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TARASCOSAURUS SALLUVICUS NOV. GEN., NOV. SP., A THEROPOD DINOSAUR FROM THE UPPER CRETACEOUS OF SOUTHERN FRANCE

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INTRODUCTION

The theropod dinosaurs of the Upper Cretaceous have not been the subject of any recent study since the work of Huene (1926, 1932). It is true that until recent years they have been known only from some very fragmentary remains, generally of Maastrichtian age (Buffetaut *et al.*, 1988). Some isolated discoveries followed (teeth, phalanges), leading to the creation of new taxa, which since they encumber the literature, current systematics are particularly confused and unsuitable. In the first part a rapid revision of these remains will permit detailing their taxonomic status and clarifying their systematics. The second part of this article is dedicated to the description of a new theropod dinosaur from the Upper Cretaceous (Campanian) of the Beausset Syncline (Bouches-du-Rhône, France). This material allows comparisons with non-European theropods of the Upper Cretaceous.

THEROPODS OF CENOMANIAN TO LOWER CAMPANIAN AGE

Until now, only seven discoveries have been noted in beds attributed with certainty to the pre-Maastrichtian Upper Cretaceous: Dumas (1876) reported a tooth from the Cenomanian of Saint-Julien-en-Peyrolas (Gard, France) as "a species near *Megalosaurus bucklandi* [Gervais (1859) had already noted this fossil, referring it to a "megalosaur"]. In 1988, Mornand referred two theropod teeth redeposited in the Miocene shell-marls of Doué la Fontaine (Maine and Loire, France) and probably belonging to Cenomanian beds (Buffetaut *et al.*, 1980) to *Carcharodontosaurus saharicus* (DÉPERET and SAVORNIN, 1927). Again in the Cenomanian of western France, Boisselier (1893) referred some bones to a "megalosaur". This material, deposited in the Musée de La Rochelle, must in fact be referred to a sauropod dinosaur.

In 1903, Dollo created the species *Megalosaurus lonzeensis* for a theropod claw from the "Hervian" (Santonian) of Lonzée (Belgium).

In Sweden, Persson (1959) noted a theropod tooth in the marine Campanian of Scania.

In 1881, Seeley referred two teeth from the lower Campanian of Muthmannsdorf (Austria) to a new species: *Megalosaurus pannoniensis* [Huene (1926) and Kuhn (1937) mentioned these remains under the name of "*Megalosaurus*" *pannonicus* (*sic*)].

THEROPODS FROM THE CONTINENTAL UPPER CRETACEOUS OF SOUTHERN EUROPE (CAMPANIAN-MAASTRICHTIAN)

Most of the other reported remains belong to the continental "Campano-Maastrichtian" deposits of France, Transylvania, Spain, and Portugal (for details concerning the correlations between different basins, see Buffetaut & Le Loeuff, 1991): we briefly mention the principal remains known from different European countries:

France - In 1899, Déperet referred some remains in very bad condition (a fragment of mandible, a fragment of maxilla, and a tooth) from the vicinity of Montouliers (Hérault, France) to *Dryptosaurus*, a theropod from the Upper Cretaceous of New Jersey (U.S.A.). In 1946, Lapparent referred these remains to *Megalosaurus pannoniensis*; in 1947, this author described supplementary material from the vicinity of Fox-Amphoux (Var) (three phalanges and two fibulae), which he also attributed to *M. pannoniensis*. Recently, Clottes & Raynaud (1983) noted a caudal vertebra of *Megalosaurus* sp. from Campagne-sur-Aude (Aude). In 1986, Buffetaut *et al.* described some small teeth from southern France, which they referred to juvenile deinonychosaurs; in 1989, Buffetaut *et al.* noted a theropod maxilla from Provence which they referred to the Abelisauridae, a family of South American carnivorous dinosaurs from the Upper Cretaceous (Bonaparte & Novas, 1985).

Portugal - In 1897-98, Sauvage described three tooth fragments of *Megalosaurus* sp. from Viso (Portugal). Lapparent & Zbyszewski (1957) referred these remains, as well as three theropod claws discovered in the same locality, to *Megalosaurus* cf. *pannoniensis*.

Spain - At Armuña (Campanian?), Sanz (1987) described a carnivorous dinosaur tooth. Casanovas-Cladellas *et al.* (1988) noted a theropod radius from la Cuenca de Tremp. Astibia *et al.* (1990) mentioned the discovery of numerous teeth and phalanges from small theropods in the Basque de Laño locality. They referred two femora from the same locality to the family Abelisauridae. These last two localities are probably Maastrichtian.

Romania (Transylvania) - In 1901, Nopsca created the species *Megalosaurus hungaricus* for a tooth from the Maastrichtian of Transylvania, which was less compressed than the teeth of *M. pannoniensis* from Muthmannsdorf [fossil figured by Nopsca (1902)]. Lapparent (1947), contesting the specific value of this character, subsumed this species into synonymy with *M. pannoniensis*. In 1915, Nopsca figured a caudal vertebra of a megalosaur (pl. 3, fig. 6-7): it is in reality a posterior caudal vertebra of a titanosaurid. Andrews (1913) noted remains of birds in Transylvania, followed by several authors (Lambrecht, 1929; Harrison & Walker, 1975); as Grigorescu (1984) and Paul (1988) suggested, they are in fact from small theropods, which will be described elsewhere (Le Loeuff *et al.*, in press). Grigorescu (1984) also briefly described some caudal vertebrae from small theropods.

THEROPODS OF MAASTRICHTIAN AGE

Some theropod remains from Belgium and the Netherlands belong to marine Maastrichtian beds: Seeley founded the species *M. bredai* on a femur from the Maastrichtian of Holland (Tuffeau de Maastricht). Ubaghs (1892) described two crenulated teeth from Tuffeau de Maastricht, in the Belgian Limbourg; he referred one (of which the two carinae were crenulated) to *Megalosaurus bucklandi*; Ubaghs considered the other tooth, crenulated only at the rear, as belonging "probably to one of the species described by Seeley" from these same beds (*i.e.*: *Megalosaurus bredai*). It seems in fact that these two teeth [of which the dinosaurian origin has been cast into doubt by Buffetaut *et al.* (1985)] belonged to mosasaurs.

SYSTEMATICS OF THEROPODS FROM THE UPPER CRETACEOUS OF EUROPE

Huene, author of the principal studies on the theropods of Europe, must have tried to recognize a little order in these confused systematics. In 1926 he underlined the inadequacy of the generic name *Megalosaurus*; as this genus was founded on incomplete remains from the Bathonian of England, it is entirely improbable that it survived until the Upper Cretaceous. Since the remains known from the European terminal Cretaceous show diagnostic value, Huene suggested designating them as "*Megalosaurus*" sp. ["*Megalosaurus*" *pannonicus* (*sic*) for the remains from Gosau and "*Megalosaurus*" *hungaricus* for the elements from Transylvania] and Ornithomimidorum gen. sp. [O. gen. a) *lonzeensis* for the claw from Lonzée and O. gen. b) *bredai* for the femur from Maastricht, which he placed near the ornithomimids]; he then suggested the following terminology:

- "*Megalosaurus*" *hungaricus* NOPSCA, 1901
- "*Megalosaurus*" *pannonicus* (sic) SEELEY, 1881
- Ornithomimidorum gen., a) *lonzeensis* (DOLLO, 1903)
- Ornithomimidorum gen., b) *bredai* (SEELEY, 1883).

In 1932, he sanctioned the denomination Gen. indet. sp. (in lieu of "*Megalosaurus*" sp.); he also founded the genus *Betasuchus* after the type *M. bredai* SEELEY. Huene therefore considered the following species:

- Gen. indet. *hungaricus* (NOPSCA, 1901)
- Gen. indet. *pannonicus* (sic) (SEELEY, 1881)
- Ornithomimidorum gen., a) *lonzeensis* (DOLLO, 1903)
- *Betasuchus bredai* (SEELEY, 1883).

With the exception of *Betasuchus bredai*, the validity of which will be discussed further, all the theropod species from the European Upper Cretaceous are founded on remains (teeth and phalanges) of which the diagnostic value is extremely weak at a lower taxonomic level.

As a consequence, it becomes necessary for us to reject the species *M. hungaricus*, *M. pannoniensis* (founded respectively on one and two teeth) and *M. lonzeensis* (of which the type consists only of an ungual phalanx), which must be considered as *nomina dubia*. The only denomination which can be applied to them is Theropoda indet. Likewise, the references to *Megalosaurus* sp. (Sauvage, 1897-98; Clottes & Raynaud, 1983), to *Megalosaurus bucklandi* (Dumas, 1876; Ubaghs, 1892) and to *C. saharicus* (Mornand, 1989) must be rejected. For this last species, the presence of oblique striations on the lateral edges of the teeth cannot be a sufficiently diagnostic character for a specific identification. Finally, given the nature of the material referred to the Deinonychosauria by Buffetaut *et al.* (1986), it may still be preferable to refer these remains to Theropoda indet. With regard to the theropods from Romania, they merit reexamination (Le Loeuff *et al.*, in press).

The maxilla from Pourcieux and the femora from Laño, as well as the remains from Beausset described below, are the only European elements permitting taxonomic identification at the family level (Abelisauridae).

DESCRIPTION OF THE THEROPOD FROM BEAUSSET

The material described here belongs to the collections of the Faculté des Sciences de Lyon. It bears for any mention of provenance "Upper Cretaceous, Lambeau de Beausset", and its discoverer is unknown. The fossils were incompletely removed from a vein-stone made of a grayish limestone. The Lambeau de Beausset is a Triassic escarpement on the Cretaceous Beausset Syncline, well-known since the works of Bertrand (1887), who illustrated the notion of tectonic overlapping by the study of this structure. The Beausset escarpement partly overlaps the continental Upper Cretaceous (the Valdo-Fuvélien, the lower limit of the continental series of Provence, is only preserved in the Beausset

Syncline): the gray limestones only exist in the Fuvélien, and it is therefore certain that the remains studied here belong to this bed. Recent magnetostratigraphic studies (Westphal & Durand, 1990) give a lower Campanian age to the Fuvélien deposits of Provence (which overlie the upper Santonian marine in the Beausset Syncline).

All the other Provençal dinosaurs belong to isolated or more often broken-up deposits (of upper Campanian to Maastrichtian age). The only European dinosaurs dated with certainty to the lower Campanian belong to Muthmannsdorf (Austria), from whence are described two theropod teeth (Seeley, 1881), in an original fauna compared to the European Maastrichtian communities (Buffetaut & Le Loeuff, 1991). The Beausset theropod is thus one of the rare dinosaurs known from this period in Europe.

Class REPTILIA Linneus, 1758
Superorder DINOSAURIA Owen, 1842
Order SAURISCHIA Seeley, 1888
Suborder THEROPODA Marsh, 1881
Family ABELISAURIDAE Bonaparte and Novas, 1985

TARASCOSAURUS NOV. GEN.

Origin of name - From the Provençal *tarasco* (the Tarasque, fabled animal, a type of dragon in Provençal legend) and the Latin *saurus* (lizard).

Type species - *Tarascosaurus salluvicus* nov. sp.

Diagnosis - The same as that for the type species.

TARASCOSAURUS SALLUVICUS NOV. SP.

Origin of name - *T. salluvicus*, from the Latin *Salluvii* (the Salluvians, a Gallic people from the environs of Marseilles).

Holotype - Proximal part of a left femur (Collections of the Faculté des Sciences de Lyon, PSL 330201).

Paratypes - Two fragments of articulated dorsal vertebrae (Collections of the Faculté des Sciences de Lyon, PSL 330202), probably belonging to the same individual as the holotype.

Referred material - A caudal vertebral centrum (Collections of the Faculté des Sciences de Lyon, PSL 330203).

Type locality - Lambeau de Beausset.

Type Stratum - Lower Campanian (Fuvélien).

Diagnosis - Small abelisaurid of which the femoral neck is particularly straight anteroposteriorly. Transverse processes very wide anteroposteriorly. Infradiapophyseal laminae of the dorsal vertebrae diverge beneath the diapophyses. Femoral head directed anteromedially. Limited dorsal projection of the lesser trochanter (or anterior trochanter). Presence of a hyposphene-hypantrum structure. Very cavernous internal structure of the vertebrae.

Description of material - The material studied is composed of part of a dorsal vertebra articulated with a fragment of the preceding vertebra, a very poorly preserved caudal vertebral centrum, and the proximal part of a left femur.

Femur (fig. 1): it is the proximal half of a left femur, well enough preserved. The summit of the greater trochanter, the posterior part of the lesser trochanter [anterior trochanter of Gauthier (1986)] and the proximal end of the head are showing; the medial face is slightly crushed; finally, a 3 x 3 cm rectangular fracture is open on the lateral wall of the shaft, beneath the lesser trochanter. The preserved length of the bone is 22 cm; the complete femur might have measured 35 cm in length, indicating an animal of fairly small size (2.5 to 3 m long). The bone is hollow, with relatively thin walls (4 to 6 mm in thickness); the medullary cavity is very wide (around 3.5 x 2.5 cm at the middle of the shaft). The general form of the bone is quite slender. The shaft is compressed in the anteroposterior plane, owing in part to the crushing of the medial face.

The anterior face is straight (slightly convex under the nutrient foramen) and very narrow: distally, it is reduced practically to a ridge rising near the lesser trochanter (it is slightly elongated at the level of the nutrient foramen, under the lesser trochanter). The result is that the cross-section of the shaft is nearly triangular, with the lateral and medial faces converging towards the anterior ridge. The lateral face is a nearly straight; nevertheless, a slight curvature is drawn towards the rear distally.

Distally, the preserved part of the posterior face is flat and nearly straight; at 8 cm from the summit of the bone it curves inferiorly, forming a clearly marked angle. Situated 8 cm from the proximal end (therefore in the upper third of the bone) the fourth trochanter measures 6 cm in length; directed backwards and slightly towards the interior, it becomes thinner near the top and bottom; on its medial face, the scar for muscular insertion is observable.

In anterior and posterior view, the bone shows a very slight upper curvature directed towards the interior: the external contour is convex, the internal contour slightly concave. Dorsally and laterally, the greater trochanter, weakly developed and partly destroyed, forms a ridge on the neck of the femur.

The lesser trochanter is separated from the head by a groove; anteriorly, it overhangs a small nutrient foramen; the development of the lesser trochanter could have been less important: the preserved part (anteriorly) is differentiated from the shaft by about 1.5 cm, and is not dorsally extended.

The neck of the femur is compressed from front to back; it is very narrow relative to the width of the shaft. The proximal articulation is directed towards the interior and slightly forwards and towards the top (in proximal view, it forms an angle of about 80° with the end of the shaft). In medial view, the head is thus oriented towards the lesser trochanter. The proximal articulation is truncated; it measures 4 cm by 3 cm; since the bone is fairly flat posteriorly, the head is practically hemispherical.

Dorsal vertebrae (fig. 2-3) - The right half of the best preserved vertebra is not preserved; the left posteroventral part of the centrum is lacking, and the left diapophysis is not complete. The fragment of the preceding vertebra is comprised only of the left posterior part of the centrum, and the neural arch with the postzygapophysis. The morphology of these vertebrae (particularly the position of the parapophyses) suggests that they correspond to the sixth and seventh dorsal vertebrae.

The anterior articular face of the centrum is flat; the posterior face of the first vertebra is concave. The planes limiting the centrum anteriorly and posteriorly are parallel to each other and perpendicular to the floor of the neural canal. Laterally, the centrum is hollowed by deep depressions; on the left side of the centrum, a pleurocoel is outlined anteriorly; in a number of theropods, the more anterior dorsal vertebrae are pierced by pleurocoels; these become smaller, then disappear towards the rear, around the 7th dorsal vertebra in *Allosaurus fragilis* (Madsen, 1976). The fractures show evidence of the very cavernous internal structure of the vertebrae; the reduction of this structure of the vertebral column is observed in numerous theropods (Bonaparte, 1986) but it is particularly slight in *T. salluvicus*. The parapophyses are slightly disengaged from the centrum: they are chiefly carried by the neural arch: in

Allosaurus, this is observed from the fifth dorsal (Madsen, 1976). The base of the centrum being broken, it is not possible to reveal the probable presence of a ventral keel.

The depressions on the neural arch - chonos: cf. Welles (1984) for the terminology - are well developed: the first (lateral chonos) opens 1.8 cm above the pleurocoel, on the lateral face of the neural arch, under the diapophysis and between the infradiapophyseal laminae; it seems to communicate by a foramen with the internal cavities of the vertebra, but the opening is perhaps due to a poor preservation of the element; an anterior chonos (between the prezygapophysis, the parapophysis, and the anterior infradiapophyseal lamina), and a posterior chonos (between the postzygapophysis and the posterior infradiapophyseal lamina) both communicate with the internal cavities of the vertebra; at present, these openings perhaps did not exist at the beginning. 1.2 cm above the lateral chonos, another depression (superior lateral chonos) is observable elsewhere at the base of the diapophysis, and does not communicate with the neural canal. The infradiapophyseal laminae diverge under the diapophysis, in contrast with those observed in other theropods; the diapophyses are directed towards the top and the rear; they form an angle of about 30° with the horizontal; they are particularly wide anteroposteriorly.

The prezygapophyses are very close together (fig. 2); their articular facets show an angulation of about 90° (convex surface); the postzygapophyses are also very close together; their articular facets show an inverse disposition (concave surface). The vertebra thus presents the outline of a hyposphene-hypantrum structure, which might be more characteristic of the more posterior dorsal vertebrae.

The neural spine is well preserved; anteriorly and posteriorly, a rugose scar corresponds to the insertion of the interspinous ligaments; the spine is enlarged dorsally, forming a swelling of rectangular shape at the summit.

Comparisons - The characters of *T. salluvicus* distinguish it from the majority of known theropods; the structure of the infradiapophyseal laminae, the anteroposterior width of the transverse processes, and the narrowness of the neck of the femur constitute an association of characters entirely unknown in North American and Asian Cretaceous theropods. Comparisons are possible with some South American and European theropods.

- *Carnotaurus sastrei* BONAPARTE, 1985 (Patagonia, Albian-Cenomanian).

Discovered recently, this abelisaurid from the "middle" Cretaceous of Argentina shows interesting resemblances with *T. salluvicus*: just as the very cavernous structure of the dorsal vertebrae, the weak dorsal development of the lesser trochanter and the anteromedial orientation of the femoral head can be considered as synplesiomorphies, so the anteroposterior width of the transverse processes and the relative thinness of the neck of the femur constitute synapomorphies of *C. sastrei* and *T. salluvicus*. This association of characters permits the assignment of *T. salluvicus* nov. gen., nov. sp. to the family Abelisauridae.

- cf. *Tarascosaurus* (Laño, Spain; Maastrichtian).

A right femur and the proximal end of a left femur noted by Astibia *et al.* (1990) show the same narrowness of the neck; they also show a nutrient foramen beneath the lesser trochanter. Distally, an anterointernal crest below the tibial condyle is very similar to that of *Carnotaurus sastrei*. However, the femora from Laño are more robust than that from Beausset, with less anteriorly oriented heads. They can be referred to Abelisauridae (probably not to the same species).

- *Betasuchus bredai* (SEELEY): the femur from Beausset and that from Tuffeau de Maastricht present some common characters (flatness of the neck of the femur, disposition and development of the fourth trochanter, triangular shape of the shaft). The two elements also show slight differences: the neck is still much more narrow in *B. bredai*, the head is not oriented towards the front, there is no foramen under the lesser trochanter; finally, the anterior face is wider in *T. salluvicus*. Towards the distal end of the bone of *B. bredai,* an anterointernal crest begins which appears homologous to the supracondylar crest of the femur of *C. sastrei*. The assignment of the Maastricht femur to the family Ornithomimidae by Huene in 1926 (Ornithomimidorun gen. b *bredai*), confirmed by Russell in 1972 in his study of the ornithomimids of Canada (ornithomimid, *nomen vanum*), appears disputable, in particular because of the narrowness of the neck and the elevated position of the fourth trochanter. The affinities of *B. bredai* will be analyzed in detail elsewhere.

CONCLUSION

The presence of representatives of the family Abelisauridae in the Upper Cretaceous of Europe, at first suggested on the basis of a lone maxilla from Pourcoeux (Buffetaut *et al.*, 1988), is today attested to by the discovery of postcranial elements belonging to diverse localities. The abelisaurids, defined at first on South American material (Bonaparte & Novas, 1985), appear to have had a much vaster distribution, including India, with *Indosuchus* (Bonaparte & Novas, 1985; Bonaparte & Kielan-Jaworowska, 1987; Buffetaut *et al.*, 1988), and probably also Africa [where Upper Cretaceous theropods are still entirely very poorly known, with principally the incomplete material from Baharija (Stromer, 1936) that Bonaparte *et al.* (1990) referred to the abelisaurids]. It is therefore a group of an essentially "Gondwanan" distribution (in other words distributed on the continents created from Gondwana). Its presence in Europe confirms the importance of southern Tethyan elements in the

Upper Cretaceous European faunas, also evidenced by the presence of diverse other groups (Titanosauridae, Trematochampsidae: see Buffetaut, 1989).

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