp., No. K 57/21;(Indian Museum, Kolkata)
Cranial rostrum fragment. A small part between the orbits and maxillaries is preserved.

Gavialis sp., No. W 20/180) (Indian Museum, Kolkata)
Nearly complete mandible (right posterior portion is broken) fixed on a stand so that the study of ventral surface is not possible. Five teeth in right jaws are seen. Teeth are slender and curved. Lateral keel and vertical striations are well marked.

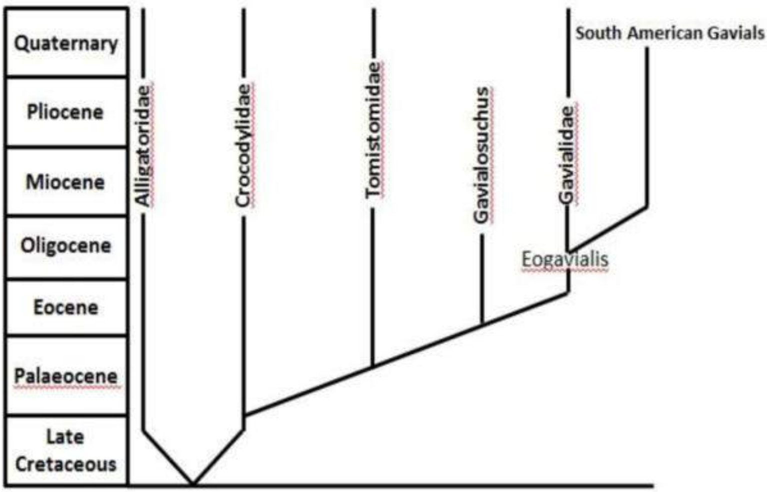
cf. ***Rhamphosuchus crassidens*** No. R 15 (FMS): Isolated tooth; crown height approx. 3 cm.

Phylogenetic and Evolutionary Aspects

In archosaur systematics, the relationships between the major groups of living crocodilians is a debated issue (NEILL, 1971; DENSMORE, 1983; BUFFETAUT, 1985; NORELL, 1989 and TARSITANO et al., 1989).
ROMER (1956) referred all of the living crocodilians in three subfamilies (Alligatorinae, Crocodylinae, Gavialinae), a procedure largely followed by KUHN (1968) but with the gavials separated as a distinct family unit and *Nettosuchus* included as meriting only subfamilial status. These reptiles are all relatively conservative forms and display fairly consistent basic morphological pattern, and there is extensive variation in skull proportions and the shape and distribution of teeth. STEEL (1973) considered these characters insignificant to be described under different families; he suggested five subfamilies under the family Crocodylidae: the Crocodylinae, Alligatorinae, Gavialinae, Thoracosaurinae (included by ROMER among the crocodylines), and the Pristichampsinae (proposed by KUHN in 1968 for *Pristichampsus* and *Weigeltisuchus*).
There are mainly two genealogies for the living crocodilian groups (NORELL, 1989). One hypothesis portrays the gavialids, crocodylids (including *Tomistoma*) and the alligatorids as monophyletic and the other hypothesis suggests a sister group relationship between *Gavialis* and *Tomistoma* with alligatorids as the sister group to other Crocodylia. Other crocodilian phylogenies are unresolved at this level (MOOK, 1934; WERMUTH, 1953; STEEL, 1973), or have cconsidered the Crocodylia as polyphyletic, with the gavialids, having thalatosuchian affinities (KÄLIN, 1933, 1955). DUMÈRIL (1806) and NORELL (1989) considered three families representing modern crocodiles Aligatoridae (including *Alligator*, *Caiman*, *Paleosuchus* and *Melanosuchus niger*), Crocodylidae (including species of *Crocodylus*, *Osteolaemus tetraspis* and *Tomistoma schlegeli* and Gavialidae (only *Gavialis gangeticus*) with a sister group relationship between the crocodylids and alligatorids. However, on the basis of molecular characterstics (DENSMORE, 1983; DENSMORE & DESSAUER, 1984 and DESSAUER & DENSMORE, (1983) and many palaeontological and morphological characters (BUFFETAUT, 1985) a sister group relationship between the crocodylid genus Tomistoma amd *Gavialis* has been favoured (DENSMORE, 1983). This reconciliation was not accepted by ANTUNES (1987) and he considered *Gavialosuchus* at subgeneric level of *Tomistoma*, maintaining the familiar concept of Gavialidae and Tomistomidae.
We agree with the arguments given by NORELL (1989) for the higher-level relationships of the Crocodylia. Although, molecular evidences (DENSMORE, 1983) are the most resolved for the approximation of crocodilian phylogeny, it is not without problems and doubts. As suggested by NORELL (1989) there is no close living outgroup of the extant crocodilians. Like other hypotheses, DENSMORE'S molecular hypothesis should also be open to discussion from both comparative anatomists and molecular systematists. In the present state of our knowledge and ignorence, the hypothesis of a sister group relationship between the crocodylids and alligatorids (sensu DUMÈRIL, 1908 and NORELL, 1989) is best supported and acceptable. On the basis of comparative and functional morphological examination of *Gavialis* and *Tomistoma* (TARSITANO,

et al., 1989), we advocate that *Gavialis* is quite different from the tomistomine lineage (KÄLIN, 1955 and HECHT & MALONE, 1972). Many aspects such as the braincase, cranial sinus systems, jaw adductor systems, pelvic and hindlimb morphplogy and epaxial musculature demonstrate that *Gavialis* is unique among the living Crocodiles (TARSITANO et al., 1989). Therefore, in phylogenetic tree, we retain the familiar concept of Gavialidae and Tomistomidae (Table 5) as discussed by ANTUNES (1987).

We consider the fish-eating longirostrine condition (elongation of jaws) in both the families as a result of functional and ecological adaptation, as this condition reoccurs many times within the Crocodilia as well as in other reptilian and amphibian taxa (ROMER, 1956, TARSITANO et al., 1989). Very interestingly, it has also been noticed from the description of the skull that the



Tab. 5. Phylogenetic tree of the main groups of eusuchians in the late Cretaceous and Cenozoic with special emphasis on Gavialidae and Tomistomidae (modified after BUFFETAUT, 1985).

method of attainment of the longirostrine condition and braincase costruction is not the same in *Gavialis* and *Tomistoma*. *Tomistoma* is constructed as a typical *Crocodylus* having attained the longirostrine condition earlier in their evolution than other living crocodylines (TARSITANO et al., 1989). The genus *Rhamphosuchus* (one of the largest known crocodilians), attaining a length of about 15-18 meters was earlier considered to be a thoracosaurine (KÄLIN, 1955; ANTUNES, 1961; 1987 and STEEL, 1973), although classified by ROMER (1956) and LYDEKKER (1886) as a gavial.

LANGSTON (1965) considered that the systematic position of *Rhamphosuchus* is questionable.
In the present state of knowledge, we classify *Rhamphosuchus* with *Tomistoma* under the Family Tomistomidae since it apparently displays most of the features found in the genus *Tomistoma* and other thoracosaurines as descirbed by STEEL (1973); however, the possibility of a convergent evolution of both the genera can not be ignored.
Among the fossil gavials from the Indian subcontinent, excepting the form *G. gangeticus,* the type material is always incomplete. Among all of the fossil gavials *Gavialis browni* MOOK is the bestpreserved record. With the incomplete material of various species an accurate comparison is not possible which opens door for misidentification and misinterpretation of the fossil specimens. Only complete material available for comparison is that of living *Gavialis gangeticus* and to some extant *Gavialis browni.*

***Crocodylus palustris* (living)**	***Crocodylus palaeindicus* (fossil)**	***Crocodylus biporcatus* (fossil)**	***Crocodylus porosus* (living)**
Maximum length 4-5 m	Maximum length 6-8 m	Maximum length 9-10 m	Maximum length 10-11 m
Fresh water form	Fresh water form	Fresh water form	Salt water form
Skull broad, short	Skull broad (broader than in *C. palustris*), short	Skull long, less broad than in *C. palustris*	Skull large, less broad than in *C. palustris.*
Snout moderately broad, short	Snout broad, small (broader than *C. palustris*)	Snout moderately sharp	Snout moderately broad
Premaxillary and maxillary are wide	Premaxillary bone stout and wide (more than in *C. palustris*), maxillary very heavy, stout and large	Premaxillary and maxillary broad, short compared to *C. palustris*	Premaxillary and maxillary broad, large compared to *C. palustris*
Upper cranial profile convex	Upper cranial profile flat	Upper cranial pfofile sloping	Upper cranial profile sloping
External narial aperture auricular, reniform	External narial aperture rounded	External narial aperture auricular	External narial aperture auricular
Palatine fenestrae oval	Palatine fenestrae rhomboid	Palatine fenestrae rhomboid	Palatine fenestrae rhomboid

Premaxillary foramen small	Premaxillary foramen large	Premaxillary foramen small	Premaxillary foramen small
Orbits large, round to suboval	Orbits large and oval	Orbits large and oval	Orbits large and oval
4-5 pairs of premaxillary teeth (3rd -4th largest)	4 pairs premaxillary teeth (3rd largest)	4 pairs of premaxillary teeth (3rd largest)	Usually 4 pairs of premaxillary teeth; rarely 5 pairs
14 pairs of maxillary teeth (5th largest)	14 pairs of maxillary teeth (4th largest)	13-14 pairs of max. teeth (5th largest)	14 pairs of maxillary teeth (5th largest)
Deep alveoles for teeth attachment	Deep alveoles for teeth attachment	Shallow alveoles for teeth attachment	Deep alveoles for teeth attachment
Lacrymals broad and stout	Lacrymals broad and stout (more than *C. palustris*)	Lacrymals long and slender	Lacrymals long and slender
Lateral margins of inter-orbital plate	Lateral margins of inter-orbital plate	Lateral margins of inter-orbital plate	Lateral margins of inter-orbital plate
slightly elevated	elevated	elevated	elevated
proportion of breadth of pre-orbital region to its length is 1:1.3.	proportion of breadth of pre-orbital region to its length is 1:1.2.	proportion of breadth of pre-orbital region to its length is 1:1.5.	proportion of breadth of the pre-orbital region to its length is 1:1.25 to 1:1.75
Inter-alveolar space 2-6 mm; its max. 2nd - 3rd (19 mm) and 8th and th (approx. 21 mm) mandibular teeth 7th - 8th maxillary teeth (approx. 10 mm) Anterioposterior diameter of alveoles between 10-15 mm; it is maximum for 1st (approx. 28 mm)	Inter-alveolar space 2-5 mm; its max. 1st - 2nd premaxillary teeth (17 mm) and 7th - 8th maxillary teeth (approx. 15 mm) Anterioposterior diameter of alveoles between 12-17 mm; it is maximum for 4th maxillary tooth	Inter-alveolar space 3-9 mm; its max. 7th - 8th maxillary teeth (approx. 17 mm) Anterioposterior diameter of alveoles between 12-17 mm; it is maximum for 3rd	Inter-alveolar space 4-10 mm; its max. 7th - 8th maxillary teeth (approx. 18 mm) Anterioposterior diameter of alveoles between 12-17 mm; it is maximum for 3rd maxillary

and 4th (approx. 26 mm) mandibular teeth and 4th (approx. 26 mm) and 5th maxillary teeeh (approx. 20 mm).	(approx. 28 mm)	premaxillary tooth (approx..22 mm) and 5th maxillary tooth (approx. 27 mm	tooth (approx. 22 mm) and 5th maxillary tooth (approx. 28 mm)

Tab 6 (above). Comparison of osteological features of *Crocodylus palustris, C. palaeindicus, C. biporcatus* and *C. porosus*

Gavialis gangeticus	***Gavialis browni***	***Gavialis curvirostris***	***Gavialis curvirostris gajensis***	***Gavialis breviceps***
Max. length about 9-10 m	Max. length about 6-8 m	Max. length about 6-7 m	Max. length about 7-8 m	Max. length about 8-10 m
Rostrum long; slight upward curved, distal expansion	Rostrum long, beak like, slender, extending from face like the handle of a frying pan; it is upward curved (more than in *G. gangeticus*), distal expanded	Rostrum consider-ably shorter than in *G. gangeticus* with marked upward curvature	Rostrum short, excessively upward curved (more than in *G. curvirostris*), term-inal expansion	Rostrum short compared to width; very massive and distal expanded, upwards curved
Skull table wide, transition from face to rostrum anterior to orbits abrupt and sharply defined	Skull massive, no apparent abrupt depression in front of the orbits	There is no abrupt depression of rostrum in front of the orbits	Profile not abruptly depressed in front of the orbits	Profile not abruptly depressed in front of the orbits

Orbits sub-rounded, lateral elongated rather than anterioposterior	Orbits sub-oval and laterally elongated than anterio-posterior	Orbits subrounded and anteroposterior elongated rather than lateral	Orbits wider transverse compared to those in *G. gangeticus*.	Orbits sub-rounded
Orbits wide separated with a concave frontal having everted margin	Orbits relatively close with a flat frontal with no prominent eversion of the borders	Orbits less wide placed compared to those of *G. gangeticus* with no eversion of the borders	Orbits less wide placed compared to *G. gangeticus*; orbital borders not prominent.	Orbital borders not prominent.
Width of parietal bar is about 1/5 to 1/3 of the width of interorbital bar	Width of parietal bar is about ½ of the width of the inter-orbital bar	Width of parietal bar is about 1/5 to 1/3 of the width of inter-orbital bar	Width of parietal bar is about 3/2 of the width of inter-orbital bar	Width of parietal bar is about 3/2 of the width of inter-orbital bar

Lacrymals long and slender	Lacrymals comparatively small	Lacrymals are smaller than in *G. gangeticus* and slender.	Lacrymas are smaller than in G. gangeticus and slenderer than in *G. curvirostris*.	Lacrymals are as long as in *G. gangeticus* and are slender (less than in *G. curvirostris*).
Supratemporal fenestrae large and equal in size and shape of orbits	Supratemporal fenestrae large equal to orbits, wider than long	Supratemporal fenestrae large, equal to orbits in size and shape	Supratemporal fenestrae large and slightly smaller than the orbits	Supratemporal fenestrae large and slightly smaller than the orbits

Maxillary teeth 27-29 and 25-26 mandibular teeth.	Maxillary teeth approx. 20; number mandibular teeth unknown	Maxillary teeth approx. 22. Mandibular teeth approx. 20.	Maxillary teeth approx. 22. Mandibular teeth approx. 20.	Maxillary teeth approx. 20. Mandibular teeth approx. 20
Maxillary occupies max. width of snout. Max. width of snout near prefrontal (158 mm)	Maxillary occupies max. width of snout. Max. width of snout is near prefrontal (140 mm)	Maxillary occupies max. width of snout. Max. width of snout is near prefrontal (120 mm)	Maxillary occupies max. width of snout. Max. width of snout is near prefrontal (115 mm)	Maxillary occupies max. width of snout. Max. width of snout is near prefrontal (150 mm)
Maxillopalatine suture appears extending upto third pair of maxillary teeth from posterior	Maxillopalatine suture appears extending upto fifth pair of maxillary teeth from posterior	Maxillopalatine suture appears extending upto sixth pair of maxillary teeth from posterior	Maxillopalatine suture appears extending upto fifth pair of maxillary teeth from posterior	Maxillopalatine suture appears extending upto seventh pair of maxillary teeth from posterior
Anterior margin of ectopterygoid reaches last maxillary tooth	Anterior margin of ectopterygoid reaches anterior margin of 2nd maxillary tooth from posterior	Anterior margin of ectopterygoid reaches anterior margin of 2nd maxillary tooth from posterior	Anterior margin of ectopterygoid reaches anterior margin of 2nd maxillary tooth from posterior	Anterior margin of ectopterygoid reaches anterior margin of 2nd maxillary tooth from posterior

Interalveolar space 4-10 mm three alveoles approx. about 1/3 to 1/2 the rostral width	Interalveolar space ranges 11- 8 mm; three alveoles approx. about 3/4 the rostral width	Interalveolar space ranges 5 - 14 mm; three alveoles approx. more than 1/2 the rostral width	Interalveolar space 9-18 mm; three alveoles approx. about 3/4 the rostral width	Interalveolar space 1-10 mm; three alveoles approx. about 1/2 the rostral width
Anterioposterior diameter of alveoles between 10 and18 mm	Anterioposterior diameter of alveoles between 10 and18 mm	Anterioposterior diameter of alveoles between 11 and14 mm	Anterioposterior diameter of alveoles between 12 and18 mm	Anteroposterior diameter of alveoles between 12 and19 mm
Palatine fenestrae oval they are long and narrow (length about twice the width)	Palatine fenestrae narrow and elongated with parallel inner margins	Palatine fenestrae narrow and elongated	Palatine fenestrae narrow and elongated	Palatine fenestrae narrow and elongated with parallel inner margins.
Anterio-posterior length of the pterygoid is equal to the length of the palatine fenestrae	Anterio-posterior length of the pterygoid is equal to 3/4 of the palatine fenestrae	Anterio-posterior length of the pterygoid is equal to 3/4 of the palatine fenestrae	Anterio-posterior length of the pterygoid is equal to 3/4 of the palatine fenestrae	Anterio-posterior length of the pterygoid is more than 3/4 of the palatine fenestrae

The distance from the anterior ends of the palatine fenestra forward to the junction of the two maillo-palatine sutures at the median line, is considerably lesser than breadth of the snout at this junction.	Distance from anterior end of palatine fenestrae to junction of two maxilla-palatine sutures at median line, measured is considerably greater than breadth of the snout at this junction.	Distance from anterior end of palatine fenestrae to junction of the two maxillae-palatine sutures at the median line, is little more than the breadth of snout at this junction.	Distance from anterior end of palatine fenestrae forward to junction of the two maxillae-palatine sutures at the median line, is considerably less than the breadth of the snout at this junction.	Distance from anterior end of palatine fenestrae to junction of the two maxillae-palatine sutures at the median line, is considerab ly less than the breadth of the snout at this junction.

Tab. 7. Comparison of osteological features of *Gavialis gangeticus, G. browni, G. curvirostris, G. curvirostris gajensis* and *G. breviceps*

Palaeoenvironmental and Palaeoecological aspects

The present-day crocodiles have a very specific habitat; they dwell in subtropical - tropical warm climate (MASKEY & SCHLEICH 1992; SCHLEICH & MASKEY, 1992, SCHLEICH et al. 2002). The fresh water genera of crocodiles do not go far away from the river system they prefer to live on the river banks; however, salt water genera for example *Crocodylus porosus* leave their salt water habitat during breeding seasons and go far away in the river channel systems (DERANIYAGALA, 1953). The presence of crocodilian skulls from various horizons of the Siwaliks suggest that the accumulation of crocodilian remains is essentially fluvial.

The condition of preservation of recovered large skull elements (with intact teeth in many cases) with no suggest nearly negligible transportation before the deposition in the fluvial channel system (SRIVASTAVA, 1993; SRIVASTAVA & KUMAR, 1996). The skull elements of crocodiles generally do not show any postmortem deformation. However, few deformed skulls are suspected to have undergone some amount of plastic deformation caused by mechanical stress and due to shrinking of the clay content of the sediments during compaction (SRIVASTAVA, 1993; SRIVASTAVA & KUMAR, 1996).

The presence of the crocodile taxa (*Crocodylus* and *Gavialis*) and the giant *Rhamphosuchus crassidens* in the Siwaliks suggest large and deep permanent fluvial channel systems with riverine shore areas as prevail today for the living species of *Crocodylus* and *Gavialis* (*Crocodylus palustris* and *Gavialis gangeticus*) and support the idea for (para-) tropical climate (at least similar or even more warmer condition) during the Miocene – Pleistocene time; the presence of number of species of *Crocodylus* and *Gavialis* in the Siwaliks suggest an open fresh water environment (PATNAIK, 1991; CORVINUS & SCHLEICH, 1994). The presence of large vertebrate fauna and flora reported so far by various workers suggest the presence of an open grassland and wooded grassland with perennial rivers and swamps where rodents and other vertebrates could survive providing suitable feeding conditions for crocodiles (FISHER, 1981; BADAM, 1984; PATNAIK, 1991; PATNAIK & SCHLEICH, 1993).

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PLATE 1

Crocodylus palaeindicus FALCONER, 1859

Fig. 1. Holotype (E – 31). Complete cranium;
a – dorsal view,
b – ventral view.

Fig. 2. Specimen E – 32. Anterior part of cranial rostrum;
a – dorsal view,
b – ventral view.

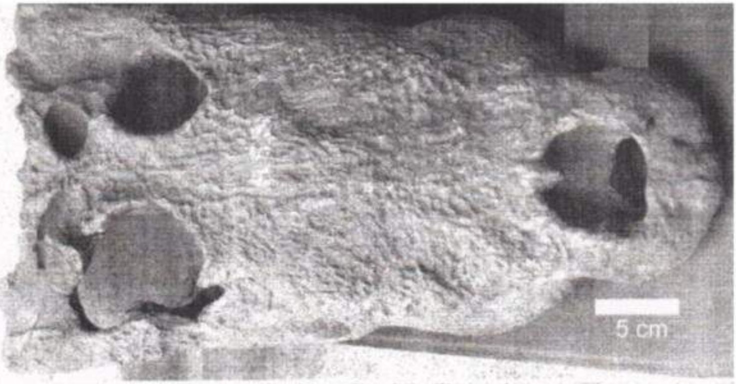


Fig. 1a

Fig. 1b

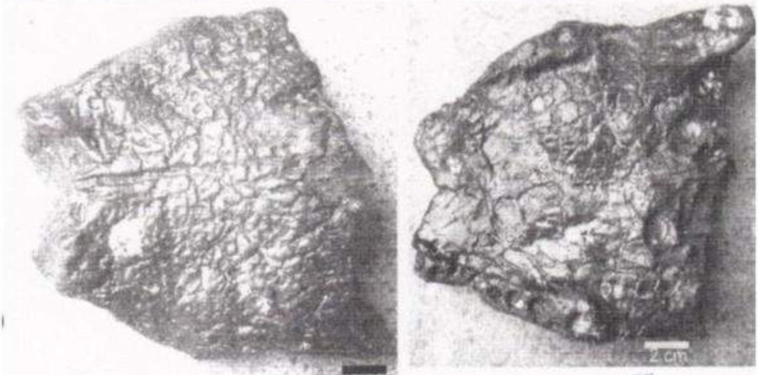


Fig. 2a,b

PLATE 2

Crocodylus palaeindicus FALCONER, 1859

Fig. 1: Specimen A-683. Posterior broken cranium;
a – dorsal view,
b – ventral view.

Fig. 2: Specimen 18136. Dorsal view of posterior broken and lateral deformed cranium.

Fig. 1a

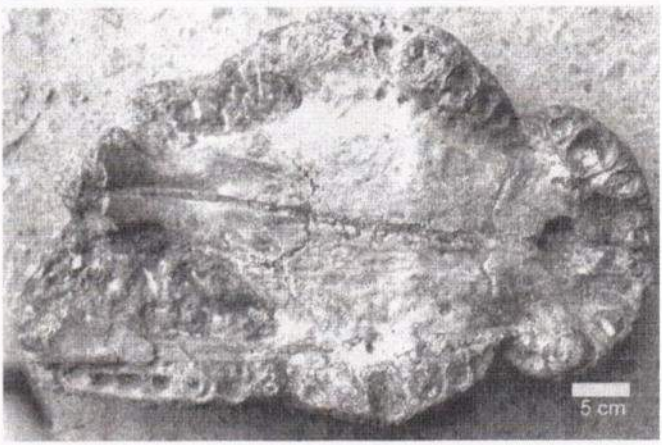


Fig. 1b

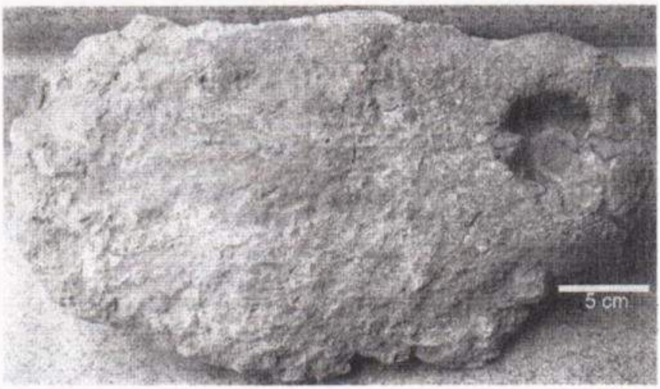


Fig. 2

PLATE 3

Crocodylus cf. *palaeindicus* FALCONER, 1859

Fig. 1: Specimen KN 751 (E – 281). Ventral view of fragmentary cranial rostrum.

Crocodylus biporcatus CUVIER, 1807

Fig. 2: Specimen A-684. Complete cranium;
a – dorsal view,
b – ventral view.

Crocodylus palustris LESSON, 1831

Fig. 3: Specimen BMNH - 39798 (cast: E – 186). Complete skull with upper and lower jaws. The specimen was described by LYDEKKER (1886) as *Crocodylus* sivalensis under the catalogue number BMNH – 39797.

Fig. 1

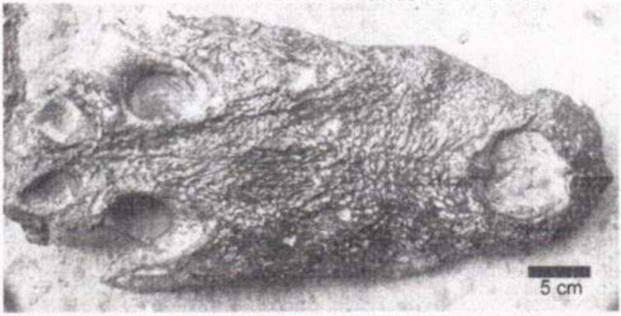


Fig. 2a

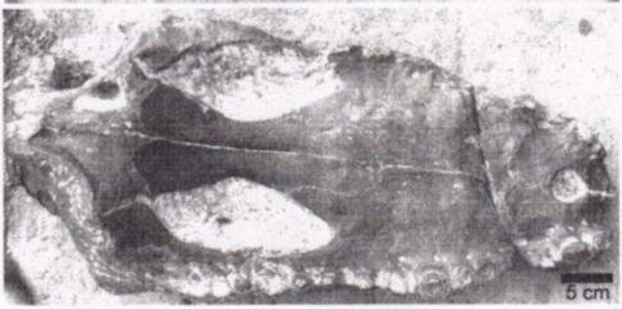


Fig. 2b

Fig. 3

PLATE 4

Crocodylus palustris LESSON, 1831

Fig. 1: Specimen SFP – 201. Mandibular rostrum;
a – ventral view,
b – occlusal view.

Fig. 2: Specimen WIF/A 463 (a). A part of right cranial rostrum;
a – ventral view,
b – dorsal view.

Fig. 3: Specimen WIF/A 463 (b). Ventral view of a part of right premaxillary and maxillary.

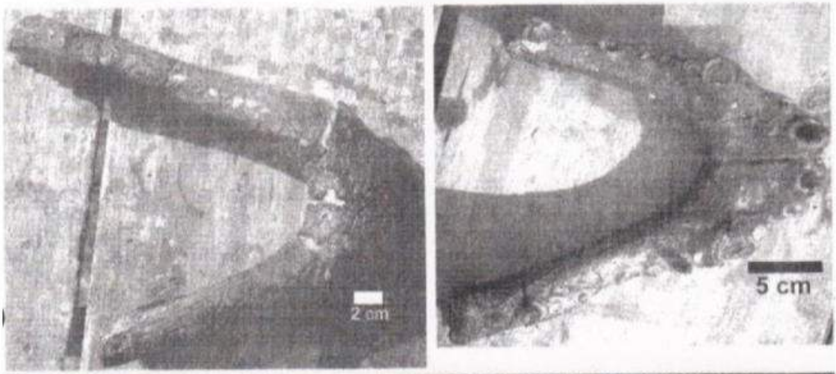


Fig. 1a,b

Fig. 2a

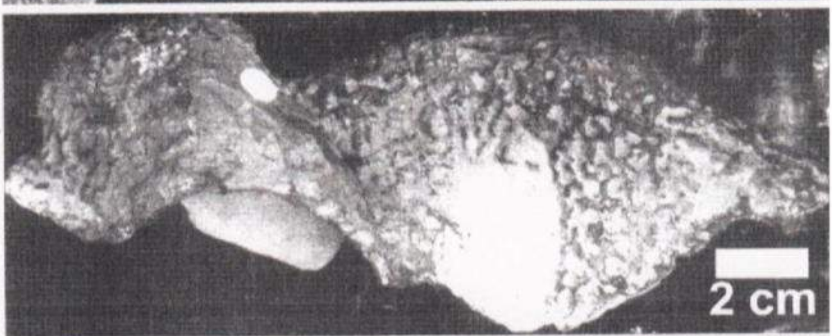


Fig.2b

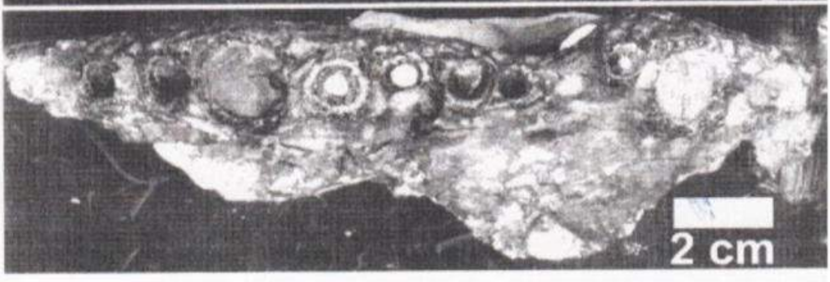


Fig. 3

PLATE 5

Crocodylus palustris LESSON, 1831

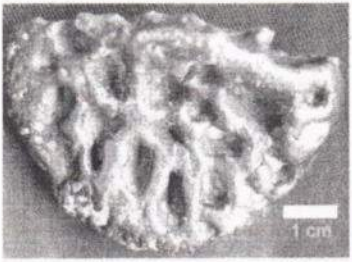
Fig. 1. Specimen NHM/TU 1989 (cast: BSP 1989 XVIII 13). Dorsal view of a fragmentary osteoscute.

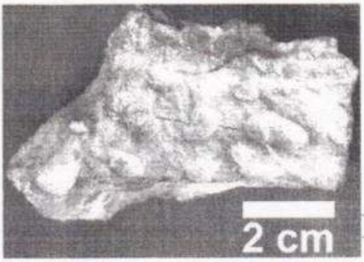
Fig. 2. Specimen NHM/TU 1989/30 (cast: BSP 1989 XVIII 12). Dorsal view of another fragmentary osteoscute.

Fig. 3. Specimen E- 34. Ventral view of right premaxillo-maxillary part of cranial rostrum.

Fig. 4. Specimen E – 42 (a). Occlusal view of left mandibular rostrum.

Fig. 5. Specimen E – 42 (b). Occlusal view of another left mandibular rostrum.





Fig, 1, 2

Fig.3

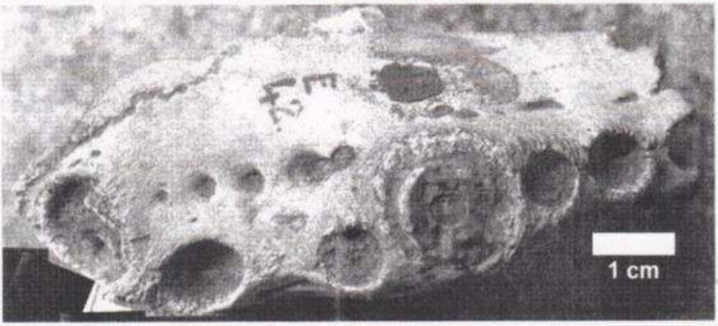


Fig. 4

Fig. 5

PLATE 6

Crocodylus cf. *palustris* LESSON, 1831

Fig. 1. Specimen SFP – 200. Complete skull with cranium and mandibles;
a – dorsal view,
b – right lateral view.

Gavialis gangeticus GMELIN, 1789

Fig. 2. Specimen SFP – 185. Posteriorly fragmentary dorsal view of cranium. The posterior view is not possible as the specimen is intact in the rock.

Fig. 3. Specimen SFP – 137. Dorsal view of fragmentary mandibular rostrum.

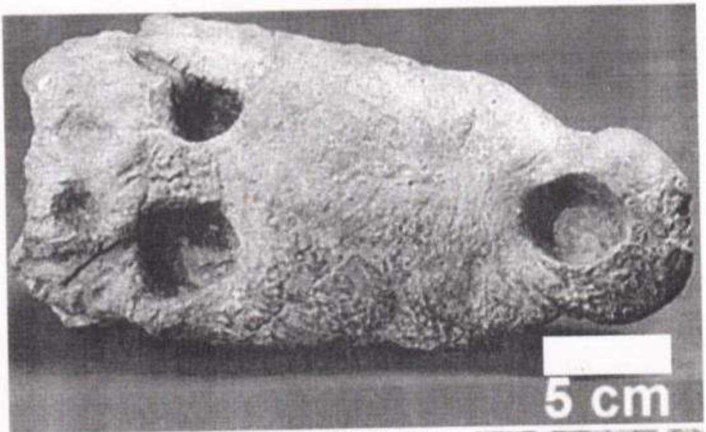


Fig. 1a

Fig. 1b

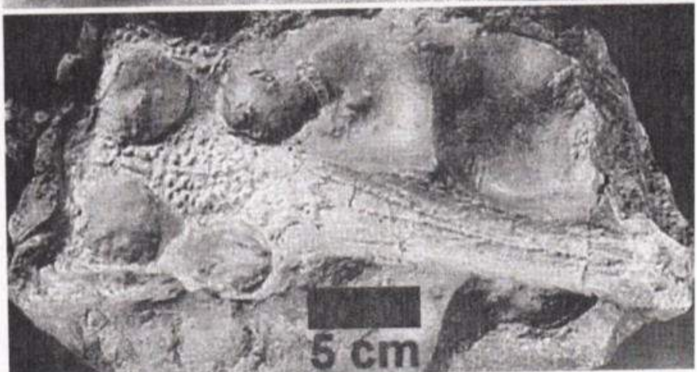


Fig. 2

Fig. 3

PLATE 7

Gavialis gangeticus GMELIN, 1789

Fig. 1. Specimen SFP – 137. Ventral view of fragmentary mandibular rostrum.

Fig. 2. Specimen E – 11. Fragmentary mandibular rostrum,
a – occlusal view,
b – ventral view.

Fig. 3. Specimen BMNH – 36727 (cast: E – 22). Lateral view of skull with anterior broken cranium and splenials

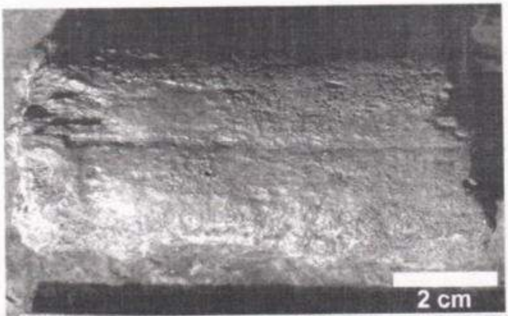


Fig. 1

Fig.2a

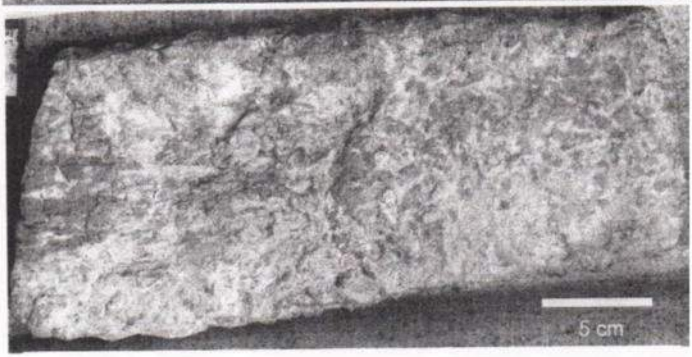


Fig. 2b

Fig. 3

PLATE 8

Gavialis gangeticus GMELIN, 1789

Fig. 1. Specimen BMNH - 36727 (cast: E – 22). Anteriorly broken skull with cranium and splenials,
a – dorsal view,
b – ventral view.

Fig. 2. Specimen BMNH - 40695 (cast: E – 184). Anteriorly broken skull with cranium and splenials,
a – dorsal view,
b – ventral view.

Fig. 3. Specimen E – 25. Dorsal view of posterior part of cranium.

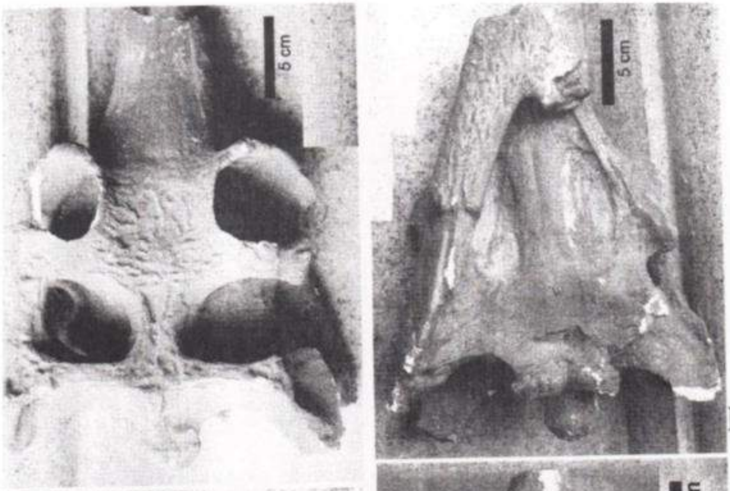


Fig. 1a,b

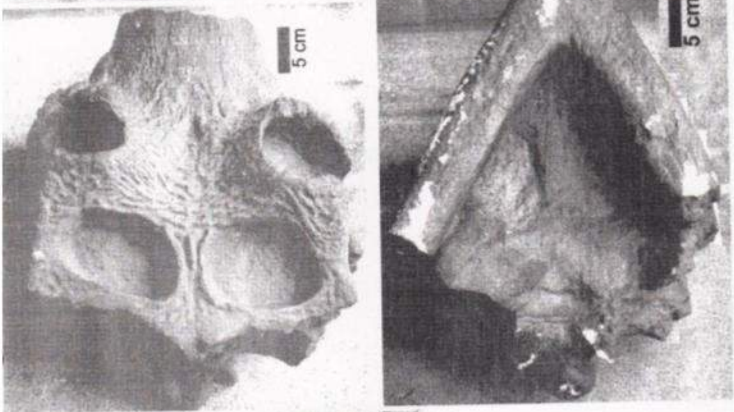


Fig. 2a,b

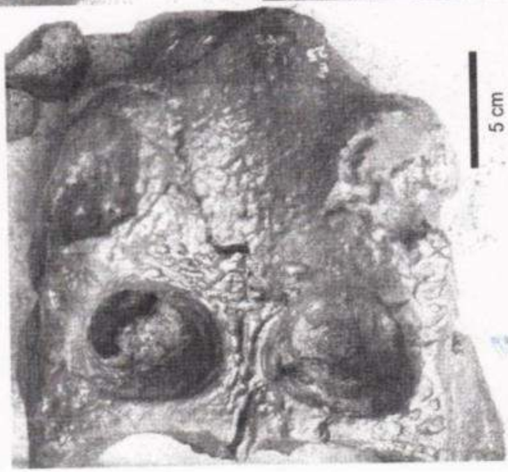


Fig. 3

PLATE 9

Gavialis gangeticus GMELIN, 1789

Fig. 1. Specimen E – 14. Anterior most part of cranial rostrum,
a - dorsal view,
b – ventral view.

Fig. 2. Specimen IM – 5 (Temporary catalogue number, the specimen is in Indian Museum). Occlusal view of complete mandibular rostrum with splenials.

Gavialis cf. *gangeticus* GMELIN, 1789

Fig. 3. Specimen NHM/TU 1989/28 (cast: BSP 1989 XVIII 9). Ventral view of anterior maxillary part of snout.

Fig. 4. Specimen E – 20 a. Ventral view of fragmentary anterior premaxillary part of snout.

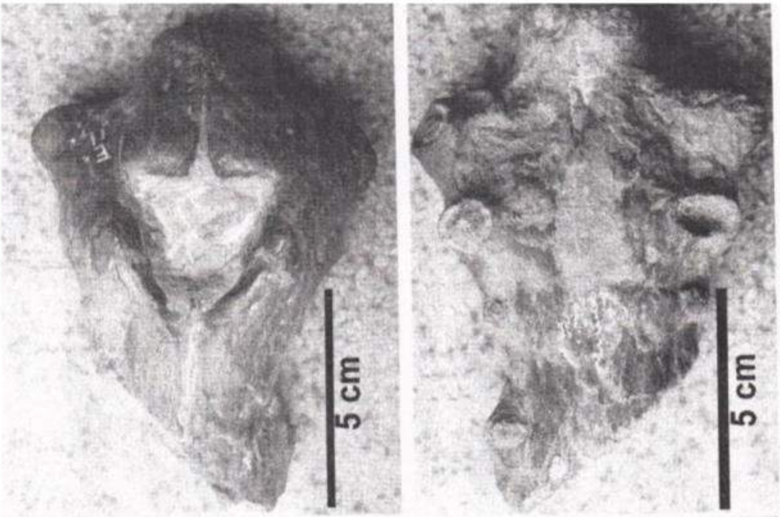


Fig. 1a,b

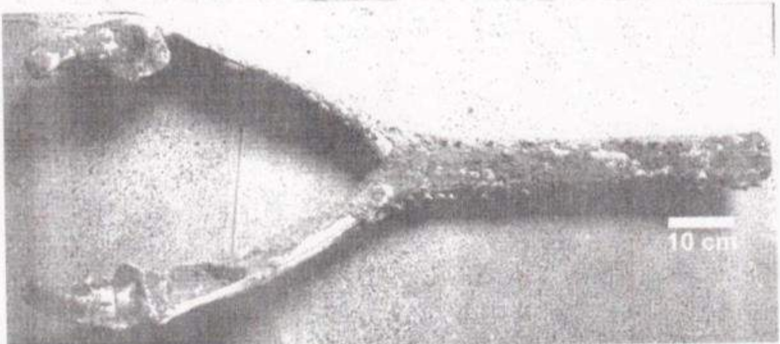


Fig. 2

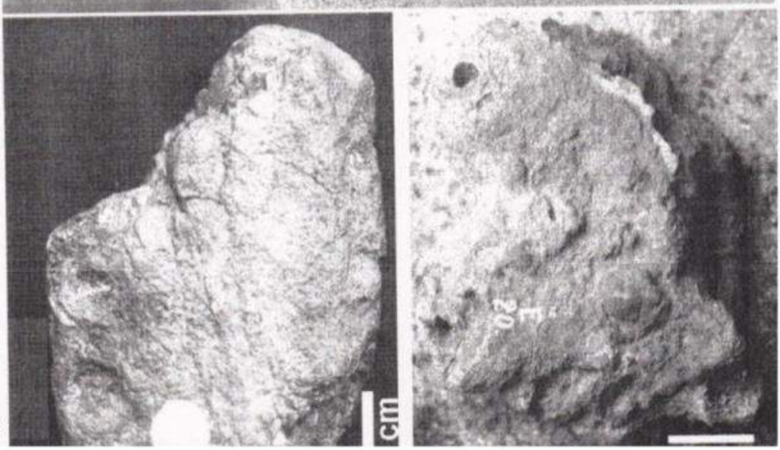


Fig. 3, 4

PLATE 10

Gavialis cf. *gangeticus* GMELIN, 1789

Fig. 1. Specimen E – 20
(b). Ventral view of fragmentary anterior premaxillary part of snout.

Fig. 2. Specimen WIF/A 461. Fragmentary posterior part of cranial rostrum,
a – ventral view,
b – dorsal view.

Fig. 3. Specimen WIF/A 460. Posterior part of cranium,
a – ventral view,
b – dorsal view.

Fig. 4. Specimen WIF/A 459. Dorsal view of a fragmentary posterior part of cranium.

Fig. 1, 2a

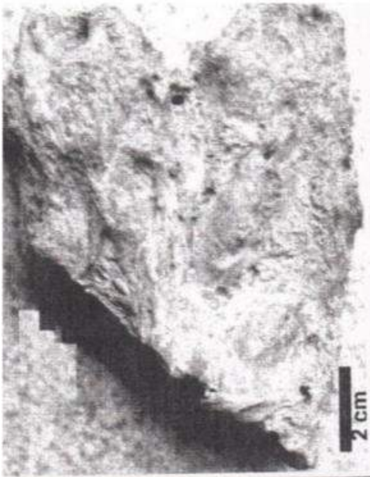


Fig. 2b, 3a

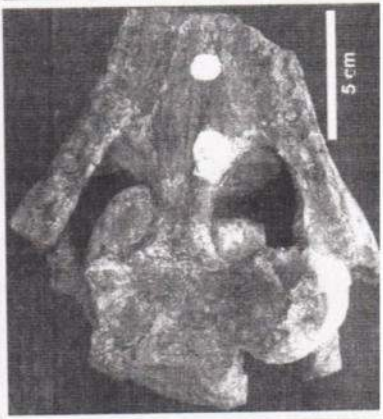
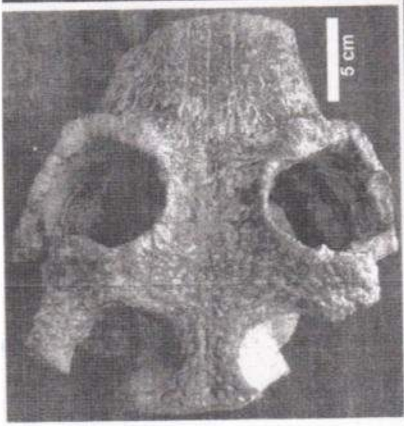


Fig. 3b, 4



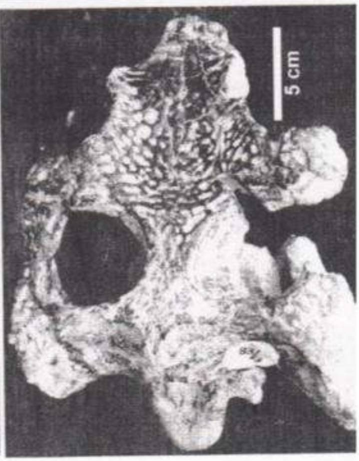


PLATE 11

Gavialis cf. *gangeticus* GMELIN, 1789

Fig. 1. Specimen WIF/A 459. Ventral view of fragmentary posterior part of cranium.

Gavialis browni MOOK, 1932

Fig. 2. Specimen WIF/A 458. Fragmentary maxillary part of snout,
a- ventral view,
b – dorsal view.

Fig. 3. Specimen E – 13. Ventral view of fragmentary posterior maxillary part of snout.

Fig. 4. Specimen E – 24. Ventral view of fragmentary mandibular rostrum.

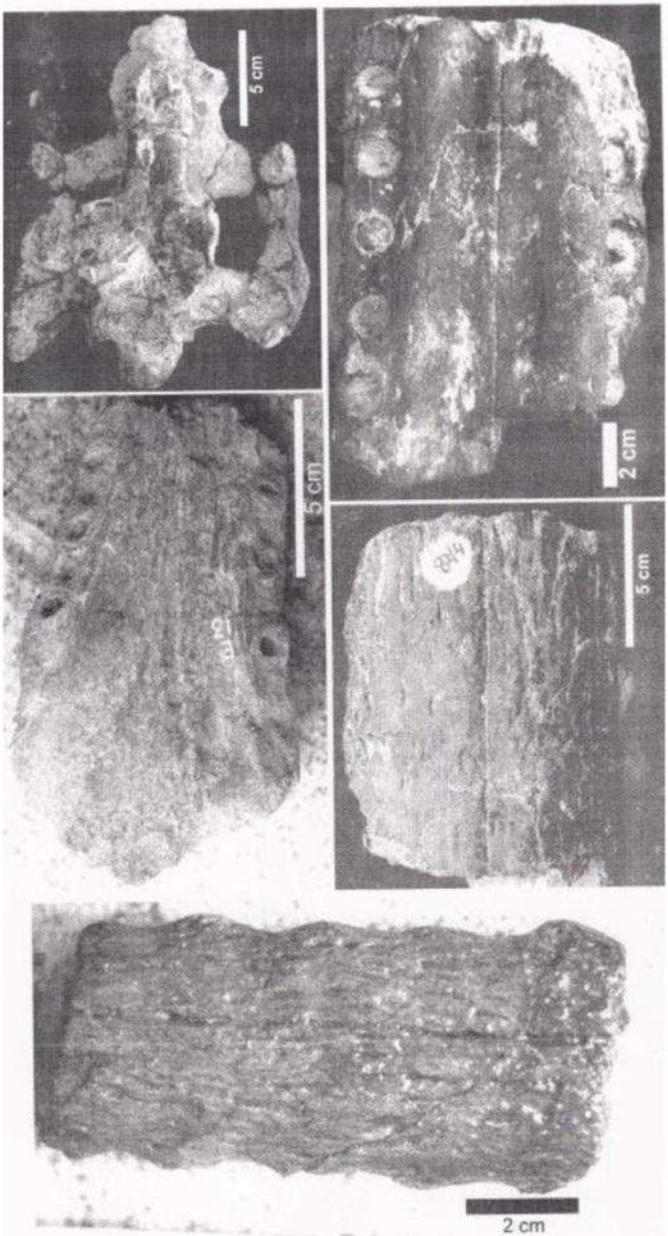


Fig. 1, 2a

Fig. 3, 2b

Fig. 4

PLATE 12

Gavialis browni MOOK, 1932

Fig. 1. Specimen E – 24. Occlusal view of fragmentary mandibular rostrum.

Gavialis curvirostris LYDEKKER, 1886

Fig. 2. Specimen E – 16. Occlusal view of maxillary part of snout.

Gavialis curvirostris gajensis PILGRIM, 1912

Fig. 3. Holotype (E – 222). Ventral view of posterior broken cranial rostrum.

Fig. 4. Specimen E – 223. Occlusal view of fragmentary mandibular rostrum.

Fig. 1

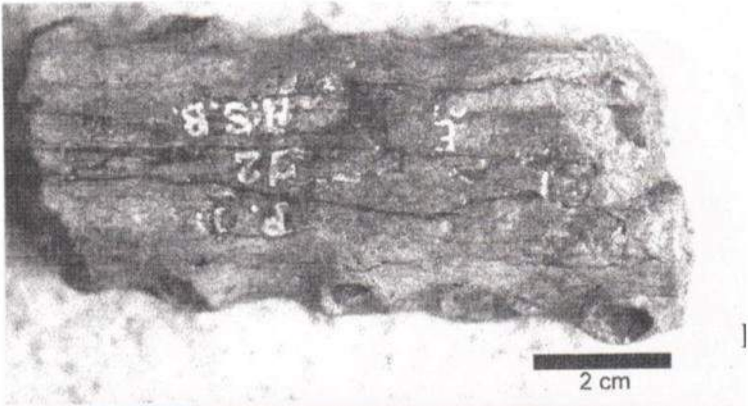


Fig. 2

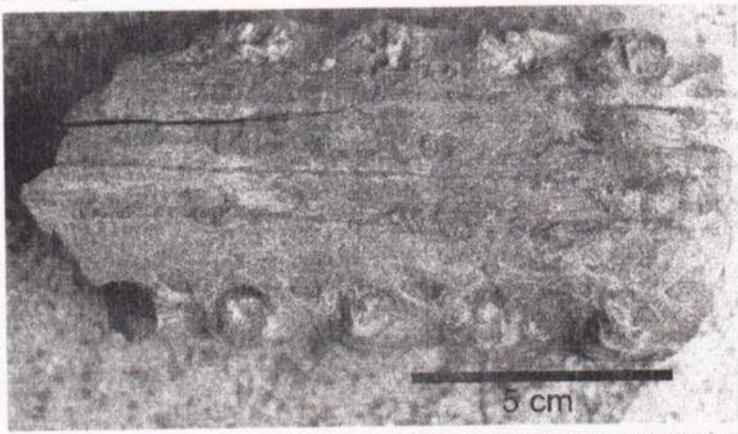


Fig. 3

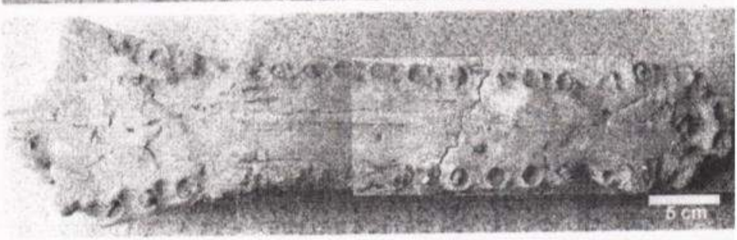


Fig. 4

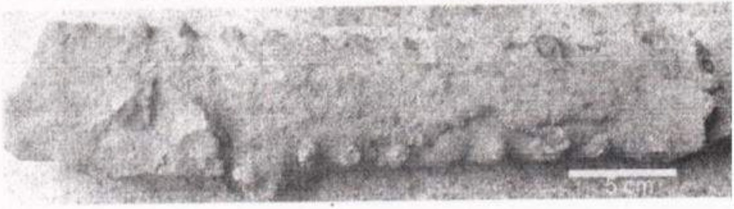


PLATE 13

Rhamphosuchus crassidens FALCONER & CAUTLEY, 1840

Fig. 1. Holotype BMNH – 39802 (cast: E – 183). Dorsal view of cranial rostrum. The specimen has upper and lower jaws intact.

Fig. 2. Specimen WIF/A 464. Fragmentary maxillary part of snout,
a – ventral view,
b – dorsal view.

Fig. 3. Specimen NHM/TU 1989/27 (cast: BSP 1989 XVIII 8). Dorsal view of premaxillary part of snout.

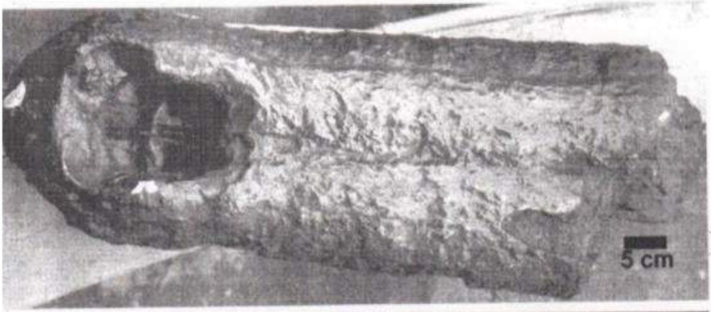


Fig. 1

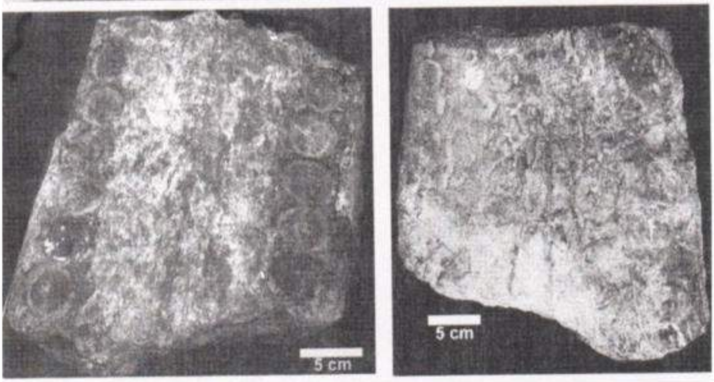


Fig. 2a,b

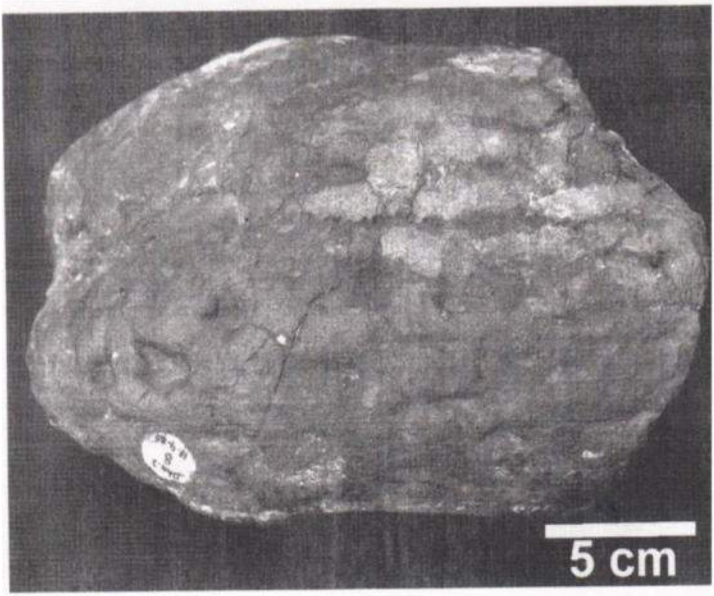


Fig. 3

PLATE 14

Rhamphosuchus crassidens FALCONER & CAUTLEY, 1840

Fig. 1: Specimen NHM/TU 1989/27 (cast: BSP 1989 XVIII 8). Ventral view of premaxillary part of snout.

Fig. 2: Specimen NHM/TU 1989/27 (cast: BSP 1989 XVIII 8). Anteriosinistral part of premaxillary showing fourth replacing tooth.

Fig. 3: Specimen NHM/TU 1989/32 (cast: BSP 1989 XVIII 10). Isolated tooth,
(a) –front view,
(b) – lateral view.

Fig. 4: Specimen NHM/TU 1989/33 (cast: BSP 1989 XVIII 11). Isolated tooth,
(a)– lateral view,
(b)– front view.

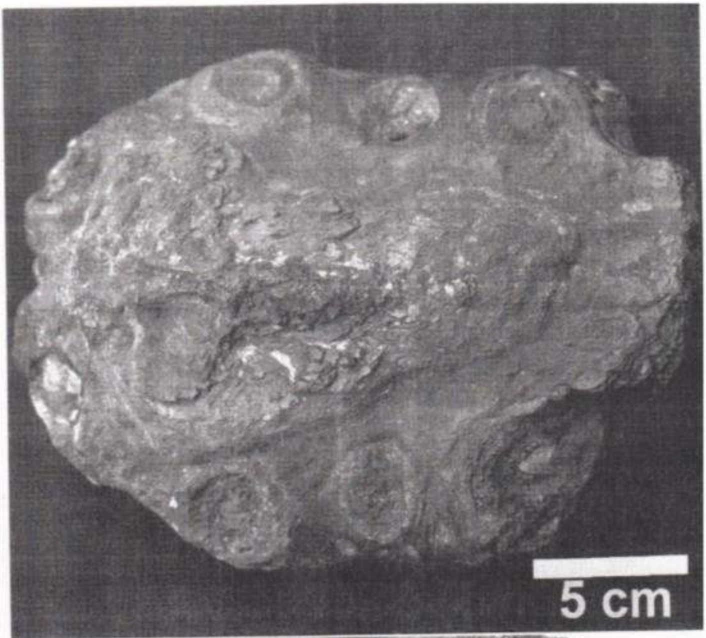


Fig. 1

Fig. 2

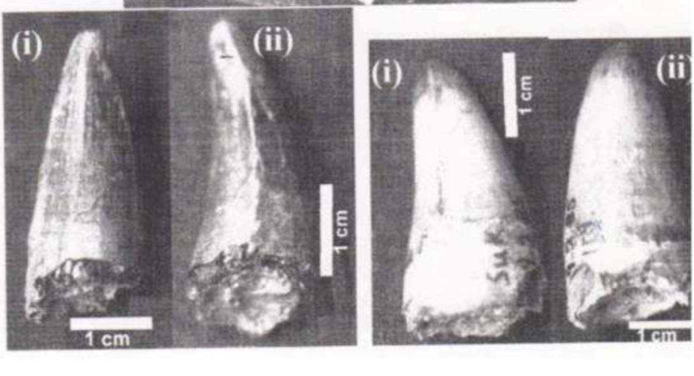


Fig. 3a,b, 4a,b

Special Part – Colour photo plates

We show here in an extraordinary way some selected fossils in colour. The material is described in the text and figured in the black-white plates. The black and white plates added to both chapters were done at the former Fuhlrott-Museum and neither the original negatives nor photographs were respected with the Museum' s demolition.

Our intention is to show to the reader the fine and real quality and also the difficult fossilisations, in how specimens are found or stored at the various places. It also shall be a small compensation of the only as drafted plates shown in the illustrations/plates of the two different chapters. Many of the colour photographs were taken by H.S. during various fieldtrips and visits to institutes in India, as sampling ideas of the material. Later it came with all casted material to a comprehensive collection that is now described and presented by both authors.

These plates also contain photos of the collaborating colleagues Dr. Rajeev Patanaik and Dr. Rahul Srivastava and technical assistant Mr. Peter Veith, from Palaeontological State Collection Munich, as well as of late Dr. Gudrun Corvinus who contributed a lot in collecting Siwalik fossil material which she purchased mostly from local collectors.

The senior author, HS, is tremendously grateful to WACKER CHEMIE Burghausen that not only donated the material for casting but also delivered it free of costs to the project to Nepal. Others not to forget with acknowledgements, are UHU (glueing products) and AKEMIE, who both have contributed and supported to facilitate the project.

Plate I/1 *Megalochelys sivalensis*, specimen restored and exposed in American Museum of Natural History, New York. Photo:https://de.wikipedia.org/wiki/Atlasschildkr%C3%B6te#/media/File:Colossochelys_atlas.jpg

Plate I/2 *Megalochelys sivalensis*. Digitally restored from Plate II/1. Indian Museum.

Plate II/1. *Megalochelys sivalensis*, Indian Museum.
a- Posteriolateral view, b- lateropygal view, c- frontal view

Plate III/1. *Megalochelys sivalensis*, Panjab University.
a- Frontal view, b- lateral view, c- dorsal view

Plate IV/1. *Indotestudo* sp. Saketi Fossil Park.
a- Lateral view, b- dorsal view

Plate V/1. *Omegachelys sahnii* nov. gen. nov spec. Saketi Fossil Park.

Plate VI/1. *Omegachelys sahnii* nov. gen. nov spec.
a- Lateral, b- dorsal. Wadia Institute.

Plate VII. *Geoclemys hamiltonii*. Wadia Institut

Plate VIII. *Geoclemys hamiltoni*. Specimen from Plate VII. Wadia Institut.

Plate IX. cf. *Geoclemys hamiltonii*. Wadia Institute.

Plate X. *Hardella thurjii*. Wadia Institute.

Plate XI. *Batagur baska*, Indian Museum.

Plate XII. *Hardella thurjii*. Indian Museum; labelled as "PHRAMYS AUFFENBERGI PRASAD" Skull. Piram Conglomerate (Dhokpatan Stage). Piram Island."
Melanochelys trijuga. Indian Museum.

Plate XIII *Lissemys* spec.; plastron. Indian Museum.

Plate XIV *Crocodylus* palaeindicus. Indian Museum.

Plate XV *Crocodylus* cf. *palaeindicus.* Indian Museum.

Plate XVI *Gavialis browni*. Wadia Institute.

Plate XVII *Gavialis* cf. *gangeticus*. Wadia Institute.

Plate XVIII *Gavialis* cf. *gangeticus* Wadia Institute.

Plate XIX *Gavialis* cf. *gangeticus* Wadia Institute.

Plate XX *Gavialis* cf. *gangeticus.* Wadia Institute.

Plate XXI *Rhamphosuchus crassidens*. Wadia Institute & British Museum Natural History.

Plate XXII
1) *Rhamphosuchus crassidens* reconstruction at Saketi Fosssil Park,N-India
2) Shell of big fossil batagurid turtle at Saketi Fossil Park showing a stage of fossil conservation typical for that area.
3) Drs. R. Srivastava (left) & R. Patnaik at Saketi Fossil Park helping with preservation for casting and studying fossil reptile material

Plate XXIII
1) At Rato khola with a student group from Munich University (LMU) searching for fossils, sampling and screen washing.

2) Late Dr. GUDRUN CORVINUS, former archeologist and palaeontologist at Natural History Museum, Tribhuwan University - Kathmandu

Plate XXIV.

1) Senior author (H.S together with D. Fuchs from Zool. State Collection (ZSM) Munich preparing fossils for casting with material kindly donated and delivered by Wacker Chemie, D-Burghausen.

2) PETER VEITH, Technical assistant from Palaeontol. Institute & Bavarian State Collection, making casts of fossil turtles being assisted by Drs. R. PATANAIK & R. SRIVASTAVA (right)

PLATE I *Megalochelys sivalensis*

1

American Mus. Nat. History

2

Digitally restored from Plate II/1c Indian Museum

PLATE II *Megalochelys sivalensis* Indian Museum

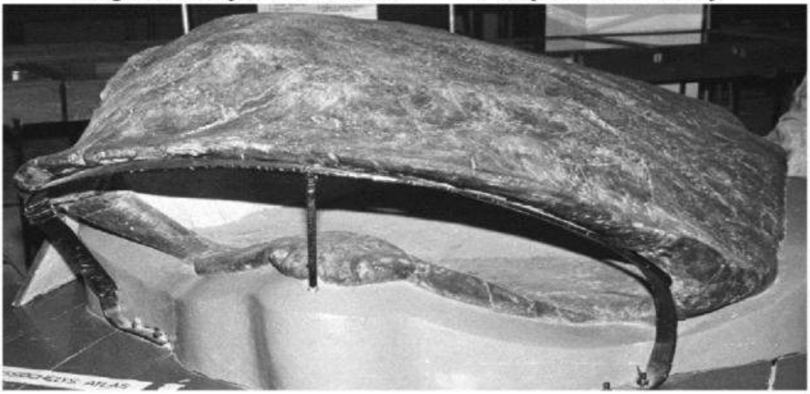
1a

1b

1c

PLATE III

Megalochelys sivalensis Panjab University



1a

1b

1c

PLATE IV

Indotestudo sp. Saketi Fossil Park

1a

1b

PLATE V *Omegachelys sahnii* Saketi FP

1

2

PLATE VI *Omegachelys sahnii* Wadia Institute 1a

1a

1b

PLATE VII

Geoclemys hamiltonii Wadia Institute

PLATE VIII

Geoclemys hamiltonii Wadia Institute

1a

1b

PLATE IX

cf. *Geoclemys hamiltonii* Wadia Institute

PLATE X

Hardella thurjii Wadia Institute

PLATE XI

cf. *Batagur baska* Indian Museum

PLATE XII

Hardella thurjii Indian Museum

Melanochelys trijuga Indian Museum

PLATE XIII

Lissemys sp.; plastron Indian Museum

PLATE XIV

Crocodylus palaeindicus Indian Museum

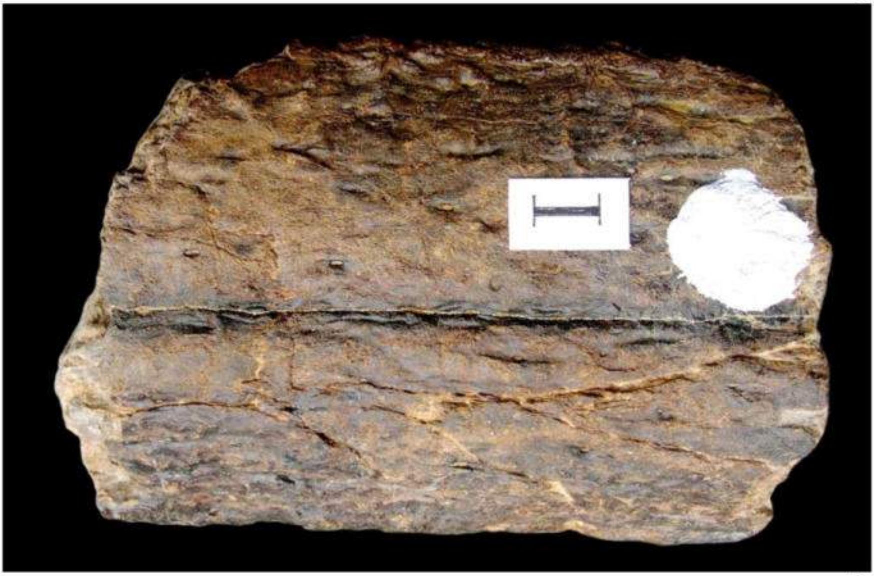
PLATE XV

Crocodylus cf. *palaeindicus* Indian Museum

PLATE XVI

Gavialis browni Wadia Institute

1a

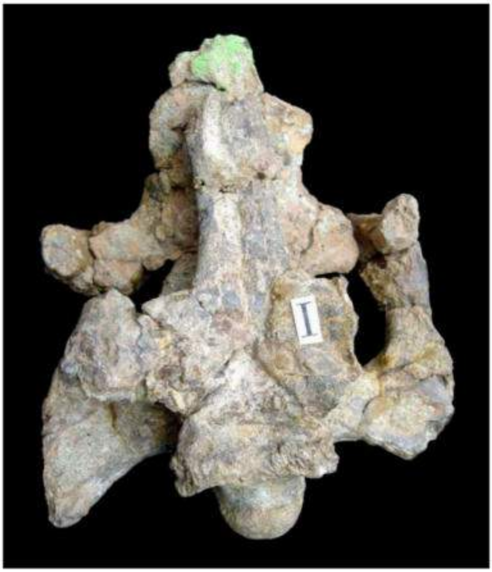


1b

PLATE XVII

Gavialis cf. *gangeticus* Wadia Institute

1a



1b

PLATE XVIII

Gavialis cf. *gangeticus* Wadia Institute

1a

1b

PLATE XIX

Gavialis cf. *gangeticus* Wadia Institute

1a

1b

PLATE XX

Gavialis cf. *gangeticus* Indian Museum

1

2

PLATE XXI *Rhamphosuchus crassidens*

1a

1b
Wadia Institute

British Museum Nat. History

PLATE XXII

1,2,3 top to bottom

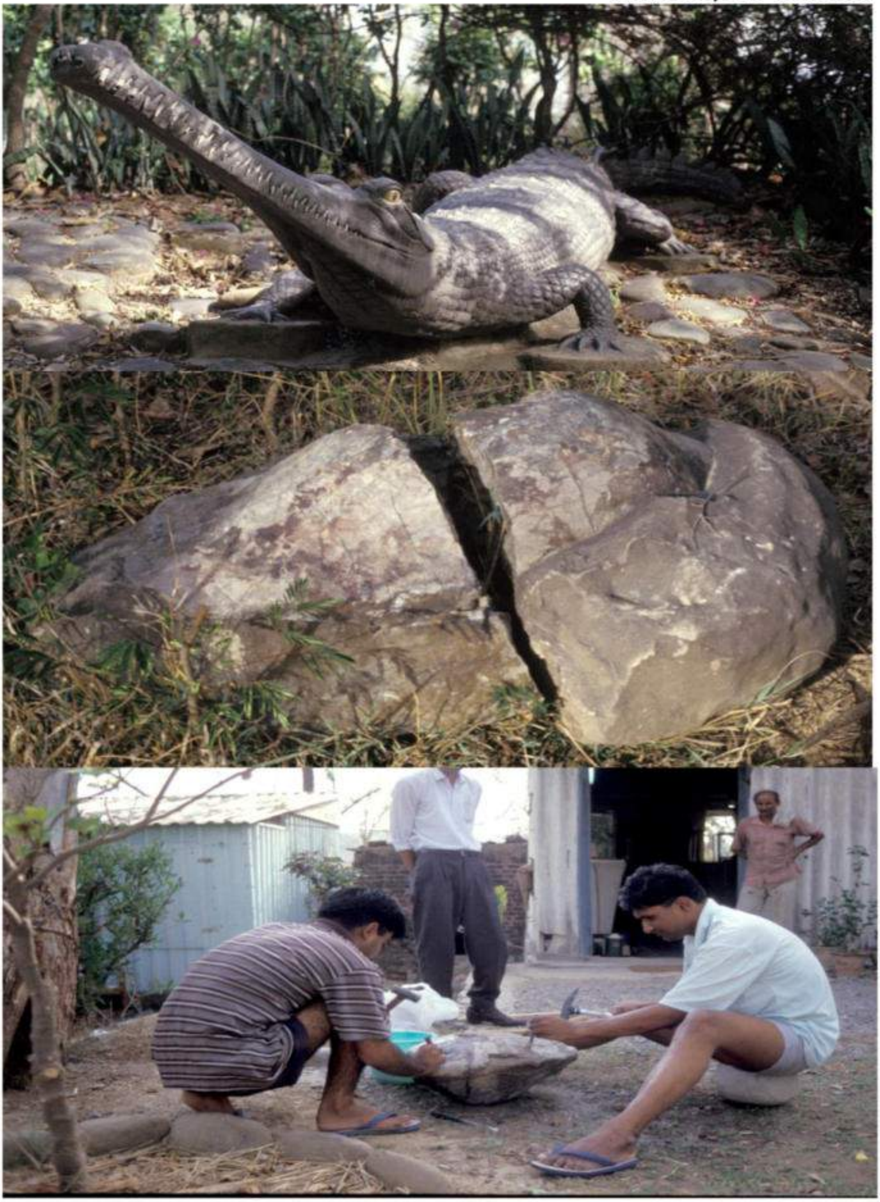


PLATE XXIII

PLATE XXIV