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Dinosaurs of France

Dinosaures de France

Ronan Allain ^{a,*}, Xabier Pereda Suberbiola ^{a,b}

^a UMR 8569 du CNRS, Département « Histoire de la Terre », Muséum national d'histoire naturelle, 8, rue Buffon, 75005 Paris, France

^b Departamento de Estratigrafía y Paleontología, Facultad de Ciencias,
Universidad del País Vasco/EHU, Apartado 644, 48080 Bilbao, Spain

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Abstract

The French dinosaur record is one of the most extensive in Europe; it ranges stratigraphically from the Late Triassic to the Latest Cretaceous. All major clades of dinosaurs but marginocephalians are known. About 20 species are based on significant material; the theropods are the best represented. Most of these taxa have been described or revised in recent years. Important specimens have been discovered in the Late Triassic of eastern France, the Middle Jurassic of Normandy, and the Late Cretaceous of Provence and Languedoc. The ichnological record is good for the Late Triassic–Early Jurassic, and the Late Cretaceous egg sites are among the richest in the world. **To cite this article:** R. Allain, X.P. Suberbiola, *Palevol* 2 (2003) 27–44.

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Résumé

Le registre fossile des dinosaures français, qui s'étend du Trias supérieur au Crétacé supérieur, est l'un des meilleurs d'Europe. Tous les principaux clades de dinosaures y sont représentés, à l'exception des marginocéphales. Une vingtaine d'espèces, connues par des restes significatifs, ont été recensées, les théropodes étant les mieux représentés. La plupart de ces taxons ont été décrits ou révisés au cours des dix dernières années. D'importants spécimens ont été découverts dans le Trias supérieur de l'Est de la France, le Jurassique moyen de Normandie et le Crétacé supérieur de Provence et du Languedoc. Les empreintes sont abondantes dans le Trias supérieur et le Jurassique inférieur, et les sites à œufs du Crétacé supérieur sont parmi les plus riches du monde. **Pour citer cet article :** R. Allain, X.P. Suberbiola, *Palevol* 2 (2003) 27–44.

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* Correspondence and reprints.

E-mail addresses: rallain@mnhn.fr (R. Allain), gppesuf@lg.ehu.es (X.P. Suberbiola).

Version abrégée

La révision des dinosaures français entreprise ici met l'accent sur les dix dernières années de recherche et vient compléter les travaux de synthèse effectués précédemment [22, 37, 106]. Si l'accent a été essentiellement mis sur les restes squelettiques, les principales découvertes relatives aux empreintes et aux pistes, d'une part, et aux œufs et coquilles de dinosaures, d'autre part, sont mentionnées.

Les premières découvertes de restes de dinosaures faites en France datent de la fin du XVIII^e siècle [154] et un bon nombre de naturalistes et paléontologues européens renommés, tels que Cuvier, Depéret, Eudes-Deslongchamps, Gaudry, Gervais, Matheron, Nopcsa, Sauvage ou Huene ont contribué à l'étude de ces restes [22, 40, 154, 155]. Le registre fossile des dinosaures français est l'un des meilleurs d'Europe, aussi bien du point de vue de la diversité, puisque tous les grands clades de dinosaures y sont représentés, à l'exception des marginocéphales, que du point de vue de la répartition stratigraphique, puisqu'il s'étend du Trias supérieur au Crétacé supérieur [37]. Les périodes les mieux connues sont le Crétacé supérieur, qui a été largement exploité durant ces dix dernières années, et dans une moindre mesure, celle s'étalant du Jurassique moyen au début du Jurassique supérieur. D'importantes lacunes apparaissent dans l'enregistrement fossile des dinosaures au Pliensbachien-Bajocien, Berriasien-Valanginien et Turonien-Santonien, ces périodes correspondant le plus souvent à des époques de hauts niveaux marins [92]. Les environnements sédimentaires de dépôt dans lesquels sont retrouvés les restes de dinosaures français sont variables, selon les époques considérées. Les taxons du Jurassique ont ainsi tous été retrouvés dans des sédiments marins [20], alors que ceux du Crétacé supérieur l'ont été en grande majorité dans des dépôts d'origine continentale.

Des restes de dinosaures ont été signalés dans de nombreuses régions françaises : la Normandie, la Picardie et le Boulonnais, au nord ; la Provence, le Languedoc et les Pyrénées, au sud ; la Lorraine, la Champagne et la Franche-Comté, à l'est ; le Poitou et les Charentes, à l'ouest, le Massif central et le Périgord dans la partie centrale du pays [22, 106]. Les principaux gisements ayant livré au cours des dix dernières années de nombreux ossements de dinosaures sont situés dans le Trias supérieur du Jura [9, 57, 58, 61], le Jurassique moyen à supérieur des côtes du Calvados [4–6, 21, 26], le Crétacé inférieur de la Haute-Marne

[125] et des Alpes-de-Haute-Provence [1], et le Crétacé supérieur du Var, des Bouches-du-Rhône, de l'Hérault, de l'Aude et de l'Ariège [3, 8, 13, 15, 23, 30, 31, 37, 44–46, 105, 110, 112, 114, 118, 119, 152]. Les plus belles pistes ou empreintes de dinosaures décrites durant cette décennie proviennent du Trias supérieur du Gard [79] et du Jurassique inférieur et supérieur du Lot [102, 103, 127, 128]. Enfin, de nombreux gisements à coquilles d'œufs de dinosaures du Crétacé supérieur du Sud de la France, depuis le bassin d'Aix-en-Provence jusqu'aux Corbières, ont été découverts et étudiés [13, 53, 80].

Une vingtaine d'espèces, basées sur du matériel diagnostique, ont été reconnues valides (Tableau 1), dont six décrites durant ces dix dernières années : le Coelophysidae *Liliensternus airelensis* Cuny et Galton, 1993 de l'Hettangien de Normandie [60], le nouveau Megalosauridae du Bathonien moyen de Conteville (Calvados) [5, 6], le cératosaure *Genusaurus sisteronis* Accarie et al., 1995 de l'Albien de Sisteron [2] (Fig. 1E), le Dromaeosauridae *Pyroraptor olympius* Allain et Taquet, 2000 du Crétacé supérieur de Provence [8] (Fig. 1G) et, enfin, le Titanosauridae *Ampelosaurus atacis* Le Lœuff [115], 1995, ainsi qu'une nouvelle espèce du Nodosauridae *Struthiosaurus* [82] (Fig. 4), tous deux du Crétacé supérieur du Languedoc. Bon nombre des taxons décrits antérieurement ont aussi été révisés pendant cette décennie : parmi eux, les deux Megalosauridae *Poekilopleuron* [7] (Fig. 1B) et *Streptospondylus* [4] du Jurassique moyen de Normandie, *Compsognathus* [129] du Jurassique supérieur de Provence (Fig. 1D), le carnosaure *Erectopus superbus* [5] du Crétacé inférieur de Lorraine, dont les moulages du type sont conservés au Muséum à Paris, les prosauropodes du Trias supérieur de Lorraine et de Franche-Comté, rattachés aux taxons *Plateosaurus longiceps* et *P. engelhardti* [75, 76] (Fig. 1A), les stégosaures *Lexovisaurus* et *Dacentrurus* [74, 78] du Jurassique moyen et supérieur de Normandie (Fig. 1C), les deux Iguanodontidae *Iguanodon atherfieldensis* et *I. bernissartensis* [125] du Crétacé inférieur de Champagne et, enfin, le petit Iguanodontia *Rhabdodon priscus* du Crétacé supérieur du Sud de la France [85, 139, 142] (Figs. 1F, 2 et 3). Il faut noter que de nombreux spécimens, comme le sauropode du Jurassique supérieur de Damparis, rattaché précédemment au genre *Bothriospondylus* [104], ou les hadrosaures du Crétacé supérieur du Sud de la France [109], sont actuellement en cours d'étude.

1. Introduction

The French record of dinosaurs is one of the best in Europe, at least in terms of stratigraphic representation: it ranges in age from Late Triassic to Late Cretaceous [37]. The first dinosaur discoveries in France were made at the end of the 18th century [154]. Leading palaeontologists such as Cuvier, Depéret, Eudes-Deslongchamps, Gaudry, Gervais, Huene, Lapparent, Matheron, Nopcsa, Sauvage and many others participated in the research on French dinosaurs [22, 40, 154, 155]. The French record is relatively good for the Late Cretaceous and, to a lesser extent, for the Middle to Late Jurassic. Important preservational gaps occur in the Pliensbachian-Bajocian, Berriasian-Valanginian and Turonian-Santonian, perhaps related to global high sea-level and climate changes [92]. French dinosaur remains occur in a variety of sedimentary environments. A large part of the record is from shallow marine rocks [20], except the Late Cretaceous dinosaur assemblages.

Dinosaur specimens have been found in various parts of France, from Normandy, Picardy and Boulonnais in the north to Provence and Languedoc in the south, from Lorraine, Champagne and Franche-Comté in the east to the Atlantic coast of Poitou and Vendée in the west, and the Massif Central and Périgord in the central part [22, 106]. The main dinosaur sites that have yielded skeletal remains are located in the Late Triassic of Jura, the Middle to Late Jurassic of Calvados, the Early Cretaceous of Haute-Marne, and the Latest Cretaceous of the foothills of Pyrenees, including Ariège, Haute-Garonne and Aude, and of Provence and Languedoc, including Hérault, Gard, Bouches-du-Rhône, and Var (see maps in [37, 106]). Interesting tracksites outcrop in the Latest Triassic to Early Jurassic of the western coast of Le Veillon (Vendée), the Early Jurassic of the Causses region of the Massif Central and Dordogne, and the Late Jurassic lithographic limestones of Crayssac and Cerin [123]. Moreover, famous egg localities are known in the Late Cretaceous of the Aix-en-Provence Basin, Mèze-Villeveyrac area, Corbières and the Upper Aude Valley [13, 53, 80].

As a whole, the French record includes representatives of all major groups of dinosaurs, except marginocephalians (ceratopsians and pachycephalosaurians). Theropods and ornithomorphs are better represented in

numbers of species and of specimens than are the prosauropods, sauropods, stegosaurs and ankylosaurs (Table 1).

This review of French dinosaurs emphasises the discoveries and contributions made in recent years. The skeletal remains are more extensively treated than more indirect evidence, but recent significant finds of both eggs or eggshells and footprints have also been included. The fossil record is presented following a stratigraphic arrangement from older to younger.

2. Middle Triassic

No dinosaur remains have been hitherto found in the Middle Triassic of France. The skeletal remains from the Muschelkalk of Lorraine, originally assigned to the prosauropod *Thecondontosaurus* are in fact lacertiform [9]. Tridactyl footprints from the Middle Triassic of the region of the Massif Central, assigned to the ichnogenera *Anchisauripus*, *Coelurosaurichnus* and *Grallator* [52], may have been made by early dinosaurs [51]. Lockley and Meyer [123] noted that these ‘dinosauroid’ tracks are extremely dinosaurian in appearance, but these authors prefer to adhere to the hypothesis regarding dinosaur origins in the Late Triassic and are inclined to point out that the tracks were probably made by non-dinosaurian archosaurs that had feet resembling those of dinosaurs.

3. Late Triassic

The oldest skeletal remains of dinosaurs yet reported from France are from the Late Triassic deposits of Lorraine, Franche-Comté and Languedoc. Prosauropod remains, including teeth, vertebrae and appendicular bones are common in the Keuper (Norian) of eastern France and have been described from several localities in the Poligny region (Jura) [9, 57, 58, 61]. The prosauropod material from the ‘Marnes irisées supérieures’ near Poligny has classically been referred to *Plateosaurus* (‘*Dimodosaurus*’) *poligniensis*, but this taxon is currently regarded as a *nomen dubium* [76]. Most of the *Plateosaurus* material from Poligny is probably referable to *P. longiceps* from the Knollenmergel of Germany [76]. Most of the additional material of *Plateosaurus* from Saint-Nicolas-de-Port

Table 1

Stratigraphic distribution of the main French dinosaur taxa based on diagnostic skeletal remains

Tableau 1

Répartition stratigraphique des principaux taxons ou genres et espèces de dinosaures français connus par des restes squelettiques diagnostiques

		PROSAUROPODA	SAUROPODA	THEROPODA	STEGOSAURIA	ANKYLOSAURIA	ORNITHOPODA	
CRETACEOUS	LATE	MA	<i>Ampelosaurus</i>	<i>Pyroraptor</i>		<i>Struthiosaurus</i>	<i>Pararhabdodon</i> sp.	
		CA					<i>Rhabdodon priscus</i>	
		SA						
		CO						
		TU						
	EARLY	AL			<i>Genusaurus</i> <i>Erectopus</i>			
		AP						<i>I. bemissartensis</i>
		BA						<i>I. bemissartensis</i>
		HA						<i>I. atherfieldensis</i>
		VA						<i>I. atherfieldensis</i>
		BE						
		JURASSIC	LATE	TI		<i>Compsognathus</i>		
KI					<i>Dacentrurus</i>			
OX	" <i>Bothriospondylus</i> "			<i>Streptospondylus</i>				
MIDDLE	CA			<i>Piveteausaurus</i>	<i>Lexovisaurus</i>			
	BA			<i>Poekilopleuron</i>				
	BA							
	AA							
EARLY	TO							
	PL							
	SI				<i>Liliensternus</i>			
LATE	HE							
	RH							
TRIAS.	LATE	NO	<i>Plateosaurus longiceps</i> <i>P. engelhardti</i>					

(Meurthe-et-Moselle) [34, 59, 91], Violot (Haute-Marne) [56] and Le Chappou (Ain) [9] is also referable to *P. longiceps* [75, 76]. In addition, most of the *Plateosaurus* remains excavated in the last years from the top of the Keuper of Lons-le-Saunier (Jura) have yet to be described [61]. In southern France, a few prosauropod postcranial bones have been described from the Keuper of Alzon (Gard) [88], which may also belong to

Plateosaurus [75]. However, one individual with a distally straight femur from Poligny, referred to *Gresslyosaurus* cf. *plieningeri* by Huene [94], provides evidence for a prosauropod taxon distinct from *P. longiceps* and may be referable to *P. engelhardti*, as may be the large, *Thecodontosaurus*-like teeth from the vicinity of Arbois (Jura) [75, 76] (Fig. 1A). A tooth with tooth-to-tooth wear from Saint-Nicolas-de-Port [62]

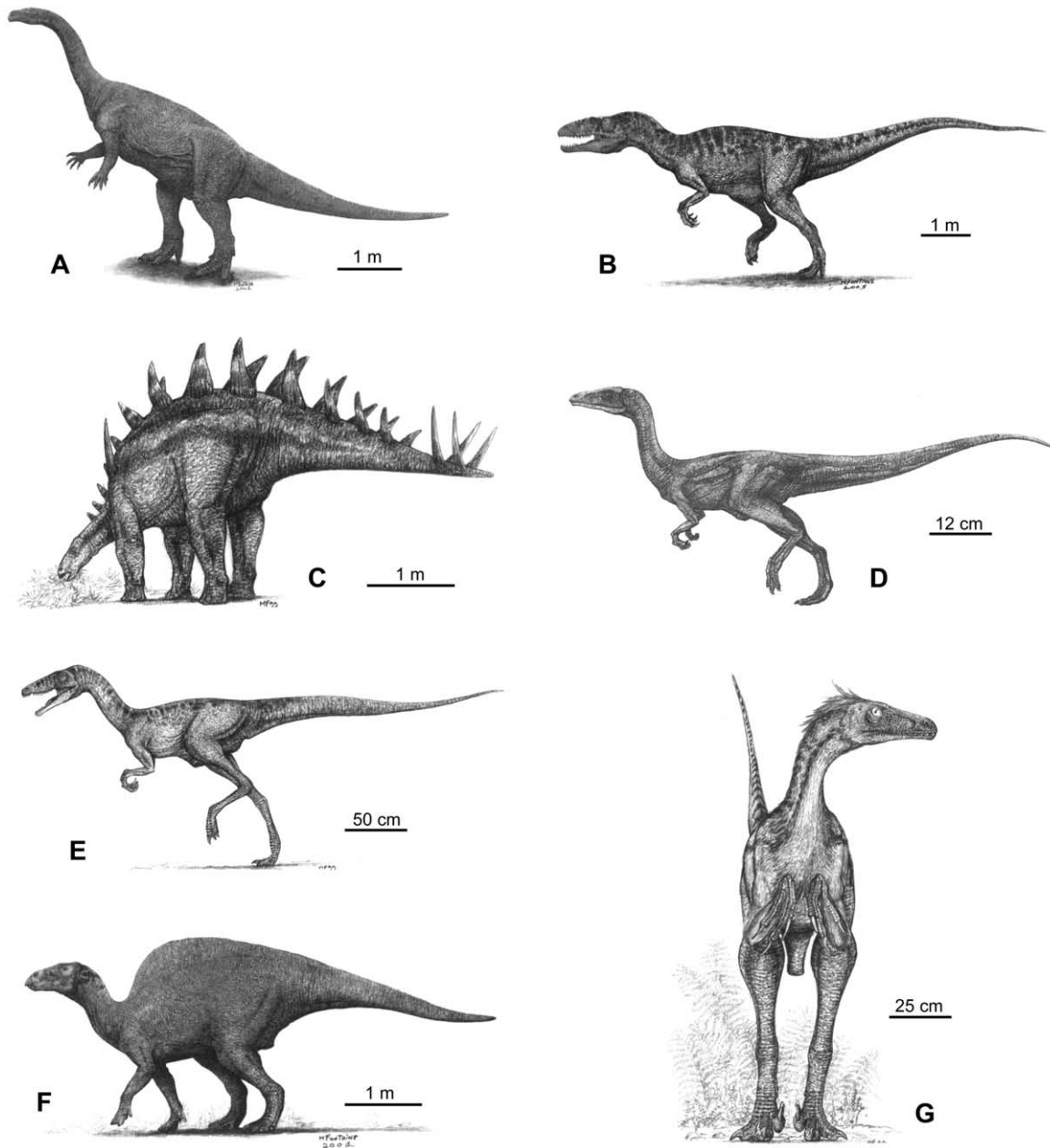


Fig. 1. **A**, *Plateosaurus engelhardti*, Upper Triassic, Norian, Jura; **B**, *Poekilopleuron bucklandii*, Middle Jurassic, Bathonian, Calvados; **C**, *Lexovisaurus durobrivensis*, Middle Jurassic, Callovian, Calvados; **D**, *Compsognathus longipes*, Late Jurassic, Tithonian, Var; **E**, *Genusaurus sisteronis*, Early Cretaceous, Albian, Alpes-de-Haute-Provence; **F**, *Rhabdodon priscus*, Late Cretaceous, Campano-Maastrichtian, southern France; **G**, *Pyroraptor olympius*, Late Cretaceous, Campanian, Bouches-du-Rhône. Restorations by Michel Fontaine. © Éditions du MNHN.
 Fig. 1. **A**, *Plateosaurus engelhardti*, Trias supérieur, Norien, Jura ; **B**, *Poekilopleuron bucklandii*, Jurassique moyen, Bathonien, Normandie ; **C**, *Lexovisaurus durobrivensis*, Jurassique moyen, Callovien, Calvados ; **D**, *Compsognathus longipes*, Jurassique supérieur, Tithonien, Var ; **E**, *Genusaurus sisteronis*, Crétacé inférieur, Albien, Alpes-de-Haute-Provence ; **F**, *Rhabdodon priscus*, Crétacé supérieur, Campano-Maastrichtien, Sud de la France ; **G**, *Pyroraptor olympius*, Crétacé supérieur, Campanien, Bouches-du-Rhône. Reconstitutions réalisées par Michel Fontaine. © Éditions du MNHN.

may represent a third sauropodomorph taxon, either a sauropod-like prosauropod or an early sauropod [75]. Prosauropod remains are abundant in the Norian, but plateosaurids have not been identified with certainty in Rhaetian strata; the only French site surely dated from the Rhaetian, in which prosauropod remains were found is Provençères-sur-Meuse (Haute-Marne) [58]. The locality of Saint-Nicolas-de-Port (Late Norian to Early Rhaetian in age) is famous for having yielded numerous mammal teeth, but also a theropod tooth [34] and a few ornithischian-like teeth, which could be the oldest representatives of this group in Europe [91]. Another ornithischian tooth has also been reported from the Rhaetian of Lons-le-Saunier [64]. These discoveries suggest that ornithischian dinosaurs reached Europe before the Rhaetian transgression [64, 91].

Footprints from the Keuper of Gard described by Ellenberger [71] could belong to prosauropods [88]. The Norian of Ardèche, in the eastern border of the Massif Central, has yielded an interesting *Otozoum/Grallator* association [79]. The *Otozoum* footprints, referable to prosauropods, are characterised by a remarkable homopody (and thus seem to differ from *Plateosaurus*). The *Grallator* ichnites are probably due to coelophysid theropods [123]. In the Atlantic coast, the Rhaetian-Early Jurassic site of Le Veillon (Vendée) has yielded many tridactyl footprints of the ichnogenera *Grallator*, *Eubrontes*, *Saltopoides*, *Anatopus*, and *Talmontopus* [107]. *Anatopus* and, probably, *Saltopoides* appear to be closely related to *Grallator*. *Talmontopus* also falls in the size range of *Grallator* and small *Eubrontes* [123]. In Ardèche, small theropod footprints have been assigned to *Coelurosaurichnus* [52], a junior synonym of *Grallator* [123].

4. Early Jurassic

The French Liassic record is mainly represented by footprints; only a few dinosaur bone remains have been reported to date from deposits of this age. The most interesting specimen is an incomplete theropod skeleton consisting of vertebrae and pelvic bones, as well as a tooth, from beds very close to the Triassic-Jurassic boundary, probably basal Hettangian in age, from the Airel quarry (Manche), Normandy. Based on this material, Cuny and Galton [60] erected the species *Liliensternus airelensis*. *Liliensternus* is regarded as a coelo-

physoid by Rauhut and Hungerbühler [144]. Serrated teeth from the Hettangian of Hettange (Moselle), Lorraine, are probably phytosaurian rather than dinosaurian [37].

Early Liassic dinosaur ichnites, most of them attributed to theropods, are well known at several French sites [123]. Tridactyl footprints and trackways have been reported from the Hettangian of the departments of Vendée, Lozère, Gard, Aveyron, Hérault and Var, and from the Sinemurian of Aveyron and Lot [66–69, 102]. The ichnofauna consists of *Grallator*, *Dilophosaurus* and *Eubrontes*, which were probably made by theropods. With regard to ornithischian ichnites, the trackway of a large quadrupedal thyreophoran has been described from the Hettangian of Dordogne [121]. The shape of the footprints suggests a protostegosaurian trackmarker, but a *Scelidosaurus*-like form could not be excluded [90].

5. Middle Jurassic

A large part of the Middle Jurassic dinosaur material pertains to theropods. The isolated remains from the Oxfordo-Callovian deposits that outcrop in the ‘Vaches Noires’ cliffs on the coast of Calvados [21, 26, 38, 145], as well as those from Haute-Saône [42], Indre [22] and Doubs [41], have systematically been referred to the waste-basket taxon *Megalosaurus*. Considering that *Megalosaurus* is a *nomen dubium*, material should not be referred to it [5, 7]. Moreover, a recent revision of the diagnostic theropod remains from the Middle to Late Jurassic of western Europe shows that the diversity of the theropod fauna has been widely underestimated [5]. The Middle Jurassic French theropod fauna is thus composed of megalosaurid spinosaurids, including *Poekilopleuron bucklandii* [72] (Fig. 1B), *Streptospondylus altdorfensis* [4] and *Poekilopleuron? valesdunensis*, a new taxon from Conteville (Calvados) represented by a nearly complete skull [5, 6], and of allosaurids represented by *Piveteausaurus* [156] and the skull of an unnamed theropod from Auberville [4, 98]. The type of *Poekilopleuron bucklandii* was kept in the University of Caen and was destroyed by an air raid in 1944 [11]. However, casts of some parts of the type skeleton have been found in the collections of the Paris Museum and have been redescribed [7]. Isolated teeth from a Bathonian locality in Aveyron [100] and postcranial material from the Callovian of Doubs

[16], both of them referred to indeterminate theropods, have also been reported.

One of the most remarkable dinosaur specimens found in the Middle Jurassic of France is a partial stegosaur skeleton consisting of parts of the vertebral column, appendicular bones and a dermal spine from the Callovian of Argences (Calvados). This material has been referred to the stegosaurid *Lexovisaurus durobrivensis* [74, 78] (Fig. 1C). Other herbivorous dinosaurs are represented by a rich collection of hypsilophodontid teeth from the Bathonian of the Larnagol site (Lot) [100].

Finally, the oldest eggshell dinosaur remains known in France have been reported from the Middle Jurassic (Bathonian) of Quercy [84]. They have been interpreted as belonging to a discretispherulitic morphology related to sauropods.

6. Late Jurassic

The Late Jurassic strata have only yielded a few dinosaur remains in the past ten years. The most complete specimens from that period have been known for a long time. These are the sauropod from Damparis (Jura) [17, 70], the stegosaur *Dacentrurus lennieri* from Octeville (Seine-Maritime) [151], and the theropod *Compsognathus longipes* from Canjuers (Var) [10].

A re-examination of the partial sauropod skeleton from the Late Oxfordian (*Bimmamatum* zone) of Damparis referred to *Bothriospondylus madagascariensis* by Lapparent [104] is currently in progress [130]. Following the phylogeny of Wilson and Sereno [165], it seems that the Damparis sauropod housed in the Paris Museum is closely related to *Haplocanthosaurus* and *Lapparentosaurus* [130], but Wilson [164] assigned it to *Brachiosaurus*. Other sauropod finds from the Late Jurassic of France include camarasaurid-like caudal vertebrae from the Portlandien of Ville-en-Blaisois (Haute-Marne) [19], vertebrae from the Tithonian of Cognac (Charente) [120], and large spatulate teeth known as *Neosodon praecursor* and referred to a camarasaurid from the Portlandian of La Crèche (Pas-de-Calais) [32]. This latter taxon is represented by scanty material not different from that of the sauropod of Damparis, and should be considered a *nomen dubium*.

The most complete dinosaur skeleton found in France is the small coelurosaurian theropod *Compsog-*

nathus from the Tithonian lithographic limestones of Canjuers (Var) (Fig. 1D). Originally described as the type of a new species *C. corallestris* [10], the specimen was later referred to *C. longipes*, known from the Solnhofen lithographic limestones of Bavaria [129, 134]. The specimen is currently under study in Paris by K. Peyer. As for the Middle Jurassic, most of the isolated large theropod remains found in the Late Jurassic rocks of France have been referred to *Megalosaurus* [37, 161], but can only be identified as Theropoda indet. These remains include teeth from the Oxfordian of the neighbourhood of Lisieux (Calvados) [35], teeth and a caudal vertebra from the Boulonnais [32], and several caudal vertebrae of a large theropod from the Oxfordian (Argovian facies) of Plaimbois-du-Miroir (Doubs) [141]. A small theropod from Cognac (Charente) [160] has also been mentioned, as well as a theropod tooth from the Tithonian of Oléron Island (Charente-Maritime) [12].

Among ornithischians, the most complete specimen is the partial skeleton that comprises the holotype of the stegosaur *Dacentrurus lennieri*. It was found at the end of the 19th century in the Kimmeridgian of Octeville (Seine-Maritime), Normandy. The specimen, which consists of vertebrae, pelvic elements and a femur, was destroyed in 1944 during World War II. However, a partial femur was discovered in the same horizon near the type locality and was referred to *Dacentrurus lennieri* by Galton and Boiné [77]. This species is currently regarded as a junior synonym of *Dacentrurus armatus* from the Late Jurassic of England and Portugal [74]. Ornithopods are represented in the Kimmeridgian of Normandy by a femur from the Octeville cliffs (Seine-Maritime), identified as *Dryosaurus* sp. [25]. The femur is dryosaurid-like, but it is too incomplete for an accurate generic identification [147]. In addition, isolated teeth of iguanodontid ornithopods and nodosaurid ankylosaurs have been reported from the Tithonian (Purbeck facies) of the Boulogne-sur-Mer area [63, 150]. The occurrence of a 'fabrosaurid' ornithischian in the same locality is doubtful [96].

With respect to the ichnological record, dinosaur prints are abundant in the Tithonian limestone of the Crayssac region (Lot), including theropod, sauropod and probably ornithopod trackways [103, 127, 128]. Trackways of *Saltosauropus* from the Kimmeridgian-Tithonian limestones of Cerin (Ain), first attributed to a

hopping theropod, may in fact have been left by turtles [157]. A theropod footprint is also known from the Tithonian of the Oléron Island [12].

7. Early Cretaceous

The Early Cretaceous record (mainly Wealden facies) of France is relatively poor by comparison with those of England, Belgium, Germany and Spain. Most of the material is from the eastern Paris Basin, although there are some remains from other regions. No dinosaurs are hitherto known in the Berriasian deposits and the only described remains from the Valanginian beds are the shoulder and forelimb bones of an allosauroid theropod from Montmirat (Gard) [140]. Remains of iguanodontid ornithopods are known from deposits of the Saint-Dizier region (Haute-Marne), which range in age from Hauterivian to Aptian. Two species of *Iguanodon* have been recognized [125]: *I. atherfieldensis*, represented by a partial skeleton that includes numerous vertebrae, parts of the pelvis and hindlimb bones; and *I. bernissartensis*, known from an incomplete skeleton that consists of tail vertebrae, pelvis and limbs. The former species occurs in the Hauterivian-Barremian, and the latter is known from the Barremian-Early Aptian [125]. Isolated sauropod remains, including vertebrae and limb bones, have been reported from the Barremian of Meuse [39] and from the Albian of Meuse, Oise, Seine-Maritime, Vaucluse [37, 126], and Aube [99]. Ankylosaurs are also represented in the Albian of Aube [97].

The main discovery of the past ten years is that of the partial skeleton of the theropod *Genusaurus sisteronis* from the Albian green clays and glauconitic sands of Sisteron (Alpes-de-Haute-Provence) [1] (Fig. 1E). It is known from parts of the pelvis and hindlimb, as well as vertebrae. The phylogenetic position of *Genusaurus* within the theropods remains debated. It is referred to coelophysoids by some authors [1, 2] and to abelisauroids by others [2, 48, 143]. The deeply excavated medial surface of the proximal fibula is unknown in Coelophysoidea, and some characters, such as the large and dorsally curved cnemial crest, are reminiscent of Abelisauroidea. Considering the recent description of the small-bodied *Masiakasaurus* [48, 148], the close affinities of *Genusaurus* with noasaurid abelisauroids should be investigated [48].

Erectopus superbus from the Lower Albian phosphate-bearing beds of the Gault of Louppy

(Meuse) has long been considered lost. Casts of the type skeleton have however been found in the collections of the Paris Museum and are currently being redescribed by the senior author [5]. Most of the unusual characters of *Erectopus* listed in the literature [37, 95, 131, 143] are due to Sauvage's misinterpretations [149] or to an incorrect restoration of some bones such as the femur. *Erectopus* seems to be related to Allosauroidea [5]. Finally, bird remains have also been found in the Neocomian of Yonne, central-eastern France [101].

8. Late Cretaceous

The dinosaurs of the early Late Cretaceous (Cenomanian-Turonian) and mainly of the Coniacian-Santonian interval are very poorly documented. Isolated finds are known in the Cenomanian of west-central France, including very fragmentary remains of theropods in Charente-Maritime and Maine-et-Loire [33], sauropods in Sarthe [18, 114] and Charente-Maritime [37], and ankylosaurs in Indre-et-Loire [24]. A number of old finds, presumably of Cenomanian age, are lost or were destroyed [37]. Dinosaur remains associated with amber that contains insects from the Lower Cenomanian of Charente-Maritime have been recently described [132]. The diagnostic material includes an ulna and the distal end of a tibia that show affinities with *Iguanodon*, and it has been questionably referred to that genus. Reworked dinosaur remains include theropod and ornithopod teeth from the Miocene deposits (probably derived from Cenomanian rocks) of Maine-et-Loire in the Loire Valley [33]. Isolated theropod teeth have also been described from the Turonian and Santonian of Vendée [33].

The Campanian-Maastrichtian of southern France is very rich in dinosaur sites and specimens. Since Lapparent [105], many discoveries have been made [13, 23, 45, 87, 110, 113]. The most productive dinosaur sites are Fox Amphoux [15, 105] and La Boucharde [3, 8] in the Aix-en-Provence Basin; Champ-Garimond [152] in Gard; Villeveyrac [44, 82] and Cruzy [46] in Hérault, the Upper Aude Valley [30, 31, 36, 113, 114] and Montplaisir [118, 119] in Aude, and the Plantaurel [112] in Ariège.

As in other countries of Europe, most of the Latest Cretaceous French dinosaur finds have been made in continental deposits, and precise dating of the locali-

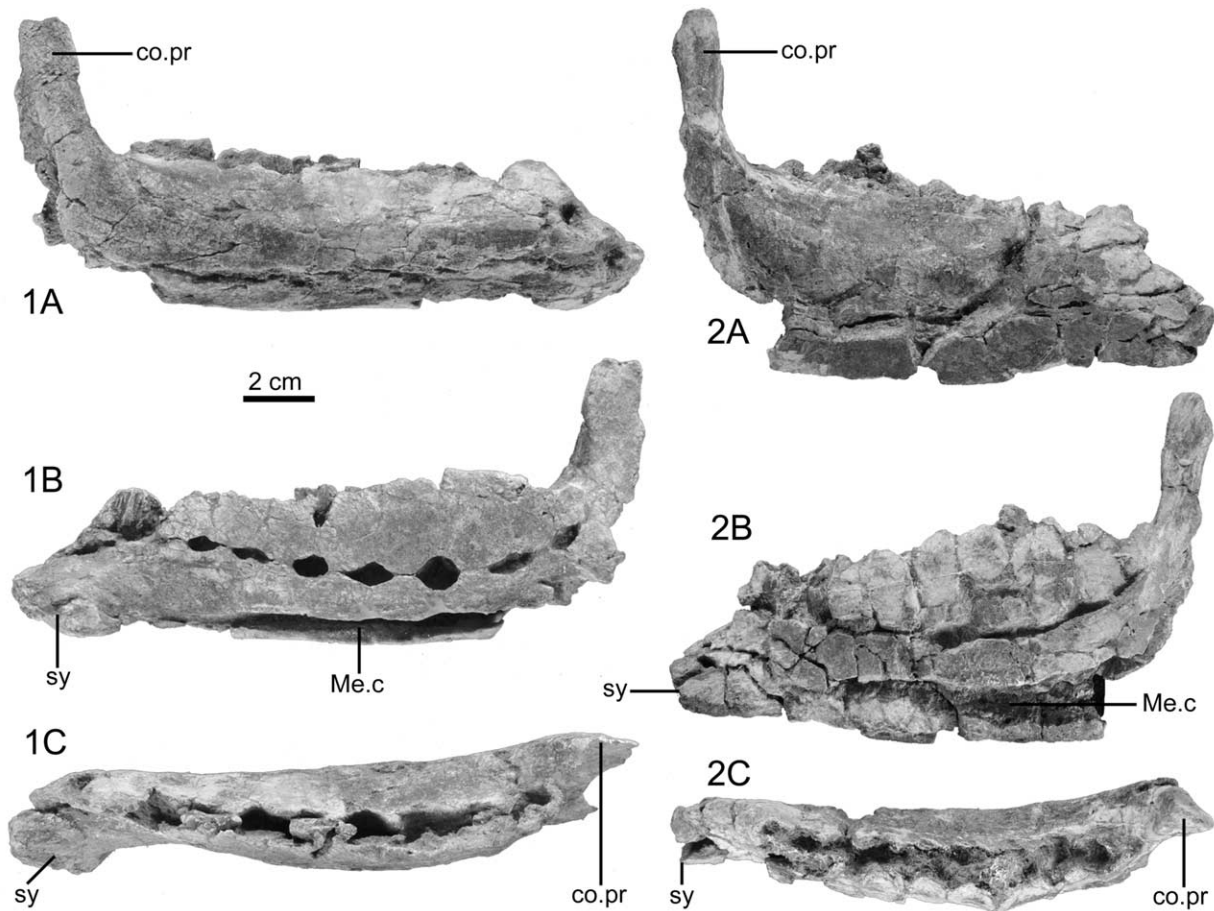


Fig. 2. *Rhabdodon priscus*, La Boucharde, Upper Campanian. **1**, Right dentary and **2**, reversed left dentary in: **A**, lateral view; **B**, medial view; **C**, dorsal view. **Co.pr**, Coronoid process; **Me.c**, Meckelian canal; **sy**, symphysis.

Fig. 2. *Rhabdodon priscus*, La Boucharde, Campanien supérieur. **1**, Dentaire droit et **2**, dentaire gauche inversé en : **A**, vue latérale ; **B**, vue médiale ; **C**, vue dorsale. **Co.pr**, Processus coronoïde ; **Me.c**, canal de Meckel ; **sy**, symphyse.

ties is usually difficult because the stratigraphic correlations are problematic [27]. For example, some dinosaur sites have been dated as Late Maastrichtian on the basis of the presence of the charophyte *Septorella ultima* [108, 109, 119]. In fact, this taxon ranges from the Latest Campanian to the Late Maastrichtian [73, 146] and cannot be used as a Late Maastrichtian biostratigraphic marker.

Late Cretaceous ornithopods consist of *Rhabdodon* and hadrosaurids. *Rhabdodon* is the most common element of the dinosaur assemblages from the Late Cretaceous of southern France (Fig. 1F). Described as early as 1869 by Matheron [155], it is currently known from a large number of Campanian-Maastrichtian localities, from Provence to the foothills of the Pyrenees

[14, 110, 142]. The *Rhabdodon* remains show great variability, but the significance of this is currently uncertain [139]. The presence of several species of *Rhabdodon* has been suggested by some authors; Buffetaut and Le Lœuff erected *R. septimanicus* on the basis of a dentary with teeth from Hérault [28]. Two morphological types of dentary have been discovered in the Late Campanian La Boucharde locality (Fig. 2) [3]. Two 'diagnostic' features of *R. septimanicus* are present on one of them (Figs. 2A-C): a coronoid process in prolongation of the alveolar row and a marked curvature of the alveolar row. Each dentary bears nine alveoli but they are quite different in shape. Such a difference has not been observed on the abundant postcranial material found in La Boucharde, even in earlier ontogenetic

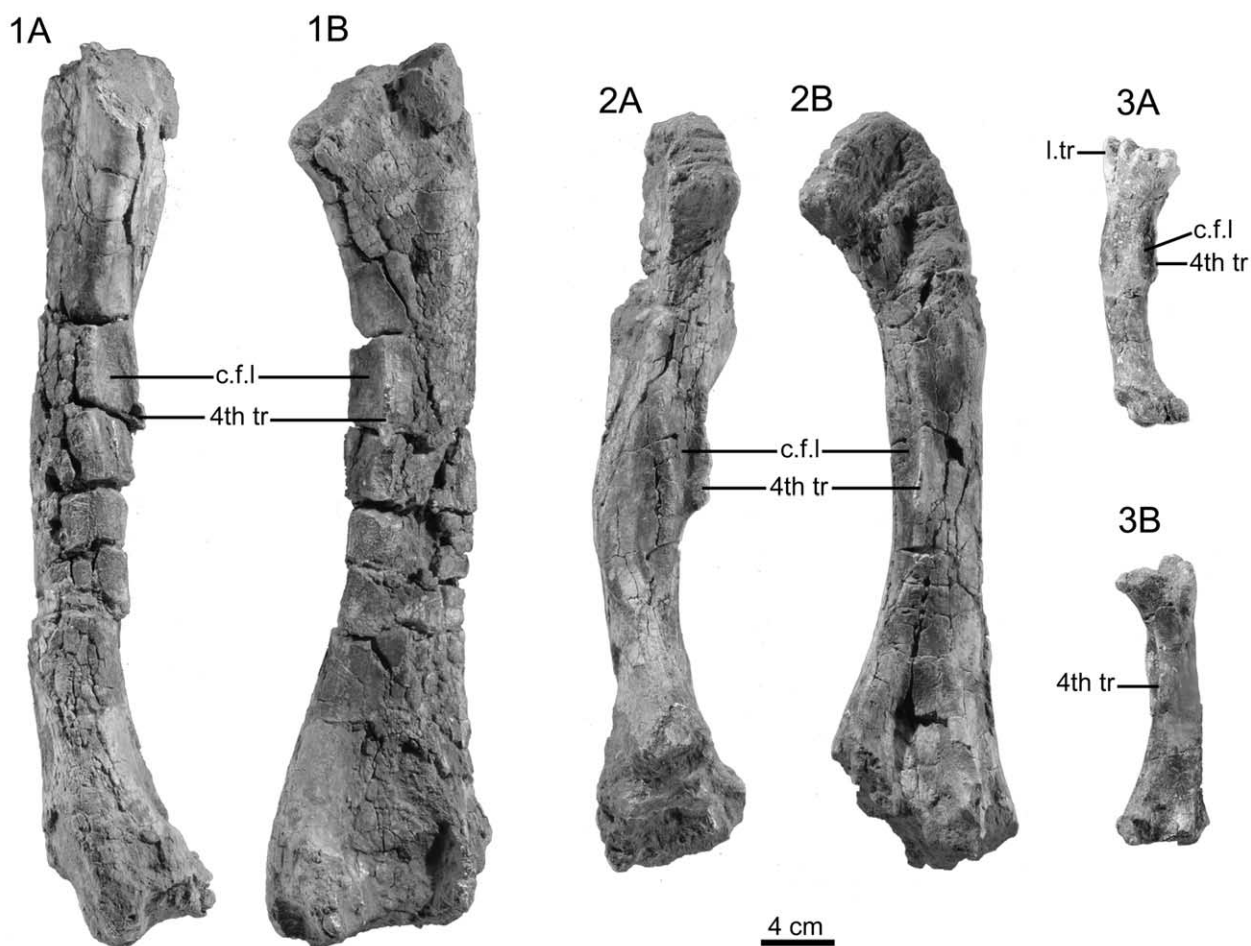


Fig. 3. *Rhabdodon priscus*, La Boucharde, Upper Campanian. **1**, Reversed left femur; **2**, right femur; **3**, right femur of a juvenile individual in: **A**, medial view; **B**, posterior view. **C.f.l.**, Insertion of the *M. caudi-femoralis longus*; **l.tr.**, lesser trochanter; **4th tr.**, fourth trochanter.

Fig. 3. *Rhabdodon priscus*, La Boucharde, Campanien supérieur. **1**, Fémur gauche inversé ; **2**, fémur droit ; **3**, fémur droit d'un individu juvénile en : **A**, vue médiale ; **B**, vue postérieure. **C.f.l.**, Zone d'insertion du muscle caudi-femoralis longus ; **l.tr.**, petit trochanter ; **4th tr.**, quatrième trochanter.

stages (Fig. 3). We consider the *Rhabdodon* remains of La Boucharde as conspecific. The polymorphism observed in French *Rhabdodon* material may reflect individual differences and/or sexual dimorphism rather than an interspecific variability. *R. septimanicus* is thus regarded here as a junior synonym of *R. priscus*. On the other hand, the systematic position of *Rhabdodon* is under debate. It has been referred either to the Hypsilophodontidae or Iguanodontidae [14]. Recent phylogenetic analyses suggest that *Rhabdodon* is a basal euornithopod closely related to *Tenontosaurus* [85, 139, 142]. A revision of the French material of *Rhabdodon* is currently in progress by M. Pincemaille.

First described in southern France in 1973 [135], the hadrosaurs are well known in localities of the Haute-Garonne [89, 108, 110, 122], Aude [109, 118] and Ariège [119]. Part of the material has been assigned to *Pararhabdodon* sp. [109], a taxon originally described from Catalonia [49]. The occurrence of a second taxon different from *Pararhabdodon* and *Telmatosaurus* is likely. The hadrosaurian material of southern France is under study by Y. Laurent.

Ankylosaur remains are not abundant, and most of the known material is indeterminate [3, 110, 136, 137]. A new species of the nodosaurid *Struthiosaurus* has recently been described from a partial skeleton that

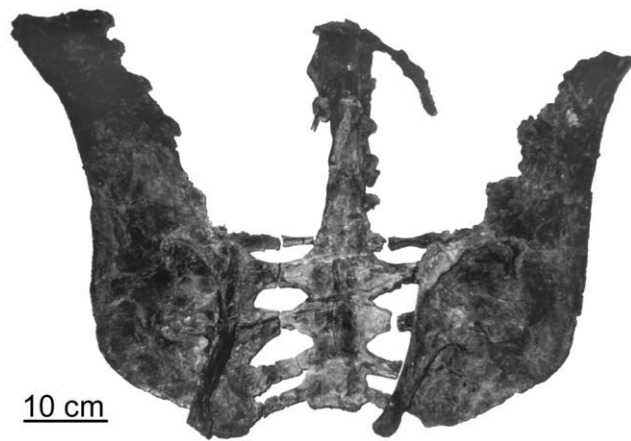


Fig. 4. *Struthiosaurus* n. sp., Villeveyrac, Lower Campanian. Synsacrum and pelvic girdle in ventral view [82].

Fig. 4. *Struthiosaurus* n. sp., Villeveyrac, Campanien inférieur. Synsacrum et ceinture pelvienne en vue ventrale [82].

includes dorsal vertebrae, synsacrum and pelvic girdle from the Early Campanian of Villeveyrac (Hérault) (Fig. 4) [13, 82]. The species *Rhodanosaurus ludgunensis* Nopcsa, 1929 is based on non-diagnostic material from Hérault and is regarded here as a *nomen dubium* [136]. All ankylosaur remains appear to belong to nodosaurids; there is no current evidence of ankylosaurids in the Latest Cretaceous of southern France [82].

Late Cretaceous sauropods are exclusively represented by titanosaurs. *Ampelosaurus atacis* from the Early Maastrichtian (or Late Campanian) of Campagne-sur-Aude (Aude) is known from a large collection of skeletal remains but has been only briefly described [115]. Additional remains of the same age from the Aude and Gard departments may belong to the same taxon [46, 119]. Indeterminate titanosaurid material has been reported from localities in Ariège [112], Hérault [114] and Var [37]. The taxon *Hypselosaurus priscus* Matheron, 1869 is based on a few scattered postcranial remains from the Aix-en-Provence Basin (Bouches-du-Rhône) and is currently regarded as a *nomen dubium* [113, 114]. However, there is evidence of the presence of several distinct titanosaurs in the Latest Cretaceous of southern France, represented by caudal vertebrae from Vaixains (Dordogne) [133], a caudal vertebra and a tibia from Le Mas-d'Azil (Ariège) [112], a braincase and postcranial material from La Boucharde [3] and additional remains from Bastide-Neuve (Bouches-du-Rhône)

[110]. Most of these remains are fragmentary and probably insufficient to erect new taxa, so they have been provisionally considered as indeterminate [113, 114]. The French titanosaurid record is clearly in need of a revision.

Most of the theropod remains described in the last few years are fragmentary. The dromaeosaurid *Pyroraptor olympius* [8] from the Late Campanian of La Boucharde locality seems to be the only taxa based on diagnostic material (Fig. 1G). *Variraptor mechinorum* is based on a poorly preserved sacrum and articulated last dorsal vertebra, problematically identified as a dromaeosaurid [117]. For one time, the identification of the holotypic material as dromaeosaurid is far from certain [143]; moreover, the association of the referred material (a humerus from the same locality and two vertebrae found in another locality) is very doubtful. As pointed out by Rauhut [143], the cervicodorsal vertebra referred to *Variraptor* is almost indistinguishable from that of the caenagnathid *Chirostenotes* [153]. *Variraptor mechinorum* is probably a chimera and can only be regarded as a *nomen dubium* [8, 143]. However, the presence of an oviraptorosaur in the Late Cretaceous of France is not excluded [143]. *Tarascosaurus salluvicus*, from the Early Campanian of the Beausset Syncline (Bouches-du-Rhône), is based on a badly preserved proximal end of a femur and has been referred to an abelisaurid ceratosaurian [116]. None of the diagnostic characters of abelisaurids [48, 93, 143, 148] is discernible on this material [3, 143]. The specimen is not diagnostic at the species or genus level and *Tarascosaurus salluvicus* should be considered a *nomen dubium* [143]. A right tibia from La Boucharde locality is reminiscent of that of abelisauroids, having a large cnemial crest, with a laterally directed hook (Fig. 5) [148]. Moreover, the end of the cnemial crest exhibits a distally directed process. Because this apomorphic character is shared with *Genusaurus* (see above), the two specimens could be closely related. Be that as it may, even if the presence of abelisauroids in the Late Cretaceous of France is likely, it should be phylogenetically demonstrated on the basis of a more abundant material. Finally, avian theropods have been described in various localities [31, 43, 47].

Previous work based on sites in southern France have concluded that an important faunal replacement related to environmental changes occurred in southern Europe during the Maastrichtian, in the form of re-

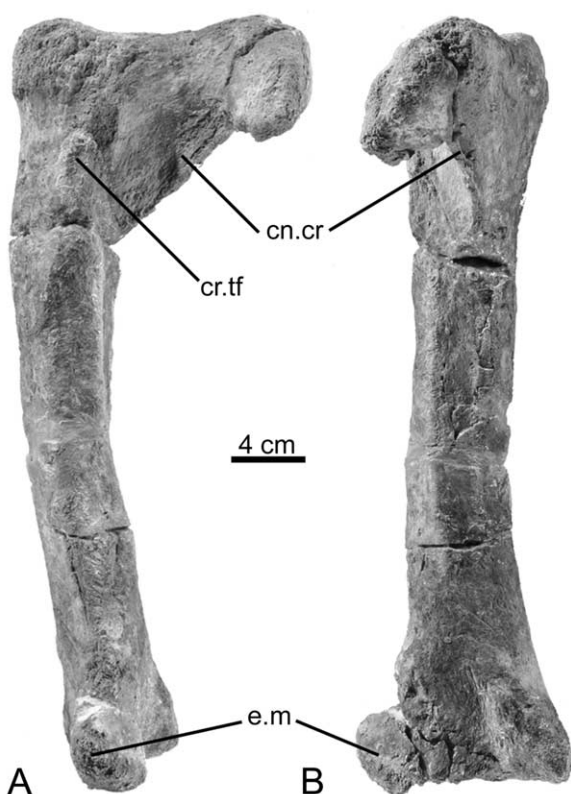


Fig. 5. *Neoceratosauria* sp., La Boucharde, Upper Campanian. Right tibia in: **A**, lateral view; **B**, anterior view. **Cn.cr**, Cnemial crest; **cr.tf**, crista tibiofibularis; **e.m**, external malleolus.

Fig. 5. *Neoceratosauria* sp., La Boucharde, Campanien supérieur. Tibia droit en : **A**, vue latérale ; **B**, vue antérieure. **Cn.cr**, crête cnémiale ; **cr.tf**, crista tibiofibularis ; **e.m**, malléole externe.

placement of an Early Maastrichtian fauna dominated by titanosaurs by a Late Maastrichtian assemblage dominated by hadrosaurs [45, 113, 119]. This hypothesis has been challenged by recent discoveries in northern Spain [124]. In fact, hadrosaurids show a continuous record from the Late Campanian to Latest Maastrichtian in southern France and the Iberian Peninsula. The Late Campanian to Early Maastrichtian dinosaur fauna of southern Europe is dominated by *Rhabdodon*, titanosaurs, and ankylosaurs, but hadrosaurs are also documented. During the Late Maastrichtian, a fauna arose that was dominated by hadrosaurs and titanosaurs, while *Rhabdodon* and ankylosaurs become more and more scarce and were probably extinct well before the Cretaceous-Tertiary boundary [124]. Theropods, mainly dromaeosaurids, are present in both faunal assemblages.

From a palaeobiogeographical point of view, the Late Cretaceous dinosaurian fauna of southern Europe has been regarded as having mixed affinities: some taxa such as dromeosaurids and nodosaurids are typically Laurasiatic, whereas titanosaurids and abelisaurids probably have a Gondwanan origin [111]. Le Lœuff [114] suggested that the appearance of titanosaurs in the Late Campanian of Europe is due to an immigration event from Africa but, as noted by Wilson and Sereno [165], this hypothesis is not supported by phylogenetic data. The occurrence of primitive hadrosaurids in Europe [65, 163] has been explained by a late dispersion via Africa [109, 113], where hadrosaurids are unknown, but they could be relict elements that evolved in isolation by vicariance in the European archipelago during the Late Cretaceous [50, 162]. In fact, vicariance could have been more important than previously thought in dinosaurian evolution, because most of the Campanian-Maastrichtian suprageneric taxa known in southern Europe were still represented in the Early Cretaceous or Late Jurassic of Laurasia [3, 55, 138].

The earliest dinosaur egg discoveries were made in southern France. Dinosaur eggshells were first found in Provence by Matheron, as early as 1846 [155]. Later, eggshell fragments were discovered in the French Pyrenees in 1859 by Pouech [29]. The egg localities of southern France are currently among the richest in the world. Eggs and eggshell remains have been collected from the Campanian-Maastrichtian continental deposits in several areas, from Provence in the east to Languedoc and Ariège in the foothills of the Pyrenees in the west. These areas include the Arc Basin near Aix-en-Provence; the Villeveyrac-Mèze syncline, close to Montpellier; the Corbières and Upper Aude valley; and Ariège [13, 54, 80, 83]. The Megaloolithidae (discretispherulitic morphotype, probably referable to titanosaurian sauropods) is the most diverse oofamily, with at least four valid oospecies of *Megaloolithus* and *Cairanoolithus* [53, 83, 159]. The Prismatoolithidae (prismatic structure, which has been referred to theropods) consists of at least three oospecies of *Prismatoolithus* and an unnamed type [81, 86, 158]. In addition, ratite (ornithoid) morphotypes have also been described [81]. The ootaxon diversity appears greatest in the Campanian deposits, and then drastically decreases during the Maastrichtian [83].

9. Conclusions

The French dinosaur record is important in several respects, mainly in terms of stratigraphic completeness, because it ranges in age from the Late Triassic to the end of the Cretaceous. But it is also important because it includes so many early discoveries, including the first dinosaur eggs found in southern France in the middle of the 19th century and the skeletal remains found in Normandy at the end of the 18th century. The osteological and oological records are good in the Late Cretaceous continental deposits of southern France, while the richest footprint sites are known in the Late Triassic-Early Jurassic formations of the Massif Central and the Atlantic coast of Vendée. Theropods and, in to a lesser extent, ornithopods are the most diversified dinosaur groups, but prosauropods, sauropods and thyreophorans are also represented. Our knowledge of French dinosaurs has been greatly improved in the last few years through the exploitation of a number of rich localities and to the discovery or revision of interesting specimens. Among the 20 species regarded as valid in this work (see Table 1), six have been described in the last decade. New French taxa include the theropods *Liliensternus airelensis* Cuny & Galton, 1993 from the Triassic-Jurassic boundary of Normandy, a megalosaurid from the Middle Jurassic of Normandy [6], the ceratosaur *Genusaurus sisteronis* Accarie et al., 1995 from the late Early Cretaceous of Provence and the dromaeosaurid *Pyroraptor olympius* Allain & Taquet, 2000 from the Late Cretaceous of Provence, as well as the sauropod *Ampelosaurus atacis* Le Lœuff, 1995 and a new species of the ankylosaur *Struthiosaurus* [82], both from the Late Cretaceous of Languedoc. The taxa *Tarascosaurus salluvicus* [116], *Variraptor mechinorum* [117] and *Rhabdodon septimanicus* [28], all from the Late Cretaceous of southern France, are here regarded as *nomina dubia*. Additional dinosaur material has been redescribed or revised in detail in the last years, including theropod remains from the Middle Jurassic of Normandy, such as *Poekilopleuron bucklandii* and *Streptospondylus altdorfensis*, *Compsognathus longipes* from the Late Jurassic of Provence, and *Erectopus superbus* from the Early Cretaceous of Lorraine; prosauropod specimens from the Late Triassic of Franche-Comté, Lorraine and other regions referred to as *Plateosaurus longiceps* and *P. engelhardti*; stegosaur remains assigned to *Lexovisaurus durobriv-*

ensis and *Dacentrurus armatus* from the Middle-Late Jurassic of Normandy; and ornithopod bones that belong to *Iguanodon atherfieldensis* and *I. bernissartensis* from the Early Cretaceous of Champagne, and to *Rhabdodon priscus* from the Late Cretaceous of Provence. It should be noted that studies of other dinosaurs, such as the Damparis sauropod from the Late Jurassic of the Jura region referred to *Bothriospondylus madagascariensis*, and the ornithopods (mostly hadrosaurs) from the Late Cretaceous of southern France are currently in progress. Titanosaurids from the terminal Cretaceous and French sauropods in general are in need of revision. Most of the dinosaur material from France is fragmentary, but specimens of *Compsognathus*, *Plateosaurus*, *Ampelosaurus*, *Dacentrurus*, *Iguanodon* and *Rhabdodon* are relatively complete or known from articulated remains. With regard to the ichnological record, a large number of footprints of *Otozoum*, *Grallator* and *Eubrontes* are known in the Late Triassic-Early Jurassic sites of the Massif Central and the Atlantic coast. Finally, the Late Cretaceous egg localities of Provence and Languedoc are among the richest in the world and have yielded several ootaxa of Megalolithidae and Prismatolithidae.

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