fossil studies

Article

Caletodraco cottardi: A New Furileusaurian Abelisaurid (Dinosauria: Theropoda) from the Cenomanian Chalk of Normandy (North-Western France) †

Eric Buffetaut [1,*], Haiyan Tong [2,3], Jérôme Girard [4], Bernard Hoyez [5] and Javier Párraga [6]

[1] Centre National de la Recherche Scientifique (UMR 8538), Laboratoire de Géologie, Ecole Normale Supérieure, PSL Research University, 24 Rue Lhomond, 75231 Paris, CEDEX 05, France
[2] Palaeontological Research and Education Centre, Mahasarakham University, Kantarawichai 44150, Mahasarakham, Thailand; htong09@yahoo.fr
[3] Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing 100044, China
[4] Société d'Etude des Sciences Naturelles d'Elbeuf, 127 rue aux Saulniers, 76320 Saint Pierre lès Elbeuf, France; j76gir@gmail.com
[5] Université Le Havre Normandie, 25 rue Philippe Lebon, 76600 Le Havre, France; bernard.hoyez@univ-lehavre.fr
[6] Muséum d'Histoire Naturelle du Havre, Place du Vieux Marché, 76600 Le Havre, France; javier.parraga@lehavre.fr
* Correspondence: eric.buffetaut@sfr.fr

† LSID: urn:lsid:zoobank.org:act:4BEA1D52-B1D2-4D60-BD12-A77AF3DE61FF; urn:lsid:zoobank.org:act:28143D7A-C622-4B19-A307-B987CCBC2493.

Abstract: An articulated group of skeletal elements comprising a sacrum, both ilia and a first caudal vertebra, plus an isolated tooth found in immediate proximity to the bones, from the lower Cenomanian Chalk at Saint-Jouin-Bruneval (Seine-Maritime, Normandy, France) is described and attributed to a new genus and species of abelisaurid theropod, *Caletodraco cottardi*, on the basis of several characters of the sacrum and pelvis. The peculiar shape of the transverse process of the first caudal vertebra shows that *Caletodraco cottardi* differs from majungasaurine abelisaurids previously described from Europe, such as *Arcovenator escotae*, and belongs to the Furileusauria, a group of derived abelisaurids hitherto recognized only from South America. The presence of a furileusaurian abelisaurid in the Cenomanian of Normandy suggests that the biogeographical history of the Abelisauridae in Europe was more complex than hitherto admitted. Several previously described European abelisaurids, such as the Albian *Genusaurus sisteronis*, may in fact belong to the Furileusauria.

Keywords: Dinosauria; Theropoda; Abelisauridae; Cenomanian; Normandy

Citation: Buffetaut, E.; Tong, H.; Girard, J.; Hoyez, B.; Párraga, J. *Caletodraco cottardi*: A New Furileusaurian Abelisaurid (Dinosauria: Theropoda) from the Cenomanian Chalk of Normandy (North-Western France). *Foss. Stud.* **2024**, *2*, 177–195. https://doi.org/10.3390/fossils2030009

Academic Editor: Federico Agnolin

Received: 10 July 2024
Revised: 2 August 2024
Accepted: 3 August 2024
Published: 19 August 2024

1. Introduction

When the family Abelisauridae was erected in 1985 by Bonaparte and Novas [1], it included the single taxon *Abelisaurus comahuensis*, a large carnivorous dinosaur from the Campanian of Patagonia. It has since become apparent that the Abelisauridae actually constitute a major radiation of neoceratosaurian theropods that played an important part in the Cretaceous continental ecosystems of South America ([2,3] and references therein), Africa [4], the Indian subcontinent ([5] and references therein) and Madagascar [6]. Although the Abelisauridae have a mainly Gondwanan distribution, an abelisaurid was reported from the Late Cretaceous of southern France as early as 1988 (the "Pourcieux maxilla" [7]), and they are now known from Cretaceous localities in several European countries [8], including France [9–12], Spain [13,14], Hungary [15] and the Netherlands (with *Betasuchus bredai* [9]). Here, we report an abelisaurid specimen from the Cenomanian

Chalk of Normandy that is unexpected in terms of both its geological occurrence in a marine deposit where tetrapod remains seldom occur and its systematic position among the Furileusauria, a derived abelisaurid subgroup previously known only from South America [16].

2. Geographical and Geological Settings

The specimen, consisting of two Chalk blocks containing bones and teeth, was found by Mr Nicolas Cottard in the course of stratigraphic and paleontological research at the foot of the sea cliffs at Saint-Jouin-Bruneval (Figure 1), on the coast of the Pays de Caux, in the department of Seine-Maritime (Normandy, north-western France) (Figure 2). Although the blocks were found on two distinct occasions in 2021 (the block containing the posterior part of the specimen) and 2023 (the block containing the anterior part), the bones they contain fit well together, with only minor loss of bony substance between the two parts.

Figure 1. The Chalk cliffs at Saint-Jouin-Bruneval (Seine-Maritime, Normandy, France), where the holotype specimen of *Caletodraco cottardi* was discovered by Mr. Nicolas Cottard.

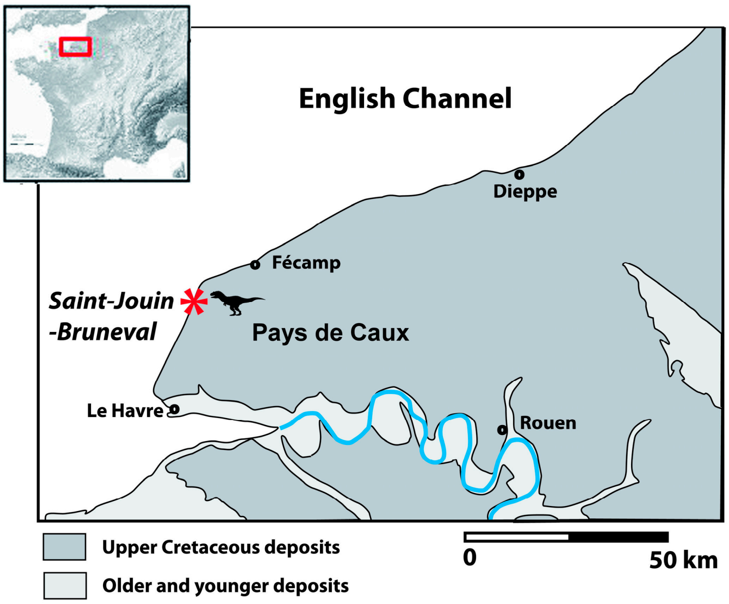

Figure 2. Location map showing the position of Saint-Jouin-Bruneval on the coast of the Pays de Caux (Normandy). The blue line is the river Seine.

Since the lithostratigraphic section at this particular location has been studied in great detail [17], the initial position of the fossil-bearing blocks in the cliff can be ascertained with some precision on the basis of the matrix. The specimen can apparently be referred to the C3 sequence of Hoyez et al. [17]), corresponding to the *Mantelliceras dixoni* zone of the lower Cenomanian glauconitic Chalk (Figure 3). The glauconitic Chalk of the Pays de Caux is a marine deposit [18], as indicated in the present case by a shark tooth present in the matrix, close to one of the bones in the anterior block (Figure 4). The nearest land area (where the dinosaur described below probably lived) must have been the Armorican Massif, about 100 km to the south-west (Figure 5, see also palaeogeographical map in Juignet and Kennedy ([19], Figure 16A). The dinosaur specimen must somehow have been carried out to sea, possibly by a stream, after which it must have floated over a fairly long distance until it sank to the bottom. According to Lasseur et al. [20], dominant winds were blowing from the SW, with a wind fetch of at least 200 km, in the Early Cenomanian, which may have facilitated the drift of a carcass from the Armorican Massif to the area where the fossil remains were found. Occurrences of dinosaur remains in marine deposits are rather frequent [21], although this seems to be the first record from the Late Cretaceous Chalk of the Pays de Caux, where the only relatively common vertebrate fossils are fish teeth [17,22], although scanty crocodile and ichthyosaur remains were reported from the Cenomanian glauconitic Chalk by Lennier [23,24].

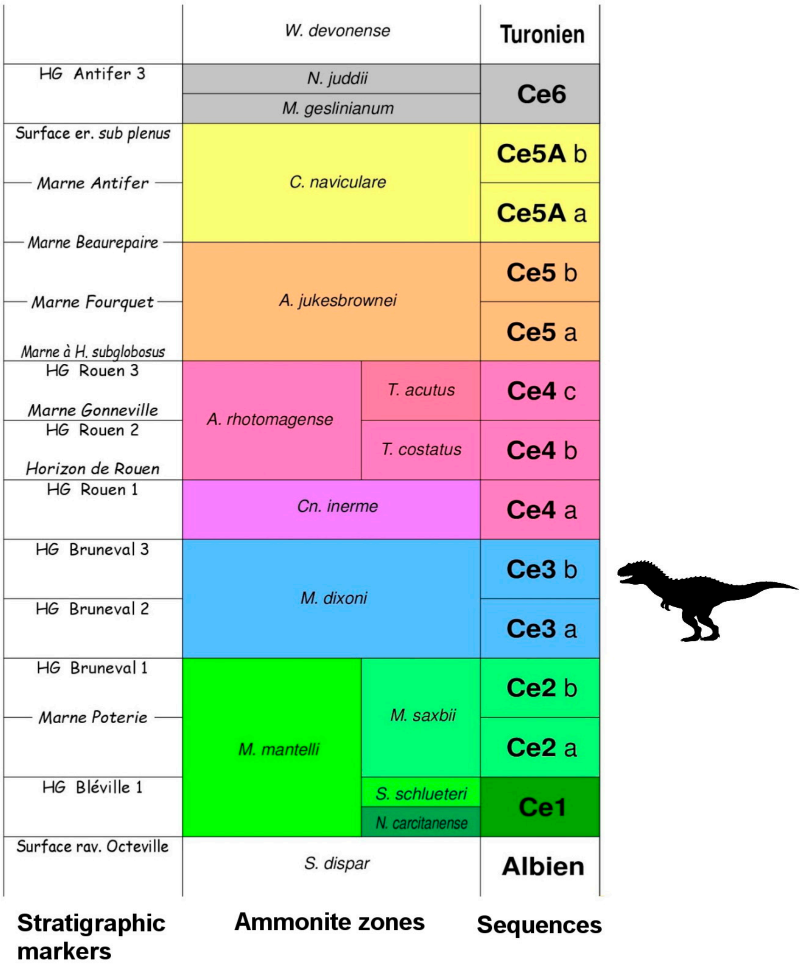

Figure 3. Probable stratigraphic origin (C3 sequence) of the type specimen of *Caletodraco cottardi* in the Lower Cenomanian glauconitic Chalk of Saint-Jouin-Bruneval. Stratigraphic column after Hoyez et al. [17].

The presence of abelisaurid remains in a marine sedimentary environment is uncommon but not exceptional. Previous records of abelisaurids in marine formations include the holotype of *Genusaurus sisteronis*, from Albian deposits in south-eastern France [25] and various remains from the Maastrichtian phosphates of Morocco [26–28] and Egypt [29,30]. However, only very few dinosaur remains, belonging to ornithopods and ankylosaurs, have hitherto been reported from the Chalk of the Anglo-Paris basin [31].

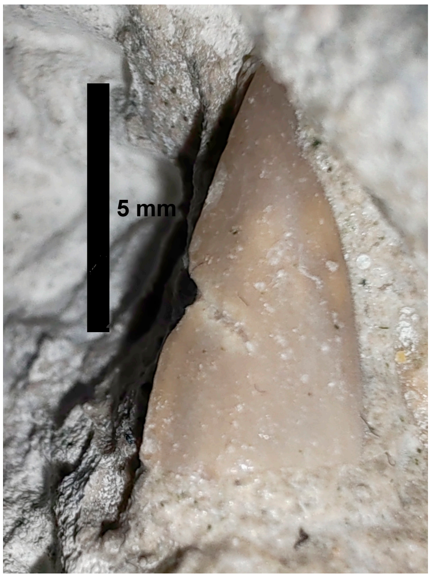

Figure 4. Shark tooth (probably lamniform) associated with the bones of *Caletodraco cottardi* in block MHNH 2024.1.1.2.

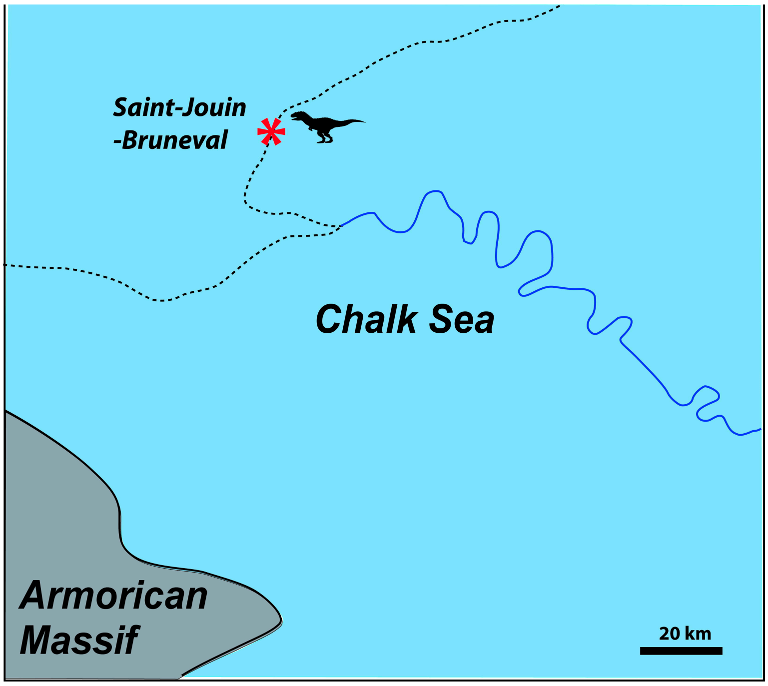

Figure 5. Simplified paleogeographical map of part of Normandy in the Early Cenomanian, superimposed on present-day landmarks: coastline (dotted) and Seine river valley (blue). The Armorican Massif was a land area in the Cenomanian. Distribution of land and sea after Juignet and Kennedy [19].

3. Material and Methods

As mentioned above, the two blocks containing the dinosaur remains were found separately on two different occasions in the course of systematic research by Nicolas Cottard. The fragile bones, encased in very hard grey chalk, have been prepared mechanically but no attempt has been made to completely free them of the matrix because of the risk of damaging them. Scanning of the blocks, although technically difficult, may be attempted at a later stage. Many of the bones are more or less damaged, following their fall from the cliff and exposure on the surface before they were noticed and collected. Moreover, they appear to have been partly crushed and distorted during fossilisation. Nevertheless, several of them are sufficiently well preserved to be clearly identified. The material consists of a sacrum with the attached partially preserved ilia, the first caudal vertebra and various poorly preserved bones that could not be accurately identified, although some of them may be ribs.

4. Systematic Paleontology

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Ceratosauria Marsh, 1884
Abelisauridae Bonaparte and Novas, 1985
Brachyrostra Canale et al., 2009
Furileusauria Filippi et al., 2016
Caletodraco cottardi, n.g., n.sp.

Derivatio nominis: genus name from the *Caleti* (or *Caletes*), a Celtic tribe that inhabited the Pays de Caux [32]), the part of Normandy on the coast of which the fossil was found, and *draco*, Latin for dragon. The species is dedicated to Mr Nicolas Cottard, who discovered the specimen in the course of his systematic research on the stratigraphy and paleontology of the Chalk of Normandy and donated it to the Muséum d'histoire naturelle du Havre.

Locus typicus: cliffs along the English Channel at Saint-Jouin-Bruneval, Seine-Maritime, Normandy (NW France).

Stratum typicum: Lower Cenomanian glauconitic Chalk, *Mantelliceras dixoni* zone, probably C3 sequence of Hoyez et al. [17].

Type specimen: a group of bones comprising a sacrum, incomplete ilia, the first caudal vertebra and various poorly preserved bones, possibly ribs (Figure 6). An isolated theropod tooth (Figure 7) found in the matrix close to the bones may belong to the same specimen or to a predator/scavenger. Muséum d'histoire naturelle du Havre, MHNH 2024.1.1.1 (subdivided into MHNH 2024.1.1.1 for the first block containing the posterior part and MHNH 2023.1.1.2 for the second block containing the anterior part, the abelisaurid tooth and the shark tooth).

Diagnosis: a large abelisaurid theropod showing furileusaurian characteristics, including a straight dorsal margin of the ilium and a distally expanded and crescent-shaped tip of the dorsally orientated transverse process of the first caudal vertebra, with a convex distal margin, differing from previously known furileusaurians by the following autapomorphy: distinctive shape of the transverse process, with a short anterior spine and a rounded and expanded fan-shaped semicircular posterodistal margin.

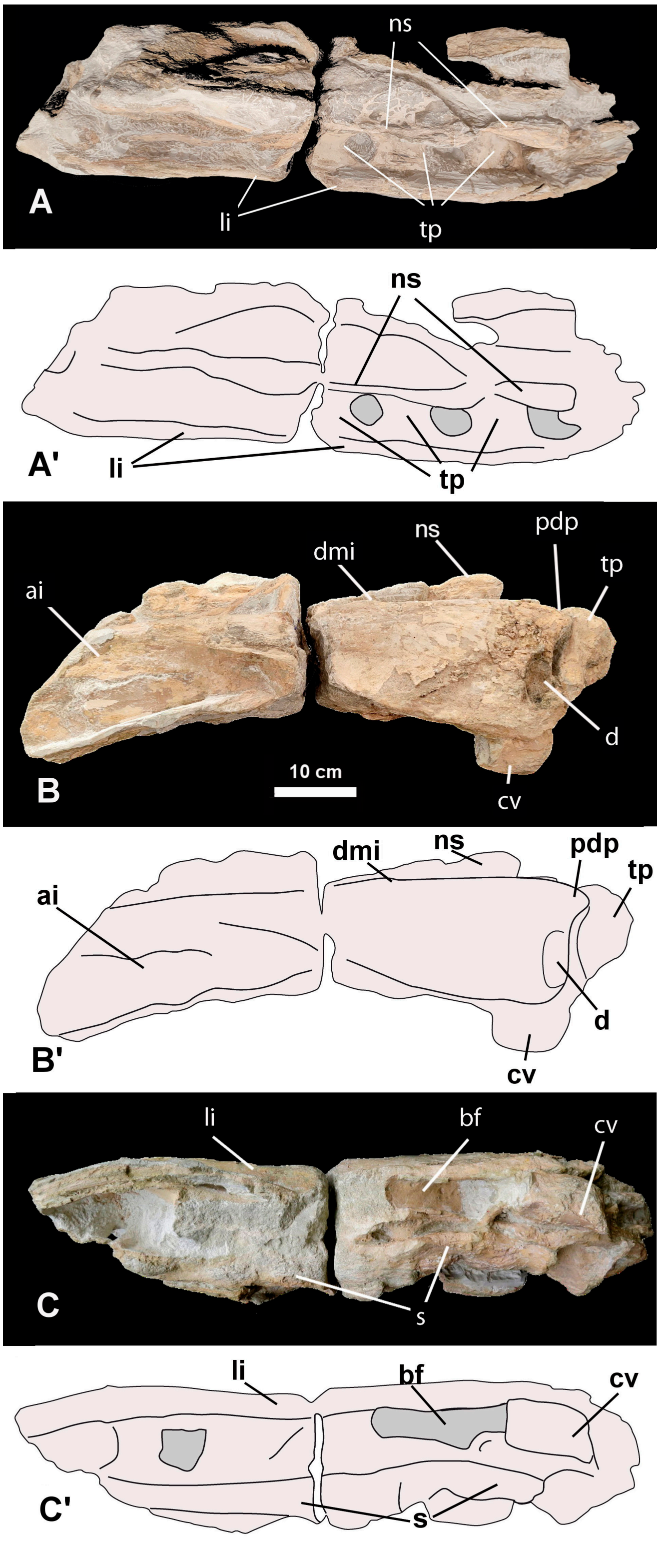

Figure 6. Holotype specimen of *Caletodraco cottardi*, MHNH 2024.1.1., in dorsal (**A**,**A′**), left lateral (**B**,**B′**) and ventral (**C**,**C′**) views, with explanatory drawings. Front is at left. Abbreviations: ai: anterior wing of ilium; bf: brevis fossa; cv: centrum of first caudal vertebra; d: depression; dmi: dorsal margin of ilium; li: left ilium; ns: fused neural spines of sacral vertebrae; pdp: posterodorsal process of ilium; s: sacrum; tpc: transverse process of first caudal vertebra; tps: transverse processes of sacral vertebrae.

4.1. Description

Tooth. An isolated tooth (Figure 7) is partly embedded in matrix close to the anterior part of the poorly preserved iliac blade. Its apical part is well preserved, while its more basal part is damaged and incomplete, so that a morphometric study is difficult. The crown is blade-like, compressed lateromedially, with sharp serrated mesial and distal carinae. The distal margin is straight, whereas the mesial margin is markedly convex. The enamel surface is faintly irregular rather than smooth. There are about 14 serrations per 5 millimetres. They are oblique (apically inclined) relative to the apicobasal axis of the crown, separated by well-marked interdenticular spaces, and with a convex external margin. No interdenticular sulci are visible.

Figure 7. Abelisaurid tooth associated with the holotype specimen of *Caletodraco cottardi*, in block MHNH 2024.1.1.2.

While this tooth shows characters strongly suggesting it is from an abelisaurid (see below), its location close to the pelvis is unusual and it can be interpreted in two different ways. Either it belongs to the same individual as the postcranial bones, which implies that it was detached from the jaws and somehow became displaced to its present position during fossilisation, or it belongs to another individual that consumed the carcass, either as a predator or a scavenger. The latter interpretation cannot be excluded, since cannibalism has been demonstrated in the Madagascan abelisaurid *Majungasaurus* [33]. This would imply that the tooth, after being lost by the predator, somehow became stuck to the carcass sufficiently solidly to remain fixed to it during transport to its burial place at the bottom of the Chalk sea. The presence of the crown of a shark tooth (possibly a lamniform: G. Cuny, pers. com.) in the same block (Figure 4), in direct proximity to the bones, is easier to explain since it simply implies scavenging on the carcass while it was floating or on the sea-floor. If the abelisaurid tooth reflects predation or scavenging, the fact that the carcass was apparently partly eaten first (on land) by a theropod dinosaur and then (at sea) by a shark is an unusual taphonomic occurrence. An oyster shell fixed on one of the bones shows that the skeleton lay on the sea bottom for some time before being buried in sediment.

Sacrum and pelvis (Figures 6, 8 and 9). Although it exhibits deformation, the sacrum appears to be complete and is visible both in ventral and dorsal views between the ilia. It is composed of apparently six strongly fused vertebrae, between which no sutures are visible. The presence of six or more sacral vertebrae is considered as a characteristic of derived abelisaurids by Baiano et al. [34]. The centra of the middle part of the sacrum are constricted by comparison with the more anterior and posterior centra, also a derived character. Because of its preservation, it is difficult to determine whether the sacrum was ventrally arched. The posteriormost sacral centrum shows a distinctly concave articular surface. The neural spines of the caudal vertebrae are thickened and fused together, showing the derived condition of abelisaurids. They are highly pneumatized, the broken bony wall showing extensive matrix-filled cavities that extend into the transverse processes of the sacral vertebrae (Figure 8).

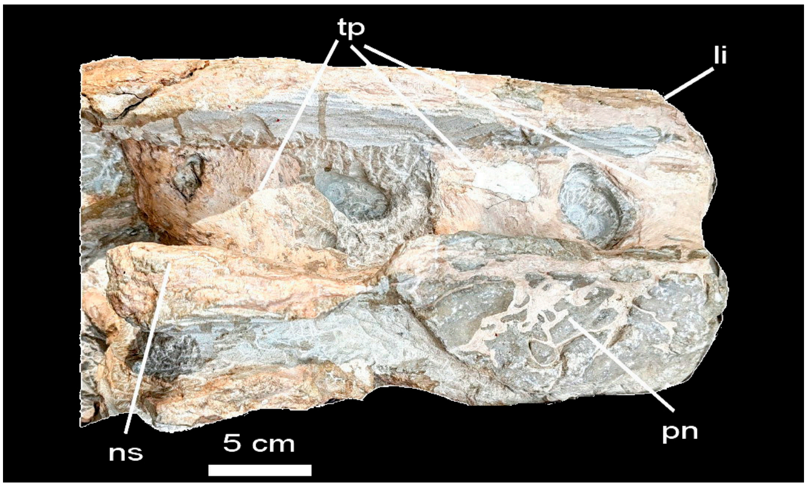

Figure 8. Close-up of part of the holotype specimen of *Caletodraco cottardi*, MHNH 2024.1.1.1. in dorsal view, showing extensive pneumatization of the sacral vertebrae. Abbreviations: li: left ilium; ns: thickened and fused neural spines of sacral vertebrae; pn: pneumatic spaces in transverse processes of sacral vertebrae; tp: transverse processes of sacral vertebrae.

The ilia are partly preserved, the left one (on which the description is based) being more complete than the right one, although both miss their ventral part and acetabular region. The real shape of the anterior wing of the ilium is difficult to ascertain because its anterodorsal margin is poorly preserved. Its outline seems to have been convex and smoothly rounded. The dorsal margin of the ilium is straight, rather than convex, thus exhibiting the derived condition in abelisaurids. The posterior margin of the ilium (Figure 9) shows a well-marked notch separating a posteriorly convex ventral part from a posterodorsal corner that forms a well-marked spur (posterodorsal process). The lateral surface of the left ilium shows a subcircular shallow depression in its posteroventral corner (Figure 9). This has not been reported in any other abelisaurid (and probably not in any theropod). It may be a pathological feature, or possibly a taphonomic artefact caused by the pressure of a rounded hard object during fossilisation. In ventral view, the posterior half of the left ilium clearly shows a deep and posteriorly wide brevis fossa.

Caudal Vertebra

The first caudal vertebra (Figures 9–11) is displaced anteroventrally relative to the last sacral vertebra. Its centrum is poorly preserved, its ventral face being much abraded, like its articular faces, so that its original shape is difficult to reconstruct. It cannot be determined whether a ventral median groove was present, as in some abelisaurids. Only the posterior aspect of the neural arch is visible (Figure 10). It is worth noting that the base of the neural arch is quite broad, apparently equaling the width of the centrum. A hyposphene is present above the neural canal. The long left transverse process is relatively well preserved. Despite the fact that it is broken near its inception on the centrum, it has been only a little displaced relative to it. The angle at which it diverges from the neural arch at its base is about 45°. The transverse process is visible mainly in ventral view and shows a peculiar shape (Figure 11). Its shaft is broad and slightly curved posteriorly. Its ventrolateral surface bears a low, rounded centrodiapophyseal lamina. The distal end of the process is much widened, forming a fan-shaped, semicircular posterodistal flange, with a convex posterior margin, while the anterodistal margin forms a sharp but not very long hook-like process.

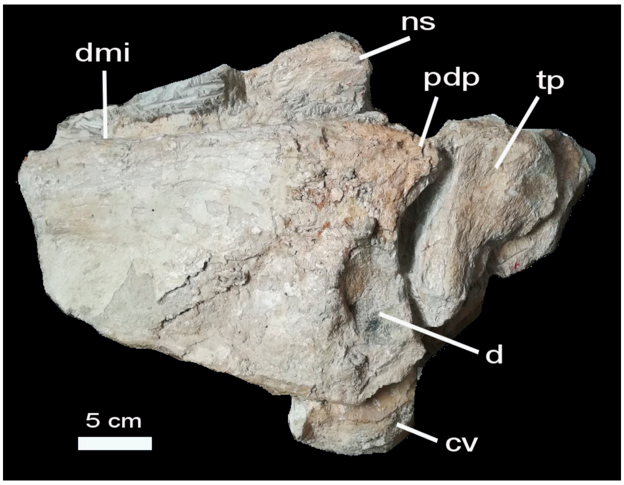

Figure 9. Posterior part of holotype specimen of *Caletodraco cottardi*, MHNH 2024.1.1.1. in lateral view, showing details of posterior part of left ilium and first caudal vertebra. Abbreviations: cv: centrum of first caudal vertebra; d: depression; dmi: dorsal margin of ilium; ns: fused neural spines of sacral vertebrae; pdp: posterodorsal process of ilium; tp: transverse process of first caudal ver.

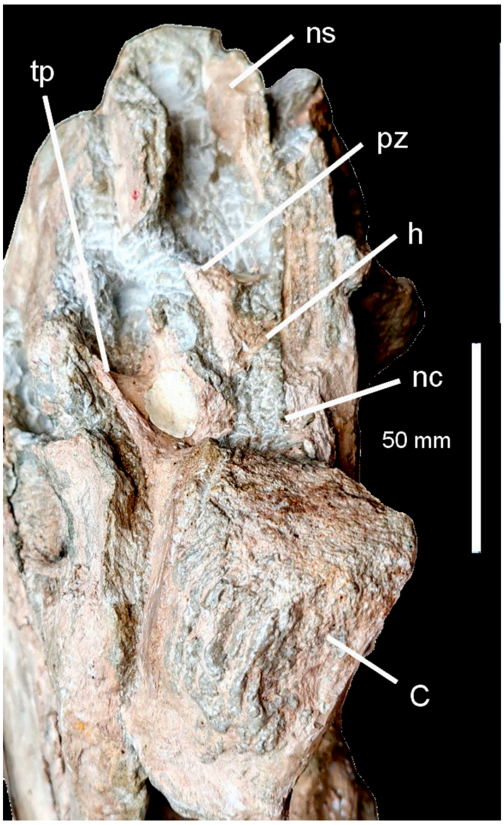

Figure 10. Close-up of first caudal vertebra in posteroventral view. Abbreviations: c: centrum; h: hyposphene; nc: neural canal; ns: neural spine; pz: postzygapophysis; tp: base of transverse process.

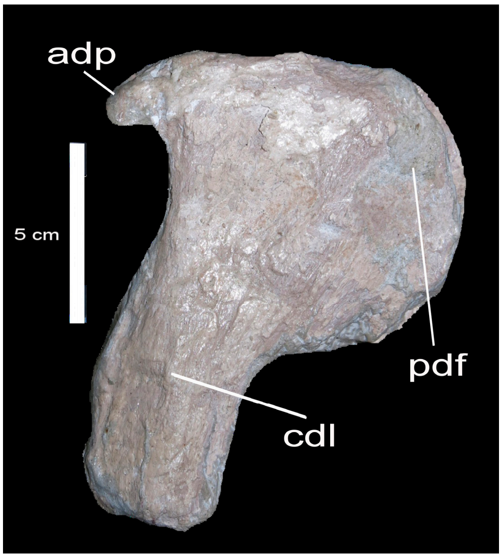

Figure 11. Distal part of transverse process of first caudal vertebra in ventral view. Abbreviations: adp: anterodistal process; cdl: centrodiapophyseal lamina; pdf: posterodistal flange.

4.2. Measurements and Size Estimate

Because of the preservation of the specimen, few significant measurements can be taken. The total length of the ilium must have been close to 700 mm or a little more, similar to that of the ilium of *Skorpiovenator* (700 mm), for which an estimated length of about 6 m has been proposed [35,36]. This would make *Caletodraco cottardi* a middle-sized abelisaurid (see body length estimates in Grillo and Delcourt [36]).

The length of the centrum of the first caudal vertebra is 95 mm. It was probably slightly longer, since both articular ends are abraded. If one assumes an original length of about 100 mm, again this measurement is close to that given by Grillo and Delcourt [36] for *Skorpiovenator* (104 mm).

4.3. Comparisons and Identification

Although the specimen from Saint-Jouin-Bruneval consists of relatively few skeletal and dental elements, they show significant characteristics, which make useful comparisons possible.

It cannot be incontrovertibly demonstrated that the tooth found in association with the bones belongs to the same individual (see above). Nevertheless, it shows clear abelisaurid characters that deserve to be discussed in some detail. With its straight distal margin and convex mesial margin, this tooth is very similar to abelisaurid teeth from various localities [37]), notably morphotype III of Meso et al. [38] from the Campanian–Maastrichtian Allen Formation of Patagonia, the isolated tooth from the Maastrichtian phosphates of Morocco described by Buffetaut et al. [26], some of the abelisaurid teeth from the Albian-Cenomanian Açu Formation of Brazil described by Ribeiro et al. [39]), or some of those from the Campanian–Maastrichtian Adamantina Formation of Brazil described by Giaretta et al. [40]. It also resembles some of the abelisaurid teeth from the Upper Cretaceous Bauru basin of Brazil figured by Delcourt et al. [41]. It differs from the probable abelisaurid teeth from the Cenomanian of Algora in Spain described by Perez-Garcia et al. [13] in that in the latter the denticles are not apically inclined. The teeth of *Arcovenator escotae*, from the upper Campanian of Pourrières in Provence [12], those of the Pourcieux maxilla [7] and comparable ones from deposits of similar age at Cruzy in southern France) [11] and Laño in Spain [14] differ from the tooth from Saint-Jouin-Bruneval in having a more slender and recurved crown.

Skeletal characters of particular significance indicating abelisauroid, abelisaurid and furileusaurian affinities are listed below (mostly taken from the list in Baiano et al. [34]).

- Presence of six strongly fused sacral vertebrae. The number of sacral vertebrae is variable in abelisauroids [34]. The furileusaurians *Carnotaurus* and *Aucasaurus* have six, the majungasaurine *Majungasaurus* only five, but the noasaurid *Masiakasaurus* has six. The degree of fusion of the sacral vertebrae is also variable. In *Majungasaurus* [42], sutures are still visible between centra and neural arches. The advanced degree of fusion seen in *Caletodraco cottardi* can probably be considered as a characteristic of derived abelisaurids.
- Sacrum constricted in its middle part. This character, resulting from the narrowness of the mid-sacral vertebrae, is present in many ceratosaurs [34] and well developed in furileusaurians such as *Carnotaurus* and *Aucasaurus*, but is apparently absent in *Majungasaurus*.
- Thickened dorsal edge of the neural spines of the sacral vertebrae. This derived character is present in *Carnotaurus*, and *Aucavenator.* It is less developed in *Koleken* [3] and absent in *Skorpiovenator* [43] and in majungasaurines such as *Majungasaurus* [42].
- Well-developed pneumaticity of the neural spines and transverse processes of the sacral vertebrae. This is a ceratosaurian character according to Carrano and Sampson [44].
- Wide base of the neural arch of the first caudal vertebra. This character is widespread among abelisauroids according to Carrano and Sampson [44].
- Presence of a hyposphene on the neural arch of the first caudal vertebra. A hyposphene–hypantrum accessory articulation is present in *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, *Skorpiovenator*, *Pycnonemosaurus* [45], *Kurupi* [46] and *Koleken* [3] but absent in *Ilokelesia*, *Majungasaurus* [45] and *Arcovenator* [12].
- Presence of a centrodiapophyseal lamina on the ventral surface of the transverse processes of the first caudal vertebra. According to Ezcurra and Méndez [47] and Méndez [45], this is an abelisauroid character.
- Distally expanded transverse processes of the first caudal vertebra, with a convex distal margin and a pointed anterior process. A great distal expansion of the transverse processes of anterior and mid-caudal vertebrae was considered as a synapomorphy of Brachyrostra by Canale et al. [35]. Filippi et al. [16] considered a convex distal edge of the transverse process, and a strong development of an anterior projection as a synapomorphy of Furileusauria. See below for a detailed discussion of this feature, which appears to be a distinguishing characteristic of furileusaurians.
- Dorsal margin of the ilium straight (Figure 11). This character is found in derived abelisaurids such as the furileusaurian Brachyrostra *Carnotaurus sastrei* [48], *Aucasaurus garridoi* [34] and *Koleken inakayali* [3]. In the less derived *Majungasaurus crenatissimus* [42] and *Skorpiovenator bustingorryi* [49], the dorsal margin of the ilium is convex, while it is possibly undulated in *Rahiolisaurus gujaratensis* [50] and *Ekrixinatosaurus novasi* [51]. Interestingly, a straight dorsal margin is also present in *Genusaurus sisteronis*, from the Albian of France, a possible furileusaurian (see below and [34]). It should be noted, however, that this character is also known in the noasaurid *Masiakasaurus knopfleri* [52].
- Posterior margin of the ilium with a deep notch and a posterodorsal process (Figure 11). This is a widespread character in Abelisauridae, being found in both majungasaurines (*Majungasaurus*) and brachyrostrans (*Aucasaurus*, *Carnotaurus*).
- Brevis fossa becoming significantly wider posteriorly. This feature appears to be widespread in abelisaurids, and more generally in ceratosaurs [43].

Because of its significance as a distinguishing character of the new taxon *Caletodraco cottardi*, the morphology of the transverse process of the first caudal vertebra (Figure 12) is discussed below at some length. As noted above, the transverse process of the first caudal vertebra is orientated dorsally, making an angle of about 45 ° with the neural spine. In this, it differs from the more horizontal processes of majungasaurines such as *Majungasaurus* [42] and *Arcovenator* [12] and is reminiscent of furileusaurians such as *Carnotaurus* [48], *Aucasaurus* [34] and *Viavenator* [53]. Similarly, the unusual and distinctive shape of the distal end of the transverse processes of the first caudal vertebra allows referring *Caletodraco cottardi* to the Furileusauria, a distinct clade of brachyrostran Abelisauridae defined by Filippi et al. [16]. The Saint-Jouin-Bruneval specimen shares with the Furileusauria an expanded and convex distal tip of the transverse process, which is crescent- or sickle-shaped, with a marked anterior projection (Figure 13). It differs from other abelisaurids [45,54] in which the tip of the transverse process is expanded but with a straight or concave distal margin, such as *Ekrixinatosaurus* [51], *Ilokelesia* [55] and *Skorpiovenator* [35]. *Caletodraco* shows clear similarities with the furileusaurians in which the transverse processes are known, such as *Carnotaurus sastrei* [48], *Viavenator exxoni* [16,53], *Pycnocnemosaurus nevesi* [56]), *Kurupi itaata* [46] and *Aucasaurus garridoi* [34,57]. However, its outline distinguishes it from all previously described furileusaurians (Figure 12). In *Carnotaurus sastrei*, the distal end of the transverse process of the first caudals is less expanded posteriorly. In *Viavenator exxoni*, the anterior projection of the transverse process is much longer than in *Caletodraco*. In *Pycnocnemosaurus nevesi*, the distal end of the transverse process is less expanded both anteriorly and posteriorly. In *Kurupi itaata*, it does not show the fan-shaped posterior flange and it bears a longitudinal ridge along the distal margin that is not present in *Caletodraco*. In *Aucasaurus garridoi*, this distal ridge is also present and there is no fan-shaped posterodistal flange, while the anterior projection is markedly longer. Because of these differences, it seems legitimate to consider the abelisaurid from Saint-Jouin-Bruneval as a new taxon, mainly because of the highly distinctive outline of the distal end of the transverse process of the first caudal vertebra, which constitutes its principal synapomorphy.

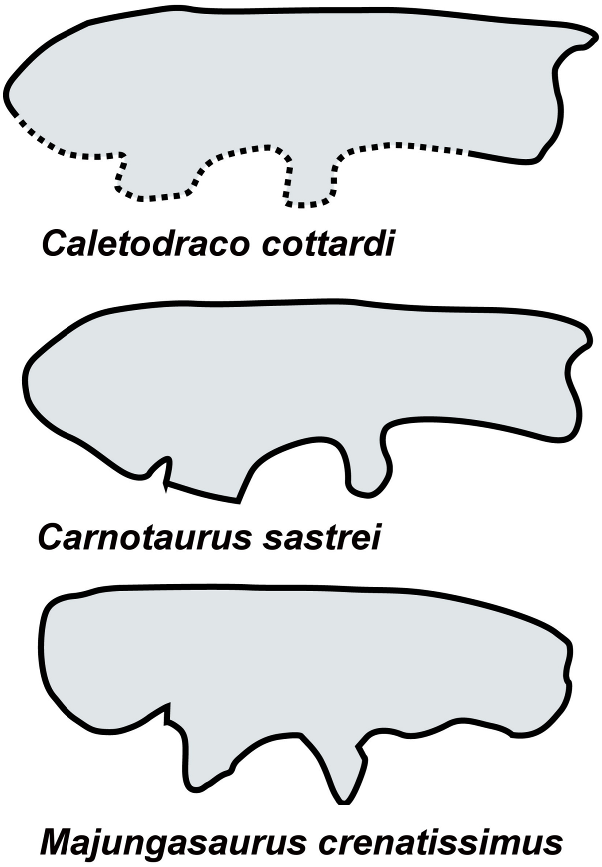

Figure 12. Outline of the ilium in three abelisaurids: the furileusaurians *Caletodraco cottardi* and *Carnotaurus sastrei* and the majungasaurine *Majungasaurus crenatissimus*. Reconstructed areas in *C. cottardi* are dotted. Not to scale.

Apart from South American forms, abelisaurids with which *Caletodraco cottardi* can be compared include the Madagascan *Majungasaurus crenatissimus*, which clearly differs from it in having quite different transverse processes of the anterior caudal vertebrae, without any significant anteroposterior expansion of the distal end [42], and an ilium with a convex rather than straight dorsal margin [58]. African abelisaurids cannot be compared with *Caletodraco cottardi* because there is no skeletal material in common (the ilium from the Cenomanian Kem Kem beds of Morocco described by Zitouni et al. [59] is too fragmentary for comparison with that from Saint-Jouin-Bruneval). Among Indian forms, *Rahiolisaurus gujaratensis* [50] has sacral vertebrae that are less strongly fused and less compressed in the median region than in *Caletodraco cottardi*, the first caudal vertebra has transverse processes that do not project much dorsally, and the ilium possibly has an undulated rather than straight dorsal margin. Other abelisaurid specimens from India [60] do not show any clear similarities with *Caletodraco*; in particular, they lack the strong constriction of the middle part of the sacrum.

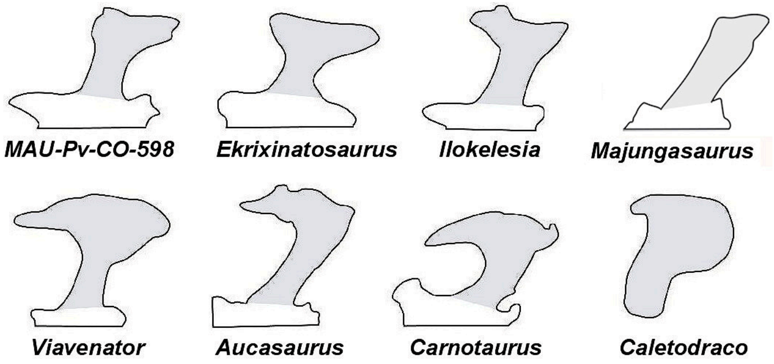

Figure 13. Outlines of transverse processes (in grey) of caudal vertebrae of various abelisaurids for comparison with *Caletodraco cottardi*. Redrawn and modified after Gianechini et al. [61], except for *Majungasaurus* and *Caletodraco.* MAU-Pr-CO-598 is a non-furileusaurian abelisaurid vertebra from the Santonian Bajo de la Carpa Formation, Argentina. *Viavenator*, *Aucasaurus*, *Carnotaurus* and *Caletodraco* are furileusaurians. Not to scale.

Comparisons with European abelisaurids are especially significant but limited by the scarcity of skeletal elements that can be directly compared with *Caletodraco cottardi.* The ilium is known in *Genusaurus sisteronis*, from the Albian of south-eastern France [25], which is clearly an abelisaurid [10], as generally accepted today, although this was initially disputed by Accarie et al. [62]), who considered abelisaurids as a dubious group, and Carrano and Sampson [44]), who considered *Genusaurus* as noasaurid. Tortosa et al. [12] place it outside Majungasaurinae in a rather basal position. Divergent opinions have been expressed by other authors about the position of *Genusaurus* among Abelisauridae (see below). The specimen is apparently a juvenile, as suggested by the incomplete fusion of the sacral vertebrae. It shows a straight dorsal margin, as in *Caletodraco.* The posterior margin may at first sight seem similar to that of *Caletodraco*, with what seems to be a wavy outline and a posterodorsal process, but the margin is in fact broken so that its original outline cannot be safely reconstructed. Although a few vertebral centra are preserved, they do not seem to be from caudal vertebrae, and no transverse processes are preserved.

In the holotype of *Arcovenator escotae*, from the late Campanian of Provence, the pelvis is not preserved but an anterior caudal vertebra is present [12]. Unlike *Caletodraco* (and other brachyrostran abelisaurids), there is no hyposphene–hypantrum articulation. The transverse processes are only slightly dorsally orientated, as in *Majungasaurus* [42], and show no trace of a distal expansion (although this part is not well preserved). According to Tortosa et al. [12], *Arcovenator* belongs to the subfamily Majungasaurinae, together with *Majungasaurus* and several Indian taxa, a phylogenetic placement accepted, with only slight variants, by various authors (e.g., [2,16,54,63]). According to recent phylogenies (e.g., [2,16,54]), Majungasaurinae and Furileusauria are very distinct clades of abelisaurids, majungasaurines being significantly more basal than furileusaurians (which are considered as the most derived abelisaurid clade). It thus appears that the Cenomanian *Caletodraco* and the Campanian *Arcovenator* were not closely related. Further phylogenetic analyses should clarify the relationships between *Caletodraco* and other European abelisaurids.

Other European abelisaurids, including *Tarascosaurus* and *Betasuchus*, plus unnamed forms from Hungary, France and Spain [8]), cannot be directly compared with *Caletodraco* because of the absence of comparable skeletal elements. It should be noted, however, that possible furileusaurian affinities can be suspected for a few previously described abelisaurids from France (see below).

5. Discussion

Caletodraco cottardi is an unexpected addition to the Cretaceous dinosaur fauna of Europe. The presence of abelisaurids in Europe has been known since the description of the Pourcieux maxilla (probably belonging to *Arcovenator*) in 1988 [7], and their record in that geographical area now spans a rather long stratigraphic interval, from the middle Albian to the late Maastrichtian [8] (Figure 14). Jurassic reports of abelisaurids in Europe should be considered as doubtful: the attribution to an abelisauroid of a tibial fragment from the Bathonian of Stonesfield (England) by Ezcurra and Agnolin [64] was disputed by Rauhut [65], and putative abelisaurid teeth from the Upper Jurassic of Portugal reported by Hendrickx and Mateus [66] more probably belong to allosauroids [67]. While their presence in Europe during the Cretaceous is now well documented, the systematic position of European forms among Abelisauridae has remained uncertain, with the exception of *Arcovenator escotae*, which is generally placed in the subfamily Majungasaurinae (e.g., [2,12,16,34,63,68]). No consensus exists about the exact position of other European abelisaurids. For instance, to mention only relatively recent phylogenies, *Genusaurus sisteronis* is considered as a noasaurid by Gianechini et al. [69], and as a majungasaurine by Filippi et al. [16] (who consider it as the sister group of *Arcovenator*) and by Gianechini et al. [68]. Tortosa et al. [12] place it in a more basal position than majungasaurines and it appears as the most basal abelisaurid in the phylogeny of Gianechini et al. [54]. However, Baiano et al. [34] place it among the Furileusauria.

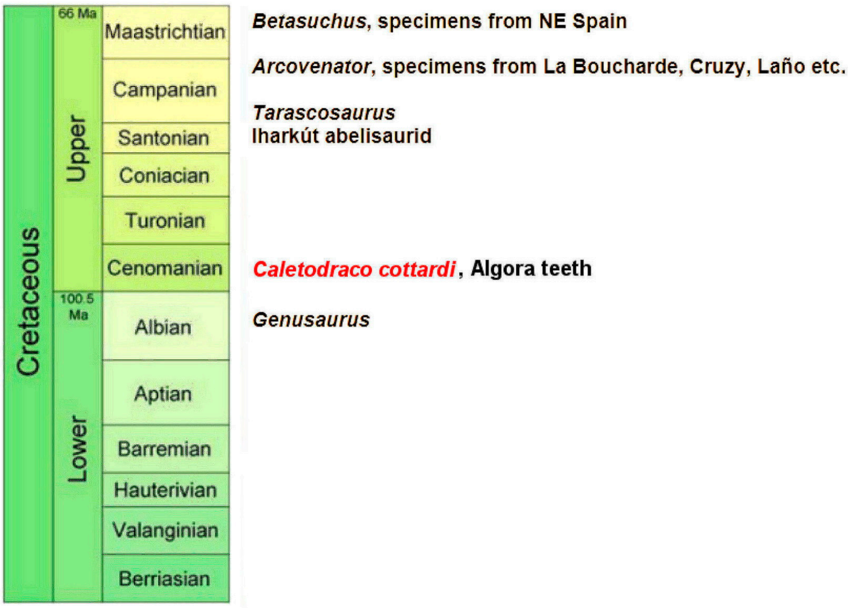

Figure 14. Stratigraphic distribution of main abelisaurid occurrences in the Cretaceous of Europe, including *Caletodraco cottardi*.

In fact, both *Genusaurus sisteronis* and the late Campanian tibia from la Boucharde, in Provence, initially described as a neoceratosaurian [70]), may in fact be brachyrostrans or even furileusaurians, like *Caletodraco cottardi*. Besides the presence of a straight dorsal margin of the ilium (see above) in *Genusaurus*, the main reason for this possible attribution is the shape of the proximal part of the tibia, with a downturned distal end of the cnemial crest ("distal process of cnemial crest" of Baiano et al. [61])—a feature listed by Canale et al. [35] as a synapomorphy of Brachyrostra and by Filippi et al. [16] as being characteristic of Furileusauria. A similar possibility was hinted at by Ezcurra and Agnolin ([71] Appendix 1), who considered that both *Genusaurus* and the La Boucharde tibia could be placed among the Carnotaurinae because of the downturned end of the cnemial crest. Furileusauria is a more inclusive taxon than Carnotaurinae and the downturned distal end of the cnemial crest is apparently not restricted to the latter—it is present, for instance, in *Elemgasem nubilus*, which is either a furileusaurian or a sister-taxon of that clade [61]. Pending a revision of both *Genusaurus* and the La Boucharde tibia, the suggestion that they belong to the Furileusauria should merely be considered as a possibility needing confirmation. Whatever the status of these two specimens, the discovery of the furileusaurian *Caletodraco* in the Cenomanian of Normandy raises an interesting question. So far, only majungasaurines had been clearly identified in Europe (mainly with *Arcovenator*) and this suggested biogeographical links with the Indian subcontinent and Madagascar, with Africa playing an essential part as a connecting landmass [12], although trans-Tethyan dispersal between Africa and the European archipelago (and more precisely the Ibero-Armorican island) had to be postulated. The discovery of a furileusaurian in Europe shows that the diversity of European abelisaurids was greater than previously recognized, since it included both majungasaurines and furileusaurians, and it poses additional problems. Furileusaurians were hitherto known only from South America, and it is difficult to conceive a direct connection between the South American continent and the European archipelago. Even according to the "Eurogondwana" hypothesis of Ezcurra and Agnolin [71], dispersal between South America and Europe had to take place via Africa. As for the European majungasaurines, a connection via Africa seems to be the only possible option, although furileusaurians have not yet been recorded from Africa. It should be noted, however, that an incomplete tibia from the upper Maastrichtian phosphates at Sidi Chennane (Morocco) shows a markedly downturned end of the cnemial crest [28]. As noted above, this is considered as a distinctive character of Furileusauria by Filippi et al. [16]. Despite the fact that the Sidi Chennane abelisaurid is a very late representative of the family, much later in age than the Cenomanian *Caletodraco*, if it is indeed a furileusaurian the occurrence of this group in Africa would make it easier to understand its presence in Europe.

Nevertheless, the stratigraphic origin of the type specimen of *Caletodraco cottardi* raises an additional question. In South America, furileusaurians are known mainly from the later part of the Late Cretaceous, with *Viavenator* [16] and *Llukalkan* [68], both from the Santonian of Argentina, as the earliest recorded representatives. The Cenomanian *Caletodraco* is roughly 10 million years older, and if *Genusaurus* is indeed a furileusaurian, it pushes the European record of that group even farther back in time. Even though the phylogenies of Filippi et al. [16] and Gianechini et al. [68] allow for ghost lineages that place the origin of Furileusauria in the Early Cretaceous (Albian), *Caletodraco* is an unexpectedly early member of that group. Interestingly, Agnolin [72] considers that exchanges between the Gondwanan continents and Europe were interrupted during the Cenomanian, which would push back the dispersal of Furileusauria between these biogeographical areas to the Early Cretaceous. The question then arises of whether furileusaurians may have appeared elsewhere than in South America, possibly in Europe. The available European material remains scanty, especially by comparison with the much more abundant and complete record from South America, and caution should be exercised when putting forward paleobiogeographical hypotheses based on only a few fossils, but it appears that the evolutionary and biogeographical history of the Abelisauridae was more complex, especially in Europe, than hitherto recognized.

6. Conclusions

The discovery of *Caletodraco cottardi* shows that dinosaur remains, although exceedingly rare, do occur in the Chalk of the Anglo-Paris basin and that a careful search for fossil vertebrates in these marine formations can yield surprising and important results. The new taxon leads to a reassessment of the fossil record of abelisaurids in Europe, showing that, contrary to what could previously be assumed, majungasaurines were not the only abelisaurid subgroup present in that geographical area, since *Caletodraco cottardi* apparently belongs to the Furileusauria, a highly derived clade of Abelisauridae. *C. cottardi* is one of the earliest known Furileusauria and its occurrence in Europe leads to reconsider the biogeographical history of this group of theropods, hitherto known from South America.

Author Contributions: Specimen preparation: J.G., J.P. and H.T.; investigation: E.B., J.G., H.T., B.H. and J.P.; writing—original draft: E.B. and H.T.; writing: E.B., H.T., B.H., J.G. and J.P. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no special funding.

Data Availability Statement: All the data used in the study are included in the paper.

Acknowledgments: We are especially grateful to Nicolas Cottard, who discovered the specimen in the course of his detailed investigations of the Chalk of the Normandy coast and donated it to the Le Havre Natural History Museum. Thanks to Damien Germain for access to abelisaurid specimens in the Muséum National d'Histoire Naturelle, Paris, and to Federico Agnolin (Buenos Aires) for helpful comments. Thanks to two anonymous reviewers for their useful comments on the initial version of the paper.

Conflicts of Interest: The authors declare no conflicts of interest.

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