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LARGE SOFT-SHELLED TURTLES FROM THE UPPER PLIOCENE ROCKS OF SAKETI (DISTRICT, SIRMAUR), HIMACHAL PRADESH, INDIA

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ABSTRACT

The Tatrot Formation exposed near Siwalik Fossil Park, Saketi (Himachal Pradesh) has yielded carapace fragments of large trionychid turtles. The characters, size of the fragments and hypothetical reconstruction of the carapace indicate towards the presence of large trionychids, *Chitra* and *Aspideretes*. The genus *Chitra* (*C. indica, C. chitra*) is characterized by a large, flat and wider than long carapace, absence of peripherals and large 8th pleural, which meet at midline, whereas, genus *Aspideretes* is characterised by round to oval carapace, a preneural and neural or one or two pairs of neurals separating the first pair of pleurals and pitted surface of carapace.

INTRODUCTION

The study of the South Asian turtles, especially that of the Siwalik turtles was initiated by Falconer and Cautley (1837, 1844), which was later continued by Lydekker until the end of the 19th century (1885, 1886, 1887 and 1889). The work done by 19th Century workers was purely taxonomical, based on the morphological characteristics as visible in the hand specimens. Following this approach, a number of Siwalik turtle genera and species were erected by Lydekker (1886). Lydekker (1886) differentiated various genera and species on the basis of trivial characters, for example he used even a slight change in the shape of epiplastron of *Megalochelys* (*Colossochelys*, Testudinidae) as one of the distinguishing characters. Some specimens described by the 19th century workers were restudied and revised by Das (1991, 1995). More recently Srivastava and Schleich (2001) carried out a comprehensive study, which includes entire Siwalik turtle material, housed at various Institutes of the world, and proposed a revised taxonomic status of batagurid, testudinid and trionychid turtles of Siwaliks of the Indian Subcontinent.

For ascertaining phylogenetic relationship of turtles, cranial features have more relevance as compared to the carapacial features (Gaffney and Meylan, 1988). However, the fossil turtle material is mostly represented by the partial or complete carapaces, plastra and very rarely skulls. In an extensive study, Gardner and Russell (1994) assessed the taxonomic and phylogenetic utility of carapacial features of turtles especially of trionychid turtles. However they also reiterated the significance of cranial and post-cranial features, but proposed guidelines using 22 carapacial features in assessing the taxonomic position and phylogenetic relationships of fossil (Meylan *et al.*, 1990) and living trionychids (Meylan, 1985, 1987, Gardner, 1992).

The present work deals with the taxonomic status of fragmentary carapacial material recovered from the Upper Pliocene Tatrot Formation of the Middle Siwalik sequences exposed near Siwalik Fossil Park, Saketi of district Sirmaur, Himachal Pradesh (figs. 1 and 2). The bony fragments represent two genera of large trionychid turtles, *Chitra indica* and *Aspideretes* cf. *gangeticus*. The size of fossil *Chitra* (total disc length approx. 600 mm) and *Aspideretes* (maximum disc length approx. 540 mm) is comparable to their living counterparts (living *Chitra* : 550 mm and living *Aspideretes* : 480 mm). The size of the fossil material described here is maximum among the so far known fossil and living trionychids. The larger size of the specimens may be related to the open environment in the area during the late Pliocene time.

The material is catalogued in the collection of the second author of the paper in the Vertebrate Paleontology Laboratory, CAS in Geology, Panjab

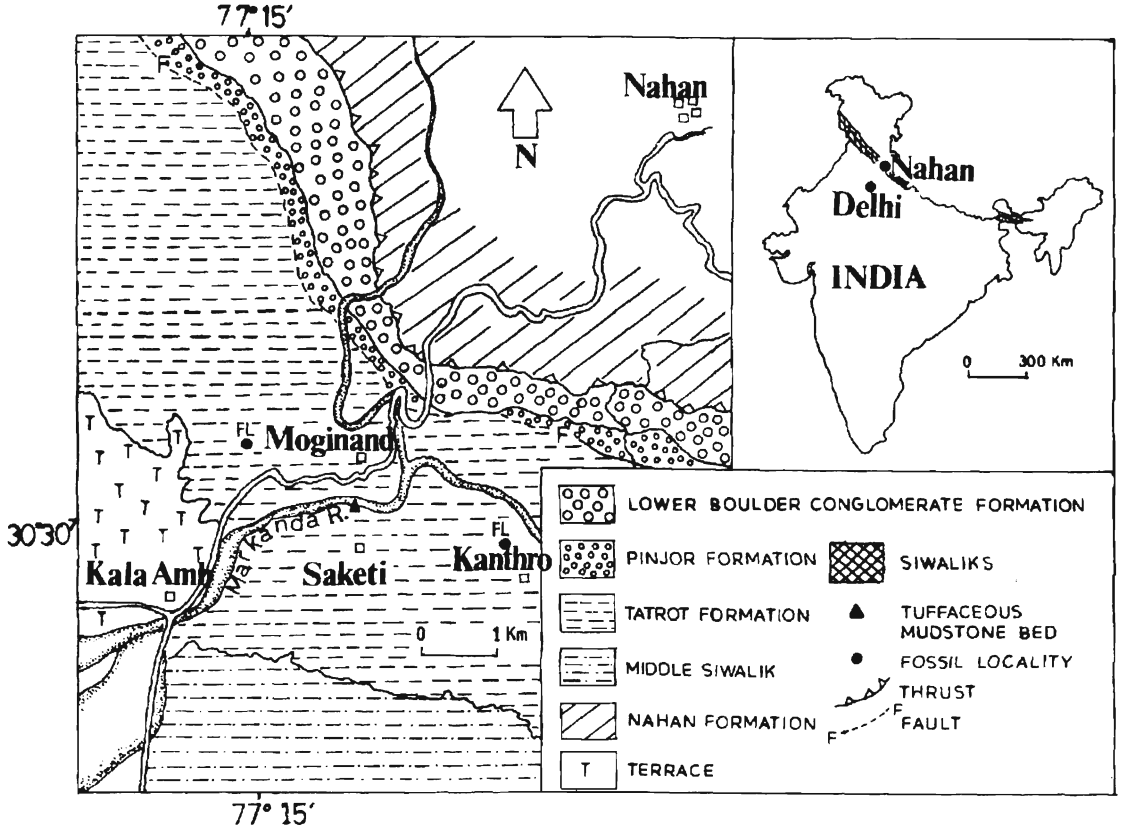


Fig. 1. Geological map of the Saketi area showing fossil turtle locality (modified after Verma and Verma, 1969; Patnaik 2001).

University, Chandigarh (VPL/RP/ST = Vertebrate Palaeontology Laboratory/Rajeev Patnaik/Siwalik Turtle).

The terms for describing the carapacial characters were used following Schleich (1980) and the measurements were taken following Gardner & Russell (1994).

SYSTEMATIC DESCRIPTION

Order **Testudines** Linnaeus 1758

Suborder **Casichelydia** Gaffney, 1975

Infraorder **Cryptodira** (Cope, 1868)

Parvorder **Eucryptodira** Gaffney 1975

Superfamily **Trionychoidea** Gray, 1870

Family **Trionychidae** Bell, 1828 (Synonym: Trionychoidea Fitzinger, 1826)

The shell depressed and covered with a continuous skin (Lydekker, 1885). The shape of the bony part of the carapace of trionychids varies from a highly arched rectangle to a nearly flat circular disc. *Lissemys* is most similar to other freshwater cryptodires, having bony carapace that is longer than wide; most *Aspideretes* have an oblong to circular bony carapace, whereas, genus *Chitra* has nearly flat and actually wider than long carapace (Meylan, 1985, 1987). As the disc becomes flatter and wider, it also constitutes a smaller portion of the total carapace, which is a derived condition (Meylan, 1987).

The horny scutes are absent; the reduction of 8th pleural is common which is a derived condition however, cyclanorbines and Old World trionychines have large 8th pleural (Meylan, 1987). There is a trend toward the loss of the 8th pleurals in New World forms (Meylan, 1985). The most posterior pair of the pleurals may meet at midline; no pygals or metaneurals. The peripherals are absent (except for possible vestiges in *Lissemys*). The distal end of the ribs is projecting freely; a plastral bridge is absent.

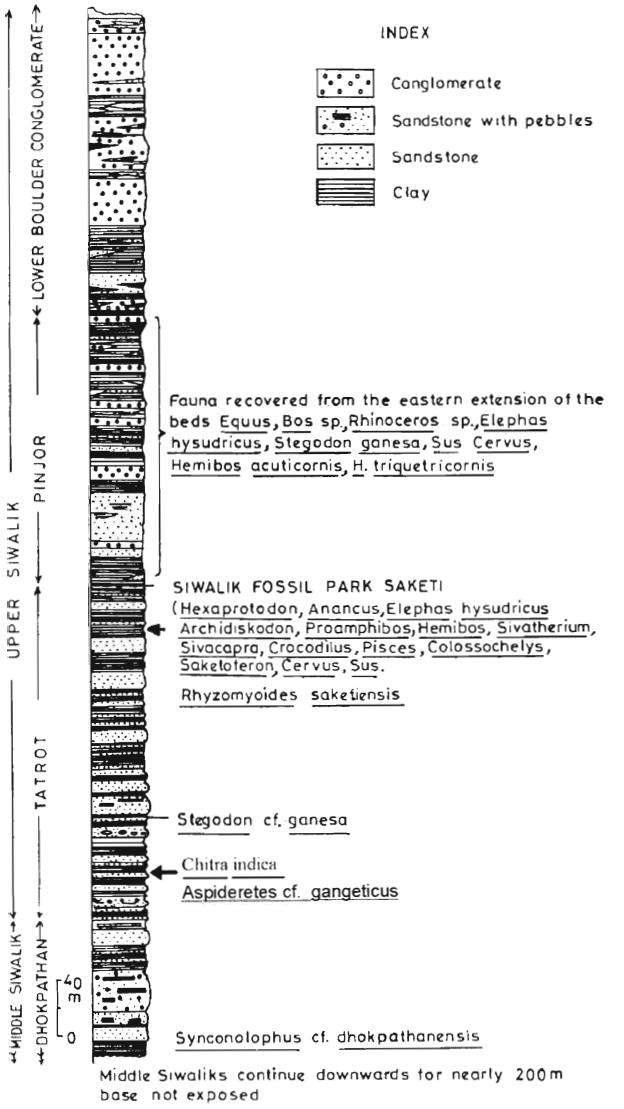


Fig. 2. Lithological column showing the turtle horizon in the south of Saketi (modified after Verma and Verma, 1969; Patnaik, 2001).

The plastron is somewhat reduced with a central lacuna in modern forms and the lateral fontanelles; as the callosities in the plastron are reduced, so are the sutures between them. Thus, the presence of callosities in the plastron is interpreted as primitive condition. Seven callosities are considered to be primitive condition and an increase or a decrease in the number is considered to be a derived condition (Meylan, 1985). The anterior portion of the plastron is highly modified; there are paired crecentric structures present apparently being neomorphs; a median V-shaped fused epiplastral callosity, an entoplastron is absent (an entoplastral callosity 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 *Aspideretes*. A small palatine fenestra is present. The pterygoid is broad, in contact with the maxillary, separated by the basiosphinoid, which is in contact with the palatines. The dentary reaches upto the posterior end of the jaw, laterally; the neck is long and retractile; there are no biconvex centra in the neck. The limbs are paddle-like; there are three claws only; the feet are elongate (Romer, 1956). The 'soft shell turtles' are seldom found far from water and feed on both plant and animal matter; *Chitra* is considered to be the most developed piscivore trionychid (Meylan, 1987). Many trionychids are aggressive, capable of inflicting serious injury (Das, 1991; 1995).

Genus ***Aspideretes*** Hay, 1904 [*Trionyx* (*Aspideretes*) Mlynarski, 1976]

The round to oval carapace (distinguishable from round and flattened carapace of *Chitra*). Several longitudinal rows of tubercles occur on the juvenile carapace, but absent on adult carapace, which is smooth. A preneural and neural or one or two pairs of neurals separate the first pair of pleurals (Ernst and Barbour, 1989). It can be differentiated from *Chitra*, in which the first pair of pleurals is separated by a single neural. The 8th pair of pleural is large and meets at the midline. The carapace bones have pitted surface. Five callosities are present on the plastron (4 are present in *Chitra*); callosities are large in the region of the hyo-hypoplastra, xiphiplastra and epiplastra. The preplastra nearly touch in front of the epiplastra which lie at obtuse or right angle to the midline; whereas in *Chitra* the preplastra are widely separated and epiplastra lie at an acute angle to the midline (Ernst and Barbour, 1989; Das, 1991 and 1995).

Aspideretes can be distinguished from *Lissemys* by the absence of peripherals, prenuchals and an entoplastral callosity (present in *Lissemys*).

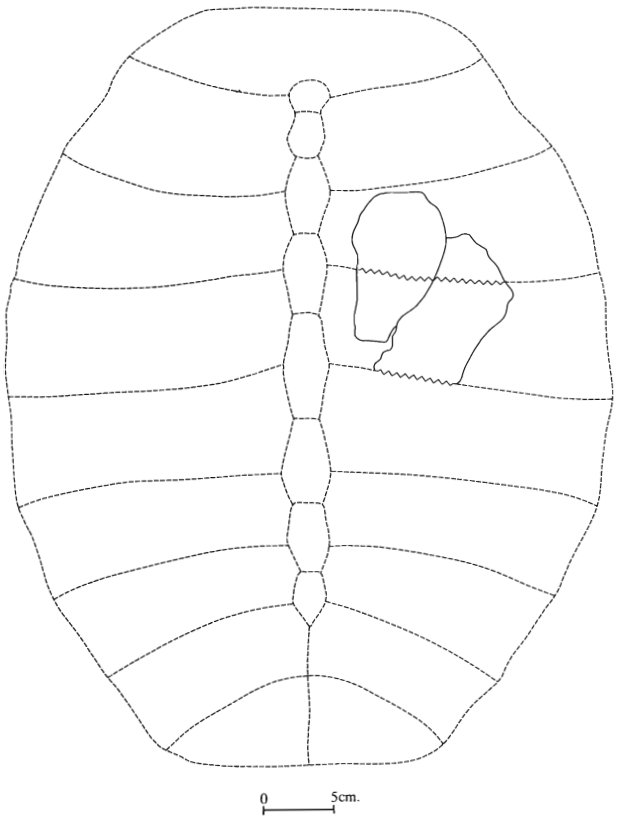


Fig. 3. Dorsal view of a reconstructed disc of larger *Aspideretes* cf. *A. gangeticus*.

Aspideretes cf. *gangeticus* Cuvier, 1825

(Pl. I, figs. a-g; figs. 3-4)

Original Name: *Trionyx gangeticus*

Syntype: 4 specimens MNHN 4148, 9387, 1887-838, A5226

Type Locality: India, river Ganges (according to Gray, 1831 "1830-35" : Plate 80)

Distribution: Indus and Ganges and Mahanadi river basins in Pakistan, Northern India Southern Nepal and Bangladesh.

Diagnosis: It is characterized by a prenural and a neural or two neurals separating the first pair of pleurals. The number of neurals may be 8 or 9. The 8th pair of the pleural is large and meets at the mid line. The carapace of an adult A. *gangeticus* is larger than the carapace of *A. leithii* and *A. hurum* but smaller than that of *A. nigricans*. In *A. gangeticus* the skull is broad and the mandibular symphysis is shorter than the diameter of the orbits; whereas, in other *Aspideretes* (*A. leithii*, *A. hurum*, and *A. nigricans*) the skull is moderate in size and the mandibular symphysis is equal to or longer than the diameter of the orbits.

This large soft-shelled turtle inhabits deep rivers, streams, and large canals with mud and sand bottoms, where it buries itself in the mud. It probably prefers turbid water (Minton, 1966). The Indian soft-shelled turtle is an aggressive species, which needs to be handled with extreme caution. It is an omnivorous species.

Horizon and Locality : Tatrot Formation in the South of Siwalik Fossil Park, Saketi (District Sirmaur), Himachal Pradesh, India.

Age: Upper Pliocene

Description: The material is represented by the partially preserved 6th pleural, partially broken and sutured right 2nd, 3rd and 5th pleural (VPL/RP/ST-03, ST-05 and ST-09 respectively).

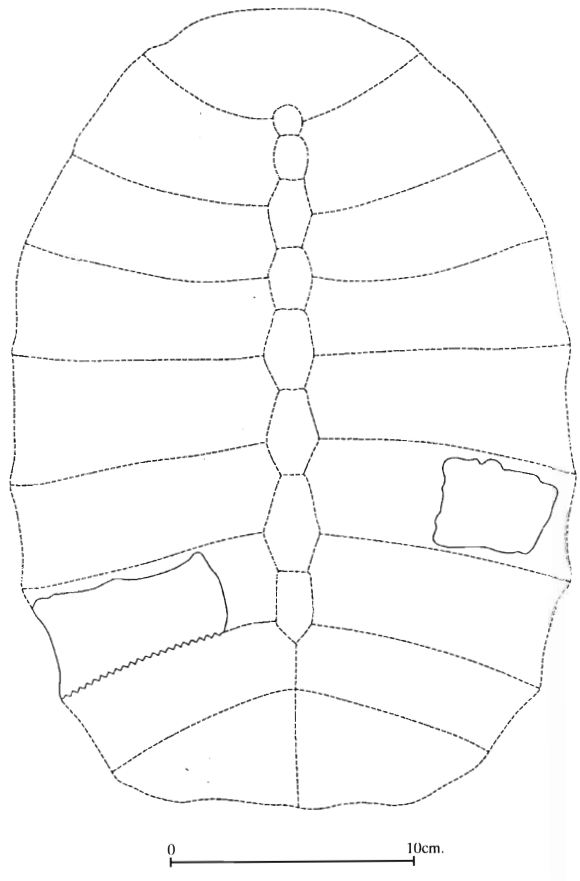


Fig. 4. Dorsal view of a reconstructed disc of smaller *Aspideretes* cf. *A. gangeticus*.

The specimen VPL/RP/ST-03 is represented by the distal part of the left 6th pleural. A small proximal and anterior portion of the pleural is broken. On the surface the pits are visible and the sculpture is distinguishable from that of *Chitra*. The distal margin of the pleural is concave whereas that of *Chitra* is angular or deeply convex. The distal end of the pleural does not show any traces or the presence of marginals (present in *Lissemys*). The pleural outline is slightly concavely twisted possibly due to post-mortem deformation. If the twisting is ignored, the pleural must have been either flat or broadly concave (*sensu* Gardner and Russell, 1994). The posterior margin of the pleural is almost flat or feebly concave. On the ventral surface of the pleural no trace of rib is visible. The preserved length of the pleural is approximately 83 mm and antero-posterior width is approximately 52 mm.

The specimen VPL/RP/ST-5 is a large specimen represented by antero-posteriorly almost complete right 3rd pleural and anteriorly broken 2nd pleural. The proximal margin and distal 1/3rd of the pleurals are also broken. The surface sculpture of the specimen is identical to that of VPL/RP/ST-03. But, VPL/RP/ST-5 (a reconstruction suggests the total disc length approximately 540 mm) is much larger than VPL/RP/ST-03 (total reconstructed disc length approximately 362 mm). The size variation in these specimens may be a result of sexual dimorphism or different ages of the individuals. The antero-posterior width of the 3rd pleural is approximately 95 mm. It is not possible to determine the size of the 2nd pleural. However, the maximum preserved width (antero-posterior) of the 2nd pleural is approximately 75 mm. The posterior margin of the 3rd pleural is not straight but slightly wavy. It is feebly concave medially and convex proximally. The anterior margin of the bone is straight.

The maximum preserved length of the specimen is approximately 170 mm and maximum preserved width is approximately 140 mm. On the internal surface of the pleurals the proximal portion of the ribs is visible. The proximal end of the rib is not flat but crested and shows a tendency of a strong suture with the vertebral centra.

The specimen VPL/RP/ST-09 represents a very small portion of the 5th pleural. The bone is nearly rectangular in shape. The margins of the bone are not preserved but it is possible to determine the nature of the margins. The posterior margin of the bone is slightly concave whereas the anterior margin is slightly convex. The total preserved length of the bone is approximately 50 mm and the width is approximately 35 mm. On the internal surface of the bone no features are visible due to thick concretion. The outline of the bone is almost flat. The surface sculpture of the bone is identical to that found in the other specimens of *Aspideretes gangeticus*.

Another partially preserved specimen VPL/RP/ST-08 (Pl. 1, fig. 8) is poorly preserved and represents a middle portion of a pleural. It is not possible to identify the location of the pleural on the carapace but the surface sculpture; shell thickness and general similarity with the specimen VPL/RP/ST-03 suggests its tentative inclusion in *Aspideretes*.

Genus ***Chitra*** Gray, 1844 (Narrow-headed soft-shelled Turtle)

Meylan (1987) and Das (1991) redefined the genus on the basis of the following characters:

- The skull long and narrow with eyes far forward
- The anterior edge of the prezygapophysis of the first thoracic vertebra lies at the anterior edge of the carapace.
- The foramen intermandibularis caudalis is never enclosed by the prearticular.
- The intermaxillary foramen is reduced by 7% of primary palate.
- The postorbital bar twice as wide as orbit
- The premaxillary is usually absent

Chitra indica (Gray, 1831)

(Narrow-headed soft-shelled Turtle)

(Pl. I, figs. h-i; Pl. II, figs. a-f; fig. 5)

Original Name: *Trionyx indicus.*

Holotype: Plate 80, Gray (1831 : "1830-35").

Type Locality: India, river Ganges (according to Gray, 1831 "1830-35" : Plate 80).

Distribution: Pakistan, India and Thailand.

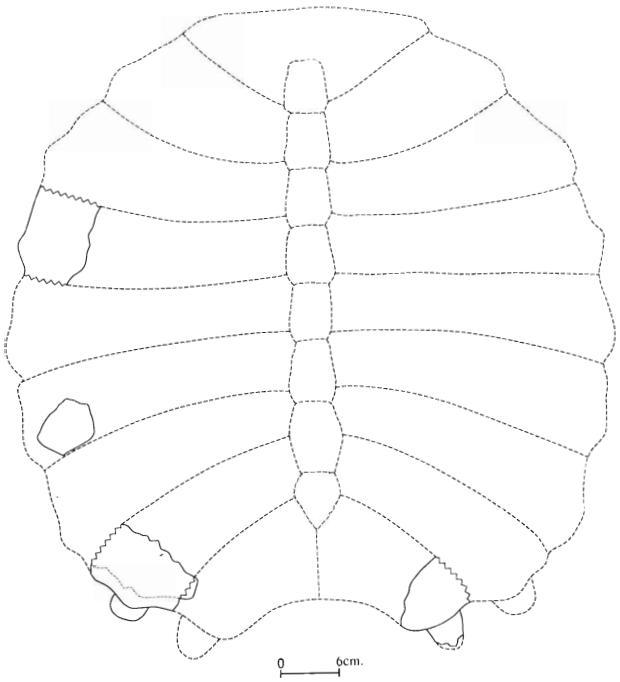


Fig. 5. Dorsal view of a reconstructed disc of Fossil *Chitra*.

Diagnosis: As for the genus.

Horizon & Locality: Tatrot Formation in the South of Siwalik Fossil Park, Saketi (District Sirmaur), Himachal Pradesh, India.

Age: Upper Pliocene

Description: Very large specimens represented by the 3rd, 5th, 7th and 8th pleurals. The size, surface sculpture, negligible curvature (flat carapace) and absence of marginals suggest that the specimen belong to the large Indian freshwater turtle *Chitra*.

The specimen VPL/RP/ST-01 is the left 7th pleural bone. It is a flat bone of which proximal 2/3rd is broken, but it is complete distally and antero-posteriorly. The bone is pentagonal in shape. The typical trionychid surface sculpture is well preserved on the pleural bone. The distal end of the bone is angular. The antero-posterior margins of the pleural are well preserved. The margins are straight. A small anterior portion of the 8th pleural is also preserved. The total preserved length of the pleural is approximately 65 mm and width (antero-posterior) is approximately 92 mm. On the internal surface the rib is strongly sutured to the pleural bone. The distal end of the rib projects out of the rim of the shell. The length of projected part of the rib is approximately 23 mm, and the width (antero-posterior) is approximately 36 mm. A hypothetical line drawn from the summit of the distal end of the pleural divides the rib antero-posteriorly into two halves. The total preserved length of the rib is approximately 83 mm. The width of the rib increases proximally. It is 45 mm at the preserved proximal end. The distal margin of the rib is convex.

The specimen VPL/RP/ST-02 represents left 3rd pleural bone. The outline of the bone is flat. The proximal more than 2/3rd of the bone is not preserved. The surface sculpture is well preserved.

EXPLANATION OF PLATE I

a-g ***Aspideretes*** cf. ***A. gangeticus*** Cuvier.

a. VPL/RP/ST-5. Dorsal view of fragmentary carapace represented by anteriorly broken 2nd pleural (on left in the photograph) and almost complete 3rd pleural (on right in the photograph). Scale Bar = 20 mm.

b. VPL/RP/ST-05. Ventral view of the fragmentary carapace showing proximal margins of the ribs on 2nd pleural (right lower side of the photograph) and 3rd pleural (left lower side of the photograph). Scale Bar = 20 mm.

c. VPL/RP/ST-09. Dorsal view of a small portion of right 5th pleural. Scale Bar = 10 mm.

d. VPL/RP/ST-09. Ventral view of the partially preserved right 5th pleural. The surface is covered with the thick layer of concretions. Scale Bar = 10 mm.

e. VPL/RP/ST-03. Dorsal view of partially broken left 6th pleural. The posterior margin is complete whereas the anterior margin is broken. The distal margin of the bone is concave (upper side of the photograph). Scale Bar = 20 mm.

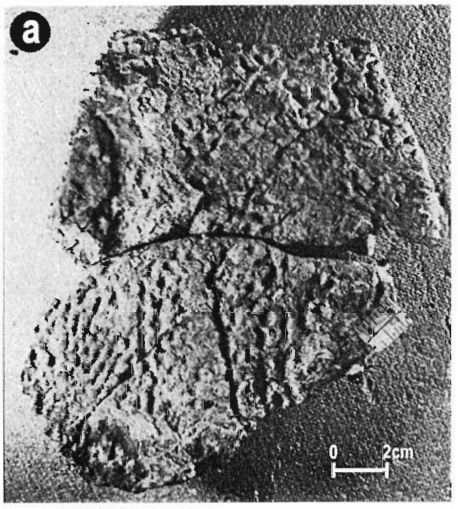
f. VPL/RP/ST-03. Ventral view of the left 6th pleural. No trace of rib is visible on the ventral surface of the pleural. Scale Bar = 20 mm.

g. VPL/RP/ST-08. Dorsal view of a small portion of a pleural bone. It is not possible to decipher the position of this bone on the carapace. The surface sculpture of the bone and also that of other bones is identical. The specimen is referable to *Aspideretes*. Scale Bar = 10 mm.

h-i ***Chitra indica*** (Gray)

h. VPL/RP/ST-01. Dorsal view of a Proximally broken 7th pleural bone. The rib is visible projecting out of the pleural bone. Scale Bar = 20 mm.

i. VPL/RP/ST-1. Ventral view of the fragmentary 7th pleural bone. A prominent and wide rib is visible on the pleural. Scale Bar = 20 mm.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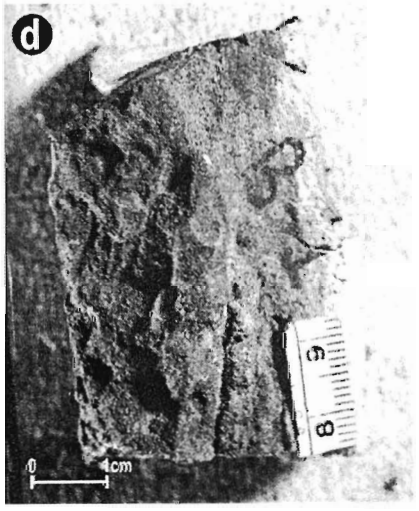
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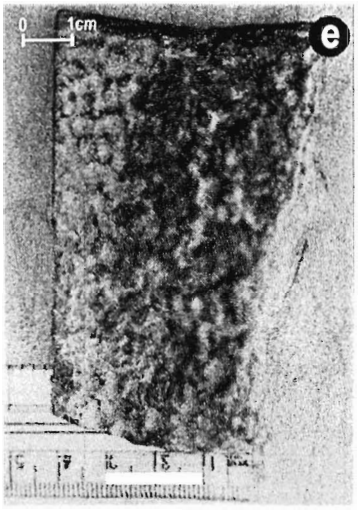
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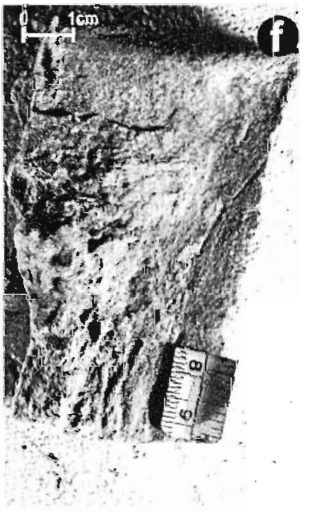
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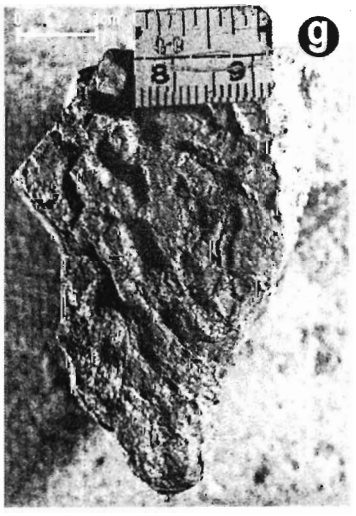
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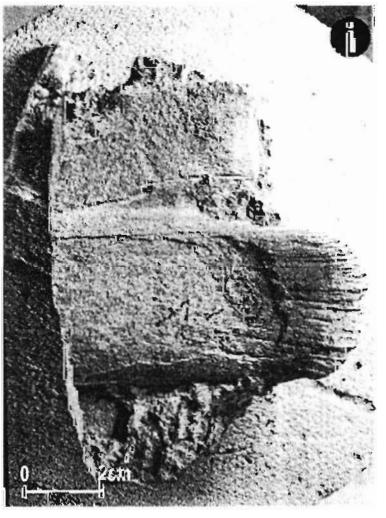
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The distal end is less angular than that of VPL/RP/ST-01, due to which the bone looks more or less rectangular in shape. The antero-posterior margins of the bone are well preserved and are straight. The anterior margin is longer than the posterior similar to that in VPL/RP/ST-01. The rib is not clearly visible on the internal surface of the specimen due to the sediment cover. The distal end of the rib is broken from the rim of the pleural but a trace of the broken margin can be marked on the distal end of the pleural. The total length of the specimen is approximately 65 mm and width (antero-posterior) is approximately 94 mm.

The specimen VPL/RP/ST-04 is represented by the right 8th pleural. The posterior and proximal portion of the bone is not preserved. The distal end is convex and firmly sutured to the rib. The surface sculpture is not well preserved; it has been eroded during the post-mortem activities. This specimen differs from others in having a broadly convex (*sensu* Gardner and Russell, 1994) shell outline. The preserved length of the specimen is approximately 53 mm and width (antero-posterior) is approximately 60 mm. On ventral surface the concave rib is firmly sutured to the bone. The distal margin of the rib is partially broken but it suggests a convex outline. The length of the freely exposed portion of the rib is approximately 37 mm and width (antero-posterior) is approximately 35 mm.

Another partially preserved specimen (VPL/RP/ST-07) is represented by the middle portion of the left 5th pleural. The specimen is broken proximally, distally and also antero-posteriorly. The rib on the internal surface is slightly wider than that of VPL/RP/ST-01 and VPL/RP/ST-2 and therefore suggests a position anterior to it. The width of the rib is comparable to that of the 5th pleural in living *Chitra indica*.

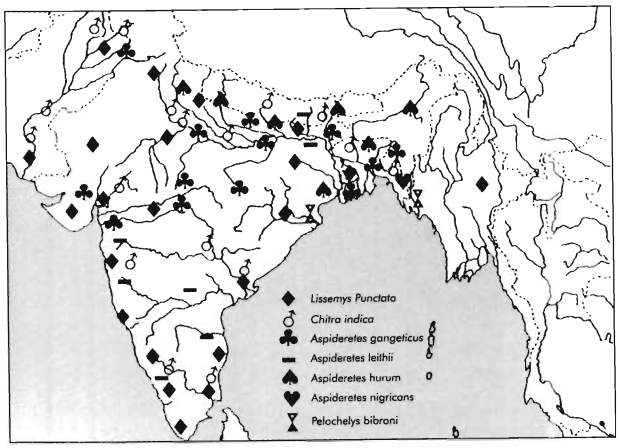

Fig. 6. A distribution map of living trionychids turtles in India (modified after Iverson, 1992).

DISCUSSION AND CONCLUSIONS

The Siwaliks have yielded a great wealth of fragmentary carapace and plastra of turtles. Most of the Siwalik material belongs to the family Testudinidae and Bataguridae (see Srivastava & Schleich, 2001). In comparison, the trionychids (soft-shelled turtles) are less abundant. Lydekker (1885) was the first to comprehensively describe the Siwalik turtle material. Since then a number of short descriptions have been published on the occurrence of the turtle carapaces and plastra from various horizons of the Siwaliks (see Das, 1991; 1995 and

EXPLANATION OF PLATE II

a-f *Chitra indica* (Gray)

a. VPL/RP/ST-02. Dorsal view of partially broken left 3rd pleural bone. The surface sculpture is well comparable to that of specimen VPL/RP/ST-01. Scale Bar = 10 mm.

b. VPL/RP/ST-02. Ventral view of the 3rd pleural bone. The surface is convered with the sediments but a trace of rib is visible beneath the sediments distal end of which is broken. Scale Bar = 10 mm.

c. VPL/RP/ST-04. Dorsal view of right 8th pleural. The proximal margin of the bone is not preserved. The rib projecting out of the pleural margin is almost complete excepting a small distal most part which is not preserved. The reconstruction suggests that shape of the rib is identical to the shape of the rib in the specimen VPL/RP/ST-01. Scale Bar = 20 mm.

d. VPL/RP/ST-04. Ventral view of the 8th pleural. A prominent and wide rib is visible which is broken on the distal margin. Scale Bar = 20 mm.

e. VPL/RP/ST-07. Dorsal view of middle portion of left 5th pleural. The surface sculpture of the bone is comparable to those found in other pleurals of *Chitra indica*. Scale Bar = 10 mm.

f. VPL/RP/ST-07. Ventral view of partially preserved 5th pleural. A wide and prominent rib is visible on the surface. The rib is wider than that of VPL/RP/ST-01 and ST-02, suggesting a position anterior to them. Scale Bar = 10 mm.


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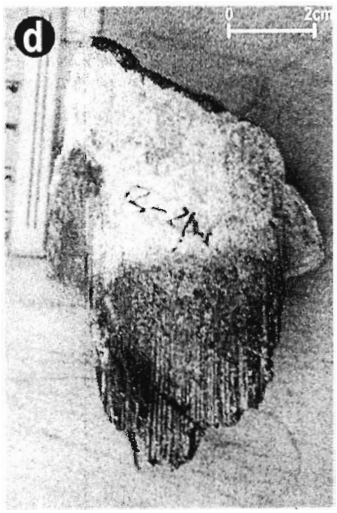
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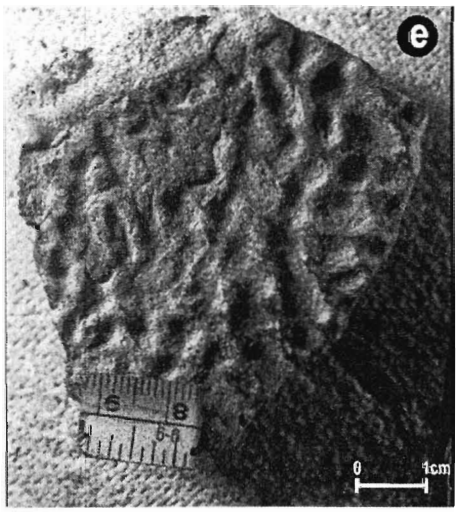
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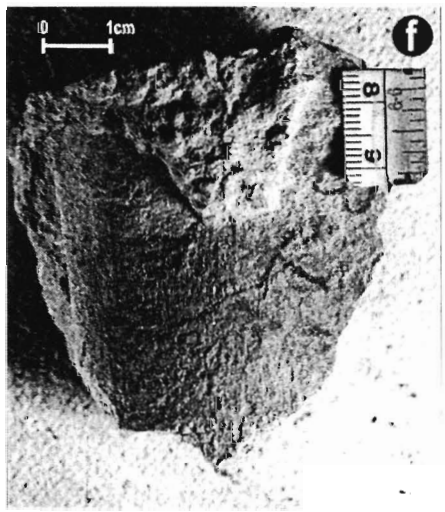
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Table 1: Carapace characters and character states for recent trionychid turtles (after Meylan, 1987). For each character the most primitive state is number 1.

Characters	Character states
1. width/length of nuchal bone	1. less than 2
	2. greater than 2
	3. greater than 3
	4. greater than 4
2. first and second neurals fused	1. no
	2. yes
3. total number of peripherals	1. 22
	2. 20
	3. 14-18
	4. 0
4. prenuchal bone	1. absent
	2. present
5. size of 8th pleurals	1. large
	2. reduce or abset
6. number of neurals (fused 1 & 2 counted as 2)	1. nine
	2. eighth or nine
	3. eight
	4. seven or eight
	5. seven of fewer
7. pleurals which meet at midline	1. eighth only
	2. seventh and eighth or eighth only
	3. sexth, seventh and eighth or seventh and eighth only
	4. more than sixth
8. depressions on 8th pleaural for contact of ilia	1. present
	2. absent
9. rib heads strongly sutured to vertebral centra	1. no
	2. yes
10. anterior and posterior costiform processes of nuchal bone united	1. no
	2. yes
11. position of anterior edge of first body vertebra relative to nuchal bone	1. posterior edge of nuchal
	2. middle of nuchal
	3. anterior edge of nuchal
12. largest adult size 200 mm or less (carpace length)	1. no
	2. yes
13. carpace margin straight to concave posterlaterally	1. no
	2. yes
14. point of reversal of orientation of neurals	1. at neural eigth
	2. at neural seven
	3. at neural six or seven
	4. at neural six
	5. at neural four, five of six

Srivastava and Schleich, 2001). This database elucidates the frequent occurrence of shell material in comparison to the skulls from the Plio-Pleistocene rocks of India. Only two skulls of batagurids and one of trionychid have been described by Lydekker (1885) in his monographic work and therefore, it becomes necessary to focus the attention on the shell characteristics and tracing the key characters of the shell that are helpful in identification at atleast generic level. The identification of batagurid and testudinid species is far more difficult in comparison to the trionychids. Family Trionychidae is represented by 14 living genera, of which four, *Lissemys, Chitra, Aspideretes,* and *Pelochelys* are found in India (fig. 6; Iverson, 1992). All the living genera and species (excepting *Pelochelys*) are found in Indian Siwaliks and there has been no report of any new genera or species that can be differentiated from the living trionychids (Srivastava and Schleich, 2001). The differentiating features of the trionychids are frequently preserved on the shell, on the basis of which it is possible to identify even a fragmentary pleural at least up to the generic level (see character analysis of Meylan, 1987 and also see Gardner and Russell, 1994). *Lissemys*, *Chitra* and *Aspideretes* are distinguishable on the basis of shell characteristics (see the previous section and also Meylan, 1987). *Lissemys* is monotypic but it is again difficult to identify the subspecies of *Lissemys punctata*. Similarly, the species of *Aspideretes* may not be easily identifiable unless a complete shell or at least anterior and posterior portions of the carapace and the plastron are recovered.

For the phylogenetic study of the Indian trionychids, 14 shell characters were used, 7 characters out of 14 were identifiable in fossil *Chitra*. The species status of the *Aspideretes* is not certain and therefore has not been incorporated in the study. The study using the PAUP (Phylogenetic Analysis Using Parsimony) produced ten equally parsimonious trees. This is possibly due to non-enforcement of topological constraints. The clade of *Chitra* (This work, fig. 7) possibly cannot be resolved only on the basis of 14 shell characters or may be the data from shell alone is not sufficient for resolving the clades (Meylan, 1987).

Table 2 Modal character states for carapace characters of the recent trionychid turtles found in the Indian subcontinent (modified after Meylan, 1987). For description of the characters and character states, see table 1.

	Characters													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Chitra indica (Pliocene age)	-	-	4	-	1	-	1	2	2	-	-	1	1	-
Chitra indica	3	2	4	1	1	1	1	2	2	2	3	1	1	3
Lissemys punctata	2	1	3	1	1	4	2	1	2	1	1	1	2	3
Asppideretes gangeticus	3	1	4	1	1	2	2	2	2	2	2	1	1	3
Aspideretes leithii	3	1	4	1	1	2	1	2	2	2	2	1	1	3
Aspideretes hurum	3	1	4	1	1	2	2	2	2	2	2	1	1	3
Aspideretes nigricans	3	1	4	1	1	1	2	2	2	2	2	1	1	3

For this reason, it stands between *Chitra indica* and outgroup (fig. 7). The outgroup has been defined as having all unknown 14 characters. The results obtained from the data are compatible with that of Meylan (1987). *Chitra* in most of the studied characters stands apart from *Aspideretes* and *Lissemys*. Further shell data of large *Chitra* and *Aspideretes* would be very important in resolving their monophyletic position in cladogram (earlier recognized by Meylan, 1987).

Chitra represents the group of largest living trionychids. The length of the bony disc (excluding the free ends of the ribs) of living *Chitra* goes maximum to 550 mm whereas that of living *Aspideretes* goes upto 485 mm (Meylan, 1987). The hypothetical reconstruction of the bony disc of Pliocene *Chitra* and *Aspideretes* shows that the living forms do not differ much in size from their Pliocene ancestors. There is no noticeable change in the size of *Chitra* and *Aspideretes,* which suggests that there has been no significant change in the habitat and living environment of these turtles since the Pliocene time. The large size of the genera may be related to the open environment, with little or no threat to life. The presence of large trionychid turtles in the Upper Pliocene rocks of Siwalik suggests a warm tropical rainy or mansoon climate with well watered streams (*sensu* Corvinus and Schleich, 1994) full of small plants and animals on which trionychid turtles generally feed (Das, 1991, 1995). This notation is in corroboration of palaeoecological studies previously done by various workers (Corvinus and Schleich, 1994; Patnaik, 1991, 1995 and Patnaik and Schleich, 1993).

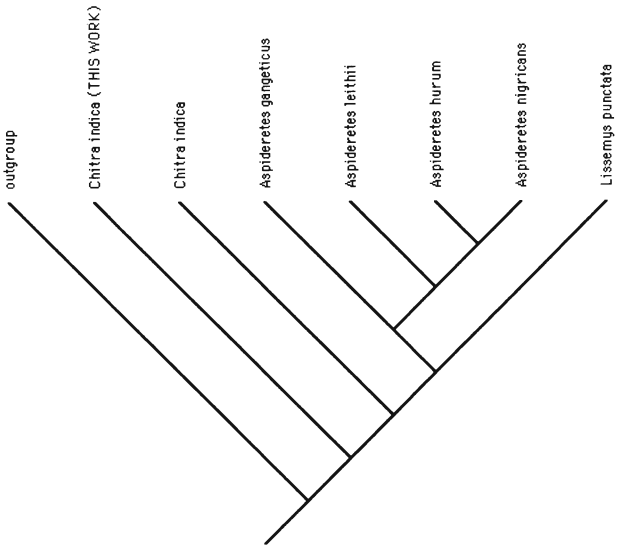

Fig. 7. A cladogram for the Indian trionychids based on 14 shell characters. Position of the fossil *Chitra* is in-between the outgroup and living *Chitra* due to many unknown shell characters. The outgroup has been defined with all 14 unknown characters.

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REFERENCES

Minton, S. A., Jr. 1966. A contribution to the herpetology of West Pakistan. *Bull. Amer. Mus. Nat. Hist.* **134** : 27-184.

Corvinus, G. and Schleich, H. H. 1994. An Upper Siwalik reptile fauna from Nepal. *Courier Forsch. – Inst. Senckenberg*, **173** : 239-259.

Das, I. 1991. *Colour guide to the turtles and tortoises of the Indian Subcontinent*. R & A Publishing Ltd., Portishead.

Das, I. 1995. *Turtles and Tortoises of India.* Oxford University Press, Bombay.

Ernst, C. H. and Barbour, R. W. 1989. *Turtles of the world.* Smithsonian Institution Press, Washington, D. C.

Falconer, H. and Cautley, P. T. 1837. On additional fossil species of the order Quadrumona from the Sewalik hills. *Jour. Asiatic Soc. Bengal*, Calcutta, **6** : 354-360..

Falconer, H. 1868. On the *Colossochelys atlas*, a gigantic tortoise from the Sewalik hills, p. 359-381. In : *Fauna Antiqua Sivalensis* (Ed. C. Murchison), Vol. 1. Robert Hardwick, **192**, London.

Falconer, H. and Cautley, P. T. 1844. On the osteological characters and palaeontological history of the *Colossochelys atlas*, a fossil tortoise of enormous size from the Tertiary strata of the Sewalik hills in the north of India. *Proc. Zool. Soc. London,* **12** : 54-55.

Gaffney, E. S. 1975. A phylogeny and classification of the higher categories of turtles. *Bull. American Mus. Nat. Hist.*, New York, **155**:387-436.

Gaffney, E. S. and Meylan, P. A. 1988. A phylogeny of turtles, p. 157-219. In: *Phylogeny and Classification of the Tetrapods. Vol. I : Amphibians, Reptiles and Birds*. Systematics Association Special volume. *Clarendon Press*, Oxford, **35A**.

Gardner, J. D. 1992. Systematics of the soft-shelled turtles (Family Trionychidae) from the Judith River Formation (Campanian). *M. S. Thesis, Univ. Calgary, Alberta.*

Gardner, J. D. and Russell, A. P. 1994. Carapacial variation among soft-shelled turtles (Testudines : Trionychidae), and its relevance to taxonomic and systematic studies of fossil taxa. *N. Jb. Geol. Palaeont. Abh.* **193 (2)** : 209-244.

Gray, J. E. 1830-1835. *Illustrations of Indian Zoology, Vols.* **1, 2.** London.

Iverson, J. B. 1992. *A revised checklist with distribution maps of the turtles of the world.* Privately printed, Richmond, Indiana.

Lydekker, R. 1885. Siwalik and Narbada Chelonia. *Pal. Indica*, **10** (3):154-205.

Lydekker, R. 1886. Catalogue of the remains of Siwalik Vertebrata contained in the geological department of the Indian Museum Calcutta. (II), Aves, Reptilia and Pisces. *Govt. India Press* : 1-23.

Lydekker, R. 1887. The fossil Vertebrata of India. *Rec. Geol. Surv. India*, **20** : 51-80;

Lydekker, R. 1889. Notes on Siwalik and Narbada Chelonia. *Rec. Geol. Surv. India*, **22**: 56.

Meylan, P. A. 1985. Evolutionary relationships of recent trionychid turtles : Evidence from shell morphology, p. 169-188. In : *Studia Palaeocheloniologica I : Comunicaciones del I Simposium Internacional Sobre Quelonios Fosiles* (Eds. F. De Broin & E. Jiménez-Fuentes).

Meylan, P. A. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). *Bull. Amer. Mus. Nat. Hist.* **186** (1): 1-101.

Meylan, P. A., Weig, B. S. and Wood, R. C. 1990. Fossil soft-shelled turtles (Family Trionychidae) of the Lake Turkana Basin, Africa. *Copeia,* **1990** (2) : pp 508-528.

Minton, S. A. 1966. A. contribution to the herpetology of West Pakistan. *Bull. Amer. Mus. Nat. Hist.* **134**: 27-184.

Mlynarski, M. 1976. *Handbuch der Palaeoherpetologie. Part 7. Testudines.* Fischer Verlag, Stuttgart.

Patnaik, R. 1991. Micropalaeontology, biostratigraphy and palaeoenvironmental analysis of the Siwalik Sequences in the Saketi-Nahan Area (H. P.). *Unpublished Ph.D. Thesis, Panjab University, Chandigarh.*

Patnaik, R. 1995. Narmada valley microvertebrates: systematics, taphonomy & palaeoecology. *Man & Environment*, **XX** (2) : 76-90.

Patnaik, R. 2001. Late Pliocene micromammals from Tatrot Formation (Upper Siwaliks) exposed near village Saketi, Himachal Pradesh, India, *Palaeontographica*, **261**(1-3):55-81.

Patnaik, R. and Schleich, H. H. 1993. Fossil crocodile remains from Upper Siwaliks, India. *Mitt. Bayer. Staatsslg. Paläont. Hist. Geol.* **33** :91-117.

Romer, A. S. 1956. *Osteology of reptiles.* University of Chicago Press. Chicago.

Schleich, H. H. 1980. Jungtertiäre Schildkröten Süddeutschlands unter besonderer Berücksichtigung der fundstelle Sandelzhausen. *Inaugural Dissertation zur erlangung des Doktorgrades der Fakultät für Geowissenschaften der Ludwigs-Maximilians Universität, München.*

Srivastava, R. and Schleich, H. H. 2001. Review of Neogene-Quaternary turtles from the Indian Subcontinent (in press). *Sonder Ousdruek von Fuhlrott Museum*, Wuppertal.

Verma, B. C. and Verma, S. N. 1969. Geological mapping of the Siwalik hills lying in parts of Ambala distt. Haryana and Sirmur distt., Himachal Pradesh and studies of vertebrate fossils. *Geol. Surv. Ind.* Unpubl. Report.

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