Discovery of a new theropod dinosaur (*Genusaurus sisteronis* n. g., n. sp.) in the marine Albian of Sisteron (Alps of Haute-Provence, France) and the extension of the ceratosaur lineage into the Lower Cretaceous*

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Abstract Elements of the pelvis and hindlimb of a new carnivorous dinosaur were found in the marine Albian of Sisteron (Alps of haute-Provence, France). This theropod, *Genusaurus sisteronis* n. g., n. sp., is a ceratosaur whose lineage had been known only from the Upper Triassic to the Upper Jurassic. These bones were associated with an abundant microflora indicating the presence on the nearby continent of a wooded countryside and the existence of a warm temperate and somewhat humid paleoenvironment.

Keywords: Albian, France, Vertebrata, Ceratosauria, biostratigraphy, systematics.

INTRODUCTION

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The Ceratosauria constitutes a monophyletic taxon of theropod dinosaurs, created by Marsh in 1888. A reexamination of the characters of different ceratosaur species by Gauthier (1986), then Rowe (1989), and finally Rowe and Gauthier (1990), allowed them to give a new diagnosis of this taxon and show that these moderately-sized carnivorous dinosaurs, having populated the earth from the Upper Triassic to the Upper Jurassic, formed the sister-group (plesiomorphic, that is to say primitive) of all other theropods.

The recovery of part of a ceratosaur skeleton in the marine middle Albian of the subalpine basin not far from Sisteron thus constitutes a surprise and an interesting discovery. We describe below the remains of this new dinosaur, as well as the data relative to the stratigraphic context and paleoecology in which it was found.

The first bones, the proximal ends of the left tibia and fibula, were discovered in 1984 by three of us (H.A., B.B., G.F.) thanks to cartographic geology work in the territory around the commune of Bevons, 4.25 km SW of the village of Sisteron. The locality is located at an altitude of 550 m on deposits south of Turkish Rock and on the west flank of the crest of the Plantayes.

A short expedition (G.F., J.G.M., P.T.) in September 1986 allowed us to recover a little more material: a tarsal, the left femur, left ilium and a sacral vertebra still in place in the fossiliferous bed. Two other visits to the terrain (J.G.M.) allowed the recovery of some supplemental vertebrae (a total of 7 articulated dorsal vertebral centra and 5 neurapophyseal fragments). But all efforts to find the rest of the skeleton were in vain, and it is very probable that erosion had already removed and destroyed the greater part of this skeleton when the discovery took place.

STRATIGRAPHIC AND PALEOECOLOGICAL CONTEXTS

The Sisteron sector occupied a unique place on the southern border of the Vocontian Basin (**figures 1, 2**) during Aptian-Albian time, due to its nodal position at the intersection of structures that were functioning during sedimentation at different periods: an intense synsedimentary tectonism associated with major discontinuities controlled the distribution of facies and particularly redeposition (Beaudoin *et al.*, 1986, Joseph *et al.*, 1989). Paleomorphologic restorations (Friès, 1987, figure 1) indicate that this sector was situated in the basin domain, downwards from an upper E-W oriented zone (the Ventoux-Lure zone), continuously from the Aptian to Cenomanian, and was characterized by platform deposits.

Aptian

Near Sisteron (**figure 3**), the Aptian series (Gargasian marls and Clansayesian marl-limestones with planktonic foraminifera and ammonites), which is very complete and thick (up to 150 m in current thickness), belongs to the bathyal domain. On Montagne de Lure, located several kilometers to the south (**figure 3**), the Gargasian (basal upper Aptian) is reduced to about twenty meters belonging to an external platform area, while the terminal Aptian (Clansayésian) is preserved locally in the form of green glauconitic marls.

Albian

The Aptian series is brutally interrupted in the Centoux-Lure zone by a major discontinuity, overlain by a decimeter-thick bed of green clay and sandy glauconitic pebbles encrusted with phosphates (**figure 3**), and dated as non-basal upper Albian by the microfauna (*Rotalipora ticinensis* zone; Friès, 1987), indicating a period of immersion of several million years from the middle of the upper Aptian to the upper Albian. This period corresponds to the installation of the "Durancian isthmus" (Masse and Philip, 1976) in a setback structural context (Joseph *et al.*, 1987). Above, the much shallower clay-sand platform deposits are organized into a large regressive sequence (Cabrol, 1985; Joseph and Cabrol, 1986; Friès, 1987).

At Sisteron the thicker and more complete marl/marl-limestone Albian series is organized into several-decimeter regressive sequences (figure 3); sedimentation is controlled by a set of accidents determining a system of vacillating traps (Beaudoin *et al.*, 1986; Friès, 1987): thus note the absence of the lower Albian in the region of Bevons and Puy, the middle Albian coming to lie in angular discordance on the various upper Aptian surfaces.

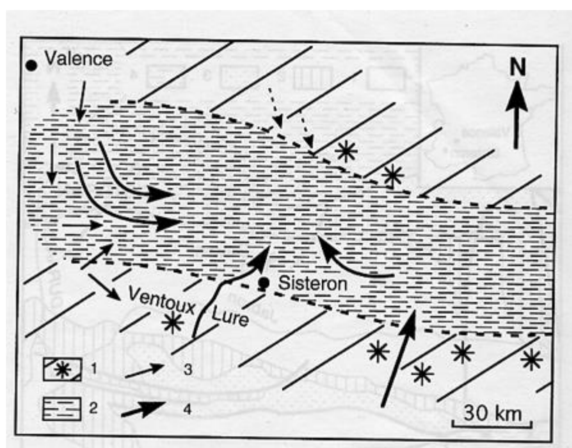

Figure 1. The subalpine Aptian-Albian basin. 1, platform domain and border with locally condensed horizons of phosphate and glauconitic concretions (*); 2, pelagic domain; 3, current direction; 4, submarine morphology (canyon).

It is 0.30 m above this discordance, in the middle Albian, that the bones of a dinosaur were recovered in a mixed green clayey and sandy glauconitic detrital sediments, overlying numerous remains of molluscs, and vertebrae and teeth of sharks.

The fossiliferous bed is composed of a 1–3 cm thick layer of broken oyster shells, attributable to *Curvostrea* sp. aff. *C. rouvillei* (Locquand, 1862) (identification by F. Freneix), mixed with sands rich in organic material, with several fragments of poorly silicified wood; the homoxylous structure of this wood with unbroken woody rays probably allies it with Coniferophytes.

Palynological analysis of the sediment produced an abundant microflora. Spores of Pteridophytes belong chiefly to Filicales; they are reported from the following species: *Deltoidospora minor* (Couper, 1953) Pocock, 1970 (Cyatheaceae, Dicksoniaceae); *Verrucosisporites rotundus* Singh, 1964 (Cyatheaceae?); *Concavissimisporites* sp. (Dicksoniaceae?); *Dictyophyllidites* sp. (Cheiropleuriaceae?); *Appendicisporites tricornitatus* (Weyland and Greifeld, 1953) Potonié, 1960, *A. erdtmanii* Pocock, 1964; *Cicatricosisporites hallei* Delcourt and Sprumont, 1955, *C. venustus* Deak, 1963 and *C. brevilaesuratus* (Couper, 1958) Kemp, 1970 (Schizaeazeae). Pollen of Coniferophytes is reported from the following species: *Araucariacites australis* Cookson, 1947 (Araucariaceae); *Classopollis* sp. (Cheirolepidaceae); *Alisporites bilateralis* Rouse, 1959 (Pinaceae; this species could also belong to Pteridospermaphytes); *Callialasporites segmentatus* (Balme, 1957) Srivastava, 1963 and *Podocarpidites deltmanni* Kemp, 1970 (Podocarpaceae). The microflora conceals no grain of pollen with angiosperm affinity. Algae are represented by various dinoflagellate cysts, reported notably from the genera *Oligosphaeridium* Davey and Williams, 1966 and *Systematophora* Klément, 1960. The palynological analysis likewise produced numerous chitinous organic threads of foraminiferans (“basals”).

The palynological analysis revealed alluvial deposits of continental origin (spores and pollen) and a clear littoral or marine influence (cysts and “basals”): this implies a setting somewhat near the coast because of the fairly well-preserved spores and pollen grains, which must not have sustained a long transport and are abundant in remains.

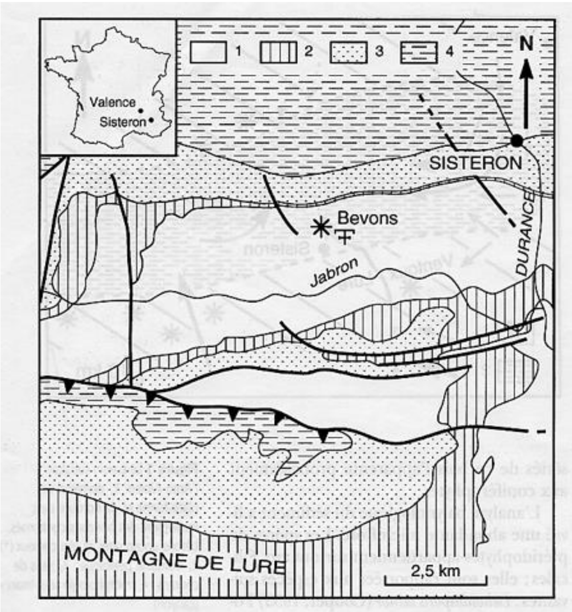

Figure 2. Geologic scheme of the Sisteron-Bevons-Montagne de Lure sector. 1, Aptian-Albian; 2, Barremian; 3, Neocomian; 4, Upper Jurassic.

The terrestrial microflora reflects a temperate-to-warm and rather humid paleoenvironment because of the abundance of Filicales spores; the countryside was probably wooded, composed principally of conifers and ferns, some of which must have been arborescent.

Situated in the Albian basin, around 5 km north of the clay-sand platform facies shown by the palynological contents, the Bevons site, which corresponded to a depth of around 500 m (Bizon, pers. comm.), received the turbid products drawn from erosive overhangs on the slope (Beaudoin and Friès, 1982).

It is in this paleomorphologic context that our locality is situated. The compaction of sediment has crushed the bones: the body of the femur and, to a lesser degree, the anterior end of the tibia are crushed and split.

The presence of these bones in articulation is evidence of the probable ocean transport of a floating cadaver that was followed by sedimentation on the bottom. The bones were not immediately covered again, as evidenced by traces of corrosion on the vertebrae and the medial face of the ilium. The accumulation of oysters indicates a taphocoenosis or a collection by transport and *post-mortem* accumulation.

PALEONTOLOGY

Dinosauria Owen, 1842.

Saurischia Seeley, 1887.

Theropoda Marsh, 1881.

Ceratosauria Marsh, 1884.

Genusaurus sisteronis n. g., n. sp.

Holotype (and only specimen) (**figure 4 A–F):** MNHN, Bev. 1. Left ilium, proximal end of the left pubis, left femur, proximal ends of the left tibia and left fibula, a tarsal, a sacral vertebral centrum, seven dorsal vertebral centra.

Type locality: Greenish clays and glauconitic sands of Bevons.

Type stratum: Bevons, 4.250 km SW of Sisteron (Alps of Haute-Provence), middle Albian.

Derivation of name: The generic name comes from the Latin word *geniculum* diminutive of *genu* (knee) and alludes to the great development of the cnemial crest situated in front of the proximal end of the tibia. The specific name refers to the nearest town of Sisteron.

Diagnosis: Ceratosaur in which the tibia has an extremely developed cnemial crest.

Commentary

This small dinosaur is incontestably a theropod as indicated by the length of the preacetabular process of its ilium, the presence of a pronounced “brevis fossa” with an indented form situated behind the acetabulum and under the posterior wing of the ilium, the anterior curvature of the femur, the union between the tibia and fibula, and finally the possession of hollow long bones with thin walls.

Theropods include the Tetanurae (with species more closely related to birds) and the Ceratosauria, considered as the most primitive carnivorous dinosaurs. The diagnostic characters of Ceratosauria were recently reviewed by Rowe (1989) and, by chance, a certain number of these characters were noticed on the pelvis, femur and fibula – skeletal elements that were preserved in the dinosaur recovered from Bevons.

These characters are the following: 1) the pubic bar is extremely oblique towards the front, 2) the pubis and ischium are fused in adults, 3) a marked trochanteric shelf exists on the anterior trochanter (= lesser trochanter) of the femur which is evidence of the important development of the puboischiofemoralis internus pars dorsalis muscle, 4) there is a lateral sulcus on the tibia at the base of the tibio-fibular crest, 5) there is a deep sulcus on the medial surface of the proximal end of the fibula.

The attachment area between the medial face of the proximal end of the fibula and the external face of the proximal end of the tibia, in the same way as the sulcus present on the fibula, resembles amazingly that described on the corresponding bones of *Syntarsus kayentakatae* by Rowe in 1989 (p. 132, figure 1B and C).

Genusaurus sisteronis thus possesses five important characters present in Ceratosauria, and short of completely revising the definition of Ceratosauria, this new Lower Cretaceous theropod cannot but be classified with the other representatives of this group of primitive carnivorous dinosaurs. Character 3 is less diagnostic since it is known to be present on the femur of the primitive dinosaur *Eoraptor*. Character 5, the presence of a sulcus on the medial face of the proximal end of the fibula, was similarly observed in tetanuran dinosaurs such as *Allosaurus* and *Tyrannosaurus* (information from J. Gauthier), but this sulcus is of a very great depth on the specimen from Sisteron.

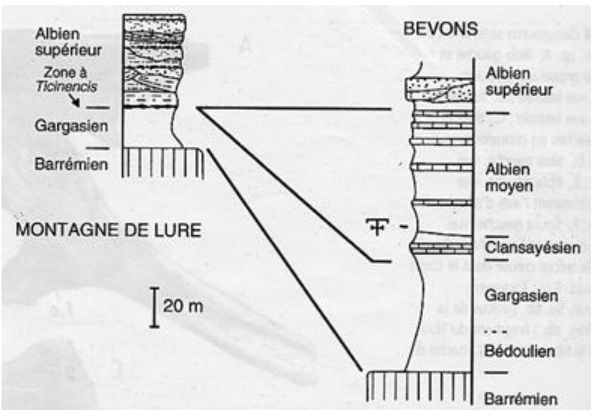

Figure 3. Lithostratigraphy of the Aptian-Albian series at Montagne de Lure and in the Bevons sector.

Several observations reinforce these indicators of relationship: the pelvis, of which the ilium and pubis are clearly fused, strongly recalls that of certain ceratosaurs like *Sarcosaurus woodi*, described by Andrews in 1921 from the Lower Jurassic of Leicestershire (Great Britain), with its very anteriorly oriented pubis – it equally recalls the pelvis of certain specimens of *Coelophysis bauri*, such as for example those described by Colbert (1989, figure 76, p. 10) or by Padian (1986, figure 5.2, p. 49). In *Genusaurus sisteronis*, the superior edge of the ilium is straight and much evokes that of *Coelophysis bauri* [Upper Triassic of New Mexico and Arizona (United States)] or of *Syntarsus rhodesiensis* [from the Lower Jurassic of Zimbabwe (Rowe and Gauthier, 1990, figures 5–7, DEF, p. 161)].

Curiously, the posterior part of the ilium seems larger than the anterior part, but this latter is very thin and not preserved in its entirety in the anteroventral region. The ilium presents the peculiarity of being fenestrated - the presence of two openings in the iliac blade could be due to poor preservation of the bone or could be the result of corrosion of the bone. However, it is very possible that these gaps in the ossification are in fact natural; the ilium of the cassowary (*Casuarius casuarius*) presents exactly the same type of fenestration, which seems to correspond to a simple reduction of the bone.

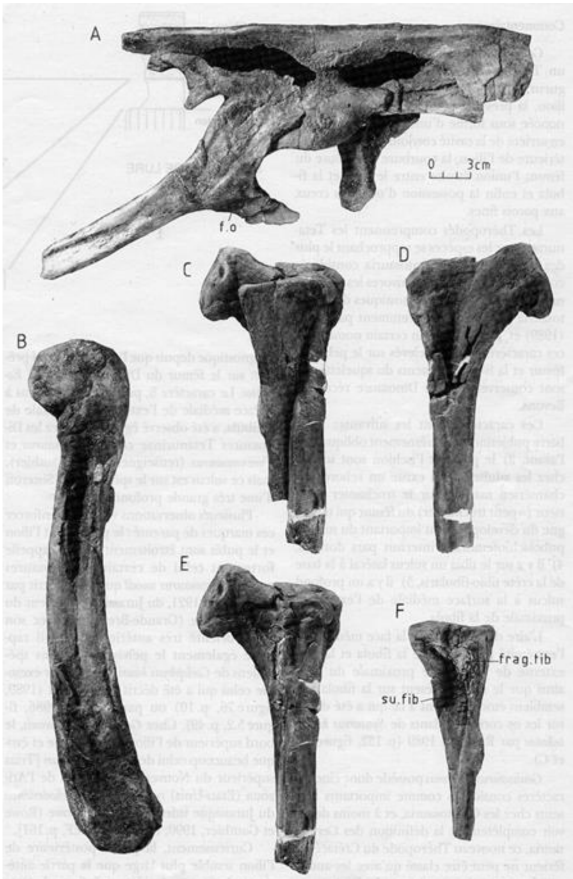

Figure 4. *Genusaurus sisteronis* nov. gen., nov. sp. A, left ilium and proximal end of the left pubis, lateral view; B, left femur, lateral view; C, left tibia and fibula in articulation, lateral view; D, left tibia, medial view; E, left tibia, lateral view showing the attachment area for the fibula; F, left fibula, medial view showing the attachment area for the tibia and the sulcus cut into the body of the fibula. F. o.: obturator foramen, Su. fib.: fibular sulcus, Frag. tib.: fragment of tibia fused to the fibula and attachment area for the tibia.

On the femur, the anterior trochanter is relatively small and occupies a position considered more primitive in other ceratosaurs, in other words at the summit of the femur just at the level of the head (Rowe and Gauthier, 1990, p. 161). In tetanurans, this condyle is more proximal, widened and laterally displaced; it is adjacent to or coossified with the greater trochanter, which is not the case here.

The tibia is remarkable for the extreme development of its cnemial crest, a development which does not exist to such a degree in any other ceratosaur, even though this crest is very developed in *Ceratosaurus nasicornis* from the Upper Jurassic of North America (Gilmore, 1920, figure 65B, p. 111). A development comparable to that of *Genusaurus sisteronis* exists on the tibia of theropod unnamed but figured in 1925 (Pl. VI, figure 5a) by Janensch and discovered in the beds of Tendaguru (East Africa – Kimmeridgian). But the cnemial crest on this tibia is directed upwards and not forwards and it does not possess a distally directed face as in *Genusaurus sisteronis* (Pl. I, figure 4C–D).

One can inquire about the function of this large and prominent cnemial crest – the hypertrophy of this part of the tibia is linked to the existence of very strong tendinous attachments joining the end of the tibia to the end of the femur. But, in the position where the skeletal elements of *Genusaurus sisteronis* were found, the femur of which the head was in place in the acetabulum, presents a very strong forward inclination parallel to the pubis, a position which seems natural. If such was the case, *Genusaurus sisteronis* would have possessed a thigh very oblique towards the front, closer to the horizontal than to the vertical. This position recalls very strongly the oblique position of the femur of certain birds such as *Struthio* and *Aepyornis*. Paul (1988, figures 4–14, p. 112 and figures 4–16, p. 115) clearly showed the differences positions of the leg segments in the ostrich and in certain theropods, and explained very well that the movement of the leg takes place at the time of the motion about the knee. In this case, the cnemial crest of *Struthio* is correspondingly well developed. The dimensions of *Genusaurus sisteronis* are relatively reduced, the femur measures 38 cm in length and this theropod might have reached the size of a cassowary, in other words 1.50 m in height.

This remarkable discovery allows us to complete the very reduced knowledge that we have of the theropod dinosaur fauna from the Lower Cretaceous of France, since the Albian in particular has given up but very few remains. The only bones attributed to a theropod came from the Albian near Louppy-le-Château (Meuse) and were described by Sauvage in 1882, under the name of *Megalosaurus superbus* and called afterwards *Erectopus sauvagei* by von Huene in 1932. This theropod, according to Molnar (1990), is a problematic “carnosaur”. The femur has a deviated head (Sauvage, Pl. XXIX, figure 1) very different from that of *Genusaurus sisteronis*, whereas the proximal end of the tibia illustrated by Sauvage (Pl. XXI, figure 1) possesses a cnemial head of normal dimensions. This theropod dinosaur is thus very different from that of Sisteron. *Genusaurus sisteronis* was the contemporary of *Aepisaurus elephantinus*, a sauropod known by a humerus described by Gervais (1852, Pl. 63, figures 3 and 4) and recovered on the southern flank of Mont Ventoux. Finally, the existence even in the Lower Cretaceous of a representative of the ceratosaurs, of which the other species were known up to then only from the Upper Triassic to the Upper Jurassic, shows that the distribution in time and space of different dinosaur families remains poorly understood and can still hold many surprises for us.

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