Journal of Vertebrate Paleontology 25(4):888–896, December 2005
© 2005 by the Society of Vertebrate Paleontology

NEW INFORMATION ON THE SKULL OF THE ENIGMATIC THEROPOD *SPINOSAURUS*, WITH REMARKS ON ITS SIZE AND AFFINITIES

CRISTIANO DAL SASSO[1], SIMONE MAGANUCO[2], ERIC BUFFETAUT[3], and MARCO A. MENDEZ[4]
[1] Museo Civico di Storia Naturale di Milano, Corso Venezia 55, 20121 Milano, Italy, cdalsasso@yahoo.com;
[2] Museo Civico di Storia Naturale di Milano, Corso Venezia 55, 20121 Milano, Italy, simonemaganuco@iol.it;
[3] CNRS, 16 cour du Liégat, 75013 Paris, France, eric.buffetaut@wanadoo.fr;
[4]University of Chicago, Department of Organismal Biology and Anatomy, 3424 W 54th Street, Chicago, IL 60632, USA, mamendez@uchicago.edu

ABSTRACT—New specimens of the unusual theropod *Spinosaurus* cf. *S. aegyptiacus* from the Late Cretaceous (early Cenomanian) of Morocco reveal new information about the structure of the snout and the very large adult body size attained by the species. The external naris is retracted farther caudally on the snout than in other spinosaurids and is bordered exclusively by the maxilla and nasal. The fused nasals preserve a longitudinal, fluted crest. The size of the snout suggests that *Spinosaurus* may well have exceeded the maximum adult body size of other large Cretaceous theropods such as *Tyrannosaurus* and *Giganotosaurus*. The new material also supports the monophyly of the Spinosaurinae and the separation of *Spinosaurus* and *Irritator*.

INTRODUCTION

In 1912, Ernst Stromer discovered several bones of a large, long-snouted, sail-backed predator from the Cenomanian of Baharija (Egypt) that he named *Spinosaurus aegyptiacus* (Stromer, 1915). Unfortunately, this material was destroyed during an air raid in the Munich bombing of April 1944 (Taquet, 1984; Taquet and Russell, 1998; Sereno et al., 1998). Although remains have been described subsequently from Morocco (Buffetaut, 1989; Russell, 1996), Tunisia (Bouaziz et al., 1988; Buffetaut and Ouaja, 2002) and Algeria (Taquet and Russell, 1998), none of them have significantly furthered knowledge about this unusual theropod. In the present paper, we describe specimens referable to *Spinosaurus* cf. *S. aegyptiacus* that provide new information on its anatomy, size, and relationships.

Fossil Location and History

MSNM V4047—Specimen MSNM V4047, now housed in the collections of the Museo di Storia Naturale di Milano (MSNM V4047), was found in southern Morocco in 1975 and remained in a private collection until 2002. The specimen was reported to have been found east of the town of Taouz, within the red beds underlying the Hammada du Guir plateau, and more precisely in the area called Kem Kem. More specific field data were not recorded but sediment adhering to the bone is closely consistent with the Kem Kem red sandstone both in colour, composition, and texture. An isolated fish vertebra associated with the specimen is embedded between the right second premaxillary alveolus and its erupting tooth and can be tentatively referred to ?*Onchopristis* sp. (Stromer, 1926:taf I, fig. 7), a sawfish that is very abundant in the Kem Kem beds.

UCPC-2—Specimen UCPC-2 (University of Chicago Paleontological Collection) was discovered in the Kem Kem beds in Northern Morocco (Location: N30° 02′ W 5° 12′, near the outpost in Keneg ed Dal) during the 1996 expedition led by Dr. Sereno (University of Chicago). The expedition produced a myriad of fossils from river washes, one being a partially eroded pair of fused nasals preserving a fluted crest. Initially thought to be an unidentifiable fragment, the specimen remained within the collection cases at the University of Chicago until 2002. It was then re-evaluated thanks to its multiple key characteristics that suggested spinosaur affinities.

Horizon—On the basis of stratigraphical and paleontological evidence (Wellnhofer and Buffetaut, 1999), the Kem Kem “Continental Red Beds” (Russell, 1996) can be referred to the early Cenomanian.

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
SPINOSAUROIDEA Stromer, 1915, sensu Sereno et al., 1998
SPINOSAURIDAE Stromer, 1915, sensu Sereno et al., 1998
SPINOSAURUS cf. *S. AEGYPTIACUS* Stromer, 1915

Comments—The genus *Spinosaurus* was erected in 1915 by Stromer (1915), with *Spinosaurus aegyptiacus* as type species, on the basis of an incomplete skeleton, including a dentary and long-spined dorsal vertebrae. Rauhut (2003) questioned this association, claiming that the dorsal vertebrae lack the strong pneumatization and laminae of the Baryonychinae and instead are comparable to the dorsal vertebrae of the Allosauroidea. The absence of these derived vertebral features in *Spinosaurus*, however, may represent a plesiomorphic feature shared by *Spinosaurus aegyptiacus* and the Allosauroidea. Consequently, we regard the cranial material and the tall-spined dorsal vertebrae of the type material (Stromer, 1915) as belonging to the same individual. A second species of *Spinosaurus*, *S. maroccanus*, was erected by Russell (1996). The holotype of *S. maroccanus* is based on inadequate material: a single cervical vertebra thought to be distinguishable from *S. aegyptiacus* by its “relatively greater central and neural arch length” (Russell, 1996:fig. 9). Rauhut (2003) attributed this difference to the more rostral position of the vertebra in the cervical series. Similarly, in our opinion, the attribution of a snout from Algeria to *S. maroccanus* (Taquet and Russell, 1998) cannot be supported. For all these reasons we regard *S. maroccanus* as a nomen dubium, following Sereno et al. (1998). The only other specimens of *Spinosaurus* for which skull material is known are the type specimen of *S. aegyptiacus*, which includes a piece of maxilla with four alveoli (not figured but described by Stromer [1915]), and a referred maxillary fragment described by Buffetaut (1989). *S. aegyptiacus* is the only species of *Spinosaurus* that we regard as valid and to which we refer the new specimens MSNM V4047 and UCPC-2. Firsthand comparison of the craniodental material previously referred to *Spinosaurus* (isolated teeth [Bouaziz et al., 1988]; maxilla fragment [Buffetaut, 1989]; snout [Taquet and Russell, 1998]; dentary fragment [Buffetaut and Ouaja, 2002]) with that of MSNM V4047 and UCPC-2 do not reveal significant differences within this genus. At present there is no evidence for the occurring of more than one species of *Spinosaurus* in the Albian-Cenomanian of North Africa.

DESCRIPTION

Specimen MSNM V4047

MSNM V4047 consists of a large snout, 988 mm long, preserved from the tip of the rostrum to the rostral portion of the antorbital fenestra. It includes both of the premaxillae and maxillae and the rostral part of the nasals, all well preserved in three dimensions (Fig. 1).

Premaxillae—The conjoined premaxillae form a long and slender rostrum that belongs to a mature animal, as shown by the fact that the sagittal suture is fused dorsally, and is clearly visible only at the rostral end. The tip of the rostrum bears numerous enlarged pits (neurovascular foramina) on its outer wall (Fig. 2A) and forms a spatulate terminal rosetta, emphasized caudally by deep emarginations. In dorsal and in ventral view, this rosetta is almost circular in outline, whereas in *Baryonyx* (Charig and Milner, 1997) and *Suchomimus* (Sereno et al., 1998) it is more oval in shape, gradually tapering caudally. Caudal to the rosetta, the articulated premaxillae taper, never exceeding a width of 80 mm. At the level of the external nares they measure only 29 mm in width. In ventral view, the medial portions of the premaxillae form a pair of elongate but massive elements ("stout ridges" in Charig and Milner, 1997:16), which are clearly divided from the lateral dentigerous portions by a premaxillary groove. Rostrally, the two elements meet medially with a strongly interdigitate median suture, about 60 mm long, whereas caudally they are separated by a narrow, deep, median gap. Contrary to the premaxillae referred to *Spinosaurus maroccanus* (Taquet and Russell, 1998), which bear 7 alveoli, MSNM V4047 bears 6 alveoli on each side. It is questionable whether varying premaxillary tooth count can be regarded as a diagnostic feature. In *Baryonyx* (Charig and Milner, 1997) there are 6 teeth on the left and 7 on the right premaxilla. In MSNM V4047, alveolus 1 is much smaller than its counterpart in the Baryonychinae, whereas it is comparable to that of *S. maroccanus* and to that of *Angaturama* (Kellner and Campos, 1996); alveoli 2 and 3 are the largest; alveoli 4 and 5 are coupled and separated from the other premaxillary teeth by two short diastemata. A third larger, asymmetrical diastema (up to 76 mm on the right side) is present between alveolus 6 and the maxillary teeth. All the alveoli having a diameter less than 35 mm (measurement that approaches the maximum width of the premaxillary dentigerous portion) are circular. This width represents a constraint that forced the largest alveoli (left 2 and right 2 and 3) to grow farther along their mesiodistal axis and to become slightly compressed labiolingually. The preserved portions of the tooth crowns (left 3 and right 3) closely resemble the teeth previously assigned to *Spinosaurus* (Stromer, 1915; Bouaziz et al., 1988), both being nearly straight, elongate, conical, and sub-circular in transverse section. In lateral view, the dentigerous margin of the premaxilla resembles *S. maroccanus* (Taquet and Russell, 1998) in being strongly downturned towards the tip, such that the front of the rostrum is not elevated above the line of the maxillary tooth row, as in *Baryonyx* (Charig and Milner, 1997), *Suchomimus* (Sereno et al., 1998), and *Angaturama* (Kellner and Campos, 1996). In the diastema region, the rostrum has a sub-oval cross section with minimum circumference of 303 mm; the dentigerous margin is smoothly concave and, at scale, seems to fit on the convex dorsal margin of the rostral portion of the dentary figured by Stromer (1915:taf I, fig. 12a). As in *S.* "*maroccanus*" (pers. obs.), the lateral wall of the diastema region is marked by three depressions. Judging by Stromer's figures (1915:taf I, fig. 12b) we can infer that the rostral portion of the dentary of *Spinosaurus* was mediolaterally wider than its premaxillary counterpart (the diastema region), so that the largest dentary teeth (2–4) were visible when the jaws closed, occupying the above-mentioned three depressions.

Maxillae—Due to the intimate rostral intrusion of the laminar rostromedial processes of the maxillae (see below), the premaxillary-maxillary connection is very complex. In lateral view, the rostral margin of the maxillae rises caudally at some 40 degrees from its tip to the level of the second maxillary alveolus. Above the third maxillary alveolus, the two bones interlock via two peg-like processes, immediately below a foramen that is homologous with the subnarial foramen of other Saurischia. Caudal to the foramen, the maxillary margin curves and flattens to project horizontally along the ventral margin of the premaxilla. The lateral surface of each maxilla bears a complete row of large vascular foramina that runs parallel to the alveolar margin. In ventral view, a deep septum formed by two unfused vertical laminae (290 mm long) emerges from the thin median gap that divides the massive premaxillary median elements. Although some authors interpreted these laminae as the rostral portion of the paired vomers (Charig and Milner, 1997), these bones are not fused and must be regarded as rostromedial processes of the maxillae ("anteromedial processes of the maxillae" in Sereno et al., 1998). This is demonstrated by the fact that in MSNM V4047 there is a clear bone continuity, via a very thin caudal passage, between the laminae and the maxillary rami (Fig. 2B). The rostralmost portions of the rostromedial maxillary processes do not contact medially; thus, it is possible to see underneath the gap between the medial rami of the articulated premaxillae. The labial edges of the maxillae appear wavy and nearly parallel each other, with the caudal half only slightly wider than the rostral one. In ventral view, the lingual half of each maxilla appears to be divided from the labial half by a wavy groove. Because of the incompleteness of other spinosaurid taxa, this groove was interpreted as a suture and the lingual half of the maxilla was misinterpreted as a vomer (Taquet and Russell, 1998). Nonetheless, at a closer view of the broken caudal edges of each maxilla of MNSM V4047 in cross section (Fig. 2C), we see that the groove does not penetrate the bone. The maxillary grooves and their premaxillary continuations contain the resorption pits of the teeth that in turn expose several replacement teeth (Fig. 2E). On the medial wall of the labial half of the maxilla, some irregular rugose areas can be seen through the grooves. Those areas correspond to the not well-defined interdental plates of *Spinosaurus* cf. *S. aegyptiacus* (Buffetaut, 1989) and *S. maroccanus* (Taquet and Russell, 1998; pers. obs.). The maxillae meet broadly along the midline, forming a deep, acutely arched (35° to 40°) secondary palate that matches the subtriangular pattern of their outer wall. The vomers and the palatines are lacking, but the attachment areas of the latter are preserved at the level of the tenth alveolus as symmetrical scars on the caudomedial wall of the maxillae. Caudally, the maxillae are broken off at the contact with the jugals; on the right lateral side, the notch that received the forward-pointing maxillary process of the jugal can be seen (Fig. 2D). As a result of the fracture, only the rostral parts of the antorbital fossae and fenestrae are visible. The preserved part of the rostromedial wall of the antorbital fossa resembles that of *Suchomimus* in being confined to the rostral end of the antorbital fenestra (Sereno et al., 1998). The maxilla of MSNM V4047 additionally resembles that of *Suchomimus* (Sereno et al., 1998) in having a simple conical pneumatocoel that extends rostrally into the body of the maxilla. A complete series of 12 subcircular alveoli is preserved on both maxillae: they are nearly identical in shape and spacing to the maxillary alveoli in the other specimens

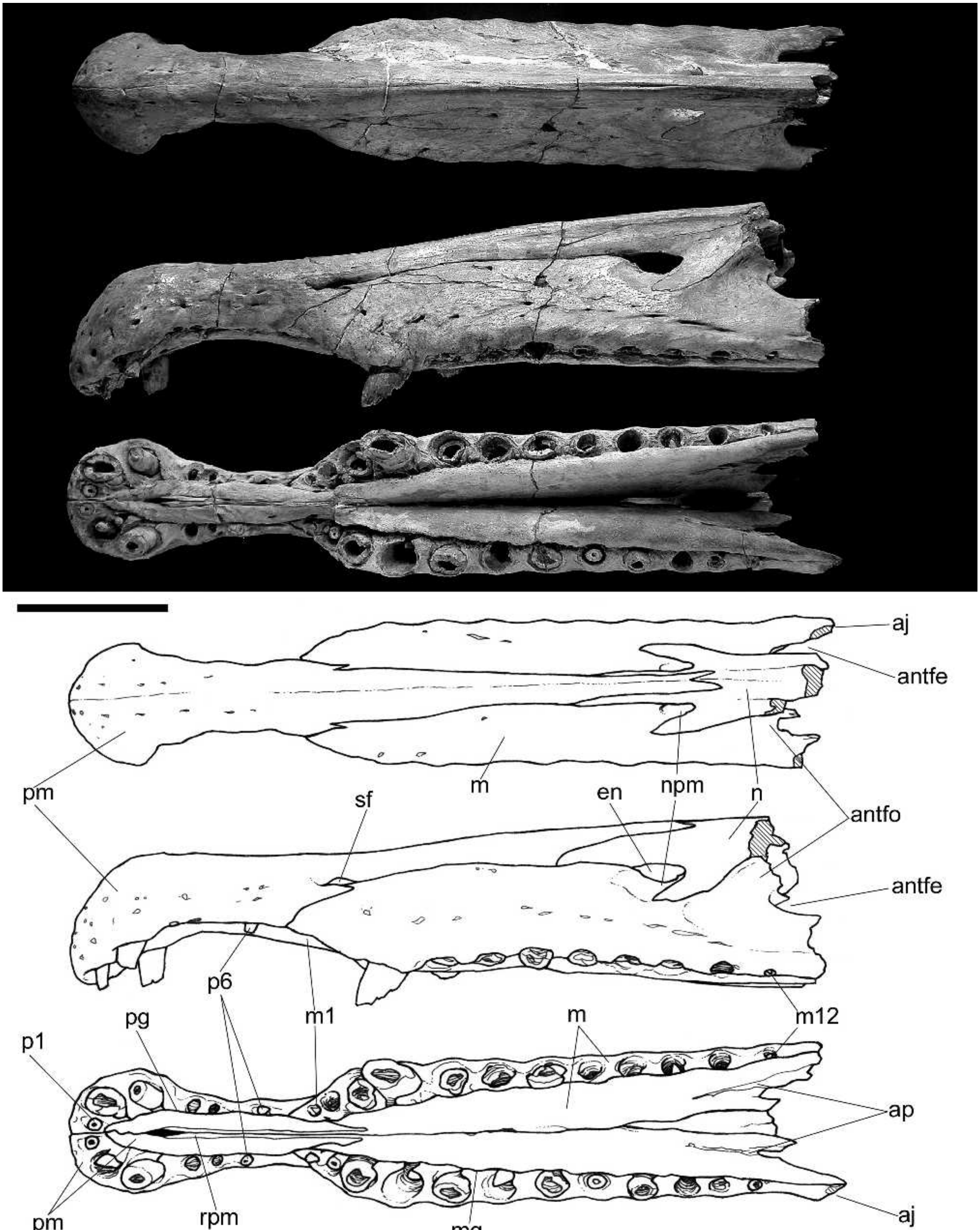

FIGURE 1. Photos and line drawings of MSNM V4047 in dorsal, lateral and ventral views. **Abbreviations**: **antfe**, antorbital fenestra; **antfo**, antorbital fossa; **aj**, articular surface for jugal; **ap**, articular surface for palatine; **en**, external naris; **m**, maxilla; **m1–12**, 1st–12th maxillary alveoli; **mg**, maxillary groove; **n**, nasal; **npm**, nasal process of maxilla; **p1–6**, 1st –6th premaxillary alveoli; **pg**, premaxillary groove; **pm**, premaxilla; **rpm**, rostro-medial processes of maxillae; **sf**, subnarial foramen. Scale bar equals 20 cm.

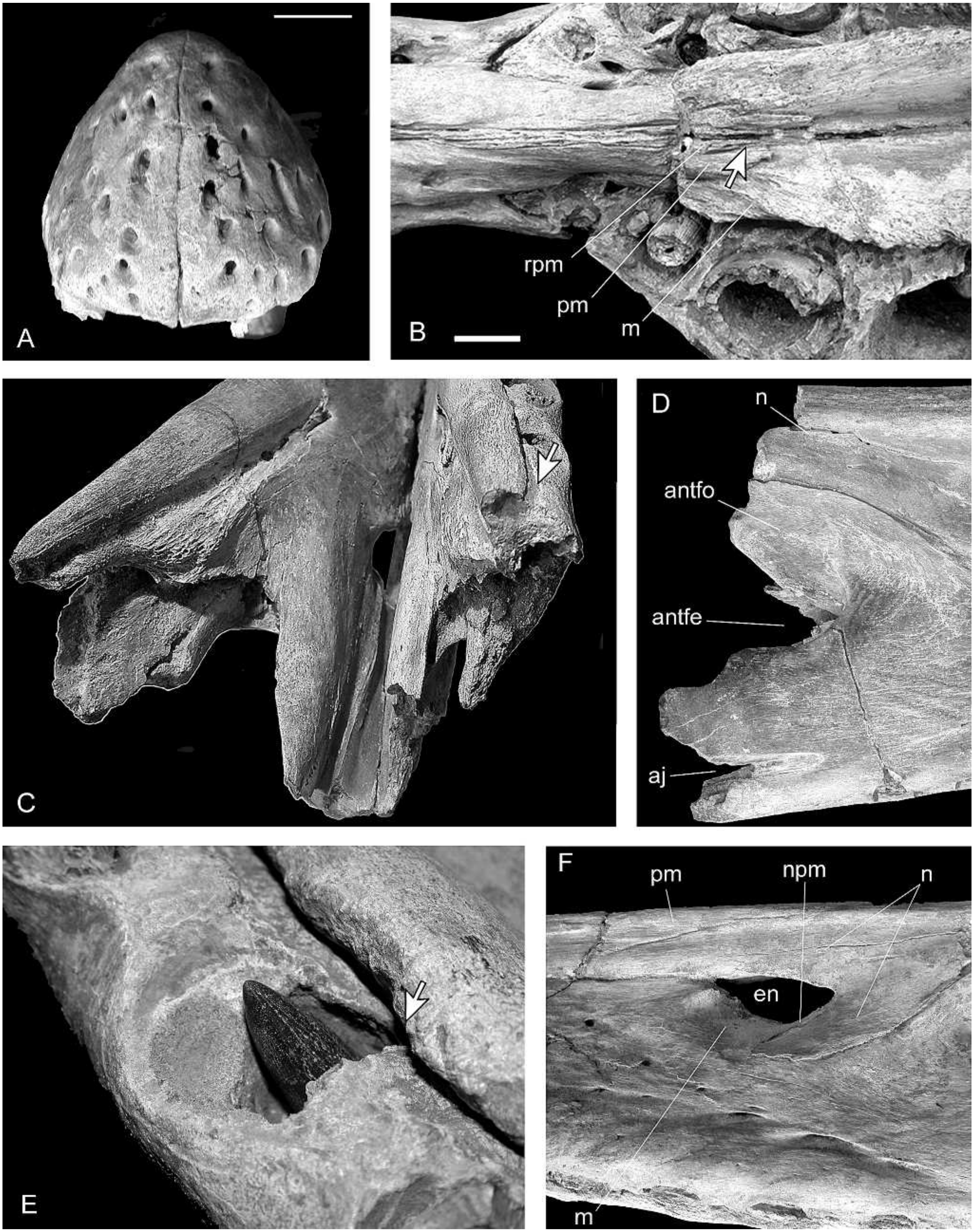

FIGURE 2. Close-ups of MSNM V4047. Abbreviations as in Figure 1. **A**, rostral view of the rostrum, showing the particularly developed pits emerging on the outer wall of the premaxillae. Scale bar equals 5 cm. **B**, ventral view of the specimen, showing the bone continuity (arrow) between the lingual halves of the maxillae and their thin rostro-medial processes. Scale bar equals 2 cm. **C**, cross section of the maxillae, viewed from upside down. Their caudal fracture highlights that the maxillary groove (arrow) does not penetrate the bone, thus it cannot be misinterpreted as a suture. **D**, right lateral view of the caudal portion of the snout, showing the preserved part of the antorbital fossa and fenestra, and the notch for the jugal attachment. **E**, right maxillary groove (arrow) with the erupting maxillary tooth 6. **F**, left external naris.

of *Spinosaurus* (Stromer, 1915; Buffetaut, 1989; Taquet and Russell, 1998). As in *S. maroccanus* (Taquet and Russell, 1998), their size increases abruptly from 1 to 4 (the basal circumference of the teeth increases from 42 mm to 146 mm), and decreases gradually from 5 to 12 (in *S. maroccanus* only alveoli 1 to 9 are preserved), resulting in an interdental gap that approaches in length the alveolar diameter toward the rear of the maxillae. Except for the replacement teeth and one fully grown tooth (left 4), the tooth crowns are missing or broken at their bases. The fourth left tooth crown is preserved from its base to one third of its reconstructed height, it also resembles the premaxillary teeth yet it is a bit more recurved. The roots are deeply implanted and converge medially, occupying almost the complete depth of the maxillae. As in the premaxillae, the largest teeth and alveoli (3 to 5 right and 3 to 4 left) were forced to grow compressed labiolingually by the width of the maxillae. The emerging tips of the replacement teeth are nearly straight, slightly flattened labiolingually and possess carinae lacking serrations. The thin enamel layer, where preserved, bears fine vertical ridges, denser lingually than labially: this fluting is variably present in some of the isolated teeth referred to *Spinosaurus* (Bouaziz et al., 1988).

External Nares—The external nares, which perforate the snout bilaterally, occur as a pair of openings that are remarkably small relative to the snout size and compared to those of other theropods (Rauhut, 2003). An autapomorphy of *Spinosaurus* revealed in this specimen is the position of the external nares, which are dramatically retracted to the level of maxillary alveoli 9–10. Unlike the condition in other dinosaurs (Sereno, 1999; Holtz, 2000), including baryonychines (Charig and Milner, 1997; Sereno et al., 1998) and perhaps *Irritator* (Sues et al., 2002), in MSNM V4047 the premaxilla does not bifurcate caudally to border the nasal cavity, but rather is completely excluded from its boundary (Fig. 2F). Uniquely, the entire concave ventral margin of each naris is formed by the main body of the maxilla and its thin, upturned nasal process, whereas the straight, dorsal margin is formed by the upper one of two finger-like, rostral rami of the nasal bone. This nasal ramus terminates rostral to the external naris, at the level of alveoli 7–8. The shape of the external naris is oval but terminates rostrally in an acute angle. According to Witmer (pers. comm.), *Spinosaurus* may have been similar to other tetrapods in having rostrally placed fleshy nostrils, situated in the rostral-most portion of the very subtle narial fossa extending from the external naris all the way rostrally up to the subnarial foramen. The complexity of this structure and other paleobiology-related features will be the basis of another investigation.

Nasals—The premaxillae taper caudally and meet a median spike of the nasals above the external nares. The preserved portion of the conjoined nasals is 280 mm long. In lateral view, the dorsal margin of the nasals projects horizontally as the morphological continuation of the narrow premaxillae, without any trace of a crest. However, the passage from the premaxillae to the nasals is marked, on the sagittal line, by an abrupt shift from an inverted U-shaped to an inverted V-shaped cross-section, suggesting that the inter-nasal suture might be the point of origin of a crested structure. The nasals of *Irritator* rise dorsally between the external nares and the antorbital fossa, whereas in the same position the nasals of MSNM V4047 have a straight dorsal margin.

Specimen UCPC-2

UCPC-2 (180 mm in length, 52 mm in width at its widest point, 62 mm in height at its apex; Fig. 3) consists of the caudal portion of a pair of conjoined narrow nasals articulated with a small fragment of a left maxilla. In lateral profile, the specimen preserves two peculiar characteristics: a ridge-like fluted crest and an inverted-V shape in at the rostral and caudal views. In right lateral profile (Fig. 3A, C) the specimen shows a smooth, non-eroded, surface. The rostral-most portion also preserves a strong sutural surface composed of horizontally oriented pores where the nasal would join the portion of the maxilla that borders dorsally the antorbital fenestra. Meanwhile, the caudal-most lower portion preserves another sutural surface that is slightly hidden by a curved protrusion and represents the attachment area for the rostral-most portion of the lachrymal. The shape of the rim formed by the nasal here is very much like the one in *Baryonyx* (Charig and Milner, 1997). The convex lateral surface of the nasal just above the sutural surfaces preserves fine longitudinal wrinkles. These wrinkles are similar to the surface texture on the bones of MSNM V4047, but are less dense. The convex lateral surface gradually becomes at first slightly curved and then vertical until it forms the real crest. This transitional point is characterized also by a change in surface texture from wrinkled to a smooth texture marked by shallow, elongate, and parallel depressions inclined caudally. Above this transitional surface there is a series of oscillating convex protrusions that form the right side of the fluted crest. The texture on the surface of the crest is very much like the lateral transitional surface below. This texture suggests the presence of highly vascularized soft tissue tightly bound to it (pers. obs. on extant comparative material). Nonetheless, erosion atop the crest does not allow for a distinct height measurement. As expected to be consistent with MSNM V4047, UCPC-2, in left lateral profile, shows a portion of the maxillary border of the antorbital fenestra without traces of the wall of the antorbital fossa. Also, the dorsoventral height of both the nasal and maxilla is consistent, at scale, with the ideal continuity of MSNM V4047.

In dorsal view, erosion has given way to insight into pneumatics of the nasal. At least 7 foramina that housed blood vessels are visible dorsally, each other apart, within the deep spongy bone. Each foramen appears to run deep into the bone but not through it and possibly forms a network within that may have regulated blood flow. The smooth medial surfaces of the two enclosing nasals indicate the presence of hollows within the crest. In ventral view (Fig. 3B, D), UCPC-2 resembles both MSNM V4047 and *Baryonyx* (Charig and Milner, 1997) in having a narrow, smooth and rather flat ventral surface. The surface also preserves two foramina that are longitudinally stretched over the rostral-most portion of the specimen. Additionally, there is a gradual expansion toward the caudal end of the fossil, where it would join with the frontal, a feature also evident in *Irritator* (Sues et al., 2002) and *Baryonyx* (Charig and Milner, 1997). Notably, a portion of co-ossified frontals figured by Russell (1996:fig. 18b) and referred to Theropoda indet. shows a ventral surface that would match perfectly the shape of UCPC-2. Considerably deep grooves form along the edge where the sutural surfaces occur with the maxilla and the lachrymal, as in *Baryonyx* (Charig and Milner, 1997). The rostral-most portion of the sutural surface of the lachrymal runs medial to the caudal-most portion of the one with the maxilla; this is particularly evident alongside the preserved left maxilla. In rostral and caudal (Fig. 3E, F) views, a key spinosaurid characteristic is visible, that of the inverted-V shape, which is also present in both MSNM V4047 and in the nasal fragments of *Baryonyx* (Charig and Milner, 1997). Unlike those of *Baryonyx*, however, the conjoined nasals of UCPC-2 apically form an inflated, hollow, and fluted crest. As mentioned above, since the bone has been eroded, its height and further morphology is not known. However, we believe the crest to be a single crest that expands but does not diverge. Additionally, the rostral-most portion of UCPC-2 resembles the shape of the caudal-most portion of the nasals of MSNM V4047, which preserves a slight lateral constriction at the apex that corresponds to a concave surface of UCPC-2. This makes for the transition between the nasal and the crest visible in Figure 5. Unlike *Baryonyx*, UCPC-2 does not have a thin parasagittal crest (Charig and Milner, 1997);

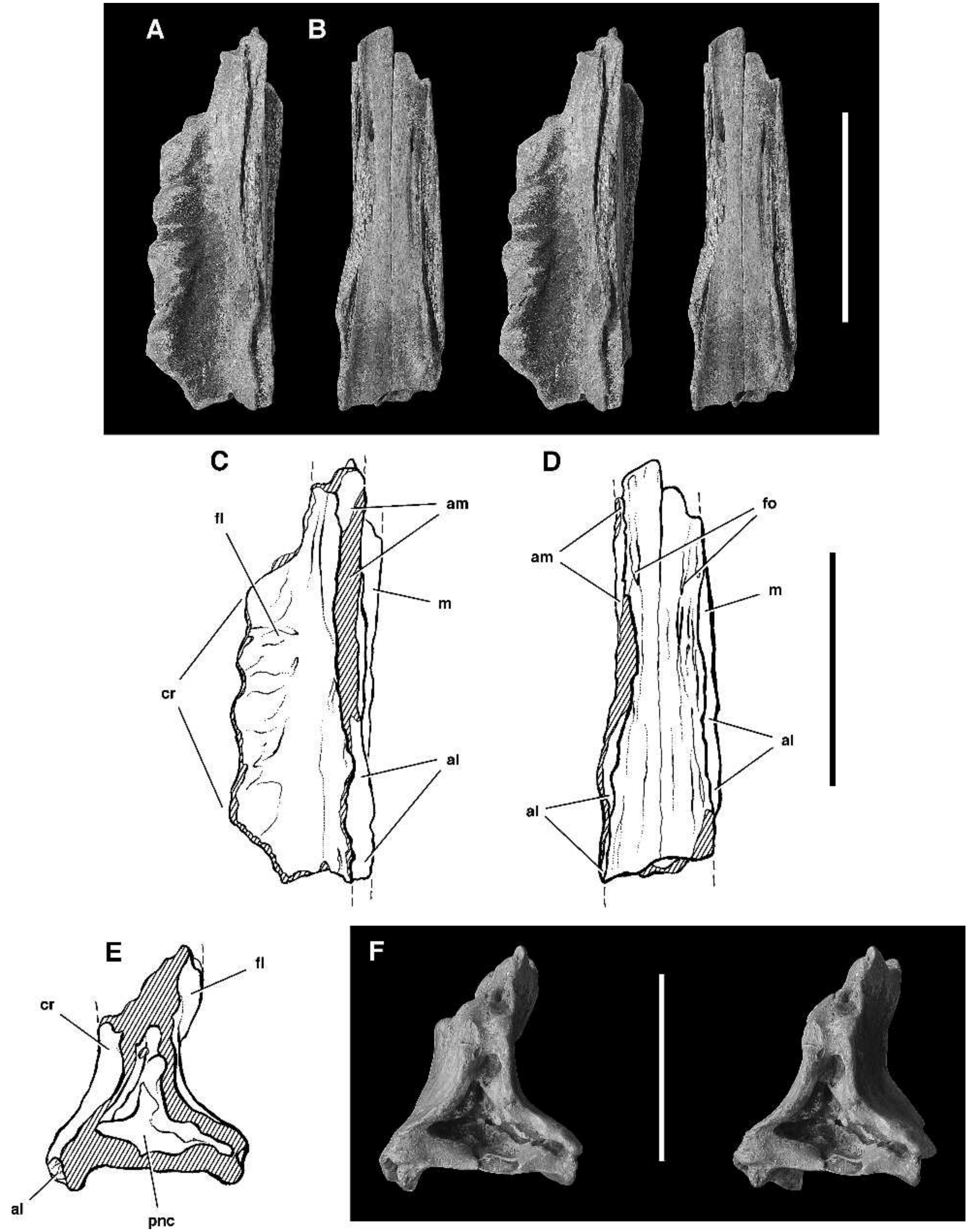

FIGURE 3. Stereophotographs (**A**, **B**, and **F**) and line drawings (**C**, **D**, and **E**) of the fused nasals UCPC-2. **A** and **C**, right lateral profile. **B** and **D**, ventral view. **E** and **F**, caudal view showing inverted V-shape. **Abbreviations**: **al**, articular surface for lachrymal; **am**, articular surface for maxilla; **cr**, crest; **fl**, fluted portion; **fo**, foramen; **m**, maxilla; **pnc**, pneumatic cavity. Scale bars equal 10 cm (**A**, **B**, **C**, and **D**) and 5 cm (**E** and **F**).

instead it is bulky and fluted with a presence of foramina. The only crested theropod that comes close to this specimen is *Irritator* (Sues et al., 2002). Sues et al. (2002) describe the crest of *Irritator* to be a single entity that stems from the inter-nasal suture. However, the skull of *Irritator* does not keep a level plane like that of *Spinosaurus*, but rather tapers rostrally and does not seem to have a fluted portion to the longitudinal crest. This level-plane character is key in assigning UCPC-2 to *S.* cf. *S. aegyptiacus*, which keeps a level plane as can be seen in both MSNM V4047 (Fig. 4) and *S. maroccanus* (Taquet and Russell, 1998).

TABLE 1. List of the spinosaurid specimens used in the comparison of craniodental features

Spinosaurinae	MSNM V4047 *Spinosaurus* cf. *aegyptiacus*
	UCPC-2 *Spinosaurus* cf. *aegyptiacus*
	IMGP 969-1 *Spinosaurus* cf. *aegyptiacus* (Buffetaut, 1989)
	MNHN SAM 124 *Spinosaurus maroccanus* (Taquet and Russell, 1998)
	USP GP/2T-5 *Angaturama limai* (Kellner and Campos, 1996)
	SMNS 58022 *Irritator challengeri* (Sues et al., 2002)
Baryonychinae	BMNH R9951 *Baryonxy walkeri* (Charig and Milner, 1986, 1997)
	MNHN GDF 366 *Cristatusaurus lapparenti* (Taquet and Russell, 1998)
	MNN GDF501 *Suchomimus tenerensis* (Sereno et al., 1998)

Institutional Abbreviations—MSNM, Museo di Storia Naturale di Milano; **UCPC**, University of Chicago Paleontological Collection; **IMGP**, Institut und Museum für Geologie und Paläontologie of the Georg-August-Universität (Göttingen); **MNHN**, Muséum National d'Histoire Naturelle (Paris); **USP**, Universidade de São Paulo; **SMNS**, Staatliches Museum für Naturkunde Stuttgart; **BMNH**, The Natural History Museum (London); **MNN**, Musée National du Niger (Niamey).

DISCUSSION

Specimen Affinities and Taxonomy

Baryonychinae and Spinosaurinae—The craniodental features of MSNM V4047 and UCPC-2 support recognition of the family-level taxon Spinosauridae Stromer, 1915, as defined and diagnosed by Sereno et al. (1998) and discussed by Sues et al. (2002). According to the phylogenetic analysis of the Spinosauridae by Sereno et al. (1998), within this derived clade of basal Tetanurae, two taxa have been recognized, the Baryonychinae and the Spinosaurinae. Herein, a comparison of previously described spinosaurid specimens (Table 1) with MSNM V4047 and UCPC-2 supports and strengthens the monophyly of the Spinosaurinae. We agree with Sereno et al. (1998) in recognizing some features of the snout that differentiate the Baryonychinae (premaxillary alveolus 1 slightly smaller in diameter than alveoli 2 and 3; curved tooth crowns; teeth with fine serrations) from the Spinosaurinae (premaxillary alveolus 1 less than one half of the diameter of alveoli 2 and 3; unserrated teeth; tooth crowns hardly curved or straight). By comparing the snouts (Fig. 4), we have found an additional difference between the Baryonychinae (external naris retracted to the first half of the maxillary tooth row) and the Spinosaurinae (external naris retracted farther caudally). The maxillary tooth count could be an additional distinctive feature, *Suchomimus* having 22 maxillary teeth and the Spinosaurinae 12 well-spaced maxillary teeth; however, the caudal portion of the maxilla in *Baryonyx* is not known, so the presence of a high number of maxillary teeth in the Baryonychinae can be inferred only on the basis of the strong resemblance of the lower jaws of both *Baryonyx* and *Suchomimus*, which bear more than 30 teeth (a clear autapomorphy of that taxon). Moreover, the external nares of the Baryonychinae seem to be larger than in the Spinosaurinae, but their exact size and shape cannot be established because in *Baryonyx* and *Suchomimus* the rostral portion of the nasals is missing. As mentioned in the description, the nasal crest of *Spinosaurus* clearly differs from that of *Baryonyx*. The features of the nasal crest may eventually characterize the Spinosaurinae, but the poor preservation in *Irritator* renders a diagnosis on the basis of this element impossible at the moment.

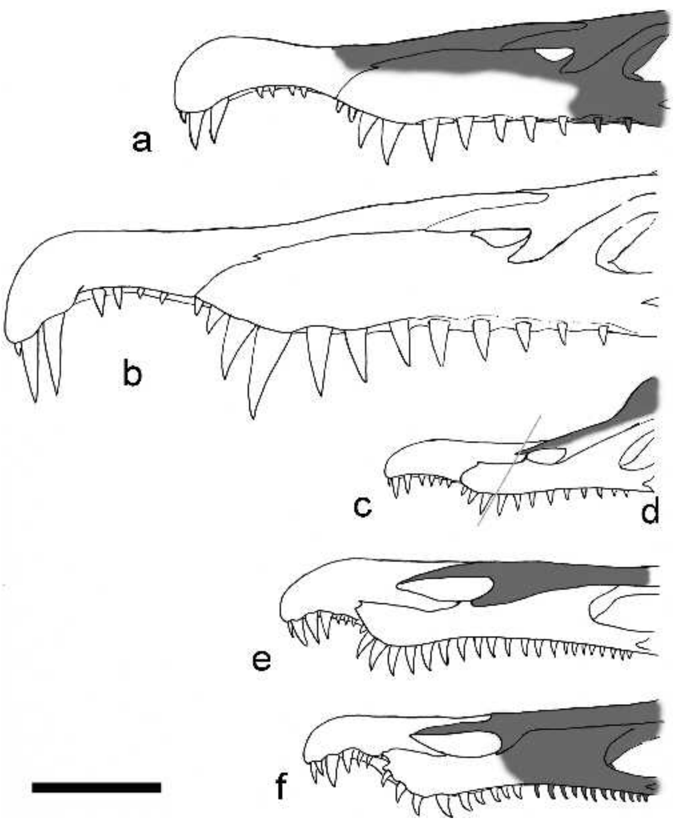

FIGURE 4. Comparison among the known spinosaurid snouts: **a**, *Spinosaurus maroccanus* (Taquet and Russell, 1998); **b**, *Spinosaurus* cf. *S. aegyptiacus* MSNM V4047; **c**, *Angaturama* (Kellner and Campos, 1996); **d**, *Irritator* (Sues et al., 2002); **e**, *Suchomimus* (Sereno et al., 1998); **f**, *Baryonyx* (Charig and Milner, 1997). Shaded areas represent unknown parts of the snout; missing elements of *Spinosaurus maroccanus* and *Baryonyx* are based respectively on MSNM V4047 and *Suchomimus*; *Irritator* and *Angaturama* are shown as two parts of the same taxon (see text). Scale bar equals 20 cm.

Irritator* and *Spinosaurus—The Spinosaurinae include *Spinosaurus*, *Irritator*, and *Angaturama*. According to several authors (Charig and Milner, 1997; Sereno et al., 1998; Buffetaut and Ouaja, 2002; Sues et al., 2002), *Angaturama limai* is a junior synonym of *Irritator challengeri*, as the two holotypes in all likelihood pertain to the same taxon (Fig. 4c, d). For this reason, information about the rostrum in *Irritator* is here taken from *Angaturama* (Kellner and Campos, 1996).

Due to the lack of adequate cranial material of *Spinosaurus* (Fig. 4a), Sues et al. (2002) suggest that *Irritator* could be congeneric with it. On the basis of both MSNM V4047 and UCPC-2, we can confirm that the two taxa are closely related but show also some differences. In particular, in *Irritator* the external nares are retracted to the mid-part of the maxillary tooth row; the premaxillae bifurcate caudally and their ventral rami participate to the rostral margin of the external nares (although their contribution in bordering the external nares seems to be markedly lower than in the Baryonychinae); the dentition is less massive than in *Spinosaurus*, as pointed out by Taquet and Russell (1998); in ventral view the labial margins of both premaxillae and

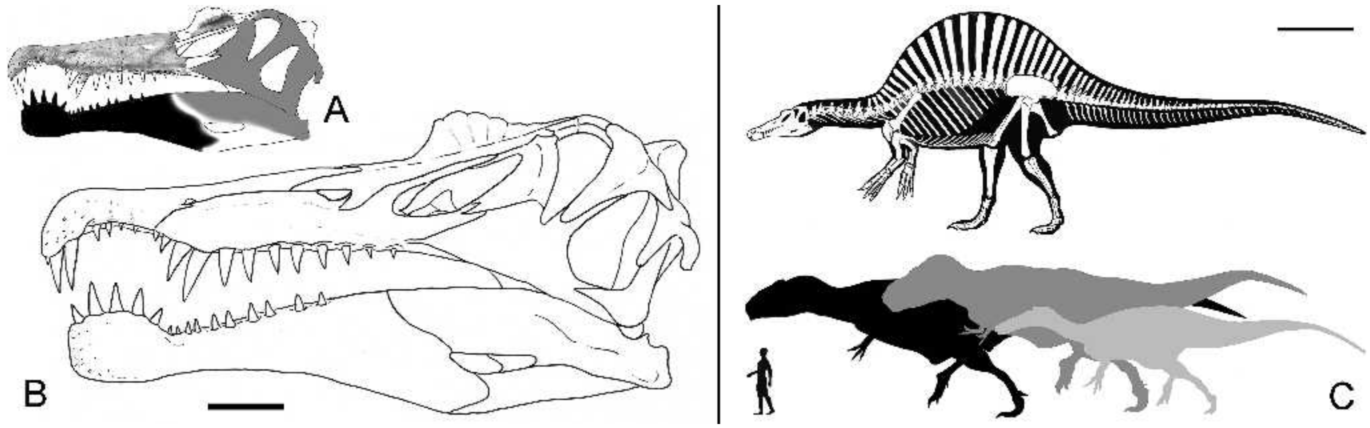

FIGURE 5. **A**, explanatory sketch showing on which material the skull reconstruction here proposed is based. The snout and the crested nasals (photos) pertain respectively to MSNM V4047 and UCPC-2, the dentary (black) is based on the holotype of *Spinosaurus aegyptiacus*, and the remaining parts of the skull (grey) are modified from *Irritator*. For more details see the text. **B**, reconstruction of the skull of *Spinosaurus* cf. *S. aegyptiacus*. With an estimated skull length of 175 cm, it represents the largest known spinosaurid skull and one of the largest theropod skulls. Scale bar equals 20 cm. **C**, estimated size of MSNM V4047 (body length about 17 m) compared, from left to right, with *Homo sapiens* and the largest known individuals of *Giganotosaurus* (Calvo and Coria, 2000), *Tyrannosaurus* (Brochu, 2003) and *Suchomimus* (Sereno et al., 1998). Scale bar equals 2 m.

maxillae are subparallel, without marked constriction caudal to the rosette; in lateral view the rostrum is less elongated than in *Spinosaurus.* In *Spinosaurus* the external nares are retracted to the level of the caudal half of the maxillary tooth row; the maxillae entirely border the rostro-ventral and caudal margins of external nares, excluding both premaxillae and nasals; the rostral-most part of the rostrum is strongly downturned and reaches the level of the dentigerous margin of the maxillary tooth row, whereas in *Irritator* the ventral margin of the premaxilla is elevated above the maxillary tooth row as in the Baryonychinae. Finally, the skull of *Irritator* tapers rostrally whereas that of *Spinosaurus* maintains a level plane. Therefore, on the basis of the above-mentioned differences, the separation of the two genera is clearly warranted.

Skull Size and Hypothetical Body Size

The exceptional size of MSNM V4047 indicates that it represents the largest known spinosaurid skull (Fig. 4). The snout of *Suchomimus*, measured from the tip of the rostrum to the notch for the jugal attachment, is only 60% that of MSNM V4047, whereas the reconstructed snout of *Irritator* is less than half that size. MSNM V4047, measured both from the tip of the rostrum to the caudal margin of maxillary alveolus 7 and from one lateral margin to the other (at the level of the maxillary alveolus 7), is about 21.5–24.5% larger than the snout of *S. maroccanus*. Our tentative reconstruction of the skull (Fig. 5B), based on MSNM V4047, UCPC-2 and other spinosaurid specimens (Fig. 5A), gives a total skull length of about 175 cm. The toothed half of the lower jaw is from the holotype (Stromer, 1915), and the sister-taxon of *Spinosaurus*, *Irritator* (Sues et al., 2002), was used for the unknown part of the skull and the rear portion of the lower jaw. Some parts of the parietals, not preserved in *Irritator*, are from the Baryonychinae (Charig and Milner, 1997; Sereno et al., 1998). Due to the uncertain maturity and small size of *Irritator* (Sues et al., 2002), in drawing some bones we have also taken into consideration the degree of variation of shape and robustness relative to age and size in the skull of other theropods, as well demonstrated in tyrannosaurids (Carr, 1999 ; Currie, 2003). With regard to body size, a comparison between the known elements (lower jaw, ribs and dorsal centra) of the holotype of *S. aegyptiacus* (Stromer, 1915) with the Baryonychinae (Sereno et al., 1998; Charig and Milner, 1997), suggests that it was about 20–30% larger than *Suchomimus* and *Baryonyx*, rivalling in size other giant theropods such as *Tyrannosaurus* (Brochu, 2003) and the Carcharodontosauridae (Sereno et al. 1996; Calvo and Coria, 2000). *Spinosaurus* specimen MSNM V4047 is roughly 20% bigger than the holotype (Stromer, 1915); therefore, it represents potentially the largest known theropod dinosaur. As some postcranial elements (i.e., the limb bones and the caudal vertebrae) are hitherto unknown in *Spinosaurus*, it is difficult to reconstruct accurately its body proportions, so the real size of MSNM V4047 can be only tentatively hypothesised. With an appropriate degree of caution, the size of the whole animal (Fig. 5C) can be calculated by reconstructing the skeleton on the basis of both the remains of the holotype of *Spinosaurus* (Stromer, 1915) and *Suchomimus* (Sereno et al., 1998). The estimated length for MSNM V4047 is about 16–18 m, and presuming that the body proportions were the same as for *Suchomimus* (Sereno et al., 1998), using Seebacher's (2001) method we obtain a weight around 7–9 t.

ACKNOWLEDGMENTS

We thank T. Holtz Jr. for the revision of a first version of the manuscript. Many thanks to four anonymous referees, as well as to M. Carrano, D. Naish, O. Rauhut, S. Sampson, and L. Witmer for their critical and helpful comments. D. Naish, S. Sampson, and P. Sereno provided useful suggestions on the presentation of the manuscript. We thank also P. Taquet for access to specimens MNHM SAM 124 and MNHN GDF 366, P. Sereno for access to specimen MNN GDF501, F. Bacchia for information about the Kem Kem area, A. Cau for unpublished data about theropod phylogeny, L. Magnoni and D. Affer for specimen preparation, L. Spezia for photos, and E. Bianchi for helpful discussion on extant comparative material. M. Mendez thanks P. Sereno, who offered him the opportunity for a great start on a career in paleontology. Drawings are by M. Auditore (Fig. 1), S. Maganuco (Figs 4, 5) and M. Mendez and C. Abraczinskas (Fig. 3).

LITERATURE CITED

Bouaziz, S., E. Buffetaut, M. Ghanmi, J.-J. Jaeger, M. Martin, J.-M. Mazin, and H. Tong. 1988. Nouvelles découvertes de vertébrés fossiles dans l'Albien du Sud tunisien. Bulletin de la Société. Géologique de France (8) 4:335–339.

Brochu C.A. 2003. Osteology of *Tyrannosaurus rex*: Insight from a

Nearly Complete Skeleton and High-Resolution Computed Tomographic Analysis of the Skull. Society of Vertebrate Paleontology Memoir 7:1–138.

Buffetaut, E. 1989. New remains of the enigmatic dinosaur *Spinosaurus* from the Cretaceous of Morocco and the affinities between *Spinosaurus* and *Baryonyx*. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1989:79–87.

Buffetaut, E., and M. Ouaja. 2002. A new specimen of *Spinosaurus* (Dinosauria, Theropoda) from the Lower Cretaceous of Tunisia, with remarks on the evolutionary history of the Spinosauridae. Bulletin de la Société Géologique de France 173:415–421.

Calvo, J. O., and R. Coria. 2000. New specimen of *Giganotosaurus carolinii* (Coria & Salgado, 1995), supports it as the largest theropod ever found. Gaia 15:117–122.

Carr, T. D. 1999. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). Journal of Vertebrate Paleontology 19:497–520.

Charig, A. J., and A. C. Milner. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. Bulletin of the Natural History Museum, London, Geology Series 53:11–70.

Currie, P. J. 2003. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia. Canadian Journal of Earth Sciences 40:651–665.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds; pp. 1–55 in K. Padian (ed.), The Origin of Birds and the Evolution of Flight. Memoirs of the California Academy of Sciences 8.

Holtz, T. R., Jr. 2000. A new phylogeny of the carnivorous dinosaurs. Gaia 15:5–61.

Kellner, A. W. A., and D. de A. Campos. 1996. First Early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, Stuttgart 199:151–166.

Marsh, O. C. 1881. Principal characters of American Jurassic dinosaurs. Part V. American Journal of Science 21:417–423.

Rauhut, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology 69:1–213.

Russell, D. A. 1996. Isolated dinosaur bones from the middle Cretaceous of the Tafilalt, Morocco. Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4 18:349–402.

Seebacher, F. 2001. A new method to calculate allometric length-mass relationships for dinosaurs. Journal of Vertebrate Paleontology 21: 51–60.

Sereno, P. C. 1999. The evolution of dinosaurs. Science 284:2137–2147.

Sereno, P.C., D. B. Dutheil, M. Iarochene, H. C. E. Larsson, G. H. Lyon, P. M. Magwene, C. A. Sidor, D. J. Varricchio, and J. A. Wilson. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. Science 272:986–991.

Sereno, P. C., A. L. Beck, D. B. Dutheuil, B. Gado, H. C. Larsson, G. H. Lyon, J. D. Marcot, O. W. M. Rauhut, R. W. Sadleir, C. A. Sidor, D. Varricchio, G. P. Wilson, and J. A. Wilson. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. Science 282:1298–1302.

Stromer, E. 1915. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Bahariye-Stufe (unterstes Cenoman). 3. Das Original des Theropodes *Spinosaurus aegyptiacus* nov. Gen., nov. Spec. Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Klasse, München 28:1–28.

Stromer, E. 1926. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîje-Stufe (unterstes Cenoman). 7. *Stomatosuchus inermis* Stromer, ein schwach bezahnter Krokodilier. 8. Ein Skelettrest des Pristiden *Onchoprisitis numidus* Haug sp. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung, 30:1–22.

Sues, H.-D., E. Frey, D. M. Martill, and D. M. Scott. 2002. *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. Journal of Vertebrate Paleontology 22: 535–547.

Taquet, P. 1984. Une curieuse spécialisation du crâne de certains Dinosaures carnivores du Crétacé: Le museau long et étroit des Spinosauridés. Comptes Rendus de l'Académie des Sciences, Paris, série II, 299:217–222.

Taquet, P., and D. A. Russell. 1998. New data on spinosaurid dinosaurs from the Early Cretaceous of the Sahara. Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des Planètes 327:347–353.

Wellnhofer, P., and E. Buffetaut. 1999. Pterosaur remains from the Cretaceous of Morocco. Paläontologische Zeitschrift 73:133–142.

Submitted 10 March 2005; accepted 25 May 2005.