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A Sauropod Braincase from the Pab Formation (Upper Cretaceous, Maastrichtian) of Balochistan, Pakistan

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Abstract

Recent geological and paleontological exploration in the Pab Formation (Upper Cretaceous) of Balochistan Province has uncovered new terrestrial vertebrate remains. Together with Cretaceous vertebrates from India, the Pab vertebrates provide information about the paleobiogeographic history of Indo-Pakistan during its northward migration towards Asia. Vertebrate remains collected from several localities in the Pab Formation include numerous, isolated postcranial bones attributable to titanosaur sauropods and a well-preserved sauropod braincase that is described here.

The Pab braincase is referable to Eusauropoda, but it does not preserve characteristics diagnostic of lower-level sauropod clades. The Pab braincase is relatively small and diagnosed by a prominent supraoccipital wedge, pronounced proatlantal facets, and a ventrally deflected occipital condyle that forms a 120° angle with the skull roof. Sauropod braincase material collected from Lameta Formation localities in India (Bara Simla, Dongargaon) closely resembles the Pab braincase in size and general morphology and shares one or more of its diagnostic features. The Indian and Pakistani braincases likely represent the same genus or species, which was distributed across Indo-Pakistan during the Cretaceous. Further exploration in both countries will better constrain the distribution of these and other vertebrate fossils, providing a clearer picture of the Cretaceous vertebrate fauna of Indo-Pakistan.

Introduction

Upper Mesozoic and Lower Cenozoic sediments of Indo-Pakistan record its geographical transition from an early connection to greater Gondwana, through a northern drift across the equator, to a later connection to Asia. All competing reconstructions of this geographical transition posit major changes in latitude and land connections that likely had a major impact on the terrestrial vertebrate lineages that evolved in Indo-Pakistan during that interval. However, the Mesozoic and Cenozoic vertebrate fossils of Indo-Pakistan are best known from Permian to Lower Jurassic sediments of India predating the transition (Jain, 1980; Bandyopadhyay and Sengupta, 1999; Ray and Bandyopadhyay, 2003) and Eocene to Miocene sediments of India and Pakistan postdating the transition (*e.g.*, Gingerich and Wells, 1983; Barry *et al.*, 1995; Gingerich *et al.*, 2001; Verma *et al.*, 2002).

Until recently, Mesozoic transitional faunas were recorded only from uppermost Cretaceous sediments of central and western India (Fig. 1), which produce numerous but often disarticulated remains (*e.g.*, Rana, 1990; Sahni and Bajpai, 1991; Prasad and Rage, 1991, 1995; Loyal *et al.*, 1996; Prasad and de Broin, 2002; Rana and Wilson, 2003). Few Upper Cretaceous Indian vertebrates are known from material whose association is documented. These include the titanosaur sauropod *Isisaurus colberti* (Jain and Bandyopadhyay, 1997), the abelisaurid theropod *Rajasaurus narmadensis* (Wilson *et al.*, 2003), and an unnamed snake (Mohabey, 1987).

Recently discovered vertebrate remains from the Upper Cretaceous Pab Formation of Balochistan, Pakistan (Fig. 1) offer a second opportunity to record late Mesozoic transitional faunas of Indo-Pakistan (Malkani and Anwar, 2000; Malkani *et al.*, 2001). Pab vertebrate fossils include the only diagnostic crocodylomorph from the Mesozoic of Indo-Pakistan (*Pabwehshi*; Wilson *et al.*, 2001) as well as numerous, isolated sauropod elements that include a well-preserved braincase (Malkani *et al.*, 2001). The Pab sauropod braincase is described here and compared to sauropod braincases collected from India. Several derived similarities suggest that the Pab braincase is very similar to remains collected from central India. Other sauropod elements from the Pab Formation share autapomorphic features with Indian material, suggesting paleobiogeographic continuity across Indo-Pakistan.

Institutional Abbrevations

ISI	—	Indian Statistical Institute, Kolkata
GSI	—	Geological Survey of India, Kolkata
GSP	—	Geological Survey of Pakistan, Quetta
UMMP	—	University of Michigan Museum of Paleontology, Ann Arbor.

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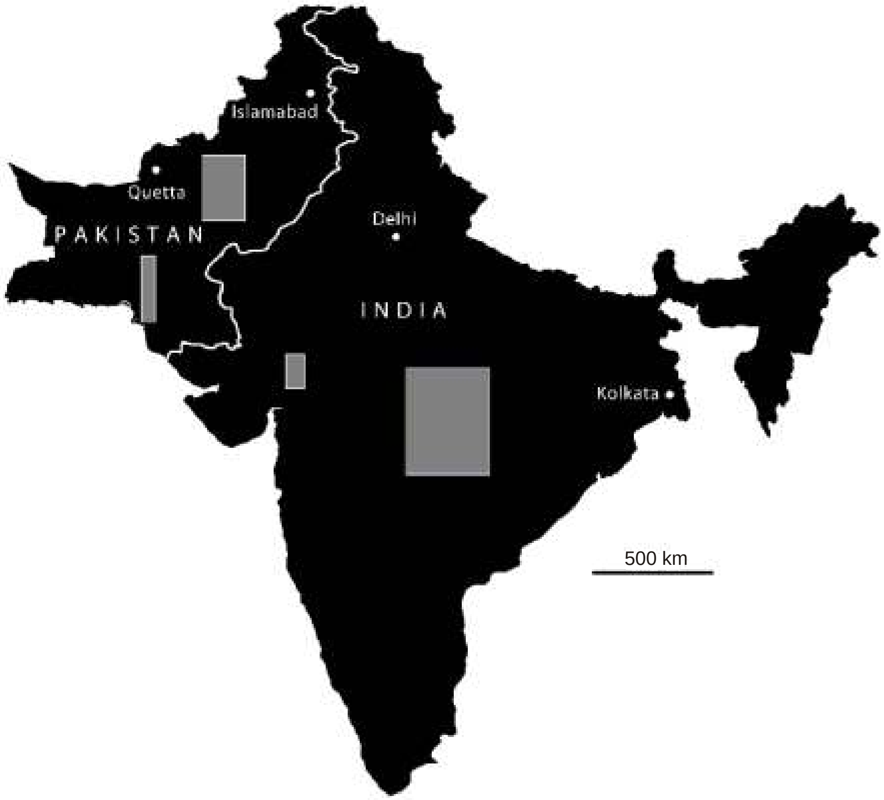

Fig.-1. Map showing the location of Upper Cretaceous fossil-bearing outcrops (gray boxes) in India (Lameta Formation) and Pakistan (Pab Formation). Capital cities (Islamabad, Delhi) and location of headquarters of the Geological Survey of Pakistan (Quetta) and Geological Survey of India (Kolkata) are shown.

Systematic Paleontology

DINOSAURIA Owen 1842
SAUROPODA Marsh 1877
EUSAUROPODA Upchurch 1995
Figure 2

Referred specimen : GSP-UM 7000, an isolated braincase that includes elements of the skull roof (frontal, parietal) and basicranium (supraoccipital, exoccipital-opisthotic, basioccipital, basisphenoid, prootic, laterosphenoid, orbitosphenoid). A cast of the specimen is housed in the University of Michigan Museum of Paleontology (UMMP 11303).

Type locality : Vitakri Locality 16. Part of a 15-20 km exposure of Pab Formation in the Dhaola range, near the village of Vitakri in eastern Balochistan Province, Pakistan.

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 (Fig. 1). In the western part of the Sulaiman Province, the formation is marginal marine to fluvial (Sultan, 1997). The age is considered to be latest Cretaceous (Maastrichtian) based on stratigraphic position within a sequence of dated formations (Nagappa, 1959; Jones *et al.*, 1960; Kazmi and Jan, 1997; Sultan, 1997).

The Pab Formation is overlain unconformably by the Paleocene Khadro Formation and is exposed, with the Paleocene Rakhi Gaj and Dungan Formations, in a series of roughly east-west trending *en echelon* folds near Vitakri. These tectonic structures are thought to have been produced by the oblique collision of the Indo-Pakistan Plate and the Afghan block (Kazmi and Jan, 1997). The Pab Formation forms the axis of the three main anticlines in the region: the Vitakri, Andari-Dhaola, Siah Koh anticlines. Thus far 18 vertebrate localities have been sampled in the Vitakri and the Andari-Dhaola anticlines. No sample has been collected *in situ* at any of these localities, so the exact fossil-bearing horizon is not yet known.

Description : The braincase is well preserved but lacks the distal ends of the paroccipital processes, basal tubera, and basipterygoid processes, as well as the anterior portions of the orbitosphenoids and latero-sphenoids. A portion of the skull roof is preserved that includes the parietals internal to the supratemporal openings and the frontals internal to the supratemporal and orbital margins and posterior of the nasal contacts. The Pab braincase is relatively small (Table-1) but sutures are tightly fused or indistingui- shable, which

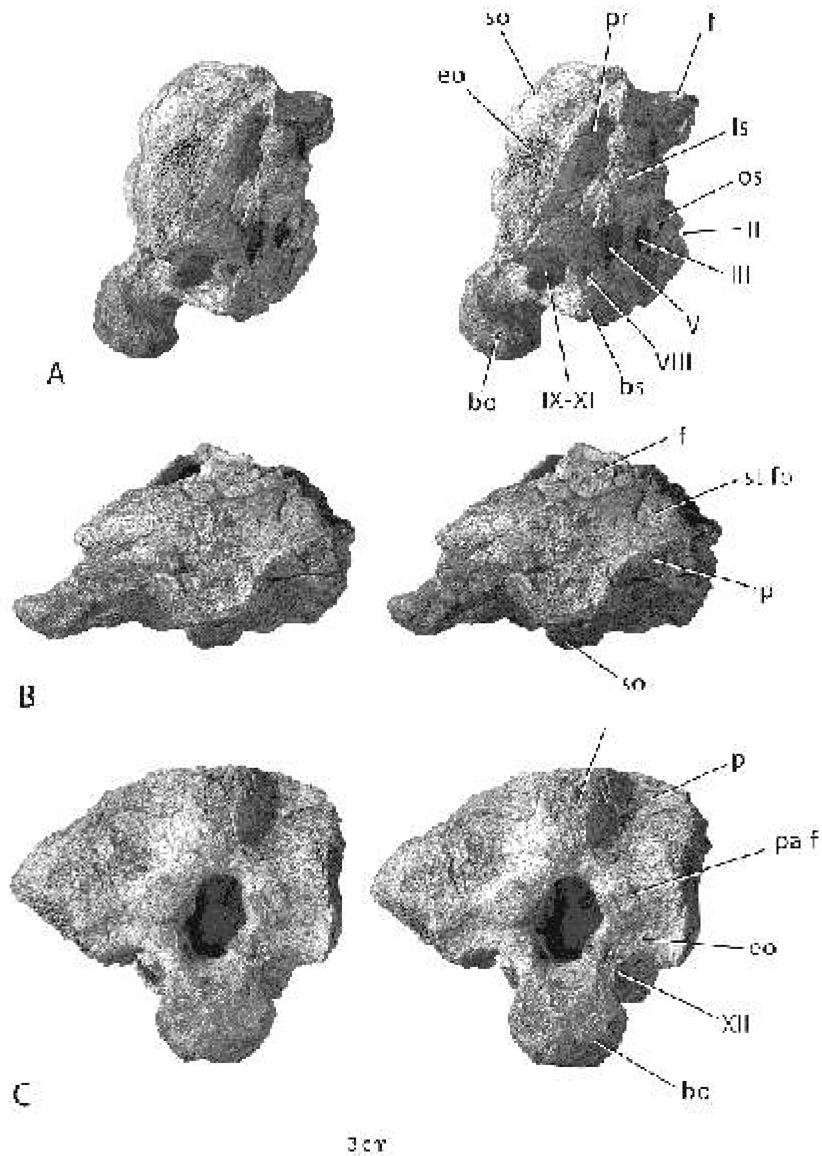

Fig-2. Stereopairs of the Pab sauropod braincase (GSP-UM 7000) in right lateral (A), dorsal (B), and posterior (C) views. Abbreviations: *bo*, basioccipital; *bs*, basisphenoid; *bt*, basal tubera; *eo*, exoccipital-opisthotic; *f*, frontal; *fm*, foramen magnum; *ls*, laterosphenoid; *os*, orbitosphenoid; *p*, parietal; *pa f*, proatlantal facet; *pr*, prootic; *so*, supraoccipital; *st fo*, supratemporal fossa. Roman numerals refer to cranial nerve openings.

suggests that GSP-UM 7000 represents a mature individual.

The **parietal** is a paired midline element that contacts the frontal anteriorly and has ventral contacts with the supraoccipital, exoccipital-opisthotic, prootic, and laterosphenoid bones. The parietal is exposed on the dorsal and posterior surfaces of the skull and typically participates in the margin of the supratemporal fenestra, which is not preserved in this specimen (Fig. 2 B, C). The midline suture of the parietal is partially fused, but traces of it can be discerned. The parietal and frontal are likewise tightly sutured, but a roughened line of bone traversing the dorsal skull probably represents their contact. As in other sauropods, the frontal-parietal contact is positioned near the contact of the laterosphenoid and prootic, and it coincides with a diminution of skull roof thickness that can be observed in lateral view. The supratemporal fenestrae are not preserved, but a shallow depression along the frontal-parietal suture, most pronounced on the right side, may represent part of the fossa surrounding it (Fig. 2B). The posterior margin of the skull is marked by low, arcuate ridges formed by the parietal on either side of the supraoccipital. The parietal is well exposed in posterior view, where it wraps over the supraoccipital wedge and extends laterally to overlay the exoccipital-opisthotic.

Table-1 : Principal dimensions of the Pab braincase (GSP-UM 7000) in millimeters.

Parietals, preserved transverse width	95
Parietals, anteroposterior length	37
Supraoccipital, dorsoventral height	38
Supraoccipital, transverse width of wedge	21
Paroccipital processes, preserved transverse width	118
Proatlantal facet (right side), transverse width	10
Proatlantal facet (right side), dorsoventral height	11
Foramen magnum, transverse width	26
Foramen magnum, dorsoventral height	32
Occipital condyle, transverse width	42
Occipital condyle, dorsoventral height	35
Basioccipital, transverse width between metotic foramina	42

The **frontal**, like the parietal, is a paired midline element. Unfortunately, little of the frontal is preserved. An available cross-section near the midline anteriorly reveals a thickness of about three millimeters. The frontal increases to nearly twice this thickness at its preserved lateral extreme; it would have been even thicker at its orbital margin, which is not preserved in GSP-UM 7000. The frontal contacts the laterosphenoid along a transverse contact that is visible on the left side. In dorsal view, the frontal forms part of the shallow supratemporal fossa (Fig. 2B).

The **supraoccipital** is the median basicranial element above the foramen magnum (Fig. 2B, C). It contacts the parietal dorsally and the exoccipital-opisthotic laterally and ventrally. Its suture with the exoccipital-opisthotic is not visible, but the supraoccipital likely contributed to the margin of the foramen magnum, as it does in other sauropods. The supraoccipital is slightly taller than the foramen magnum (Table-1) and bears a prominent wedge that extends noticeably from the plane of the occiput, as seen in lateral view (Fig. 2A). The prominence of the supraoccipital wedge, which is not quite complete in GSP-UM 7000, may be diagnostic.

The **basioccipital** is the median element that forms most of the occipital condyle and the ventral margin of the foramen magnum (Fig. 2C). Its contact with the exoccipital-opisthotic dorsally is tightly sutured, as is its contact with the basisphenoid anteriorly. The occipital condyle is D-shaped, with a flattened dorsal surface and a hemispherical posterior surface. A shallow groove on the left side of the occipital condyle suggests that the exoccipital-opisthotic formed its dorsolateral corner. A single opening for cranial nerve XII pierces the neck of the occipital condyle, it is likely that this opening passed through the basioccipital, rather than through the exoccipital-opisthotic or between the two, but this requires confirmation. The occipital condyle is strongly deflected ventrally and forms an angle of approximately 120 degrees with the skull roof. This deflection is not preservational and may be a diagnostic feature. The basioccipital and basisphenoid form the basal tubera, which are incomplete in GSP-UM 7000. The basioccipital forms the posterior margin of the metotic foramen; a trace of its suture with the basisphenoid is visible in the floor of this opening (Fig. 2A).

The **basisphenoid** is the median element that forms the posterior portion of the braincase floor. It contacts the basioccipital posteriorly and the prootic, laterosphenoid, and orbitosphenoid dorsally. The basisphenoid is incomplete ventrally and anteriorly, so the basipterygoid processes and parasphenoid rostrum are not preserved in GSP-UM 7000. The basioccipital forms the anterior margin of the metotic foramen as well as the floor of the openings for cranial nerves III and V (Fig. 2A). A small opening on the left side of the braincase may represent the opening for cranial nerve VII or VI, but the corresponding region is damaged on the right side.

The **exoccipital-opisthotic** forms the lateral margins of the foramen magnum, the shoulders of the occipital condyle, and the paroccipital processes. It contacts the parietal, supraoccipital, prootic, basioccipital, and basisphenoid. Although the paroccipital processes are not completely preserved, the preserved portion suggests that they were arched ventrally. Two rounded prominences on either side of the foramen magnum are facets for articulation with the proatlas (Fig. 2C). Proatlantal facets are uncommon in sauropods and may be diagnostic.

The **prootic** is a large, paired basicranial element that forms the anterior surface of the paroccipital processes. The prootic of GSP-UM 7000 lacks only its distal end. It contacts the laterosphenoid anteriorly, the exoccipital-opisthotic posteriorly, the parietal and possibly the frontal dorsally, and the basisphenoid ventrally. The prootic forms the forms the anterodorsal margin of the metotic foramen and the posterior margin of the trigeminal foramen. The fenestra ovalis opens is positioned between these openings.

The **laterosphenoid** is a transversely oriented paired braincase element that forms part of the wall of the endocranium and separates the supratemporal and orbital regions of the skull. The laterosphenoid of GSP-UM 7000 is only partially preserved, lacking its distal head and anterodorsal margin. It contacts the frontal and parietal dorsally, orbitosphenoid anteroventrally, and the basisphenoid ventrally. The laterosphenoid contribution to the dorsal margin of the openings for cranial nerves V and III is preserved, but its contribution to the opening for cranial nerve IV is not. Cranial nerve foramina V, III, and II are aligned with one another and oriented parallel to the skull roof (Fig. 2A).

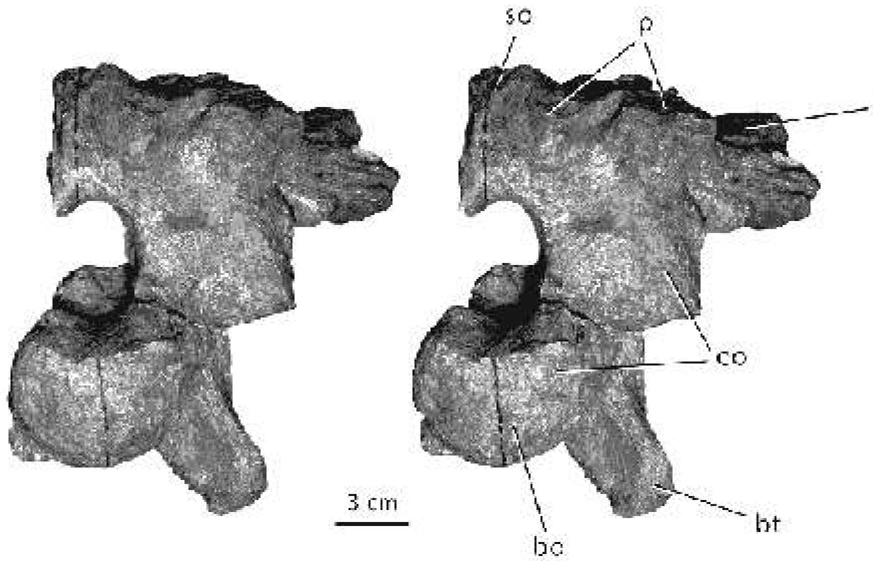

Fig-3. Stereopairs of the *Jainosaurus* (= "*Antarctosaurus*") *septentrionalis* braincase (GSI K27/497) in posterior view. Abbreviations are as in Figure 2.

The paired **orbitosphenoids** enclose the anterior portion of the endocranial cavity. Only the posterior-most portion of the orbitosphenoid is preserved, extending forward from its contacts with the basisphenoid and laterosphenoid near the opening cranial nerve III to the posterior margin of cranial nerve II (Fig. 2A).

Phylogenetic affinities : Although all diagnostic sauropod postcranial remains recovered from India and Pakistan are referable to Titanosauria, the Pab braincase (GSP-UM 7000) does not bear synapomorphies supporting this or any other lower-level affinities. The presence of a relatively flat occipital region with paroccipital processes projecting transversely is a synapomorphy of Eusauropoda (Wilson, 2002). The Pab braincase can be scored for few other braincase or skull roof characters, which themselves account for a small percentage of the total characters that have been identified in phylogenetic studies of sauropods.

Sauropod Braincases from India

Four braincases have been described from Maastrichtian-aged sediments of the Lameta Formation in central India (Bara Simla, Dongargaon) and western India (Rahioli). Indian braincases have typically been separated into "*Antarctosaurus*" and "*Titanosaurus*" morphs, which agrees with the recognition of two distinct sauropod genera (Wilson and Upchurch, 2003:132). These are briefly discussed below.

Jainosaurus (= "*Antarctosaurus*") *septentrionalis*. — Huene and Matley (1933) distinguished material Matley collected from the "Sauropod bed" at Bara Simla as the new species *Antarctosaurus septentrionalis*. Huene and Matley (1933:11-23) listed several elements that may pertain to one individual, and these may be considered the type series of "*A.*" *septentrionalis*: a partial braincase, anterior caudal vertebra, fragmentary chevrons and ribs, scapulae, partial forelimb, and sternal plate fragment. Although McIntosh (1990) formally removed "*A.*" *septentrionalis* from *Antarctosaurus*, the species has been treated as valid. Hunt *et al.* (1994:266) proposed the new generic name *Jainosaurus* for the Indian material and designated the braincase (GSI K27/497; Huene and Matley, 1933:fig. 5) as the lectotype. Following Berman and Jain (1982:408), who stated that the braincase "has been either lost or misplaced", Hunt *et al.*, (1994:266) suggested, "in case the lectotype cannot be located…we propose as a neotype the left scapula" (GSI unnumbered; Huene and Matley, 1933:pl. 3, fig. 2). We confirm that the braincase, now in two parts (Fig. 3), is present in the collections of the Geological Survey of India in Kolkata, as is a portion of the fragment identified by Huene and Matley (1933:fig. 7) as the "left squamosum". The latter element is quite heavy and may not be correctly identified as a squamosal; moreover, its association with the braincase was not documented by Huene and Matley (1933). The *Jainosaurus* braincase is characterized by transversely broad basal tubera that may have contacted the quadrate laterally, as in the titanosaur *Nemegtosaurus* (Wilson, 2002, in press). It bears a prominent crest on the dorsal surface of the parietal, which is quite narrow anteroposteriorly. The occipital condyle is large, kidney shaped, and oriented parallel to the skull roof. The neck of the occipital condyle bears a shallow depression on its ventral surface.

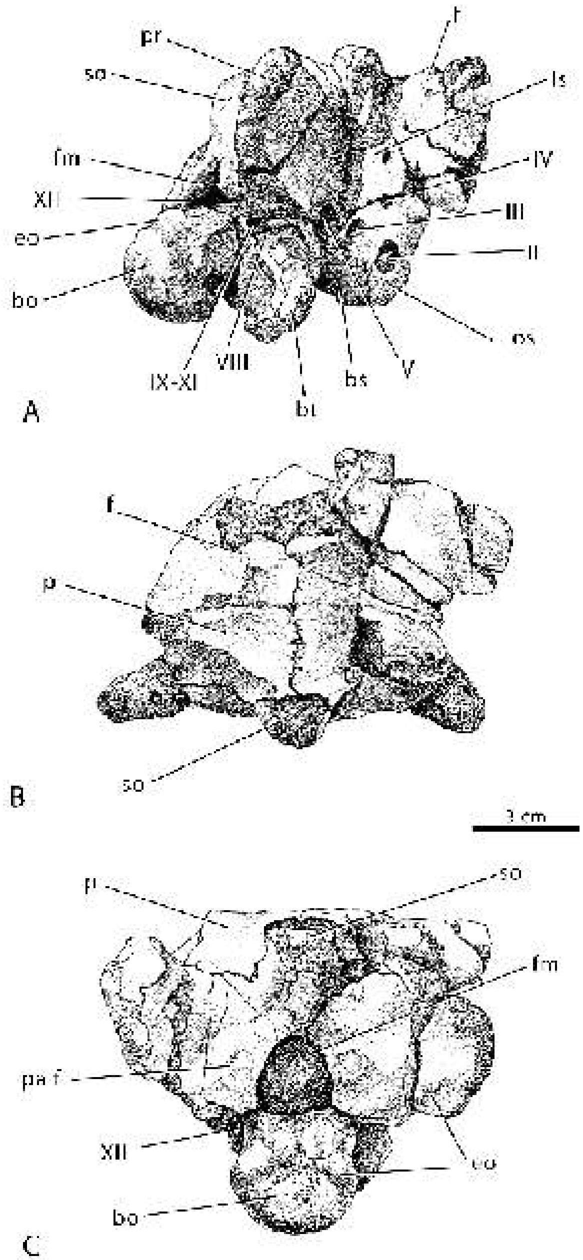

Fig-4. Line drawings of the Dongargaon braincase (ISI R199) in right lateral (A), dorsal (B), and posterior (C) views. Abbreviations are as in Figure 2. This figure was modified from Berman and Jain (1982:figs. 2-4).

Chatterjee and Rudra (1996:515) referred a braincase from Rahioli, Gujarat (ISI R162) to "*Antarctosaurus*" *septentrionalis*. Although it lacks the skull roof, laterosphenoids, and orbitosphenoids, the posterior portion of the braincase is much more complete than is the lectotype of *Jainosaurus*. Like *Jainosaurus*, ISI R162 has transversely broad but fairly thin basal tubera, but it differs slightly in its rounded, rather than kidney-shaped occipital condyle. The incomplete paroccipital processes of *Jainosaurus* are slightly arched, but their distal ends are not preserved.

Mohabey (1989:pl. 1) described a dinosaur braincase from Rahioli, Gujarat (GSI/GC/2905) that he considered to be of possible ornithischian affinity. This braincase has been re-identified as a dorsal vertebra of a titanosaur (D. M. Mohabey, personal communication).

"Titanosaurus indicus". — Two "*Titanosaurus*" morph braincases have been recovered from central India, one from Dongargaon and the other from Bara Simla.

In 1968-1969, collecting parties of the Indian Statistical Institute discovered several unassociated dorsal and caudal vertebrae and a well-preserved braincase from Lameta sediments of Dongargaon, near

Pisdura (ISI R199; Fig. 3). Because they considered the vertebrae similar to "*Titanosaurus indicus*", the braincase – although not associated – was likewise at least informally considered related to "*T. indicus*". Berman and Jain (1982) later described the braincase, but neither referred it to a preexisting genus nor assigned it a genus of its own. Subsequent ISI excavations (1984-1986) recovered an associated postcranial skeleton from a nearby locality that was described as *Titanosaurus colberti* by Jain and Bandyopadhyay (1997). These remains are diagnostic but cannot be referred to "*Titanosaurus*", which is invalid, and so they have received the new generic name *Isisaurus* in honor of the Indian Statistical Institute (Wilson and Upchurch, 2003). Jain and Bandyopadhyay (1997:131) claimed that "all this material [from Dongargaon] belongs to *T. colberti*", but the braincase does not appear on the quarry map and cannot be considered associated with the skeleton until future associations are discovered. Berman and Jain (1982:419) identified several differences between the Dongargaon braincase and that of *Jainosaurus* (= "*Antarctosaurus*") *septentrionalis* (Figs. 3, 4). The Dongargaon specimen, although apparently mature, is approximately half the size of *Jainosaurus*. They also noted that the Dongargaon braincase bears prominent proatlantal facets on either side of the foramen magnum, which are absent in *Jainosaurus*. There are some proportional differences in the skull roof, and the strong parietal ridge present on the skull roof of *Jainosaurus* is absent in the Dongargaon braincase. Berman and Jain (1982) also remarked on the strong supraoccipital wedge present in their material, which is less pronounced in *Jainosaurus*. Perhaps the most striking difference is the pronounced downward inclination of the occipital condyle of the Dongargaon material, which is oriented nearly 120 degrees from the plane of the skull roof (Berman and Jain, 1982). This condition is distinct from that in diplodocoids, in which the occipital condyle and skull roof are roughly parallel to one another but rotated ventrally relative to the anterior portion of the skull (*e.g., Diplodocus*; Wilson and Sereno, 1998:fig. 6). Both conditions resulted in a skull tipped downwards relative to the axis of the vertebral column.

Chatterjee and Rudra (1996:515-516) described a second "*Titanosaurus*" morph braincase (ISI R467) from Bara Simla. Although they reported an association with postcranial remains, this has not yet been documented. ISI R467 shares with the Dongargaon braincase general proportions as well as the characteristic strong ventral inclination of the occipital condyle. However, several minor differences are notable. The ISI R467 braincase lacks proatlantal facets, which are prominent in the Dongargaon specimen. It also has a much less pronounced supraoccipital wedge. There are also differences in the configuration of the cranial nerves. In the Dongargaon specimen, openings for cranial nerves II, III, and V are collinear and II is relatively large (Berman and Jain, 1982:figs. 4-5), whereas in the ISI R467 braincase these openings are arched and the opening for cranial nerve II is relatively small (Chatterjee and Rudra, 1996:fig. 12B). The phylogenetic value, if any, of these differences is not yet known, and some of them may vary with maturity (*e.g.*, prominence of proatlantal facets). The general shape of the braincase and the orientation of the occipital condyle strongly suggest that the Bara Simla braincase (ISI R467) and Dongargaon braincase (ISI R199) pertain to closely related taxa.

Indo-Pakistan Sauropod Fauna

The Pab braincase (GSP-UM 7000) closely resembles the Dongargaon braincase (ISI R199) in size and general morphology, and shares with it a ventrally deflected occipital condyle that forms an angle of 120 degrees with the skull roof, well-marked proatlantal facets, and a prominent supraoccipital wedge. These similarities and the absence of major differences suggest that these two specimens are congeneric or conspecific. A braincase from Bara Simla (ISI R467), which is similarly proportioned and shares the ventrally deflected occipital condyle, may also be closely related. Thus, these three braincases probably represent a single taxon that has thus far been recovered across Indo-Pakistan (Bara Simla and Dongargaon, central India; Vitakri, western Pakistan). Although none have been discovered in association with postcranial remains, the Dongargaon braincase was collected very close to the type locality of *Isisaurus colberti*, a partial titanosaur skeleton (Jain and Bandyopadhyay, 1997). *Isisaurus* is characterized by several autapomorphies in the presacral vertebral column, as well as by gracile ulna with reduced cross-sectional area. An ulna recovered from Vitakri (Malkani *et al.*, 2001) shares the extremely reduced cross-sectional area and may be referable to *Isisaurus*. Thus, *Isisaurus* postcranial remains have been found with the "*Titanosaurus*" braincase morph at both Vitakri and Dongargaon. Although field associations are still required, this at least suggests that *Isisaurus* and the "*Titanosaurus*" morph braincase pertain to the same taxon, which is distributed across Indo-Pakistan.

The second Indian sauropod genus, *Jainosaurus*, is represented by a braincase that may have been associated with a caudal vertebra, fragmentary chevrons and ribs, scapulae, a partial forelimb and sternal plate fragment. The braincase is incomplete but may have had the quadrate-basal tubera contact diagnostic of titanosaurs such as *Nemegtosaurus*. The *Jainosaurus* braincase is distinguishable from the "*Titanosaurus*" morph braincase in size and general proportions. The postcranial elements thought to be associated with the braincase (Huene and Matley, 1933) are not diagnostic. Thus far, *Jainosaurus* has been recovered at Bara Simla and Rahioli but not Pakistan.

Conclusions

The first Mesozoic vertebrate fossils from Pakistan were collected only recently from the Upper Cretaceous Pab Formation of Balochistan (Malkani and Anwar, 2000). Sauropod dinosaur remains from the Pab Formation shared derived similarities with remains collected from central India. The Pab sauropod braincase described in this contribution bears diagnostic features of Eusauropoda and appears to be congeneric or conspecific with braincase material recovered from Bara Simla and Dongargaon. Together, these braincases have been referred to as the "*Titanosaurus*" morph. Both the Pab braincase and the Dongargaon braincase were found at localities preserving postcranial remains of the titanosaur *Isisaurus*. Although further associations are required, these discoveries suggest that the "*Titanosaurus*" morph braincase pertains to *Isisaurus*. The other Indian sauropod genus, *Jainosaurus*, is represented by braincase material that has been recovered only from central and western India. Postcranial remains attributed to *Jainosaurus* are not diagnostic. Cranial and postcranial associations for *Isisaurus* and *Jainosaurus* are weakly established but consistent.

Although preliminary, these results suggest some Cretaceous vertebrates were distributed across Indo-Pakistan. It is not coincidental that it is the most complete and most diagnostic vertebrate taxon (*Isisaurus*) that has been identified at multiple localities across the subcontinent. Further work in India and Pakistan will better constrain the distribution and augment the completeness of newly described, diagnostic material such as *Isisaurus*, *Jainosaurus*, the baurusuchid crocodylomorph *Pabwehshi*, and the abelisaurid theropod *Rajasaurus*.

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