

New data on spinosaurid dinosaurs from the Early Cretaceous of the Sahara

Nouvelles données sur des dinosaures spinosaurides du Crétacé inférieur du Sahara

Philippe Taquet^{a*}, Dale A. Russell^b

^a Laboratoire de paléontologie du Muséum national d'histoire naturelle, and URA 12 CNRS, 8, rue Buffon, 75005 Paris, France

^b North Carolina State Museum of Natural Sciences, and North Carolina State University, Department of Marine, Earth and Atmospheric Sciences, Box 8208, Raleigh, North Carolina, 27695-8208, USA

Abstract—New occurrences of spinosaurid dinosaurs from the Aptian of Niger and Albian of Algeria augment our knowledge of *Spinosaurus maroccanus* and permit the description of a new taxon: *Cristatusaurus lapparenti* from the Gadoufaoua locality (Niger). Spinosaurids may be separated into two distinct groups: one with longirostrine muzzles and premaxillae which are rounded in cross-section, and a second with brevirostrine muzzles possessing a dorso-posteriorly expanded crest. The Spanish genus *Pelecanimimus* may be related to spinosaurids, rendering spinosaurids a more diversified group than previously thought. (© Académie des sciences / Elsevier, Paris.)

Aptian / Albian / Algeria / Niger / Morocco / Vertebrata / Theropoda / dinosaur

Résumé — La découverte de nouveaux restes de dinosaures spinosauridés dans l'Aptien du Niger et dans l'Albien de l'Algérie permet de compléter nos connaissances sur *Spinosaurus maroccanus* et de décrire un nouveau taxon : *Cristatusaurus lapparenti* du gisement de Gadoufaoua (Niger). Les rostres de spinosaures peuvent être séparés en deux groupes bien distincts : le premier avec des museaux longirostres et des prémaxillaires arrondis en section, le second avec des museaux brévirostres pourvus d'une crête dorsale développée vers l'arrière. Le genre espagnol *Pelecanimimus* pourrait être apparenté aux spinosauridés, qui forment un groupe beaucoup plus diversifié qu'on ne le pensait. (© Académie des sciences / Elsevier, Paris.)

Aptien / Albian / Algérie / Niger / Maroc / Vertebrata / Theropoda / dinosaure

Version abrégée (voir p. 352)

1. Introduction

In 1915, Stromer described a fragmentary skeleton of a large theropod from the Cenomanian of Egypt, including a well-preserved mandible, isolated teeth and several vertebrae. He placed it in a new genus, *Spinosaurus*, in reference to dorsal spines measuring up to 165 cm long. The type specimen was destroyed during the Second World War, but Stromer's excellent descriptions and illustrations amply define the peculiar theropod. Another, more com-

plete skeleton was described by Charig and Milner (1986), Milner and Croucher (1987), Charig and Milner (1997) from the Barremian of England, and named *Baryonyx* after a large, recurved manus claw. Its relationship to *Spinosaurus* has been much discussed (Paul, 1988; Buffetaut, 1989a and b; Charig and Milner, 1990; Buffetaut, 1992; Milner, 1997; Charig and Milner, 1997), although the two genera seem to be closely allied. Spinosaurids are considered to have diverged from ancestral tetanurans (Milner, 1996, 1997; Charig and Milner, 1997), or with ancestral

Note présentée par Philippe Taquet.

Note remise le 5 mars 1998, acceptée après révision le 24 août 1998.

* E-mail: taquet@mnhn.fr

torvosaurus within tetanurae in Toarcian time (Serenio et al., 1994; Sereno et al., 1996; Sereno, 1997). More recently, two new genera from the Albian of Brazil have been considered as spinosaurs (*Angaturama*, Kellner and Campos, 1996; *Irritator*, Kellner, 1996, Martill et al., 1996). 'Spinosaurus B' of Stromer (1934) was removed from the Spinosauridae, and placed within a new and unrelated group of theropods (Russell, 1996; see also the cervical vertebra figured by Sereno et al., 1996, figure 2D). Should the aberrant Hauterivian–Barremian Spanish 'ornithomimisaure' (Pérez-Moreno et al., 1994) also be related to the spinosaurs, as suggested below, a highly diverse group of substantial antiquity is indicated.

The purpose of this note is to characterise spinosaurian remains from two localities within the western Sahara. Gadoufaoua is of Aptian age, and is situated south of the Air Massif in northern Niger (Taquet, 1976, 1994). Gara Samani is of Albian age and is located on the northwestern edge of the Tademaït in the Algerian Sahara (de Broin et al., 1971; Lefranc and Toutin, 1971).

2. Systematics

Family

Spinosauridae Stromer 1915

Spinosaurus Stromer 1915

Spinosaurus maroccanus Russell 1996

Referred specimens

MNHN SAM 124, rostrum containing both premaxillae, maxillae, vomers and fragment from midshaft of right dentary; SAM 125, fragment of premaxilla; SAM 126–127, centra of two cervical vertebrae; SAM 128, neural arch of dorsal vertebra (figure, a–d).

Differential diagnosis (from *Cristatusaurus lapparenti*, see below)

Premaxilla bulbous, slightly 'hooked' in lateral profile, decreases in height posteriorly. Posterodorsal surface rounded in cross-section; anteriormost premaxillary alveolus relatively small, lateral alveoli grouped into two pairs. Maxillary and dentary teeth circular in cross-section, maxillary teeth procumbent both anteriorly and posteriorly. Dentary markedly constricted vertically in mid-section, alveoli grouped into pairs. Maxillary and dentary teeth with smooth carinae.

Spinosaurus may be separated from *Baryonyx* by lack of dental serrations, from *Irritator* by more massive and less homodont dentition, and *Angaturma* by longirostrine condition of premaxilla.

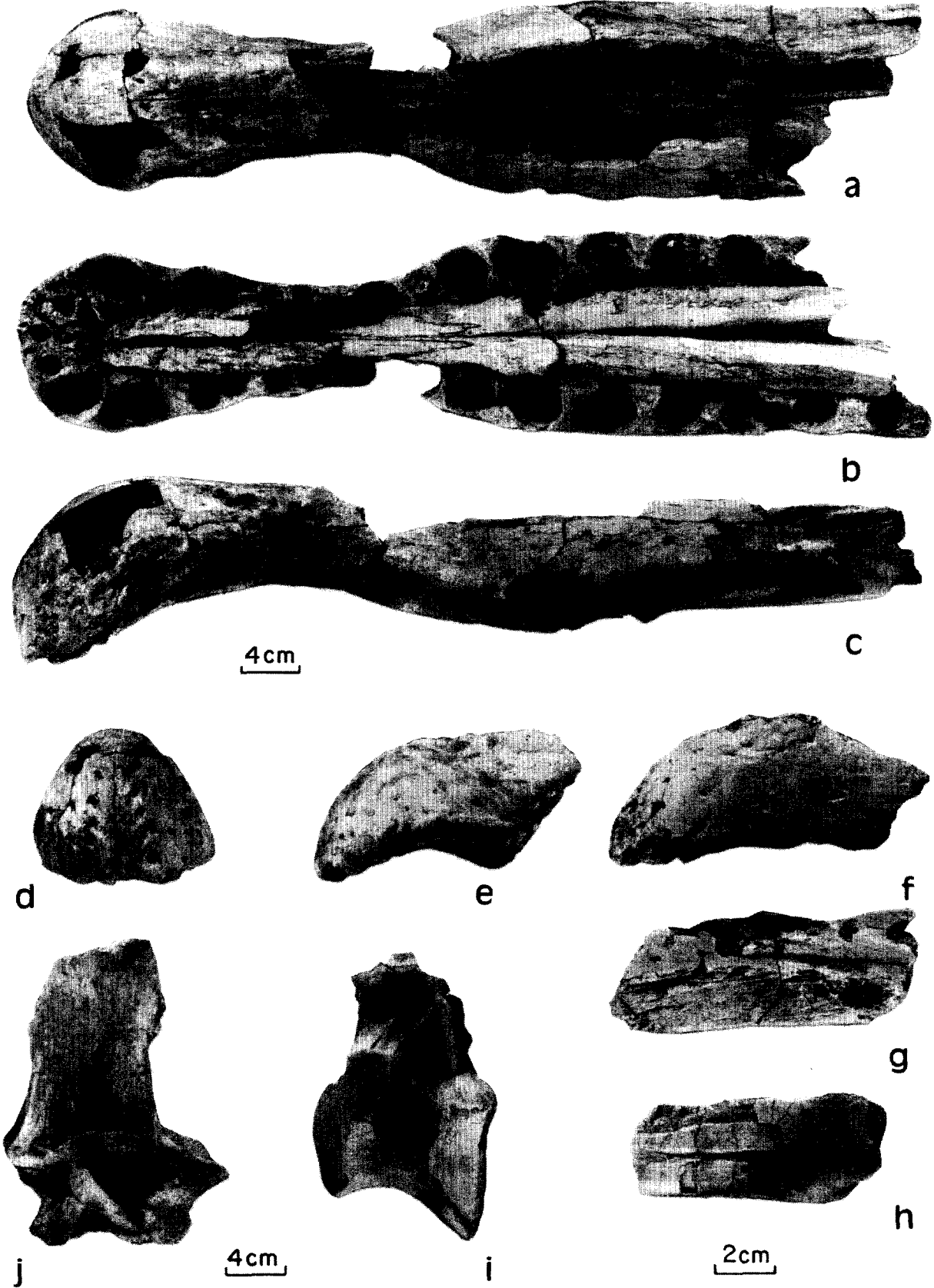
Discussion

Spinosaurus maroccanus was originally separated from *S. aegyptiacus* on the basis of the greater length of the mid-cervical centra relative to the height of the posterior articular facet (yielding a length/height ratio of 1.5 versus 1.1 in the Egyptian species; Russell, 1996). The average of the length/height ratios in two cervical centra from Gara Samani (which lack neural arches so that their position in the neck is uncertain) approximates that in the Moroccan species. The diagnosis given above is based upon the anterior portion of a skull and fragment of the right dentary from Gara Samani. The rostrum pertains to a mature animal, for the sutures separating the premaxillae are closed, though not obscured. It contains characters which further distinguish *S. maroccanus* from cranial elements of *C. lapparenti* from Gadoufaoua.

The structure of the rostrum in MNHN SAM 124 (figure, a–d) probably reflects conditions in spinosaurs generally. The articulated premaxillae (anteriorly) and maxillae (posteriorly) are of about equal width across the rostrum at their widest extent (134 vs. 137 mm), and are constricted laterally in the region of the alveolar margin between them containing the premaxillary-maxillary suture (width 74 mm). There are alveoli for seven teeth in the premaxilla (figure, b), as there are in *C. lapparenti* from Gadoufaoua (see below), the Brazilian spinosaur *Angaturma* (Kellner and Campos, 1996) and, interestingly, also in *Pelecanimimus* (Pérez-Moreno et al., 1994). The regular occurrence of such a high but constant number of premaxillary teeth in these genera is unique among theropods. The first alveolus is small (15 mm in anteroposterior diameter), is followed by two large, procumbent alveoli (33 and 38 mm), and finally by two pairs of alveoli which decrease in diameter posteriorly (from 21 to 13 mm). The alveoli are bordered medially by a rounded crest which appears to be distinct from the alveolar margin, and which Kellner and Campos (1996) suggested might be a vomer. No suture was found between this structure and the alveolar margin in an immature premaxilla from Gadoufaoua (see below), either on the anteromedial region of the premaxillary suture or the area of the premaxillary-maxillary suture posteriorly. The structure is here considered to belong to the median palatal process of the premaxilla.

Figure. *Spinosaurus maroccanus*. Rostrum with premaxillae, maxillae, vomers. SAM 124. a. Dorsal view. b. Ventral view. c. Left lateral view. d. Anterior view. *Cristatusaurus lapparenti* nov. gen., nov. sp. e. Anterior portion of premaxillae, left lateral view. GDF 365. f. Anterior portion of premaxillae, left lateral view. GDF 366. g. Portion of right maxilla, medial view. GDF 366. h. Portion of right dentary, medial view. GDF 366. i. Anterior dorsal vertebra, left lateral view. GDF 330. j. Neural arch and base of a spine of anterior dorsal vertebra, right lateral view. GDF 359.

Spinosaurus maroccanus. Rostre avec prémaxillaires, maxillaires, vomers. SAM 124. a. Vue dorsale. b. Vue ventrale. c. Vue latérale gauche. d. Vue antérieure. *Cristatusaurus lapparenti* nov. gen., nov. sp. e. Portion antérieure des prémaxillaires, vue latérale gauche. GDF 365. f. Portion antérieure des prémaxillaires, vue latérale gauche. GDF 366. g. Portion d'un maxillaire droit, vue médiale. GDF 366. h. Portion de dentaire droit, vue médiale. GDF 366. i. Vertèbre dorsale antérieure, vue latérale gauche. GDF 330. j. Arc neural et base d'une épine d'une vertèbre dorsale antérieure, vue latérale droite. GDF 359.



The maxilla described by Buffetaut (1989a, 1992) clearly belongs to *Spinosaurus*, and is nearly identical in size to the maxillae in the rostrum from Gara Samani. The maxillae are easily distinguishable from those of *Carcharodontosaurus* in that their lateral surfaces are more convex externally in a longitudinal direction, and slightly convex rather than concave vertically (Stromer, 1931; Russell, 1996; Sereno et al., 1996). Furthermore, the alveoli are rounded in *Spinosaurus maroccanus* and sub-rectangular in *Carcharodontosaurus*. The Gara Samani rostrum demonstrates that the lateral surfaces of the maxillae are inclined dorsomedially towards each other at an angle of about 45 degrees; this angle is slightly steeper anteriorly than posteriorly. A horizontal suture for the premaxilla is preserved on the maxilla described by Buffetaut. Scaling to the Gara Samani specimen, the horizontal rami of the premaxillae must have been very narrow, their combined width being of the order of 40 mm in the latter specimen. Alveoli for at least 9 maxillary teeth are preserved in this rostrum, increasing from 14 to 38 mm in diameter from the first to the fourth (they increase in size from first to third alveolus in *Angaturama* (Kellner and Campos, 1996; p. 155), and decreasing thereafter to 28 mm. All are procumbant, but become decreasingly so posteriorly where they are more widely separated from each other along the alveolar margin. Replacement teeth are present on the medial surface of several alveoli. A tooth within the second alveolus clearly bears vertical ridges on its medial face. A narrow tongue of the premaxilla extends back to a position medial to the third maxillary alveolus, at which point the anterior palatal bar becomes entirely replaced by the vomer (*figure, b*). This heavy element is inclined toward the opposite vomer at an angle paralleling that of the lateral surface of the maxilla. Both vomers are firmly sutured together along the midline of the rostrum in a manner such that the sutural contact narrows and rises posteriorly. The medial rim of the alveolar channels enters the vomerine surface dorsally. There is no indication of a suture for the palatine posteriorly, nor any indication of choanal passages.

The dentary, to the extent that it is known, appears to be similar to that of *S. aegyptiacus*. Small, medially situated alveoli in dentary fragments from Morocco are grouped into two pairs (Russell, 1996, p. 357, figures 5–6); the dentary fragment from Gara Samani contains larger alveoli (measuring about 24 mm in anteroposterior diameter) located, according to size and spacing, more posteriorly in the bone, opposite the sixth to ninth maxillary alveoli. The dentary alveoli are similarly procumbant. The carinae are smooth in unerupted maxillary and dentary teeth from Morocco (Buffetaut, 1989a; Russell, 1996); they are also smooth in *S. aegyptiacus* (Stromer, 1915) and *Angaturama* (Kellner and Campos, 1996, p. 155).

Buffetaut (1992) proposes that the neck of *Spinosaurus* did not form an upward curve when articulated. This curve is clearly indicated in the central facets of the vertebra from Gara Samani, as well as those from Morocco (Russell, 1996, figure 4).

Cristatusaurus, n.g.

Etymology:

Cristatus: crested (Latin).

Sauros: (Greek) lizard.

Type species: *Cristatusaurus lapparenti*, new species.

Diagnosis: The same as that of the type species.

Cristatusaurus lapparenti, n. sp.

Etymology: *Cristatusaurus lapparenti*, in recognition of Albert F. de Lapparent, S.J., for his contributions to the knowledge of Saharan dinosaurs, and his generous assistance during the field season of 1966.

Type locality: Gadoufaoua; GAD 5, *niveau des Innocents*, Tegama Formation, Aptian. Niger.

Type specimen: (*figure, f–h*) MNHN GDF 366, both premaxillae, portion of right maxilla and dentary.

Referred specimens (*figure, e, i, j*) MNHN GDF 365 fused premaxillae; dorsal vertebrae 357–359, 361.

Differential diagnosis (from *S. maroccanus*)

Premaxilla short, strongly 'hooked' in lateral profile, increases in height posteriorly. Dorsal surface narrows into crest posteriorly. Anteriormost premaxillary alveolus relatively large, lateral alveoli uniformly closely spaced. Maxillary and dentary teeth laterally compressed in cross-section, maxillary teeth vertically oriented posteriorly. Dentary slightly constricted vertically in mid-section, alveoli closely spaced. Maxillary and dentary teeth with finely serrated carinae.

Cristatusaurus may be separated from *Angaturama* and *Irritator* by presence of dental serrations, from *Baryonyx* by brevirostrine condition of premaxilla.

Discussion

The type and referred premaxillae have been well described and figured (Taquet, 1984; Kellner and Campos, 1996). The suture separating the premaxillae is not fused in the type specimen, indicating that the animal was immature. The anteriormost preserved maxillary alveolus (posterior margin only) is possibly homologous with the third position in the Gara Samani rostrum. The ratio of the combined lengths of alveoli five to nine in the type and Gara Samani rostra indicates the former was about 44 % of the length of the latter. According to the average lengths of the alveoli, the referred premaxillae are about 1.5 times larger than those in the type. However, dorsal vertebrae from Gadoufaoua (GDF 358 with a centrum length of about 135 mm) are as large as the largest known vertebrae of *S. maroccanus*, although no known western Saharan specimen is known to be as large as the type of *S. aegyptiacus* (Stromer, 1915, p. 24). The largest alveolus preserved among fragmentary tooth bearing elements in an infantile spinosaur from Gadoufaoua, is 7 mm long, suggesting that the creature was less than one-fifth as long as an adult. A substantial range in age is indicated by materials referred to this species.

The maxilla (*figure, g*) is the most complete of any so far referred to the Spinosauridae. On its dorsal margin, one suture ends above the ventral opening of the sixth alveolus and a bevelled surface widens posteriorly from a point above the ventral opening of the eighth alveolus. The anatomical significance of these surfaces is unclear, for there are no indications of choanae medially, and the external naris and antorbital fenestra are not confluent in *Irritator* (Martill et al., 1996). The external nares are displaced posteriorly on the rostrum of the latter genus, perhaps as an adaptation to piscivory in spinosaurs (Taquet, 1984; Charig and Milner, 1997). The roots of teeth are in the positions of alveolus four to nine and possibly ten open onto the dorsal surface of the maxilla. In all, a posteriorly incomplete series of eleven maxillary alveoli is suggested. Alveolar lengths decrease from 21 mm in the third position to 11 mm in the tenth.

A dentary fragment (*figure, h*) exhibits an anterior constriction similar to, but less marked than in *S. aegyptiacus* and in *S. maroccanus*. Semicircular alveoli are preserved for ten teeth, which decrease in diameter from 9 to 7.5 mm (the eight central alveoli span 77 mm). In view of their very close spacing, it is possible that a complete dentary of this species might contain in the order of 20 alveoli. Although *S. aegyptiacus* has only 15 dentary teeth, *Baryonyx* has 32 (Buffetaut, 1992) and *Pelecanimimus* about 75 (Pérez-Moreno et al., 1994). Fine serrations are present on the carinae, unlike in *Angaturama*, where the posterior premaxillary teeth are also more widely spaced. Vertical striations are present on teeth of the juvenile type specimen, although they have not been observed in GDF 365. These striations appear to be variably present in *S. maroccanus*, and we are uncertain of their taxonomic significance. A sagittal crest is present on the premaxilla in *Angaturama*, but the element is not as expanded laterally as in the Gadoufaoua form (Taquet, 1984; Kellner and Campos, 1996). Buffetaut (1992, p. 92) suggests that the Gadoufaoua premaxillae closely resemble those of *Baryonyx*. The teeth of *Baryonyx* are described by him as possessing fine serrations and a curvature of the crown, unlike in *Spinosaurus*, but resembling those of *S. aegyptiacus* in the circular in cross section of the crowns (Buffetaut 1992, p. 93–94).

The base of a spine preserved on the neural arch of an anterior dorsal vertebra (*figure, j*) (GFD 359, cited by Taquet, 1976, p. 53) is less robust than a spine from a neural arch of similar dimensions of *S. maroccanus* (15 versus 25 mm in transverse diameter, cf. Russell, 1996, *figure 8*). It is possible that the neural spines were not so elevated in the species from Gadoufaoua. A transitional cervico-dorsal vertebra (*figure, i*) (GDF 330) bears a heart-shaped anterior central facet and a pleurocoel beneath the parapophysis, but lacks a hypapophysis. No other dorsal vertebrae possess pleurocoels.

The anterior margin of the transverse process of anterior dorsal vertebrae is linked by a ridge to the anterior zygopophysis; a similar ridge descends from the centre of its ventral surface to the posterior base of the neural arch. Two smaller laminae project anteroventrally from the descend-

ing ridge across a deep lateral excavation within the neural arch. The neural arch is apparently often interrupted completely behind the posteriorly descending ridge, and the posterior zygopophyses are supported by a separate pillar of bone rising from the posterior end of the neural arches. Zygosphene-zygantrum articulations are present.

3. Conclusion

Spinosaur remains are relatively common in the western Sahara, but appear so far to be limited to the anterior part of the cranial rostrum, teeth and presacral vertebrae. At least two successive taxa are known, which may or may not be in an ancestor–descendant relationship. Milner (1997) places taxonomic significance on the presence or absence of serrations on the dental carinae. According to this, *Spinosaurus maroccanus* from the Albian of Gara Samani and Morocco (which lacks serrations, as do *Angaturama* and *Irritator* from the Aptian-Albian of Brazil) would be separated on a familial level from *C. lapparenti* from the Aptian of Gadoufaoua and *Baryonyx* from the Barremian of Britain (which possess them). The rostra of spinosaurs also appear to be separable into two major kinds, a longirostrine form in which the rostrum is rounded in transverse section (*figure, d*) (as in *Spinosaurus maroccanus*, *Baryonyx* and *Irritator*), and a brevirostrine form in which it abruptly narrows into a dorsoposteriorly rising longitudinal crest (*figure, f*) (*C. lapparenti* and *Angaturama*).

Kellner (1996), Milner (1997) and Charig and Milner (1997) concur on several spinosaur synapomorphies: a) elongation of rostrum with external nares displaced posteriorly, b) ventral margin of premaxilla concave, anterodorsal margin of dentary upturned, c) teeth subcircular in cross-section, with straight or slightly recurved crowns, and d) the presence of seven teeth in premaxilla. *Irritator*, which is based on a moderately large, articulated cranium, was recognised as a spinosaur by Kellner (1996). Its morphology suggests several additional possible synapomorphies (cf. Martill et al., 1996): e) orbits posterolaterally inclined, f) reduced supratemporal fenestra, g) median longitudinal crest projecting posteriorly over temporal region, and h) tooth roots occupy almost complete depth of maxilla (as is also the case in *C. lapparenti*).

Pelecanimimus, a small theropod from Hauterivian-Barremian strata in Spain, exhibits several unusual autapomorphies, including over 200 teeth, premaxillary and anterior teeth which are “D” shaped in cross-section (the remaining teeth are laterally compressed), and a manus resembling that in ornithomimids (Pérez-Moreno, 1994). The premaxilla also contains seven premaxillary teeth, a number unequalled in other dinosaurs (plateosaurids and primitive ornithischians possess up to six premaxillary teeth (Galton, 1990; Sereno, 1991), except spinosaurs. The Spanish theropod possesses a median longitudinal crest in the temporal region (Briggs et al., 1997), as does *Irritator*. Other attributes which occur in *Pelecanimimus* and spinosaurs include: jugal does not reach antorbital fenestra (cf. Martill et al., 1996, *figure 3*), maxillary teeth

larger than dentary teeth, dentary teeth unusually numerous (cf. Charig and Milner, 1990, 1997), absence of interdental plates (cf. Buffetaut, 1989a), skull narrow and shallow with elongated facial region (cf. Charig and Milner, 1990, 1997).

Pelecanimimus should be evaluated to determine whether or not it is an 'ornithomimid-mimic' related to the

spinosaurus. If so, spinosaurus were a much more diverse group than previously suspected. Three family group names apply to them: Spinosauridae (Stromer, 1915), Baryonychidae (Charig and Milner, 1986) and Irritatoridae (Martill et al., 1996). The morphology of spinosaurus is too poorly understood at present to attempt to assess the validity of the latter two.

Version abrégée

En 1915, Stromer a décrit une partie du squelette d'un grand théropode du Cénomaniens d'Égypte. Il créa pour ce matériel un nouveau genre, *Spinosaurus*, en référence à la longueur des épines neurales des vertèbres dorsales. Un autre squelette plus complet a été décrit par Charig et Milner (1986, 1997) du Barrémien d'Angleterre et nommé *Baryonyx*. Les relations de celui-ci avec *Spinosaurus* ont été largement discutées (Buffetaut, 1989a et b, Charig et Milner, 1990, Buffetaut, 1990, Charig et Milner, 1997), et les deux genres semblent étroitement apparentés. Récemment, deux nouveaux genres de l'Albien du Brésil ont été considérés comme faisant partie des spinosaures : *Angaturama* (Kellner et Campos, 1996) ; *Irritator* (Martill et al., 1996 ; Kellner, 1996). Enfin l'étrange « ornithomimosaure » (Pérez Moreno et al., 1994) de l'Hauteriviens-Barrémien d'Espagne pourrait être apparenté également aux spinosaures, ainsi que nous le suggérons.

Cette note a pour objet de décrire des restes de spinosaures de deux localités du Sahara : ceux de l'Aptien de Gadoufaoua du Nord du Niger (Taquet, 1976, 1994) et de l'Albien de la Gara Samani du Nord-Ouest du Tadémaït en Algérie (De Broin et al., 1971 ; Lefranc et Toutin, 1971).

Systématique

Famille Spinosauridae Stromer 1915

Spinosaurus Stromer 1915

Spinosaurus maroccanus Russell 1996

Spécimens en référence : rostre avec prémaxillaires, maxillaires, vomers et fragment de dentaire (figure, a-d).

Diagnose différentielle

De *Cristatusaurus lapparenti*, voir ci-dessous ; prémaxillaires bulbeux, légèrement en forme de bec en vue latérale et dont la hauteur décroît postérieurement ; surface postéro-dorsale arrondie en section ; alvéoles prémaxillaires antérieurs relativement petits ; alvéoles latéraux groupés en deux paires ; dents maxillaires et dentaires avec des carènes peu marquées.

Spinosaurus peut être séparé de *Baryonyx* par l'absence de crénélures sur les dents, d'*Irritator* par sa dentition plus massive et moins homodonte, et d'*Angaturma* par la condition longirostre des prémaxillaires.

Discussion

Spinosaurus maroccanus a été séparé de *S. aegyptiacus* (Russell, 1996) sur la base des proportions différentes des vertèbres cervicales. La diagnose peut être complétée grâce au fragment antérieur de crâne et de dentaire de la Gara Samani. Les caractères de ce rostre permettent également de distinguer *S. maroccanus* de *C. lapparenti*.

Les caractères du rostre (SAM 124) semblent typiques de celui de tous les spinosaures. Il y a, en particulier, des alvéoles pour sept dents sur le prémaxillaire, tout comme chez *C. lapparenti*, ainsi que chez le spinosaure brésilien *Angaturama* et chez *Pelecanimimus*. Ce nombre, élevé et constant, des dents prémaxillaires est unique chez les théropodes. Le rostre de la Gara Samani montre que les surfaces latérales des maxillaires sont inclinées dorso-médialement à 45°. Le cou de *Spinosaurus* forme une courbe vers le haut, ainsi que le montrent les facettes centrales des vertèbres de l'espèce de la Gara Samani, tout comme celles de l'espèce marocaine.

Cristatusaurus lapparenti n.g.

Cristatusaurus lapparenti n.g., n.sp. est un nouveau spinosaure de l'Aptien de Gadoufaoua (Niger), représenté par deux extrémités antérieures de prémaxillaires, une portion de maxillaire, une portion de dentaire et par des vertèbres.

Diagnose différentielle de *S. maroccanus*

Les prémaxillaires sont courts et plongent en bec vers l'avant, mais leur hauteur augmente postérieurement. La surface dorsale forme une crête vers l'arrière ; les alvéoles prémaxillaires les plus antérieurs sont relativement larges. Les dents des maxillaires et des dentaires sont comprimées en section ; la partie supérieure des dents maxillaires est oblique vers l'arrière ; les dentaires sont légèrement comprimés verticalement dans leur partie moyenne, leurs alvéoles sont contigus ; les dents maxillaires et dentaires ont des carènes finement crénelées.

Cristatusaurus peut être séparé d'*Angaturma* et d'*Irritator* par la présence de crénélures sur les dents, de *Baryonyx* par la condition brévirostre des prémaxillaires.

Discussion

Le type de cette nouvelle espèce appartient à un jeune individu, dont la suture entre les deux prémaxillaires n'est pas encore fermée. Le maxillaire droit est assez complet et le dentaire possède une constriction antérieure, moins marquée toutefois que chez *S. aegyptiacus* et *S. maroccanus*.

Conclusion

En fonction de la présence ou de l'absence de crénélures sur la carène des dents, il est possible de distinguer deux groupes parmi les spinosaures : l'un avec *Spinosaurus maroccanus* de l'Albien du Maroc et de l'Algérie, et *Angaturama* et *Irritator* de

l'Aptien–Albien du Brésil ; l'autre avec *Cristatusaurus lapparenti* de l'Aptien du Niger et *Baryonyx walkeri* du Barrémien d'Angleterre, qui possèdent des crénelures sur les carènes de leurs dents.

De même, le rostre des spinosaures peut être séparé selon deux formes différentes : une forme à museau long, avec un rostre de section arrondie dorsalement (comme chez *S. maroccanus*, et *Irritator*) et une forme à museau plus court, qui se

rétrécit brusquement dorso-postérieurement en une crête longitudinale (comme chez *C. lapparenti* et *Angaturama*).

Pelecanimimus, petit théropode de l'Hauterivien–Barrémien d'Espagne, doit être réexaminé pour que l'on puisse déterminer si cet animal « mimétique des ornithomimides » est apparenté aux spinosaures. Si cela était le cas, les spinosaures, auxquels il faut ajouter le nouveau genre saharien décrit ci-dessus, se seraient plus diversifiés qu'on ne le pensait.

Acknowledgements. D.A.R. is grateful to D.E. Russell and D. Sigogneau-Russell for their gracious hospitality while he visited collections in Paris. Photographs were taken by D. Serrette, plate by F. Pilard.

4. References

- Briggs D.E.G., Wilby P., Pérez-Moreno B.P., Sanz J.L. and Fregenal-Martinez M. 1997. The mineralization of dinosaur soft tissue in the Lower Cretaceous of Las Hoyas, Spain, *J. Geol. Soc. London*, 154, 587–588
- Broin F de, Grenot C. and Vernet R. 1971. Sur la découverte d'un nouveau gisement de vertébrés dans le Continental intercalaire saharien : la Gara Samani (Algérie), *C. R. Acad. Sci. Paris*, 272, Series D, 1219–1221
- Buffetaut E. 1989a. New remains of the enigmatic dinosaur *Spinosaurus* from the Cretaceous of Morocco and the affinities between *Spinosaurus* and *Baryonyx*, *Neues Jahrb. Geol. u. Paläont. Monatshefte*, 2, 79–87
- Buffetaut E. 1989b. New remains of *Spinosaurus* from the Cretaceous of Morocco, *Archosaurian Articulations*, 1, 65–68
- Buffetaut E. 1992. Remarks on the Cretaceous theropod dinosaurs *Spinosaurus* and *Baryonyx*, *Neues Jahrb. Geol. u. Paläont. Monatshefte*, 2, 88–96
- Charig A.J. and Milner A.C. 1986. *Baryonyx*, a remarkable new theropod dinosaur, *Nature*, 324, 359–361
- Charig A.J. and Milner A.C. 1990. The systematic position of *Baryonyx walkeri*, in the light of Gauthier's reclassification of the Theropoda, in: Carpenter K. and Currie P.J. (Eds.), *Dinosaur systematics: approaches and perspectives*, Cambridge University Press, Cambridge, 127–140
- Charig A.J. and Milner A.C. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey, *Bull. Natural history Museum, Geology Series*, 53, 1, 11–70
- Galton P.M. 1990. Basal Sauropodomorpha-Prosauroptera, in: Weishampel D.B., Dodson P. and Osmolska H. (Eds.), *The Dinosauria*, University of California Press, Berkeley, 320–344
- Kellner A.W.A. 1996. Remarks on Brazilian dinosaurs, *Memoirs of the Queensland Museum*, 39, 611–626
- Kellner A.W.A. and Campos D. de A. 1996. First Early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae, *Neues Jahrb. Geol. u. Paläont. Abhandlung*, 199, 151–166
- Lefranc J.P. and Toutin N. 1971. Un gisement de *Desertella foureaui* (Lamellibranche préhétérodonte) dans le soubassement albien du Tademait ouest (Sahara algérien), *Bull. Soc. Histoire Naturelle de l'Afrique du Nord*, 62, 103–111
- Martill D.M., Cruickshank A.R.I., Frey E., Small P.G. and Clarke X. 1996. A new crested maniraptoran dinosaur from the Santana Formation (Lower Cretaceous) of Brazil, *J. Geol. Soc. London*, 153, 5–8
- Milner A.C. 1996. Morphology, relationships and ecology of spinosaurs, aberrant longsnouted Cretaceous theropods, *J. Vertebrate Palaeontology*, 16, (supplement to 3), 53A
- Milner A.C. 1997. Spinosauridae and Baryonychidae, in: Currie P.J. and Padian K. (Eds.), *Encyclopedia of dinosaurs*, Academic Press, New York, 699–700
- Milner A.C. and Croucher R. 1987. 'Claws' the story (so far) of a great British dinosaur, British Museum (Natural History), Equus Print, London, 17 p.
- Paul G. 1988. *Predatory dinosaurs of the world*, Simon and Schuster, New York, 464 p.
- Pérez-Moreno B.P., Sanz J.L., Buscalioni A.D., Moratalla J.J., Ortega F. and Rasskin-Gutman X. 1994. A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain, *Nature*, 370, 363–367
- Russell D.A. 1996. Isolated dinosaur bones from the Middle Cretaceous of the Tafilalt, Morocco, *Bull. Muséum national d'Histoire naturelle*, Paris, série 4, 18, section C, 349–402
- Sereno P.C. 1991. *Lesothosaurus*, 'Fabrosaurids', and the early evolution of Ornithischia, *J. Vertebrate Palaeontology*, 11, 168–197
- Sereno P.C., Wilson J.A., Larsson H.C.E., Dutheil D.B. and Sues H.D. 1994. Early Cretaceous dinosaurs from the Sahara, *Science*, 266, 267–271
- Sereno P.C., Dutheil D.B., Iarochene M., Larsson H.C.E., Lyon G.H., Magwene P.M., Sidor C.A., Varrichio D.J. and Wilson J.A. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation, *Science*, 272, 986–991
- Sereno P.C. 1997. The origin and evolution of dinosaurs, *Annual Review Earth and Planetary Sciences*, 25, 435–489
- Stromer E. 1915. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharijje Stufe (unterstes Cenoman). 3 Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. sp., *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse*, XXVIII, 3, 1–32
- Stromer E. 1931. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharijjestufe (unterstes Cenoman). 10. Ein Skelett-rest von *Carcharodontosaurus* nov. gen., *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung, Neue Folge*, 9, 1–23
- Stromer E. 1934. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharijjestufe (unterstes Cenoman). 13. Dinosauria, *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung, Neue Folge*, 22, 1–79
- Taquet P. 1976. Géologie et paléontologie du gisement de Gadoufaoua (Aptien du Niger), *Cahiers de Paléontologie*, Éditions du CNRS, 191 p.
- Taquet P. 1984. Une curieuse spécialisation du crâne de certains dinosaures carnivores du Crétacé : le museau long et étroit des spinosauridés, *C. R. Acad. Sci. Paris*, 299, Series II, 217–222
- Taquet P. 1994. *L'empreinte des dinosaures*, Éditions Odile-Jacob, Paris, 363 p.