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ANN ARBOR

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NEW CROCODYLIFORM (REPTILIA, MESOEUCROCODYLIA)
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JEFFREY A. WILSON¹, M. SADIQ MALKANI², AND PHILIP D. GINGERICH¹

Abstract — Fossil remains from the upper part of the Pab Formation in eastern Balochistan, Pakistan, provide the first diagnostic remains of a Cretaceous crocodyliform from the Indian subcontinent, and provide important information for assessing its biogeographic history. Specimens collected to date include the well preserved rostrum of a new genus and species, *Pabwehshi pakistanensis*. The rostrum has a foreshortened anterior snout, with serrated teeth that interlock to form a zig-zag cutting edge. The anterolaterally directed external nares are bordered ventrally and laterally by a well-marked narial fossa. Comparisons with crocodyliforms of equivalent age indicate that *Pabwehshi* is a baurusuchid mesoeucrocodylian related to *Baurusuchus* from Brazil and *Cynodontosuchus* from Argentina. *Pabwehshi* is the first baurusuchid known outside South America. It provides further evidence of a Cretaceous biogeographic link between South America and Indo-Pakistan.

INTRODUCTION

Indo-Pakistan, initially interlocked with the Gondwanan landmasses of Africa, Australia, Antarctica, and Madagascar early in the Mesozoic, drifted northward during the Cretaceous to collide with Laurasian landmasses during the Cenozoic. Indo-Pakistan thus appears to have experienced a 100-million-year period of isolation during a 9,000-kilometer migration across the equator that can be expected to have influenced the character of its native biota. Fossils from this period of biogeographic isolation are relatively scarce. Thus far, the Late Cretaceous (Maastrichtian) Lameta Formation of India has served as the sole source of information on Cretaceous vertebrates of the subcontinent.

The recorded dinosaurian fauna includes only one genus known from associated elements (*Titanosaurus colberti*; Jain and Bandyopadhyay, 1997) among the thirteen Indian dinosaurs currently recorded (Loyal et al., 1996). Based on present evidence, it is likely that herbivorous titanosaurian sauropods and carnivorous abelisauroid theropods predominated in India during the Late Cretaceous (Lydekker, 1877, 1879; Huene and Matley, 1933; Chatterjee and Rudra, 1996; Jain and Bandyopadhyay, 1997). The coarseness of these taxonomic identifications, however,

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precludes any phylogenetic link to another continental landmass. Titanosaurians had achieved a near-global distribution in the Late Cretaceous (Wilson and Sereno, 1998; Curry Rogers and Forster, 2001), and abelisauroids are known from South America, Madagascar, Europe, and Africa (Bonaparte, 1991; Sampson et al., 1998; Accarie et al., 1995; Russell et al., 1996; P. Sereno, pers. comm.). Indian crocodyliforms are known only from teeth and vertebrae (Rana, 1987, 1990) that are not diagnostic beyond *Crocodyliformes* (Brochu, 1999:80; Sereno et al., 2001).

The small vertebrate fauna of India has been more intensely studied, but offers no clearer picture of the biogeographic history of the subcontinent. Localities in central India have yielded a variety of microvertebrates, including mammals (Prasad and Sahni, 1988; Prasad et al., 1994), sharks (Prasad and Cappetta, 1993), frogs (Prasad and Rage, 1991, 1995), and squamates (Rage and Prasad, 1992). Although very few of these remains can be identified to the generic level, this fauna has been considered similar to that of Eurasia by several authors (Prasad and Rage, 1991; Sahni and Bajpai, 1991; Chatterjee and Scotese, 1999). However, Krause et al. (1997) argued that the dinosaurian and microvertebrate faunas of India are cosmopolitan, bearing affinities to both northern and southern faunas. The existing coarse taxonomic identifications of these fossils again offer little signal of India's former geographic connectedness and/or isolation.

New discoveries from the Upper Cretaceous (Maastrichtian) Pab Formation of Balochistan Province, Pakistan, provide a new vantage point from which to assess the evolution of the Indian subcontinent. Continental strata in the Vitakri region of eastern Balochistan (Fig. 1) have produced a variety of large vertebrate remains that include a new slender-limbed titanosaurian (Malkani and Anwar, 2000; Malkani et al., 2001) and the new crocodyliform described here. Although fragmentary, the new specimens represent the most diagnostic crocodyliform remains from the Indian subcontinent and facilitate comparison to other crocodyliforms, especially those from Africa, South America, and Madagascar. Here we describe the morphology of the new crocodyliform, underscoring features that are phylogenetically informative. The new fossil is relevant to current hypotheses of the paleogeographic history of the Indian subcontinent.

INSTITUTIONAL ABBREVIATIONS

GSP-UM — Geological Survey of Pakistan-University of Michigan collection, Quetta
 UM — University of Michigan Museum of Paleontology, Ann Arbor

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Hay 1930
 MESOEUCROCODYLIA Whetstone and Whybrow 1983
 BAURUSUCHIDAE Price 1945

Pabwehshi pakistanensis, new genus and species
 Figs. 2-4

Holotype.— GSP-UM 2000, an isolated rostrum bearing complete premaxillae and portions of the maxillae, nasals, vomer, dentaries, and right splenial (Figs. 2-3). The holotype is housed in the collections of the Geological Survey of Pakistan, Quetta. A cast of the specimen has been deposited in the University of Michigan Museum of Paleontology collection (UM 14127).



FIG. 1 — Map of Pakistan with inset showing the northeastern portion of Balochistan Province. The inset map indicates the position of the Vitakri localities ($29^{\circ}41.9'$ N latitude, $69^{\circ}23.9'$ E longitude), which produced the new mesoeucrocodylian crocodyliform, as well as other archosaur remains that include a titanosaurian sauropod. Inset map based on Anwar and Malkani (in press).

Type locality.— The holotype was discovered by one of us (MSM) in an area designated Vitakri locality 16. This locality is part of a 15–20 km exposure of Pab Formation in the Dhaola Range, near the village of Vitakri in eastern Balochistan Province, Pakistan.

Referred specimens.— GSP-UM 2001, an anterior portion of left and right mandibular rami fused at the symphysis (Fig. 4). This specimen was collected at Vitakri locality 3. A cast of this specimen has also been deposited in the University of Michigan Museum of Paleontology collection (UM 14128).

Formation, age, and distribution.— The Pab Formation is exposed in two widely separated areas of eastern Balochistan: the Pab and Kirthar ranges bordering Sind in the south, and the Sulaiman Range bordering Punjab in the north. In the western part of the Sulaiman Province, the formation is marginal marine to fluvial. Fluvial deposits include cycles of fining-upward grain size, poor sediment sorting, decreasing-upward bed thickness, trough cross-bedding, reddish brown overbank deposits, and silty to muddy matrix in upper parts of sandstones (Sultan, 1997). The age is generally believed to be Maastrichtian (latest Cretaceous), based on stratigraphic position within a sequence of dated formations (Nagappa, 1959; Jones et al., 1960; Kazmi and Jan, 1997; Sultan, 1997). To date, *Pabwehshi pakistanensis* has been found only at Vitakri localities 3 and 16.

Diagnosis. — Medium-sized crocodyliform sharing with the baurusuchid *Baurusuchus*: a reduced anterior portion of the rostrum retaining only three premaxillary teeth, the third of which is enlarged and overhangs the dentary; a reduced first maxillary tooth positioned along the posterior margin of the premaxillary-maxillary notch; and an enlarged, caniniform second maxillary tooth. *Pabwehshi pakistanensis* is characterized by the following autapomorphies: a dorsally inset first premaxillary alveolus; a prominent premaxillary lip overhanging the external nares; a diverticulum in the posterodorsal corner of the external naris; an enlarged, caniniform sixth dentary tooth; reduced fourth and fifth dentary teeth; and a diastematic fossa positioned just posterior to the second maxillary tooth.

Etymology. — *Pab*, name of formation in which crocodyliform was discovered; *wehshi*, Urdu word for beast. The specific epithet refers to the country of origin.

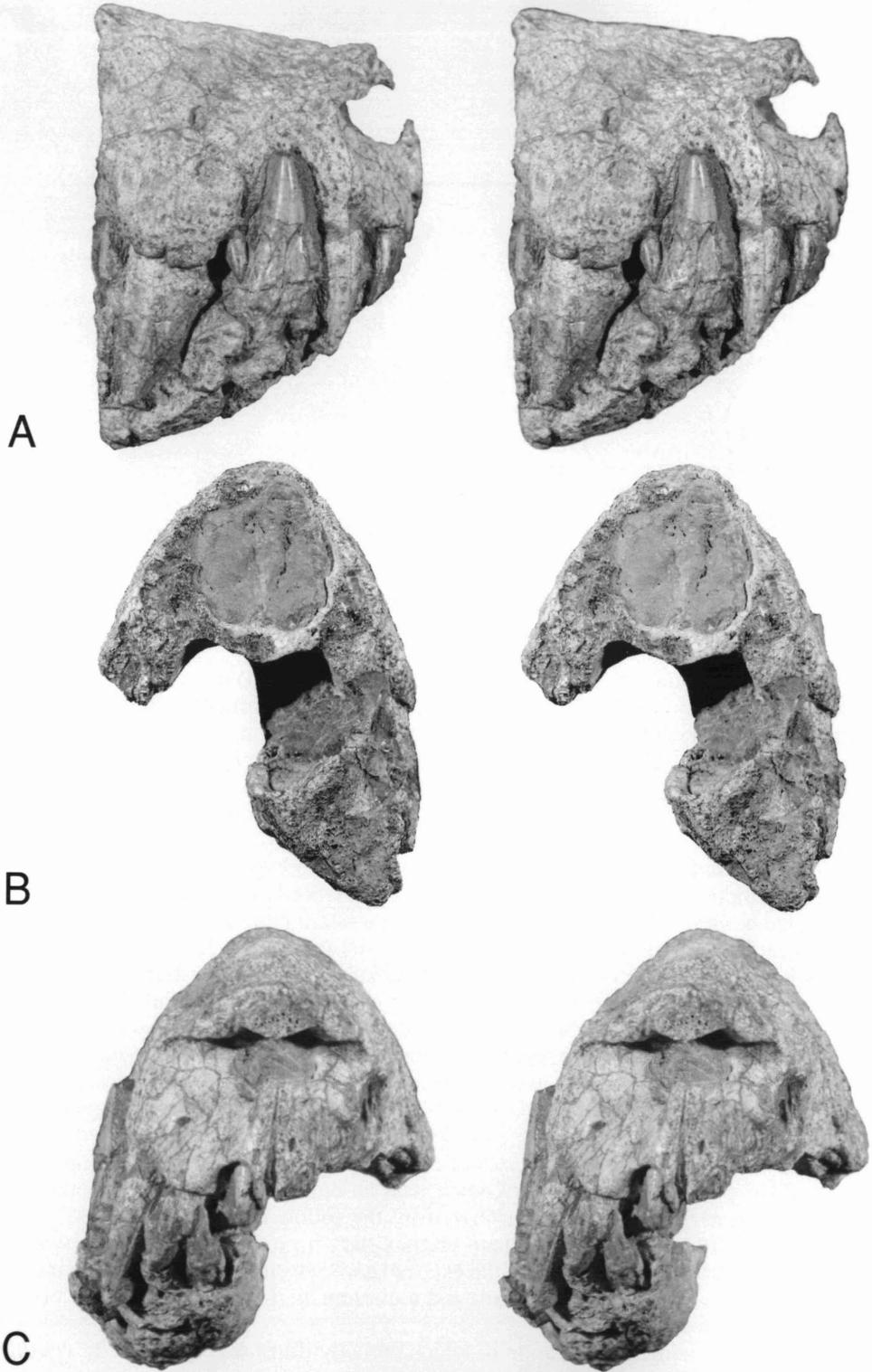
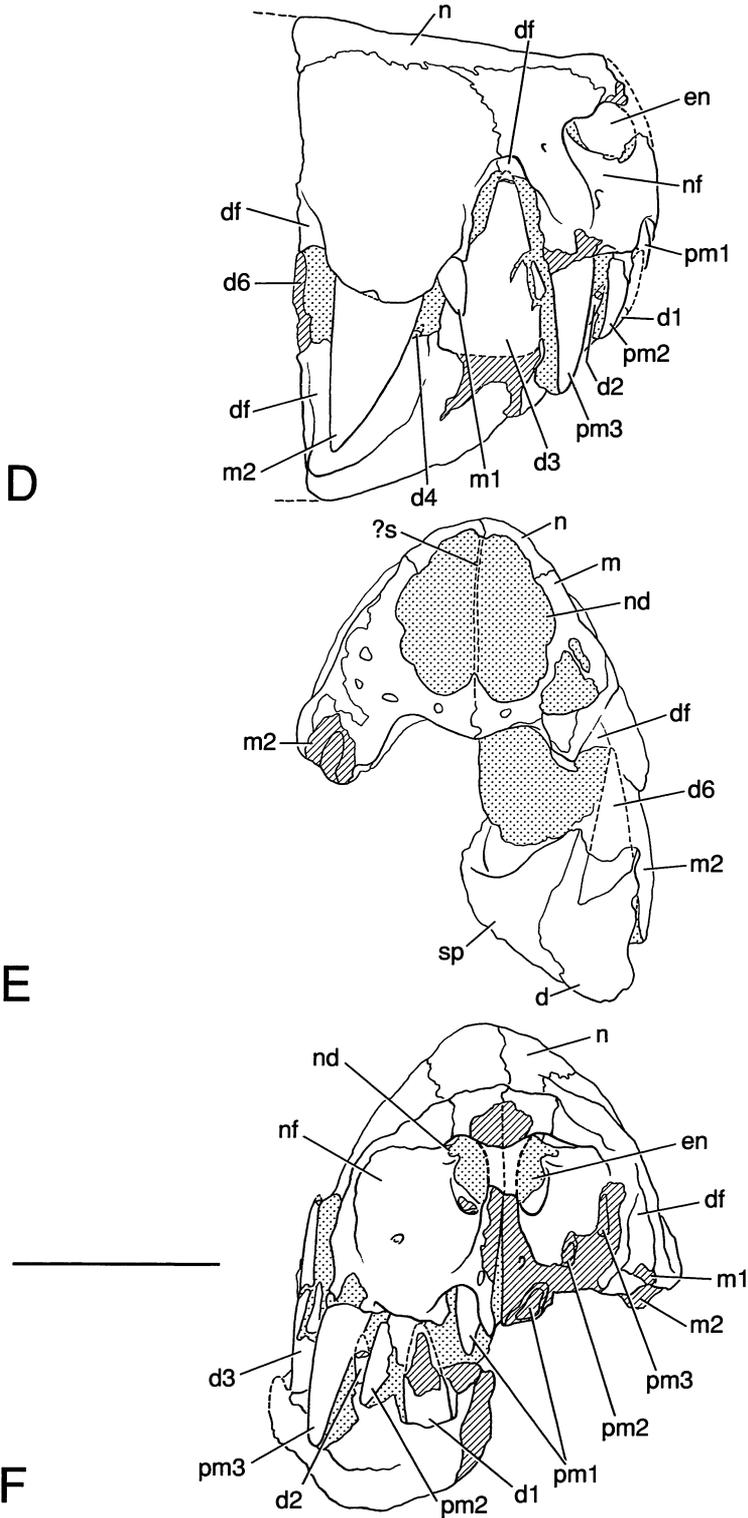


FIG. 2 — Holotypic rostrum of *Pabwehshi pakistanensis* (GSP-UM 2000). Stereophotographs (A-C) and line drawings (D-F) of the rostrum in right lateral (A, D), internal (B, E), and anterior (C, F) views. Abbreviations: *d*, dentary; *df*, diastematic fossa; *en*, external naris; *f*, foramen; *m*, maxilla; *n*, nasal;



nd, narial diverticulum; *nf*, narial fossa; *pm*, premaxilla; *sp*, splenial. Arabic numerals following abbreviations refer to tooth position (e.g., *pm3*). Stipple pattern indicates matrix, hatching pattern indicates broken bone surface. Scale equals 5 cm.

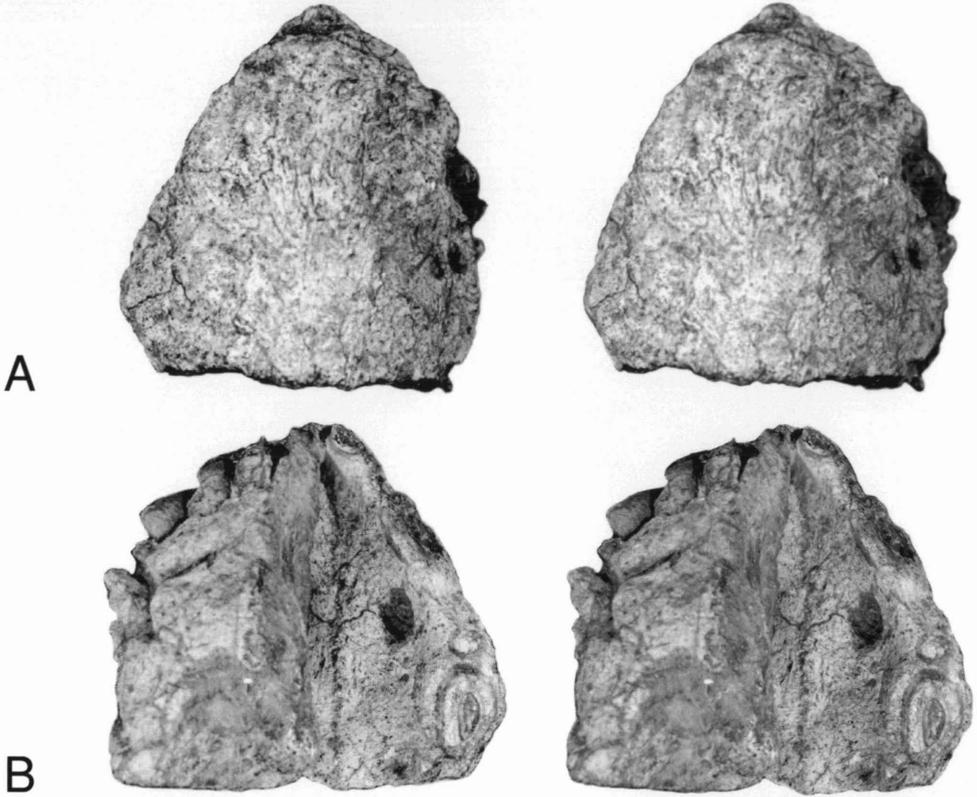
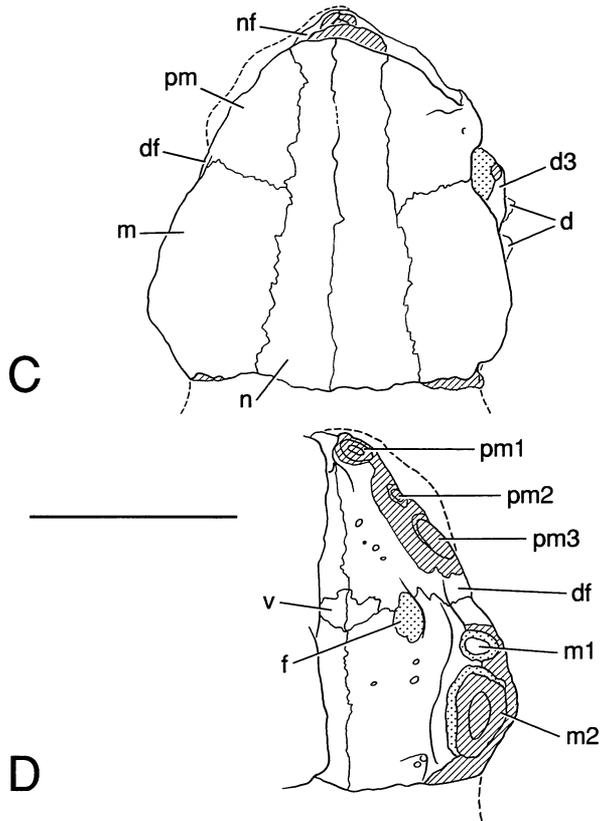


FIG. 3 — Holotypic rostrum of *Pabwehshi pakistanensis* (GSP-UM 2000). Stereophotographs (A, B) and line drawings (C, D) of the rostrum in dorsal (A, C) and ventral (B, D) views. Abbreviations: *d*,

DESCRIPTION

The holotype consists of the anteriormost portion of the rostrum, preserving the upper and lower teeth in place and interlocked on the right side (Figs. 2-3). The left portion of the rostrum has been weathered, exposing the interior margins of the premaxillary alveoli and the inner portion of the anterior end of the left mandibular ramus. The internarial bar is tapered to a narrow strut, but the portion between the premaxillae and nasals is broken away. The right side of the rostrum is nearly perfectly preserved from its tip to the fifth tooth position on the upper jaw and mandible. A referred partial mandibular ramus (GSP-UM 2001) consists of fused dentaries and splenials preserved from their posterior margin at the sixth alveolus forward (Fig. 4). GSP-UM 2001 matches the size, tooth count, and general shape of the holotypic lower jaw, and furnishes additional morphological details not available in the holotype.

General. — The surface of the rostrum is lightly ornamented with small pits that are distributed most densely in the vicinity of the maxillary tooth row and on the underside of the dentary. The rostrum is D-shaped to subtriangular in cross-section throughout its length. The available cross-section at the fifth tooth position shows that the height of the rostrum is three-quarters its width (Fig. 2E). Toward the tip of the rostrum, these dimensions are nearly equal. The external nares are terminal and extend posteriorly to the level of the third alveolus (Fig. 2D). They face anterolaterally and are bordered laterally and ventrally by a broad, smooth fossa. The referred mandible is also D-shaped in cross-section, becoming more narrow transversely and more shallow dorsoventrally toward its anterior end.



dentary; *df*, diastematic fossa; *f*, foramen; *m*, maxilla; *n*, nasal; *nf*, narial fossa; *pm*, premaxilla; *v*, vomer. Stipple pattern indicates matrix, hatching pattern indicates broken bone surface. Scale equals 5 cm.

Premaxilla. — The premaxilla is roughly quadrangular in lateral view and contacts the nasal dorsally and the maxilla posteriorly. The premaxilla and nasal meet along a horizontal suture that dips slightly ventrally as it approaches the external naris. These two elements enclose the external naris—the nasal forming the dorsal margin, and the premaxilla the anterior and lateral margins. Laterally, the premaxilla joins the maxilla along a nearly vertical butt joint. A shallow notch is present near the base of this contact. More dorsally, a triangular fossa is present that receives the caniniform crown of the third dentary tooth. The premaxilla bears three teeth that increase in size posteriorly. The first and smallest premaxillary tooth is located in a relatively large alveolus that is inset dorsally from the remainder of the alveolar margin. Posterior to this recessed alveolus, the jaw margin drops sharply to the level of the second and third premaxillary teeth. The tip of the third and largest premaxillary tooth crown projects below the lower jaw and is accommodated by a small notch and diastema between the second and third dentary teeth, which is best seen in the referred mandibular ramus (Fig. 4D,F).

The well-marked narial fossa extends anteroposteriorly from the symphysis to the third alveolus, and vertically from the alveolar margin to a point halfway up the external naris (Fig. 2D,F). The posterodorsal corner of the narial fossa is roofed by the premaxilla and bears a small diverticulum at its lateral extreme (Fig. 2F). This diverticulum is semicircular and apparently extends posteriorly the length of the preserved portion of the rostrum (Fig. 2E). A large foramen is present near the anteroventral margin of the naris. The tip of the internarial process of the

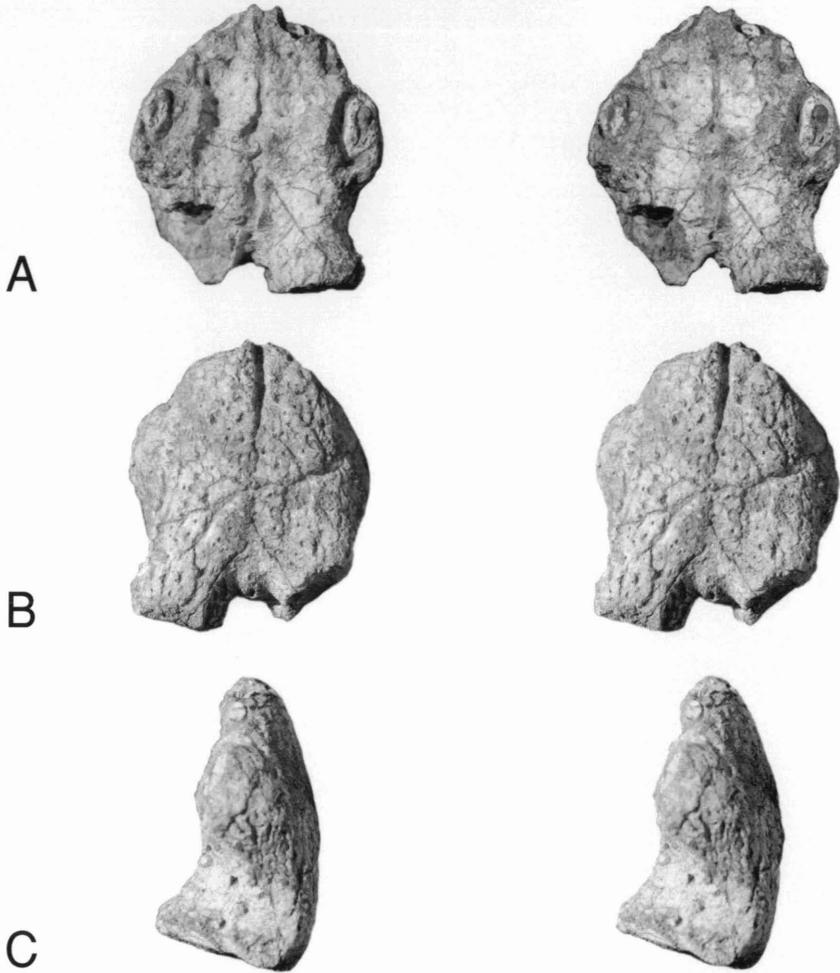
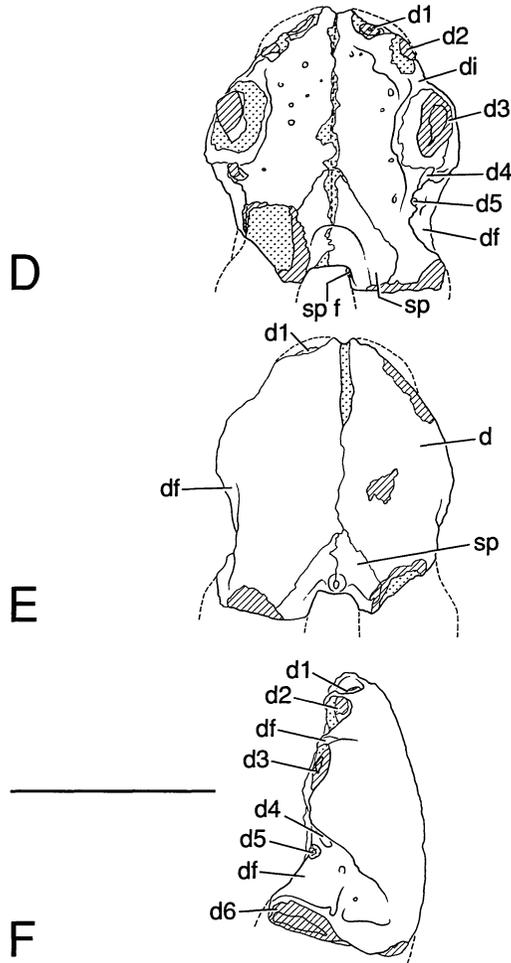


FIG. 4 — Referred mandible of *Pabwehshi pakistanensis* (GSP-UM 2001). Stereophotographs (A-C) and line drawings (D-F) of the mandible in dorsal (A, D), ventral (B, E), and right lateral (C, F) views.

premaxilla is preserved on the upper portion of the internarial bar, indicating that the premaxilla extended to the dorsal edge of the rostrum on the midline.

Ventrally, the premaxillae contact one another at the midline to form the anterior portion of the secondary palate. The premaxillary portion of the palate contacts the maxillary palate along a transversely oriented suture that is interrupted by the vomer and two large, paramedian fenestrae (Fig. 3D). These palatal fenestrae do not accommodate teeth from the lower jaw; there are no occlusal pits preserved on the premaxilla.

Maxilla. — The maxilla is preserved from its contact with the premaxilla to just behind the second maxillary tooth. Like the premaxilla, the maxilla forms the side wall of the rostrum and a part of the palate. The contact with the nasal is straight and parallels the midline, as seen in dorsal view (Fig. 3C). Laterally, the maxilla extends slightly below the premaxilla, creating a small step in the tooth row at their junction. The maxilla does not participate in the border of the external naris and has no anterior process. The two preserved maxillary teeth differ considerably in size, position, and orientation. The first maxillary tooth is less than one-third the size of the second and angles forward from its position on the posterior margin of the premaxillary-maxillary notch (Fig. 2D). The second maxillary tooth, in contrast, is caniniform and overhangs the lower jaw, its



Abbreviations; *d*, dentary; *df*, diastematic fossa; *di*, diastema; *f*, foramen; *sp*, splenial. Stipple pattern indicates matrix, hatching pattern indicates broken bone surface. Scale equals 5 cm.

crown lodged in a fossa between the fifth and sixth dentary teeth (Figs. 2D, 4F). Two diastemata are preserved on the maxilla. The first is shared with the premaxilla and accommodates the caniniform third dentary tooth. The anterior half of the second diastema is preserved just posterior to the second maxillary tooth (Fig. 2D) and receives the caniniform sixth dentary tooth (Fig. 2E).

Nasal. — The strap-like nasals roof the rostrum. Their width diminishes only slightly before their termination at the border of the external naris (Fig. 3C). The nasals are slightly arched posteriorly but nearly flat anteriorly. The nasals form the upper one-third of the margin of the external naris as well as a small portion of its overhanging lip (Fig. 2F). It appears that the nasals contribute to the internarial bar, but their anterior tips are broken away.

Vomer. — The small median element interposed between the premaxillae and maxillae on the palatal surface of the skull appears to be the vomer (Fig. 3D). The vomer is diamond-shaped, transversely elongate, and does not contact the pterygoid.

Dentary. — The holotypic dentary is preserved in articulation with the upper jaw on the right side. It bears six teeth that interdigitate with the corresponding upper teeth. The first and second dentary teeth are preserved between the first pair (pm 1 and 2) and second pair (pm 2 and 3) of

upper teeth, respectively (Fig. 2F). There is a small gap between the second and third dentary teeth that is occupied by the enlarged third premaxillary crown (Figs. 2D, 4D,F). The third and sixth dentary teeth are enlarged and caniniform, extending into diastematic fossae on the upper jaw; between these are positioned two very small teeth. The first small tooth can be seen in the holotype (Fig. 2D), but the second, which is positioned medial to the diastematic fossa, can only be seen in the referred specimen (Fig. 4D). These two small teeth are opposed by a small upper tooth.

Splénial. — Only the portion of the splénial anterior to the splénial foramen is preserved (Figs. 2E, 4D,E). The splénial contacts the medial aspect of the dentary along its height from the base of the jaw ramus to the alveolar margin. The splénial extends medially to the midline and participates in the symphysis. The dentary portion of the mandibular symphysis extends from the back of the third alveolus anteriorly, whereas the splénial makes up the portion from the back of the third dentary alveolus posteriorly.

Teeth. — All preserved tooth crowns are elongate and transversely compressed, with serrated anterior and posterior carinae. They are slightly asymmetrical. The posterior edge is straighter and shorter than the more convex anterior edge. Despite the convex anterior crown, the crowns are not recurved. The average number of serrations per mm is 2.8. This value varies with tooth size and, to a small extent, with position along the tooth edge itself (Table 1). Longitudinal striae are present on all teeth and are most conspicuous near the base of the crown. In cross-section the teeth are convex labially and slightly convex lingually. The convexity of the labial aspect of the tooth varies along the tooth row; the small, anterior teeth have D-shaped cross-sections whereas the larger, posterior teeth have elliptical cross-sections. Other differences between the teeth are attributable to size.

The arrangement of teeth and diastemata results in an interlocking occlusion. Two upper teeth (pm3, m2) and two lower teeth (d3, d6) occlude in opposing diastematic fossae. This zig-zag shearing occlusion between upper and lower teeth begins just posterior to the external naris. It is unknown how far this interdigitating occlusion extended along the tooth row.

PHYLOGENETIC AFFINITIES

Huxley (1875) arrayed fossil crocodile-like archosaurs into a graded series of three suborders—Parasuchia (which is no longer considered crocodylian), Mesosuchia, and Eusuchia—that appeared sequentially in the fossil record. The intermediate “mesosuchian” crocodylians were common during the Jurassic and Cretaceous and were characterized by a bony secondary palate composed of premaxillae, maxillae, and palatines, among other features (Huxley, 1875:427). This basic arrangement of fossil crocodylians was reflected in the first major numerical phylogenetic analysis of crocodylomorph relationships by Benton and Clark (1988), which identified a paraphyletic series of intermediate taxa that were more derived than the basal “protosuchians,” but outgroups to Neosuchia, the clade including crown-group crocodylians (Eusuchia) and their closest fossil relatives. Benton and Clark (1988) and later Clark (1994) employed the term “Mesoeucrocodylia” to refer to the clade uniting these intermediate forms and Neosuchia.

Among late Mesozoic and early Tertiary non-neosuchian mesoeucrocodylians are several South American forms that were considered members of Notosuchia, an endemic group of Late Cretaceous crocodylians (Gasparini, 1971). Gasparini (1971) originally defined the group to encompass Notosuchidae (*Notosuchus*) and Uruguaysuchidae (*Uruguaysuchus*, *Araripesuchus*) to the exclusion of several other South American genera (*Baurusuchus*, *Cynodontosuchus*, *Ilchunaia*, *Peirosaurus*). Although Romer (1956) and Huene (1956) noted the notosuchid affinities of the African genus *Libycosuchus* (Stromer, 1914), Gasparini (1971:97) excluded it from Notosuchia. However, later discoveries of West African crocodyliforms closely related to *Notosuchus* and *Araripesuchus* (Buffetaut and Taquet, 1979; Clark et al., 1989) provided strong evidence that

TABLE 1 — Measurements of teeth of *Pabwehshi pakistanensis* (GSP-UM 2000) in millimeters (mm), and counts of serrations per mm. Abbreviations: *d*, dentary; *m*, maxilla; *pm*, premaxilla. Parentheses indicate estimated measurements.

Tooth	Crown height	Crown length at base	Serrations/mm
pm 1	13.6	—	—
pm 2	21.0	10.1	—
pm 3	33.1	11.6	2.8
m 1	11.7	6.8	3.7
m 2	40.1	20.1	2.3
d 1	(26)	10.8	—
d 2	(9)	—	—
d 3	(40)	19.6	2.6
d 4	—	—	—
d 5	—	—	—
d 6	(35)	—	—

notosuchians were present outside of South America. Based on this evidence, Bonaparte and Kielan-Jaworowska (e.g., 1987) suggested notosuchians had a Gondwanan distribution.

Currently more than a dozen non-neosuchian mesoeucrocodylians are known. Phylogenetic analyses disagree on the monophyly of the principal notosuchian genera. Some show a paraphyletic Notosuchia (sensu Gasparini), linking *Araripesuchus* more closely to Neosuchia than *Notosuchus* and *Uruguaysuchus* (Gasparini et al., 1991; Clark, 1994; Wu and Sues, 1996; Buckley and Brochu, 1999; Buckley et al., 2000; Ortega et al., 2000). Others have found evidence for notosuchian monophyly (Pol, 1999; Sereno et al., 2001).

None of these higher taxa were associated with phylogenetic definitions that would clarify membership. For this reason, Sereno et al. (2001) formalized the definition of Notosuchia as “all crocodyliforms more closely related to *Notosuchus terrestris* than *Crocodylus niloticus*”. This stem-based definition guarantees notosuchian monophyly whether the group encompasses all principal notosuchian genera and their close relatives or *Notosuchus* alone.

Although no consensus exists on basal mesoeucrocodylian relationships, several points of agreement exist. Notosuchidae includes *Notosuchus*, *Malawisuchus*, *Simosuchus*, *Uruguaysuchus*, and *Chimaerasuchus*, taxa that are characterized by an anteroposteriorly elongate glenoid on the articular, with resultant fore-aft (proal) jaw motion (Gasparini, 1971; Clark et al., 1989; Wu et al., 1995; Gomani, 1997; Buckley et al., 2000). *Araripesuchus* and *Mahajangasuchus* are usually resolved as closely related to Peirosauridae (Buckley and Brochu, 1999; Buckley et al., 2000). Baurusuchidae is an enigmatic group that has been resolved in a position between notosuchids and peirosaurids (Gasparini et al., 1991; Clark, 1994; Gomani, 1997; Buckley and Brochu, 1999), as an outgroup to notosuchids (Buckley et al., 2000), or in an unresolved polytomy involving several taxa (Larsson and Gado, 2000; Sereno et al., 2001). Baurusuchids (*Baurusuchus*, *Cynodontosuchus*) have foreshortened rostra and enlarged teeth (Price 1945; Gasparini, 1972). *Sebecus* has been suggested to be the sister-taxon to Baurusuchidae (Colbert, 1946; Gasparini et al., 1991; Ortega et al., 1996; Gomani, 1997; Buckley et al., 2000; Sereno et al., 2001).

Pabwehshi pakistanensis preserves two mesoeucrocodylian synapomorphies: the premaxilla and maxilla meeting along a simple butt joint on the lateral aspect of the skull, and a bony secondary palate formed by these same two bones (Clark, 1994). Its relatively deep rostrum, and divided, anterolaterally-facing external nares exclude *Pabwehshi* from Neosuchia, which is characterized by a dorsoventrally compressed rostrum and confluent, dorsally facing external nares (Clark, 1994). *Pabwehshi* has a smooth narial fossa surrounding the ventral and lateral portions of the external naris, as in baurusuchids (*Baurusuchus*), peirosaurids (*Peirosaurus*, *Stolokrosuchus*),

and *Araripesuchus*. *Chimaerasuchus* also bears this narial fossa but differs in this respect from other notosuchids (*Notosuchus*, *Malawisuchus*, *Simosuchus*). Among these forms, *Pabwehshi* bears strongest affinities with Baurusuchidae. Like *Baurusuchus* (Price, 1945:2) and *Cynodontosuchus* (Gasparini, 1972:29, fig. 2), *Pabwehshi* has a reduced anterior portion of the snout, retaining only three premaxillary teeth, a reduced first maxillary tooth positioned in the premaxillary-maxillary notch, and an enlarged, caniniform second maxillary tooth. Additionally, *Pabwehshi* shares with *Baurusuchus* an enlarged, caniniform third premaxillary tooth (not present in *Cynodontosuchus*). Among basal mesoeucrocodylians only *Chimaerasuchus* has a more reduced dental complement, bearing only two premaxillary teeth and four maxillary teeth (Wu and Sues, 1996:fig. 1B). Derived features in the lower jaw (among others), however, have suggested that *Chimaerasuchus* is a notosuchid rather than a baurusuchid (Wu and Sues, 1996: figs. 2B, 9).

Based on diagnostic characters in the rostrum and dentition, we suggest that *Pabwehshi* is referable to Baurusuchidae, which currently includes *Baurusuchus* and *Cynodontosuchus*. *Pabwehshi* can be distinguished from all other basal mesoeucrocodylians on the basis of six characters: an elevated first premaxillary alveolus; a prominent roof over the external nares; a diverticulum in the posterodorsal corner of the external naris; reduced fourth and fifth dentary teeth; an enlarged, caniniform sixth dentary tooth; and a diastematic fossa positioned just posterior to the second maxillary tooth.

PALEOBIOGEOGRAPHIC IMPLICATIONS

Although basal mesoeucrocodylians are common throughout Gondwana, claims for their endemism have been countered by discovery of related forms on Laurasian landmasses, including Asia (*Chimaerasuchus*; Wu and Sues, 1996:680) and Europe (*Iberosuchus*; Antunes, 1975; Ortega et al., 1996). However, the prevalence of these crocodyliforms on southern landmasses makes them particularly useful in assessing biogeographic consequences of the breakup of Gondwana.

Based on the anatomical evidence provided above, *Pabwehshi* is most closely related to Baurusuchidae, a group previously known only from Argentina (Woodward, 1896; Gasparini, 1972) and Brazil (Price, 1945; Bertini et al., 1999). Inclusion of *Pabwehshi* in Baurusuchidae does not change the temporal range of the lineage (mid-Cretaceous to Maastrichtian) but expands its spatial distribution to include Indo-Pakistan. Despite geographic proximity during the Cretaceous, baurusuchids have not yet been discovered on other Gondwanan landmasses. Taking this absence literally, baurusuchid distribution can be explained by one of two mutually exclusive hypotheses: (1) dispersal between Indo-Pakistan and South America across an oceanic barrier, or (2) dispersal across Gondwana along a corridor between South America and Indo-Pakistan. The former requires that Baurusuchidae evolved after continental connections had been severed, whereas the latter requires the opposite. Additionally, the latter implies that baurusuchids traversed intervening landmasses—their absence there must be explained by regional extinction or by poor sampling. Dispersal across an oceanic barrier seems the less likely explanation for baurusuchid distributions, because the earliest record of the group (mid-Cretaceous) occurred when a land connection still existed between Indo-Pakistan and South America.

A land corridor between South America and Indo-Pakistan is present in the two main paleogeographic reconstructions. Smith et al. (1994) reconstruct a corridor between South America and Indo-Pakistan via Antarctica that existed until the Hauterivian (Early Cretaceous) at ca. 130 million years ago (mya). Hay et al. (1999) reconstruct the same corridor, but propose that it lasted until the Campanian (Late Cretaceous) at ca. 80 mya. Both depict a land connection between Africa and South America until the Albian-Cenomanian (mid-Cretaceous) at ca. 100 mya, as well as a connection between Indo-Pakistan and Madagascar that persisted until roughly the same time. However, because these two paleocoastline reconstructions indicate different durations for the corridor stretching between South America and Indo-Pakistan, they predict different landmasses

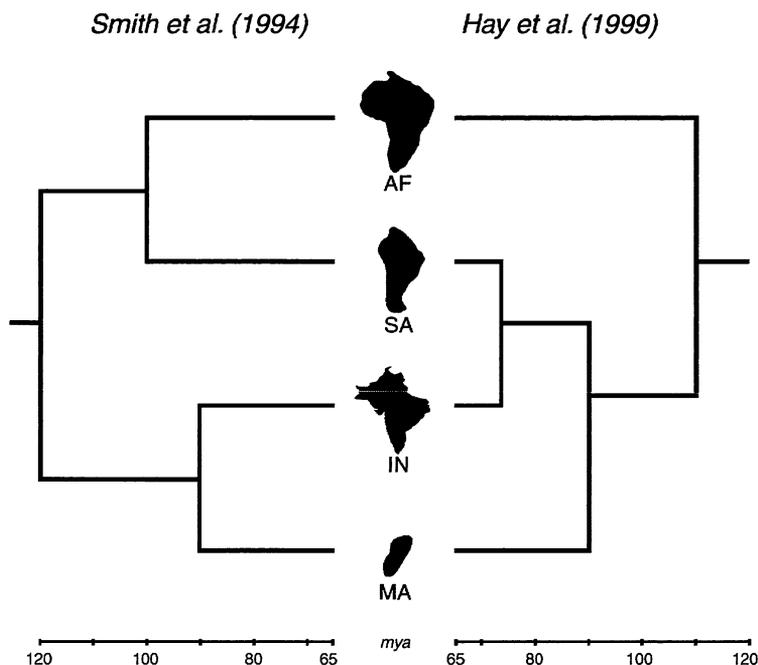


FIG. 5 — Hierarchical diagram of connections between Gondwanan continents during the last 55 million years of the Cretaceous, as implied by the paleocoastline reconstructions of Smith et al. (1994) and Hay et al. (1999). The former leads one to expect that Indo-Pakistan should show greatest faunal similarity to Madagascar, whereas the latter predicts close affinity to South America (via Antarctica). Abbreviations: *AF*, Africa; *IN*, Indo-Pakistan; *MA*, Madagascar; *mya*, million years ago; *SA*, South America.

to show greatest faunal affinity with the Indian subcontinent (Fig. 5). The paleogeography of Smith et al. (1994) leads one to expect that Indo-Pakistan's Cretaceous fauna should display greatest similarity to that of Madagascar, whereas the paleogeography of Hay et al. (1999) leads one to expect greatest similarity to South America and Antarctica. Furthermore, based on their presence in South America and Indo-Pakistan, the Smith et al. (1994) reconstruction predicts baurusuchids to have been in Africa and Madagascar; that of Hay et al. (1999) anticipates their presence in Antarctica.

Although the reconstruction by Hay et al. (1999) best accommodates the available data, the absence of baurusuchids from intervening landmasses— real or artifact— precludes favoring either one of these hypotheses at this time. Continent-level affinities of the crocodyliforms of Indo-Pakistan will be better understood with continued exploration in Pakistan, Madagascar, and Africa, as well as Australia and Antarctica, which have yet to yield diagnostic basal mesoeucrocodylian remains from the Late Cretaceous. Sampling issues aside, *Pabwehshi* provides the first record of Baurusuchidae outside South America, and provides further evidence of intercontinental biogeographic ranges for the various basal mesoeucrocodylian lineages.

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