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FROM THE MIDDLE EOCENE DRAZINDA FORMATION
OF THE SULAIMAN RANGE, PUNJAB (PAKISTAN)**

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ANN ARBOR**

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Philip D. Gingerich, Director

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FROM THE MIDDLE EOCENE DRAZINDA FORMATION
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KENNETH D. ANGIELCZYK¹ AND PHILIP D. GINGERICH

Abstract — A new crocodyloid tentatively assigned to *Asiatosuchus* is described from the Drazinda Formation of the Sulaiman Range, Pakistan. It is known from partial skull and jaw material, and associated vertebrae, ribs, and left pubis. The presence of a very horizontally-angled descending process of the articular bone in the lower jaw suggests that the new specimen may have especially close affinities to *Asiatosuchus nanlingensis*, but further characterization is difficult because of a lack of definitive morphological characters. The specimen was found in a silty reddish-brown marine shale of mid-Bartonian age (late middle Eocene) that has also produced several specimens of the archaeocete whale *Babiacetus*.

Asiatosuchus has been suggested as a possible sister taxon of the Australian mekosuchine crocodiles, although some doubt has been cast on this hypothesis by morphological differences and by previous restriction of *Asiatosuchus* and mekosuchines to terrestrial deposits. Discovery of this Pakistan specimen in marine sediments suggests that *Asiatosuchus* may have been capable of long distance dispersal, providing support for the proposed link to Mekosuchinae. Tolerance of marine environments may also explain the wide distribution of *Asiatosuchus* in Europe and Asia.

INTRODUCTION

The middle to late Eocene Drazinda Formation of Pakistan has yielded an important marine fauna, including cartilaginous and bony fish fossils (Case and West, 1991; Nolf, 1991), a large trionychid turtle (Head, Raza, and Gingerich, in preparation), and mammals such as *Protosiren*, *Babiacetus*, *Basilosaurus*, and *Basiloterus* (Gingerich et al., 1995; Gingerich et al., 1997). Crocodylians have been described from other formations in the Paleocene and the early to middle Eocene of Pakistan (Buffetaut, 1977, 1978; Gingerich, 1977; Gingerich et al., 1979; Storrs, 1986), India (Sahni and Mishra, 1975; Sahni and Srivastava, 1976, 1977), and Nepal (Sah and Schleich, 1990), but crocodylian remains have not been reported previously from the Drazinda Formation.

A partial skeleton of a eusuchian crocodile, tentatively referred to the genus *Asiatosuchus*, is described here. It was found in 1996 near Satta Post in the Sulaiman Range of southwestern Punjab, Pakistan. Initially, vertebrae and other bones were found in a jumble of reworked sedi-

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ment and surface scree plugging a small gully exposed in the side of a larger tributary of Bara Nadi. With further excavation, more of the specimen was found in place in a silty reddish-brown shale unit just below the *Discocyclus sowerbyi* marker bed of Gingerich et al. (1997). This unit has also yielded specimens of *Babiacetus indicus* (Gingerich et al., 1995).

As explained below, the presence of cf. *Asiatosuchus* in the Drazinda Formation of Pakistan has biogeographic significance for crocodyloids, and it even has implications for interpretation of cetacean evolution.

INSTITUTIONAL ABBREVIATIONS

- GSP-UM — Geological Survey of Pakistan–University of Michigan collection, Islamabad (Pakistan)
 UM — University of Michigan Museum of Paleontology, Ann Arbor

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Hay, 1930
 NEOSUCHIA Benton and Clark, 1988
 EUSUCHIA Huxley, 1875
 CROCODYLIA Gmelin, 1788
 BREVIROSTRES von Zittel, 1890
 CROCODYLOIDEA Fitzinger, 1826

Asiatosuchus Mook, 1940

Type species. — *Asiatosuchus grangeri* Mook, 1940.

Referred species. — *A. nanlingensis* (Young, 1964), *A. germanicus* (Berg, 1966), *A. zajsanicus* (Efimov, 1982), *A. volgensis* (Efimov and Yarkov, 1993), *A. monsvialensis* (Franco and Piccoli, 1993).

Age and distribution. — *A. nanlingensis*, Paleocene?, Nanhsiung, Kwangtung, China (Young, 1964); *A. volgensis*, upper Paleocene of the Syzran Group, Volga Basin, Russia (Efimov and Yarkov, 1993); *A. germanicus*, middle Eocene (Lutetian), Europe (Berg, 1966; Vasse, 1992); *A. grangeri*, upper Eocene Irdin Manha Formation, Inner Mongolia (Mook, 1940); and *A. monsvialensis*, “lower Oligocene” Castelgomberto Limestone, Italy (Franco and Piccoli, 1993).

Diagnosis. — Similar to *Crocodylus*, but with at least seventeen teeth in each ramus of the lower jaw, and splenial bones that do not reach forward to the symphysis (Mook, 1940).

cf. *Asiatosuchus* sp.

Specimen. — GSP-UM 3210: skull fragments, jaw fragments, teeth, proatlas, atlas intercentrum, vertebrae, chevron, ribs, ventral ribs, pubis, and dermal osteoderms, found disarticulated but in close association and undoubtedly representing the same animal. A cast is available for study in the UM collection.

Locality. — Bari Nadi west of Satta Post of the Border Military Police, at 30°47.23' north latitude, 70°26.21' east longitude (Fig. 1; Survey of Pakistan topographic quadrangle 39 J/5; Dhodak geological quadrangle of Bhatti et al., 1986). A photograph of the locality is shown in Figure 2.

Referred specimens. — None.

Age and distribution. — This specimen was found in the silty reddish-brown shales of the middle Drazinda Formation, immediately below the *Discocyclus sowerbyi* marker bed of Gingerich et al. (1997). These shales are middle Bartonian in age (Gingerich et al., 1997), and are calibrated at approximately 40.5 Ma on the time scale of Haq et al. (1987, 1988) or about 39 Ma on the time scale of Berggren et al. (1995).

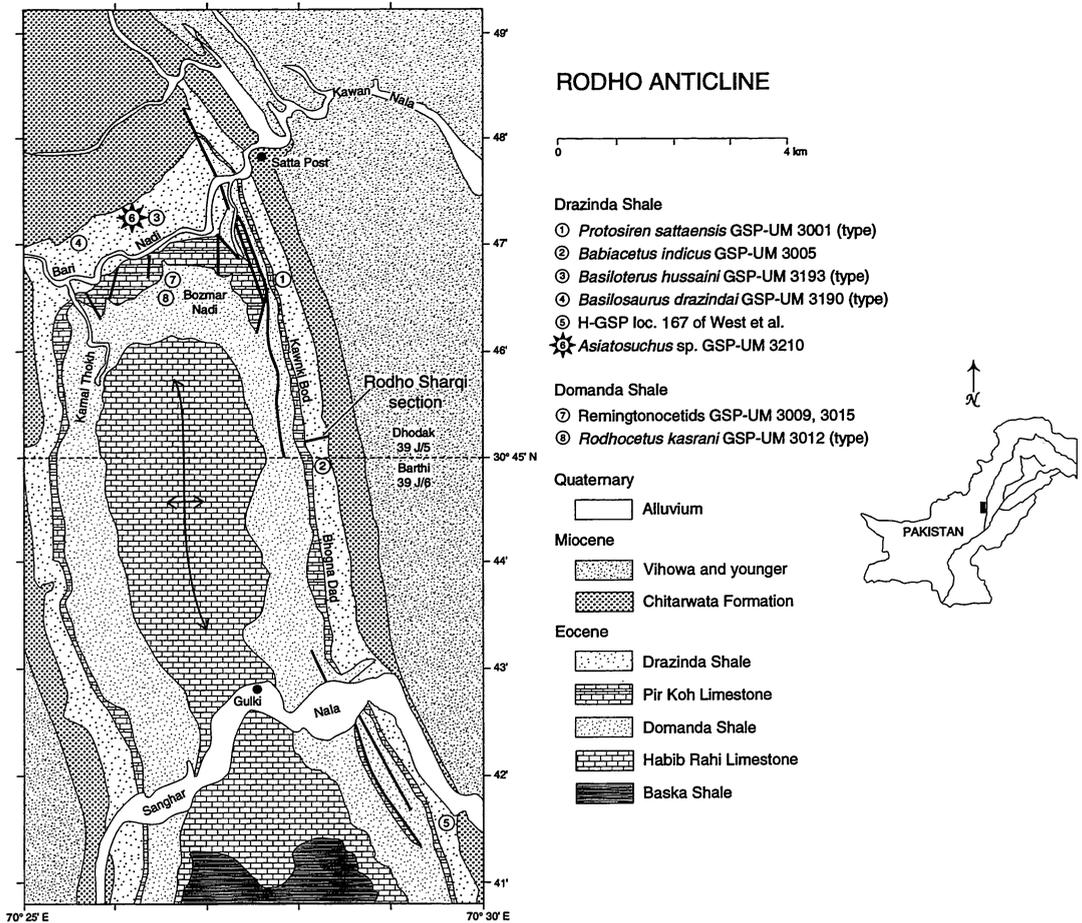


FIG. 1 — Location map showing geology of the Rodho anticline in the Zinda Pir anticlinorium bordering the Sulaiman Range west of Taunsa in southwestern Punjab, Pakistan. Localities 1 and 2 are where the type specimen of *Protosiren sattaensis* and a skull and lower jaws of *Babiacetus indicus* were found (see Gingerich et al., 1995, for details). Localities 3 and 4 are the type localities of *Basiloterus hussaini* and *Basilosaurus drazindai* described in Gingerich et al. (1997). Locality 5 is the locality H-GSP 167 from the 1978 survey of West et al. (1991). Locality 6 (asterisk) is the locality where cf. *Asiatosuchus* (GSP-UM 3210) described here was found. Locality 7 was the source of two partial skeletons of *Remingtonocetus* cf. *R. harudiensis* described by Gingerich et al. (1993, 1995). Locality 8 is the type locality of *Rodhocetus kasrani* described by Gingerich et al. (1994). Geology is from Bhatti et al. (1986) and Kahn et al. (1986). Map modified from Gingerich et al. (1995, 1997).

DESCRIPTION

Skull

Cranium. — The cranium is very poorly preserved. Most of the known cranial material consists of small isolated fragments that do not warrant description. Two fragments of maxilla and a portion of the right quadrate are the only identifiable elements preserved (see Figs. 3a-c and Fig. 4a-c).

Right quadrate. — Only the lateral condyle of the right quadrate is preserved. It is round and has some dorsoventral swelling. The surface of the condyle is slightly rugose. Part of the



FIG. 2 — Photograph of locality where cf. *Asiatosuchus* (GSP-UM 3210) was found (arrow) in Bari Nadi west of Satta Post. View is to the northeast. Note two collectors in white shirts for scale. Locality is at 30°47.23' north latitude, 70°26.21' east longitude (Survey of Pakistan topographic quadrangle 39 J/5; Dhodak geological quadrangle of Bhatti et al., 1986). The specimen was found weathering from the silty reddish-brown shales of the middle Drazinda Formation, immediately below the lighter *Discocyclusina sowerbyi* marker bed of Gingerich et al. (1997).

quadratojugal is also preserved laterally and a faint suture between the two bones is visible. A small foramen is present on the ventral surface of the quadratojugal, just lateral to the suture. The ventral surface of the fragment is relatively flat, except where the quadratojugal begins to sweep ventrally. The dorsal surface is convex medially and becomes concave laterally.

Maxilla fragment 1. — This fragment is from the lateral portion of the left maxilla. Three tooth alveoli are preserved, one of which has a piece of tooth root in it. The dorsal and lateral surfaces of the maxilla fragment have a rugose ornamentation, and show some signs of weathering. The ventral surface is smooth. The tooth-bearing portion of the bone is fairly thick, thinning as the bone curves dorsomedially to form what would be part of the roof of the nasal passage. The fragment also becomes thicker posteriorly.

Maxilla fragment 2. — This fragment is from the posterodorsal portion of the left maxilla. The dorsal surface is somewhat rugose, but not to the degree of the other maxilla fragment, and is slightly convex. The medial portion of the ventral surface is smooth. This surface broadens laterally to form an elongate ridge that constituted the lateral wall of the nasal passage. The anterior end of the nasolacrymal duct is also present at the posterior edge of the ventral surface of this fragment. The suture between the maxilla and the lacrymal is not preserved.

Left mandible. — The greatest portion of the skull preserved is a large section of the left mandible (Figs. 5a-b, 6a,b). It measures some 442 mm in length, and preserves the retroarticular process, articular, substantial portions of the angular, surangular (in two discrete pieces), splenial,

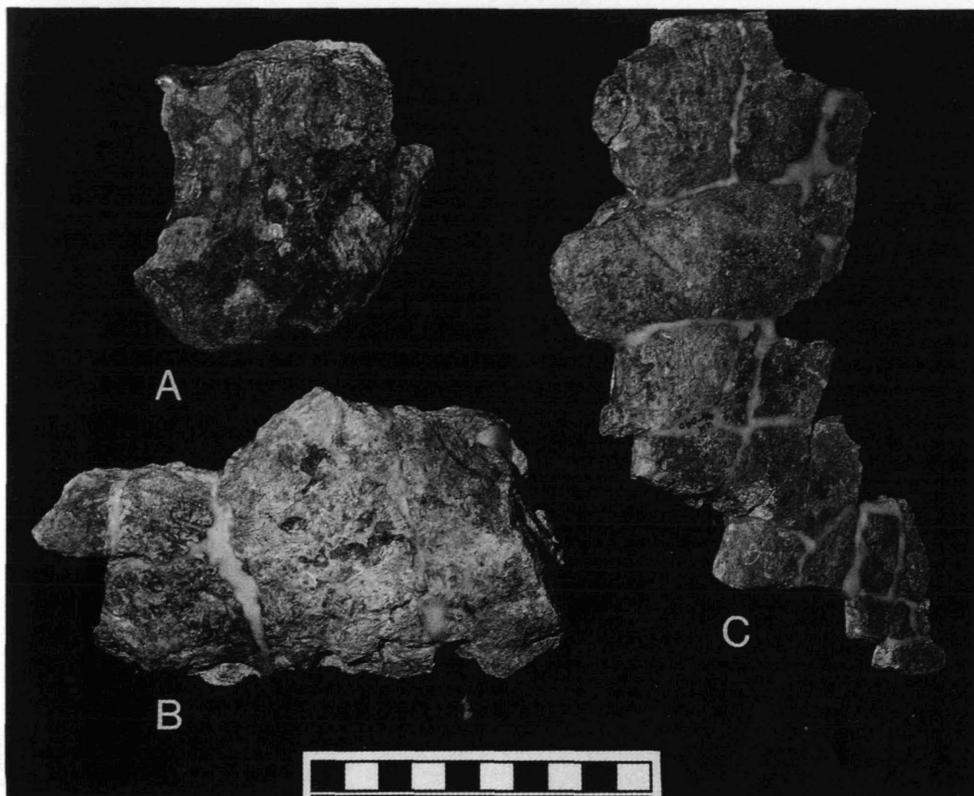


FIG. 3 — Cranial fragments of cf. *Asiatosuchus* (GSP-UM 3210). A, dorsal view of the lateral condyle of the right quadrate (anterior is at top, lateral is to right). B, Lateral view of maxilla fragment 1 (anterior is to left, ventral is at bottom). C, dorsal view of maxilla fragment 2 (anterior is at top, lateral is to left). Scale is in cm.

and a small part of the dentary. In addition, two smaller fragments of the mandible are known that will be described separately (Fig. 7a-b).

The glenoid of the articular is large and robust, and is divided into two fossae in a typically crocodilian manner. The lateral fossa is larger and deeper, and is roughly oval in shape. The medial fossa is smaller, shallower, and rectangular. A small ridge, which is most developed anteriorly, separates the two fossae. The long axis of the descending process of the articular is very anteroposteriorly directed and is close to horizontal for most of the length of the process. The dorsal surface of the process is convex, and tapers anteriorly. The overall shape of the descending process is unlike that seen in most extant crocodilians, but is very similar to that figured by Young (1964) for *Asiatosuchus nanlingensis*. The medial surface of the articular forms a large, rugose, slightly concave depression for muscle attachment. The lateral edge of the glenoid overhangs part of this depression anteriorly, and the muscle scar continues posteriorly to form the ventromedial surface of the retroarticular process. The glenoid measures 50.7 mm in maximum length anteroposteriorly and 83.5 mm in width transversely.

Parts of three bones make up the retroarticular process. As noted above, the articular makes up the medial surface and part of the ventral surface. It also forms the dorsal surface of the process. The angular bone forms most of the ventral surface of the process, and part of the lateral surface. The surangular also forms part of the lateral surface of the retroarticular process. It is present as a tapering, triangular piece of bone between the articular and angular bones that extends to the tip of

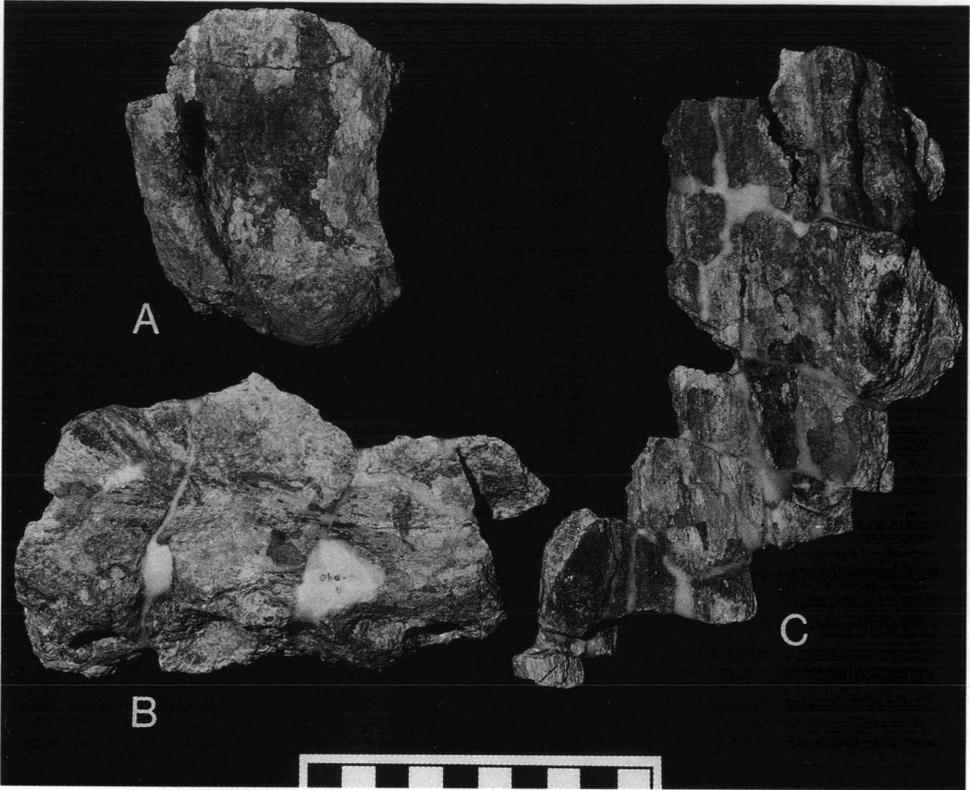


FIG. 4 — Cranial fragments of cf. *Asiatosuchus* (GSP-UM 3210). A, ventral view of the lateral condyle of right quadrate (anterior is at top, lateral is to left). B, medial view of maxilla fragment 1 (anterior is to right, ventral is at bottom). C, ventral view of maxilla fragment 2 (anterior is at top, lateral is to right). Scale is in cm.

the process. This trait is derived in crocodylians and is the state found in *Asiatosuchus germanicus* (Brochu, 1997a), but not in *A. nanlingensis* (Young, 1964). The sutures between these bones on the retroarticular process are clearly preserved. The retroarticular, as preserved, measures 86.8 mm.

The retroarticular process is broad, but not very long. It sweeps posterodorsally at a shallow angle. The posterior edge is rounded. The floor of the retroarticular fossa is slightly concave, and is not divided into separate fossae as in *Crocodylus* (Norell and Clark, 1990). The process is saddle-shaped in cross-section, with the “hump” of the saddle offset medially. The ventromedial surface is concave. In many ways, the retroarticular process is similar in morphology to that of *Tomistoma schlegelii*. The medial edge of the process is slightly broken, but it is unlikely that this significantly changes the preserved morphology.

The surangular is incomplete and is preserved as two separate pieces (Fig. 5a). The first of these is still attached to the large piece of the left mandible. As noted above, it forms part of the lateral surface of the retroarticular process. Anteriorly, the surangular borders the glenoid fossae. The suture between these elements is well preserved, and is strongly bowed laterally. The suture becomes increasingly indistinct anteriorly, but this is likely to be preservational. The dorsal surface of the surangular is slightly higher than the glenoid fossae.

The second piece of the surangular is a long, flattened piece of bone. There is not an exact fit between this piece and the other preserved on the mandible, but it is clear that they are associated. The dorsal and lateral surfaces are flattened and are nearly perpendicular to each other. The



FIG. 5 — Mandible of cf. *Asiatosuchus* (GSP-UM 3210). A, lateral view of the partial left mandible and an isolated piece of the left surangular (anterior is to left). Note the bite mark near the anterior end of the piece of surangular. B, dorsal view of the partial left mandible (anterior is to left). Scale is in cm.

anterior processes of the surangular are partially preserved, as well as a small piece of the dentary. Unfortunately, the sutures between the anterior processes and the dentary are not well preserved. A small foramen is located between the anterior processes of the surangular. The posterior portion of the medial surface is also flattened, but a shallow anteroposteriorly-directed sulcus is developed more anteriorly. At the posterior end of this sulcus is a small, deep, oval-shaped foramen that appears to connect to an anteriorly-directed canal. The posterodorsal corner of the external mandibular fenestra appears to be preserved on the ventral edge of the lateral surface. There is a large circular depression (~11.7 mm in diameter) on the lateral surface, just below the anterior processes of the surangular. It shows evidence of crushing and is likely to be a bite mark.

Most of the angular is preserved. The suture between it and the articular on the retroarticular process is visible, as is the suture with the descending process of the surangular. On the ventral surface of the angular is a small foramen and a few small pits that appear to be real features. There is also small oval pit that shows some crushing on the ventromedial surface of the angular that is likely to be another bite mark. The anterior sutures where the angular would meet the dentary and splenial are not clearly preserved. However, the length of the preserved mandible is great enough to suppose that these bones must be partially present.

The anterior section of the jaw is quite narrow as preserved. The ventral surface of the mandibular canal is present, as are small parts of the walls of the canal. The surface is generally smooth, and slightly concave. The lateral, ventral, and medial surfaces of the anterior portion of the jaw show some ornamentation in the form of shallow pits and sulci, but these are not as strongly developed as on the maxilla fragments. The jaw shows very little curvature along its length, although it does appear to curve slightly medially and dorsally along its length.

Mandible fragment 1. — The first mandibular fragment is smaller than the second and appears to be from the left mandible (Fig. 7a). It shows some ornamentation, although this has undergone weathering. The fragment is slightly concave medially. The anterior end of the fragment appears



FIG. 6 — Mandible of cf. *Asiatosuchus* (GSP-UM 3210). A, enlarged view of the medial side of the articular area of the partial left mandible (anterior is to right). Note the very horizontal angulation of the descending process of the articular bone. B, enlarged view of the dorsal surface of the partial left mandible (anterior is to left). Scale is in cm.

to sweep upward, which is unexpected. The splenial is preserved in a manner similar to that of the second mandibular fragment. It appears to widen toward the dorsal surface. Three tooth alveoli are preserved. These are located in the center of the dorsal surface posteriorly, and more laterally anteriorly. Two of these are of comparable diameter, while the most anterior is somewhat larger. One small occlusal pit is also preserved.

Mandible fragment 2. — The second mandibular fragment is tooth-bearing and appears to be from the anterior portion of the right mandible (Fig. 7b). It is noticeably concave medially and convex laterally, and shows some weathered ornamentation. The fragment becomes thicker dorsally. It appears to consist mainly of the dentary bone, although part of the splenial is sutured onto the medial surface. Posteriorly, the splenial extends more dorsally, nearly reaching the level of the dorsal surface of the jaw. Anteriorly, the splenial becomes progressively lower on the medial surface. Six alveoli with tooth roots are preserved. These are located in the center of the fragment posteriorly, but become offset toward the lateral side medially. The posterior two alveoli are similar in diameter. The third alveolus is somewhat larger, and the fourth alveolus is the largest of

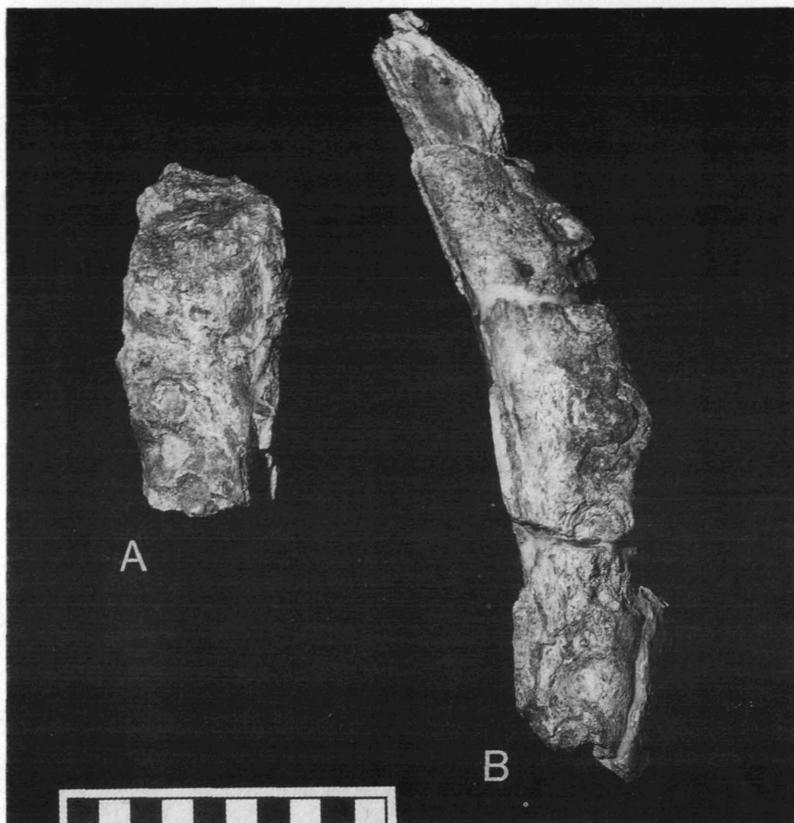


FIG. 7 — Mandible of cf. *Asiatosuchus* (GSP-UM 3210). A, dorsal view of mandible fragment 1 (anterior is at top). B, dorsal view of mandible fragment 2 (anterior is at top). Scale is in cm.

those preserved. The last two alveoli are somewhat smaller, comparable in diameter to the first two. One occlusal pit exists between the two posterior alveoli.

Teeth. — Three isolated teeth are preserved, but only one of these is in good condition (Fig. 8a-c). The teeth are large and nearly conical, with only slight lateral compression. The enamel layer on the teeth is very thin (~0.2 mm) and somewhat crenulated. Fore and aft serrations are present, and are offset toward the medial side of the crown (Fig. 8a). Mook (1940) and Young (1964) described similar fore and aft ridges and irregular striations on the teeth of *Asiatosuchus grangeri* and *A. nanlingensis*, and figures in Vasse (1992) and Keller and Schaal (1992) show that the teeth of *A. germanicus* also had comparable features. The largest tooth shows what appears to be a strong apical wear facet, although this may be preservational (Fig. 8c). No tooth crowns are preserved in any of the known tooth-bearing bones of the skull or mandible.

Vertebrae

Sixteen vertebrae and some additional vertebral elements are complete enough to warrant description. Measurements of the vertebrae are listed in Table 1.

Proatlas. — The proatlas is rarely preserved in fossil crocodylians and is infrequently described in extant taxa (Brochu, 1997b; Mook, 1921). Here the proatlas is “boomerang-shaped” (Brochu, 1997a), with the anterior and posterior edges concave ventrally (Fig. 9a). There is a weak ridge on the center of the dorsal surface. The ventral tuberosities are wider than the width of the dorsal

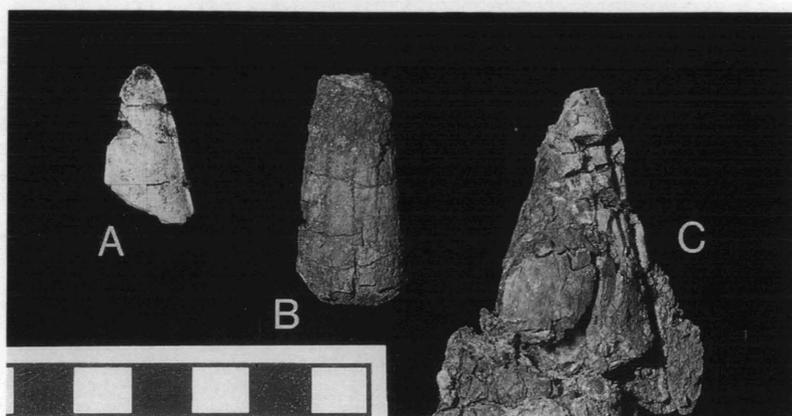


FIG. 8 — Teeth of cf. *Asiatosuchus* (GSP-UM 3210). A, tooth crown. Note fore and aft serrations and slightly crenulated enamel. B, incomplete tooth crown. C, damaged tooth crown. Note possible wear facet at tip. Scale is in cm.



FIG. 9 — Proatlas and atlas of cf. *Asiatosuchus* (GSP-UM 3210). A, dorsal view of the proatlas (anterior is at top). B, dorsal view of the atlas intercentrum (anterior is at top). Scale is in cm.

crest, and they flare posteriorly. There is a slight depression on the ventral surface of the flared area of the tuberosities. The proatlas measures 34.7 mm in maximum length at the edge, 32.1 mm in maximum length in the center, and 65.1 mm in width, as preserved.

Atlas intercentrum. — The atlas intercentrum is wedge-shaped in lateral view, with insignificant parapophyseal processes (Fig. 9b). The anterior articulating surface is concave. The dorsal surface has bilaterally-paired, obliquely-angled facets for articulation with the atlas neural arch elements. The posterodorsal surface is flat and angled posteroventrally. The parapophyses are located posteroventrally and have the form of bilaterally-paired, obliquely-angled facets. The axis intercentrum measures 32.7 mm in maximum length, 61.0 mm in maximum width, and 34.4 mm in maximum height.

Cervical vertebrae. — Five cervical vertebrae are preserved (Fig. 10a-e). Of these, three are highly broken and eroded centra that cannot be identified to position. They are tentatively identified as “anterior cervical vertebrae” and will not be described here (Fig. 10a-c). Two cervical vertebrae are well preserved and are identified as cervicals five and six (Fig. 10d-e). Both have a typically eusuchian appearance.

C5. — The fifth cervical vertebra is anteroposteriorly compressed (Fig. 10d). The centrum is procoelous with a strong posterior ball and a prominent hypophyseal keel. The left anterior

TABLE 1 — Measurements of vertebrae of cf. *Asiatosuchus* sp. (GSP-UM 3210). Abbreviations: *CL*, maximum centrum length anteroposteriorly; *CWA*, centrum width maximum at the anterior or cranial end of centrum; *CWM*, centrum width minimum (mid-centrum); *CWP*, centrum width maximum at the posterior end of centrum; *TPL*, transverse process length; *TPS*, transverse spread (maximum width of vertebra); *ZYA*, transverse width or spread across anterior zygapophyses; *ZYP*, transverse width across posterior zygapophyses; *CHA*, centrum height maximum at anterior end of centrum; *CHP*, centrum height at posterior end of centrum; *NSH*, neural spine length or height; *VH*, total vertebral height. Measurements are in mm.

Vert.	CL	CWA	CWM	CWP	TPL	TPS	ZYA	ZYP	CHA	CHP	NSH	VH
C5	56.6	42.3	47.4	41.1	23.9	85.8	—	67.1	40.1	42.1	85.3	162.4
C6	57.2	42.0	51.1	45.9	41.1	—	—	—	—	42.2	96.4	—
T3	71.8	49.0	48.4	37.3	83.3	216.6	—	—	51.7	44.8	95.9	186.7
T5	—	54.7	—	40.7	103.2	255.3	—	—	51.0	—	—	—
MT1	73.2	53.6	50.1	36.8	—	—	—	—	49.8	44.9	90.1	149.8
MT2	72.4	—	50.7	39.0	—	—	—	—	—	41.3	—	—
MT3	79.6	55.7	48.7	40.1	—	—	—	—	49.3	42.3	91.6	149.6
PT1	81.4	53.7	52.1	37.1	63.5	—	—	—	53.4	48.5	101.6	167.3
PT2	80.5	56.2	51.5	37.8	108.0	263.6	81.1	—	56.8	46.2	83.9	149.1
PT3	80.8	56.2	54.7	40.5	99.6	—	—	—	50.7	46.7	92.1	155.1
L1	82.0	55.0	55.6	39.2	—	—	90.4	80.9	51.8	48.4	93.9	156.1
L2	78.5	63.6	55.8	40.8	76.1	197.7	—	—	51.5	46.1	101.1	155.0
AC1	75.6	—	48.4	37.0	—	—	—	—	—	43.4	—	—
AC2	77.7	50.1	43.8	34.6	—	—	—	—	50.2	43.4	84.2	144.5
AC3	81.3	48.8	39.9	30.2	—	—	—	—	45.5	40.7	—	—
AC4	77.7	48.8	40.7	26.3	—	—	—	—	41.1	38.5	66.0	134.2

zygapophysis is preserved, and it is broad and tall relative to the overall size of the vertebra. It has a small metapophyseal tubercle on its anteromedial surface. The posterior zygapophyses are also relatively wide and tall.

The neural spine is thin and narrow, and of uniform width over its length. Mook (1921) described lateral flanges on the posterior surface of the spine of this vertebra in extant crocodylians, but these are poorly preserved here. The neural spine is located toward the posterior end of the neural arch pedicles. The pedicles are tall and wide relative to the centrum. The neural canal is round and equant anteriorly, but becomes taller and narrower posteriorly. The rib facets are separated. Each tubercle is situated slightly below the level of the neural canal and these form short, distinct processes that are angled ventrally. The right tubercle has a piece of the tuberculum of the associated cervical rib preserved in articulation with it. The capitular facets are located at the level of the base of the centrum. They form distinct processes posteriorly that are shorter than the tubercular processes and merge with the centrum anteriorly.

C6. — The sixth cervical vertebra is similar to the fifth in most ways (Fig. 10e). The centrum is anteroposteriorly compressed and procoelous, although the ventral anterior margin is partly broken. The hypopophysis is now missing but clearly one was once present.

Only the right anterior zygapophysis is preserved. It is slightly longer and more dorsally projecting than those on *C5*, although the width is similar. The metapophysis is not preserved, but one appears to have existed. The left posterior zygapophysis is preserved, and it is similar to posterior zygapophyses on the fifth cervical.

The neural spine has the posterior flanges described by Mook (1921), as well as a partial flange preserved on the anterior surface. The spine is about the same length as that of *C5*, but it flairs dorsally, giving it a triangular cross-section at the top. It too is located toward the rear of the neural arch pedicles, as on the fifth cervical.

The rib facets are also separated here. The tubercle is located at about the same level as the neural canal. The tubercular process is angled ventrally, although it is larger than that in *C5*. The

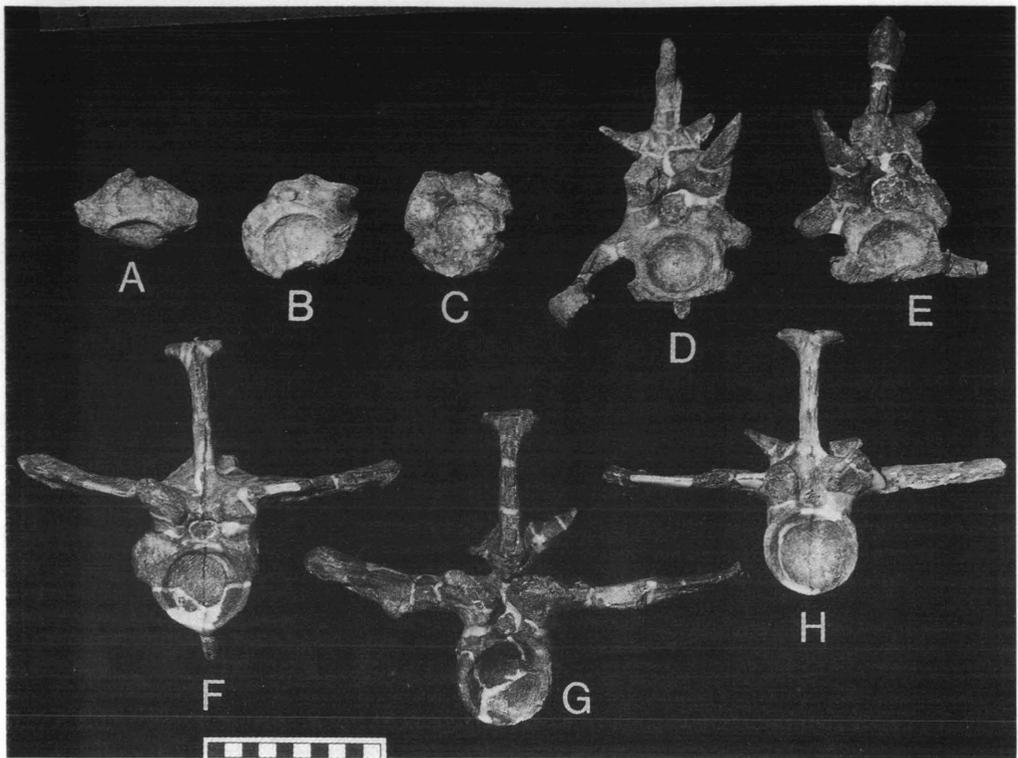


FIG. 10 — Vertebrae of cf. *Asiatosuchus* (GSP-UM 3210). A, anterior view of the first “anterior cervical vertebra”. B, anterior view of the second “anterior cervical vertebra”. C, anterior view of the third “anterior cervical vertebra”. D, anterior view of the fifth cervical vertebra. E, anterior view of the sixth cervical vertebra. F, anterior view of the third thoracic vertebra. G, anterior view of the fifth thoracic vertebra. H, anterior view of the first “mid-thoracic vertebra.” Dorsal is at top. Scale is in cm.

capitular facets form distinct processes posteriorly, but merge with the centrum anteriorly. The left capitular facet is preserved in articulation with the capitulum of the associated cervical rib.

Thoracic vertebrae. — Eight vertebrae have been identified as belonging to the thoracic column (Fig. 10f-h and Fig. 11a-e). The third and fifth thoracics (T3 and T5) are clearly identifiable, but too much information is missing from the others to make exact identification possible. They are identified here as mid-thoracics “MT1,” “MT2,” and “MT3,” and posterior thoracics “PT1,” “PT2,” and “PT3.” All are generally well preserved, and all are typically eusuchian in appearance.

T3. — Thoracic vertebra T3 is well preserved except for some plastic distortion in the left transverse process (Fig. 10f). The centrum is procoelous, with a strong posterior ball. It is less compressed anteroposteriorly than the cervical vertebrae, but is more compressed than the other thoracics. The centrum broadens toward the front and has a large, posteroventrally directed hypophyseal keel.

None of the zygapophyses are preserved. The neural spine is tall, flattened, and anteroposteriorly wider than the cervical spines. It shows some transverse flaring at the apex and is located toward the posterior end of the neural arch pedicles. The neural arch pedicles are narrower and shorter relative to the centrum than are those of the cervical vertebrae. The neural canal is smaller and more equant than in the cervicals.

The transverse processes (diapophyses) are long, angled slightly dorsally, and have a flattened, triangular shape in cross-section. The tubercular facets are located at the ends of the transverse processes. Each facet is a rounded flaring of the process, oriented laterally. Only the right capitu-

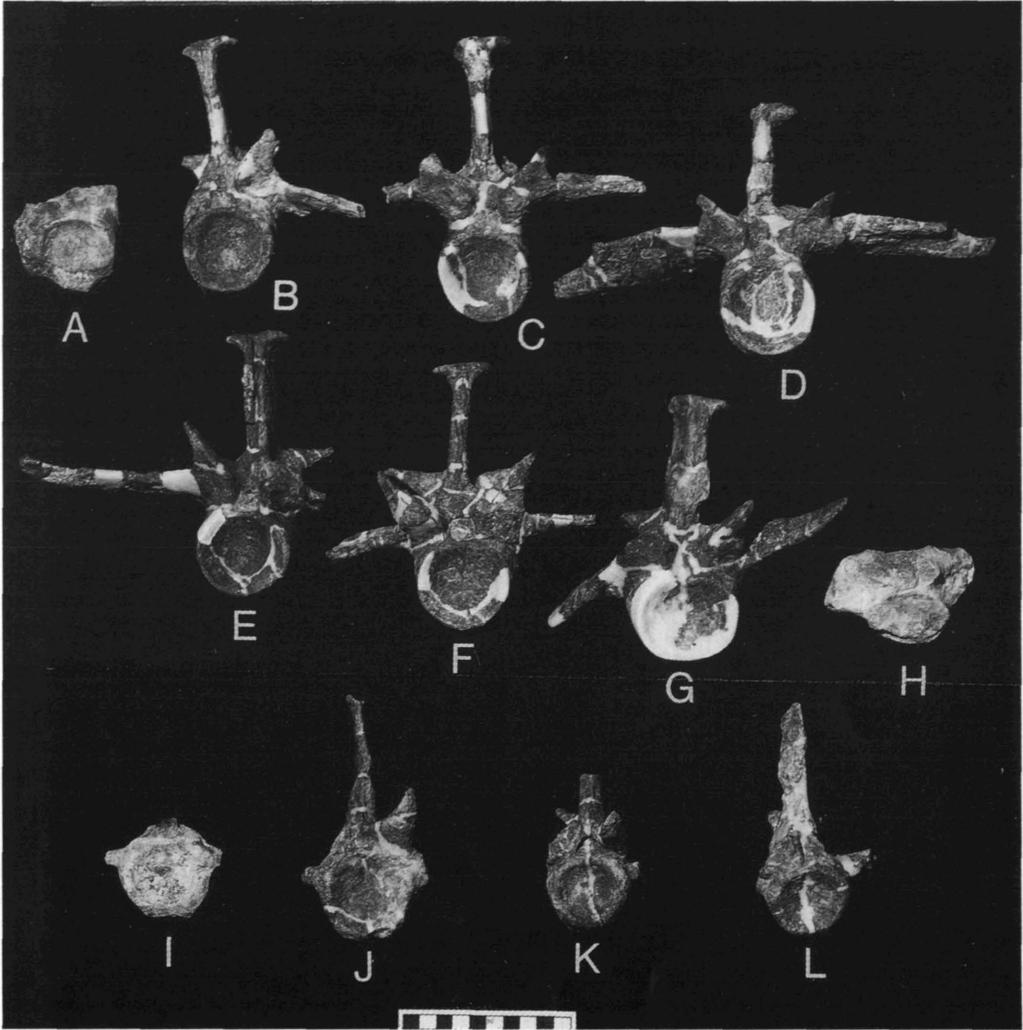


FIG. 11 — Vertebrae of cf. *Asiatosuchus* (GSP-UM 3210). A, anterior view of the second “mid-thoracic vertebra”. B, anterior view of the third “mid-thoracic vertebra”. C, anterior view of the first “posterior thoracic vertebra”. D, anterior view of the second “posterior thoracic vertebra”. E, anterior view of the third “posterior thoracic vertebra”. F, anterior view of the first lumbar vertebra. G, anterior view of the third lumbar vertebra. H, anterior view of the second sacral vertebra. I, anterior view of the first “anterior caudal vertebra”. J, anterior view of the second “anterior caudal vertebra”. K, anterior view of the third “anterior caudal vertebra”. L, anterior view of the fourth “anterior caudal vertebra”. Dorsal is at top. Scale is in cm.

lar facet is preserved. It is located just below the level of the neural canal. The facet is located on a lateral flaring of the anterior rim of the centrum.

T5. — The fifth thoracic vertebra is preserved as two separate pieces, a centrum and a neural spine (Fig. 10g). The posterior ball of the centrum is covered with sulfurous matrix, which has not been removed due to the damage that would occur to the vertebra in the process. The centrum is procoelous, long, and constricted dorsoventrally and bilaterally at the center, giving it a slightly waisted appearance. There is a very weak hypophyseal keel toward the anterior end of the centrum. This is the last vertebra to have a hypophyseal keel.

There are no zygapophyses preserved on the body of the vertebra, although one posterior zygapophysis is preserved on the neural spine piece. It is fairly long and broad, but not as large as those found on the cervical vertebrae.

The neural spine is similar in width and height to that of T3, and it shows the same transverse flaring at the apex. It would also have been located posteriorly on the neural arch, in a manner similar to that of the T3. The neural arch pedicles are broad, but not as broad as those of more anterior vertebrae.

The right transverse process is completely preserved. It is wider than the transverse processes of T3. The tubercular facet is located at the end of the transverse process, and it is oriented somewhat ventrolaterally. The capitular facet is also located on the transverse process, although it is more ventrally and medially placed. The process has a flattened, triangular shape in cross-section. The left transverse process is incompletely preserved, although it appears to have been slightly longer than the right transverse process. Left tubercular and capitular facets are not preserved.

"MT1." — The centrum of the first "mid-thoracic" vertebra (Fig. 10h) is long and procoelous with a strong posterior ball, although the centrum is not as wide as that of T5. It shows the same bilateral and dorsoventral constriction at the center of the centrum. The posterior ball has a slight constriction running around its anterior edge. There is a shallow vertical sulcus on the ventral surface of the centrum that becomes more strongly developed on the more posterior vertebrae.

Neither of the anterior zygapophyses are preserved. Both posterior zygapophyses are present, although the left is partially broken. These are shorter and narrower than those of the more anterior vertebrae.

The neural spine is about the same height as that of T5, although it is slightly wider. It is strongly flared at the apex, and this flaring is most pronounced anteriorly. The pedicles of the neural arch are slightly smaller than those of the fifth thoracic vertebra, and the neural canal is very round and equant.

Both the left and right transverse processes are partially preserved, although neither has preserved rib facets. Both are located at about the same level as the neural canal. The left process is long, but incompletely preserves both length and width. The length of the right transverse process is not known, but its width is less than that of the transverse processes of the T5. This process is also more flattened in cross-section.

"MT2." — The second "mid-thoracic" vertebra is preserved as a highly weathered centrum without transverse processes or neural arch elements (Fig. 11a). The centrum is procoelous, about the same length as "MT1," and shows the same constriction at the center. The posterior ball is slightly constricted around its anterior margin. The vertical sulcus on the ventral surface of the centrum is somewhat more pronounced than on "MT1."

"MT3." — The third "mid-thoracic" is very similar to the other two (Fig. 11b). The centrum is procoelous and has similar dimensions to the other "mid-thoracics." It has the same waisted appearance due to bilateral and dorsoventral constriction. The posterior ball is slightly constricted around its anterior margin. The ventral sulcus is present and developed to a similar degree as in the other "mid-thoracics."

The left anterior zygapophysis is partially preserved. It is slightly longer and wider than the posterior zygapophyses of "MT1." Both posterior zygapophyses are also incompletely preserved. They appear to be larger than the posterior zygapophyses on "MT1" as well.

The neural spine is about the same height as that of "MT1," although it is anteroposteriorly wider. It shows a transverse flaring at the apex that is most strongly developed anteriorly. The spine is located somewhat posteriorly on the neural arch pedicles, and the neural canal is round and equant.

The left transverse process is not preserved and the right transverse process is only partially preserved. No rib facets are preserved. The right process appears to be wider than that of "MT1," and it appears to widen distally.

"PT1." — Three vertebrae have been identified as "posterior thoracics." These vertebrae are larger than the "mid-thoracics," but are not well enough preserved to allow exact identification. Again, relative positions have been assigned by changes in vertebral size and morphology (Fig. 11c-e).

"PT1" is procoelous with a strong posterior ball (Fig. 11c). The posterior ball is larger and less constricted than those of the "mid-thoracics." The centrum is about the same length and width as "MT3," although the vertebra as a whole is taller. The centrum shows the same dorsoventral and bilateral constriction as in the "mid-thoracics." The sulcus on the ventral surface is not as well developed as on the "mid-thoracics."

One anterior zygapophysis is preserved. Its length and width are similar to those of the anterior zygapophysis on "MT3." Neither posterior zygapophysis is preserved.

The neural spine is taller than that of any of the "mid-thoracics," and it is somewhat shorter anteroposteriorly. The spine flares transversely at the apex, and this flaring is most developed anteriorly. The neural arch pedicles are tall, and the neural spine is positioned toward the posterior of the neural arch. The neural spine is located somewhat posteriorly on the neural arch. The neural canal is round and equant.

Both transverse processes are very incompletely preserved, and these are positioned at a higher level than the neural canal. No rib facets are preserved. The processes are anteroposteriorly wider than those of the "mid-thoracics" and appear to widen distally. In addition, the processes are much thicker anteriorly than posteriorly. In cross-section, the processes are rounded anteriorly and flattened posteriorly.

"PT2." — The second "posterior thoracic" is very well preserved (Fig. 11d). The centrum is procoelous with a well developed posterior ball that shows slight constriction along its anterior margin. The dimensions of the centrum are similar to those of "PT1." The bilateral and dorsoventral constriction of the centrum is strongly developed. The ventral sulcus is poorly formed.

Both anterior zygapophyses are preserved, although the right one is incomplete. These are similar in length to those of "PT1," but are considerably wider. Neither posterior zygapophysis is preserved.

The neural spine is shorter dorsoventrally and shorter anteroposteriorly than that of "PT1." The spine flares transversely at the apex and, unlike the more anterior vertebrae, this flaring does not decrease posteriorly. The neural arch pedicles are damaged, but they appear to be slightly smaller than those of "PT1." The neural spine is located somewhat posteriorly on the neural arch.

Both transverse processes are completely preserved, with rib facets, although they have been plastically deformed. The processes are very long, wide, and flattened in cross-section. They are located at about the same level as the neural canal. Both rib facets are located at the same level on the transverse processes, although the capitular facet is located anteriorly and medially relative to the tubercular facet. Both facets are very small relative to those preserved on the more anterior vertebrae.

"PT3." — The centrum of the third "posterior thoracic" vertebra is procoelous with a strong posterior ball that is more constricted at its anterior margin than those of the other "posterior thoracics" (Fig. 11e). The centrum is about the same size as the other "posterior thoracics," although it is not as strongly constricted bilaterally and dorsoventrally. The ventral sulcus is better developed than in the other "posterior thoracics."

The right anterior zygapophysis is preserved. Its length is comparable to those of the other "posterior thoracics," although it is narrower and tapers distally. The left posterior zygapophysis is also preserved. It is about the same length as the anterior zygapophysis, although it is wider.

The neural spine is slightly longer than that of "PT2," although the anteroposterior length is similar. The spine flares transversely at the apex and this flaring is more developed anteriorly. The neural arch pedicles are somewhat smaller than those of "PT1" and the neural canal is round and equant. The neural spine is located slightly posteriorly on the neural arch.

The right transverse process is preserved, although it lacks the tubercular facet. It is at the same level as the neural canal. The process's length is similar to those of "PT2," but its width may be slightly less. The process is flattened in cross-section and the capitular facet is small.

Lumbar vertebrae. — Two lumbar vertebrae are preserved, although incomplete preservation has made it difficult to identify them exactly. Relative positions have been assigned by differences in the size of the vertebrae (Fig. 11f-g).

L1. — The centrum of the first lumbar is very similar in size and shape to that of "PT3" (Fig. 11f). It is procoelous with a strong posterior ball that is constricted dorsoventrally and

bilaterally. The ventral sulcus is wider than those of the "posterior thoracics," although it is somewhat shallower.

Both of the anterior and posterior zygapophyses are fully preserved. They are very crocodylian in their form and orientation. The lengths and widths of the zygapophyses are similar to those of the anterior zygapophyses of "PT2."

The neural spine is about as high as that of "PT3," although it is shorter anteroposteriorly. The spine is transversely flared at its apex, and this is more strongly developed anteriorly. The neural arch has about the same height as "PT3," and the neural spine is located slightly at the posterior end of the neural arch. The neural canal is round and equant.

Both the left and right transverse processes are partially preserved. They are located below the level of the neural canal and are flattened in cross-section. As preserved, the processes are not as wide as those of the "posterior thoracics," although they appear to broaden distally.

L3. — The centrum of the third lumbar vertebra is procoelous with a strong posterior ball, although the anterior articulating surface is poorly preserved (Fig. 11g). The posterior ball is wide and shows very little constriction along its anterior margin. The centrum is about the same length as the first lumbar vertebra, although it is wider. The bilateral and dorsoventral constriction at the center of the centrum is only weakly developed. The ventral sulcus is also poorly formed.

The left anterior zygapophysis is preserved, as is the right posterior zygapophysis. Both are similar in width to those of the first lumbar vertebra, although they are narrower.

The neural spine is about the same length as that of the first lumbar vertebra, although it is wider anteroposteriorly. The spine shows some plastic deformation, and it is located posteriorly on the neural arch. The neural arch pedicles are similar in size to those of the first lumbar vertebra.

The left and right transverse processes are completely preserved, although they are both highly plastically deformed. The processes are shorter and anteroposteriorly narrower than those of the "posterior thoracic" vertebrae. They are flattened in cross-section and have no rib facets.

Sacral vertebra S2. — One sacral vertebra is preserved as a highly eroded centrum (Fig. 11h). It has been identified as the second sacral based on how the sacral ribs appear to have curved. The centrum is shorter than that of thoracic or lumbar vertebrae, and it is similar in width to that of L2. It shows no constriction and it has no ventral sulcus. The anterior articulating surface is broken, although it appears to have been flat. The posterior articulating surface is also incompletely preserved, but it appears to have been slightly concave.

Caudal vertebrae. — Four caudal vertebrae are preserved (Fig. 11i-1). The relatively large size and evidence of transverse processes suggest that all four vertebrae are from the anterior part of the caudal series (Mook, 1921). These are here called "AC1-4." No vertebra could be identified exactly, and relative positions were assigned on the basis of size. The caudal vertebrae are all typically eusuchian in general appearance.

"AC1." — The largest of the preserved caudal vertebrae consists of an eroded centrum with a partial endocast of the neural canal (Fig. 11i). The centrum is procoelous, although the posterior ball is not as well developed as those of the more anterior vertebrae. The length and width of the centrum are comparable to those of the "mid-thoracic" vertebrae. The posterior part of the centrum is weakly constricted bilaterally. The anterior margin of the posterior ball shows a slight constriction. The ventral sulcus is wide and shallow. Two facets for chevron articulation are present at the posterior end of the ventral surface, although these have undergone some weathering. The base of the right transverse process is partially preserved, and the process appears to have been slightly thinner than those of the "posterior thoracic" and lumbar vertebrae.

"AC2." — The second "anterior caudal" vertebra is more completely preserved than the first (Fig. 11j). The centrum is somewhat smaller than that of "AC1." The vertebra is procoelous with a less well developed posterior ball than those of thoracic or lumbar vertebrae. The ventral sulcus is wide and shallow, although it narrows posteriorly. Two anteroposterior ridges run parallel to the sulcus. Mook (1921) described these ridges as "skids." The centrum shows moderate bilateral and dorsoventral constriction. Two facets for chevron articulation are preserved on the posterior portion of the ventral surface.

The left anterior zygapophysis is preserved. It is long and directed anterodorsally at about a 45° angle above the horizontal. Its width is similar to that of the anterior zygapophysis of "PT1" The

base of this zygapophysis meets the anterior edge of the centrum. Neither of the posterior zygapophyses are preserved.

The neural spine is well developed, although it is not as high as those of some of the more anterior vertebrae. It is also anteroposteriorly shorter than those of the thoracic or lumbar vertebrae. There is a very slight bilateral flaring at the apex that is not developed to the degree seen in the more anterior vertebrae. The spine is centered on the neural arch pedicles. The pedicles are wide at the base but narrow toward the neural spine. The neural canal is small, but round and equant.

Only the bases of the transverse processes are preserved. They are located below the level of the neural canal and are slightly thinner than those of "AC1."

"AC3." — The centrum of the third "anterior caudal" vertebra is similar in length to those of "AC1" and "AC2," although it is narrower (Fig. 1k). It is procoelous and the posterior ball is developed to the same degree as those of other "anterior caudals." The centrum shows strong bilateral and dorsoventral constriction toward the middle. The ventral sulcus is wide and narrow, and it is bordered by parallel "skids." The paired facets for chevron articulation on the ventral surface are well developed.

The left anterior zygapophysis is preserved. It is comparable in size to that of the second anterior caudal, although it is more horizontally angled (about 20° above the horizontal). The right posterior zygapophysis is also preserved. It is shorter than the anterior zygapophysis, but the width is similar. Its long axis is nearly vertically oriented and the dorsal edge of the zygapophysis flairs laterally.

The neural spine is incompletely preserved. It is anteroposteriorly narrower than the spine of the other "anterior caudals," although it is somewhat thicker. It is oval-shaped in cross-section and placed somewhat posteriorly on the neural arch pedicles. The pedicles are similar in size to those of "AC2" and show a comparable narrowing toward the spine. The neural canal is round and equant, but small. Neither transverse process is preserved, although it is clear that they were once present.

"AC4." — The centrum of the fourth "anterior caudal" vertebra is shorter and narrower than those of the other preserved caudal vertebrae (Fig. 11l). It is procoelous and the posterior ball is only moderately developed. The ventral sulcus is shallow and appears to have been bordered by parallel ridges, although these are poorly preserved. The paired facets for chevron articulation are present, but have been somewhat weathered. The centrum shows some dorsoventral and bilateral constriction near the center.

Neither of the anterior zygapophyses are preserved. The right posterior zygapophysis is partially preserved. It is comparable in width to the posterior zygapophysis of "AC3," although its length cannot be determined.

The neural spine is incompletely preserved. It is shorter both dorsoventrally and anteroposteriorly than the spine of "AC2." It does not appear to flare at the apex, although this may be due to preservation. The neural arch is poorly preserved, and parts of it are still covered by a sulfurous matrix that would be difficult to remove.

The base of the left transverse process is partially preserved. It is somewhat oval in cross-section and appears to be similar in width to those of the other "anterior caudal" vertebrae. The base of the process is located at a lower level than the neural canal.

Ribs

Seven ribs are sufficiently well preserved to warrant description (Fig. 12a-g). Two of these are right ribs, and five are left ribs. Some can be identified to position, but most have been assigned tentative positions based on size and morphology. Besides those described here, there are a number of fragments of cervical and thoracic ribs that are too poorly preserved to warrant description. Measurements of ribs are listed in Table 2.

RC8. — Right cervical rib 8 is completely preserved except for the tuberculum (Fig. 12f). Mook (1921) described this rib in modern crocodylians as intermediate in morphology between the ante-



FIG. 12 — Ribs of cf. *Asiatosuchus* (GSP-UM 3210). A, tenth right thoracic rib (?), lateral is to left. B, seventh right thoracic rib (?), lateral is to left. C, fifth right thoracic rib (?), lateral is to left. D, third right thoracic rib, lateral is to left. E, first right thoracic rib (?), lateral is to left. F, eighth right cervical rib, lateral is to right. G, second right thoracic rib, lateral is to right. Scale is in cm.

rior cervical ribs and the thoracic ribs. This one is relatively short and not highly curved. The shaft is triangular in cross-section proximally and becomes more flattened distally. The rib tapers more strongly than the other ribs and comes to a fine point. The anterior and posterior surfaces of the shaft each have a wide, shallow sulcus. A well formed anterior ridge is present that gradually blends with the shaft distally.

The tuberculum is not preserved, although the capitulum and capitular process are complete. The capitular facet is oval-shaped and of a constant, shallow depth. The capitular process is relatively long and slightly curved.

RT2. — Right thoracic rib 2 is longer and more robust than RC8 (Fig. 12g). It is also more strongly curved. The shaft has small anterior and posterior processes that gradually become less pronounced distally. In cross-section, the shaft has a flattened oval shape proximally, and becomes more rounded and triangular distally. The shaft appears to swell slightly near the distal end.

The tuberculum is located at the end of a short process. The facet is oval-shaped and deepens toward the capitulum. The capitulum itself is not preserved, although part of the capitular process is present. It is less robust than the capitular process of RC8 and is nearly perpendicular to the tubercular process.

LTI(?). — Only the very proximal portion of the shaft of left thoracic rib 1(?) is preserved (Fig. 12e). The shaft is flattened and has an anterior process partially preserved. The anterior process is not as well developed as on RC8 described above. A longitudinal sulcus is present on the anterior ventral surface. There does not appear to be a posterior process. The rib is roughly triangular in cross-section.

Both the tuberculum and capitulum are completely preserved. The tubercular process is less robust than that of RT2. The tubercular facet is also smaller, and shallower, although it deepens toward the capitulum. The capitular process makes a very acute angle with the tubercular process.

TABLE 2 — Measurements of ribs of cf. *Asiatosuchus* sp. (GSP-UM 3210). Abbreviations: *RL*, rib length; *RCL*, rib chord length; *RW*, rib width across capitulum and tuberculum; *CL*, capitulum length; *CFL*, capitulum facet length; *CFW*, capitulum facet width; *TH*, tuberculum height; *TFL*, tuberculum facet length; *TFW*, tuberculum facet width. Measurements are in mm.

Vert.	RL	RCL	RW	CL	CFL	CFW	TH	TFL	TFW
RC8	—	162.1	—	62.3	20.8	16.6	—	—	—
RT2	248.8	248.5	—	—	—	—	36.7	25.9	20.2
LT1(?)	—	109.1	66.3	57.2	18.7	15.0	25.4	29.7	15.8
LT3	259.6	256.6	119.9	91.2	23.0	17.2	29.4	24.5	21.5
LT5(?)	—	—	—	76.1	20.8	18.8	—	—	—
LT7(?)	—	—	103.7	84.5	—	12.2	28.3	28.1	19.2
LT10(?)	271.3	269.4	—	—	—	—	—	20.7	18.8

The process is shorter and thinner than that of RC8 and it widens distally. The capitular facet is shallow and oval in shape.

LT3. — The left third thoracic vertebra is completely preserved (Fig. 12d). The rib shaft is of moderate length and is more strongly curved than that of RT2. A small anterior process is present that gradually blends with the shaft distally. The posterior edge of the vertebra is slightly flattened, but does not form a distinct process. In cross-section the rib is oval in shape proximally, but becomes more rounded and then triangular distally. There is a slight flaring toward the distal end.

The tuberculum is located at the end of a short process. The tubercular facet is round, equant, and of nearly uniform depth (it is slightly deeper toward the capitulum). The capitular process is nearly perpendicular to the tubercular process and is long and robust. The process is curved and thickens distally. The capitular facet is oval in shape and uniformly deep.

LT5(?). — This rib is nearly completely preserved; only the tuberculum is missing (Fig. 12c). The rib appears to articulate well with the fifth thoracic vertebra, although the incomplete preservation of both prevents an exact identification. The shaft is not as long or as strongly curved as that of the left third thoracic rib. A weak anterior process is present and the posterior edge is also slightly flattened. In cross-section the rib maintains its flattened shape nearly to the distal tip, where it becomes tear-drop shaped.

As noted above, the tuberculum is not preserved. The apparent absence of a tubercular process supports an identification posterior to thoracic rib 3 (Mook, 1921). The capitular process is shorter and more robust than that of LT3. The process widens distally and would make an acute angle with the tuberculum. The capitular facet is oval in shape and uniformly shallow in depth.

LT7(?). — The shaft of this rib is incompletely preserved and shows some plastic deformation (Fig. 12b). The anterior edge is somewhat flattened, but not enough to form a distinct process. In cross-section the rib is flattened proximally and becomes more rounded and triangular distally.

Both the tuberculum and capitulum are preserved. The tuberculum does not have a distinct process. Instead there is simply a facet at the proximal end of the shaft. The tubercular facet is oval in shape and nearly flat. There appears to have been a small process at the same level as the facet that would merge with the capitular process, although it is incompletely preserved. The capitular process is of comparable length to that of LT5, although it is slightly less robust and does not flare distally. The facet is oval-shaped and flat.

LT10(?). — The shaft of this rib is the longest of those preserved (Fig. 12a). The anterior edge is somewhat flattened toward the proximal end of the rib, but not enough to form a distinct anterior process. Most of the shaft shows little curvature, but the distal end is markedly curved toward the sagittal plane. In cross-section the rib remains flattened for most of its length and becomes rounded near the distal tip.

The tuberculum is not located on a distinct process, but is simply a facet at the proximal end of the shaft. The tubercular facet is flat, round, and equant. There is very little distance between it



FIG. 13 — Additional bones of cf. *Asiatosuchus* (GSP-UM 3210). A, ventral rib. B, ventral rib. C, chevron (dorsal is at top). D, left pubis (anterior is at top). Scale is in cm.

and the capitular process, with which it forms a very acute angle. The capitular process is incompletely preserved. It appears to have been long and comparable in width to that of LT7.

Ventral ribs. — Two ventral ribs are preserved (Fig. 13a-b). Both are short and flattened. One lacks distinct articular facets and has a sharp bend approximately mid-shaft. The other is straighter and has one well developed articular facet. Both are uniformly thick throughout the length of the shaft. One ventral rib measures 136.5 mm in length and 12.8 mm in width, and the other measures 137.4 mm in length and 11.8 mm in width.

Appendicular Skeleton

Pectoral girdle. — No elements of the pectoral girdle are preserved.

Pelvic girdle. — The left pubis is nearly complete and is the only element of the pelvic girdle that is preserved (Fig. 13d). It is characteristically crocodylian in form. The anterior portion is broad, flattened, and rounded. The anterior edge thickens medially and the dorsal surface is slightly concave. The flattened anterior area of the bone tapers posteriorly to form a sub-cylindrical shaft that is somewhat concave medially. The shaft flares posteriorly to form a facet for articulation with the ischium. This facet is rounded, nearly equant, and its surface is rugose. The left pubis measures 146.8 mm in maximum length, 32.1 mm in maximum width proximally, 29.0 mm in minimum width proximally, and 104.1 mm in maximum width distally.

Limbs. — There are no limb elements preserved.

Miscellaneous

Chevron. — One caudal chevron is partially preserved (Fig. 13c). It is long and has a strong inferior process with a rounded distal end. Only the basal parts of the dorsal processes are pre-

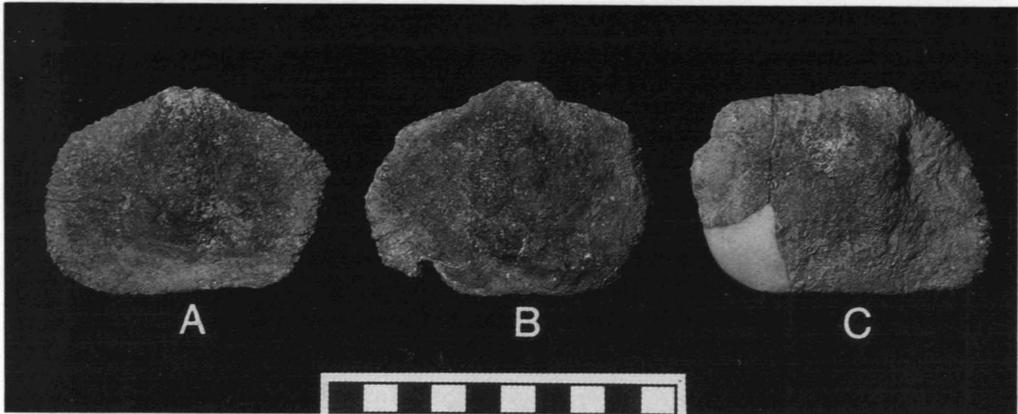


FIG. 14 — Dorsal osteoderms of cf. *Asiatosuchus* (GSP-UM 3210). A-C, scutes, in dorsal view. Scale is in cm.

served. These are flattened in cross-section, and one has been plastically deformed. As preserved, the central canal is fairly narrow, although it appears to widen dorsally. The large size of this element (larger than any described in Mook, 1921) suggests that it is probably one of the more anterior chevrons, but its exact position cannot be determined. The chevron measures 104.0 mm in maximum length.

Scutes. — Three scutes (dorsal osteoderms) are preserved (Fig. 14a-c). All have a rounded rectangular shape with a slight midline swelling on the anterior edge. All are dorsally keeled with flatter ventral sides. The dorsal surfaces have a somewhat rugose, pitted texture, while the ventral surfaces are smoother. The three scutes measure 50.9×80.7 , 60.1×82.4 , and 59.5×82.1 mm in length and width, respectively.

Stomach contents(?). — Four pieces of bone-like material found in association with the skeleton appear to be stomach contents (Fig. 15a-d). These specimens have an irregularly rounded shape, and are clearly not skeletal elements or fragments. Their surfaces are rough in texture and somewhat pitted, suggesting that they underwent at least partial digestion (Fisher, 1981). Also, they strongly resemble the preserved stomach contents of a specimen of *Rodhocetus* found in the underlying Domanda Formation (Gingerich et al., 1995).

Young (1964) described coprolites found in association with specimens of *Asiatosuchus nanlingensis* and *Eoalligator chunyii* in China, and Sahni and Mishra (1975) have reported crocodylian coprolites from Bartonian shales in India. In both cases the specimens figured are considerably larger, smoother in texture, and have a more regularly elongate shape than any of the material described here. These inconsistencies make it seem unlikely that the elements represent coprolites.

Gastrolith(?). — One pebble-sized rock was found in association with the skeleton (Fig. 15e). The reddish-brown shales the specimen was found in contain silt but nothing coarser (Gingerich et al., 1997), suggesting this was not an original component of the bed. The granule is rounded and shows some polish. However, it does not show the high degree of rounding common for gastroliths (Gillette, 1994), and there are a number of scratches and abrasions on the surface. This suggests it may not have been used for digestion, but it may be a stone swallowed for ballast.

DISCUSSION

Taphonomy

The specimen described here was found weathering on a hillside from a reddish-brown shale bed. It was excavated as deeply as possible with the tools available, although there may be some



FIG. 15 — Stomach contents(?) and gastrolith of cf. *Asiatosuchus* (GSP-UM 3210). A-D, possible stomach contents. E, possible gastrolith. Scale is in cm.

additional material still buried. Much breakage of bone appears to have been caused by erosion and weathering because most fragments recovered in the field have been reassembled to make complete or nearly complete bones. Cranial elements are an exception. Although a large number of very small cranial and jaw fragments were collected, few could be reassembled and identified. The absence of any remains from the forelimbs, pectoral girdle, and hind limbs suggests that these were missing from the body at the time of burial. They may have fallen from a floating carcass or been removed by scavengers. The presence of tooth marks on jaw elements suggests that the carcass was scavenged before burial. If the skeleton had been randomly disarticulated it is likely that some girdle and limb elements would be present.

The taphonomy of the specimen makes it impossible to say whether the animal died in the marine environment in which it was buried, or if it was washed there post mortem from a freshwater environment. At the time, eastern Tethys was a warm, shallow sea on a passive continental margin (Gingerich et al., 1995; 1997) with high organic productivity that would have made it an important potential food source. Crocodylians of Drazinda time may have exploited this by adopting the type of semi-marine habit exhibited by *Crocodylus porosus*, which spends much of its life in marine and estuarine environments but is also frequently found in freshwater settings. The morphological similarity of this specimen to fossil and extant taxa known from freshwater environments suggests that, while it may have had some sort of salt-secretion system analogous to the lingual salt glands of some modern crocodylians (Taplin and Grigg, 1989a,b), it probably lacked adaptations for a dedicated pelagic marine life.

Identification and Relationships

The name *Asiatosuchus* has been given to a number of eusuchians known from the Paleocene to Oligocene of Europe and Asia (Mook, 1940; Young, 1964; Berg, 1966; Efimov, 1982; Efimov and Yarkov, 1993; Franco and Piccoli, 1993). Unfortunately, much of the material assigned is very fragmentary and poorly studied (e.g., *A. volgensis* and *A. nanlingensis*). The lack of skull material for four of the species has made relationships of the genus especially hard to quantify. In addition, the characters that Mook (1940) used to diagnose the genus (at least 17 teeth in the lower jaw, splenials do not participate in the symphysis) are not unique to it and are included in the diagnosis of the Australian genus *Kambara* (Willis et al., 1993; see revision in Salisbury and Willis, 1996). There is also considerable variation between the species of *Asiatosuchus*. For example, Brochu

(1997a) noted that *A. germanicus* retained the plesiomorphic states of a frontoparietal suture that barely enters the supratemporal fenestra, and a splenial that participates in the symphysis, states not seen in *A. grangerii*. The monophyly of *Asiatosuchus* has never been tested and recent studies of crocodylian phylogeny (Salisbury and Willis, 1996; Brochu, 1997a,b) have only used the most completely known species, *A. germanicus*.

Despite (or perhaps because of) these problems, *Asiatosuchus* has been used frequently as a "wastebasket" taxon. For example, Berg and Crusafont (1970) and Vasse (1992) suggested synonymizing *Atacisaurus crassiproratus* (Astre, 1931), known only from jaw fragments, with *Asiatosuchus germanicus*, based on the length of the symphysis alone. Ortega et al. (1995) later redescribed these specimens as cf. *Iberosuchus* (Antunes, 1975), a metasuchian also known from the Eocene of Spain. Vasse (1992) also felt that "*Crocodylus*" *affinus* of Marsh, 1871, and "*Crocodylus*" *clavis* of Cope, 1872, from the Eocene of North America, as well as "*Crocodylus*" *depressifrons* of Blainville, 1855, of Europe, should be included in the genus. However, analysis by Brochu (1997a) showed that "*C.*" *affinus* and *A. germanicus* are separate taxa. Brochu (1997a) also noted that while "*C.*" *clavis* is somewhat younger than "*C.*" *affinus*, it is distinguishable only by minor differences in the shape of the palatine process and it is thus likely to be distinct from *Asiatosuchus*.

Salisbury and Willis (1996) felt the similarities between these two taxa and *A. germanicus* described by Berg (1966) and Vasse (1992) are likely to be symplesiomorphic. "*C.*" *depressifrons* does not have a splenial that participates in the jaw symphysis, nor a frontoparietal suture that enters the supratemporal fenestra, both of which are seen in *A. germanicus*. The three most recently described species, *A. zajsanicus* (Efimov, 1982), *A. volgensis* (Efimov and Yarkov, 1993), and *A. monsvialensis* (Franco and Piccoli, 1993), are also problematic. *A. zajsanicus* is known only from a fragment of the left jaw symphysis (Efimov, 1982). The fragment shows that the symphysis reached the level of the sixth tooth and that the splenial reached the posterior margin of the symphysis (Efimov, 1982). *A. volgensis* is known only from a fragment of the jaw preserving the symphysis, isolated teeth, and isolated osteoderms (Efimov and Yarkov, 1993). The splenial does not participate in the symphysis in this specimen. However, variation seen in this character in specimens assigned to *Asiatosuchus*, the probable paraphyly of the genus, and the lack of any truly diagnostic material makes the naming of these species premature. *A. monsvialensis* is known from several specimens that preserve most of its skeletal elements (Franco and Piccoli, 1993). The basis for its assignment to this genus is the presence of at least 17 teeth in each ramus of the jaw, similarities to the teeth Mook (1940) described for *A. grangeri*, and undescribed resemblances to specimens of *A. germanicus*. These characters are not unique to *Asiatosuchus*, however, and until further description of these specimens occurs, their true phylogenetic position will remain uncertain. Due to an uninformative diagnosis, the morphological variability of included species, and the poor quality of many assigned specimens, *Asiatosuchus* is in need of revision before its position in crocodylian evolution can be fully understood. Such a revision is beyond the scope of this paper.

Identification of the specimen described here has been difficult. The jaw symphysis and complete tooth rows are not preserved, so it is impossible to compare their features with those of the described species of *Asiatosuchus*. In addition, the lack of preserved cranial material has made cladistic analysis nearly impossible. Recently published matrices that include *Asiatosuchus* (Salisbury and Willis, 1996; Brochu, 1997a; 1997b) have focused mainly on cranial characters. This specimen has 2 codable characters out of 44 in the matrix of Salisbury and Willis (1996), and 14 codable characters out of 164 in Brochu's (1997a) matrix (which has a fairly large number of non-cranial characters). An experimental run of Brochu's (1997a) matrix, including this specimen, using Paup, 3.1.1 (Swofford and Begle, 1993) recovered 32,300 most parsimonious trees before it was terminated. A strict consensus of these trees had all of Crocodyloidea collapsed into a polytomy. An Adams consensus returned some resolution to Crocodyloidea, and placed this specimen within a polytomy including *A. grangeri* and *C. affinus* near the base of Crocodyloidea. *Asiatosuchus germanicus* was not included in this polytomy, reflecting the likely paraphyly of the genus. While these results are suggestive, additional fossils of Pakistan cf. *Asiatosuchus* that preserve more morphological characters must be found before its relationships will be understood.

This specimen has been assigned tentatively to the genus *Asiatosuchus* based on similarities of the posterior part of the jaw that it shares with jaws figured by Mook (1940) and Young (1964). However, it does not match any of this material exactly. The large fragment of the left ramus of the jaw of GSP-UM 3210 is 441.8 mm long, which is comparable to lengths given for *A. grangeri* (476 mm as preserved) and *A. nanlingensis* (375 mm as preserved, estimated total length of the left jaw ramus 550 mm). The length and breadth of the glenoid (50.6 mm and 83.5 mm) are much larger than values given by Mook (31 mm and 56 mm) or Young (33 mm and 59 mm). Despite such a size difference, the shapes of the glenoid fossae, as well as the shape of the suture between the surangular and articular in Mook's (1940) figures are similar to those of this specimen. Unfortunately, specimens of *A. grangeri* do not preserve the retroarticular process (Mook, 1940) nor the descending process of the articular (Brochu, pers. com., 1998), which would very useful for comparison with GSP-UM 3210.

The glenoid fossae of *A. nanlingensis*, as figured by Young (1964), are unlike those of this specimen. The medial fossa of *A. nanlingensis* is more rounded and the shape of the suture between the surangular and the articular is more semicircular. However, the posterior edge of the glenoid has a similar shape in both *A. nanlingensis* and GSP-UM 3210. The retroarticular process of *A. nanlingensis* is more steeply angled and the retroarticular fossa is more convex and appears to be divided into separate fossae as in *Crocodylus* (Norell and Clark, 1990). The surangulars of both *A. nanlingensis* and GSP-UM 3210 are alike in having flattened dorsal and lateral surfaces that are nearly perpendicular to each other. However, the surangular is pinched off anterior to the end of the retroarticular process in *A. nanlingensis*, while in GSP-UM 3210 the surangular continues to the end of the process. The shape and orientation of the descending process of the articular is an important similarity that *A. nanlingensis* shares with this specimen. In both cases, the descending process is much more anteroposteriorly directed than in most crocodylians, so that its long axis is nearly horizontal for much of its length. When viewed from above, the processes are convex and taper slightly to a rounded anterior end. The orientation of the descending processes in *A. nanlingensis* and GSP-UM 3210 is very unusual for crocodylians and may suggest a close relationship between these two animals even if the genus *Asiatosuchus* is paraphyletic. However, the morphological differences described above, as well as the disparity in ages (late Paleocene versus middle Eocene), make it unlikely that GSP-UM 3210 represents *A. nanlingensis*.

Biogeographical Implications

A cladistic analysis by Salisbury and Willis (1996) suggested that *Asiatosuchus germanicus* may be the sister taxon to the Australian Mekosuchinae, although the authors questioned the validity of this hypothesis. *A. germanicus* shares a number of features with mekosuchines, but these features are also convergently derived in a number of other crocodyloids (Salisbury and Willis, 1996). Also, Brochu (1997a; 1997b) included one mekosuchine, *Australosuchus clarkae*, in his analyses and found that *A. germanicus* was not closely related to it; *A. germanicus* was identified as a basal crocodyloid, while *A. clarkae* was found to be near the base of the crown group Crocodylidae. The stratigraphic ranges of the taxa also argue against this hypothesis (*Kambara*, the oldest mekosuchine, is Ypresian while *A. germanicus* is Lutetian, Salisbury and Willis, 1996). Both groups are known only from freshwater depositional environments. Salisbury and Willis (1996) felt these problems to mean that dispersal of *Asiatosuchus* across large marine barriers was unlikely, while they found no evidence to support dispersal across land bridges.

The presence of a slightly younger form of *Asiatosuchus* in a marine shale bed that has also produced archaeocetes in Pakistan (Gingerich et al., 1995) suggests that *Asiatosuchus* or *Asiatosuchus*-like crocodylians were capable of tolerating sea water, and perhaps spent much of their lives in marine seas. Berg (1966) also felt that *Asiatosuchus* was capable of navigating marine environments, which he thought may have contributed to its wide distribution in Europe and Asia (see also Keller and Schaal, 1992). If *A. volgensis* is truly *Asiatosuchus* (and there is no guarantee of this), it provides further evidence of the marine habitat of the genus. It is known from

near-shore sediments that have also produced remains of sharks, rays, chimaeras, sturgeons, teleosts, and chelonians (Efimov and Yarkov, 1993). Even if *Asiatosuchus* is paraphyletic, and this is very likely, the similarity of the orientation of the descending process of the articular in *A. nanlingensis* and GSP-UM 3210, which is unlike that seen in nearly all other crocodylians, suggests that these animals may be closely related. If this is the case, this lineage is old enough (*A. nanlingensis* is known from the Paleocene; Young, 1964) to have dispersed to Australia where it could have given rise to the mekosuchines. Discovery of GSP-UM 3210 in marine sediments also suggests that the lineage was tolerant of saline conditions and thus able to cross the marine barrier separating Asia and Australia.

Monophyly of the mekosuchine genus *Kambara* is supported by a single synapomorphy, a deep fossa on the pterygoids anterior to the internal nares. Salisbury and Willis (1996) interpreted this as possibly housing a salt-secreting gland, similar to the lingual salt glands of some modern crocodylians (Taplin and Grigg, 1989a,b). Most modern crocodylians are found mainly in fresh water, although many species are found in salt water in part of their range (Taplin and Grigg, 1989a,b). Salisbury and Willis (1996) interpreted close proximity to the coast of the site where the type specimen of *Kambara murgonensis* (Willis et al., 1993) was found to suggest that it easily could have ranged into the sea. Even if *Kambara* was salt-intolerant, the possible presence of (non-functioning?) salt-glands could indicate that its ancestors were salt-tolerant and capable of trans-oceanic dispersion (Salisbury and Willis, 1996). The presence of an *Asiatosuchus*-like crocodyloid with possible close affinities to *A. nanlingensis* in a marine shale bed in Pakistan lends some biogeographical support to Salisbury and Willis's (1996) hypothesized sister-group relationship between this taxon (or one or more of the species included in it if *Asiatosuchus* is paraphyletic) and Mekosuchinae. However, the discovery of more complete specimens of both *A. nanlingensis* and Pakistan cf. *Asiatosuchus* is necessary before hypotheses concerning their relationship to mekosuchines can be tested rigorously.

Competition with Archaeoceti

Finally, the Drazinda Formation has produced a diverse mammalian fauna, including a partial cranium and dentary of the archaeocete *Babiacetus indicus* (Trivedy and Satsangi, 1984) described by Gingerich et al. (1995). This whale is large (preserved cranial length 85 cm), shows cranial adaptations to an aquatic life mode (few postcrania are known), and presumably fed on large fish and other aquatic vertebrates (Gingerich et al., 1995a). Remains of two other large archaeocete species, *Basilosaurus drazindai* and *Basiloterus hussaini* (Gingerich et al., 1997), as well as the sirenian *Protosiren sattaensis* (Gingerich et al., 1995a), have been recovered a little higher stratigraphically and thus slightly younger geologically (Gingerich et al., 1997). *Asiatosuchus* is known to have attained large sizes (at least 4 m, Keller and Schaal, 1992; Vasse, 1992), and it was clearly capable of consuming large prey. Hence it was potentially a predator feeding on archaeocetes or competing for food with archaeocetes that shared its marine habitat.

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