Redescription of *Streptospondylus altdorfensis*, Cuvier's theropod dinosaur, from the Jurassic of Normandy

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ABSTRACT

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The theropod dinosaur remains from the Callovo-Oxfordian of the Vaches Noires, figured for the first time by Cuvier are redecrisbed. The systematic revision shows that *Streptospondylus altdorfensis* is the valid name to which the whole of the material should be assigned. A few vertebral features suggest the close relationships existing between *Streptospondylus* and *Eustreptospondylus* from the Callovian of England : both genera are related to the Spinosauroidea. The diversity of the European theropods at the end the Middle Jurassic and the beginning of the Late Jurassic is outlined.

INTRODUCTION

The main part of the bones described in this paper belongs to a private collection initially constituted by the Abbé Bachelet in the 1770 (Cuvier 1800a). The material, collected in the region of Honfleur, comprised cranial and postcranial material of two teleosaurs, as well as some theropod postcranial remains. It was then given to the Museum under Comte Beugnot's requisition by C. Guersent who was at the time professor at the Museum in Rouen (Cuvier 1800a). This collection was then attached by Cuvier (1812) to some material found in the region of Le Havre and described in 1776 by the Abbé Dicquemare. The exact origin of the Bachelet Collection remains however dubious. Cuvier (1824 : 143) mentions, without precising their exact origin, that these bones have been collected « near Honfleur » and that « it is only by the labels attached to these bones that I have been able to know their geographic origin, as well as the name of their collector, and his idea that they were sperm whale bones .» On the same aspect, the exhaustive content of the Bachelet collection has never been published, neither by its finder nor by Cuvier. The vertebrae described herein were in fact figured by Cuvier along with the remains of the "Gavial de Honfleur" (1824 : pl.VIII ;IX), whereas the distal end of the pubis, the tibia, the astragalus and the calcaneum were associated with remains from Buckland's *Megalosaurus* (1824 : pl. XXI), without it being indicated if this second batch originally belonged to the Bachelet collection. Cuvier (1824), nevertheless precising that all these pieces come form Honfleur's surroundings, suggests that they have a common origin. An examination of the collection catalogue of the Muséum national d'Histoire naturelle, Paris, tells us as well that the pubis, the tibia, the astragalus and the calcaneum have been found at the Vaches Noires. It's probably on the basis of these data that Piveteau (1923 : 121) grouped the whole of the material and precised its origin. The anatomic relations between the vertebrae, the identical aspect of the fossilisation of the various bones and the clod partially covering these bones all go the same way. Except for the distal end of the femur, acquired long after by the Museum, the whole material described thereafter is then considered coming from the shale of the Vaches Noires cliffs, dated Upper Callovian-Lower Oxfordian. These theropod remains were the first to be described from diagnostic remains. It's also the first theropod

antedated by the genus name *Megalosaurus* Buckland, 1824.

Abréviations
MNHN Muséum national d'Histoire naturelle, Paris;
OUMJ Oxford University Museum, Oxford.

SYSTEMATICS

In the second edition of *Ossements Fossiles* (1824), Cuvier refers some material found in the region of Honfleur to two species of gavials that he distinguishes one from the other by the length of the snout (« Long snouted head », Short snouted head »).Cuvier comforts this distinction by accentuating the differences existing between the two vertebral systems found « in association » with the skulls. Each of these systems is thus referred to one or the other of the skulls : the « proximal convex system » to the long snouted species, the « concave system » to the short snouted one. Meanwhile, Geoffroy Saint-Hilaire (1825) unites both species under the genus name *Steneosaurus*. He distinguishes the long snouted species, *S. rostromajor*, whose type specimen (MNHN 8900) is the skull figured by Cuvier (1824 : pl.8, figs 1 ; 2), from the short snouted species, *S. rostrominor*, whose type (MNHN 8902 ; Cuvier 1824 : pl. X, figs 1-4) is represented by a complete mandible. The study and description by Geoffroy Saint-Hilaire are solely based on the cranial anatomy of the two crocodiles. The two binomial names thus created apply only to the skulls and in no way to the vertebrae already described by Cuvier and which Geoffroy Saint-Hilaire doesn't include in his work. Von Meyer (1832) separates the two crocodiles at the genus level. He creates the names *Metriorhynchus geoffroyii* for the short snouted species and *Streptospondylus altdorfensis* for the long snouted one, but differing in this way from Geoffroy Saint-Hilaire, includes all the material already described by Cuvier. Meyer perpetuates Cuvier's mistake by assigning the vertebrae and the skull to the same taxon. Although the name *Streptospondylus* that he proposes, as he outlines it himself (Meyer 1832: 227), makes reference to the peculiar structure of the vertebrae, he doesn't define any type specimen within the material referred to the species. *Streptospondylus altdorfensis* Meyer, 1832 is then an animal composed of theropod vertebral remains as well as

Geoffroy Saint-Hilaire as the type species of *Steneosaurus rostromajor*. This same skull is in fact composed of the remains of two distinct teleosaurs species (Eudes-Deslongchamps 1870: 303), *Steneosaurus edwardsi* Deslongchamps, 1866 and *Metriorhynchus superciliosum* Blainville, 1853 (Steel 1973). Following the ICZN (1999 : art. 73.1.5), a part of the material having been excluded from the composite type and transferred to other taxa, *Streptospondylus altdorfensis* is de facto only characterised by postcranial material, and the theropod vertebrae are designed here as a lectotype of this taxon. The specific name chosen by von Meyer is a reference to the cranial remains of teleosaurs found in Altdorf (Walch 1776 ; Collini 1784) and which, following Meyer's opinion, belong to the same taxon as those found near Honfleur. Bronn (1837 : 517) notes that the specific name *altdorfensis* is inappropriate for the Norman material, as he denotes a distribution not applicable to Cuvier's material. This condition is however not enough to invalidate the specific name. *Streptospondylus altdorfensis* is thus the good name to which the vertebrae originally described by Cuvier are to be referred.

This conclusion, also reached by Wells (unpublished), hasn't imposed itself to all. Most of the works following von Meyer's don't recognise the validity of the specific name and bring forth confusion. In 1842, Owen creates a new species, *Streptospondylus cuvieri*, and compares it with the Honfleur vertebrae which he names *Streptospondylus rostromajor*. The type of *S. cuvieri* is the anterior half of a dorsal vertebra coming from the Lower Bathonian of Chipping Norton. This isolated vertebra and whose description by Owen holds no scientific value, has never been figured and is nowadays lost : *S. cuvieri* is then considered *nomen dubium*. In 1861, Owen still associates the skulls and the vertebrae from Honfleur and places them, within crocodiles, in the suborder Opisthocoelia. More confusion is added when he includes in this suborder composite material (theropod, crocodile, sauropod) coming from various English localities and that he puts in its whole to the genus *Cetiosaurus* Owen, 1842. This arrangement doesn't prevent him to recognise the validity of the genus *Streptospondylus* ; but, without any explanation, Owen now designate the material under the specific name *cuvieri* and no more *rostromajor*. From then, several authors (Lennier 1870 ; Phillips 1871 ; Nopsca 1906, Huene 1926 ; Piveteau 1923) take the material kept in Paris for the type species *Streptospondylus cuvieri*. These works are

Honfleur material can be referred to *S. cuvieri* which is based on a lost fragment of vertebra with no specific value. However, if such were the case, *Streptospondylus cuvieri* would be a junior synonym of *S. altdorfensis* and become invalidated.

More recently, Walker (1964), after having shown that the type of *Streptospondylus cuvieri* wasn't Honfleur material and after having placed *Streptospondylus altdorfensis* in synonymy with *Steneosaurus rostromajor*, referred Cuvier's theropod material to a new species, *Eustreptospondylus divesensis* and chose for type of this new species the skull described by Piveteau in 1923. By doing so, he made closer the material from Normandy and the almost complete skeleton of *Eustreptospondylus oxionensis*, Walker, 1964 type species of the genus, although it does exist, as we shall see, differences between the two type materials. It has since then been demonstrated (Taquet & Welles 1977) that the postcrania described by Piveteau and the skeleton kept at the Oxford University Museum belonged to two distinct genera, *Piveteausaurus* Taquet & Welles, 1977 and *Eustreptospndylus* Walker, 1964. Moreover, nothing indicates that the Honfleur vertebrae are co-specific with the postcrania of *Piveteausaurus divesensis*. Walker's conclusions (1964) are only acceptable if one considers *Streptospondylus altdorfensis* a junior synonym of *Steneosaurus rostromajor*. But, in contradiction to what Walker (1964) assumes, the bibliographic list is not the same for the two species. *Steneosaurus rostromajor*, differing in that point with *Streptospondylus altdorfensis*, is only based on the skull figured by Cuvier (1822 : pl. X, figs 1-4) as specified by Geoffroy Saint-Hilaire (1825 : 147). It has been shown here above that this skull could be excluded from the type material and referred to another taxon. That's what Geoffroy Saint-Hilaire (1825) has done and that Walker (1964) doesn't take into account. The conclusions of the latter are thus rejected.

Superorder DINOSAURIA Owen, 1842
Order THEROPODA Marsh, 1881
Suborder TETANURAE Gauthier, 1986
Superfamily SPINOSAUROIDEA Stromer, 1915
Genus *Streptospondylus* Meyer, 1832

Streptospondylus altdorfensis Meyer, 1832

Streptospondylus altdorfensis Meyer, 1832, 106, 226.
Streptospondylus rostromajor sensu Owen

Streptospondylus cuvieri Owen, 1842 – Owen 1859 : 23.
 Laelaps gallicus Cope, 1867 : 235.
Megalosaurus cuvieri (Owen, 1842) – Huene 1908 : 332, figs 312, 313.
Eustreptospondylus divesensis Walker, 1964, *partim* : 124.

CHRESONYMY
Crocodile fossile Cuvier 1800b : 159
Espèce inconnue de crocodile Cuvier 1808 : 95, pls 1, 2.
Espèce inconnue de crocodile Cuvier 1812 : 16, pls 1, figs 3, 6, 10, pl. 2, figs 12, 13.
Espèce gigantesque de saurien Cuvier 1824 : 343, pl. 21, figs 34-39.
Streptospondylus cuvieri Owen, 1842 – Lennier 1870 : 42, pl. 8, fig. 1. – Phillips 1871 : 321, fig. 124. – Zittel 1890 : 724, fig. 627. – Nopsca 1905 : 289. – Piveteau 1923 : 121, pl. 1, fig. 4, pl. 3, figs. 1-3, pl. 4, figs 1-5. – Lapparent & Lavocat 1955 : 934.
Megalosaurus cuvieri (Owen, 1842) – Huene 1932 : 222. – Swinton 1955 : 132.
Eustreptospondylus divesensis Walker, 1964 – Welles & Long 1974 : 205.

LECTOTYPE - Last cervical vertebra and two first dorsals (MNHN 8787) ; last dorsal vertebra and two first sacrals (MNHN 8794) ; last sacral vertebra and first caudal (MNHN 8788) ; series of three dorsal vertebrae (MNHN 8907) ; dorsal vertebra (MNHN 8789) ; anterior dorsal vertebra (pectoral) (MNHN 8789) ; anterior dorsal vertebra (pectoral) (MNHN 8793) ; distal end of left pubis (MNHN 8605); distal end of right fibula (MNHN 8606) ; distal end of right tibia (MNHN 8607) ; right astragalus (MNHN 8606) ; right calcaneum (MNHN 8609).

REFERRED MATERIAL – Distal end of left femur (MNHN 9645).

HORIZON – Shales from Upper Callovian or Lower Oxfordian of the Vaches Noires cliffs, Calvados, France.
DIAGNOSTIC – Middle size theropod. Two hypapophyses on anterior dorsal vertebrae ; centrum of anterior dorsal vertebrae strongly opisthocoelous and ventrally flattened, posterior dorsal vertebrae platycoelous ; centrum of median and posterior dorsal vertebrae elongated ; lateral extension of the medial buttress above the dorsomedial edge of the ascending process of the astragalus doesn't reach the median part of the distal end of the tibia. ; large depression at the base of the ascending process of the astragalus, lack of posteromedial process on the astragalus.

DESCRIPTION
Cervical and anterior dorsal vertebrae
The series of three anterior vertebrae in relation with Honfleur is at the base of Cuvier's «convex system» (1824) and of the generic name *Streptospondylus* from Meyer. Although the position of the parapophyses may suggest that we are in fact dealing with the two last cervicals and the first dorsal (Welles, unpublished), the anatomy of the proximal end of the rib associated with this series, the presence of hypapophyses on two of the centra and the lack of epipophyses on the two neural arches preserved, suggest that this series is in fact composed of the last cervical vertebra and the two first dorsals (fig. 1).Only the posterior part of the last cervical is preserved. The postzygapophyses are high above the centrum, overhanging the neural canal about 50 mm. The articular facet of each postzygapophysis faces lateroventrally at an angle of 45° with the horizontal. The neural spine measures 32 mm at its base and only 16 mm at its end. From a square to a rectangular section , it culminates at 80 mm above the neural canal. Its anterior and posterior edges are not totally parallel, the anterior edge being inclined of a few degrees distally. It is in a rear position on the centrum, its posterior margin being at less than 1 cm in front of the posterior articular facet of the centrum.

The first dorsal vertebra, the second of the series, is nearly complete except the transverse processes partially broken. The centrum is 58 mm in length to which are added the 18 mm of the distal articular facet. Of hemispheric shape, it is fairly convex, unlike the proximal articular facet corollary concave. The centrum is 54 mm high proximally and, due to its posteroventral extension, 70 mm distally. The parapophyses situated 5 mm under the suture between the centrum and the neural arch are vertically oval. Posterodorsally to each parapophysis, a deep pleurocoel runs through the lateral face of the centrum and continues posteriorly for nearly 35 mm. The centrum is relatively large ventrally and displays two parallel ridges (hypapophyses) that thicken and diverge anteriorly. The presence of two hypapophyses is only known for *Eustreptospondylus*, *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993) having only one hypapophysis ventrally. The surface of the centrum is slightly concave between these two ridges. The neural arch is strongly fused to the centrum, but the suture remains visible and draws the dorsal limit of the pleurocoel. The neural arch is high and laterally

infrazygapophyseal fossa is the anteriormost. 26 mm in height, it forms an isosceles triangle composed of centroprezygapophyseal lamella proximally, prezygadiapophyseal lamella dorsally and proximal centrodiapophyseal lamella distally (Wilson 1999). The high infradiapophyseal fossa is bordered anteriorly by the anterior centrodiapophyseal lamella, posteriorly by the posterior centrodiapophyseal lamella, and opens ventrally on the centrum. The infrapostzygapophyseal fossa is widely open laterally and posteriorly. It is bordered anteroventrally by the posterior centrodiapophyseal lamella and by the postzygadiapophyseal lamella anterodorsally. These three lateral fossae are very deep compared to those seen in *Allosaurus* or *Monolophosaurus* (Zhao & Currie 1993). The distance between the ends of the pre- and postzygapophyses is 78 mm. The prezygapophyses are strongly curved at the top and reach 55 mm above the centrum. Anteriorly, they extend as far as the articular convexity of the centrum. The postzygapophyses posterolaterally oriented overtake the level of the posterior face of the centrum by 12 mm. The articular facets slope down medially forming a 35° angle with the horizontal. The neural spine culminates 60 mm above the neural canal. 30 mm in length at its base, it gets thinner dorsally to become equally long and wide (12 mm) at its end.

The third vertebra of the series, the second dorsal, possesses parapophyses extending to the base of the neural arch. The transverse processes haven't been preserved. The strongly opisthocoelous centrum is 58 mm long dorsally and 64 mm ventrally for a total height of 70 mm proximally and 68 mm distally. The longitudinal depression into witch the pleurocoel is situated extends for nearly 35 mm on the lateral face of the centrum. The ventrolateral concavity situated between the hypapophysis and the thick bony edge boarding the pleurocoel ventrally is much more pronounced than the one on the last cervical. In a similar way, the two hypapophyses situated on the ventral face of the centrum are much more prominent and close, and diverge more strongly proximally. They form the attach point of *M. longus colli ventralis*. In posterior view, the centrum is 64 mm high for an almost equal width. The neural canal is 14 mm high, 16 mm wide, and is not dug in the centrum. The prezygapophyses reach 50 mm and the postzygapophyses 62 mm above the centrum. The articular facet of the postzygapophyses form an angle of 45° with the horizontal, more important than in the last cervical. The neural spine reaches 76 mm above the neural canal, is rounded at its top and is very short anteroposteriorly. There is hyposphene-hypantrum type articulation between the first dorsal vertebrae.
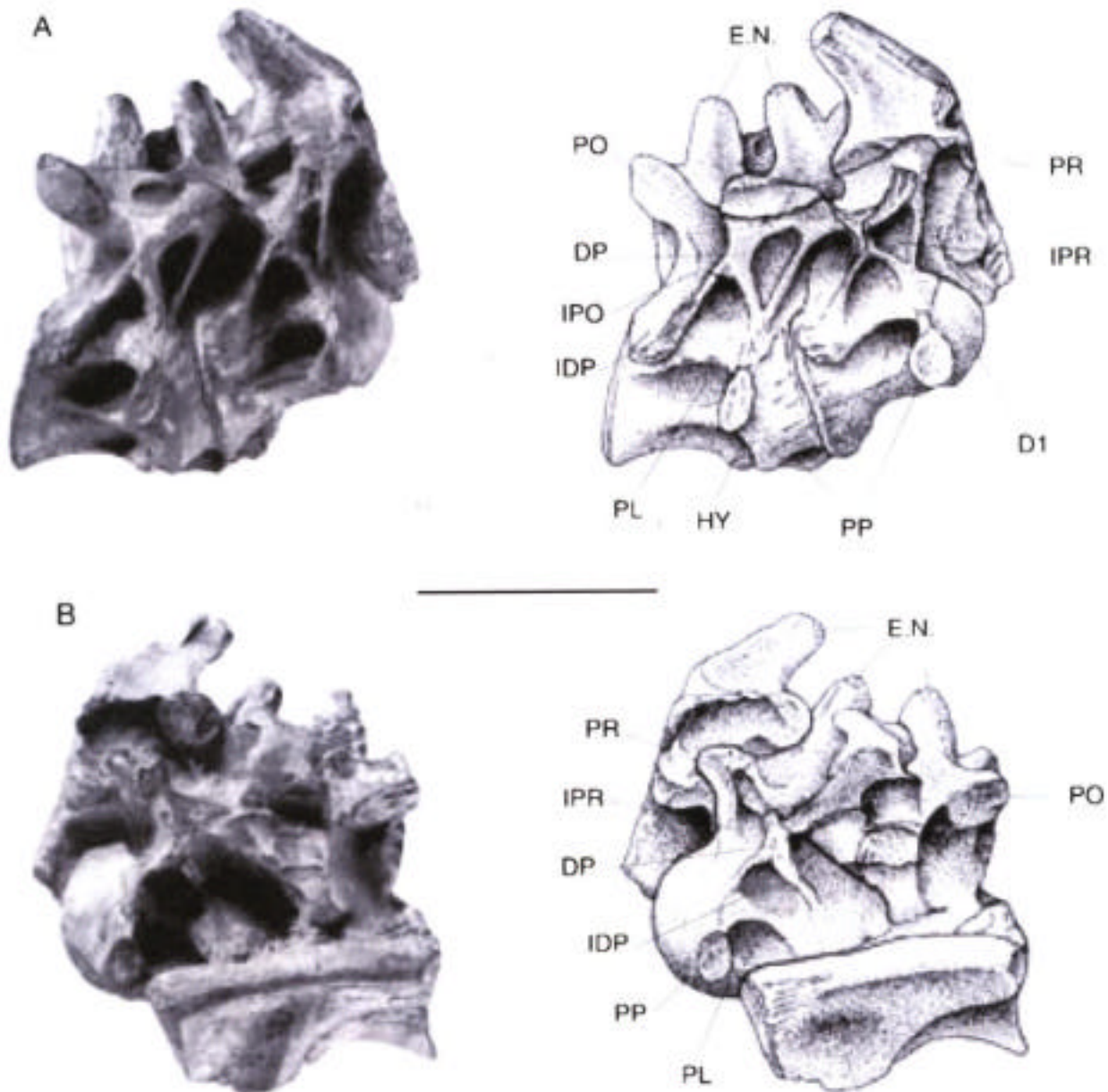
Fig. 1 – *Streptospondylus altdorfensis* Meyer, 1832 (MNHN 8787), last cervical vertebra, first and second dorsal; **A**, right lateral view; **B**, left lateral view. Abbreviations : **C**., **D**. dorsal rib; **E.N.**, neural spine; **DP**, diapophysis; **D1**, first dorsal vertebra; **HY**, hypapophysis; **IDP**, infradiapophyseal fossa; **IPO**, infrapostzygapophyseal fossa; **IPR**, infraprezygapophyseal fossa; **PL**, pleurocoel; **PO**, postzygapophysis; **PP**, parapophysis; **PR**, prezygapophysis. Scale bar : 9 cm.

Dorsal vertebrae

The two isolated centra (MNHN8793 and 8789) belong undoubtedly to anterior dorsal vertebrae. Like the first dorsal, here above described, they can be defined as pectoral due to the position of the parapophyses across the centrum and the neural arch. The first centrum (MNHN8793), 72 mm long and 62 mm high, is slightly opisthocoelous. Its ventral and lateral faces are fairly concave. Two deep depressions, 35 mm long by 22 mm, dig anterodorsally the lateral faces of the centrum, anteriorly deepening. If the parapophyses are higher than those of the type series, this vertebra doesn't seem to continue this series. It could constitute the fourth or the fifth dorsal. The second isolated centrum (MNHN 8789) seems to possibly articulate with the preceding one : it would then be the fifth or the sixth dorsal. The parapophyses have an even higher position on the centrum. This one, 74 mm long and 65 mm high, has a lightly pronounced convexity between opisthocoely and amphicoely. The lateral depressions are a bit longer (40 mm) and higher (25 mm) than the preceding vertebra. On these two vertebrae, the suture between the centrum and the neural arch is
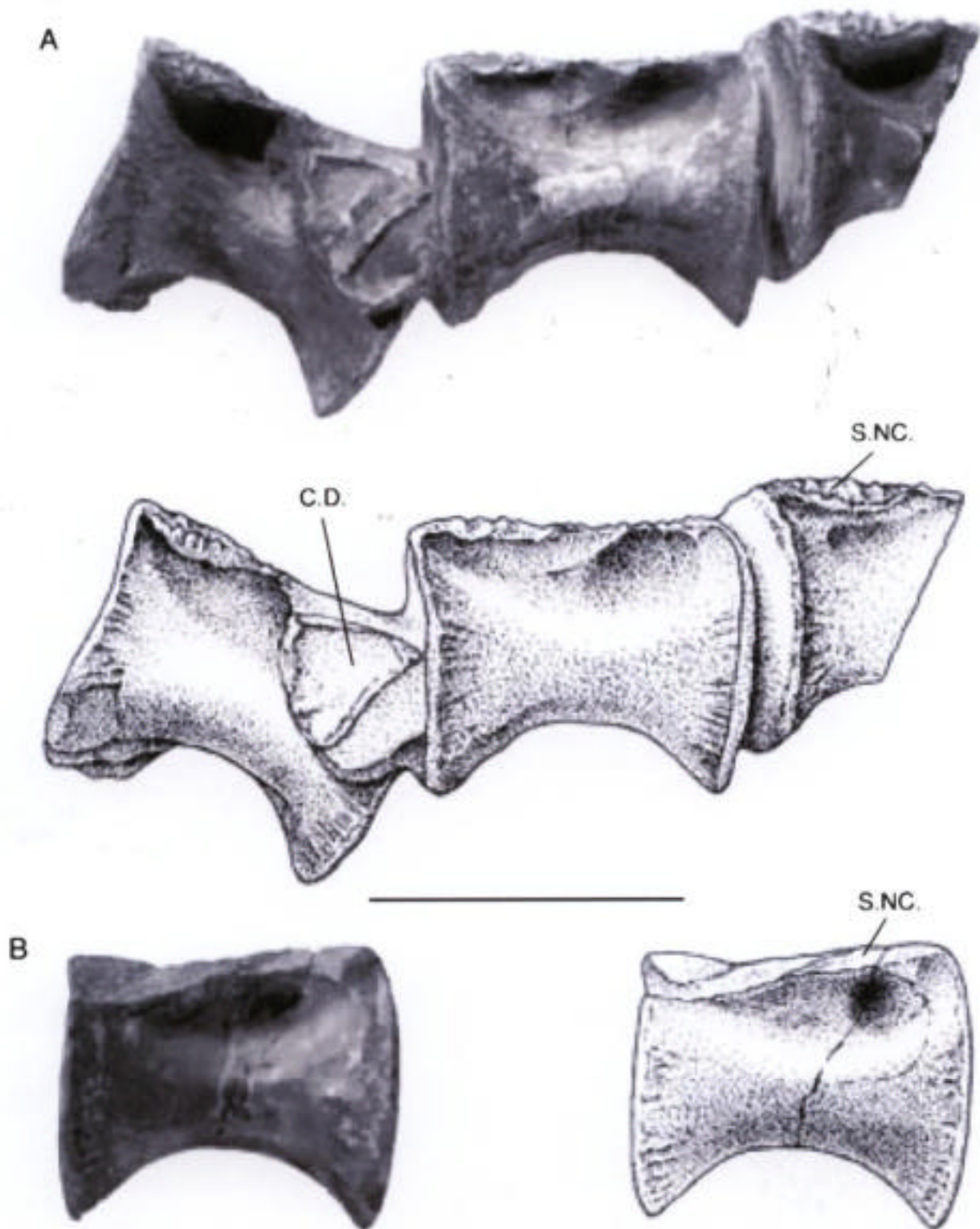
Fig. 2 – *Streptospondylus altdorfensis* Meyer, 1832; **A**, dorsal vertebrae (MNHN 8907), right lateral view; **B**, dorsal vertebra (MNHN 8789), right lateral view. Abbreviations : **C.D.** dorsal rib; **S.NC.**, neurocentral suture. Scale bar : 9 cm.

open and not broken and might indicate the relative immaturity of the specimen. The three vertebrae in connection (MNHN 8907) already figured by Cuvier (1812) and Piveteau (1923) cannot any more be interpreted as pectoral vertebrae due to the absence of parapophyses

vertebrae, the suture between centrum and neural arch is open, the latter having not been preserved. The first centrum is incomplete anteriorly. It is 74 mm high posteriorly and displays a pronounced lateral depression just below the suture with the neural arch. The

respectively 90 mm and 95 mm long for a height of 76 mm and 79 mm. These three amphicoelous centra possess laterally a large and lightly deep anterodorsal depression and are characterised by their ventral face. This one is actually strongly concave as in the pectoral vertebrae, but differ from the latter in that the ventral surface is here clearly flattened and form a plate 20 mm wide for the anteriormost vertebra, and 30 mm wide for the posteriormost vertebra. A last isolated centrum from a dorsal vertebra (MNHN 8789), 97 mm long and 80 mm high, posteriorly completes this series of three vertebrae (fig. 2B).

Posterior dorsal and anterior sacral vertebrae
Another series of vertebrae in connection (MNHN 8794), described and figured by Cuvier (1812), Nopsca (1906) and Piveteau (1923), includes a small fragment of the postzygapophyses of the penultimate dorsal vertebra, the half of the last dorsal, the first sacral and the anteriormost part of the second sacral (fig. 3A). The section of the hyposphene of the penultimate dorsal vertebra is unusual and consists in two distinct branches extending to the hypantrum of the last dorsal (Nopsca 1906 : fig. 4). The preserved distal end of the last dorsal is 96 mm high at its articular facet. This one displays a sigmoid curvature, its posterodorsal part extending distally to cover the centrum of the first sacral vertebra. The suture between the centrum and the neural arch is open. This last one is nevertheless kept associated to the centrum, maintained into place by 3 mm of sediment acting like cement at the level of the suture. The infraprezygapophyseal fossa is small and anteriorly open. The infradiapophyseal fossa is of a more important size than the preceding one, its base extending almost all along the neural arch. The anterior centrodiapophyseal lamella is a lot thicker (8 mm) than the posterior one (3 mm) which melts with the neural arch above the suture. The two lamellae meet under the diapophysis giving the dorsal edge of the infradiapophyseal fossa a rounded shape. The infrapostzygapophyseal fossa is the deepest of the three and opens widely distally. The zygapophyses have the same height, 57 mm above the centrum, and form, along with the pre- and postzygadiapophyseal fossae, a horizontal plate, slightly concave in its centre in lateral view. The postzygapophyses are continuous for 18 mm behind the centrum. The neural spine is broken. It is 7 mm wide and 40 mm long at its base and is strongly distal to the centrum. Its anterior edge is deflected by 50° distally. Although not entirely preserved, there are two postspinal lamellae which probably originated on the posterior edge of the neural spine. The neural canal is 22 mm wide that is 6 mm more than the first dorsal and digs the dorsal face of the centrum for 10 mm.

This last dorsal vertebra is very different from that reported for *Megalosaurus bucklandi* (OUMJ.13577). The centrum is more elongated than in *Streptospondylus*. The posterior face of the centrum is flat and not concave as in *Megalosaurus*. The dorsal third of the posterior face is distally bending in *Megalosaurus bucklandi* and it is the superior third which is bending distally in *Streptospondylus*. The sigmoid curvature in lateral view is thus inverted in both genera. The pleurocoel is deeper and above all longer in *Megalosaurus bucklandi*. The ventral surface is a lot flatter and the postzygapophyses do not extend beyond the length of the centrum in *Megalosaurus bucklandi.* The infraprezygapophyseal, infradiapophyseal and infrapostzygapophyseal fossae are distinct in *Streptospondylus* but the infraprezygapophyseal and infradiapophyseal fossae are continued in *Streptospondylus*.

The first sacral vertebra is complete except for the neural spine. The centrum is 98 mm long, 80 mm high and widely concave ventrally. There are no pleurocoel on its lateral faces. The neural arch is completely fused to the centrum, even if the suture remains visible.
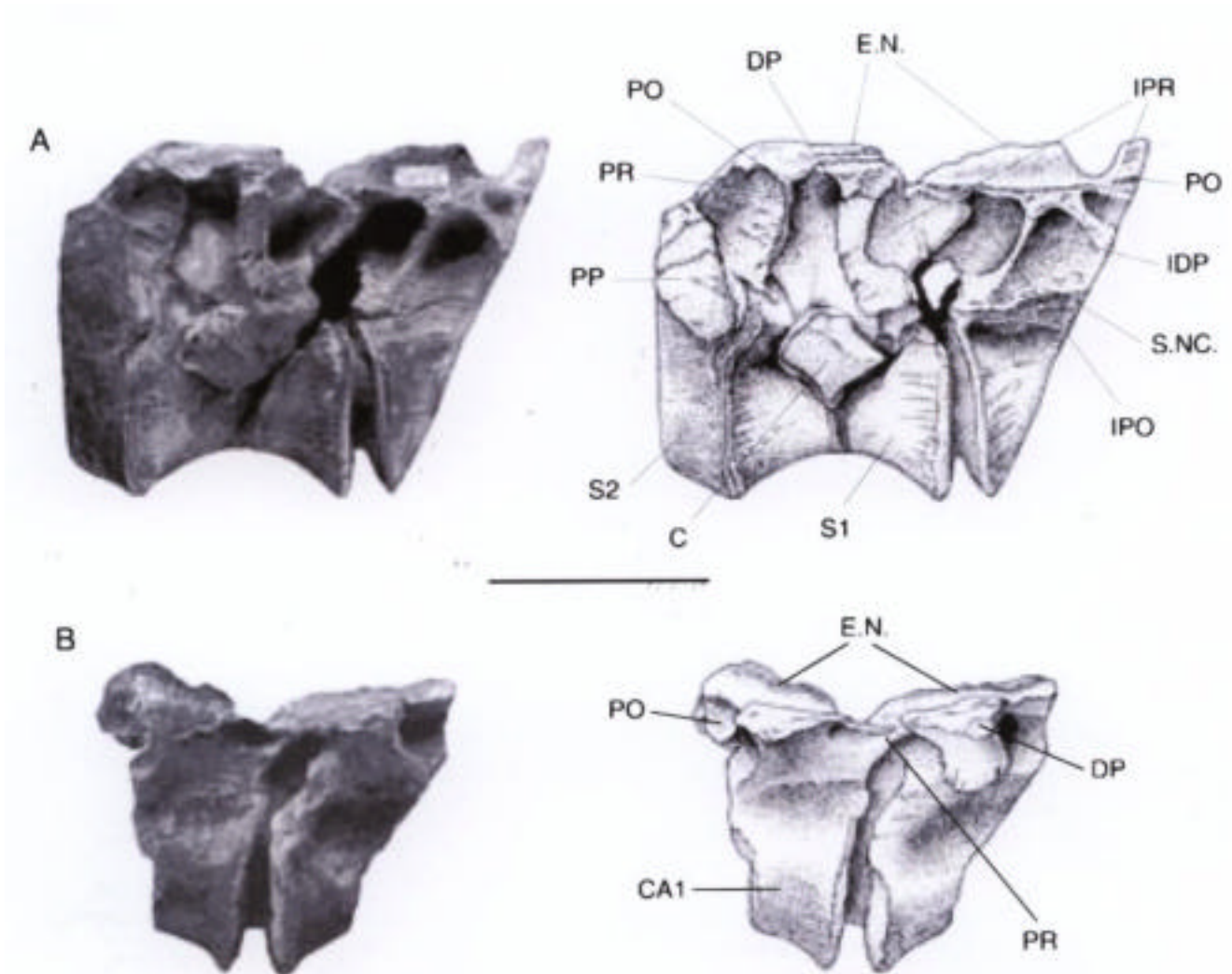
Fig. 3 – *Streptospondylus altdorfensis* Meyer, 1832; **A**, dorsal and sacral vertebrae (MNHN 8794), right lateral view; **B**, Last sacral and first caudal (MNHN 8788) right lateral view. Abbreviations : **C.**, rib; **CA1**, first caudal; **E.N.**, neural spine; **DP**, diapophysis; **IDP**, infradiapophyseal fossa; **IPO**, infrapostzygapophyseal fossa; **IPR**, infraprezygapophyseal fossa; **PO**, postzygapophysis; **PP**, parapophysis; **PR**, prezygapophysis; **S1**, first sacral; **S2**, second sacral; **S.NC**, neurocentral suture. Scale bar : 9 cm.

The articular facet for the first sacral vertebra is prominent, 36 mm long and 35 mm high. This articular facet is connected to the diapophysis through a bony lamella, 14 mm thick. This lamella, which seems to correspond to the anterior centrodiapophyseal lamella of the dorsal vertebrae, is concave anteriorly and forms the distal wall of the infraprezygapophyseal fossa opened anterolaterally. The diapophysis is situated proximally on the centrum. The infradiapophyseal fossa is not very deep, perforated in its centre by a small foramen and limited distally by a bony ridge very slightly pronounced (posterior centrodiapophyseal lamella).

Abbreviations: **L**, anteroposterior length; **W**, width; **H** height.

Pubis diaphysis (8605)	L	29
Pubis diaphysis (8605)	W	48
Pubic foot (8605)	L	104
Pubic foot (8605)	W	60
Tibia diaphysis (8607)	L	50
Tibia diaphysis (8607)	W	68
Tibia distal end (8607)	W	140
Astragalus (8608)	W	114
Astragalus (8608)	H	87
Calcaneum (8609)	L	60
Calcaneum (8609)	H	35
Calcaneum ant. (8609)	W	19
Calcaneum post. (8609)	W	285
Femur (9645)	W	135

Table 1. – Measures in mm of some bones of

Like the infradiapophyseal fossa, the infrapostzygapophyseal fossa is not very deep and nearly not visible in lateral view. The prezygapophyses originate at the articular facets level destined to the sacral vertebrae and extend 60 mm above and 13 mm in front of the centrum. Their articular facets are medially inclined at an angle of 45°. The base of the prezygapophyses is concave anteriorly and forms the dorsal margin of a large (20 mm) intervertebral foramen. The postzygapophyses culminate at 78 mm above the centrum. The neural spine, 55 mm long, is broken at its base. Posteriorly, the centrum is fused with the second sacral's centrum. Only the anteriormost 35 mm of the centrum of the second sacral and the base of the corresponding neural arch are preserved. The centrum ventral face is strongly squeezed transversely. The parapophyses destined to bear the second sacral ribs are 55 mm high and oriented ventrally. The neural arch is fused with the one from the preceding vertebra. The neural canal has an elliptic section along with a large vertical axis of 33 mm and a small horizontal axis of 29 mm.

Posterior sacral vertebrae and first caudal vertebra
The two last vertebrae in connection known from *Streptospondylus altdorfensis*, described by Nopsca (1906), are the last sacral and the first caudal (fig. 3B). Only the posterior half of the centrum and a little more of the neural arch are preserved. The centrum is a lot more rounded ventrally than on the two first sacral vertebrae. There is no pleurocoel. Its posterior articular facet is higher than wide and slightly sigmoid in lateral view. The neural arch is fused to the centrum and bears a large rectangular articular facet on which is fixed the last sacral rib. The diapophyses are situated just above the articular facets. They are horizontal, 45 mm long anteroposteriorly and inclined at nearly 40° distally. The postzygapophyses faces, strongly inclined laterally, are at the same height than the diapophyses, i.e. 50 mm above the centrum. The neural spine is broken. It is at least 70 mm long and displays a deep postspinal groove. The first caudal vertebra is connected to the last sacral but is not fused with it. The diapophyses display a more pronounced distal orientation (50°) than those of the last sacral for an equal anteropostrior length.

Fig. 4 - *Streptospondylus altdorfensis* Meyer, 1832; distal end of left pubis, lateral view (MNHN 8605). Scale bar : 3 cm.

The infraprezygapophyseal fossa is strongly restricted and nearly closed compared to that of the last sacral vertebra. The internal spongy structure of the centrum of the first caudal is also a lot more "opened" than that of the the centrum of the first caudal of *Streptospondylus*. The diapophyses are longer anteroposteriorly and show a more

sacral vertebra (Nopsca 1906 : fig. 7). Here again, numerous characters allow to differentiate the first caudal vertebra of *Streptospondylus* from that reported for

Megalosaurus bucklandi. The infraprezygapophyseal fossa is strongly restricted and nearly closed compared to that

spongy structure of the centrum of the first caudal is also a lot more "opened" than that of the last sacral vertebra (Nopsca 1906 : fig. 7). Here again, numerous characters allow to differentiate the first caudal vertebra of *Streptospondylus* from that reported for *Megalosaurus bucklandi* (OUMJ.13578). There isn't, in fact, no apparent pleurocoel on the longer centrum of the first caudal of *Streptospondylus*. The diapophyses are longer anteroposteriorly and show a more pronounced orientation than those of *Megalosaurus bucklandi*.

Pubis
The distal end of the left pubis has been, by turns, identified by Cuvier (1824) as a fibula, by Nopsca (1906), Piveteau (1923) and Huene (1926) as an ulna, before Walker (1964) identified it correctly (Fig. 4). At the breakage level, the diaphysis is wider transversely than longer anteroposteriorly (Table 1). The pubic foot is of triangular section like in *Allosaurus* (Madsen 1976), and not inverted L shaped like in *Sinraptor* (Currie & Zhao 1993), *Torvosaurus* (Galton & Bensen 1979; Britt 1991) or *Metriacanthosaurus* (Huene 1926; Walker 1964). Its posterior extension, comparable to that observed in *Eustreptospondylus*, remains modest and the anterior projection is quasi inexistent compared to that of *Allosaurus*, *Ceratosaurus* (Gilmore 1920) and the Tyrannosauridae. If the preserved part of the diaphysis displays medially no contact zone with the right pubis, the foot, however, is flattened medially along all of its length to define the symphysis at which the two pubes met. The buttress beginning at the anteriormost point of pubic foot medial face and extends posteriorly on nearly 40 mm seems to define a co-ossification zone between the two pubes.

Tibia, astragalus and calcaneum
The distal end of a right tibia associated with the astragalus, the calcaneum and the distal end of the fibula were first described by Cuvier back in 1824. None of these bones is fused with the other. The distal end of the tibia is thin anteroposteriorly (fig. 5) (Table 1). Its anterior surface is depressed where the astragalus, the calcaneum and the fibula contact. This depression is limited by a buttress overhanging the dorsomedial edge of the astragalus ascending process. This buttress has a very limited lateral extension since it doesn't reach the median part of the tibia distal end. This character helps distinguish the tibia of *Streptospondylus* from that of other Jurassic European theropods such as *Poekilopleuron* (Eudes-Deslongchamps 1837), *Megalosaurus* (Owen 1856) or *Eustreptospondylus* whose buttress displays a lateral extension much more pronounced which rejects even more the ascending process of the astragalus. The astragalus covers the distal end of the tibia (fig. 5). The articular cavity in which the latter fits is less deep and narrow that the one observed in *Sinraptor*. It is subdivided into two depressions, the lateral one situated below the ascending process being the deepest (fig. 6). As in *Poekilopleuron*, and unlike what can be observed in *Allosaurus* and *Sinraptor*, there is no real process on the posterior margin of the astragalus to cover the posteromiedial corner of the tibia. The contact between astragalus and fibula is restricted to a small facet, incompletely preserved, anterolateral to the ascending process. The ascending process is about 4 cm high (Table 1). In anterior view, it represents the half of the astragalus height, which is proportionately more important that what can be observed in *Sinraptor*, *Eustreptospondylus* or *Torvosaurus*.
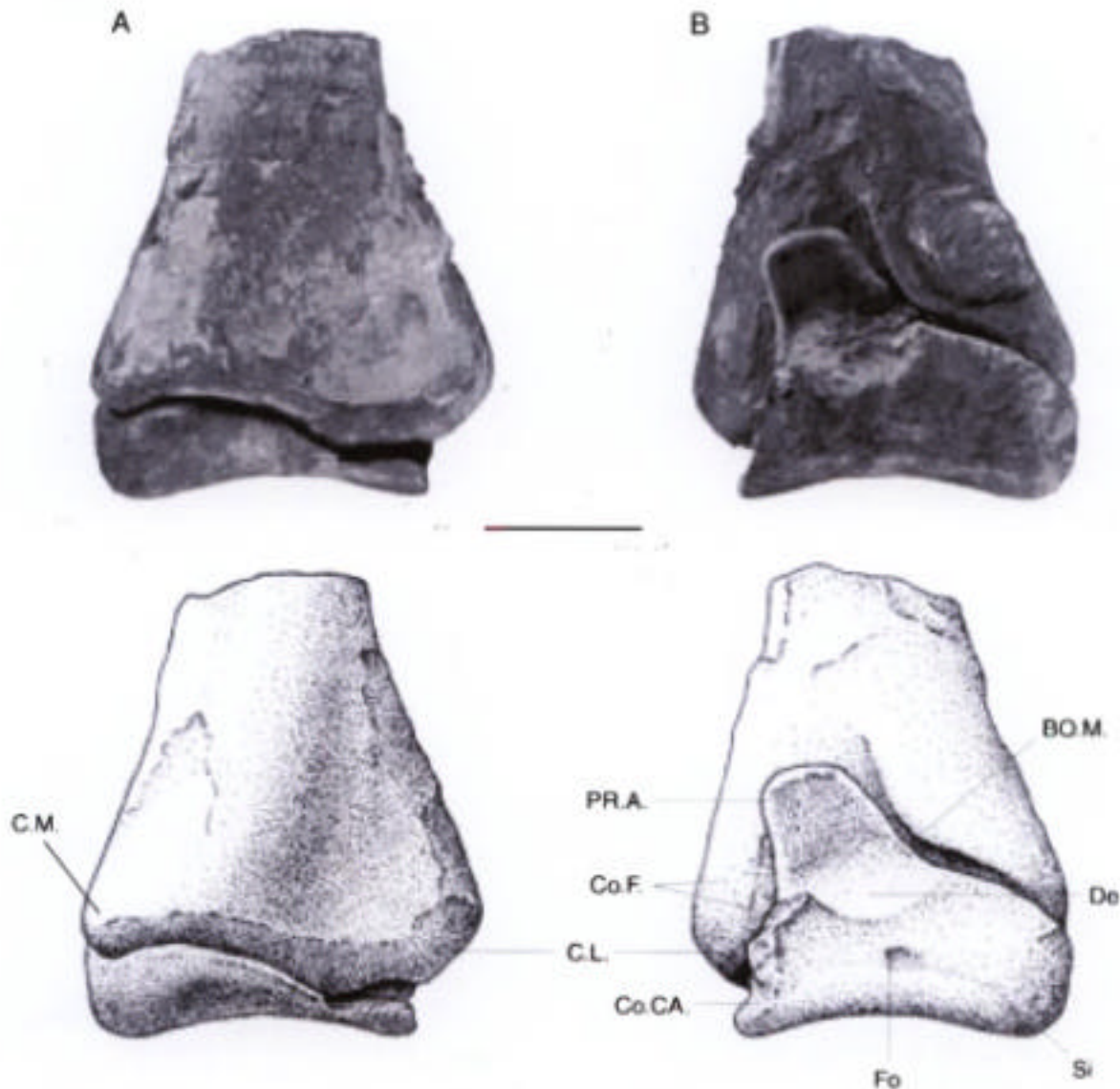
Fig. 5 - *Streptospondylus altdorfensis* Meyer, 1832; distal end of right tibia and right astragalus (MNHN 8607, 8608); **A** posterior view; **B**, anterior view. Abbreviations : **B.O.M.**, median buttress; **C.L.**, lateral condyle; **C.M.**, median condyle; **Co.Ca.**, contact zone with the calcaneum; **Co.F.** contact zone with the fibula; **De.** basal depression; **Fo.**, foramen; **PR.A.**, astragalus ascending process; **Si.**, anterior groove. Scale bar: 5 cm
.

The astragalus covers the distal end of the tibia (fig. 5). The articular cavity in which the latter fits is less deep and narrow that the one observed in *Sinraptor*. It is subdivided into two depressions, the lateral one situated below the ascending process being the deepest (fig. 6). As in *Poekilopleuron*, and unlike what can be observed in *Allosaurus* and *Sinraptor*, there is no real process on the posterior margin of the astragalus to cover the posteromiedial corner of the tibia. The contact between astragalus and fibula is restricted to a small facet, incompletely preserved, anterolateral to the ascending process. The ascending process is about 4 cm high (Table 1). In anterior view, it represents the half of the astragalus height, which is proportionately more important that what can be observed in *Sinraptor*, *Eustreptospondylus* or *Torvosaurus*.

An anterior depression marks the base of the ascending process, as in *Sinraptor*. The shape of the process is similar to that of *Allosaurus* more than to any other theropod. It is actually more or less symmetrical and its distal part is rounded and not unravelled like in *Poekilopleuron*, *Sinraptor*, *Eustreptospondylus* or *Megalosaurus*. The groove running along the anterior faces of the astragalus condyles is much less pronounced than in *Allosaurus* or *Sinraptor*. It runs through a foramen situated
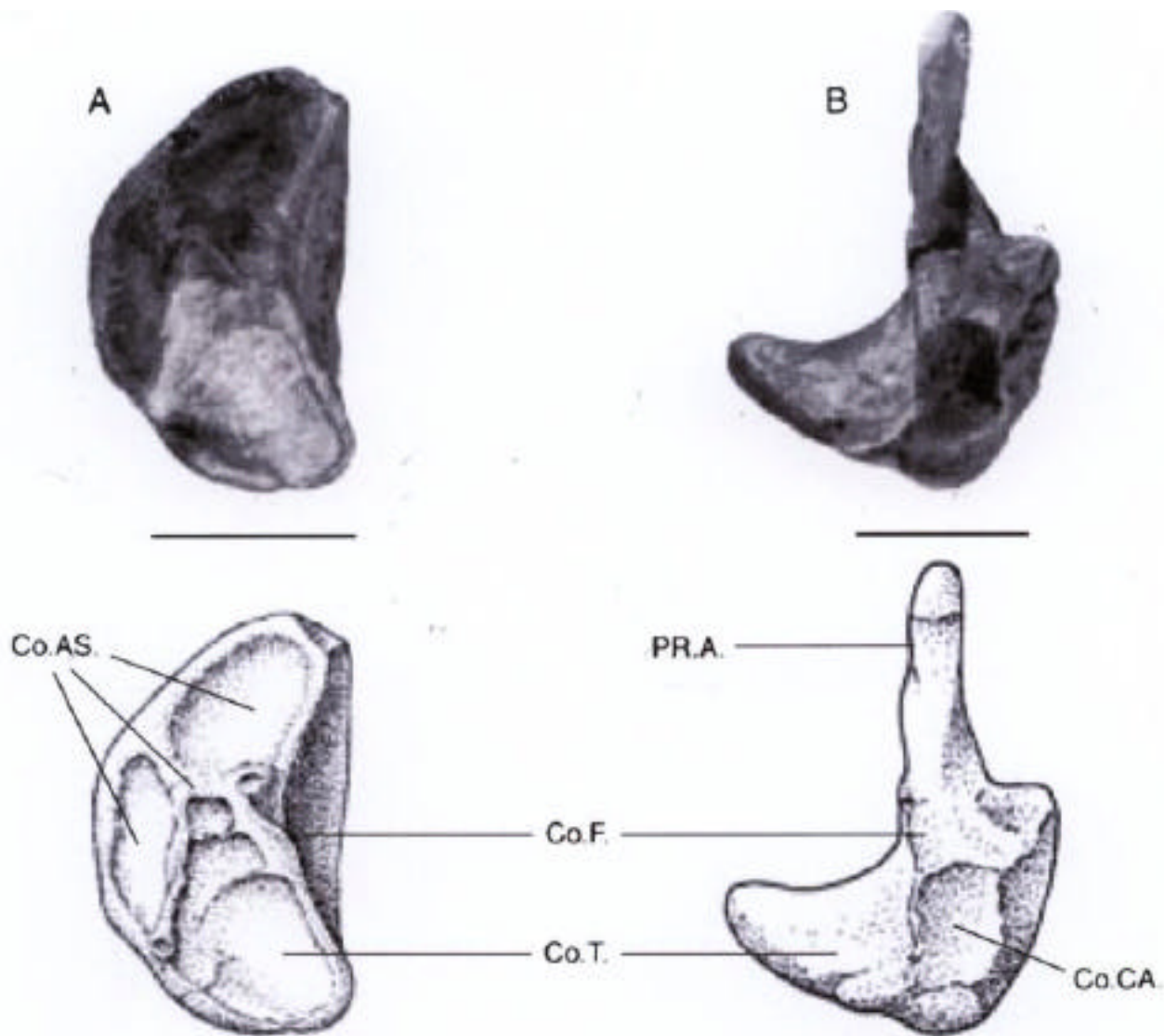
Fig.6 - *Streptospondylus altdorfensis* Meyer, 1832; **A**, right calcaneum (MNHN 8609), lateral view; **B**, right astragalus (MNHN 8608), lateral view. Abbreviations : **Co.AS.**, contact zone with the astragalus; **Co.F.**, contact zone with the fibula; **Co.T.**, contact zone with the tibia; **PR.A.**, ascending process. Scale bars : 3 cm

35 mm under the base of the ascending process.

The calcaneum is of a more or less triangular shape in lateral view. In distal view, unlike in *Allosaurus*, the calcaneum is less wide anteriorly than posteriorly (Table 1). It does not cover completely the fibula which articulates as well in a less important way with the astragalus. The lateral face of the calcaneum is flat, whereas its dorsal face, destined to receive the fibula, is slightly concave on all of its length. In medial view, the bone surface is divided into three distinct depressions. The posteriormost depression contacts the tibia (fig. 6A). The ventral and anterior cavities are separated by a small ridge a lot less pronounced than that in *Allosaurus* and

Sinraptor, the whole assuring a narrow and unmoveable contact between the astragalus and the calcaneum.

Femur
The distal end of a left femur (fig. 7A), first figured by Gaudry (1890), was given to the Muséum d'Histoire naturelle by the small seminary of Beauvais and certainly does not belong to the Bachelet collection. The source of this femur part remains unknown and its association with the aforementioned described material is only due to the similarity between the clod covering this bone and the one preserved onto the vertebrae.

In distal view, the median condyle lies longitudinally, is narrow transversely, whereas
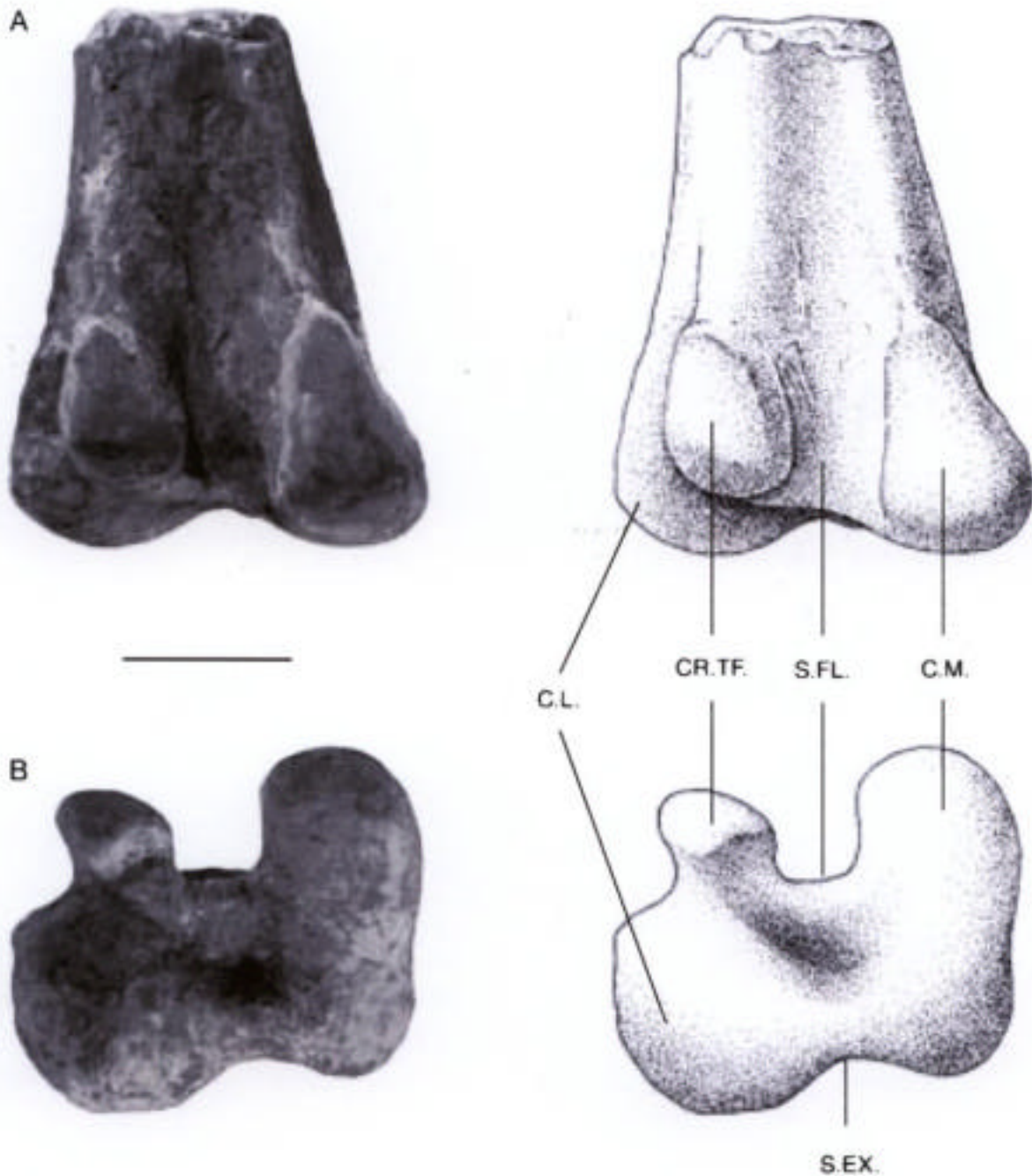
Fig. 7 - *Streptospondylus altdorfensis* Meyer, 1832; distal end of a left femur (MNHN 9645); **A**, posterior view; **B**, distal view. Abbreviations: **C.L.**, lateral condyle; **C.M.**, median condyle; **CR. TF.**, crista tibiofibularis; **S.EX.**, extending groove; **S.FL.**, flexing groove. Scale bar: 5 cm.

the lateral condyle appears more rounded (fig. 7B). As in all theropods except *Baryonyx* (Charig & Milner 1997), the median condyle shows a ventral extension more pronounced than the lateral condyle. Its posterior extension is more important than what is observed in *Megalosaurus bucklandi* (Owen 1856). The condyles are anteriorly separated by the extending groove and posteriorly by the flexing groove. The extending groove is just slightly concave compared to the flexing groove, a lot deeper. A buttress lightly pronounced but

crossed ligaments, runs longitudinally at the bottom of the flexing groove. This buttress, present in *Megalosaurus*, *Allosaurus* or *Sinraptor* has not been observed in *Eustreptospondylus*. The flexing groove is laterally boarded by the crista tibiofibularis which originates at the level of the posteromedial face of the lateral condyle. The crista tibiofibularis is slightly laterally deflected and lays posteriorly as far as the median condyle, to form a lateral depression, the trochlea fibularis, in which fits the proximal end

groove of *Megalosaurus bucklandi* appears deeper and less open than that of *Streptospondylus*.

DISCUSSION

The Callovio-Oxfordian of the Vaches Noires and its surroundings has already given numerous remains of theropod dinosaurs (Douvillé 1885; Buffetaut, Pennetier & Pennetier 1991; Buffetaut & Enos 1992; Buffetaut 1994), including the postcrania of *Piveteausaurus divesensis* (Piveteau 1923; Taquet & Welles 1977) and that of an indeterminate theropod (Knoll, Buffetaut & Bülow 1999). The whole of this material has most of the time been compared and assigned to the Megalosauridae family, known in the Bajocian and the Bathonian of England (Buckland 1824; Owen 1856; Phillips 1871; Waldman 1974) and of the region of Caen (Eudes-Deslongchamps 1837). If some recent phylogenetic analyses suggest the close relationship existing between the genera *Megalosaurus*, *Afrovenator, Torvosaurus* and *Eustreptospondylus*, grouped within the clade Spinosauroidea (Sereno *et al.* 1994, 1996), the exact affinities of the Vaches Noires material are far from being resolved. The discovery of *Lourinhanosaurus antunesi* (Mateus, 1998) in the Upper Kimmeridgian of Portugal and of *Neovenator salerii* (Hutt, Martill & Barker, 1996) in the Barremian of the Isle of Wight confirms the presence of Allosauroidea in Europe as soon as the Upper Jurassic and puts the question about the relations existing between the theropod material of the Vaches Noires either with Spinosauroidea or Allosauroidea. A quick examination of the Vaches Noires postcrania (Knoll, Buffetaut & Bülow, 1999) seems to confirm its close relationships, already suggested, with the allosauroids. The ventral extension of the paraoccipital processes under the foramen magnum is a character only found effectively in *Acrocanthosaurus* (Stovall & Langston, 1950) and *Allosaurus* (Madsen 1976). In the same way, the extremely reduced participation of the supraoccipital to the superior margin of the foramen magnum, character also present in *Piveteausaurus*, *contra* what shows the last figure of the cranium (Taquet & Welles, 1974 : fig. 5), is found in numerous Allosauroidea like *Allosaurus, Acrocanthosaurus, Sinraptor, Monolophosaurus* or *Giganotosaurus* (Carolini & Salgado, 1995). In the Spinosauroidea like *Eustreptospondylus* (Huene 1932) and *Baryonyx* (Charig & Milner, 1997), the supraoccipital on the contrary largely participates to the foramen magnum superior edge. *Piveteausaurus* and the Vaches Noires

postcrania are thus considered here belonging to two different Allosauroidea.

Streptospondylus belongs undoubtedly to Tetanurae and displays numerous synapomorphies of this clade (Sereno *et al.* 1996; Holtz 2000): cervical and anterior dorsal vertebrae strongly opisthocoelous, presence of an extension groove in the femur anterodistal region, distal end of tibia extended lying on the calcaneum, presence of a horizontal extending groove on the astragalus condyles, astragalus condyles anteroventrally oriented, astragalus ascending process mediolaterally reduced. The position of *Streptospondylus* within Tetanurae, among Spinosauroidea or Allosauroidea, is more than problematic. First of all *Streptospondylus* is only known from a small quantity of postcranial material, then the phylogenetic relationships between Allosauroidea and Spinosauroidea are still much debated, the monophyly of this group being still contested (i.e. Sereno *et al.* 1994, 1996, 1998; Charig & Milner 1997; Holtz 2000).

The presence of hypapophyses on the first dorsal vertebrae is, following Holtz (2000), a synapomorphy of clade Allosauroidea (*sensu* Sereno *et al.* 1996). If this character is absent in certain Spinosauroidea like *Torvosaurus* or *Baryonyx*, it is nevertheless present in one of them, *Eustreptospondylus*. The hypapophyses are in fact strongly developed and prominent in *Allosaurus* and *Sinraptor*, whereas they are a lot more discreet in *Monolophosaurus*, *Eustreptospondylus* and *Streptospondylus*. In the two latter genera, the ventral surface of the centrum does not bear a simple hypapohysis which prolongs the ventral keel like in *Allosaurus* or *Sinraptor*, but two hypapophyses clearly individualised one from the other anteriorly. This character, showing the close relationships existing between *Streptospondylus* and *Eustreptospondylus*, is present in none other theropod. The presence of a ventral keel on the centrum of the dorsal vertebrae seems to be a synapomorphy of Tetanurae (Rauhut 2000). This character is consequently found in all Allosauroidea such as *Allosaurus*, *Monolophosaurus*, *Sinraptor*, *Acrocanthosaurus* (Harris 1998), but also in some Spinosauroidea like *Torvosaurus* and *Baryonyx*. This ventral keel is absent in only two Teanurae, *Streptospondylus* and *Eustreptospondylus*. A last vertebral character underlines the close relationships of these two genera from the Late Middle Jurassic. Although in most theropods the dorsal vertebrae centrum length is inferior to equal to its height, in Coelophysoidea, *Streptospondylus* and *Eustreptospondylus*, the centrum significantly

morphology of *Streptospondylus* is similar to that observed In Spinosauroidea, the distal being poorly developed posteriorly and even less anteriorly as is the case in *Eustreptospondylus, Torvosaurus, Baryonyx* and *Afrovenator.* On the other hand, the pubic foot shows a posterior extension significant in most of Allosauroidea (i.e. *Acrocanthosaurus, Allosaurus, Giganotosaurus, Sinraptor*). Last, like most theropods, *Streptospondylus* shows no posteromedial process of the astragalus. This process, which covers the distal end of the tibia, is found in Allosauroidea for which an astragalus is known (*Allosaurus, Sinraptor, Acrocanthosaurus*). *Streptospondylus altdorfensis* appears then very close to *Eustreptospondylus oxionensis* from the Callovian of England, as was already noted by Nopsca (1906) and Walker (1964). This last genera, known from an almost complete skeleton, is from the clade Spinosauroidea (Sereno *et al.* 1994, 1998), to which is also attached here *Streptospondylus.*

The diversity of European theropods during the Late of the Middle Jurassic and the Early Late Jurassic seems confirmed by the present study, with at least six distinct forms including 3 spinosauroids (*Streptospondylus, Eustreptospondylus, Metriacanthosaurus*) and 3 allosauroids (*Piveteausaurus,* the Vaches Noires specimen and *Lourinhanosaurus*). This theropod fauna differs noticeably from that of the Middle Jurassic (Bathonian) of Europe which is constituted of taxon attached to Spinosauroidea and particularly Megalosauridae. The recent discovery in Normandy of a megalosaurian skeleton should allow to precise the exact phylogenetic relationships of this family within the Spinosauroidea. However, the diversity of megalosaurs from the Bajocian-Bathonian of France and England seems to have been under-estimated. An examination of the Oxford University Museum and of the Muséum d'Histoire naturelle of Paris collections have shown that at least five different theropods (Eudes-Deslongchamps 1837;Owen 1856; Phillips 1871; Waldman 1974; pers. obs.) can be identified. The emergence in Europe of Allosauroidea in the Early Late Jurassic would then coincide with a regression of Spinosauroidea diversity. This period could then correspond to a faunal renewal, with the gradual passage of a fauna dominated by the Megalosauridae to a fauna dominated by the Allosauroidea. Any hypothesis on the origin and on the paleogeographic history of the European Allosauroidea remains however a cautious subject as long as the phylogeny of

certainty is that Western Europe has undoubtedly played an important role in the establishment of the most important group of large carnivorous dinosaurs.

Acknowledgements

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