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Furileusaurian osteological characters in *Genusaurus sisteronis* Accarie *et al.*, 1995, an abelisaurid dinosaur from the Albian (Lower Cretaceous) of south-eastern France

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Abstract

A revision of the type material of *Genusaurus sisteronis*, from the Albian of Bevons in south-eastern France, confirms that it belongs to the family Abelisauridae. Several osteological characters (6 fused sacral vertebrae, thickened dorsal rim of the fused neurapophyses of the sacral vertebrae, straight dorsal margin of the ilium, hatchet-shaped cnemial crest of the tibia) indicate that it should be placed within Furileusauria, a derived clade of Abelisauridae. The dinosaur from Bevons is the earliest known furileusaurian. The evolutionary and biogeographical implications of the presence of Furileusauria in Europe as early as the Albian are discussed. Two distinct lineages of abelisaurids, Furileusauria and Majungasaurinae, appear to have been present in Europe during the Cretaceous, but whether they co-existed is uncertain.

Key words : Dinosauria, Theropoda, Abelisauridae, Furileusauria, Europe, Cretaceous, *Genusaurus*.

Caractères ostéologiques furileusauriens chez *Genusaurus sisteronis* Accarie *et al.*, 1995, dinosaure abelisauridé de l'Albien (Crétacé inférieur) du Sud-Est de la France

Résumé

Une révision du matériel type de *Genusaurus sisteronis*, de l'Albien de Bevons, dans le Sud-Est de la France, confirme qu'il appartient à la famille des Abelisauridae. Plusieurs caractères ostéologiques (6 vertèbres sacrées fusionnées, bord dorsal épaissi des neurapophyses fusionnées des vertèbres sacrées, bord dorsal de l'ilion rectiligne, crête cnémiale du tibia en forme de hache) indiquent qu'il faut le placer parmi les Furileusauria, un clade dérivé d'Abelisauridae. Le dinosaure de Bevons est le plus ancien furileusaurien connu. Les implications évolutives et biogéographiques de la présence de Furileusauria en Europe dès l'Albien sont discutées. Deux lignées distinctes d'Abelisauridae, Furileusauria et Majungasaurinae, semblent avoir été présentes en Europe au Crétacé, mais il n'est pas certain qu'elles aient coexisté.

Mots-clés : Dinosauria, Theropoda, Abelisauridae, Furileusauria, Europe, Crétacé, *Genusaurus*.

1. Introduction

Genusaurus sisteronis was described by Accarie *et al.* (1995a) on the basis of vertebral, pelvic and hind limb elements from marine deposits of middle Albian age in the Alpes de Haute-Provence in south-eastern France. While Accarie *et al.* (1995a) originally referred the specimen to Ceratosauria and claimed that it was the first occurrence of the ''ceratosaurian lineage'' from the Cretaceous, Buffetaut & Le Loeuff (1995) interpreted it as an abelisaurid, a conclusion questioned by Accarie *et al.* (1995b), who claimed that the family Abelisauridae was a poorly defined group. Since then, various interpretations have been put forward for *Genusaurus sisteronis,* although it has frequently been placed among the Abelisauroidea. Following a re-examination of the type specimen, the present paper discusses several of its osteological features which suggest that *Genusaurus sisteronis* is probably an early representative of the abelisaurid clade Furileusauria.

2. Geographical and geological setting

The type specimen of *Genusaurus sisteronis* is kept at the Muséum national d'Histoire naturelle (MNHN) in Paris, under collection number Bev.1. It was discovered in the course of geological mapping in 1984, at Bevons, near the city of Sisteron, in the department of Alpes de Haute-Provence, in south-eastern France (see map in Accarie *et al*., 1995a). The geological setting of the specimen was described in great detail by Accarie *et al.* (1995a). The bones were found in a middle Albian detritic sandy and clayey bed containing abundant oyster shells as well as shark teeth, wood remains, palynomorphs and

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dinoflagellates. The specimen was interpreted as the remains of a floating carcass originating from a nearby emergent area.

3. History of previous research

Accarie *et al.* (1995a) considered *Genusaurus sisteronis* as a ceratosaur and claimed it was the first occurrence of the ceratosaurian lineage from the Cretaceous. While accepting the ceratosaurian affinities of the taxon, Buffetaut & Le Loeuff (1995) concluded that it could be referred to the family Abelisauridae on the basis of various characters, including the straight dorsal margin of the ilium and the shape of the cnemial crest of the tibia, and pointed out that it could not be considered as the first discovery of a Cretaceous ceratosaur. Accarie *et al.* (1995b) did not agree with this interpretation and claimed that *Genusaurus sisteronis* was closer to Triassic and Early Cretaceous ceratosaurs, while considering Abelisauridae, as defined by Bonaparte (1991), as an unacceptable «catch-all» group.

Subsequently, *Genusaurus sisteronis* received various interpretations. Allain & Pereda-Suberbiola (2003) considered that it could be a noasaurid. The life reconstruction by Michel Fontaine they published (Allain & Pereda-Suberbiola, 2003, fig. 1E) shows a very gracile, rather coelophysoid-like dinosaur and is probably inaccurate. In their comprehensive review of the Ceratosauria, Carrano & Sampson (2008) placed it among the Noasauridae, an interpretation shared by Wang *et al.* (2017) and Delcourt (2018). Tortosa *et al.* (2014) considered it as a rather basal abelisaurid, a conclusion also reached by Baiano *et al.* (2021). Filippi *et al.* (2016) placed it as the sister-group of *Arcovenator* among Majungasaurinae, an interpretation followed by Gianechini *et al.* (2021). A different interpretation was proposed by Juárez-Valieri & Fiorelli (2004), who placed *Genusaurus* among the Carnotaurinae, considered as the most derived abelisaurid clade, on the basis of its hatchet-shaped cnemial crest. This interpretation was followed by Ezcurra & Agnolin (2012). Despite differences concerning its exact position among the Abelisauridae, it appears that in most recent papers, *Genusaurus* is considered as belonging to that family, as initially suggested by Buffetaut & Le Loeuff (1995).

In order to better assess the position of *Genusaurus* among Abelisauridae, the type specimen of *G. sisteronis* has been re-examined. Significant osteological characters are listed below.

4. Material and methods

As noted by Accarie *et al.* (1995a), the type specimen of *Genusaurus sisteronis* is a partial skeleton consisting of vertebral centra, parts of the pelvis (left ilium and incomplete left pubis) and hindlimb elements (left femur, incomplete left tibia and fibula, one tarsal). An element not listed by Accarie *et al*. (1995a) is an elongate and laterally flattened bony bar apparently formed by the fused neurapophyses of the sacral vertebrae (**Fig. 1**).

Seven vertebral centra were identified as belonging to dorsal vertebrae by Accarie *et al.* (1995a). The examined material in fact consists of several mostly broken centra that are long, low and strongly constricted in their middle part, giving them a hourglass-like shape (**Fig. 2**). They may be caudal rather than dorsal centra, although facets for chevron bones cannot be clearly seen ; however, as noted by Erickson *et al.* (2005), in

Fig. 1 - *Genusaurus sisteronis*, holotype (MNHN Bev.1). Fused neural arches of sacral vertebrae, showing thickening of the dorsal edge, in left (A) and right (B) lateral views. Scale bar : 5 cm.

Fig. 2 - *Genusaurus sisteronis*, holotype (MNHN Bev.1). Fragmentary vertebral centra, probably from caudal vertebrae, showing lack of fusion with the neural arches. Scale bar : 5 cm.

archosaurs the anteriormost caudal vertebrae do not bear chevrons bones. As usual in theropods, the dorsal centra of abelisaurids are shorter and taller, whereas the caudal centra are elongate and constricted (Gianechini *et al.,* 2022), as seen, for instance, in *Aucasaurus* (Baiano *et al.,* 2023), *Koleken* (Pol *et al*., 2024) and *Majungasaurus* (O'Connor, 2007). In addition, two poorly preserved fused vertebrae are probably sacrals. The fact that the vertebral centra are separated from the neural arches shows that the specimen corresponds to an immature individual, which explains its relatively small size (estimated body length 3.6 m according to Grillo & Delcourt, 2017). Accarie *et al.* (1995a) noted the presence of fairly large openings in the ilium. They seem to be an artefact of preservation rather than real anatomical features.

The aim of the present paper is not to provide a detailed redescription of the osteology of *Genusaurus sisteronis*, but to discuss various osteological characters that appear to be significant for the placement of that taxon among Abelisauridae, with special emphasis on those that suggest furileusaurian affinities.

5. Notable osteological characters

5.1. Number of sacral vertebrae.

Sacral centra are apparently represented by only one poorly preserved element consisting of a centrum fused with part of the next vertebra. However, the total number of sacral vertebrae can be estimated with some precision thanks to the above-mentioned bony bar formed by the fused neural spines of the sacral vertebrae (**Fig. 1**). The ventral margin of the bar shows several notches corresponding to spaces between the individual neurapophyses, as seen for instance in *Carnotaurus sastrei* (Bonaparte *et al.,* 1990). On this basis, the number of fused neural spines (forming a synsacrum) can be counted, showing that at least five fused sacral vertebrae were present. Since the specimen is broken posteriorly, it is highly probable that in fact there were six fused neural spines. Additional unfused sacrals may have been present, as in *Carnotaurus sastrei*, in which the first sacral is not fused to the second one (Bonaparte *et al.,* 1990). Derived abelisaurids, such as the furileusaurians *Carnotaurus* (Bonaparte *et al.,* 1990) and *Aucasaurus* (Baiano *et al.,* 2023), have six fused sacral vertebrae, while the majungasaurine *Majungasaurus* only has five (O'Connor, 2007). This suggests that *Genusaurus sisteronis* is a more derived abelisaurid than majungasaurines. It should be noted, however, that the noasaurids *Elaphrosaurus* (Janensch, 1925) and *Masiakasaurus* (Carrano *et al.,* 2011) have six coossified sacral vertebrae (see below).

5.2. Thickened dorsal margin of fused neurapophyses of sacral vertebrae.

The above-mentioned fused neurapophyses of the sacral vertebrae have a straight dorsal margin that is thickened by comparison with the more ventral areas, especially in the cranial part (**Fig. 1**). This thickening is a derived character present in *Carnotaurus* (Bonaparte *et al.,* 1990), *Aucasaurus* (Baiano *et al.,* 2023) and *Caletodraco* (Buffetaut *et al.,* 2024). It is less developed in *Koleken* (Pol *et al.,* 2024) and absent in majungasaurines such as *Majungasaurus* (O'Connor, 2007). Together with the high number of fused sacral vertebrae, the dorsal thickening of the fused neural spines suggests a furileusaurian-like sacrum in *Genusaurus sisteronis*.

5.3. Straight dorsal margin of ilium.

As already noted by Buffetaut & Le Loeuff (1995), the very straight dorsal margin of the ilium of *Genusaurus sisteronis* (**Fig. 3**) is reminiscent of some abelisaurids, notably *Carnotaurus* (Bonaparte *et al.,* 1990). Other furileusaurians such as *Aucasaurus* (Baiano *et al.,* 2023) and *Koleken* (Pol *et al.,* 2024) show the same condition, whereas the less derived *Majungasaurus* (O'Connor, 2007) and *Skorpiovenator* (Cerroni *et al.,* 2022) have an ilium with a convex dorsal margin. *Rahiolisaurus gujaratensis* (Novas *et al.,* 2010) and *Ekrixinatosaurus novasi* (Calvo *et al.,* 2004) seem to have an undulated dorsal margin of the ilium. However, a straight dorsal margin of the ilium is also present in the noasaurids *Masiakasaurus knopfleri* (Carrano *et al.,* 2011) and *Berthasaura leopoldinae* (Alves de Souza *et al.,* 2021).

At first sight, the posterior margin of the ilium of *Genusaurus sisteronis* may seem to show a slight notch and a small posterodorsal process, as in various abelisaurids, including the furileusaurian *Caletodraco cottardi*, from the Cenomanian of north-western France

Fig. 3 - *Genusaurus sisteronis*, holotype (MNHN Bev.1). Left ilium and pubis in left lateral view, showing straight dorsal margin of the ilium. Scale bar : 5 cm.

(Buffetaut *et al.,* 2024). However, this posterior margin is in fact broken, so that its original outline cannot be determined.

5.4. General morphology of the femur.

The femur of the holotype of *Genusaurus sisteronis* is complete but has undergone considerable mediolateral compression (**Fig. 4**). It shows various abelisaurid characters, including a ridge-like very proximally located fourth trochanter, a well individualized lesser trochanter and a strongly developed medial epicondylar crest. It generally resembles the femur of *Xenotarsosaurus bonapartei* (Ibiricu *et al.,* 2021), but its shaft is less curved. According to Ibiricu *et al.* (2021), abelisaurids more derived than *Xenotarsosaurus*, such as *Carnotaurus* and *Aucasaurus*, have a straighter femur.

5.5. Shape of the cnemial crest of the tibia.

One of the most salient features of *Genusaurus sisteronis* is the hatchet-like shape of the cnemial crest of the tibia (**Fig. 5**). It was considered as highly characteristic by Accarie *et al*. (1995a), who coined the genus name *Genusaurus* (from the Latin *genu*, «knee») to reflect the great development of the cnemial crest. The crest rises markedly and obliquely above the level of the proximal articular surface with the femur. The crest shows a slight constriction, after which its extremity is thickened and expanded not only proximally (upward), as in many theropods, but also distally (downward), giving it its characteristic hatchet-like shape. This peculiar shape distinguishes *Genusaurus sisteronis* from some other abelisaurids, such as *Majungasaurus crenatissimus*, in which the cnemial crest rises obliquely well above the level of the proximal articular surface of the tibia but shows no distal expansion (Carrano, 2007). Comparisons with other European abelisaurids are not easy because few well preserved tibiae are available. In the holotype of the late Campanian *Arcovenator escotae*, the cnemial crest is incompletely preserved (Tortosa *et al.,* 2014), so that its outline cannot be reconstructed with any accuracy (**Fig. 6**). Similarly, in an abelisaurid tibia from the presumably upper Campanian Massecaps locality at Cruzy (Hérault, southern France), which may belong to *Arcovenator*, the cnemial crest is very poorly preserved (Tortosa, 2024). A better preserved abelisaurid tibia was reported from the upper Campanian La Boucharde locality at Trets (Bouches-du-Rhône, south-eastern France) by Allain & Pereda-Suberbiola (2003), who identified it as «Neoceratosauria sp.». Unlike the condition in *Genusaurus sisteronis*, the well-preserved cnemial crest does not rise much above the level of the proximal articular surface and it is slightly expanded distally, but not proximally, at its extremity (**Fig. 6**). *Contra* Allain & Pereda-Suberbiola (2003), the cnemial crest of the La Boucharde tibia is not closely similar to that of *Genusaurus sisteronis*. As noted by Tortosa (2024), the La Boucharde tibia resembles that of *Arcovenator,* and it may belong to that taxon.

The tibia of *Genusaurus sisteronis* is therefore not closely similar to that of majungasaurines such as *Majungasaurus* and *Arcovenator.* Its hatchet-like shape is much more reminiscent of the tibiae of the South American abelisaurids *Aucasaurus* (Coria *et al.,* 2002), *Pycnocnemosaurus* (Delcourt, 2017) and *Quilmesaurus* (Juárez-Valieri *et al.* 2007), which are all considered as belonging to the clade Furileusauria (Filippi *et al.,* 2016, Gianechini *et al.,* 2021). Interestingly, in *Skorpiovenator bustingorryi* the cnemial crest is hatchet-shaped (Cerroni *et al.,* 2022), while the dorsal rim of the ilium is clearly convex. *Skorpiovenator* is placed within Brachyrostra

Fig. 4 - *Genusaurus sisteronis*, holotype (MNHN Bev.1). Left femur in medial view ; mec : medial epicondylar crest ; t4 : fourth trochanter. Scale bar : 5 cm.

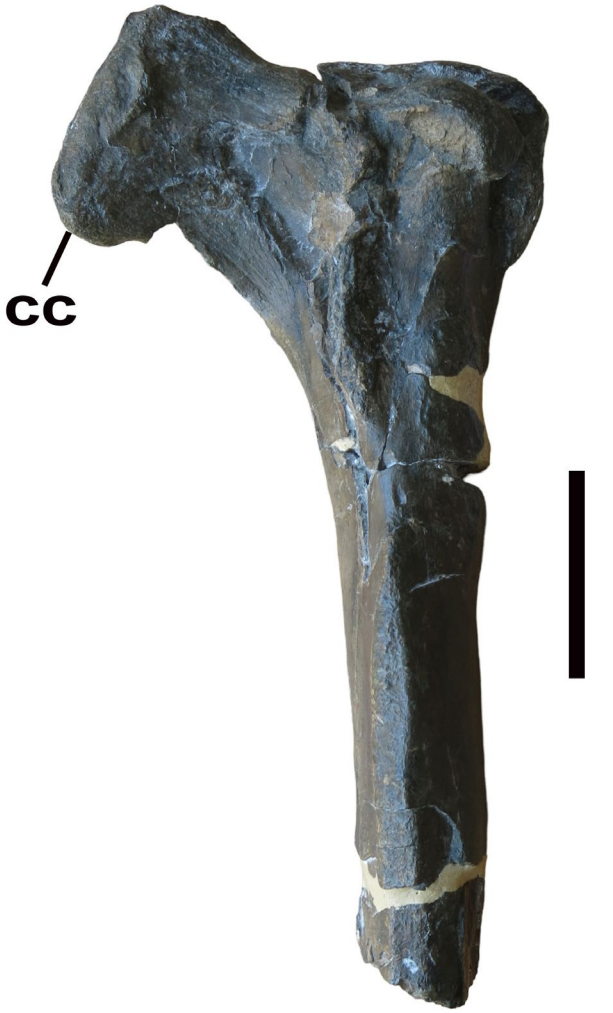

Fig. 5 - *Genusaurus sisteronis*, holotype (MNHN Bev.1). Left tibia in lateral view ; cc : cnemial crest. Scale bar : 5 cm.

and just outside Furileusauria in the cladogram of Cerroni *et al.* (Cerroni *et al.,* 2022). Less derived South American abelisaurids such as *Xenotarsosaurus* (Ibiricu *et al.,* 2021) do not show a hatchet-shaped cnemial crest. It is worth noting that an unnamed abelisaurid from the upper Maastrichtian of Morocco (MHNM.KHG.1398) shows a similar hatchet-shaped cnemial crest, as noted by Longrich *et al.* (2023).

5.6. Medial fossa of fibula.

The proximal part of the left fibula shows a large medial fossa that is open both medially and posteriorly (**Fig. 7**). According to Carrano (2007) this fossa was an insertion area for M. popliteus. A very similar fossa is known in several abelisaurids, such as *Majungasaurus*, *Xenotarsosaurus* (Ibiricu *et al.,* 2021) and *Arcovenator* (Tortosa *et al*., 2014). In less derived Ceratosauria, such as *Ceratosaurus* (Madsen & Welles, 2000), the fossa opens more posteriorly than medially. In *Genusaurus*, the iliofibularis tubercle is well developed, as usual in ceratosaurs.

6. Discussion

As mentioned above, Accarie *et al.* (1995a) correctly identified *Genusaurus sisteronis* as a ceratosaur but did not accept (Accarie *et al.,* 1995b) its referral to the Abelisauridae by Buffetaut & Le Loeuff (1995). Carrano & Sampson (2008) placed it in the family Noasauridae, an interpretation followed by Wang *et al*. (2017) and Delcourt (2018). *Genusaurus sisteronis* does show similarities with some noasaurids. Two of the above-mentioned characters, viz. the six coossified sacrals and the straight dorsal margin of the ilium, also occur in the noasaurid *Masiakasaurus knopfleri*, from the Late Cretaceous of Madagascar (Carrano *et al.*, 2011), and in the probable noasaurid *Elaphrosaurus bambergi*, from the Late Jurassic of Tanzania (Janensch, 1925).

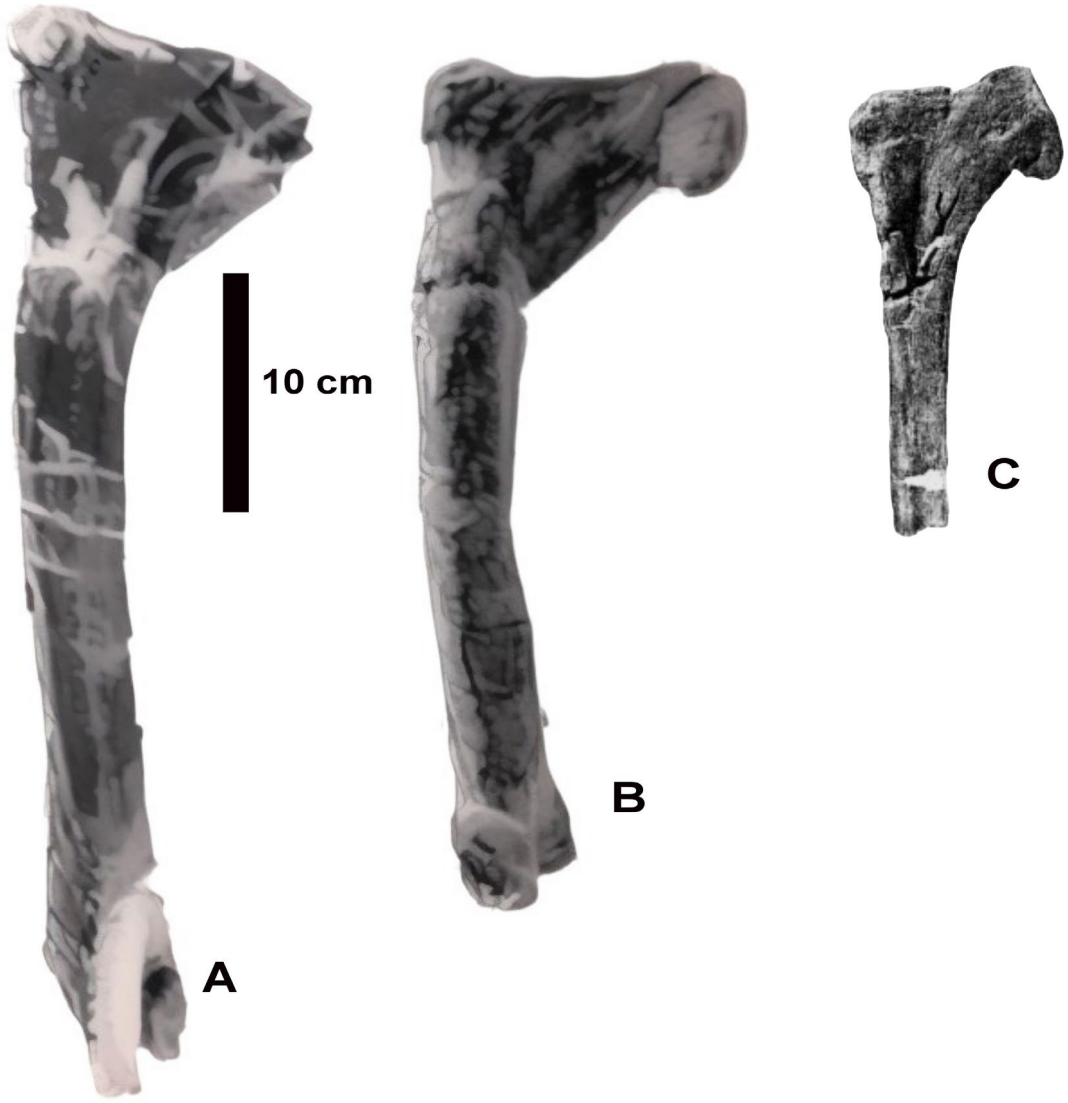

Fig. 6 – Comparison between the tibiae of *Arcovenator escotae* (**A**), the specimen from La Boucharde (**B**) and *Genusaurus sisteronis* (**C**), showing differences in the outline of the cnemial crest. A and B in lateral view, C in medial view.

However, in *Masiakasaurus* the dorsal rim of the fused sacrals is not thickened and the cnemial crest of the tibia is not hatchet-shaped. In *Elaphrosaurus*, the dorsal rim of the ilium is convex, not straight, and the cnemial crest of the tibia is not hatchet-shaped. In the noasaurid *Berthasaura leopoldinae*, from the Early Cretaceous of Brazil, the dorsal margin of the ilium is straight, but there are only five fused sacral vertebrae and the cnemial crest of the tibia is not hatchet-shaped (Alves de Souza *et al*., 2021). Other noasaurids show no special similarities with *Genusaurus* – for instance, in *Ligabueino andesi*, from the Early Cretaceous of Argentina, the ilium is markedly different from that of *Genusaurus*, with a convex dorsal margin (Bonaparte, 1996). Various other noasaurids cannot be significantly compared with *Genusaurus* because there are no sufficiently well preserved skeletal elements in common between the available specimens. The similarities between *Genusaurus* and some noasaurids are probably the result of convergent evolution.

Inclusion of *Genusaurus* among Abelisauridae has gradually become generally accepted (see above), although there is no real consensus about its position within that family. Among the osteological characters listed above, several confirm that *Genusaurus* is indeed an abelisaurid. They include the morphology of the femur, as already noted by Buffetaut & Le Loeuff (1995), as well as the orientation of the medial fossa of the fibula. Other characters point to a particular clade among Abelisauridae, viz. the Furileusauria, as defined by Filippi *et al.* (2016). The furileusaurian characters of *Genusaurus sisteronis*, which, taken in combination, distinguish it from more basal abelisaurids, can be summarised as follows :

- six coossified sacral vertebrae ;
- thickened dorsal margin of the fused neural spines of the sacral vertebrae ;
- straight dorsal margin of the ilium ;
- hatchet-shaped cnemial crest of the tibia.

In view of the above-mentioned distinctive characters observable in *Genusaurus sisteronis*, it seems reasonable to consider it as belonging to the Furileusauria. This contrasts with various recent phylogenies in which *Genusaurus* is interpreted as a rather basal abelisaurid (Tortosa *et al.,* 2014 ; Baiano *et al.,* 2021 ; Gianechini *et al.*, 2022) or as closely related to *Arcovenator* (Filippi *et al.,* 2016 ; Delcourt, 2017). However, several authors have already considered *Genusaurus* as a derived, rather than basal, abelisaurid. Because of the shape of its cnemial crest, Juárez-Valieri & Fiorelli (2004) placed it among the Carnotaurinae, now usually considered as a clade within Furileusauria. Ezcurra & Agnolin (2012) accepted the interpretation put forward by Juárez-Valieri and Fiorelli. It may actually be difficult to refer *Genusaurus* to the Carnotaurinae on the basis of the available osteological characters, but an attribution to the slightly more inclusive clade Furileusauria seems to be well supported.

Accarie *et al.* (1995a) gave the following diagnosis for *Genusaurus sisteronis* : «Ceratosaur whose tibia bears an extremely developed cnemial crest». A hatchet-shaped cnemial crest is now considered as a distinctive character of Furileusauria as a whole, and is not sufficient to characterise the taxon *Genusaurus sisteronis*. In fact, the characters that may have seemed distinctive for *Genusaurus sisteronis* now appear to be widespread among Furileusauria. If no really distinctive characters can be found, it may be necessary to consider the dinosaur from Bevons as an indeterminate furileusaurian.

Placing *Genusaurus* among Furileusauria has some interesting implications for abelisaurid evolution and biogeography. The Furileusauria were initially known only from South America, but the recent discovery of *Caletodraco cottardi* in the Cenomanian of Normandy (Buffetaut *et al.,* 2024) showed that they were present in Europe too, and that at quite an early date. The Albian *Genusaurus sisteronis* pushes the European record of furileusaurian abelisaurids even farther back in time. As already noted by Buffetaut *et al.* (2024), the Albian and Cenomanian furileusaurians from Europe antedate the earliest known South American furileusaurians, the Santonian *Viavenator* and *Llukalkan*. *Genusaurus sisteronis* is currently the earliest known furileusaurian worldwide.This raises the question of a possible origin of the Furileusauria outside South America.

The fossil record of the Abelisauridae in Europe extends from the Albian to the Maastrichtian (Buffetaut, 2024 ; Malafaia *et al.,* 2025), and with the identification of *Genusaurus* and *Caletodraco* as furileusaurians, it becomes clear that two distinct groups of abelisaurids were present in Europe during the Cretaceous, since *Arcovenator escotae*, from the late Campanian of southern France is placed within the Majungasaurinae (Tortosa *et al.,* 2024), a clade less derived than the Furileusauria. Whether the Furileusauria and the Majungasaurinae coexisted at some stage in Europe is uncertain. Various European abelisaurids, such as *Tarascosaurus salluvicus* and *Betasuchus bredai* (Le Loeuff & Buffetaut, 1991), plus unnamed specimens from France, Spain and Hungary, can hardly be referred to a definite abelisaurid subgroup on the basis of the available material. The late Campanian tibia from La Boucharde in Provence (SE France), originally described as Neoceratosauria sp. by Allain & Pereda-Suberbiola (2003), was considered as belonging to the Carnotaurinae by Ezcurra & Agnolin (2012) because of the downturned end of its cnemial crest. Although Buffetaut *et al.* (2024) found this attribution worth considering, it seems in fact more likely that the La Boucharde tibia belongs to *Arcovenator* or a related taxon (see above). Unlike the condition in Furileusauria, in which the cnemial crest is hatchet-shaped, with its end expanded both upward and downward, the cnemial crest of the La Boucharde tibia is not upturned. In the holotypic tibia of *Arcovenator escotae*, the cnemial crest is poorly preserved but what is preserved is similar to the La Boucharde specimen (see figure in Tortosa, 2024). There is presently no really solid evidence of Furileusauria in Europe later than the Cenomanian (with *Caletodraco cottardi*), while the well-attested European majungasaurines are later in age, with notably the late

Fig. 7 - *Genusaurus sisteronis*, holotype (MNHN Bev.1). Left fibula in medial view ; mf : medial fossa. Scale bar : 5 cm.

Campanian *Arcovenator escotae.* However, as noted above, the status of various Late Cretaceous abelisaurid specimens from Europe remains uncertain.

Be that as it may, the presence of both furileusaurian and majugasaurine abelisaurids in Europe during the Cretaceous points to a complex biogeographical history, all the more so that the more derived furileusaurians appear in the European fossil record earlier than the more basal majungasaurines. Juárez-Valieri & Fiorelli (2004) rightly pointed out that Africa must have been involved in the dispersal of abelisaurids between South America and Europe, and this is also implied in Ezcurra and Agnolin's «Eurogondwana» model (Ezcurra & Agnolin, 2012). As far as furileusaurians are concerned, their occurrence in Africa is supported by the above-mentioned late Maastrichtian tibia from Morocco, with its hatchet-shaped cnemial crest (Longrich *et al.,* 2023). While the specimen is much later in age than *Genusaurus* and *Caletodraco*, it does suggest that furileusaurians were once present on the African continent. Juárez-Valieri & Fiorelli (2004) rightly pointed out that the occurrence of *Genusaurus* in the Albian of Europe suggested dispersal of abelisaurids between Gondwana and Europe before the complete separation between South America and Africa. Nevertheless, the timing and modalities of furileusaurian dispersal remain rather obscure and only new discoveries in Europe, Africa and South America may shed some light on this complicated question.

7. Conclusions

A re-examination of the type specimen of *Genusaurus sisteronis* confirms that this taxon belongs to the family Abelisauridae, as initially claimed by Buffetaut & Le Loeuff (1995) and subsequently accepted by many authors. In addition to general abelisaurid features, the specimen exhibits several characters which appear to be distinctive for the clade Furileusauria. The significance of the hatchet-like shape of the cnemial crest of the tibia had already been pointed out in several studies, and additional characters are adduced, including the dorsal thickening of the bony bar formed by the fused neural spines of the sacral vertebrae, a skeletal element that had hitherto not been identified in the holotype of *Genusaurus sisteronis*.

Together with *Caletodraco cottardi*, from the Cenomanian of Normandy, the Albian *Genusaurus sisteronis* provides evidence for the presence of furileusaurian abelisaurids at a geologically early date in Europe, apparently prior to the earliest record of Furileusauria in South America. This has possible implications for the geographical origin of that clade, although the evidence admittedly remains scanty. Whatever the place of origin of Furileusauria, dispersal between South America and Europe, must have taken place via Africa. This implies either the crossing of marine barriers between that continent and the European archipelago or the establishment of temporary land connections during the Cretaceous. Although it is late Maastrichtian in age, a record of a probable furileusaurian from Morocco apparently confirms the presence of this group of abelisaurids in Africa. Although it should be remembered that quite a few abelisaurid remains from Europe cannot be identified beyond the family level, there seems to be at the moment no very solid evidence of Furileusauria in Europe after the Cenomanian, since the La Boucharde tibia, which had been considered as possibly belonging to that group, more probably belongs to the majungasaurine *Arcovenator* or to a related taxon. Be that as it may, the presence of furileusaurians in Europe can be considered as well established, and raises a number of interesting questions about the evolutionary and biogeographical history of the Abelisauridae, in which the European archipelago of the Late Cretaceous apparently played a significant part.

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