

A juvenile *Steneosaurus* in the Callovian of Normandy (France); a genus too hastily consigned to the wastebasket?

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Abstract

This paper describes a fragment of a sub-adult specimen of *Steneosaurus* cf. *heberti* (Crocodylia, Thalattosuchia, Teleosauridae) found in the Callovian of the “Vaches Noires” (Normandy, France). The small size of the specimen makes it particularly interesting, as few Teleosauridae of this size have been found in the Callovian in Europe. A recent revision, based solely on the existing material of the genus *Steneosaurus*, proposes that the genus be abandoned for ten other monospecific genera. We intend to show that in addition to this being a misinterpretation, it also skews diagnoses, such as the one presented here. A reassessment of the paleoecology of Teleosauridae is also provided.

Keywords: Teleosauridae, *Steneosaurus*, Juvenile, Callovian, ICZN, systematic, palaeoecology.

Résumé

Un juvénile de *Steneosaurus* dans le Callovien de Normandie (France) ; un genre trop vite mis à la poubelle ?

Il est décrit ici un fragment de spécimen subadulte de *Steneosaurus* cf. *heberti* (Crocodylia, Thalattosuchia, Teleosauridae) trouvé dans le Callovien des Vaches Noires (Normandie, France). L'intérêt de ce spécimen réside dans sa petite taille car peu de Teleosauridae de cette dimension ont été trouvés dans le Callovien en Europe. Récemment une révision basée uniquement sur le matériel existant du genre *Steneosaurus*, propose son abandon pur et simple pour dix autres genres monospécifiques. Cette proposition repose sur une interprétation incomplète du code de nomenclature et provoque une instabilité de ce genre créé il y a deux siècles. Une réinterprétation de la paléocologie des Teleosauridae est aussi proposée.

Mots-clés : Teleosauridae, *Steneosaurus*, Juvénile, Callovien, CINZ, systématique, paléocologie.

Introduction

Teleosauridae are Jurassic marine crocodylians of longirostrine type which have been discovered in numerous deposits in Europe and the rest of the world (e.g. Buffetaut 1982 ; Vignaud 1995 ; Mueller-Töwe 2006). They are particularly abundant in certain levels of the Lower to Middle Jurassic of Europe, to the extent that statistical approaches can be implemented: as in the Toarcian of Holzmaden (e.g. Westphal 1962 ; Mueller-Töwe 2005), and Belgium-Luxembourg (Godefroit 1994) in the Callovian of

the Oxford Clay (Martill *et al.* 1994)) and of Poitou (Vignaud 1995). Unfortunately, the unique Norman collections of Le Havre and Caen (described by J.A. Eudes-Deslongchamps 1869) have disappeared. Alongside these particularly rich sites, there are numerous deposits throughout the world covering the entire Jurassic period. These deposits range from fluvial to decidedly marine, but none has yielded juvenile or small Teleosauridae with the exception of one example from Holzmaden. The discovery of this Norman specimen changes the situation.

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Location and level of deposit

This specimen (**Pl. 1**) was discovered by two of the authors (E.P. & G. P) in March 1989 within the “Marnes de Dives” Formation at Villers-sur-Mer, which belongs to the Upper Callovian, Lamberti Zone H2 H3 (Lebrun & Couville 2013). The specimen is housed at the Villers-sur-Mer Paleospace Museum (Calvados, France) under the number MPV 2021.1.1. These levels have already yielded a significant number of marine vertebrate fossils, including numerous metriorhynchid and teleosaurid marine crocodylians: *Steneosaurus heberti* Morel de Glasville, 1876, *S. edwardsi* (Eudes-Deslongchamps, 1869) and *Lemnisuchus obtusidens* (Andrews, 1909) (cf. synthesis by Vignaud 1995). The Callovian “Marnes de Dives” (Dives marls) correspond to a shallow epicontinental sea with rapid burial of remains due to the supply of fine terrigenous material (Lebrun & Courville 2013).

Description of the specimen

The specimen is a small piece of mandibular symphysis, 9 cm long, with an ovoid section (**Pl. 1.4**) (posterior section $l = 1.2 \text{ cm} \times H = 1.2 \text{ cm}$), which bears 7 dental alveoli, spaced about 1 cm apart, on each sides (**Pl. 1.1, 2, 3**). Four of these alveoli still bear a tooth root with fluted ornamentation (**Pl. 1.6**). The regular aspect of the alveoli and the straightness of the jaw are typical features of purely ichthyophagous, longirostrine crocodylians. The diameter of the alveoli is constant, always around 5 mm. The alveolar edges are well outlined, and the two rows are 1.5 cm apart. This dental morphology, combined with a mandible featuring evenly spaced alveoli and an ovoid cross section, are typical of the Teleosauridae, a family of marine mesosuchian crocodylians of gavialoid appearance. The anterior width of 1.8 cm versus the posterior width of 2.3 cm means that this piece is from the anterior 1/3 of the jaw. If we refer to the more complete jaws of animals like the type of *S. heberti* Morel de Glasville, 1876, which was retrieved from the same stratigraphic level and geographical locality, a section with 7 alveoli represents a length of 20 cm which means that our skull would have been about half the size, i.e. around 60 cm long. This skull length corresponds to a young adult, which explains the appearance of the medial sutures of the mandible (corresponding to dentarues) which are not open like those of juveniles but are still sufficiently marked. The ornamentation of the bones, with slight longitudinal grooves, seems to corroborate the hypothesis that this

is a young adult. We did not use *S. leedsi* Andrews, 1913 for our comparisons because the latter has a very particular ultralongirostrine rostrum (length of the rostrum $> 66\%$ of the length of the skull, Hua, 1997) in which the alveoli are small, very close-set and have unraised or slightly raised edges, which is not the case here. The edges of the crowns are in every way typical of the type described by Morel de Glasville (1876) and visible at the Muséum National d'Histoire Naturelle de Paris (MNHN 13.1890). Leaving aside its size, the shape of the mandible, the alveolar margins and the dental ornamentation all correspond to the type; in addition, the stratigraphic level of the finds further connects our specimen to this species.

There are 3 unhealed bite marks, possibly *post mortem*, on each side of the front of the jaw; one of these marks is deeper on the tooth socket on the left side (**Pl. 1.5**). Another point to note, and one which is quite remarkable for the “Marnes de Dives” context, is the absence of serpulids on the fossil. This fact and the presence of replacement teeth still in place within the sockets suggest rapid burial.

Systematic. The genus *Steneosaurus* in the “wastebasket”?

Order Crocodylia Owen, 1842
Suborder Thalattosuchia Fraas, 1901
Family Teleosauridae Geoffroy, 1831
Genus *Steneosaurus* Geoffroy, 1825

Steneosaurus cf. *heberti* Morel de Glasville 1876

This specimen is related to *S. cf. heberti* by virtue of the configuration of its mandible and teeth and the fact that it was found in the type locality and type level.

The genus *Steneosaurus*, initially described by Geoffroy Saint-Hilaire in 1825, has been discussed many times because it has been found in all of the European deposits (Andrews 1913 ; Kalin 1955 ; Steel 1973, cf. synthesis *in* Buffetaut 1982). More recently, it has been described within the abundant fauna from Holzmaden, where more than 80 specimens have been recorded (Westphal 1962 ; Mueller-Töwe 2006), and in several other accounts (Buffetaut 1982 ; Godefroit, 1994 ; Godefroit *et al.* 1995 ; Vignaud 1995). These studies, which apply either classic, statistical or cladistic approaches, all converge on the same result, i.e. the justification and redefinition of the genus *Steneosaurus* through species that have been correctly redefined since the first descriptions, even

in the absence of a designated holotype, the original specimens having been destroyed.

The studies by Johnson *et al* 2020a and 2020b, which are based on existing material with no unpublished specimens, uses the cladistic approach. Curiously, this paper ignores recent studies, whether cladistic or not, carried out on rich bodies of material (Westphal 1962 ; Buffetaut 1982 ; Vignaud 1995 ; Mueller-Töwe 2006). As Johnson *et al.* (2020b, p. 435) state: "Curiously, while there has been little discussion on what the type species of *Steneosaurus* is since the 1860s, the genus *Steneosaurus* has become widely accepted and the most predominately used generic name when establishing new teleosauroid species". Each of these previously cited studies (Westphal 1962 ; Buffetaut 1982 ; Vignaud 1995 ; Mueller-Töwe 2006) were nevertheless carried out each time on new material and they take into account the entire bibliography, correcting it using all possible approaches be they statistical, sedimentological and/or cladistic. Johnson *et al.* 2020b only includes recent articles, often co-written by the same authors and using the same approaches: "In addition, multiple recent phylogenetic studies on, or including, teleosauroids (e.g. Wilberg 2015a ; Foffa *et al.* 2019 ; Johnson *et al.* 2020a, 2020b ; Martin *et al.* 2019 ; Sachs *et al.* 2019) have recovered various *Steneosaurus* species as either polyphyletic or paraphyletic, further adding to its taxonomic instability". This borders on circular reasoning : on the basis of this biased bibliographical base, lacking any new material, the authors propose a polyphyletic *Steneosaurus* genus and break it down into ten distinct genera, all of which are almost monospecific, and they literally "trash" the genus *Steneosaurus* (Johnson *et al.* 2020a, 2020b). This is a rigorous approach to the ICZN code from the point of view of 'rationalising' the genera, but it ignores the other requirement of the ICZN, namely an obligation of stability.

The revision of a two-hundred year old genus such as this generates great instability within the classification and, under the Nomenclature Code, can only be carried out by presenting the case to the Commission (Article 65.2). This article of the code states that when a genus has been incorrectly identified (Article 65.2.3), i.e. when the *de jure* species differs from the *de facto* species, the case must be referred to the Commission for a ruling. The authors must choose a more clearly defined type species (Article 70.3), while still keeping the genus for stability purposes; this must always occur following presentation of the case to the Nomenclature Commission (Article 13).

Although the goal of the ICZN is to clearly define species, it also aims to promote taxonomic and nomenclatural stability: this was the reason why Vignaud (1995) opted not to create "taxonomic chaos".

The ideal candidate for designating the type species of the genus *Steneosaurus* would be *Steneosaurus megistorhynchus* (Geoffroy, 1831), the earliest still existing species to be well described and figured (Eudes-Deslongchamps 1866). The type figured by Cuvier in 1824 was lost during the bombing of Caen in 1944, as were many Thalattosuchian specimens. The specimen had been discovered in the Calcaire de Caen Formation belonging to the Lower and Middle Bathonian in the village of Quilly in Calvados (Normandy). Although it has disappeared, it has a well-defined type locality and E. Eudes-Deslongchamps (1869) provided a sufficiently detailed diagnosis of the species. This diagnosis was subsequently amended by Vignaud (1995) who already considered the specimen a perfect candidate as a type species of the genus:

"A very elongated and slender snout, representing on average more than 70% of the total length of the skull. The anterior-orbital width of the base of the snout represents about 30% of its length measured in front of the orbits. The maximum width of the skull, measured between the external angles of the articular processes of the quadrates is 28% on average of the total length of the skull. The premaxillae are greatly enlarged. The orbits are elliptical in shape, elongated anteriorly and posteriorly. The frontal is relatively wide and short. The supratemporal fossae are quadrangular in shape and are proportionally short (the length represents only 12 to 15% of the total length of the skull); the anterior and posterior angles are rounded. The ornamentation is essentially marked on the frontal. The mandible is very compressed dorso-ventrally. The symphysis is long, it represents between 52 and 57% of the total length of the mandible. The anterior mandibular plate is very elongated and generally raised. The teeth are long, curved in a conical shape, regularly and finely striated and slightly carinated. The premaxilla bears 4 pairs of teeth, the maxilla between 30 and 34 pairs and the mandible between 37 and 40".

This amended diagnosis provided by Vignaud (1995) is accompanied by the designation of the original specimens described by Cuvier (1824) as syntypes, pl.7, figs. 6, 8, 9, 11 to 13, in the absence of an explicit holotype.

This author completes his diagnosis by attaching existing specimens which could very well be designated as neotypes (such as the most complete

MMT P28 1) and paraneotypes in the case of others:

- MMT P28 1 (skull, mandible + post cranial elements, Godefroit *et al.* 1995) - Musée municipal de Toul,
- OUM J 1414 (mandible, Phillips, 1871) - Oxford University Museum,
- OUM J 1415 (fragmentary skull, Vignaud 1995),
- LPP T1 (mandible, Mazin *et al.* 1995) - Poitiers Paleontology Laboratory.

This gives the species the following geographical and stratigraphic distribution: Lower and Middle Bathonian of Normandy, Middle Bathonian of Poitou, Middle and Upper Bathonian of Oxfordshire and Gloucestershire and Upper Bathonian of Lorraine.

This species of the genus *Steneosaurus* is considered as a *nomen dubium* by Johnson *et al.* (2020a & b) but curiously it appears in the phylogenetic analyses of these authors. They consider the species to be valid but refuse to amend the genus *Steneosaurus*, and instead create an umpteenth monospecific genus of Teleosauridae. Their interest in the MMT P28 1 specimen is noteworthy, since they use it as a neotype of their new genus, while still keeping the old species.

Although these authors are of the opinion that the use of "*Steneosaurus*" risks causing confusion, under article 13 and especially 70.3, they must present their case to the commission - which has not yet been done - and they should not create new taxa which risk creating confusion or chaos.

Pending this presentation to the commission and its outcome, we will therefore not take their classification into account. For the moment, in order to maintain a semblance of objectivity, we will retain a more "classic" and "stable" systematic through new discoveries.

Clearly this position is subject to change with the addition of new material, and not just a revision of existing material, as has already been done in the past (Westphal 1965 ; Buffetaut 1982 ; Martill *et al.* 1985 ; Godefroit 1994 ; Vignaud 1995). Here our specimen shows the potential limits of this proposed classification: according to the Johnson

et al. classification, 2020a, our specimen would be classed as a Teleosaurini indet, whereas the hitherto valid classic classification (pending redefinition), which is not perfect but is at least stable, proposes a *Steneosaurus cf. heberti*.

These authors (as contributors in Kean *et al.* 2020) seem to be aware of the limits of their classification and the instability it creates. In describing a specimen from the Isle of Skye, they acknowledge that it is probably a *Steneosaurus bollensis* alias "*Macrospondylus*". However, using their own taxonomic revision, they cannot go below the super family Teleosauroidea, thus showing the weakness of their own revision!

Once again, the description of new specimens, in this case this small *Steneosaurus cf. heberti*, allows us to clarify the debate and to assess whether a new hypothesis is objectively pertinent or not, or, in this case, whether it is constructive in the sense of being stable or not. In the case of the Teleosauridae, rediscovery, such as that of *M. mosae* (Hua 1999), has led to a clear definition of the genus (Young *et al.* 2006) through the designation of a new neotype. The example of *Steneosaurus megistorhynchus* described by Godefroit *et al.* (1995) has thus led to a better understanding of this species and will perhaps contribute to a better definition of the future neotype of the type species of the genus as part of a forthcoming study.

For the time being, this specimen and the one from the Isle of Skye (Kean *et al.* 2020) do not seem to argue for the redesignation of *Steneosaurus* as presented by Johnson *et al.* 2020a & b. We therefore prefer not to take these conclusions into account pending a detailed study in progress which will take into account all of the ICZN recommendations, including those established to avoid confusion within this genus and its historically related species.

Palaeoecology

Since the first published work of J.A. Eudes-Deslongchamps (1869) the palaeoecology of Teleosauridae has been approached on the basis of dental morphofunctionality; it was with the work of

Plate 1 - Portion of *Steneosaurus cf. heberti* mandible (MPV 2021.1.1) (vertical bar = 1 cm)

1. Dorsal view
2. Left side view
3. Ventral view
4. Anterior view showing the ovoid section
5. Detail of the jaw showing bite marks
6. Detail of the dental alveoli and the ornamentation at the base of the crowns



Westphal (1965) and Buffetaut & Thierry (1977) that the sedimentological dimension was added in order to identify the palaeoecological framework. Vignaud (1997) specified the major dental categories associated with the degree of longirostria within the Teleosauridae. However, as Mueller-Töwe (2005) reminds us, the palaeoecological interpretation based solely on dental morphology and longirostria of an animal whose diet varies according to age, and which in the wild proves opportunistic, should not be pushed too far. As proof, we refer the reader to this video ([Video: A shark and Crocodylus share a dead whale | National Geographic](#)) where a Tiger shark and a *Crocodylus porosus* share a carcass, and yet both have a very different dental morphology and skull shape. Similarly, *C. porosus* when young is rather ichthyophagous in a broad sense (including insects and amphibians) before becoming macrophagous and eventually, as an adult in the marine environment, eating whatever it finds as a downright opportunist (Allen 1974). The tooth morphology remains the same but the diet does not. Here again, actualism shows us that we must be very careful and not push interpretation too far. Massare (1987), Vignaud (1997) and Hua (1997, 1999) did not link the palaeodiet to the paleoenvironment on this basis alone because they are two quite distinct things. For example, the Ganges gavial strongly resembles *Steneosaurus leedsi* in that they are both longirostrine with pointed teeth, and yet one is fluvial and the other marine. Curiously, however, Johnson *et al* (2020b) propose a palaeoecological reconstruction based solely on dental and cranial morphology, without any other form of verification such as, for example, sedimentological or geochemical criteria.

As this specimen shows, we can only make a decision on the paleoecology of a given species when we know all of the stages of growth, thus avoiding any biased vision skewed by environments that are more fossiliferous than others.

In the absence of arguments other than the shape of the skull and teeth, the conclusions of Johnson *et al.* 2020b cannot therefore be used.

Conclusion

Because of its size, this specimen is rare in the context of Callovian deposits. It had a skull about 60 centimetres long, similar to the young specimens of *Steneosaurus bollensis* described by Westphal (1962) and Mueller-Töwe (2005). The Toarcian levels of Holzmaden correspond to a shallow sea. The Callovian environment of the “Vaches Noires” cliffs corresponds to an epicontinental sea close to the

continent. Mueller-Töwe (2005) considers that this is the size limit for young adults of this type and rightly asks where are the smaller individuals and the egg-laying areas? Particularly since we know that in living crocodylians, such as the Nile Crocodile (Cott 1961), distribution is a function of age group and size. In the Indo-Pacific crocodile (Grigg *et al.* 1980), juveniles are found upstream and large adults are found in estuaries and in the open sea. Given the total absence of juveniles in the European marine Jurassic levels, it is therefore reasonable to think that we are dealing with a similar situation and that the spawning areas must have been further upstream and, hence, that we have not yet found the correct continental Jurassic deposits. Martin *et al* (2019) describe fluvial Teleosauridae in Thailand (on a sedimentological basis and not just on dental evidence): since the first juveniles, with a skull length of less than 60 cm, are found in these deposits, then we can be reasonably hopeful that we are close to the spawning areas. We will only have a good understanding of, and be able to reconstruct, the palaeoecology of the Teleosauridae when we have an overview of the populations and their entire growth cycle. For the moment, the presence of only adults or young adults in marine levels suggests that we have a biased view of their palaeoecology. We must therefore remain cautious and not push a palaeoecological interpretation based on a single criterion until we have a more global vision of the Teleosauridae populations and, in particular, before we have found the juveniles.

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References

- Allen G.R. (1974) - The marine crocodile *Crocodylus porosus* from Ponape, Eastern Caroline islands, with notes on the food habits of crocodiles from the Palau Archipelago. *Copeia*, Lawrence. 553 p.
- Andrews C.W. (1909) - On some new Steneosaurs from the Oxford Clay of Peterborough. *Annals of the Magazine of Natural History*, London, 3(15) : 299-308.
- Andrews C.W. (1913) - A descriptive catalogue of the marine reptiles of the Oxford Clay. Part II. *British Museum (Natural History)*, London. 206 p.

- Buffetaut E. & Thierry J. (1977) - Les crocodiliens fossiles du Jurassique moyen et supérieur de Bourgogne. *Geobios*, Lyon, 10 (2) : 151-194.
- Buffetaut E. (1982) - Radiation évolutive, paléoécologie et biogéographie des crocodiliens méso-suchiens. *Mémoire de la Société Géologique de France*. Paris. 142. 88 p.
- Cott H.B. (1961) - Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Transactions of the Zoological Society of London*, London, 29 (4) : 211-357.
- Cuvier G. (1824) - Sur les ossements fossiles de Crocodiles. In *Recherches sur les ossements fossiles*, 1ère éd., Deterville (éd.), Paris, 5 (3) : 1-38.
- Eudes-Deslongchamps E. (1869) - Mémoire sur les Téléosauriens de la Normandie. *Bulletin de la Société Linnéenne de Normandie*, Caen (année 1868), 2 (3) : 124-221.
- Eudes-Deslongchamps J.A. (1866) - Sur la découverte d'un mâchoire inférieure entière de *Teleosaurus megistorhynchus* (Geoffroy) trouvé à Allemagne et comparaison avec le *Teleosaurus larteti* (Deslongchamps). *Bulletin de la Société Linnéenne de Normandie*, Caen (années 1864-1865), 10 : 80-85.
- Foffa D, Johnson M.M., Young M.T., Steel L. & Brusatte S.L. (2019) - Revision of the Late Jurassic deep-water teleosauroid crocodylomorph *Teleosaurus megarhinus* Hulke, 1871, and evidence of pelagic adaptations in Teleosauroidea. *PeerJ* 7:e6646 <https://doi.org/10.7717/peerj.6646>
- Geoffroy Saint-Hilaire E. (1825) - Recherches sur l'organisation des gavials, sur leurs affinités naturelles desquelles résulte la nécessité d'une autre distribution générique : *Gavialis*, *Teleosaurus*, *Steneosaurus* ; et sur cette question, si les gavials (*Gavialis*), aujourd'hui répandus dans les parties orientales de l'Asie, descendent, par voie non interrompue de génération, des gavials antédiluviens, soit des gavials fossiles, dits crocodiles de Caen (*Teleosaurus*), soit des gavials fossiles du Havre et de Honfleur (*Steneosaurus*). *Mémoires du Muséum National d'Histoire Naturelle de Paris*, Paris, 12 : 97-155.
- Geoffroy Saint-Hilaire E. (1831) - Recherches sur les grands sauriens trouvés à l'état fossile aux confins maritimes de la Basse Normandie, attribués d'abord au Crocodile, puis déterminés sous les noms de *Teleosaurus* et *Steneosaurus*. *Mémoire de l'académie des sciences de Paris*, Paris, 12 : 1-138.
- Godefroit P. (1994) - Les reptiles marins du Toarcien (Jurassique inférieur) belgo-luxembourgeois. *Mémoire pour Servir à l'Explication des Cartes Géologiques et Minières de la Belgique*, Bruxelles, 39. 98 p.
- Godefroit P., Vignaud P. & Lierger A. (1995) - Un Teleosauridae (Reptilia, Mesosuchia) du Bathonien supérieur lorrain, France). *Bulletin de la Société Géologique de Belgique*, Bruxelles, 104 (1-2) : 91-107.
- Hua S. (1997) - Adaptations des crocodiliens méso-suchiens au milieu marin. Thèse de Doctorat de l'Université de Paris 6. 211 p.
- Hua S. (1999) - Le Crocodilien *Machimosaurus mosae* (Thalattosuchia, Teleosauridae) du Kimméridgien du Boulonnais (Pas-de-Calais, France). *Palaeontographica*, Stuttgart, A, 252 : 141-170.
- Johnson M.M., Young M.T. & Brusatte S.L. (2020a) - Emptying the wastebasket: a historical and taxonomic revision of the Jurassic crocodylomorph *Steneosaurus*. *Zoological Journal of the Linnean Society* 189(2): 428-448, <https://doi.org/10.1093/zoolinnean/zlaa027>
- Johnson M.M., Young M.T. & Brusatte S.L. (2020b) - The phylogenetics of Teleosauroidea (Crocodylomorpha, Thalattosuchia) and implications for their ecology and Evolution. *PeerJ* 8:e9808 <https://doi.org/10.7717/peerj.9808>
- Kalin J. (1955) - Crocodilia. In *Traité de Paléontologie* : J. Piveteau (éd.), Masson, Paris, 5 : 695-784.
- Kean J., Foffa D., Johnson M. M. & Young M., Greitens G. & Brusatte S.L. (2020) - First and most northern occurrence of a thalattosuchian crocodylomorph from the Jurassic of the Isle of Skye, Scotland, *Scottish Journal of Geology*, 57 (1): sjg2020-013.
- Lebrun P. & Courville P. (2013) - Le jurassique des falaises des Vaches-Noires. *Fossiles, Revue française de paléontologie*, Hors série, Paris :16-28.
- Martill D. M. ; Taylor, M.A. Duff K.L. Riding J.B. & Bown P.R., 1994 - The trophic structure structure of the biota of Peterborough Member, Oxford Clay Formation (Jurassic), UK, *Journal of the Geological Society of London*, London, 151 : 173-194.
- Martin J.E., Suteethorn S., Lauprasert K., Tong H., Buffetaut E., Liard R., Salaviale C., Deesri

- U., Suteethorn V. & Claude J. (2019) - A new freshwater Teleosaurid from the Jurassic of northeastern Thailand. *Journal of Vertebrate Paleontology*, Oklahoma, 38(6): e1549059.
- Massare J.A. (1987) - Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology*, Oklahoma, 7: 121-137.
- Mazin J.M., Bardet N., Vignaud P. & Hua S. (1995) - Marine reptiles faunas from the Middle and Upper Jurassic of Western Europe. 6. *Congreso Argentino de Paleontología y Bioestratigrafía*, Treleu : 35-36.
- Morel de Glasville M. (1876) - Sur la cavité crânienne et la position du trou optique dans le *Steneosaurus heberti*. *Bulletin de la Société Géologique de France*, Paris, 3(4) : 342-348.
- Mueller-Töwe I.J. (2006) - Anatomy, phylogeny, and palaeoecology of the basal thalattosuchians (Mesoeucrocodylia) from the Liassic of Central Europe. Am Fachbereich 09 Chemie, Pharmazie und Geowissenschaften der Johannes Gutenberg-Universität Mainz, Mainz. 369 p.
- Phillips J. (1871) - Geology of Oxford and the valley of the Thames. Clarendon Press, Oxford. 523 p.
- Sachs S., Johnson M.M., Young M.T. & Abel P. (2019) - The mystery of *Mystriosaurus* Kaup, 1834: redescribing the poorly known Early Jurassic teleosauroid thalattosuchians *Mystriosaurus laurillardi* Kaup, 1834 and *Steneosaurus brevior* Blake, 1876. *Acta Palaeontologica Polonica*, Varsovie 64 : 565-579.
- Steel R. (1973) - Crocodiles: Christopher Helm, London. 198 p.
- National Geographic (2020) : Vidéo : un requin et un crocodile se partagent une baleine morte | National Geographic. <https://www.nationalgeographic.fr/video/tv/video-un-requin-et-un-crocodile-se-partagent-une-baleinemorte?fbclid=IwAR1ZrWB8rKmMelCLa5emoUW9rflK1sGILr8c7HA9q4twRZYY SopYwgcZCws>
- Vignaud P. (1993) - Thalattosuchians from the Callovian of Poitou (Vienne, France). *Revue de Paléobiologie*, Genève, 7 : 251-261.
- Vignaud P. (1995) - Les Thalattosuchia, crocodiles marins du Mésozoïque: Systématique phylogénétique, paléoécologie, biochronologie et implications paléogéographiques. Thèse de Doctorat de l'Université de Poitiers, France. 271 p.
- Vignaud, P. (1997) - La morphologie dentaire des Thalattosuchia (Crocodylia, Mesosuchia). *Palaeovertebrata*, Montpellier, 26 (1-4) : 35-59.
- Westphal F. (1962) - Die Krokodilier des deutschen und englischen oberen Lias. *Palaeontographica*, Stuttgart 116 : 23-118.
- Wilberg E.W. (2015) - What's in an outgroup? The impact of outgroup choice on the phylogenetic position of Thalattosuchia (Crocodylomorpha) and the origin of Crocodyliformes. *Systematic Biology* 64(4) : 621-637 <https://doi.org/10.1093/sysbio/syv020>

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