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A Dyrosaurid Crocodile (Crocodylia: Mesosuchia) from the Paleocene of Pakistan

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Abstract

A nearly complete vertebral column and portions of an associated pelvis and hind limb from Sind Province, southern Pakistan, are described and identified as those of a marine crocodile belonging to the poorly known family, Dyrosauridae. The fossil is the most complete of its kind yet known from Asia and adds to our knowledge of the postcranial anatomy of the dyrosaurs. Its occurrence in the late Paleocene (Thanetian) Lakhra Formation places it among the earliest of Asian dyrosaurid crocodiles and strengthens the view that the Dyrosauridae spread from Africa to Asia along the shores of Tethys. The source rocks are of marine origin. Remains of dyrosaurid crocodiles are generally restricted to marine sediments of Africa, North America, and South America but have been only rarely found in marine rocks of Asia.

Key Words

Crocodylia, Dyrosauridae, Mesosuchia, Pakistan, Paleocene, Sind Province, Thanetian.

Introduction

During the period of 23 December 1981 to 1 January 1982 a joint field expedition from the Yale Peabody Museum of Natural History and the Geological Survey of Pakistan (GSP) under the direction of J. D. Archibald and H. Shaheed conducted a geological and paleontological survey of the Paleocene rocks of the Ranikot Group in the northern Lakhi Range of the Lower Indus Basin, Pakistan. This work was carried out under the auspices of the University of Michigan Museum of Paleontology and the Geological Survey of Pakistan as part of a continuing survey of Paleocene and Eocene continental sediments in Pakistan. The Yale-GSP field area comprised three ephemeral stream valleys, known locally from north to south as Rahman Doro (which dissects Bara Dome or the Lakhra anticline), Bara Nala (Bara Nai), and Lohige Nala (including, south of the main drainage, its tributary Barhi Nala). These valleys lie in the foothills at the northern end of the Lakhi Range, a group of north–south trending mountains in the Dadu District of Sind Province at the southern end of Pakistan (Fig. 1). During the course of field investigations, the articulated vertebral column of a large crocodilian was discovered and collected from the field area (Fig. 2) approximately 10 kilometers due east from the British colonial rest house settlement of Amri and the west bank of the Indus River, and approximately 170 kilometers from and 27° northeast of Karachi. Approximate coordinates of the field area are 26°10′N latitude; 67°53′E longitude.

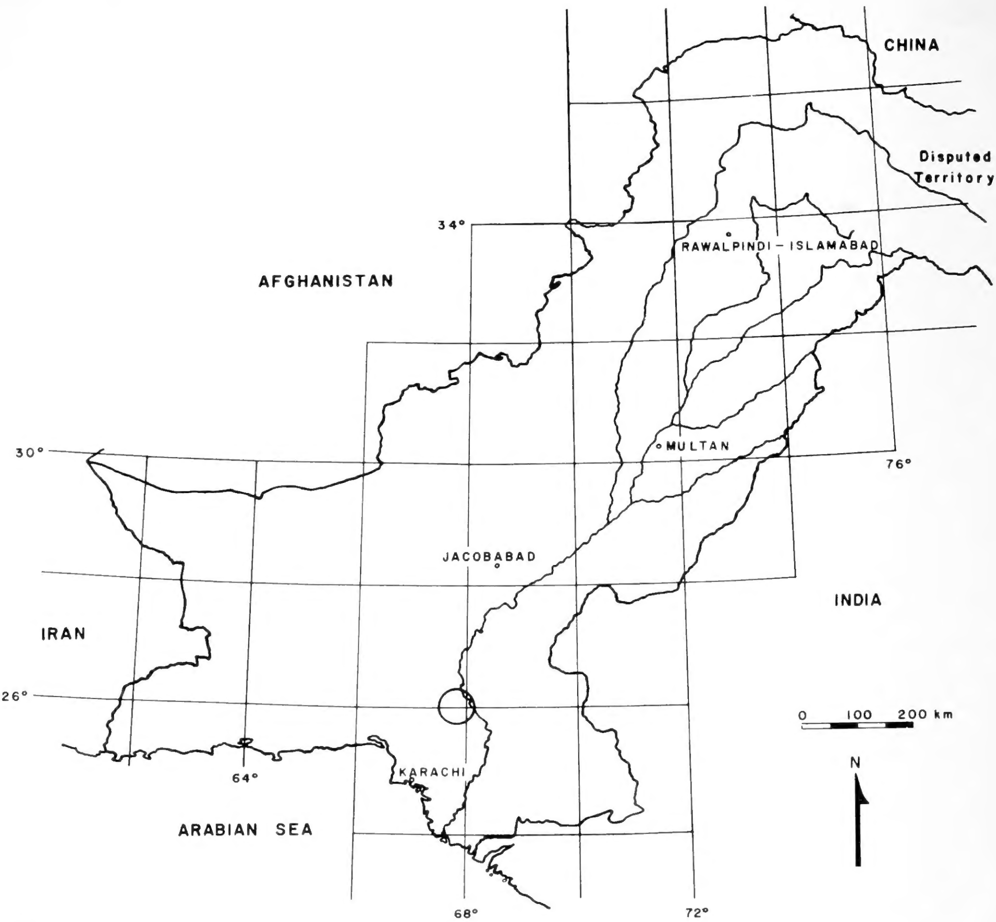

Fig. 1
Outline map of Pakistan. Northern Lakhi Range is located within circle and detailed in Fig. 2.

Geologic Setting

Several stratigraphic units are exposed in the field area. The disposition, description, and nomenclatural history of these formations has been discussed in detail by numerous authors (e.g., Gingerich et al. 1979; Hunting Survey Corporation 1961; Khan 1956; Shah 1977; Vredenburg 1909, 1928; Williams 1959; etc.). Lowermost in the section lies the Pab Sandstone of latest Cretaceous (Maastrichtian) age. Above this are found the three formations of the Ranikot Group, oldest of which is the Khadro Formation of Williams (1959) ("*Cardita beaumonti* beds" of Blanford 1876; "Daphro Beds" of Gingerich et al. 1979). On the basis of abundant foraminifera, the Khadro has been labeled Late Cretaceous to (primarily) early Paleocene or "Danian" in age (Shah 1977). The top of the Khadro Formation is marked by a basaltic trap possibly related to the Peninsular India Deccan Vent volcanism of the early Tertiary. The specific flow found in the Khadro has not, to my knowledge, been dated. Above the "Deccan trap" lie the Paleocene Bara and Lakhra formations, respectively, which are unconformably overlain by the Eocene Laki

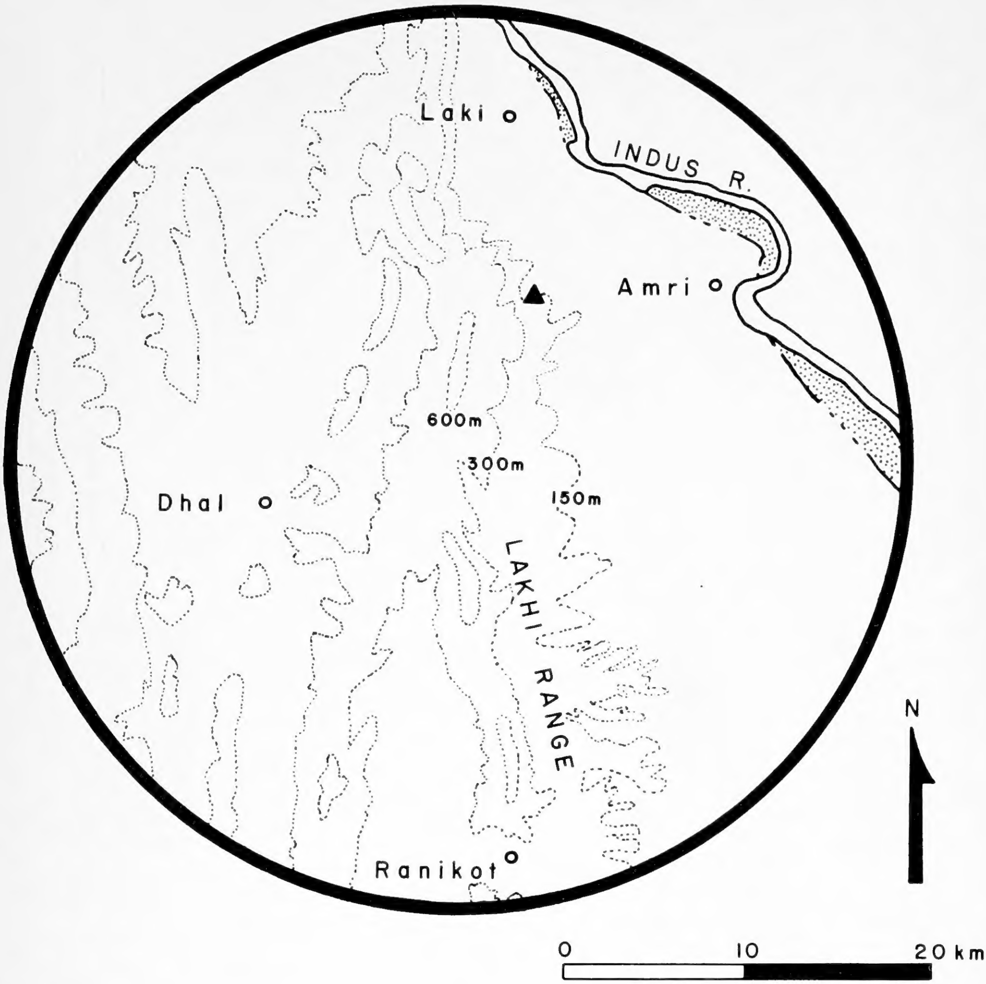

Fig. 2
Detail of Fig. 1 with approximate topographic contours in meters above sea level. Approximate locality (W1) of dyrosaur fossil, GSP No. 1020, is indicated by triangle.

Formation (Shah 1977). The Deccan trap basalt and the resistant, cliff-forming limestone of the Laki Formation present convenient and easily recognizable markers that delimit the local extent of the Bara and Lakhra sediments.

While the primary research interest of the Yale-GSP field party centered around the Paleocene Bara Formation (Lower Ranikot Formation of Hunting Survey Corporation 1961), the overlying Lakhra Formation (Upper Ranikot Formation) was also surveyed. The Lakhra Formation is approximately 242 m thick at the type section on the southern flank of the Lakhra anticline (Rhaman Doro) and invertebrate fossils from its richly fossiliferous sediments indicate a late Paleocene (Thanetian) age (Shah 1977). The Lakhra Formation consists of alternating calcareous sands, silts, shales, and dominant foraminiferal

Fig. 3
Barhi Nala, Sind Province, Pakistan. Khadro Formation shales and dyrosaur locality (W1) lie in foreground. Cliff-forming Laki limestone rises in distance.

limestones of varying thicknesses. All gradations between limestone and shale can be found. The sands are varicolored and poorly sorted, fine to coarse grained, thin to thick bedded, with cross-stratification and occasional ferruginous nodules. The shales, are clayey, gypsiferous, and poorly indurated. The characteristic limestones are richly fossiliferous, thin to thick bedded, nodular, brecciated, and arenaceous. They are generally brown weathering (Shah 1977).

Although of marine origin at the base, the Bara Formation has generally been regarded as predominantly representing fluvial environments, owing in part to the paucity of invertebrate fossils (Gingerich et al. 1979). The Lakhra Formation is unquestionably marine, however, and suggests frequent, short-lived regressions of intertidal mudflat and estuarine environments between episodes of transgression and offshore marine deposition.

On 30 December 1981, while prospecting in Barhi Nala within Lohige Nala, J. D. Archibald discovered the skeleton of a fossil crocodile in marine sediments of Paleocene age (Yale-GSP locality W1) which are unquestionably part of the Lakhra Formation. These were greensand rocks situated some distance (although unmeasured) below the obvious cliffs of the Laki limestone (Figs. 3, 4) and presumably above the Deccan trap. The Deccan trap is believed to lie subsurface in this area. The locality consisted of nearly horizontal beds of soft, brown and greenish-gray, gypsiferous shales. A NNW-to-SSE-trending fault separated these rocks from steeply dipping (about 60°) beds to the east. Approximately 150 m to the west, limestones were discovered approximately 15 m below the shales. The poorly exposed strata above the locality were also dominated by limestones (Yale-GSP field notes). Fossil

Fig. 4
Detail of dyrosaur locality (W1) in Barhi Nala. Laki Formation cliffs beyond.

invertebrates recovered from the matrix and surrounding area match those collected by the Yale team in the Lakhra Formation at Rhaman Doro and include *Ostrea* sp., *Venericardia* sp., *Crassatella* sp., ?*Conus* sp., ?*Turritella* sp., numerous indeterminate bivalves and gastropods, solitary scleractinians, worm tubes, and fragments of crab shell. Shark teeth, fish vertebrae, and rare carbonized plant debris were also found at both localities.

Preservation of the Fossil

The skeleton was discovered weathering from the side of a small hill. A large section of the articulated cervical and thoracic regions of the vertebral column was separated from the tail section by a break in the column. These sections lay in a coil which extended into, and was excavated from, the hillside (Figs. 5, 6). The sacral vertebrae and pelvis had been

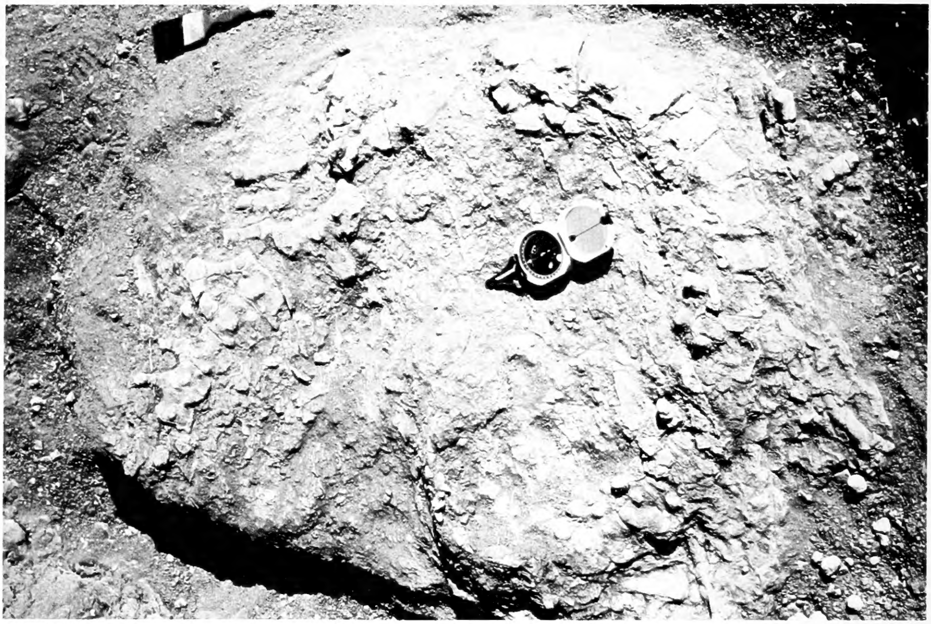

Fig. 5
Dyrosaur vertebral column, GSP No. 1020, *in situ,* after partial excavation. Left lateral surface exposed. Caudal vertebrae to left. Break in column at top.

destroyed by erosion, but parts of some of these elements, ribs, and portions of a hind leg were collected below the site as float. No part of the skull was found.

The condition of the bones is only fair and although harder than the crumbly siltstone matrix, they are delicate, easily broken, and badly fractured. Occasionally, the common veins of secondarily deposited gypsum have entered and distorted individual bones. The skeleton is for the most part encrusted with an extremely hard, ferruginous, concretionary layer averaging approximately 5 mm in thickness. Although the concretion has been mechanically removed from the bone in some places, it has often made detailed study of specific features difficult. However, the concretion takes the general form of the bones and so with the use of composite reconstructions incorporating fully prepared areas, little information about the external appearance of the bones has been lost. The configuration of the vertebrae indicate the skeleton is that of a dyrosaurid crocodile. Most strikingly, the vertebrae are platycoelous, indicating that the animal was a mesosuchian in the classical sense (although the Mesosuchia is likely to be an artificial grouping). Additionally, the fossil was discovered, presumably untransported, in marine sediments of Paleocene age. The Dyrosauridae represent the last radiation of marine mesosuchians (Buffetaut 1981) and the only family of mesosuchians (possibly excluding the problematic terrestrial Sebecidae of South America) to survive past the Cretaceous—Tertiary boundary. While it is as yet virtually impossible to identify isolated postcrania of the dyrosaurs to genus, as the postcranial skeleton exhibited very little variation within the family (Buffetaut, personal communication, 1984; Moody and Buffetaut 1981), the completeness of this fossil warrants its description. The fossil is number 1020 in

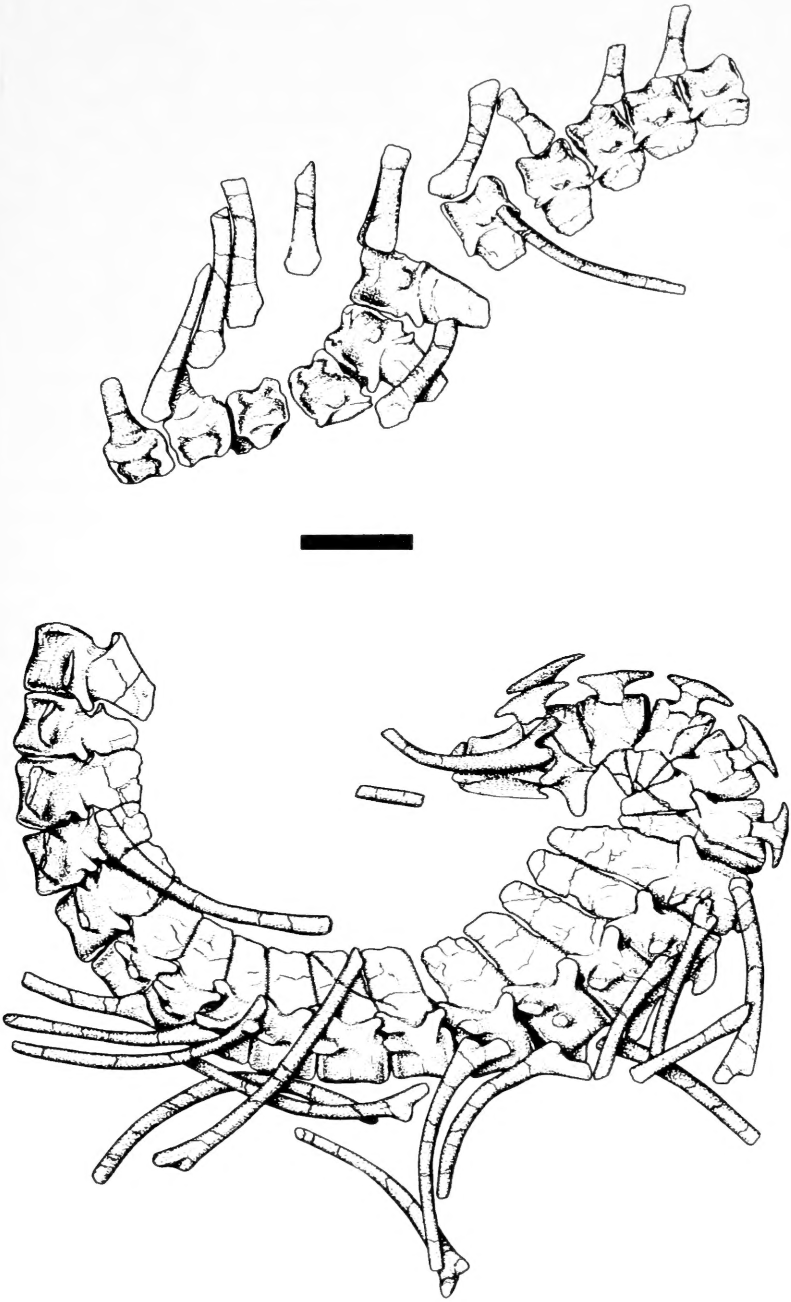

Fig. 6
Illustration of dyrosaur vertebral column, GSP No. 1020, after preparation. Right lateral surface shown. Caudals at top. Bar = 10 cm.

the collection of the Geological Survey of Pakistan.

Description

ORDER Crocodylia GMELIN, 1788
SUBORDER Mesosuchia HUXLEY, 1875
FAMILY Dyrosauridae DE STEFANO, 1903

The total length of the anterior series of articulated vertebrae is approximately 135 cm. This series begins with the fused atlas centrum and axis intercentrum. The neural arch and the intercentrum of the atlas are missing. This is followed by the axis, seven additional cervical vertebrae (totaling nine as is typical for most crocodilians), and fourteen dorsals. Typical cervical ribs remain articulated with the third through seventh cervicals. Seventeen thoracic ribs lie across the vertebral column, some articulated with their transverse processes. A few isolated rib fragments were also collected. The second group of articulated vertebrae consists entirely of caudals and is approximately 60 cm long. Eleven proximal caudals are present. The first ten are complete with their respective chevrons. All of the preserved caudal vertebrae have transverse processes. From between the two vertebral series an isolated dorsal vertebra and a single sacral vertebra are preserved. The second sacral is missing, along with perhaps one posterior dorsal, one or more anteriormost caudals, and the greater part of the tail's extremity.

The fact that most of the spines and all of the arches are intact throughout the column is noteworthy. Dyrosaurid vertebrae are usually found as isolated centra and it is very rare for the neural arch to remain attached. This is due to the frequently weak neurocentral sutures of dyrosaurs (Buffetaut 1978b).

Part of the pelvic girdle and right hind leg are present. These are composed of the articulated right ilium and proximal part of the right ischium, three fragments of the right pubis, the acetabular portion of the left ilium, the proximal end of the right tibia, and the right astragalus. A single crocodilian tooth fragment was discovered in the matrix of the skeleton. However, as other crocodile teeth were found in the vicinity, this is possibly from a separate individual.

Atlas-axis Complex

The atlantal centrum forms a small, wedge-shaped lozenge approximately 3 cm wide and 3 cm high. It is fused with the axial intercentrum. This bone is thickest dorsally. It is articulated with the anterior face of the much larger axis centrum. The centrum of the axis is approximately 5 cm long, 3 cm wide, and carries a neural arch with a long (7.5 cm), low neural spine, which projects past the posterior end of the centrum. In this regard, the vertebra resembles the axis of the living *Gavialis gangeticus*. Indeed, the atlas-axis complex of *Gavialis* is closely similar to that of the fossil, except for the platycoelous nature of the latter.

Third through Ninth Cervical Vertebrae

The centra of these vertebrae are cylindrical and platycoelous. The eighth cervical centrum is approximately 4 cm high, 4 cm wide, and 5.5 cm long. The capitular facets of the vertebrae are situated low on the centrum and the tubercular facets lie at the tip of the transverse processes of the neural arches. The ribs of vertebrae 3 through 7 are short and bladelike and resemble those of *Gavialis*. Each is supported by a V-shaped brace formed by the capitulum and tuberculum. The "blade" projects both craniad and caudad parallel to the axis of the column.

The posterior two cervical vertebrae are transitional to the dorsals and bear parapophyses that are located progressively higher on the centra than those of the anterior cervicals. The diapophyses are long and stout. The ribs of these transitional vertebrae resemble those of the dorsals as they are long and robust. The posterior two cervical vertebrae also possess strong, keellike hypapophyses much as in other dyrosaurs, for example, *Hyposaurus* from the Cretaceous of New Jersey (Owen 1849) and Brazil (Cope

1886) and the Paleocene of Mali (Buffetaut 1980; Dollo 1914; Swinton 1930). Those of the Pakistani crocodile are swept back, subtriangular in lateral outline, and approximately 2.5 cm long from base to tip. In contrast, the small hypapophyses of the modern *Alligator mississippiensis* are present on all cervicals and point craniad. Similarly, all parapophyses of *Alligator* are located near the anterior end of each centrum, whereas in the fossil each is found at the approximate midpoint.

It is in the neural spines that differences from other crocodilians are most evident. The spines of vertebrae 3 through 7 are short and narrow with rounded tops, whereas the last two cervicals have very tall (maximum 12 cm), rectangular spines. The spines of *Hyposaurus* are more rounded. The tall spines of the Pakistani crocodile begin abruptly and then, together with the anterior dorsal spines, gradually decrease in size caudad. Dyrosaurids are distinguished from other crocodilians by such tall cervical spines and Buffetaut (1979a) has suggested that they provided surfaces of attachment for powerful neck muscles from the occiput. Dyrosaurids had large, longirostrine skulls and a strong nuchal ligament at this point probably supported the heavy head.

Dorsal Vertebrae

The dorsal vertebrae continue the pattern observed in the cervicals in that long, rectangular, anterior neural spines become progressively shorter toward the middle of the column where they become nearly equal (approximately 6 cm) in height. Throughout the column each spine is uniformly thin with little or no lateral thickening at its top. The last few preserved dorsals have neural spines that are directed somewhat craniad. These spines are also rectangular in outline. These last dorsals represent the lumbar region because they have stout transverse processes but no associated ribs. The long transverse processes of the anterior dorsals are swept backwards at an angle of approximately 45° from the perpendicular. This angle decreases posteriorly. The dorsal diapophyses of *Alligator* are, on the other hand, all set nearly perpendicular to their centra.

The anterior dorsal centra of the fossil are only slightly taller than they are wide. The centrum of the fourth dorsal is 3.5 cm wide, 4.5 cm high and 5 cm long. Caudad the centra become more nearly cylindrical. The thirteenth dorsal is 4 cm wide, 4 cm high, and 5 cm long. Well-developed hypapophyses are characteristic of the anterior dorsals of dyrosaurs, and they are present on the first three dorsals of the fossil. These are similar to those of the cervicals. Vertebrae 13 and 14 each have a small hypapophysis. The parapophyses of the first two dorsals lie along, and are divided by, faint neurocentral sutures. There are no uncinate processes on any of the associated dorsal ribs.

Sacral Vertebra

This isolated bone, though poorly preserved, is large and robust. The centrum is approximately 5.5 cm long and 4.5 cm wide, but is only 3.5 cm high. It is thus semielliptical in cross section. The articular faces of the centrum are expanded. A single fused sacral rib, (7 cm) long and stout, is intact.

Caudal Vertebrae

These vertebrae are characteristically dyrosaurian and strikingly similar to those of *Hyposaurus*. They indicate a powerful, laterally compressed tail. The centra are deeper than they are broad (3.5 cm by 3 cm, respectively, in the third preserved vertebra); preserved centra average approximately 4.5 cm in length. The articular surfaces are subrectangular and the ventral surfaces are deeply concave. Prominent chevron facets are present at both ends of the centra. The chevrons are long and rectangular as are the neural spines. The complete chevron of the third preserved caudal is 13 cm in length whereas that of the tenth is only about 6 cm long. The spine of the sixth preserved caudal is approximately 7 cm tall.

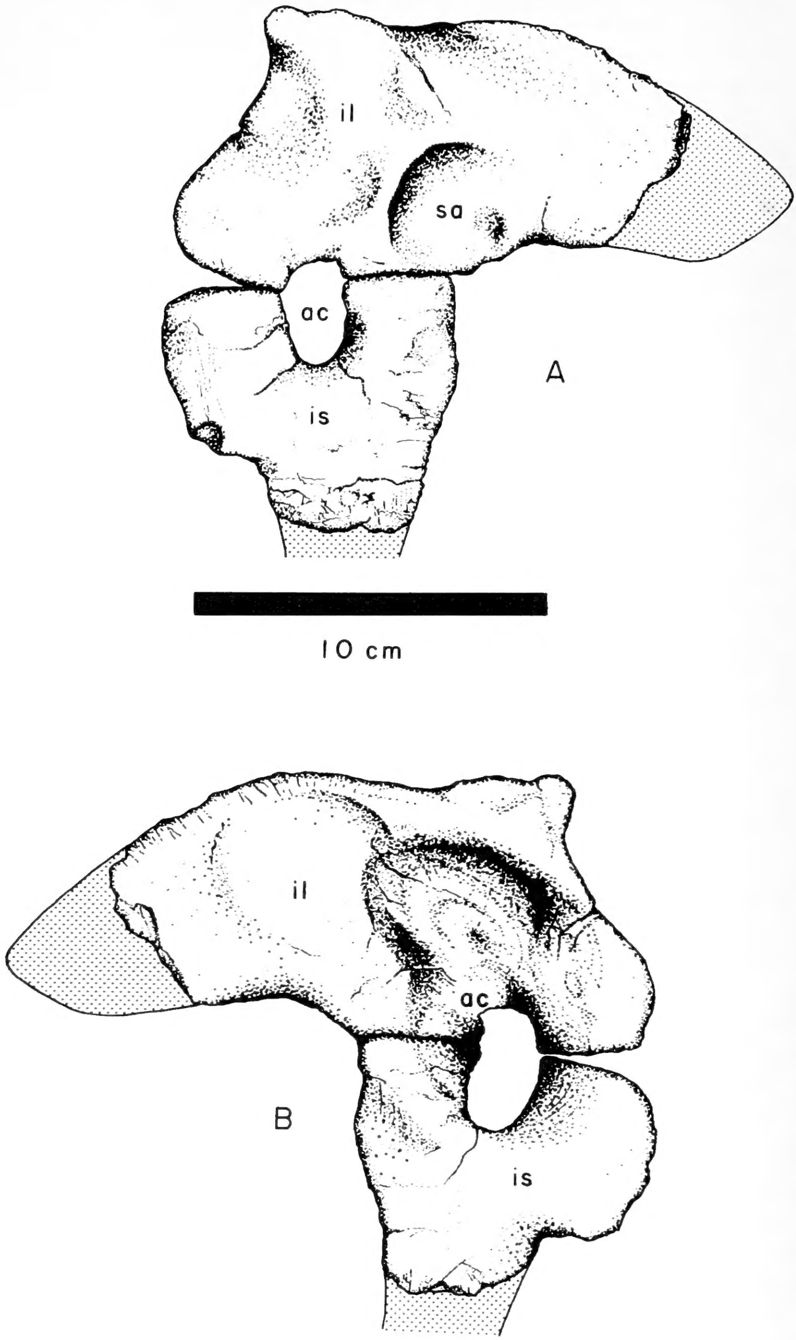

Fig. 7

Right ilium and ischium, GSP No. 1020. *A*, medial aspect; *B*, lateral aspect. *ac*, acetabulum; *il*, ilium; *is*, ischium; *sa*, sacral articulation. Shaded portions are reconstructed.

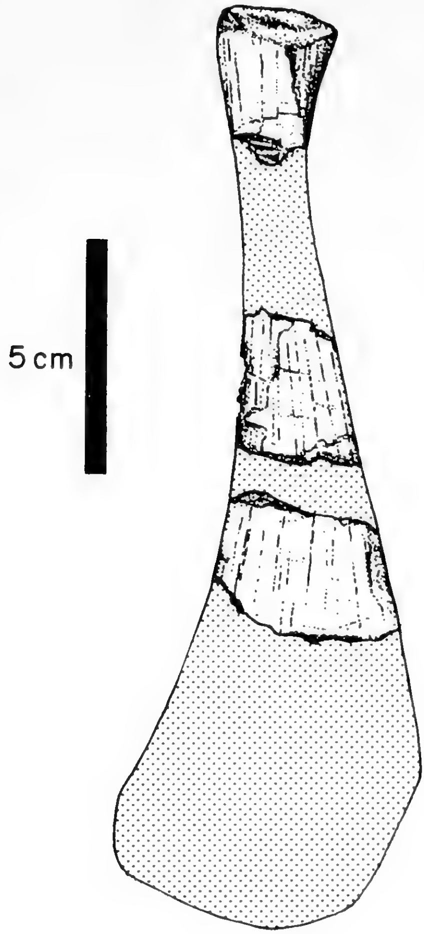

Fig. 8
Right pubis, GSP No. 1020, dorsal aspect. Proximal end at top. Shaded portions reconstructed after *Hyposaurus*.

Pelvic Girdle

The ilium and ischium (Fig. 7), except for their larger sizes, are little different from those of *Alligator*. Slight differences are found in the shape of the acetabulum and the high anterodorsal spur, or costalis tubercle, on the ilium of the fossil. This spur, and indeed the entire pelvis, is virtually identical to that of the *Hyposaurus* specimen described by Troxell (1925). As in *Hyposaurus*, the acetabular perforation is deeply incised into the ischium, and although filled with concretionary material, the anterior opening of the acetabulum appears to be more nearly closed by the ilium and ischium than in *Alligator*. The right pubis is represented by three fragments which indicate a very long (possibly 20 cm), spatulate blade as in *Hyposaurus* (Fig. 8), and not the short, broad type found in *Alligator*. The longest dimension of the right ilium is approximately 15 cm. The posterior tip of the

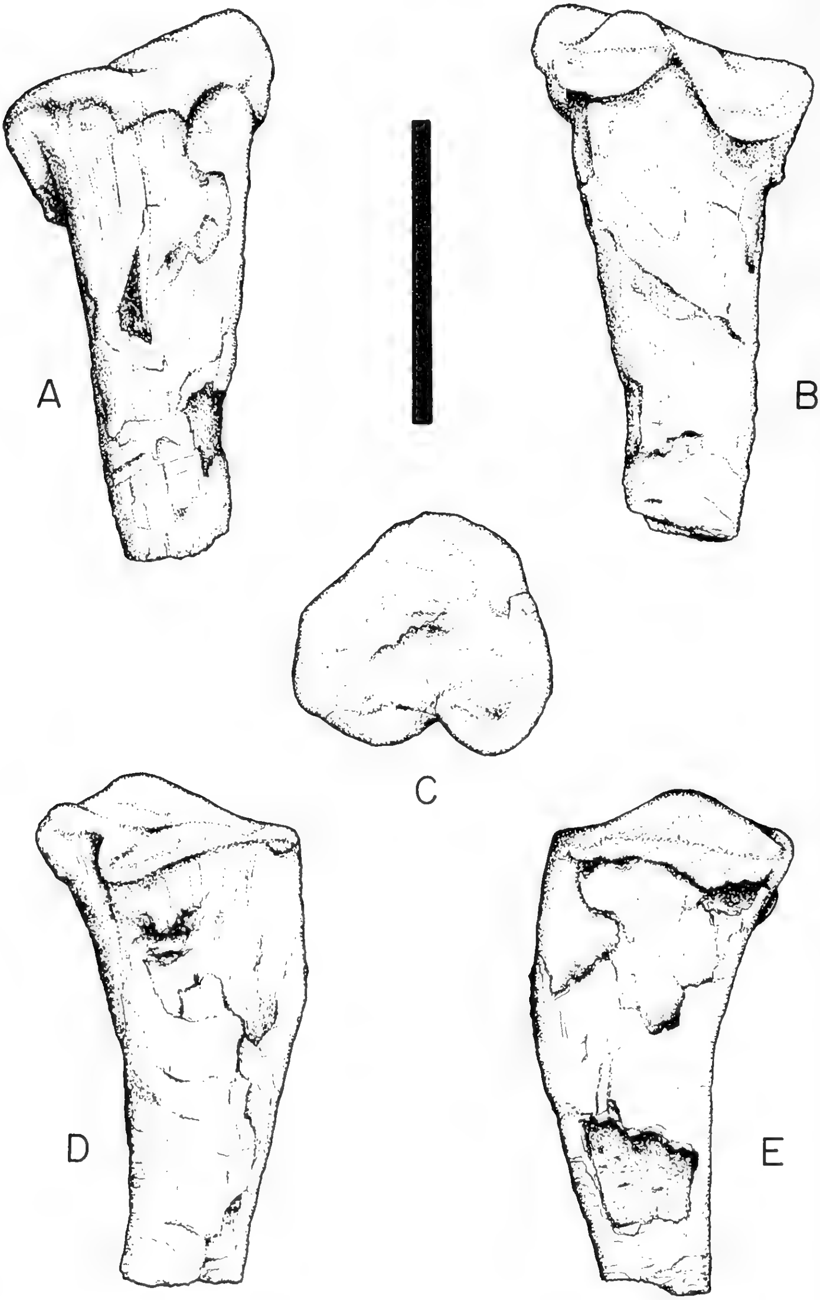

Fig. 9
Right tibia, GSP No. 1020. *A*, extensor aspect; *B*, flexor aspect; *C*, proximal aspect, anterior to top; *D*, posterior aspect; *E*, anterior aspect. Bar = 5 cm.

bone is missing. The breadth of the right ischium at the iliac articulation and across the acetabulum is approximately 8 cm.

Tibia

The proximal end of the right tibia (Fig. 9) has a maximum diameter of approximately 4.5 cm. The articular region is well formed, indicating an adult animal. The head is robust and the two areas of contact with the femoral condyles are individually distinct. The posterior articulation is much larger than that of *Alligator,* creating a more nearly triangular proximal surface. This surface is much higher anteriorly than it is posteriorly and laterally. A well-defined trough is present between the condylar articulations on the flexor surface of the bone. On the extensor surface the cnemial crest is prominent.

Astragalus

The astragalus is not unlike that of *Alligator.* The ball joint for articulation with the first metatarsal is well defined, as are the peg for the calcaneum, the facet for the tibia, and the contact with the fibula. The bone is approximately 4.5 cm long.

Discussion

The late Mesozoic and Paleogene Dyrosauridae is a family of poorly known, longirostrine mesosuchian crocodilians. Most were large (up to 9 m in length), and they were probably powerful swimmers primarily adapted to life in the littoral marine environment. They are so far known from the Maastrichtian through the Eocene, most notably from northern Africa. During the Paleogene, dyrosaurid crocodiles diversified, exhibiting several combinations of jaw structure and dentition (Buffetaut 1979a). Thevenin (1911) first proved the crocodilian affinities of the familial type, *Dyrosaurus* Pomel, 1894, from the early Tertiary phosphate beds of southern Tunisia (see also De Stefano 1903; Nopcsa 1905; Sauvage 1904; Thomas 1893). Additional dyrosaur fossils representing several taxa (e.g., *Atlantosuchus, Dyrosaurus, Hyposaurus, Phosphatosaurus, Rhabdognathus, Sokotosuchus, Tilemsisuchus*) have since been collected from marine deposits in Algeria, Angola, Egypt, Ivory Coast, Mali, Morocco, Niger, Nigeria, Saudi Arabia, Senegal, and Togo (Buffetaut 1979a). Bergounioux (1955, 1956), Buffetaut (1976a, 1976b, 1978c, 1979a, 1979b, 1980), Buffetaut and Wouters (1979), Buffetaut et al. (1982), Halstead (1975), Madden et al. (1979), Moody and Buffetaut (1981), and others have studied and discussed many of these specimens. Buffetaut has also shown that *Hyposaurus* from New Jersey, Brazil, and Mali ("*Congosaurus,*" "*Sokotosaurus,*" "*Wurnosaurus*") is a dyrosaurid (1976a, 1980), and that indeterminate dyrosaurs occur in Pakistan (1977, 1978b) and possibly also in Burma (1977, 1978a).

The occurrence of Asian dyrosaurid crocodile remains has been reviewed by Buffetaut (1978a, 1978b). One caudal vertebra of a possible dyrosaur is known from the late Eocene of Burma. It is from a freshwater deposit and is perhaps the latest and the easternmost dyrosaur occurrence known (Buffetaut 1978a). However, the caudals of certain terrestrial mesosuchians are quite similar (Buffetaut, personal communication, 1984). Asian marine dyrosaurids are surprisingly rare. With the exceptions of a single vertebra from an Eocene oyster bed limestone of Punjab (northern Pakistan) and one dorsal and one caudal centrum from the "Danian" Khadro Formation of the Lakhi Range (described by Lydekker 1879), all previously known Pakistani dyrosaur fossils have come from freshwater deposits (Buffetaut 1978b). Virtually every specimen from Africa, North America, and South America is known to be from marine rocks.

Dyrosaur fossils from freshwater deposits in Pakistan are numerous, but usually consist of isolated vertebral centra, occassional skull and jaw fragments, scutes, and teeth, suggesting considerable postmortem transport. All of them are Eocene in age

(Buffetaut 1978b). Buffetaut (1978b) suggests that they may represent immature individuals that were hatched from inland broods and had not yet journeyed seaward to live along the coast as adults. Most of the vertebrae are small (about 4 cm in length). The abraded nature of the bones is consistent with riverine or estuarine transport.

The present specimen represents by far the most complete dyrosaurid yet discovered in Asia. The preserved portion of the column and the average vertebral length of approximately 5 cm suggests an adult individual of about 4 m length. The fossil is one of the oldest Asian finds, excepting the two above-mentioned vertebrae from the Khadro Formation. Apparently the individual (from its deep caudals, presumably an active swimmer) was part of the littoral fauna. Shallow-water marine invertebrates (e.g., *Ostrea* sp., corals, decapods, etc.) and the ubiquitous teeth of the sand shark *Odontaspis* sp. and the nurse shark *Ginglymostoma* sp. confirm the near-shore marine nature of the matrix. The glauconitic content of the siltstone (approximately 80%) and its calcite cement also support this interpretation. The articulated condition of the column suggests little transport of the carcass and only moderate disruption after deposition. The animal, though deposited in shallow water, was presumably lying below wave base where some of its exposed bones provided a temporary substrate for small epifaunal oysters and solitary scleractinians. There is also, incidentally, no direct evidence that any of the sharks were scavenging upon the carcass. Their teeth are common throughout the sediments of the locality.

The dyrosaurs of Pakistan, owing to their fragmentary record, have not yet been identified generically. At least some of them may be congeneric with African forms where the dyrosaurid record is most complete (Maastrichtian to middle Eocene) and where their greatest known diversity was achieved in the Paleocene (Buffetaut 1978b). Northern Africa and Pakistan are geographically related as components of the Tethyan maritime province, and it is not unlikely that crocodilians, especially such strong swimmers as dyrosaurs, could have spread from one area to the other. The present specimen, while similar to *Hyposaurus* in most respects, cannot be positively linked with any of the African forms. Part of a slender, curved tooth associated with, and probably belonging to it, may rule out the large *Phosphatosaurus* whose teeth were generally massive and stout. However, the other and smaller Tertiary dyrosaurs had long slender teeth. Only when good skull material of Pakistani dyrosaurids is found can more definitive identifications be made.

Acknowledgments

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