

## Fossil crocodile remains from the Upper Siwaliks of India

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With 10 plates, 9 figures and 5 tables

### Abstract

Crocodile remains from two Pliocene localities, Moginand and Saketi (Himachal Pradesh) from the Upper Siwaliks of India are described. A comparative analysis of the fossil teeth, jaw remains and eggshell fragments with the relevant extant taxa of fresh-water crocodiles from India is presented.

### Kurzfassung

Von zwei pliozänen Fundstellen der Oberen Siwaliks Indiens (Moginand und Saketi - Himachal Pradesh) werden fossile Krokodilnachweise beschrieben. Die fossilen Zähne, Kieferreste und Eischalenfragmente sind im Vergleich mit den rezenten Taxa dargestellt.

### Introduction

Research on Upper Siwalik sequences exposed near Saketi Fossil Park (Himachal Pradesh/India) has been carried out during the last four years (1989-1992). These activities resulted in the recovery of several crocodylid remains associated with lizards, fishes, frogs, molluscs, ostracodes, charophytes and a diverse micromammalian assemblage.

### Geological Setting

In the area around Saketi Fossil Park (Himachal Pradesh/India), Middle and Upper Siwalik units add up to around 780 m thick sequences. The contact between Middle and Upper Siwalik rocks is of tectonical origin. The Middle Siwalik sediments are characterized by massive grey sandstones and subordinate orange, red, yellow and grey mudstones. The overlying Tatrot are characterized by alternating bands of grey friable and occasionally pebbly sandstone/siltstone and variegated mudstones of red, pink, yellow and grey colours. The total thickness of the Tatrot units in this area is about 260 m. Approximately 40 cycles of sandstones and mudstones can be recognized in the

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Markanda River Section from Kala Amb to Saketi, each cycle starting with a coarse sandstone and ending up with fine clays. A volcanic ash bed has been discovered by one of the authors (RP) in the Markanda river valley (fig. 1). This tuffaceous mudstone bed has been tentatively correlated to those (around 2.5 m. y. old) occurring in the Upper Siwalik sequences in India (RANGA RAO et al. 1988) and from Pakistan (OPDYKE et al. 1979).

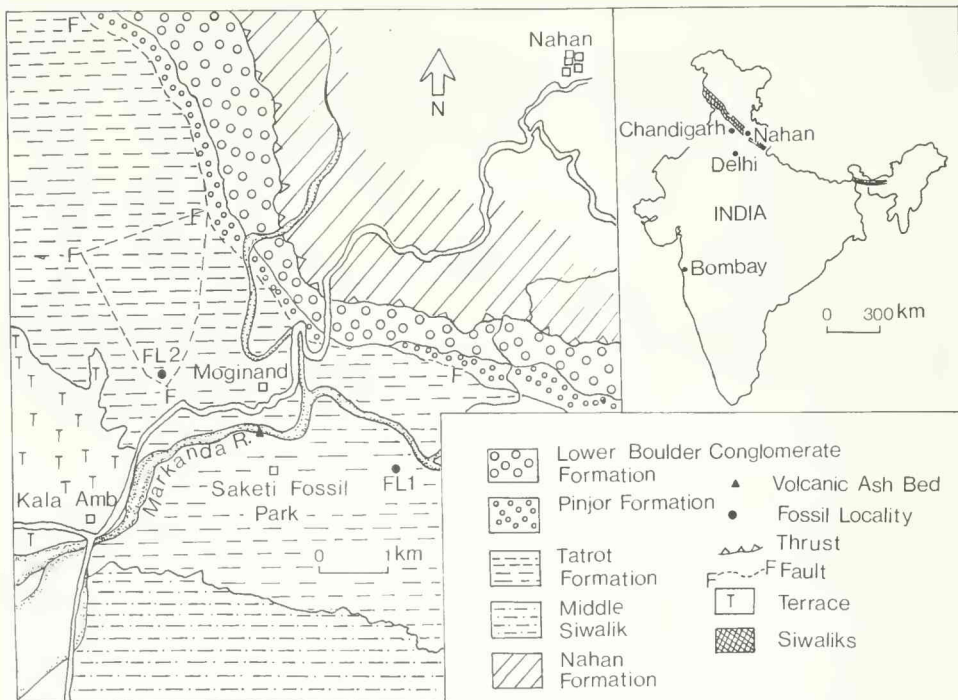


Fig. 1: Geological map of the Saketi-Nahan Area (modified after VERMA et al., 1969).

### Palaeoenvironment

The fossils bearing mudstone units, both at Saketi and Moginand are of limited lateral extent (around 50 m) and their thickness ranges from 20 to 50 cm. These mudstones have been recognized as overbank flood-plain deposits which have undergone pedogenesis, a situation that is known from the recent habitats of gharials e. g. in the Narayani area, S-Nepal. The diagnostic features indicative of pedogenesis include: the presence of tabular variegated coloured units with calcium, iron, manganese and aluminium rich nodules; bioturbation features; local calcitic cementation in sandy mudstones; absence of bedding and presence of microtopography at the contacts of coloured units.

Studies concerning taphonomy and palaeoecology of the fossil mammals and associated microfossils collected from these horizons have been carried out by Patnaik for a PhD thesis and will be published in detail elsewhere. These studies reveal that there was a gradual accumulation of micro- and mega-fossil remains in shallow seasonal ponds of broad flood-plains. It has been observed that the concentration of fossils was partly biogenic and partly fluvial. A reconstruction of the palaeocommunity indicates derivation of the faunal elements at least from four different ecological regions: bushland, grassland, pond and pondbank.

The knowledge being deductable from the study on the habitats of extant *Crocodylus palustris* and *Gavialis gangeticus* (see MASKEY & SCHLEICH, SCHLEICH & MASKEY, 1992) in the area of the Siwaliks allows to give rather detailed ecological informations for the presence of these both taxa and confirm the paleocological interpretations. Tropical woodlands with wide river systems, deep permanent water channels and associated riverine shore areas ranging from rocks, sand banks, grassbanks are to expect for *Gavialis* while *Crocodylus palustris* seems to be more restricted to hot swamp areas ranging from small riverine forests with side channels, streams to ponds, lakes and slower river parts of similar tropical climates. These data coincide well with the palaeoenvironmental constraints being drawn from the sedimentological and geological informations.

### Previous references on Siwalik Crocodiles

Reports on Siwalik crocodiles go back till 1836, when CAUTLEY & FALCONER described cranial fragments of *Gavialis leptodus* from the Upper Pliocene of the Siwalik Hills. This was followed by descriptions of *Crocodylus palaeindicus* (FALCONER, 1859) and *Crocodylus bombifrons* (FALCONER, 1868) from the Pliocene of Siwaliks, *Crocodylus sivalensis* and *Ramphosuchus crassidens* from the Pliocene, *Gavialis hysudricus* from the Upper Pliocene, *Gavialis pachyrhynchus* from the Upper Miocene and *Gavialis curvirostris* from the Lower Pliocene of the Siwalik Hills, India (LYDEKKER, 1886). In the early 20th century, PILGRIM (1912) reported *Gavialis curvirostris* var. *gajensis* and *Gavialis breviceps* from Lower Miocene deposits of Bugthi Hills, Baluchistan. MOOK (1932) described *Gavialis browni* from the Lower Pliocene, LULL (1944) described *Gavialis lewisi* from the Middle Pliocene and BADAM (1974) reported *Gavialis browni* from Lower Pleistocene sediments of the Indian Siwaliks. Recently, SCHLEICH (in CORVINUS & SCHLEICH, 1994) reports *Gavialis* cf. *gangeticus*, *Crocodylus* aff. *palustris* and *Ramphosuchus crassidens* from the Upper Siwaliks of Nepal. SCHLEICH (1993) provided a rather complete listing of the palaeoherpetological records from the Siwaliks.

### Some Aspects on the fossil History and Systematics of Gavialid Crocodiles

Fossil gavialids had been described from several cenozoic outcrops from Eurasia and South America. *Hesperogavialis* is according to BOCQUENTIN VILLANUEVA & BUFFETAUT (1981: 415) „... the only known South American gavialid in which, as in the Gavialidae from the Indian region, the nasals do not come into contact with the premaxillae . . .“, what has been interpreted as convergent evolution.

In 1982, BUFFETAUT recognizes on the basis of shared synapomorphies following genera (p.127) „... of gavials from the Tertiary of South America: *Gryposuchus*, *Ikanogavialis*, *Hesperogavialis* hav(e)ing been originated from the Paleogene *Eogavialis* of Africa“.

Fossil Gavialid crocodiles have been reported from Europe as *Gavialosuchus* (BUFFETAUT, 1978) and primitive Gavialids from the Palaeogene of Africa (op. cit.). From the Upper Miocene of Iraq, *Gavialis* spec. has been studied by BUFFETAUT & THOMAS (1981).

Systematically, BUFFETAUT (1985) documents in a quite appreciable paper the relationship between *Tomistoma* and *Gavialis* by palaeontological data, as neontological investigations don't consider them as being related. Due to palaeontological-morphological constraints both genera are to unify in the family Gavialidae, and are closer related to the crocodylia than to the Alligatorinae. According to BUFFETAUT their lineages have diverged already in the lower Paleogene. ANTUNES (1987) considered *Gavialosuchus* at subgeneric level of *Tomistoma* and does not accept the



arguments presented by BUFFETAUT (1985), maintaining the familiar concept of Gavialidae and „Tomistomidae“.

## Systematical Description

### Methods:

Most of the skeletal elements described here were collected on the surface of the outcrops. Around 1200 kg of rock samples, quarried from the two fossiliferous horizons were macerated in the Laboratory (Department of Geology, Panjab University, Chandigarh/India) treating them initially with Kerosene and later with mild acetic acid to recover microfossils from the harder residue.

Comparative analysis (statistical) have been undertaken using the teeth and alveolar dimensions (fig. 2, 5) of 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.

Eggshell fragments and a few teeth were examined by SEM at the Institute of Palaeontology and Historical Geology, Munich, to study their ultrastructure.

### Abbreviations

ZSM: Zoologische Staatssammlung München, BSP: Bayerische Staatssammlung für Paläontologie, VPL: Vertebrate Paleontology Laboratory, Univ. Chandigarh (Dept. Geology).

Measurements of crocodylid skull elements used in this study: Straight Teeth Length (TL), Teeth Width A (compressed) and B (extended) (TWA & TWB), Alveolar Diameter A (extended) and B (compressed) (ADA & ADB), Intervalveolar Length (IAL) and Mandibular Width (MW).

Class Reptilia LAURENTI 1768  
Order Crocodylia GMELIN 1788  
Family Crocodylidae CUVIER 1807  
Genus *Crocodylus* LAURENTI 1768

### *Crocodylus* cf. *palustris* (pl. I, II)

**M a t e r i a l:** One fragmentary mandible (VPL/RP-R 11), nine isolated teeth (VPL/RP-R 12-20), four partly broken vertebrae (VPL/RP-R 21-24), and one complete and three partly broken osteoscutes (VPL/RP-R 25-28).

**L o c a l i t y:** Mogninand, Himachal Pradesh (India).

**D e s c r i p t i o n:** The mandibular fragment (VPL/RP R 11; pl. I/1) possesses two alveoles with teeth broken at their bases. The posterior alveole is much larger than the anterior one and is placed relatively at a higher level.

The teeth VPL/RP-R 12,13 (pl. I/1, 2) are larger (Tab. 1), keeled and with a sharp apex. They show vertical striations on the enamel's surface. The teeth numbered 18, 19, 20 have sharp apices and clearly visible vertical striations. The remaining teeth (VPL/RP-R 14-17) are rather blunt, have well developed ornamented keels (pl. I/10 b) and show a complex network of enamel striations (pl. I/10 a).

Fig. 2: Scatter diagram showing alveolar dimensions of *Crocodylus palustris* (o- maxillary and x- mandibular alveoles): a, specimen number ZSM 34/1912 (lower jaw length = 18,63 cm & skull length = 15,83 cm; b, ZSM 517/1911 (lower jaw length = 41,03 cm & skull length = 34,07 cm); c, ZSM 231/0 (lower jaw length = 30,75 cm & skull length = 25,87 cm) and *Crocodylus* cf. *palustris* (■ mandibular alveoles).

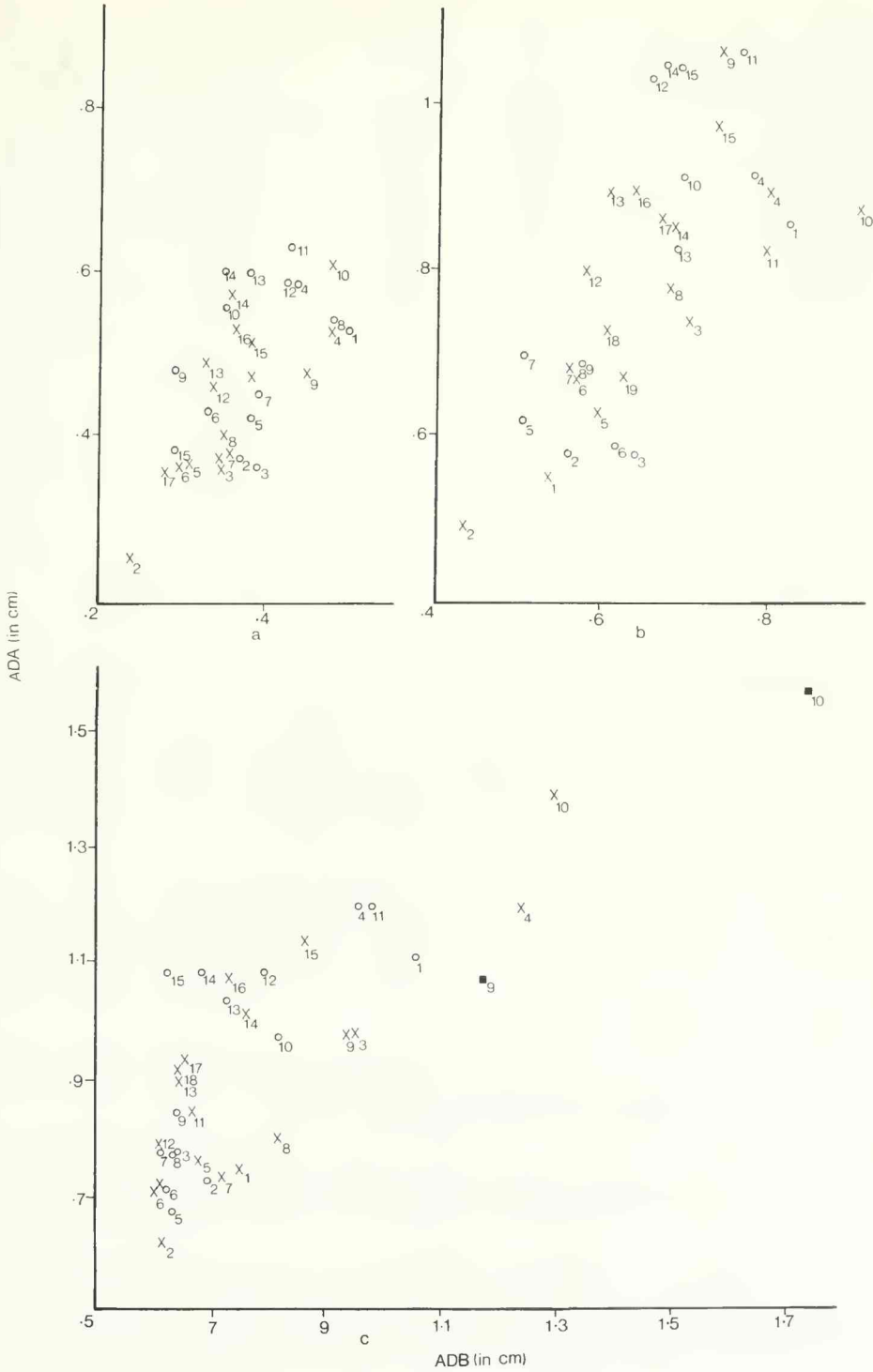


Table 1:

Specimen Number	TL	TWA	TWB
<i>Crocodylus cf. palustris</i>			
VPL/RP-R-12	2.885	1.56	1.74
VPL/RP-R-13	2.575	1.565	1.75
VPL/RP-R-14	1.78	1.31	1.385
VPL/RP-R-15	.88	.875	1.035
VPL/RP-R-16	.87	.85	1.085
VPL/RP-R-17	.805	.715	.805
VPL/RP-R-18	–	.625	.745
VPL/RP-R-19	.685	.54	.75
VPL/RP-R-20	.88	.48	.54
<i>Gavialis cf. gangeticus</i>			
VPL/RP-R-2	–	.8	.93
VPL/RP-R-3	–	.75	.86
VPL/RP-R-4	–	.815	.89
VPL/RP-R-5	–	.8	.95
VPL/RP-R-6	–	.94	1.12
VPL/RP-R-7	–	.74	1.13
VPL/RP-R-8	–	.565	.695
VPL/RP-R-9	–	.51	.53

Table 1: Measurements of teeth dimensions of *Crocodylus cf. palustris* and *Gavialis cf. gangeticus*.

The alveoles preserved in the mandibular fragment were found to resemble most closely to the 9th and 10th alveoles of comparative recent specimens of *Crocodylus palustris* (see pl. 3, 4). The scatter plots (fig. 3 a, b, c) indicate that the fossil fragment probably belongs to a much bigger mandible as compared to those of the recent specimens examined. In all the recent specimens the 10th alveole is much larger in size than the 9th and is placed relatively at a higher level. It has been observed that the 10th and 2nd maxillary alveoles show the longest and the shortest labio-lingual diameter respectively. The 11th mandibular alveole has been found to have the longest antero-posterior diameter (fig. 3 a, b, c).

Opposite to the rather homodont jaws of *Gavialis*, *Crocodylus palustris* shows a typical heterodont dentition pattern. The first 12 maxillary and 8 mandibular teeth in the recent specimens of *Crocodylus palustris* are slender, have a well developed keel, sharp apex and vertical striations. The 13 to 19 maxillary and 9 to 15 mandibular teeth are relatively wider, low crowned, blunt and show a complex pattern of striations (pl. I/11). The 1st and 4th mandibular and the 4th and 10th maxillary teeth are large and caniniform (see also Tab. 2).

The scatter plots (fig. 4, 5) show that the dimensions of most of the fossil teeth fall very much within the range of *Crocodylus palustris*. The few teeth which fall beyond the range of the recent specimens examined might belong to a larger *Crocodylus palustris*.

For better comparison different skull views of the recent *Crocodylus palustris* are shown on plate III and IV.

The complete osteoscuta (pl. I/13) and three osteoscuta fragments (pl. I/12, 14, 15) exhibit well developed deep grooves and a prominent medial keel. The complete osteoscuta is of oval to subcircular outline.

The cervical vertebra (pl. II/1 a, b) has a moderately elongated centrum and a partly broken ventral facet, situated on the anterior part of the centrum. Its partly broken transverse processes slant down from the lateral surface of the centrum. The zygapophyses are situated at a higher level as compared to that of the neural canal.

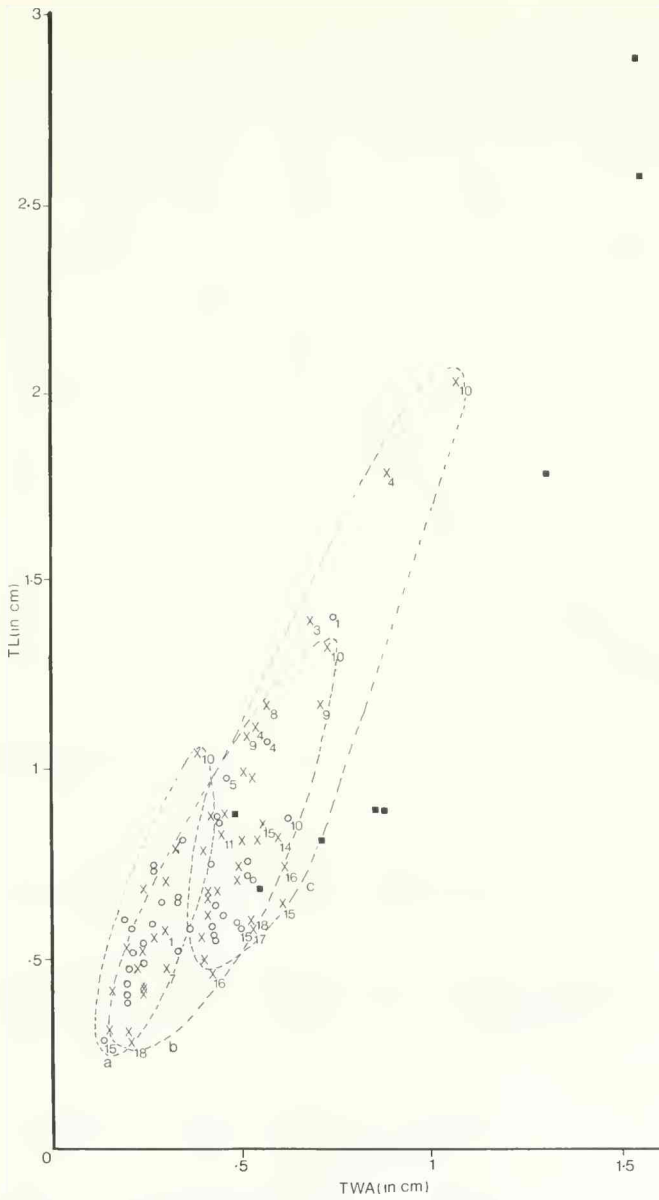


Fig. 3: Scatter diagram showing teeth dimensions (TL/TWA) of *Crocodylus palustris* (o-maxillary & x-mandibular teeth) and *Crocodylus cf. palustris* (■): a, ZSM 34/1912; b, ZSM 517)1911 and c, ZSM 231/0.

The caudal vertebra VPL/RP-R 22 (pl. II/2 a, b) possesses a somewhat reduced centrum, partly broken posterior zygapophyses that slant posterio-dorsally, a partly broken dextral transverse process, sinistral and dextral anterior zygapophyses and the neural spine.

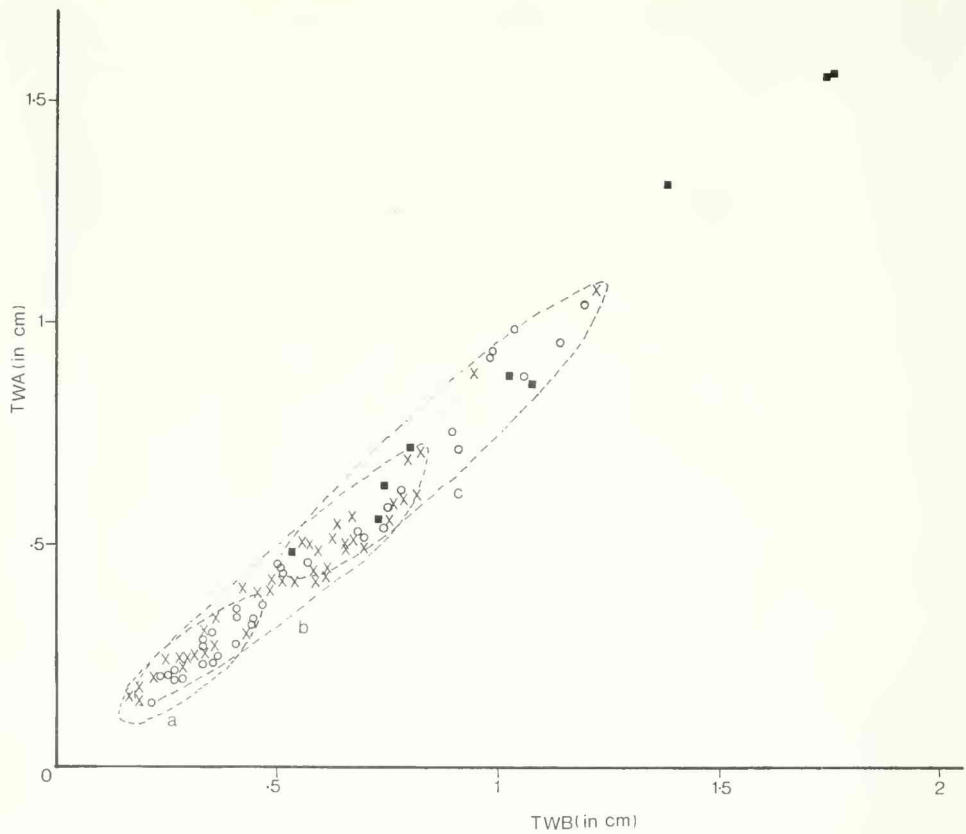


Fig. 4: Scatter diagram showing teeth dimensions (TWA/TWB) of *Crocodylus palustris* (o-maxillary & x-mandibular teeth) and *Crocodylus cf. palustris* (■); a, ZSM 34/1912; b, ZSM 517/1911 and c, ZSM 231/0.

The caudal vertebra VPL/RP-R 23 (pl. II/3 a, b) has a moderately elongated centrum and broken transverse processes and zygapophyses. In the caudal vertebra VPL/RP-R-24, transverse processes are highly reduced, no dorsal process is present and a small spine is situated anterior on the ventral surface of the centrum (pl. II/4 a, b).

Family Gavialidae ADAMS 1954

Genus *Gavialis* OPPEL 1811

*Gavialis cf. gangeticus* (pl. V, VI)

**Material:** Two mandibular fragments (VPL/RP-R 1 a, b) and eight isolated and broken teeth (VPL/RP-R 2-9).

**Locality:** Saketi, Himachal Pradesh (India).

**Description:** The anterior mandibular fragment (pl. V) exposes four complete and one partly preserved sinistral alveoles and four partly preserved dextral alveoles. The posterior dextralateral mandibular fragment has 3 well preserved alveoles. Two interdental pits and a medial suture can be seen on the occlusal surface of the posterior fragment.



Specimen Number	TL:X				N	TWA:Y			
	R	M	S	V		R	M	S	V
231/0 mandible	.515-1.065	.689	.148	.214	13	.33-57	.410	.078	.190
231/0 maxilla	.46-1.31	.753	.229	.304	18	.3-555	.443	.098	.221
34/1912 mandible	.28-.74	.459	.120	.242	15	.2-.295	.222	.038	.171
34/1912 maxilla	.275-1.04	.506	.179	.353	17	.15-385	.248	.059	.238
517/1911 mandible	.545-1.07	.773	.164	.212	12	.38-.75	.509	.090	.177
517/1911 mandible	.5-2.20	.993	.449	.452	17	.4-1.075	.597	.168	.281
		TWA:X				TWB:Y			
231/0 mandible	.33-.57	.410	.078	.190	13	.41-.705	.451	.107	.197
231/0 maxilla	.3-.555	.443	.098	.221	18	.34-.825	.564	.130	.230
34/1912 mandible	.2-.295	.222	.038	.171	15	.225-.415	.311	.056	.180
34/1912 maxilla	.15-.385	.248	.059	.238	17	.17-.455	.319	.082	.257
517/1911 mandible	.38-.75	.509	.090	.177	12	.5-.915	.659	.145	.220
517/1911 maxilla	.4-1.075	.597	.168	.281	17	.5-1.22	.716	.178	.248
		AWA:X				AWB:Y			
231/0 mandible	.58-1.045	.811	.186	.229	15	.5-.775	.644	.096	.149
231/0 maxilla	.49-1.07	.785	.146	.185	19	.43-.905	.651	.110	.168
34/1912 mandible	.37-.595	.510	.094	.184	15	.28-.49	.375	.061	.162
34/1912 maxilla	.36-.615	.439	.093	.211	19	.23-.47	.339	.065	.191
517/1911 mandible	.665-1.195	.931	.188	.201	15	.61-1.05	.743	.144	.194
517/1911 maxilla	.615-1.385	.902	.194	.215	19	.6-1.29	.774	.20	.258

Table 2: Measurements of teeth dimensions of *Crocodylus palustris*. Range (R), mean (M), standard deviation (S), variations (V), and number (N). Only unbroken and fully erupted teeth of right mandible and maxillae have been used for measurements (in cm).

Eight isolated partly broken teeth are slender, antero-posteriorly compressed (Tab. 1) and exhibit well developed vertical striations and lateral keels.

For comparison with the recent *Gavialis* see plates VII, VIII.

The scatter plots (fig. 6) of the dimensions (Tab. 3) of the mandibular alveoles of the fossil specimen indicate that the two mandibular fragments probably belong to a larger specimen than the recent ones studied here (ZSM 2528/0 being the largest amongst the for us available recent specimens Tab. 4).

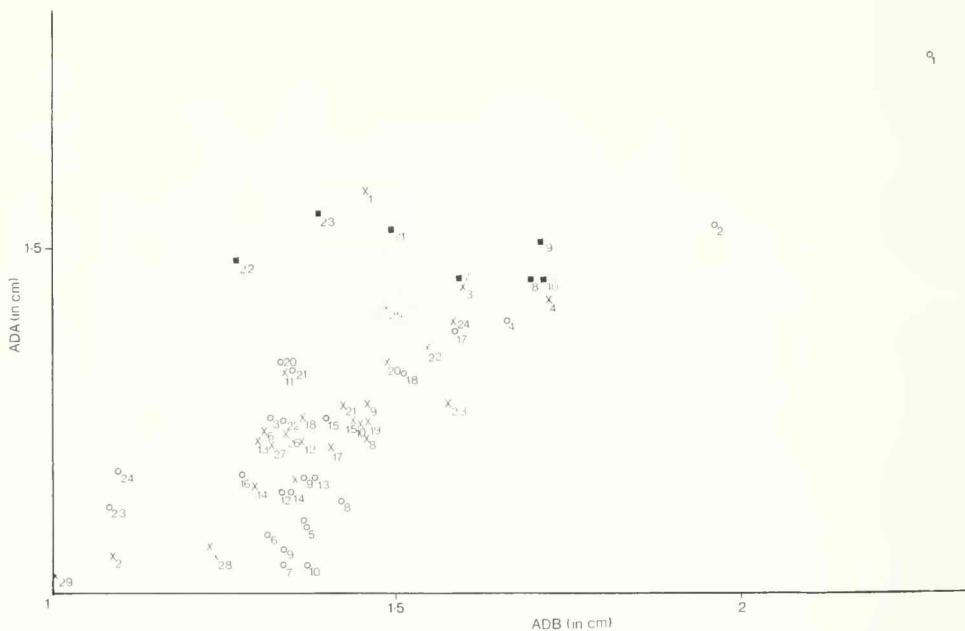


Fig. 5: Scatter diagram showing alveolar dimensions of *Gavialis gangeticus* (ZSM 2528/0, o-maxillary & x-mandibular alveoles) and *Gavialis* cf. *gangeticus* (■-mandibular alveoles).

Table 3:

*Crocodylus* cf. *palustris* (VPL/RP-R-1)

Alveole Number	AXA	AWB
?9	1.055	1.17
?10	1.58	1.735

*Gavialis* cf. *gangeticus* (VPL/RP-R-11)

?7	1.455	1.595
?8	1.45	1.70
?9	1.505	1.715
?10	1.45	1.72
?21	1.525	1.495
?22	1.48	1.27
?23	1.55	1.39

Table 3: Measurements of alveolar dimensions of *Crocodylus* cf. *palustris* and *Gavialis* cf. *gangeticus*.

Table 4:

Specimen Number	TWA:X				N	TWB:Y			
	R	M	S	V		R	M	S	V
2528/0 mandible	.66-1.055	.824	.107	.129	23	.795-1.32	1.069	.116	.108
2528/0 maxilla	.58-1.04	.821	.124	.151	23	.765-1.285	1.026	.137	.133
62/1959 mandible	.535-.93	.673	.080	.118	25	.725-1.21	.844	.093	.110
62/1959 maxilla	.56-.84	.695	.070	.100	13	.72-1.01	.870	.079	.090
29/1912 mandible	.29-.555	.402	.066	.164	23	.395-.72	.535	.079	.147
29/1912 maxilla	.37-.53	.485	.039	.085	20	.45-.6	.528	.034	.064
		AWA:X				AWB:Y			
2528/0 mandible	1.035-1.78	1.224	.172	.140	24	1.085-2.29	1.425	.252	.176
2528/0 maxilla	1.02-1.58	1.253	.125	.099	29	1.005-1.725	1.398	.149	.106
62/1959 mandible	.88-1.37	1.055	.169	.160	25	.86-1.575	1.148	.153	.133
62/1959 maxilla	.9-1.335	1.064	.122	.114	28	.685-1.59	1.138	.190	.166
29/1912 mandible	.525-.91	.665	.082	.123	25	.5-.98	.716	.101	.141
29/1912	.51-.84	.685	.084	.122	28	.435-.92	.711	.103	.144

Table 4: Measurements of teeth and alveolar dimensions of *Gavialis gangeticus*. Range (R), mean (M), standard deviation (S) variation (V) and Number (N). Only unbroken and fully erupted teeth of right mandible and maxillae have been used for measurements (in cm).

We attempt to place the two dentary fragments at their right position by comparing their widths with the ones from the recent specimens; a reconstruction is tried in fig. 7. It was observed that all the recent specimens have 25 teeth on the right dentary jaw and the 23rd alveoli lies nearest to the junction of right and left mandible. We measured the width of the right mandible at the alveoli nearest to the junction assuming it to be the 23rd alveoli (pl. V/1 a, Tab. 5). Shape and size of the anterior mandibular fragment and the position of the alveoles suggest that it belongs most probably to a part of the mandible posterior to the position of the 4th alveole (in recent specimens an abrupt difference in the mandibular width at the 4th and 5th alveoles can be recognized, pl. VIII/1 b). Therefore the mandibular width at the 7th alveole was selected for reference. By taking average widths at the 23rd and 7th mandibular alveole and the distance between them (Tab. 5) an approximate position of the anterior mandibular fragment has been estimated (fig. 6).

Size, shape and ornamentation on the enamel surface of the fossil teeth are very similar to those seen in the teeth of recent forms (pl. V). Close resemblance of the present isolated teeth to those of recent *Gavialis gangeticus* is further supported by the scatter plots (fig. 8), where their dimensions fall very much within the range of those of the latter (Tab. 4).

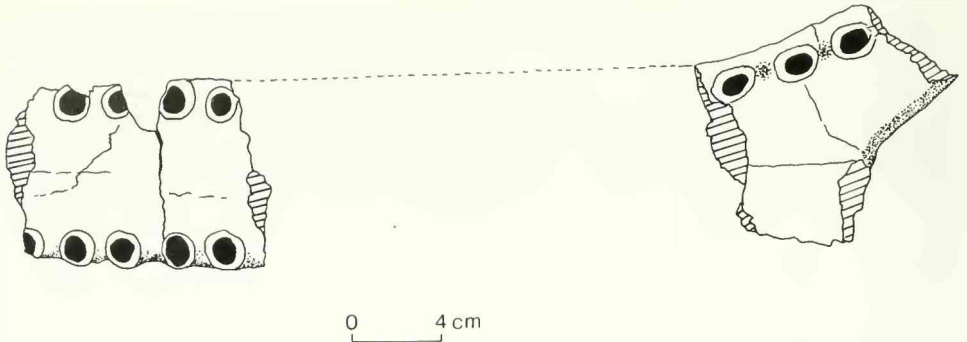


Fig. 6: Approximate placement of the two mandibular fragments of *Gavialis cf. gangeticus* (VPL/RP-R-11).

Table 5: Specimen no.	MW(23)	MW(7)	IAL (7-10)	IAL (7-23)
521/1911	1.75	2.475	3.5	19.7
29/1912	2.735	3.78	5.3	27.3
62/1959	4.08	5.745	5.4	29
2528/0	5.20	7.18	6.6	33.085
Mean	3.42	4.795	5.2	27.27
VPL/RP-R-1	5.835	appr. 8.30	7	appr. 36.7

Table 5: Measurements of mandibular dimensions of *Gavialis gangeticus* and *Gavialis cf. gangeticus*.

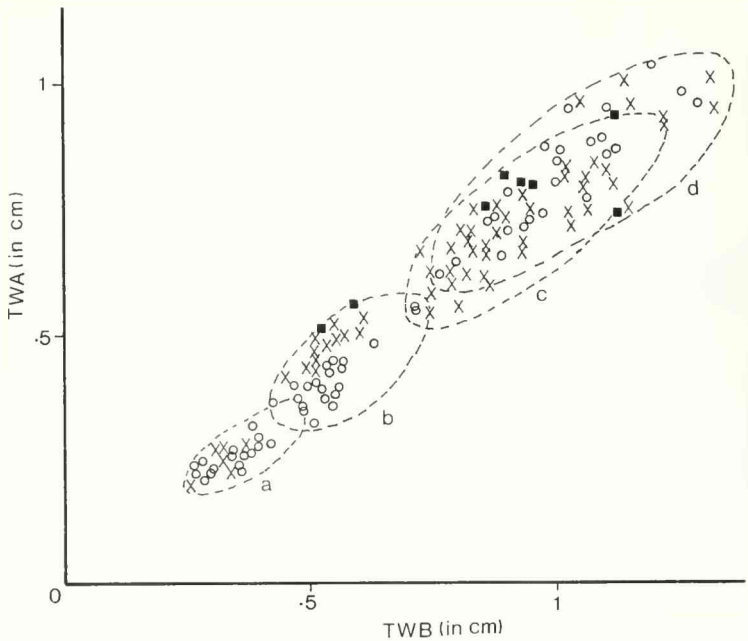


Fig. 6: Scatter diagram showing teeth dimensions of *Gavialis gangeticus* (o-maxillary & x-mandibular teeth) and *Gavialis cf. gangeticus* (■): a, ZSM 521/1911 (lower jaw length = 45,98 cm and skull length = 41,54 cm); b, ZSM 29/1912 (lower jaw length = 65,04 cm and skull length = 57,76 cm); c, ZSM 62/1959 (lower jaw length = 77,86 cm and skull length = 67,52 cm) and d, ZSM 2528/0 (lower jaw length = 91,05 cm and skull length = 79,67 cm).

## Crocodylian Eggshell Fragments

This is the first description of crocodile eggshell fragments from the Siwaliks. Records on fossil crocodile eggshells from other parts of the world is meager, too. The few findings include eggshells from the Eocene of Halle, Germany (HELLER, 1931); from Upper Cretaceous of Wyoming, U.S.A. (ERIKSON, 1978); from Eocene of Colorado and Upper Cretaceous of Montana, U.S.A. (HIRSCH, 1985; HIRSCH & QUINN, 1990 respectively) and from the Lower Miocene of Ulm, S-Germany (KÖHRING, 1992). For further information on that topic see SCHLEICH & KÄSTLE (1988).

### *Gavialis cf. gangeticus* & *Crocodylus cf. palustris* (pl. IX, X)

**Material:** Approx. 140 eggshell fragments. The four fragments described and illustrated here, bear the numbers VPL/RP-RE 1-4.

**Locality:** Moginand, Himachal Pradesh (India).

**Description:** The eggshell fragments in the present collection range in thickness from 1.9 to 6.6 mm (fig. 9). As shown by SCHLEICH, GASSNER & MASKEY (1994) even prominent differences in thicknesses might be due only to the different loci on the egg shell and do not really allow

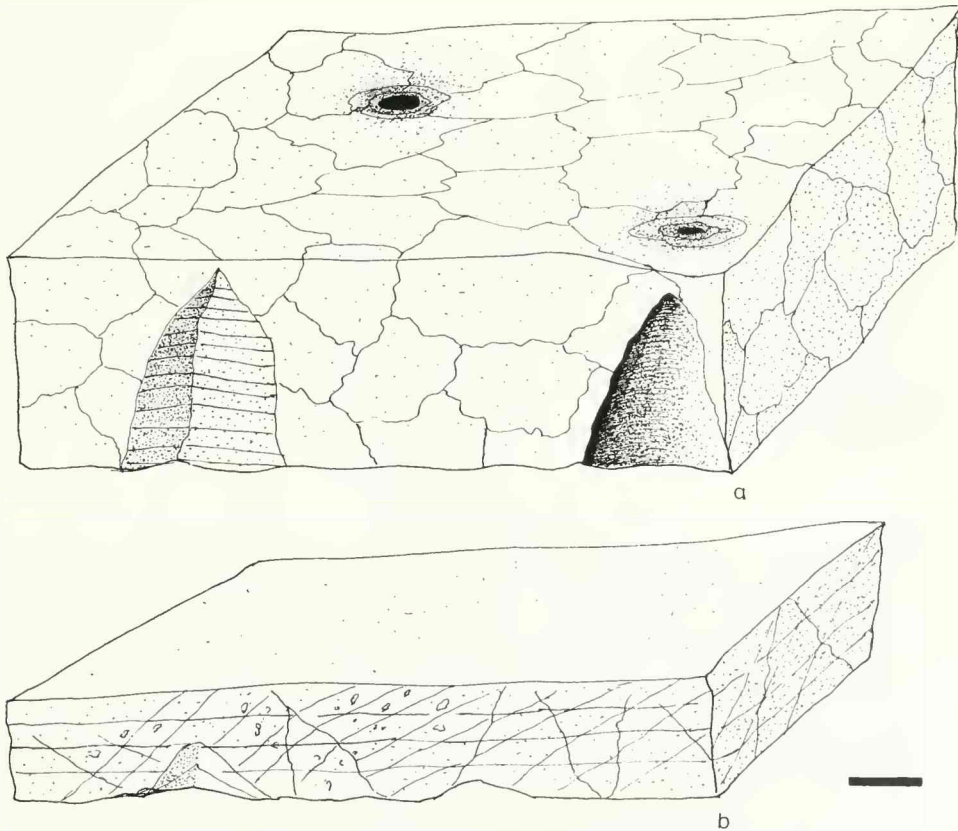


Fig. 8: Gross surface morphology and cross-section of Crocodylidae indet. eggshell fragment. a, thicker and b, thinner eggshell fragments. Bar represents 100  $\mu$ .



taxonomic interpretations. Supposedly the ranges between 3.5 to 5.5 and 5.8 to 6.6 mm reflect the thickness of polar and equatorial pieces of gavialid egg shells (see SCHLEICH et al., op.cit.) while the ranges from 1.9-2.9 and those till 3.3 mm thickness respectively might be interpreted as belonging to *Crocodylus*.

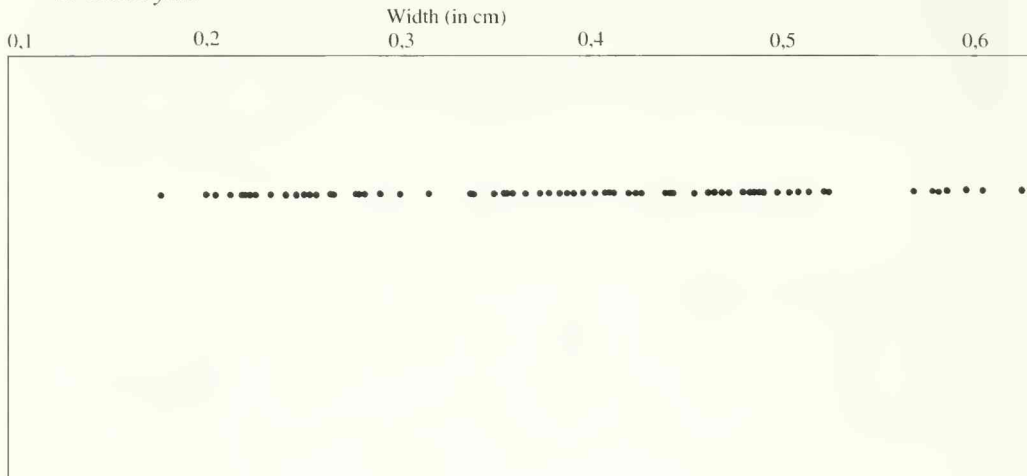


Fig. 9: Variation seen in the thickness of the Crocodylidae indet. eggshell fragments.

The outer surface of the thicker (?gavialid) eggshell fragments is smooth and is divided into irregular blocks by fractures. The pores are large, round and sunken (pl. IX/1, fig. 9 a). Very few specimens show erosion craters around the pores (pl. IX/7). In cross-section large pores and caverns can be seen (pl. IX/2). A freshly broken eggshell shows diverging wedges running all across the shell thickness (pl. IX/8). The enlarged cavern exhibit horizontal layers (pl. X/1). The inner surface shows closely spaced mamillae and large pore openings (pl. IX/5, 6).

Very few (approx. 5) eggshell fragments have rather rough outer surfaces, probably due to etching (pl. X/2). In cross-section they show horizontal and diagonal cleavages, which may have formed due to diagenesis (fig. 9 b). On the inner surface very well preserved, closely packed mamillae can be seen (pl. X/7, 8).

### Acknowledgements

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### Plate I

- Fig. 1-8, 10, 12-15: *Crocodylus* cf. *palustris*, Moginand (Himachal Pradesh), India.
- Fig. 1:            occlusal view of the mandibular fragment (VPL/RP-R 11); bar = 1 cm.
- Fig. 2, 3, 6, 7:   lateral views of anterior teeth (VPL/RP-R 12-15); bar = 1 cm.
- Fig. 4, 5:        lateral views of posterior teeth (VPL/RP-R 18, 19); bar = 1 cm.
- Fig. 8, 9:        magnified anterior teeth (VPL/RP-R 18 and of *Crocodylus palustris* ZSM 34/1912, respectively) bar = 1 mm;
- Fig. 10 a, b, 11: magnified posterior teeth (VPL/RP-R 16, a part of its keel and of *Crocodylus palustris* ZSM 517/1911); bars of 10a, 11 = 1 mm, 10b = 100  $\mu$ .
- Fig. 12-15:      surface views of the osteoscutes (VPL/RP-R-25-28), bar = 1 cm.

### Plate II

- Fig. 1, 2:        *Crocodylus* cf. *palustris*, Moginand (Himachal Pradesh), India.
- Fig. 1 a, b:      anterior, posterior view of cervical vertebrae (VPL/RP-R 21);
- 2 a, b, 3 a, b, 4 a, b: anterior and posterior views of caudal vertebra (VPL/RP-R 22-24); bar = 2 cm.

### Plate III

- Fig. 1:           *Crocodylus palustris* (ZSM 517/1911), skull from recent specimen; scale in cm. a) lateral, b) dorsal

### Plate IV

- Fig. 1:           *Crocodylus palustris* (ZSM 517/1911), skull from recent specimen.
- a) ventral, b, c) occlusal views of lower and upper jaw respectively; scale in cm.

### Plate V

- Fig. 1:           *Gavialis* cf. *gangeticus*, Moginand (Himachal Pradesh), India. Anterior mandibular fragment (VPL/RP-R 1a).
- a) occlusal, b) ventral; bar = 2 cm.

### Plate VI

- Fig. 1-4: *Gavialis cf. gangeticus*, Moginand (Himachal Pradesh), India. posterior mandibular fragment (VPL/RP-R 1b).  
a) occlusal b) ventral; bar = 2 cm.
- Fig. 2, 3: partly broken teeth (VPL/RP-R 2,3). lateral, bar = 1 cm.
- Fig. 4: magnified tooth (VPL/RP-R 4); bar = 1 mm.
- Fig. 5: *Gavialis gangeticus* (ZSM 62/1959), recent comparative specimen, magnified tooth; bar = 1 mm.

### Plate VII

- Fig. 1: *Gavialis gangeticus* (ZSM 2528/0); recent comparative skull. a) lateral b) dorsal; scale in cm.

### Plate VIII

- Fig. 1: *Gavialis gangeticus* (ZSM 2528/0); recent comparative skull.  
a) ventral b,c) lower and upper jaw respectively, occlusal. Scale in cm.

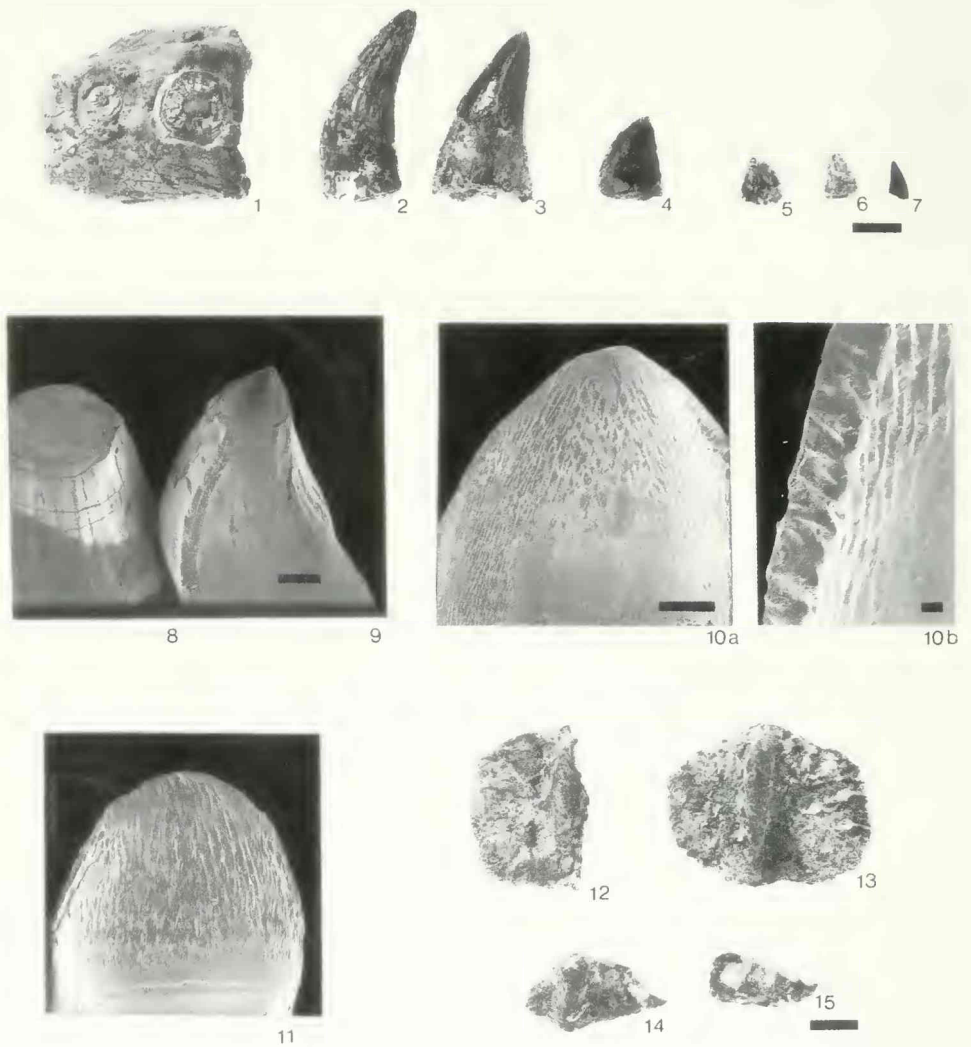
### Plate IX

- Fig. 1-8: *Gavialis cf. gangeticus* & *Crocodylus cf. palustris*, Moginand (Himachal Pradesh), India. Eggshell fragments, SEM-photographs.
- |   |                                 |
|---|---------------------------------|
| 1) outer surface (VPL/RP-RE 1);               | 5) inner surface (VPL/RP-RE 1); |
| 2) cross-section (VPL/RP-RE 1);               | 6) pore canal (VPL/RP-RE 1);    |
| 3) upper half of cross-section (VPL/RP-RE 1); | 7) pore opening (VPL/RP-RE 2);  |
| 4) lower half of cross-section (VPL/RP-RE 1); | 8) cross-section (VPL/RP-RE 2). |

### Plate X

- Fig. 1-8: *Gavialis cf. gangeticus* & *Crocodylus cf. palustris*, Moginand (Himachal Pradesh), India. Egg shell fragments, SEM-photographs.
- |                                    |                                 |
|------------------------------------|---------------------------------|
| 1) cavern magnified (VPL/RP-RE 3); | 5) lower half of cross-section; |
| 2) outer surface (VPL/RP-RE 4);    | 6) cavern magnified;            |
| 3) cross section;                  | 7) view of the inner surface;   |
| 4) upper half of cross-section;    | 8) inner surface magnified.     |

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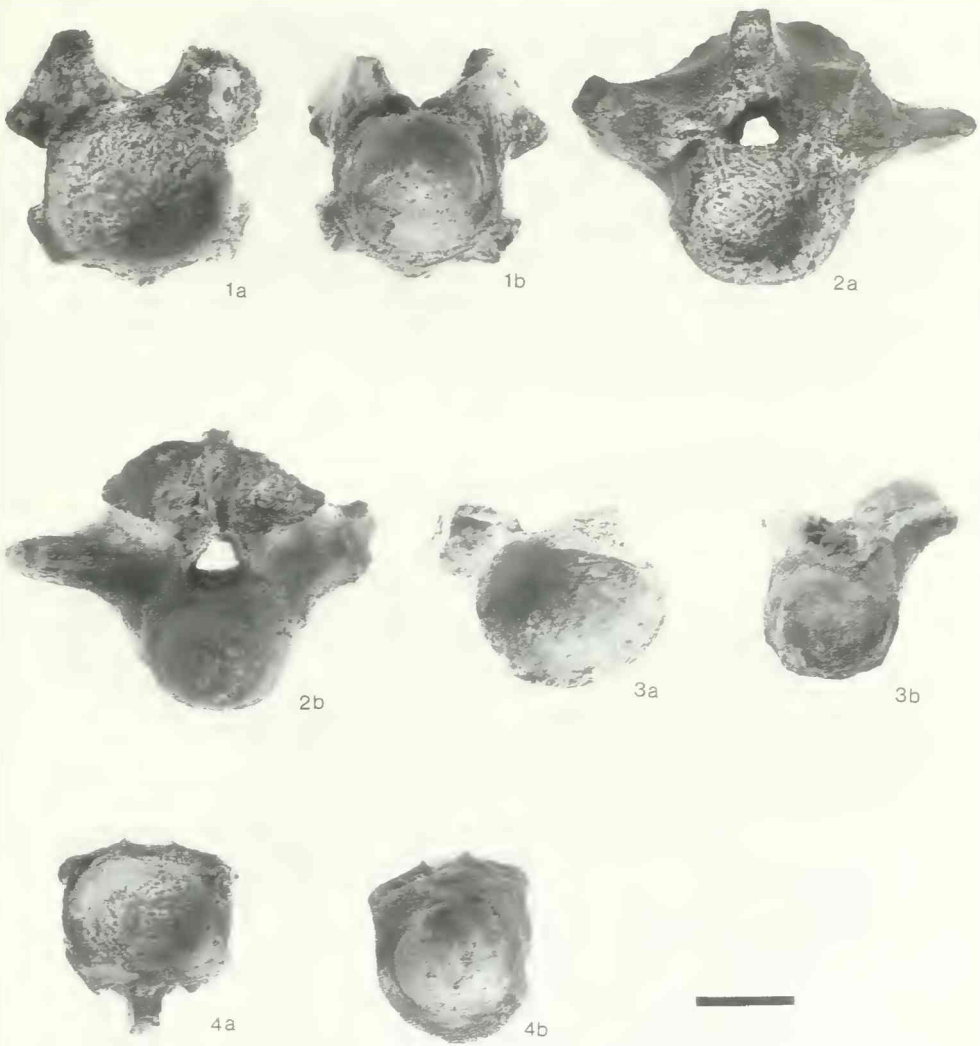


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Plate I



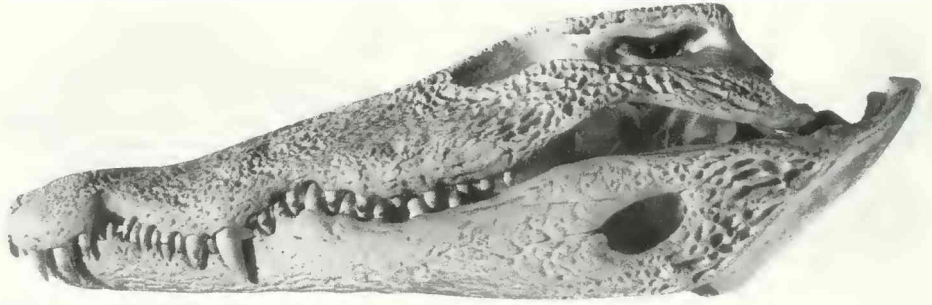
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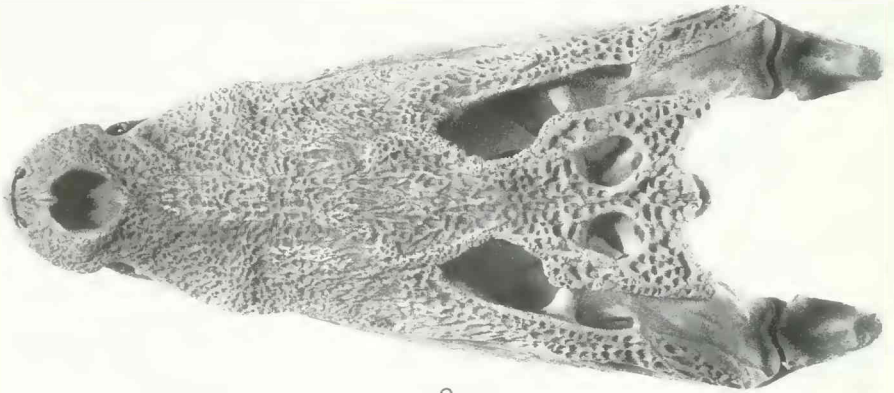
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Plate II

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1



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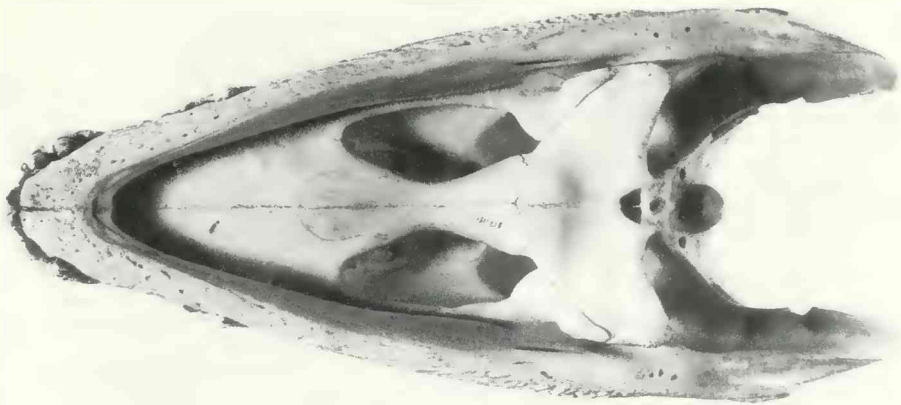
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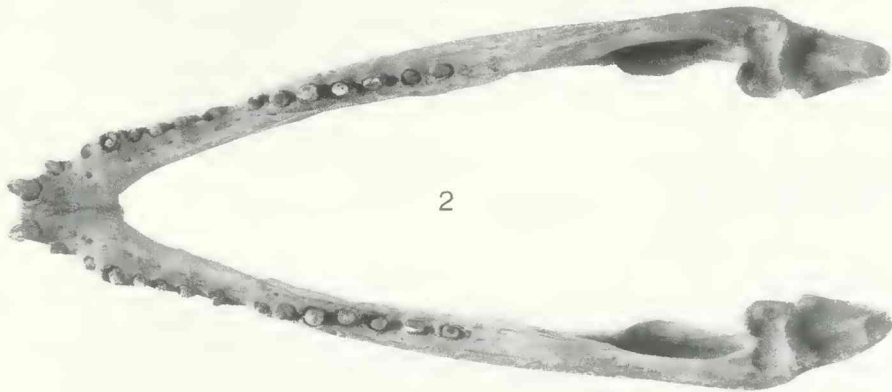
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Plate III

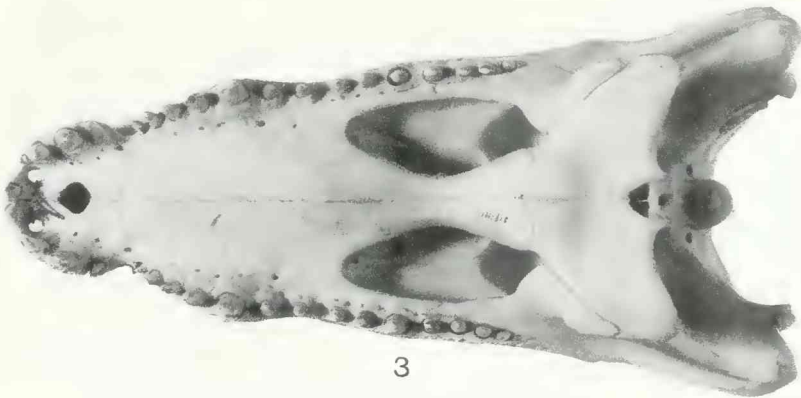
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2



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Plate IV

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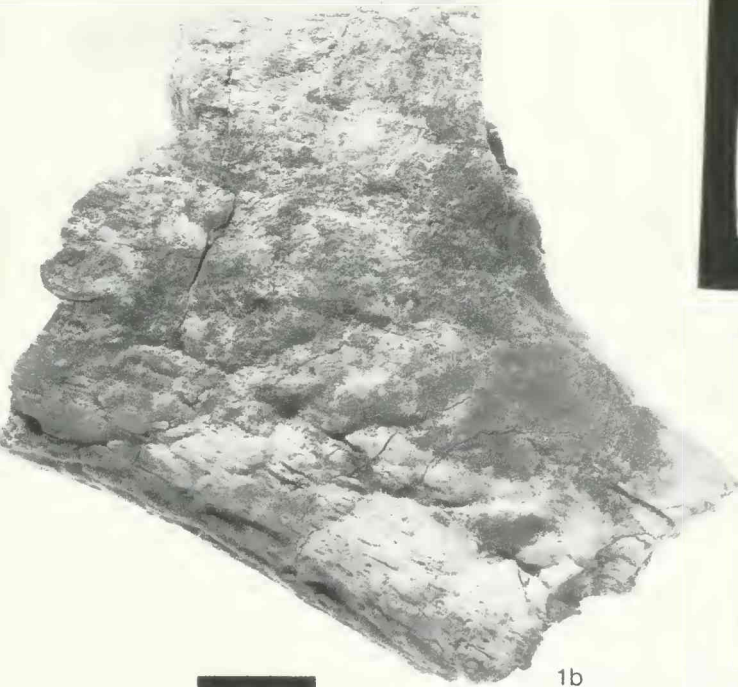
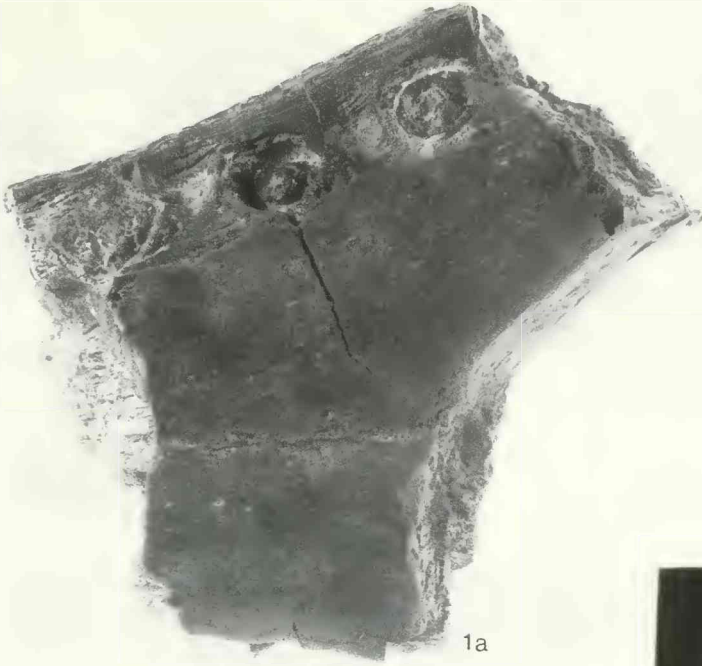
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1b

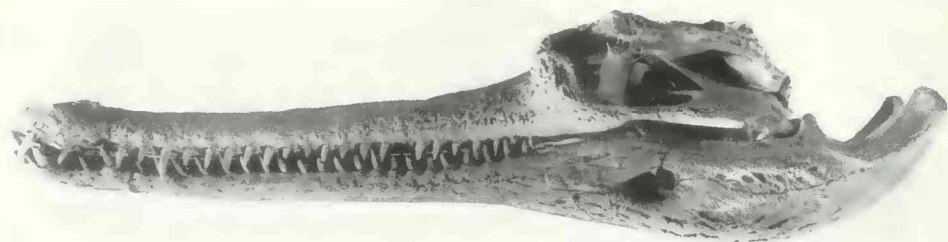
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Plate V

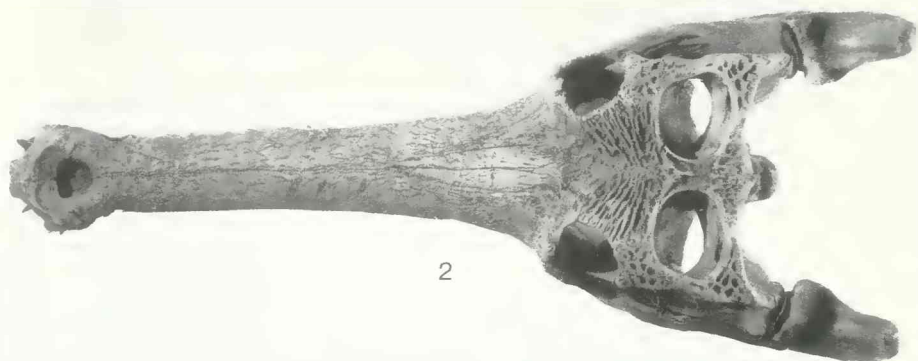




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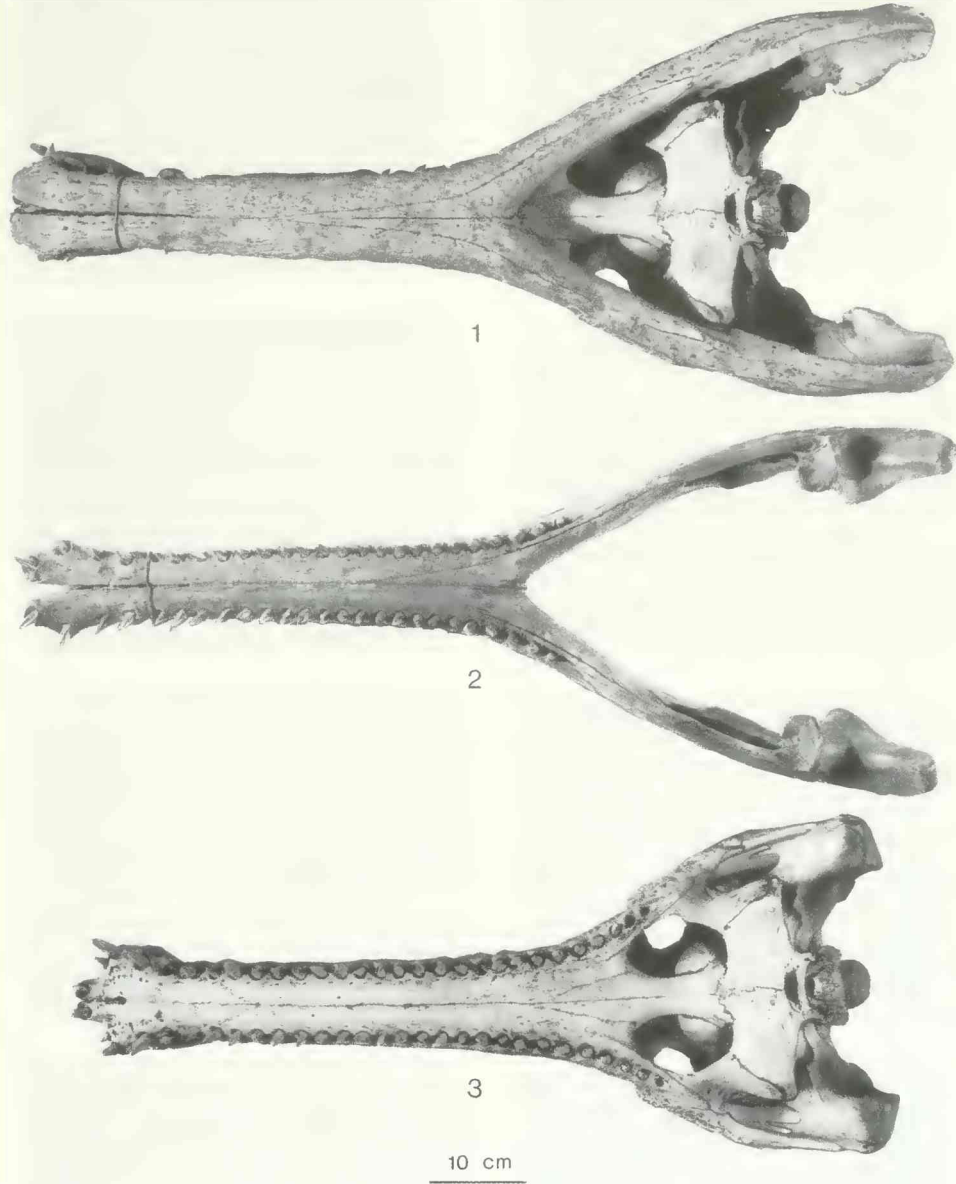
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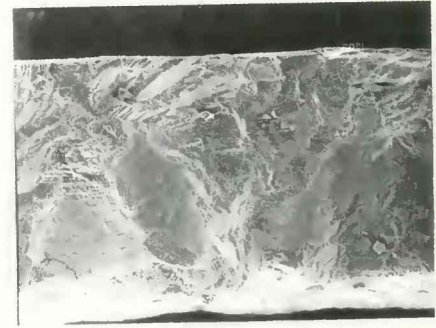
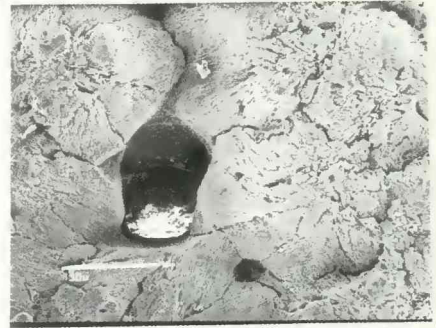
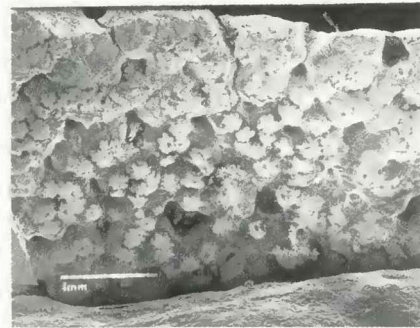
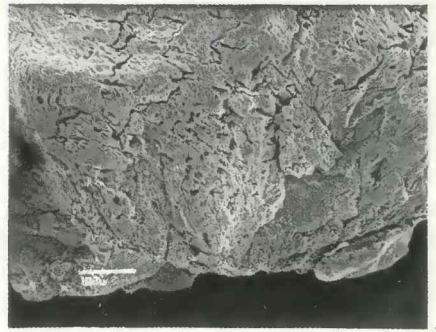
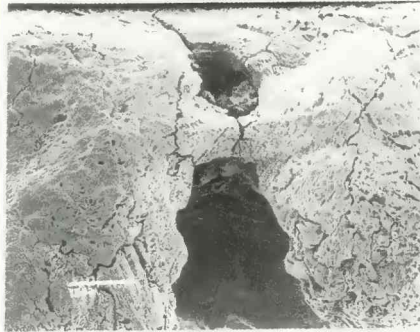
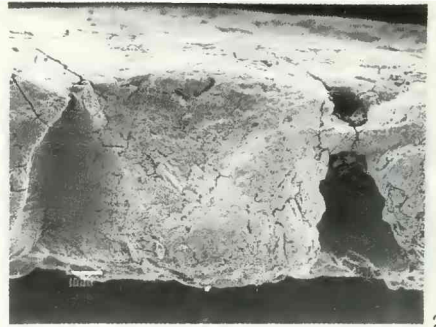
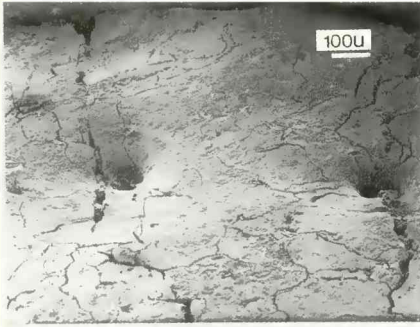
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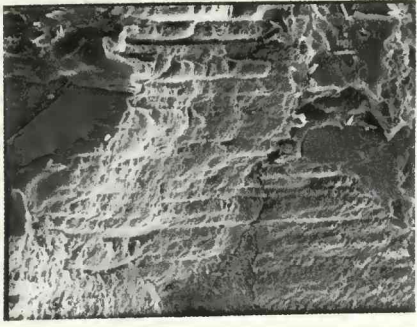


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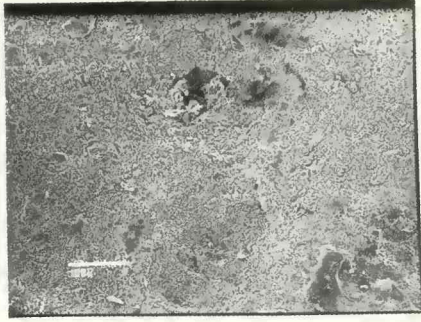
Plate VIII



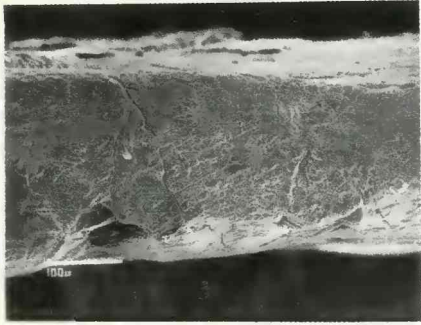




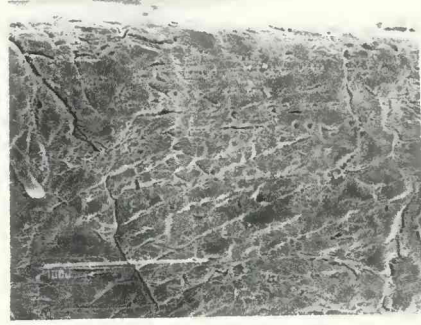
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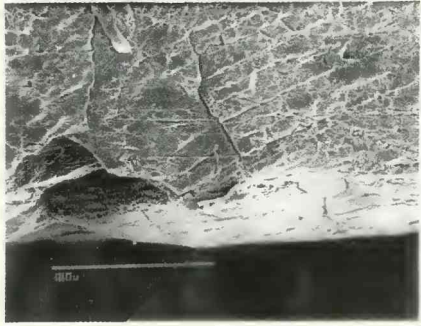
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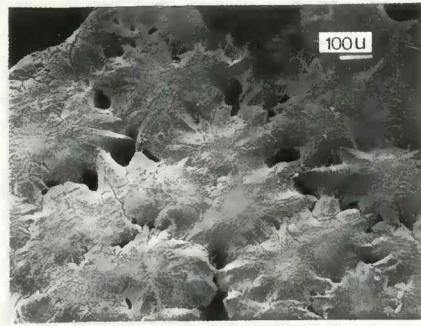
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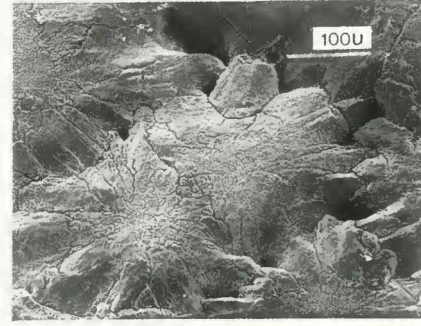
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Artikel/Article: [Fossil crocodile remains from the Upper Siwaliks of India 91-117](#)