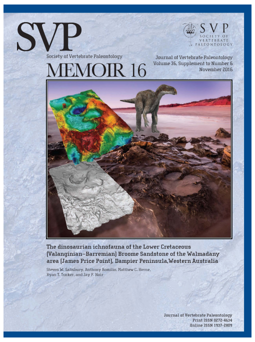

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SHORT COMMUNICATION

A LARGE CROCODYLOID FROM THE OLIGOCENE OF THE BUGTI HILLS, PAKISTAN

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Cenozoic continental deposits of the Bugti Hills crop out south of the Sulaiman Range in Balochistan, Pakistan. These have been renowned since Vickary (1846) for their exceptionally rich vertebrate-bearing Miocene localities. This led G. E. Pilgrim (Geological Survey of India) and later C. Foster-Cooper (University of Cambridge) to conduct expeditions there in the beginning of the 20th century. More recent expeditions in the late 1990s have reported the occurrence of successive fossiliferous horizons spanning the Eocene–Pleistocene interval (Welcomme et al., 1997, 2001; Welcomme and Ginsburg, 1997). Fossil-yielding series around Dera Bugti document marine, coastal, then fluviolacustrine depositional environments during the Eocene, the earliest Oligocene, and the late Oligocene–Pleistocene, respectively (Welcomme et al., 2001; Métais et al., 2009b; Roddaz et al., 2011; Antoine et al., 2013). The most species-rich intervals, at least for mammals, are Oligocene and Miocene in age (Marivaux et al., 1999, 2001, 2002a, 2002b, 2005; Antoine and Welcomme, 2000; Antoine et al., 2003, 2004, 2010, 2013; Marivaux and Welcomme, 2003; Métais et al., 2003, 2006, 2009a, 2017; Orliac et al., 2009, 2010). As for crocodylians, fossil remains were initially described from the Bugti Hills by Pilgrim (1908, 1912), but their precise stratigraphic provenance has not been recorded. Most of those fossils are quite fragmentary, and they consist of large tomistomine skull fragments (Martin, 2018) formerly referred to species of *Gavialis* (Pilgrim, 1908, 1912). Together with these remains, *Crocodilus bugtiensis* Pilgrim, 1908, was erected from a left maxilla and associated skull fragments of remarkable size found at Pishi Nala. Since its formal description four years later (Pilgrim, 1912), the taxon has been briefly recorded from several levels in the Bugti Hills (Welcomme et al., 1997), but no detailed account has been given since. Here, we describe partial, yet diagnostic, mandibular elements of a large crocodyloid recovered from upper Oligocene deposits of the Bugti Hills, that are morphologically compatible with the skull elements described by Pilgrim (1912). This material was collected from a well-identified Oligocene horizon within the framework of the field campaigns that took place in Baluchistan between 1995 and 2000. We also report a partial mandible collected in the 1920s from Baluchistan but with no provenance data. Finally, we mention the presence of tooth marks on associated megaherbivore remains.

Institutional Abbreviations—**IM**, Indian Museum, Calcutta, India; **MHNL**, Musée des Confluences, Lyon, France; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**, Natural History Museum, London, U.K.; **UM-DB-LC**, Université de Montpellier-Dera Bugti, Lundo Chur locality.

GEOLOGICAL SETTING

Pilgrim (1912) states that the holotype specimen IM E221 comes from the lowest beds in the series in Pishi Nala, Bugti Hills. Unfortunately, this information remains ambiguous, and depending on the occurrence and current understanding of the systematics of co-occurring ruminant mammals, one may consider its provenance to be lower Oligocene or upper Oligocene–lower Miocene (Pilgrim, 1912; Antoine et al., 2013; Métais et al., 2017). For this reason, we consider IM E221 to be Oligocene in age. On the other hand, the age and the provenance of UM-DB-LCJ1-02 are clearer. This specimen was collected later in the Bugti Hills (Baluchistan, Pakistan) by the members of the 'Mission Paléontologique Française au Baloutchistan' (MPFB), in deposits situated in the south of the Zin Anticline, Lundo Chur section, and is upper Oligocene in age (see Welcomme et al., 2001; Antoine et al., 2003, 2004; Métais et al., 2009b; Orliac et al., 2010). Specimen UM-DB-LCJ1-02 originates from the J1 horizon (lower elephantoid-bearing horizon; Antoine et al., 2003, 2004) of the Lundo Chur section, about 25 km south of Dera Bugti (Welcomme et al., 2001; Métais et al., 2009b).

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin, 1789
CROCODYLOIDEA Fitzinger, 1826
Family incertae sedis
ASTORGOSUCHUS, gen. nov.

*Corresponding author.
Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

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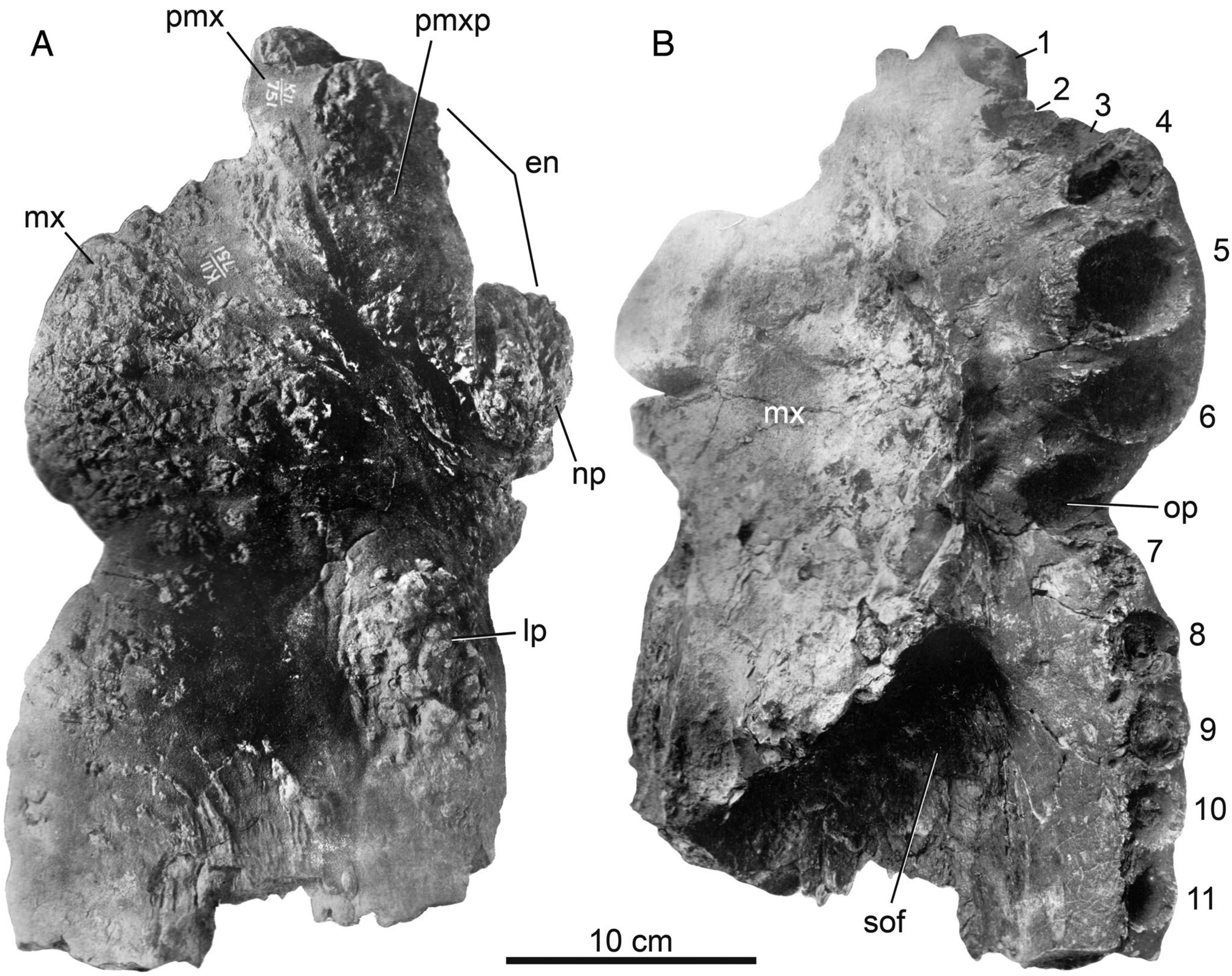

FIGURE 1. Holotype specimen (IM E221) of *Astorgosuchus bugtiensis*, comb. nov., modified after Pilgrim (1912:pls. 26, 27), Oligocene, Pishi Nala, Bugti Hills, Pakistan, in **A**, dorsal and **B**, ventral views. Numerals denote the maxillary alveolar number. **Abbreviations**: **en**, external nares; **lp**, lacrimal prominence; **mx**, maxilla; **np**, nasal prominence; **op**, occlusal pit; **pmx**, premaxilla; **pmxp**, premaxillary prominence; **sof**, suborbital fenestra.

Type Species—*Crocodilus bugtiensis* Pilgrim, 1908.

Diagnosis—As for the type and only known species.

Etymology—From the Greek 'astorgos,' meaning merciless or inexorable, and 'souchos,' from the Greek name of the crocodile-headed god in Egyptian mythology (Sobek); referring to the inexorable fate of animals being seized in such powerful jaws.

ASTORGOSUCHUS BUGTIENSIS, comb. nov.
(Figs. 1–4)

Holotype—IM E221, parts of a single cranium including a nearly complete left maxilla and connected fragments of a premaxilla, a nasal, and a lacrimal (Fig. 1; Pilgrim, 1912). Pilgrim (1912) reports this specimen as originating from Pishi Nala in the Bugti Hills.

Referred Material—UM-DB-LCJ1-02, a mandibular symphysis including the dentaries and splenials (Figs. 2, 3). NHMUK R.5266 (Fig. 4) was presented to NHMUK in 1925 by Clive Foster-Cooper and is labeled as originating from the Miocene of Baluchistan. However, its precise origin (locality) and age (horizon) remain unknown.

Locality and Horizon—Oligocene of the Bugti Hills, Baluchistan, Pakistan.

Diagnosis—*Astorgosuchus bugtiensis* is characterized by the following unique combination of skull characters as noted by Pilgrim (1912) (autapomorphies are denoted with *): total skull length greater than 80 cm for mature individuals; short-snouted skull as indicated by a rostrum only twice as long as wide; broad-headed skull as indicated by a rostrum at level of largest maxillary alveolus as wide as the width in front of the orbits; largest maxillary alveolus is the fifth; presence of a deep notch lateral to premaxillary-maxillary suture; presence of a deep notch located between sixth and seventh maxillary alveoli for reception of the 11th dentary tooth; enlarged external nares extending far posteriorly, almost reaching level of enlarged fifth maxillary alveolus*; nasals contributing to external nares; and presence of swollen and rugose prominences on dorsal surface of lacrimal (not contributing to orbital margin)*, premaxilla, and anterior part of the nasals. *A. bugtiensis* also displays a unique combination of mandibular characters among Crocodyloidea, including a mandibular symphysis encompassing first seven dentary alveoli*; fused splenials penetrating mandibular rostrum to the level of sixth dentary alveolus*; and elevated contiguous large fourth and diminutive fifth dentary

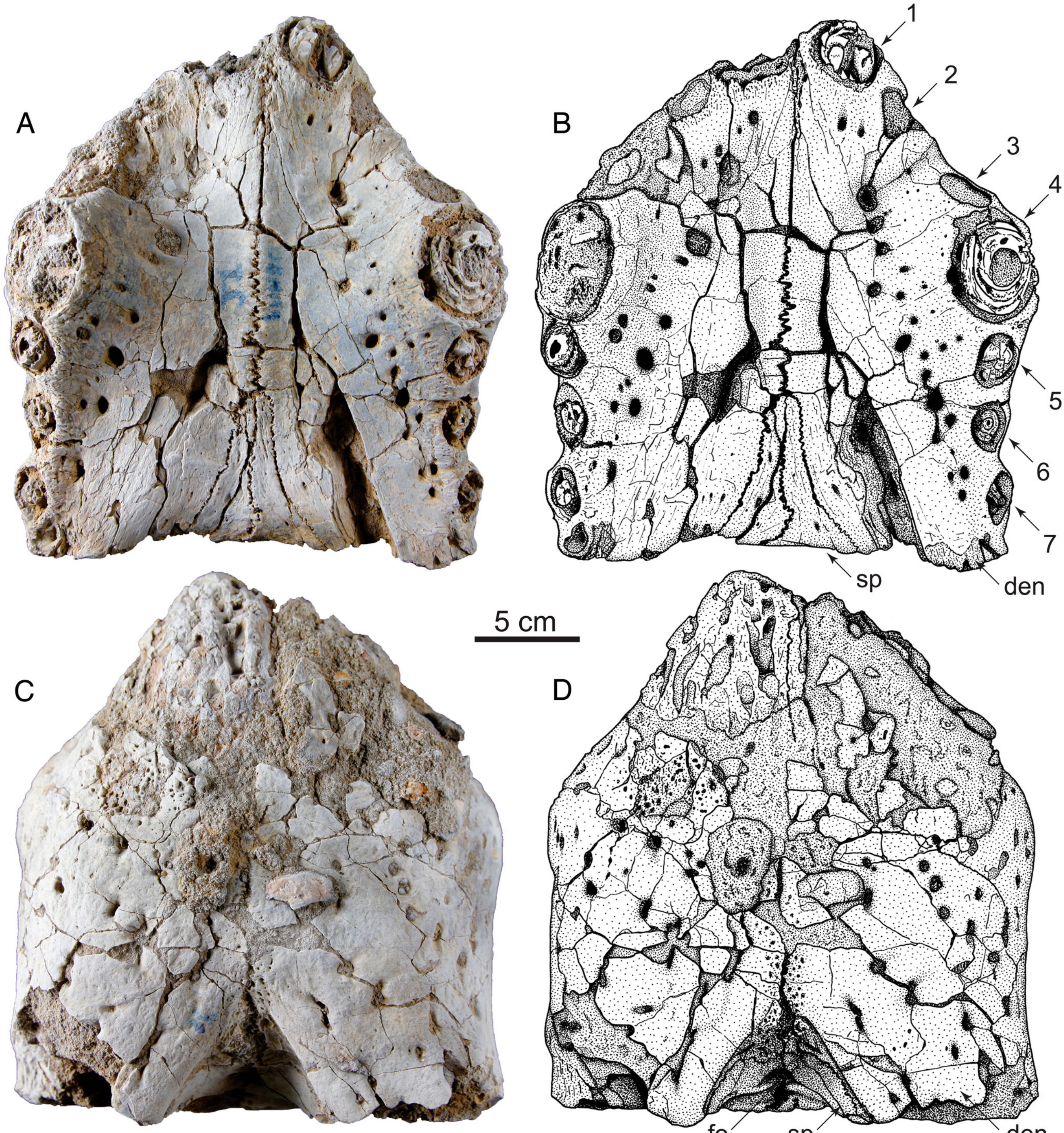

FIGURE 2. Photographs and associated drawings of UM-DB-LCJ1-02, mandibular rostrum of *Astorgosuchus bugtiensis*, comb. nov., from the upper Oligocene of the Bugti Hills, Pakistan, in **A**, **B**, occlusal and **C**, **D**, ventral views. Numerals denote the alveolar number. **Abbreviations**: **den**, dentary; **fo**, foramen; **sp**, splenial.

alveoli*. Differs from crocodylines, mekosuchines, and the basal crocodyloid *Asiatosuchus* in having splenials involved in the mandibular symphysis; differs from tomistomines in having a shorter mandibular rostrum.

Description—The two newly reported specimens (NHMUK R.5266 and UM-DB-LCJ1-02) comprise the fused left and right anterior portions of the mandibular rami (Figs. 2–4). In NHMUK R.5266, the left mandibular ramus is preserved to the level of the ninth alveolus and the associated splenial is flanked on the entire preserved medial surface of the dentary ramus. However, the symphysial surface is somehow damaged, and the extent to which the splenial contributes to it is difficult to precisely ascertain (Fig. 4A–C). The relative dimensions and positions of dentary alveoli are identical to those of UM-

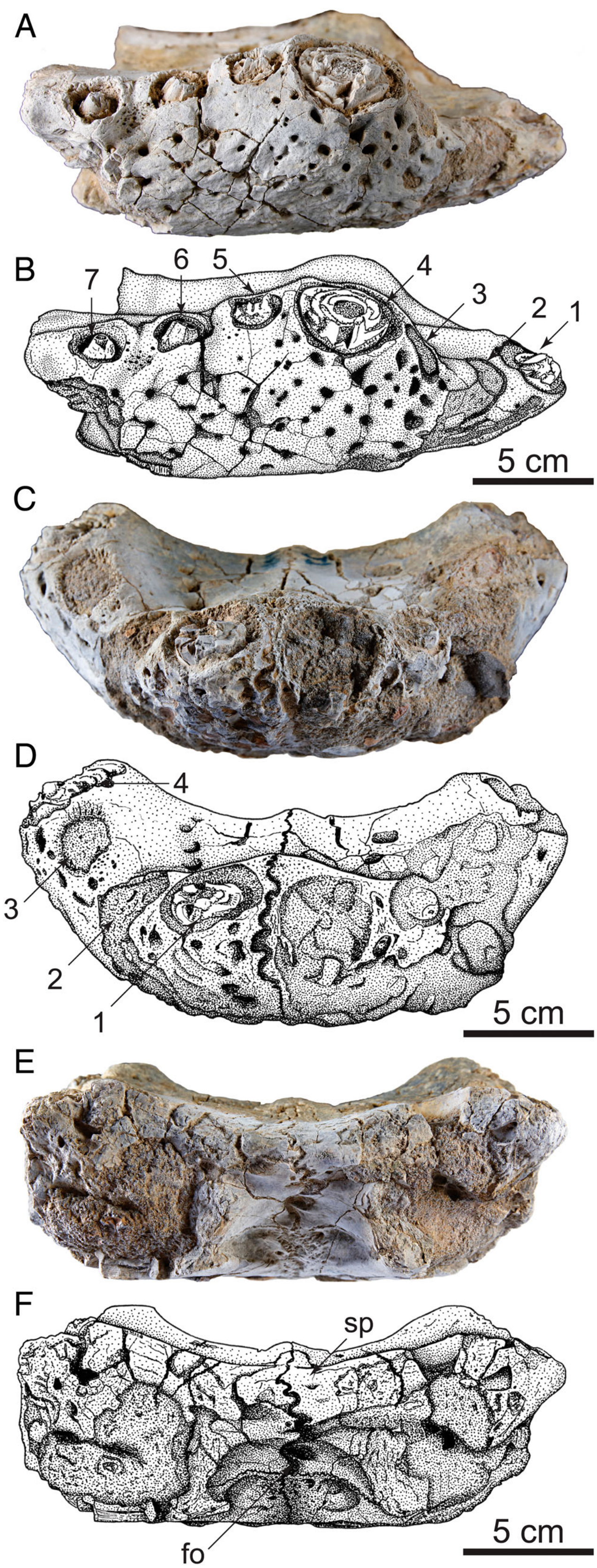

FIGURE 3. Photographs and associated drawings of UM-DB-LCJ1-02, mandibular rostrum of *Astorgosuchus bugtiensis*, comb. nov., from the upper Oligocene of the Bugti Hills, Pakistan, in **A**, **B**, right lateral, **C**, **D**, anterior, and **E**, **F**, posterior views. Numerals denote the alveolar number. **Abbreviation**: **fo**, foramen; **sp**, splenial.

DB-LCJ1-02. For these reasons, our description focuses on UM-DB-LCJ1-02.

Specimen UM-DB-LCJ1-02 preserves each dentary from the first to the seventh dentary alveolus. Several cracks run through the specimen, the anterior-most edge of the left dentary is slightly worn, some of the ventral surface of the right dentary is eroded, and teeth have been broken away with only roots remaining in some alveolar positions. The specimen has not undergone deformation, and the left and right rami are symmetrical. The lateral surface of the dentary is profusely ornamented with deep circular foramina. They are sparsely distributed and slightly larger on the ventral surface.

The robust mandibular rostrum is slightly longer than wide, giving to it a general spoon-shaped appearance when viewed dorsally (Figs. 2, 3). Anterior to the largest alveoli, the outline of the rostrum forms an isosceles triangle in dorsal view, whereas the lateral margins behind the largest alveoli are parallel to each other. The dentaries meet medially from the level of the first to fifth alveoli. As observed in occlusal view, the mandibular symphysis is strongly serrated and it forms a median ridge, which stops at the level of the adjoining anterior splenial processes.

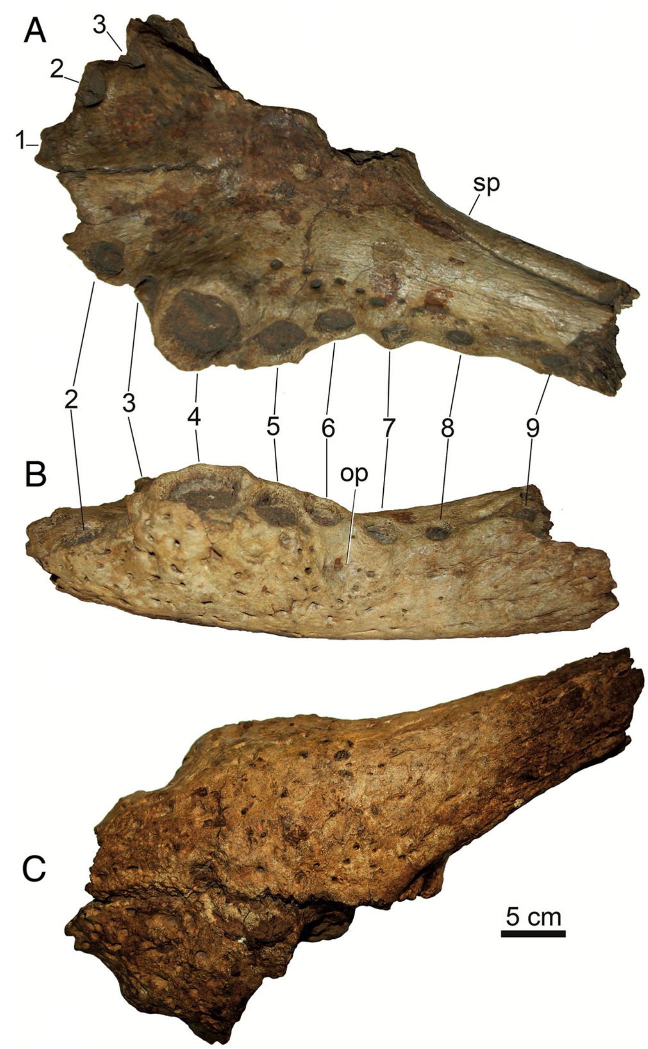

FIGURE 4. Photographs of the partial mandibular rostrum of NHMUK R.5266, *Astorgosuchus bugtiensis*, comb. nov., from the Oligocene of the Bugti Hills, Pakistan, in **A**, occlusal, **B**, left lateral, and **C**, ventral views. Numerals denote the alveolar number. **Abbreviations**: **op**, occlusal pit; **sp**, splenial.

TABLE 1. Alveolar dimensions (in mm) of UM-DB-LCJ1-02, the dentary of *Astorgosuchus bugtiensis.*

Dentary alveolus	Left AP length	Left ML length	Right AP length	Right ML length
1	34[a]	33[a]	33	30
2	22	21	24[a]	?
3	—	—	25	23
4	46	42	44	44
5	24	23	23	20
6	23	20	22	17
7	23	20	19	19

Abbreviations: **AP**, anteroposterior; **ML**, mediolateral.
[a]Damaged alveolar border.

The splenials penetrate the mandibular rostrum in the shape of an inverted 'Y' process; their anterior two-thirds running nearly parallel to the outer mandibular margin. Here, the occlusal surface of the splenials is faintly concave. The portion of the splenials contributing to the mandibular rostrum extends posteriorly to a point level with the sixth and seventh dentary alveoli. The splenials do not contribute to the ventral surface of the mandible. As seen in posterior view, their dorsal margin forms a shelf in the mandibular rostrum. Below this shelf, the splenials enclose the small meckelian foramen, which opens posteroventrally (Fig. 3E, F).

Alveolar dimensions are presented in Table 1. All preserved dentary alveoli are nearly circular in outline (Figs. 2A, B, 3A, B). The first alveolus faces anterodorsally and seems to have hosted a procumbent tooth. The first right alveolus hosts a broken tooth root, which is markedly curved. The second alveolus is slightly smaller than the first and is separated from it by less than a centimeter. It is also anterodorsally directed. A 2-cm diastema separates the second from the third alveolus. The third alveolus opens on the anterior everted surface of the large fourth alveolus, the two alveoli being contiguous but not confluent. The fourth alveolus is the largest of all preserved alveoli, and it projects in a dorsolateral direction. Its lingual alveolar wall bulges along the occlusal surface of the mandibular rostrum. The fifth alveolus is much smaller and is also contiguous with the fourth alveolus, its dorsal margin protruding at the same level as the fourth alveolus. The sixth and seventh alveoli open at the level of the main occlusal surface of the dentary and are of about the same size. They are separated from each other, with the seventh alveolus possessing a distinct outline along the lateral border of the dentary. Occlusal pits occur on the lateral margin of the dentary between the sixth and seventh alveoli. The medial margin of the dentary tooth row is pierced by numerous foramina of variable dimensions. The largest (about 13 mm in diameter) are observed at the level of the diastema between the second and third alveoli as well as medial to the fourth through sixth alveoli. A single tooth crown is preserved in the left third dentary alveolus of NHMUK R.5266 (Fig. 4). Despite a circular cross-section, the crown is heavily worn and no features of the enamel can be described.

TABLE 2. Maximum total body length (TBL) of crocodylomorphs surpassing 7 m, sorted stratigraphically from oldest to youngest.

Age	Taxon	Estimated TBL	Reference
early Cretaceous	*Chalawan thailandicus*	7–8 m	Martin et al., 2014
Aptian–Albian	*Sarcosuchus imperator*	11–12 m	Sereno et al., 2001
Cenomanian	*Stomatosuchus inermis*	10 m	Stromer, 1925
Campanian	*Deinosuchus* sp.	9.1 m	Erickson and Brochu, 1999
early Eocene	*Phosphatosaurus gavialoides*	9 m	Buffetaut, 1979
late Oligocene	*Astorgosuchus bugtiensis*	8 m	This study
late Miocene	*Mourasuchus mirandai*	11.5 m	Aguilera et al., 2006
Miocene	*Purussaurus brasiliensis*	12.5 m	Aureliano et al., 2015
Mio-Pliocene	*Gryposuchus croizati*	10.15 m	Riff and Aguilera, 2008
Mio-Pliocene	*Rhamphosuchus crassidens*	8–11 m	Head, 2001
Pleistocene	*Crocodylus thorbjarnarsoni*	7.6 m	Brochu and Storrs, 2012
Pleistocene	Kali Gedeh *Crocodylus*	7 m	Delfino and De Vos, 2013

DISCUSSION

Pilgrim (1908, 1912) was the first to describe and name several crocodylian species from the Bugti Hills, including a number of longirostrine forms (Martin, 2018). With these remains, Pilgrim (1908) erected *Crocodilus bugtiensis*, which was later described (Pilgrim, 1912) and represented by a portion of the rostrum (IM E221) from Pishi Nala near Dera Bugti. Although no overlapping material exists to relate the skull material described by Pilgrim (1912) with the mandibular material described above, we consider all these specimens to represent a single species for the following reasons: first, IM E221, NHMUK R.5266, and UM-DB-LCJ1-02 are all of large dimensions (i.e., skull length estimated over 80 cm; Appendix 1) and all retain characters of the Crocodyloidea, as explained in the paragraph below. The skull (IM E221), as well as the two mandibles described here, points to an animal with a remarkably broad cranium (Appendix 1; Pilgrim, 1912). The morphology of the maxillary and dentary tooth rows shares the same pattern of occlusion. Among crocodylians, at the level of the premaxillary-maxillary suture, a marked notch on the lateral margin of the rostrum always accommodates an enlarged dentary tooth of the anterior part of the lower jaw. Compatible with the deeply excavated premaxillary-maxillary notch, the mandibular specimens described herein show a distinctly enlarged fourth dentary tooth that was occluding at this level. Finally, the enlarged fifth maxillary tooth occludes laterally at the level of the sixth to seventh dentary alveoli, where an occlusal pit is clearly visible in NHMUK R.5266.

In light of these observations, we view all these three specimens as conspecific. The generic name '*Crocodilus*' has traditionally been applied to a variety of fossil crocodylians with a 'generalized non-alligatorid-like' morphology (Delfino et al., 2007). The new taxon from the Bugti Hills cannot be assigned to the genus *Crocodylus* or to any members of the Crocodylinae because of the significant posterior extent of the external nares and because its splenial is involved in the mandibular symphysis. For these reasons, we propose the name *Astorgosuchus bugtiensis* as a new combination for the Bugti crocodylian represented by IM E221, NHMUK R.5266, and UM-DB-LCJ1-02.

The fragmentary nature of *Astorgosuchus bugtiensis* does not facilitate a clear taxonomic attribution beyond Crocodyloidea. Although we did not examine the holotype firsthand, we view IM E221 as a large crocodyloid, as evidenced by its enlarged fifth maxillary alveolus (Pilgrim, 1912:pl. 26). The presence of an enlarged fourth dentary alveolus is plesiomorphic and observed in alligatorines, caimanines, and crocodyloids. The most notable character is the participation of the splenial in a relatively short mandibular symphysis, which extends posteriorly to a point level with the seventh dentary alveoli. This character is not encountered in basal eusuchians or alligatoroids, nor in any

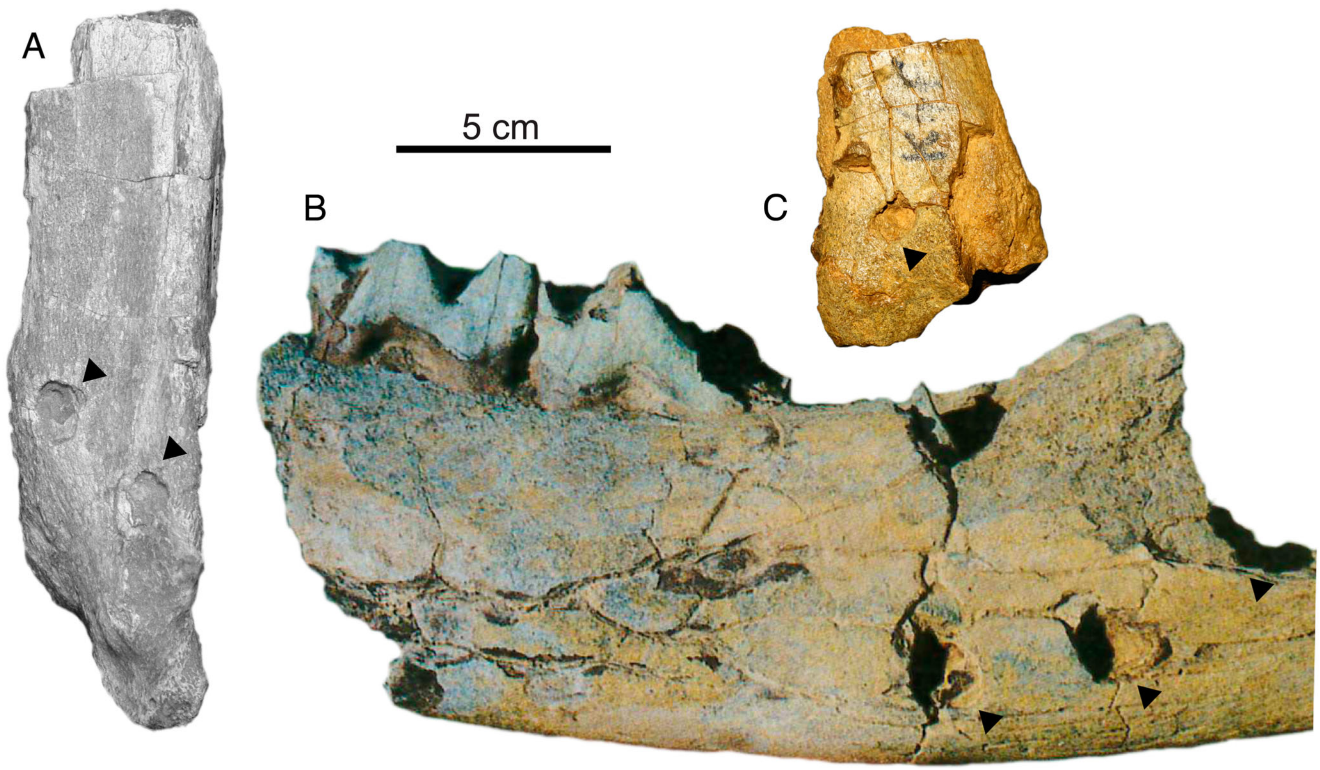

FIGURE 5. Selected perissodactyl specimens from the upper Oligocene–lower Miocene deposits of the Bugti Hills, Pakistan, presenting tooth marks attributable to large crocodylomorphs. **A**, cf. *Rhinoceros* sp. (MNHN-Pak 2221 field number), distal fragment of a left ulna, in anterior view (DB6 locality, early Miocene). **B**, *Paraceratherium bugtiense*, juvenile jaw, in lingual view (Lundo Chur J2 locality, upper Oligocene). **C**, Chalicotheriidae indet. (MNHN-Pak 1715 field number), fragmentary right tibia, in posterior view (Kumbi 4F locality, earliest Miocene). Black arrows denote crocodylomorph tooth marks.

short-snouted basal eusuchians. In contrast, deep splenial participation in the mandibular symphysis is observed in longirostrine forms, such as tomistomines and gavialids, where the mandibular symphysis is extensive and encompasses most of the mandibular length, a condition not approached in *A. bugtiensis*. In alligatoroids, the mandibular symphysis extends posteriorly to the level of the fourth dentary alveolus. In crocodyloids, the symphysis is slightly more elongate, extending posteriorly to a point level with the fifth alveolus. In some extinct crocodyloids, such as species of the mekosuchine *Kambara* from Australia (Salisbury and Willis, 1996) or the basal crocodyloids '*Crocodilus*' *depressifrons* from Europe (Delfino and Smith, 2009) and *Asiatosuchus* (Mook, 1940; Berg, 1966), the symphysis extends to the level of the sixth or seventh alveolus. In *Kambara* and '*C.*' *depressifrons*, however, the splenials do not participate in the mandibular symphysis, although they approach it. Mook (1940) describes the splenial in *Asiatosuchus grangeri* as almost approaching the symphysis but not actually doing so. The taxon most closely resembling *A. bugtiensis* is *Asiatosuchus germanicus*, in which the splenials are slightly involved in the symphysis (Berg, 1966), but admittedly, *A. bugtiensis* displays a stronger splenial involvement in the symphysis, reaching the sixth dentary alveoli. Although the precise placement of *A. bugtiensis* in a phylogenetic framework is beyond the scope of this study, we view *A. bugtiensis* as a probable basal crocodyloid close to *As. germanicus* in light of the following shared characters: mandibular symphysis extending to the level of the seventh alveolus; participation of the splenial in the mandibular symphysis; diastema between the second and third alveoli; and enlarged fourth alveolus. *Astorgosuchus bugtiensis* differs from *As. germanicus* in the relative dimensions of the fourth alveolus relative to the much smaller fifth dentary alveolus, and in its more extensive participation of the splenial in the mandibular symphysis. *Astorgosuchus bugtiensis* is recovered in much younger strata (Oligocene) than *As. germanicus*, which is Lutetian in age (i.e., middle Eocene). Although the affinities of the *Asiatosuchus*-like taxa remain unclear (Delfino and Smith, 2009), *A. bugtiensis* will require more complete specimens for its affinities to be assessed.

Total body length (TBL) of *Astorgosuchus bugtiensis* is estimated using mandibular width at the level of the largest dentary alveolus. A regression equation using skull and mandibular measurements of 13 individuals of the genus *Crocodylus* (Appendix 1) allowed us to estimate skull lengths for *A. bugtiensis* of 80 and 91 cm for UM-DB-LCJ1-02 and NHMUK R.5266, respectively. Measurements taken on a large series of *Crocodylus porosus* have demonstrated that the skull becomes shorter relative to the body length during ontogeny (Fukuda et al., 2013, and references therein). For this reason, the total length versus head length ratio (TL/HL) changes from 1:7 to well over 1:8 for *C. porosus* individuals with a skull length around 60 cm (Fukuda et al., 2013). Using a 1:8 ratio would result in a minimum TBL estimate for *A. bugtiensis* of 6.4 m for UM-DB-LCJ1-02 and of 7.3 m for NHMUK R.5266. A TL/HL of 1:8.8 was established for the longest *C. porosus* ever measured, which possesses a skull length of 70 cm (Britton et al., 2012), which is significantly smaller than the skull length estimated above for *A. bugtiensis*. Here, applying this ratio gives a TBL of 7 m for UM-DB-LCJ1-02 and of 8 m for NHMUK R.5266. Estimates should be taken with caution, but one can reasonably consider probable that the largest representatives of *A. bugtiensis* approached or surpassed 8 m in TBL (Fig. S1 in Supplemental Data).

The estimated size of adult *A. bugtiensis* falls in the range of other large fossil *Crocodylus* (Brochu and Storrs, 2012; Delfino and De Vos, 2014). The fossil record offers repeated instances of gigantism among semiaquatic crocodylomorphs (Table 2), and based on cranial material, the largest exemplars could be estimated to surpass a TBL of 10 m (Head, 2001; Sereno et al., 2001; Aguilera et al., 2006; Riff and Aguilera, 2008). *Astorgosuchus bugtiensis* was retrieved in the same fluviolacustrine deposits as the large tomistomines '*Gavialis*' *curvirostris* and '*Gavialis*' *breviceps* (Pilgrim, 1908, 1912; Martin, 2018). Both '*Gavialis*' taxa cooccur with several megaherbivores, such as rhinocerotoids and chalicotheriids among perissodactyls, anthracotheriid artiodactyls, and proboscideans (Antoine et al., 2003, 2004, 2013; Métais et al., 2009a; Lihoreau et al., 2017). Indeed, predator-prey interactions due to crocodylians are recorded on a wide array of mandibular and postcranial remains of rhinocerotoids, including the gigantic rhinocerotoid *Paraceratherium bugtiense*. The jaw of a juvenile specimen referred to as *P. bugtiense* has several large conical unhealed bisected tooth marks (Fig. 5B) unambiguously left by a giant crocodylian (compare with Njau and Blumenschine, 2006), as for several postcranial remains of *P. bugtiense*, rhinocerotoids, and chalicotheriids (Fig. 5), which would support the conspicuous nature of such predator-prey interactions at those times. Nevertheless, it is not possible to differentiate between tooth marks inflicted by *A. bugtiensis* or by other large tomistomines due to their similar tooth morphology. Presumably, these different crocodylians inhabited the same streams but did not share the same microhabitats, as is possibly the case today in India with gharials and muggers (Da Silva and Lenin, 2010) or as previously discussed for various Mesozoic and Cenozoic aquatic habitats where both mesorostrine and longirostrine forms have been described (e.g., Salas-Gismondi et al., 2015; Martin et al., 2016; Souza et al., 2016). Whatever the predator-prey interactions, this ecosystem is remarkable for the gigantic sizes attained by several of its organisms, calling for further investigation of the underlying evolutionary mechanisms accounting for increase in body size.

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APPENDIX 1. *Crocodylus niloticus* skull measurements (in cm) used in a regression equation to derive total body length of *Astorgosuchus bugtiensis* (Fig. S1). **A**, skull length from tip of snout to posterior edge of cranial table; **B**, width at level of the fourth dentary alveolus including both mandibular rami.

Specimen number	Taxon	A	B
MHNL50.001389	*Crocodylus porosus*	39	8.6
MHNL50.001387	*Crocodylus* sp.	47	9.6
MHNL50.001390	*Crocodylus porosus*	44	9.7
MHNL50.001392	*Crocodylus* sp.	45	10.4
MHNL50.001397	*Crocodylus niloticus*	45.4	9.8
MHNL50.001394	*Crocodylus niloticus*	41.3	9.6
MHNL50.001399	*Crocodylus niloticus*	36.7	7.1
MHNL50.001398	*Crocodylus* sp.	48.2	13.2
MHNL50.001404	*Crocodylus* sp.	56.4	13.3
MHNL50.001403	*Crocodylus* sp.	52.8	13
MHNL50.001402	*Crocodylus porosus*	53.4	11.4
NHMUK 47.3.5.33	*Crocodylus porosus*	71.8	18
UM-DB-LCJ1-02	*Astorgosuchus bugtiensis*	See Fig. S1	20.4
NHMUK R.5266	*Astorgosuchus bugtiensis*	See Fig. S1	23.6