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REVIEW

Emptying the wastebasket: a historical and taxonomic revision of the Jurassic crocodylomorph *Steneosaurus*

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Teleosauroidea is a clade of ancient crocodylomorphs that were integral components of coastal marine environments throughout the Jurassic. For nearly two centuries, one of the most familiar genera of teleosauroids has been *Steneosaurus*, encompassing nearly every teleosauroid species at some point. However, no type species has been designated for *Steneosaurus* under ICZN Code rules; the type specimen of the presumed type species *S. rostromajor* Geoffroy Saint-Hilaire, 1825 (MNHN.RJN 134c-d) is a chimera that has been largely neglected in the literature. Moreover, there is confusion as to which teleosauroid species it pertains to, and the genus *Steneosaurus* is often recovered as paraphyletic or polyphyletic in phylogenetic analyses. As such, the validity of *Steneosaurus* is uncertain. Here we formally designate *S. rostromajor* as the type species of *Steneosaurus*, designate a lectotype and re-evaluate MNHN.RJN 134c-d. We compare it with several well-known teleosauroids, including *Lemmysuchus* and '*S.*' *edwardsi*. Due to lack of autapomorphic characters, poor preservation and a tortured taxonomic history, we find MNHN.RJN 134c-d to be an undiagnostic and unreliable specimen. Thus, we consider *S. rostromajor* as a *nomen dubium* and propose that the genus *Steneosaurus* is undiagnostic. This has profound implications for teleosauroid phylogenetics, which we will clarify in an upcoming paper.

ADDITIONAL KEYWORDS: Crocodylomorpha – Cuvier – taxonomy – Teleosauroidea – Thalattosuchia.

INTRODUCTION

Teleosauroids (one of the two major clades of Thalattosuchia), were a near-global group of extinct crocodylomorphs that inhabited marine, brackish and freshwater ecosystems throughout the Jurassic (Andrews, 1913; Buffetaut *et al.*, 1981; Buffetaut, 1982; Hua, 1999; Foffa *et al.*, 2015, 2019; Martin *et al.*, 2016, 2019; Johnson *et al.*, 2018a, b, 2019) and Early Cretaceous (Fanti *et al.*, 2016; Cortes *et al.*, 2019; Young & Sachs, 2020). They are often viewed as Jurassic analogues of extant gavials, as many species have an elongate and tubular snout, dorsally directed orbits and high tooth count, suggesting a primarily piscivorous diet (Andrews, 1909, 1913; Westphal, 1961, 1962; Buffetaut, 1982). Traditionally thought to be morphologically conservative, recent studies have shown teleosauroids to have been a diverse group in terms of anatomy, species richness and ecology (Buffetaut, 1982; Young *et al.*, 2014a; Jouve *et al.*, 2016; Johnson *et al.*, 2018a, 2019; Foffa *et al.*, 2019; Johnson, 2019; Martin *et al.*, 2019; Sachs *et al.*, 2019).

Arguably, the most historically important and commonly discussed teleosauroid genus is *Steneosaurus*. Originally coined by Geoffroy Saint Hilaire in 1825, it has since become a wastebasket containing a multitude of species named throughout the 19th to 20th centuries (e.g. Geoffroy Saint-Hilaire, 1825; J. A. Eudes-Deslongchamps, 1868a, b; E. Eudes-Deslongchamps, 1867–69; Hulke, 1871; Sauvage, 1872; Blake, 1876; Morel de Glasville, 1876; Hulke, 1877; Newton, 1893; Andrews, 1909, 1913; Phizackerley, 1951; Westphal, 1961; Buffetaut, 1980; Vignaud, 1998). However, it is unclear what *Steneosaurus* actually represents; it has long been

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recognized as a 'wastebasket taxon' by researchers, one that nearly every known teleosauroid species has at some stage been placed into. In addition, no type species has been formally designated for *Steneosaurus* under the International Commission on Zoological Nomenclature (ICZN) Code rules (see below for further details). However, the presumed type species, *Steneosaurus rostromajor* Geoffroy Saint-Hilaire, 1825 (MNHN.RJN 134c-d), has been largely ignored in the literature. These taxonomic complications undoubtedly play a significant part in the ongoing problems of larger teleosauroid taxonomic and phylogenetic studies, in which *Steneosaurus* has been considered paraphyletic (e.g. Mueller-Töwe, 2006; Jouve, 2009; Foffa *et al.*, 2019; Johnson *et al.*, 2019).

Herein we provide an in-depth historical overview of the genus *Steneosaurus* and act as first reviser. We designate a type species for *Steneosaurus*, designate a lectotype for this type species and provide a detailed redescription of the type specimen MNHN.RJN 134c-d. We then compare MNHN.RJN 134c-d with corresponding teleosauroid taxa, declare it a *nomen dubium*, and thus consider the genus *Steneosaurus* to be invalid.

Historical background

The works of Georges Cuvier (1808, 1812 and 1824) and his 'tête à museau plus allongé et court' *fossils*

Georges Cuvier (1769–1832), a famed French zoologist and naturalist, initially described a longirostrine fossil 'crocodilian' snout from Honfleur (Cuvier, 1800), adding more detailed information about the specimen in 1808 and 1812. This specimen was part of a large assortment of fossils from the Honfleur area, originally assembled by Father Bachelet (in actuality Father Bacheley; the name Cuvier mentioned was a typographical error; Brignon, 2016). Bacheley's fossils were presented to the Museum d'Histoire Naturelle (MNHN) in Paris on the orders of Count Beugnot, an advisor of the State (Cuvier, 1812). Cuvier's 'crocodilian species' consisted of a partial rostrum and orbital region of the skull. Oddly, Cuvier (1812) wrote that the rostral piece (pl. II, figs 3–5), was part of the collection of M. Bexon, a renowned and respected mineralogist, and that the skull portion (pl. II, fig. 9) belonged to Father Bacheley. Why Cuvier (1808, 1812) believed that the snout and skull were from the same animal is unclear (Cuvier's original figures confirm it to be MNHN.RJN 134, with the snout eventually labelled MNHN.RJN 134c-d and skull MNHN.RJN 134a-b). Nevertheless, all fossils were collected from '*un banc de marne calcaire endurcie, d'un gris bleuâtre, qui devient presque noirâtre quand il est humide*' ('a bed of calcareous marl, a bluish grey which becomes almost black when [it is] wet') (Cuvier, 1808: 3) found along the Seine and present in many areas such as Caux, Touque, Dives and Vaches Noires in France. Cuvier (1808, 1812) briefly compared the rostrum and skull to that of the gavial, stating that they are similar in generic characters but differ in specific ones, most notably snout length and width, as well as frontal configuration.

In his 1824 book, *Recherches sur les ossemens fossils, Tome V*, Cuvier (1824) labelled the rostrum/skull specimen he had previously described as '*tête à museau plus allongé*' (head with a more elongated snout). It is slightly clearer in the text who collected certain fossils and how Cuvier eventually acquired them, and it is implied that this specimen was assembled together using many pieces. Three of these pieces [previously noted and figured in Cuvier (1808, 1812)] were amassed to form the partial skull of one 'species': two came from Father Besson (a priest who received the fossils from Father Bacheley) and one from Mr Faujas, which had been initially given to him by Besson (Cuvier, 1824); thus it is unclear why Cuvier (1812) initially mentioned M. Brexon as the possessor of two pieces. Six additional pieces from three different collections were also collected and assembled: two had remained with Father Bacheley, two had passed into the collection of M. de Drée and two arrived from Geneva sent by the late M. de Jurine (it was not stated which pieces were with which person). Cuvier's (1824: 149) reasoning for combining these pieces together was that '*j'ai vu que ce museau s'adaptoit si bien à ce crâne, qu'il ne me reste aucun doute qu'il n'y ait appartenu*' ('I saw that this snout fitted so well to this skull, that I have no doubt that it belonged to it') and that they had been '*dispersés par l'incurie et le peu de connoissances de leur premier possesseur*' ('dispersed by the carelessness and lack of knowledge of their first possessor').

Like in 1812, Cuvier (1824) described several characters of the original assembled specimen, referring to it as '*tête à museau plus allongé*', in which it differed from the modern gavial. However, his 1824 description was noticeably more in-depth than in 1812, noting several characteristics:

1. The fossil specimen is overall more oblong than that of the gavial.
2. In the fossil specimen, the supratemporal fenestrae are more elongate and oval, with a narrow sagittal crest, as opposed to the gavial. In addition, '*l'arcade*' ('the arch') (presumably meaning the anterior rim of the fenestrae) is not as straight as in the gavial.
3. The frontal, lachrymal and jugal are not concave and the orbits are not as indented, in contrast to the gavial.
4. The frontal is much larger in the fossil specimen.
5. The (posterior) nasals widen to accommodate the anterior tip of the frontal in the fossil specimen.
6. The palatines are much more 'bulging' in the fossil specimen than in the gavial.

Cuvier (1824: 151) also noted that an additional specimen resembling that of his '*tête à museau plus*

allongé' was found in the Darmstadt cabinets by Mr Bauder (when is not known) and illustrated by Mr Schleyermacher (Cuvier, 1824: pl. VI, figs 10–15). It is unknown if this specimen is still housed at the Darmstadt collections, or what its identification (specimen) number may be, but fig. 14 in Cuvier (1824) appears to illustrate the rostrum of the *Mystriosaurus laurillardi* Kaup, 1834, holotype HLMD V946-948 (see: Sachs *et al.*, 2019).

In his notes, Cuvier (1824) also described a new specimen and referred to it as '*tête à museau plus court*' (head with a more shortened snout) (pl. X, figs 5–7). This specimen, consisting of two snout fragments, had been housed at the Academy of Geneva, and was initially drawn by Cuvier in 1811 and subsequently published in a life-size lithograph by M. de La Bêche (Cuvier, 1824). Cuvier (1824: 153) described this specimen as being different from both the gavial and the '*tête à museau plus allongé*' fossil mainly due to its shorter and broader shape. In addition, he figured a second specimen from Honfleur (pl. VIII, figs 6, 7) that, based on its form, '*…est absolument la même que dans le museau de Genève, et je ne vois pas comment il s'adapteroit à ma première tête*' ('…is absolutely the same as in the muzzle of Geneva, and I do not see how it would adapt to my first [skull]') (his 'first skull' refers to the '*tête à museau plus allongé*' fossil). Despite describing and figuring both of these 'species' in relative detail, Cuvier (1812, 1824) did not assign them scientific names, continuing to refer to them as '*tête à museau plus allongé et court*' ('head[s] with an elongated snout and a shortened snout').

Geoffroy Saint-Hilaire (1825 and 1831) and the creation of the genus Steneosaurus

Étienne Geoffroy Saint-Hilaire (1772–1844), another well-known French naturalist, also contributed substantially to the study of fossil teleosauroids. Most notably, he erected the genus *Steneosaurus*, differentiating it from the then commonly used *Teleosaurus* and modern crocodile genera. He introduced and conceptualized *Steneosaurus* in a series of papers in the early-mid 1800s.

In 1825, he classified both of Cuvier's 1824 '*tête à museau plus allongé et court*' specimens. Geoffroy Saint-Hilaire (1825: 147) initially discussed the '*tête à museau plus allongé*' fossil (which he prematurely called the species *rostromajor*, before actually assigning a genus and species to the specimen), stating '*Toutefois, l'un des reptiles des carrières d'Honfleur,* rostro-major*, doit aux travaux ardens et persévérans de M. Cuvier une restitution presque entière. Il manque peu de chose à son crâne; mais comme ce sont les hérisséaux et toutes les parties sous-orbitaires et sous-temporales, je ne puis aujourd'hui comprendre utilement ce précieux morceau dans les précédentes comparaisons*' ('However, one of the reptiles of the quarries of Honfleur, *rostro-major* owes to the ardent and persevering M. Cuvier an almost complete restitution. It is missing [some of] its skull; but as these are the [bristles] and all the suborbital and subtemporal parts, I do not today usefully understand this precious piece in previous comparisons.') Importantly, in a small footnote, Geoffroy Saint-Hilaire (1825: 147) stated that *rostromajor* refers to one of the fossil Honfleur 'crocodilians' described by Cuvier in 1824, specifically the one with '*longues mâchoires*' (longer jaws) (referring to the '*tête à museau plus allongé*' specimen). Geoffroy Saint-Hilaire believed that, after a thorough comparison of *S. rostromajor* with other crocodylian taxa had been completed, *S. rostromajor* would not belong to the genus *Teleosaurus* or modern *Crocodylus* (1825: 147) and lists certain aspects that he alleged differentiated the Honfleur specimen from both *Gavialis* and *Teleosaurus*:

1. Disproportionate eyes that are laterally placed.
2. '*L'arc, dont le jugal fait partie, est singulièrement descendu et rentrant*' ('The arch, [of which] the jugal part, is singularly descended and returning'; presumably referring to the slight concavity of the dorsal rim of the jugal) (Geoffroy Saint-Hilaire, 1825: 148).
3. Thinning of the temporal regions.
4. Higher occipital 'wings'.

Geoffroy Saint-Hilaire (1825) also recognized that the elongate snout did not necessarily mean that one extant or extinct animal was related to another, but rather that this was a plastic condition that had developed multiple times throughout the animal kingdom. He therefore omitted rostral characters in his comparisons of *S. rostromajor* with *Teleosaurus* and *Crocodylus*.

Based on the above characteristics, most notably those in the temporal region, Geoffroy Saint-Hilaire (1825) put forth the names *Steneosaurus rostro-major* (Cuvier's '*tête à museau plus allongé*' specimen) and *Steneosaurus rostro-minor* (Cuvier's '*tête à museau plus court*' specimen), with the genus *Steneosaurus* specifically referring to the 'gavials de Honfleur'. *Steneosaurus rostro-major* was the first species named, and in the greatest detail, while *Steneosaurus rostro-minor* was an accompanying species (Geoffroy Saint-Hilaire 1825: 149). Geoffroy Saint-Hilaire implored '*Cependant les naturalistes voudroient-ils accueillir dès ce moment les dénominations suivantes?*' ('However, would naturalists like to welcome the following names?') (Geoffroy Saint-Hilaire, 1825: 149). According to Article 67.2.1 and Article 67.2.2, of the ICZN Code, 'In the meaning of the Code the "originally included nominal species" comprise only those included in the newly established nominal genus or subgenus,

having been cited in the original publication by an available name' and 'If a nominal genus or subgenus was established before 1931, the nominal species that were first subsequently and expressly included in it are deemed to be the only originally included nominal species'. Therefore, either *S. rostromajor* or *S. rostrominor* must be designated as the type species. While Geoffroy Saint-Hilaire (1825: 149) considered *S. rostromajor* to be the '*première espèce*' ('first species'), he did not designate a type species, as this was not customary at the time. It is possible that this is also why there were varying interpretations of what *Steneosaurus* should be applied to during the 19th century.

In 1831, Geoffroy Saint-Hilaire declared that an in-depth, comprehensive analysis between *Teleosaurus* and his new genus *Steneosaurus* was needed to make the distinction between both genera '*parfaitement senti*' ('perfectly felt'). Geoffroy Saint-Hilaire (1831: 5) also wrote '*Réservant cette discussion pour la fin de mes recherches, je vais m'occuper aujourd'hui d'établir ce que sont véritablement les* teleosaurus *et les* steneosaurus*, c'est-à-dire leur assigner l'existence zoologique qui leur appartient*' ('Reserving this discussion for the end of my research, I am going [to be busy today] to establish what *Teleosaurus* and *Steneosaurus* really are, that is to say, to assign to them the zoological existence that belongs to them'). Geoffroy Saint-Hilaire (1831) then proceeded to define what is today interpreted as 'Teleosauridae' (although he did not assign a name to this group). Crucial features include: large 'vertical holes' (supratemporal fenestrae); vertically placed eyes; the parietal bone not intervening between the jugal and temporal; two arches ['*l'une supérieure jugo-temporale, l'autre inférieure maxillo-tympanique*' ('one superior jugotemporal, the other lower maxillofacial')]; the development of the nasal (craniorespiratory) canal and temporal region; and a 'beak-like' snout. At the end of this description, he wrote '*Cette dernière combinaison remarquable dans les êtres téléosauriens devient des éléments caractéristiques pour une nouvelle famille; des éléments d'une puissance et d'une valeur à rendre en effet obligatoires les distinctions zoologiques de cette famille, c'est-à-dire l'érection des genres téléosaurus et sténéosaurus*' ('This last remarkable combination in teleosaurs becomes characteristic elements for a new family; elements of power and value to make compulsory the zoological distinctions of this family, that is to say the erection of the genera *Teleosaurus* and *Steneosaurus*') and '*L'indépendance de ces deux combinaisons anormales existe de fait: elle nous est révélée par l'organisation des sauriens fossiles du calcaire de Caen*' ('The independence of these two abnormal combinations exist in fact: it is revealed to us by the organization of fossil lizards [in] limestone [at] Caen') (Geoffroy Saint-Hilaire, 1831: 37–38). As mentioned previously, it is unclear at what taxonomic level Geoffroy Saint-Hilaire was referring to; just before writing this description, he refers to '*un cachet crocodilien*' ('a crocodilian character'), suggesting that he is describing the main features of teleosauroids (although this is never explicitly stated, but perhaps his declaration to establish what *Teleosaurus* and *Steneosaurus* really were pertained to both of them as a group, not individually). As with his 1825 work, Geoffroy Saint-Hilaire (1831: 37) considered '*la région supérieure et vers la fin de l'arrière-crâne; et d'autre part le museau*' ('the upper region and towards the end of the back of the skull; and [on the other hand] the snout') to be the most important features when distinguishing teleosauroid fossil species, along with '*le canal nasal et le palais*' ('the nasal canal and the palate').

When defending the creation of the genus *Steneosaurus*, Geoffroy Saint-Hilaire (1831: 40) stated that '*…ce genre est exactement intermédiaire entre nos téléosaurus et le démembrement du grand genre Crocodile…*' ('…this genus is exactly intermediary between *Teleosaurus* and the [dismemberment] of the big genus Crocodile…'). Geoffroy Saint-Hilaire (1831: 41) also briefly noted his reason for the creation of the genus, in that '*Le nouveau genre sténéosaurus est en outre justifié par l'existence de plusieurs espèces: à Caen, j'en connais deux bien distinctes; à Honfleur, une troisième. Le crocodile fossile du cabinet de Genève est encore une autre espèce se rapportant aussi au genre sténéosaurus*' ('The new genus *Steneosaurus* is further justified by the existence of several species: in Caen, I know two well distinct; in Honfleur, a third. The fossil crocodile of the Geneva cabinet is yet another species pertaining [also] to the genus *Steneosaurus*'). One major feature Geoffroy Saint-Hilaire (1831: 52) described as differentiating *Steneosaurus* and *Teleosaurus* was '*l'extrême différence de leur museau*' ('extreme difference of their muzzle') in that '*…les sténéosaures répètent assez bien l'arrangement que montrent à cet égard les gavials. Les narines y sont ouvertes supérieurement, et les intermaxillaires qui se développent autour, chacun en demi-cercle, leur fournissent un bord évasé, mais sans relief sensible. Les narines des téléosaures sont au contraire tout à fait antérieures et terminals…*' ('…the stenosaurs repeat quite well the arrangement that shows in [this respect] the gavials. The nostrils are open superiorly, and the intermaxillaries which develop around each, in a semicircle, give them a flared edge, but without any appreciable relief. The nostrils of the telosaurs are on the contrary quite anterior and terminal…'). Another feature used to distinguish between the two genera was dentition: the teeth of *Teleosaurus* were

'*grêles et déjetées latéralement*' ('thin and laterally spindly'), whereas in *Steneosaurus* '*les dents diffèrent peu de celles des gavials*' ('the teeth differ little from [those of] gavials') (Geoffroy Saint-Hilaire, 1831: 52).

Realities of Cuvier and Geoffroy Saint-Hilaire's specimens

As mentioned previously, in Cuvier (1808, 1812, 1824) the original '*tête à museau plus allongé*' specimen (labelled *S. rostromajor* by Geoffroy Saint-Hilaire in 1825) was composed of three main parts: a two-part rostrum (MNHN.RJN 134c-d) and an orbital region (MNHN.RJN 134a). However, while both Cuvier (1808, 1812, 1824) and Geoffroy Saint-Hilaire (1825, 1831) thought all pieces originated from the same animal, in reality they did not; the rostral material (MNHN.RJN 134c-d) comes from a teleosauroid, whereas the orbital section (MNHN.RJN 134a-b) represents the metriorhynchid *Metriorhynchus superciliosus* de Blainville, 1853 (Steel, 1973). The prefrontal of MNHN.RJN 134a-b has the characteristic enlarged, 'teardrop' shape of all metriorhynchids (e.g. Andrews, 1913; Herrera *et al.*, 2013), which is an immediate diagnostic feature; in contrast, MNHN.RJN 134c-d displays the distinctive, posteriorly curving teleosauroid premaxilla–maxilla suture (both dorsal and ventral) and an overall elongated snout (particularly the maxilla bones), deeper maxillary reception pits and lack of a deep midline trench (= groove). Therefore, Cuvier's '*tête à museau plus allongé*' specimen is a chimera. In contrast, Cuvier's '*tête à museau plus court*' specimen (classified with the Geneva specimen as *S. rostrominor*, MNHN 8902, by Geoffroy Saint-Hilaire in 1825), is a complete mandible that belongs to a metriorhynchid, not a teleosauroid.

Post-Geoffroy Saint-Hilaire: von Meyer and colleagues (1830s and 1840s), J. A. and E. Eudes-Deslongchamps (1860s) and recent interpretations of 'Steneosaurus'

While Holl (1829) followed on from the work of Geoffroy Saint-Hilaire (1825), instead of using Geoffroy Saint-Hilaire's species epithets *rostro-major* and *rostro-minor*, Holl (1829: 88) altered them to *longirostris* and *brevirostris*. Although, the nominal authority next to both species was 'Geoffr.', Holl (1829) also provided short diagnoses for both species, stated from where the species were known and provided an indication to which of Cuvier's (1824) plates the species were figured on. *Steneosaurus longirostris* was stated to be from Honfleur, and on plate 8 of Cuvier (1824), but no figures were specifically referred to. Although plate 8 is referred to rather than plate 10 [Geoffroy Saint-Hilaire (1825) referred to Cuvier's pl. 10 for *S. rostro-major*], *S. longirostris* is an objective junior synonym of *S. rostro-major*. This is because Holl (1829) gave the nominal authority of his species to Geoffroy Saint-Hilaire, and the description was clearly meant to be the same taxon (even if he did not refer to the same plate as Geoffroy Saint-Hilaire had).

Gray (1831) used a different taxonomy than both Geoffroy Saint-Hilaire (1825) and Holl (1829). Instead, Gray (1831: 57) established two species in the genus *Gavialis*. Cuvier's '*tête à museau plus allongé*' and Geoffroy Saint-Hilaire's *Steneosaurus rostro-major* were referred to the new taxon *Gavialis Bacheleti* [sic]. No description was provided, but an indication to Cuvier's (1824) plates was (= pl. 6, figs 10, 15; pl. 8, figs 8, 9, 13; pl. 9, figs 3, 12; pl. 10, figs 1, 4, 8, 10). As the species was established for Cuvier's '*tête à museau plus allongé*', and does have an indication that includes the figures for that chimeric skull (pl. 10, figs 1–4), we consider *Gavialis bacheleti* Gray, 1831 to be an objective junior synonym of *Steneosaurus rostro-major*.

In 1832, von Meyer (1832) separated both of Cuvier's specimens on a generic level, assigning the name *Metriorhynchus geoffroyii* von Meyer, 1832 to *Steneosaurus rostrominor* and *Streptospondylus altdorfensis* von Meyer, 1832 to *Steneosaurus rostromajor*. Von Meyer (1832) included additional vertebrae previously documented and described by Cuvier (1808, 1812) that were not associated with his '*tête à museau plus allongé*' specimen and that had been ignored by Geoffroy Saint-Hilaire (1825) when establishing '*S.*' *rostromajor* (Allain, 2001). The generic name *Streptospondylus* refers to the unusual structure of the vertebrae (von Meyer, 1832: 227), but these vertebrae are from a theropod dinosaur and not a crocodylomorph (Allain, 2001). According to Article 67.2.1 of the ICZN, 'A nominal species is only eligible to be fixed as the type species of a nominal genus or subgenus if it is an originally included nominal species (Art.67.2)'. Therefore, the generic name *Streptospondylus* does not have any reference to '*S.*' *rostromajor*, as the vertebrae on which this name was based were originally not included with the type *S. rostromajor* skull material.

Bronn (1835–37) initially established the genus *Leptocranius* for Cuvier's '*tête à museau plus allongé*' (*S. rostromajor*) specimen, and referenced Cuvier's 1824 figure of the specimen (therefore, the genus *Leptocranius* is an objective junior synonym of *Steneosaurus*). Bronn (1835–37) diagnosed *Leptocranius* based on the following characteristics:

1. A narrow, elongated skull that is higher than it is wide.
2. Approximately 36 to 40 conical teeth with well-separated alveoli.
3. Large, forward-directed orbits.
4. Broad temporal (frontal) pits.

Because Bronn (1835–37) included features of the orbits and posterior skull in his description, it is likely that he considered all of the associated fossil material (both MNHN.RJN a-b metriorhynchid and MNHN. RJN 134c-d teleosauroid) assembled by Cuvier to be from a single animal. Fitzinger (1843) included *Leptocranius* in his teleosauroid classification and Geinitz (1846) briefly described the *Leptocranius*-type specimen, affirming that it was indeed originally Geoffroy Saint-Hilaire's (1825) *S. rostromajor*. Giebel (1847), also confirming that Bronn's new genus was based on Cuvier's first '*gavial de Honfleur*', stated that Bronn (1835–37) separated *Leptocranius* from Geoffrey Saint-Hilaire's *Steneosaurus* and von Meyer's *Streptospondylus* '*…weil beide die converconcaven Wirbelkörper des Metriorhynchus ihren Gattungen zugeeignet und dieſem biconcave Wirbel zugeſchrieben haben*' ('…as both have assigned their [hourglass] vertebrae of *Metriorhynchus* to their genera and to this biconcave vertebrae'), and wrote a brief description of *Leptocranius* that is nearly identical to that found in Bronn (1835–37) and Geinitz (1846). After Giebel's (1847) work, the genus *Leptocranius* is scarcely mentioned in the literature and it seems to have become considered a synonym of *Steneosaurus*.

Despite Geoffroy Saint-Hilaire's (1825, 1831) brief classification of both the genus *Steneosaurus* and the two *Steneosaurus* species, French father-and-son palaeontologists, Jacques Amand and Eugène Eudes-Deslongchamps, neglected the existence of both *S. rostromajor* and *S. rostrominor*, believing them to be invalid names. They were not alone in their opinion: the younger Eudes-Deslongchamps (1867–69: 109) mentioned that, in a letter to his father, de Blainville referred to *S. rostromajor* as a '*monstre anatomique*' ('anatomical monster'). The younger Eudes-Deslongchamps (1867–69: 242) cited the poor preservation of *S. rostromajor* (MNHN.RJN 134c-d) as one of the major reason why it was an insupportable taxon, describing the '*diverses brisures ou plutôt fendillements*' ('various breaks or [rather] cracks') that adorned the specimen '*profondément altéré les caractères*' ('profoundly altered the characters'). The Eudes-Deslongchamps briefly referred to *Leptocranius*, stating that Bronn (1835–37) '*le changea contre celui de* Leptocranius *et conserva celui de* Metriorhynchus' ('changed it [presumably the *S. rostromajor* type specimen] to that of *Leptocranius* and conserved [that] of *Metriorhynchus*; Eudes-Deslongchamps, 1867–69: 116). However, they did not acknowledge nor describe it as a valid genus. Indeed, they appeared to criticize its existence, and scolded previous researchers for allowing problems associated with *S. rostromajor* to manifest, by not viewing the type specimen themselves: '*…leurs jugements sont-ils presque tous entachés d'erreurs et souvent d'erreurs grossières*' ('… their judgments are almost all tainted with errors and often with gross errors') and '*…qui avaient prétendu juger Cuvier et Geoffroy Saint-Hilaire et s'étaient eux-mêmes trompés de la manière la plus manifeste*' ('… who had pretended to judge Cuvier and Geoffroy Saint-Hilaire and who were themselves most clearly mistaken') (Eudes-Deslongchamps, 1867–69: 107).

Due to this, both Eudes-Deslongchampses stated that the taxon to represent the genus *Steneosaurus* should be either '*Steneosaurus*' *megistorhynchus* Eudes-Deslongchamps, 1866, or '*Steneosaurus*' *edwardsi* Eudes-Deslongchamps, 1868c. Eugène Eudes-Deslongchamps (1867–69: 220) described the situation as follows: '*E. Geoffroy-Saint-Hilaire donna le nom de Sténéosaurus aux longs maxillaires à l'espèce qui nous occupe; mais il avait également en vue une autre espèce qu'il croyait être la même que celle-ci, c'est-à-dire le Gavial à museau allongé d'Honfleur que nous décrivons plus loin sous le nom de* Steneosaurus Edwardsi*; toutefois, comme E. Geoffroy-Saint Hilaire applique surtout ce terme de Sténéosaure au crocodile aux longs maxillaires de Quilly, nous conservons le nom de Sténéosaure aux longs maxillaires celui que nous décrivons en ce montent. Plusieurs auteurs ont diversement traduit ce nom de Sténéosaure aux longs maxillaires: les uns ont mis rostro-major, d'autres longirostris. Le nom de* megistorhynchus *a sur ces divers noms l'avantage d'exprimer parfaitement le caractère de longueur démesurée du museau, et en second lieu d'avoir été choisi par E. Geoffroy-Saint Hilaire lui-même, puisqu'il désigne ainsi cette espèce dans la longue correspondance qu'il a eue avec mon père au sujet des Téléosauriens; c'est également sous ce nom que mon père le signale dans ses lettres à M. de Blainville sur les crocodiles vivants et fossiles. Pour ces diverses raisons, nous croyons qu'il est convenable de préférer le nom de* megistorhynchus' ('Geoffroy-Saint-Hilaire gave the name *Steneosaurus* to long maxillae of the species that occupies us; but he also had in view another species that he believed to be the same as this one, that is to say, the Gharial with the extended muzzle of Honfleur which we describe below under the name of *Steneosaurus Edwardsi*; However, as E. Geoffroy-Saint Hilaire applies the term "*Steneosaurus*" to the crocodile in the long maxillae of Quilly, we retain the name "*Steneosaurus*" with the long maxillary teeth that we describe. Several authors have variously translated the name of *Steneosaurus* to the long maxillaries: some have put *rostro-major*, others *longirostris*. The name of *megistorhynchus* has on these various names the advantage of perfectly expressing the character of excessive length of the muzzle, and secondly of having been chosen by E. Geoffroy-Saint Hilaire himself, since he thus designates this species in the long correspondence he had with my father concerning the Teleosaurians; it is also under this

name that my father indicates it in his letters to M. de Blainville on living and fossil crocodiles. For these reasons, we believe that it is convenient to prefer the name of *megistorhynchus*').

However, other than the fact that '*S.*' *megistorhynchus* possessed a long rostrum and was a name chosen by Geoffroy Saint-Hilaire when corresponding with J. A. Eudes-Deslongchamps, E. Eudes-Deslongchamps (1867–69) did not give any anatomical reason as to why he and his father decided that '*S.*' *megistorhynchus* is representative of this genus. In a footnote, Eudes-Deslongchamps (1867–69: 112) stated that '*Quelques auteurs s'étant imaginé, je ne sais pourquoi, que Geoffroy Saint-Hilaire avait en vue le crocodile à museau court d'Honfleur quand il créa le genre* Steneosaurus*, ont donné ce nom aux espèces que je désignerai sous le nom de* Metriorhynchus *d'après Hermann de Meyer. Il y a. à la vérité, assez d'obscurité dans le passage de Geoffroy Saint-Hilaire à ce sujet; mais c'est surtout au grand crocodile de Quilly, à son* Steneosaure aux longs maxillaires *ou* Megistorhynchus*, que s'applique le nom de* Steneosaurus*, comme la correspondance avec mon père en fait foi*' ('Some authors having imagined, I do not know why, that Geoffroy Saint-Hilaire had in mind the short-nosed crocodile of Honfleur when he created the genus *Steneosaurus*, giving this name to the species that I will describe under the name of *Metriorhynchus* after Hermann de Meyer. There is, in truth, enough obscurity in the wise step of Geoffroy Saint-Hilaire on this subject; but it is especially to the large crocodile of Quilly, to its *Steneosaurus with long maxillae* or *Megistorhynchus*, that the name of *Steneosaurus* applies, as the correspondence with my father proves'). However, it is not explicitly stated if the two Eudes-Deslongchampses considered *S. rostromajor* to be the same as '*S.*' *megistorhynchus* or if they rejected *S. rostromajor* altogether.

Jacques Amand Eudes-Deslongchamps (1896: 33) stated that Lamouroux acquired a specimen of '*Steneosaurus quillensis*' (*Teleosaurus cadomensis* Lamouroux, 1820) in 1822, sent some drawings to Cuvier in 1824 (see Brignon, 2013) and determined that Cuvier '*crut que ce second crocodilien était de la même espèce que celui dont il possédait une moitié de crâne et qu'il ne différait du premier que par un âge plus avancé, mais c'était tort*' ('[Cuvier] believed that this second crocodylian was of the same species as the one in which he had half a skull and that he differed from the first only by a more advanced age, but was wrong'), and stated that the specimen belonged to '*S.*' *megistorhynchus*. However, the whereabouts of the specimen from Quilly are unknown (either destroyed or missing) and there is no way to validate this declaration. Interestingly, when both Eudes-Deslongchamps (1866, 1867–69) described '*S.*' *megistorhynchus*, they focused on specimens from '*Fuller's Earth*' and the Caen Limestone (both Bathonian in age) in France; this is a drastically different age than that proposed for *S. rostromajor*, as discussed below.

Curiously, E. Eudes-Deslongchamps (1867–69: 242) then noted in his description of '*Steneosaurus*' *edwardsi* Eudes-Deslongchamps, 1868a, that it was '*une espèce qui était évidemment identique avec celle dont Cuvier avait connu le museau seulement et qu'il avait désigné sous le nom de gavial à museau allongé d'Honfleur*' ('a species which was obviously identical with that of which Cuvier had known the muzzle only and which he designated as the gavial from Honfleur with the elongated muzzle'). The younger Eudes-Deslongchamps then allegedly showed his father the illustrations he had made of the specimen, prompting J. A. Eudes-Deslongchamps to name the specimen '*S.*' *edwardsi* in honour of a famous scholar (possibly M. Milne-Edwards, but this is never explicitly stated), whose friendship he treasured (Eudes-Deslongchamps, 1867–69: 242–243). It is, therefore, uncertain which of these two taxa E. Eudes-Deslongchamps originally considered *S. rostromajor* to belong under, or if he considered either as a viable option; he refers to '*S.*' *edwardsi* as being the most viable candidate, as indicated in a short footnote (Eudes-Deslongchamps, 1867–69: 110), but then writes 'Steneosaurus *aux longs maxillaires ou* Megistorhynchus*, que s'applique le nom de* Steneosaurus' ('*Steneosaurus* with long maxillaries, or *Megistorhynchus*, that the name of *Steneosaurus* is applied') (Eudes-Deslongchamps, 1867–69: 112).

Following the work of both Eudes-Deslongchamps, the MNHN specimen of *S. rostromajor* was seldom mentioned and never figured in the literature. Geoffroy Saint-Hilaire's (1825) *S. rostrominor*, despite being classified as *Metriorhynchus* by von Meyer (1832), continued to serve as the generic basis for many metriorhynchid specimens, including *Steneosaurus gracilis* (= *Cricosaurus gracilis* Phillips, 1871), *Steneosaurus palpebrosus* (= '*Metriorhynchus*' *palpebrosus* Phillips, 1871), *Steneosaurus dasyceps* (= subjective junior synonym of *Metriorhynchus superciliosus* de Blainville, 1853), *Stenosaurus* [sic] *elegans* (= *Cricosaurus elegans* Wagner, 1852) and *Steneosaurus manselii* (= *Plesiosuchus manselii* Hulke, 1870).

Richard Owen (1841) continued to use the genus *Steneosaurus* in reference to metriorhynchids, and was heavily criticized for this (e.g. Woodward, 1885: 501). Allain (2001) mentioned both of Cuvier's 'gavials' in his redescription of *Streptospondylus altdorfensis* (a theropod dinosaur), and verified that Geoffroy Saint-Hilaire (1825) united the two specimens under the genus *Steneosaurus* and that both names did not apply to additional vertebrae that were previously described by Cuvier (1812) and disregarded by Geoffroy Saint-Hilaire (1825). Brignon (2016) briefly mentioned

Cuvier's '*gavials de Honfleur*' when describing Father Bacheley's contributions to French palaeontology, confirming that Cuvier's '*tête à museau plus allongé*' specimen did indeed belong to the French priest's collection (but it is uncertain when this specimen received its official museum label, MNHN.RJN 134c-d).

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 (e.g. Morel de Glasville, 1876; Hulke, 1871, 1877; Newton, 1893; Andrews, 1909, 1913; Phizackerley, 1951). Almost all teleosauroid species have at one point in their taxonomic history been included in the genus *Steneosaurus* (excluding those within the genus *Machimosaurus*, which had been well established since von Meyer's 1837 and 1838 work). In addition, multiple recent phylogenetic studies on, or including, teleosauroids (e.g. Wilberg, 2015a; Foffa *et al.*, 2019; Johnson, 2019; Johnson *et al.*, 2019; Martin *et al.*, 2019; Sachs *et al.*, 2019) have recovered various *Steneosaurus* species as either polyphyletic or paraphyletic, further adding to its taxonomic instability.

Geology

The exact age of *S. rostromajor* (MNHN.RJN 134c-d) is a subject of debate, as it is either Callovian or Oxfordian. It is confidently agreed upon, first noted by Bacheley (1778a, b) and then by Cuvier (1808, 1812), that the fossil originated from Vaches Noires (Calvados, France). The Vaches Noires cliffs stretch approximately 5 km along the coast of France and are situated between the towns of Villers-sur-Mer (east) and Houlgate (west) (Buffetaut & Tabouelle, 2019). This site has yielded numerous vertebrate remains, including dinosaurs (von Meyer, 1832; Eudes-Deslongchamps, 1849; Bigot, 1898; von Huene, 1926b; Knoll *et al.*, 1999), crocodylomorphs (Cuvier, 1824; Eudes-Deslongchamps, 1867–69; Wenz, 1970; Lepage *et al.*, 2008; Brignon, 2016), marine reptiles (Bigot 1938; Blain *et al.*, 2003; Bardet 2014) and fishes (Liston, 2008; Dutel *et al.*, 2014; Liston & Gendry, 2015; Brignon, 2016). There are two main formations exposed within the Vaches Noires cliffs: the Marnes de Dives (MD) Formation (Upper Callovian) and the Marnes de Villiers (MV) Formation (Lower Oxfordian) (Buffetaut, 1983; Brignon, 2016). Both formations consist of bioclastic mudstones (namely marl) and limestone; the MD Formation is approximately 8 to 10 m thick with lumachelle patches, and the MV Formation is roughly 25 m thick and interbedded with calcareous nodules (Dugé *et al.*, 1998; Lebrun & Courville, 2013; Brignon, 2016). Both Bacheley (1778a, b) and Cuvier (1808, 1812) have suggested that MNHN.RJN 134c-d comes from the MV Formation. If this is correct, then this fossil would be Lower Oxfordian in age, which in itself is significant, as there are few teleosauroid fossils from this time period.

Abbreviations

Institutional: CAMSM, Sedgewick Museum, Cambridge, UK; LPP (PALEVOPRIM-CVCU), Institut de paléoprimatologie, paléontologie, humaine; évolution et paléoenvironnements Université de Poitiers, Poitiers, France; MNHN, Muséum national d'histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, UK; NOTNH, Nottingham Natural History Museum, Nottingham, United Kingdom; OUMNH, Oxford University Museum of Natural History, Oxford, UK; PRC, Palaeontological Research and Education Centre, Maha Sarakham University, Thailand.

Anatomical: M10, maxillary alveolus 10; mx, maxilla;?pal, possible palatine; pmx, premaxilla.

RESULTS

SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA Hay, 1930 (*sensu* Nesbitt, 2011)

THALATTOSUCHIA Fraas, 1901 (*sensu* Young & Andrade, 2009)

TELEOSAUROIDEA Geoffroy Saint-Hilaire, 1831 (*sensu* Young & Andrade, 2009)

STENEOSAURUS Geoffroy Saint-Hilaire, 1825

Steneosaurus rostromajor Geoffroy Saint-Hilaire, 1825 (type species, designated here)

(Fig. 1)

Etymology: Named *rostro-major* (from Latin *major*, elongated, and *rostrum*, snout) by Geoffroy Saint-Hilaire (1825), to emphasize the elongation of the maxillae. According to the ICZN Code, Article 32.5.2.3: 'In a compound species-group name published as words united by an apostrophe or a hyphen, the words are to be united by removing the mark concerned.' Therefore, *S. rostro-major* is recognized as *S. rostromajor*.

v 1800	'Crocodilian' snout; Cuvier, p. 159
v 1808	'Crocodilian' snout; Cuvier, pp. 20–21, pl.II, figs 3, 4
v 1812	'Crocodilian' snout; Cuvier, pp. 20–21, pl. II, figs 3, 4

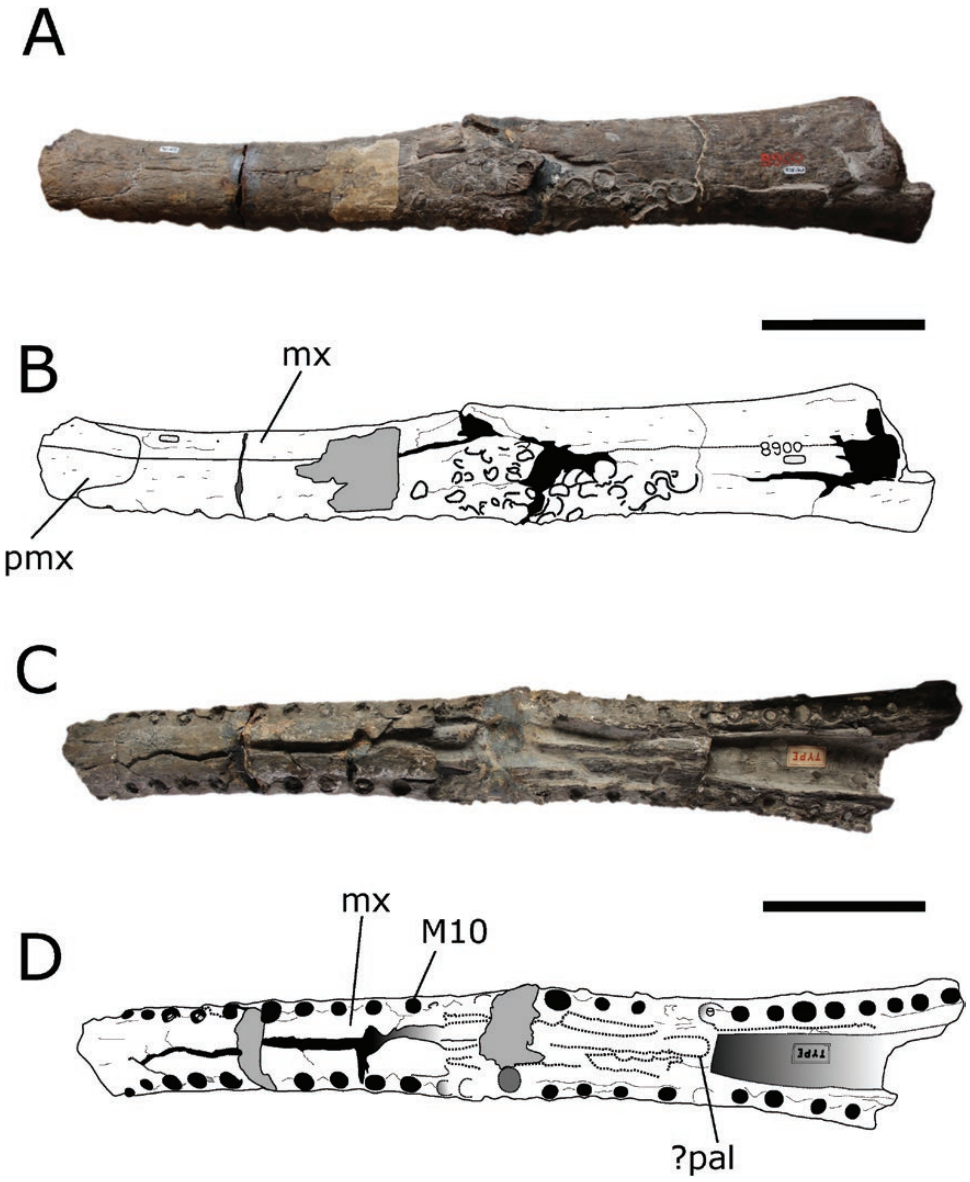

Figure 1. Photographs (A, C) and line drawings (B, D) of *Steneosaurus rostromajor*, MNHN.RJN 134c-d, type specimen. Refer to the main text for the abbreviations list. Scale bars: 10 cm.

v 1824	'*Tête à museau plus allongé*'; Cuvier, p. 148, pl. VII, figs 3, 4; pl. X, fig. 1
v 1825	*Steneosaurus rostromajor* **nov. sp.**; Geoffroy Saint-Hilaire, pp. 146–147
v 1829	*Steneosaurus longirostris*; Holl, p. 88
v 1831	*Gavialis bacheleti*; Gray, p. 57
v 1831	*Steneosaurus rostromajor*; Geoffroy Saint-Hilaire, p. 40
v 1832	*Streptospondylus altdorfensis*; von Meyer, p. 227
v 1835–37	*Leptocranius* **nov. gen.**; Bronn, p. 516
v 1841	*Steneosaurus rostromajor*; Owen, p. 88
v 1846	*Leptocranius*; Geinitz, p. 87
v 1847	*Leptocranius*; Giebel, p. 113–114

Designation of type species: Jacques Amand and Eugène Eudes-Deslongchamps (1867–69) attempted to rectify the taxonomic issues associated with *S. rostromajor* (MNHN.RJN 134c-d) and selected a new type species for *Steneosaurus* (either '*S.*' *megistorhynchus* or '*S.*' *edwardsi*, see above). However, the ICZN did not exist during that time and, unfortunately, their selection does not conform to the current articles of the Code. Herein we formally designate *S. rostromajor* as the type species of *Steneosaurus*. In order to be in full

accordance of Article 67 of the ICZN Code, in particular Article 67.2, we make the following statements:

1. This designation is made with the express purpose of clarifying the taxonomic status of *S. rostromajor*.
2. MNHN.RJN 134c-d is an originally included nominal specimen and, therefore, is eligible to be fixed as the type. In addition, the name *Steneosaurus rostromajor* was established for MNHN.RJN 134c-d before 1931 and, therefore, is deemed to be the only originally included nominal species.
3. The type species can be recognized through both the description below and Figure 1, as well as in the works of Cuvier (1808, pl. II, figs 3, 4; 1812, pl. II, figs 3, 4; 1824, pl. VII, figs 3, 4; pl. X, fig. 1) and Geoffroy Saint-Hilaire (1825, 1831).
4. Cuvier's '*tête à museau plus allongé*' specimen (1808, 1812, 1824) was attributed to the name *Steneosaurus rostro-major* by Geoffroy Saint-Hilaire in 1825 as the '*première espèce*' ('first species) of *Steneosaurus* (i.e. position precedence).
5. The type species is the property of a recognized scientific institution, MNHN, which maintains a research collection with proper facilities for preserving name-bearing types and is accessible for study.

Designation of type specimen: Given that the type specimen of *Steneosaurus rostromajor* is a chimera of teleosauroid and metriorhynchid material (see above), we herein rectify this issue. Following Article 74.7 of the ICZN Code we hereby designate MNHN.RJN 13c-d as the lectotype of *S. rostromajor*. This ensures that the teleosauroid component of the original specimen is now formally the type specimen of *S. rostromajor*, and ensures taxonomic stability.

Lectotype: MNHN.RJN 134c-d, a partial rostrum covered in ironstone sediment and oysters, and severely broken and dorsally displaced in the middle.

Lectotype age: Callovian or Oxfordian, Middle or Late Jurassic (Lower Oxfordian if from Marnes de Villiers Formation).

Lectotype locality and stratigraphic horizon: Vaches Noires, Calvados, France. Suggested to be from the Marnes de Villiers Formation.

Description: The type specimen of *Steneosaurus*, *Steneosaurus rostromajor* (MNHN.RJN 134c-d), is represented by a partial rostrum that is preserved up until the 27th maxillary alveolar pair. The majority of the premaxillae are missing, so none of the premaxillary alveoli are preserved. At approximately the 12th maxillary alveolus, the remaining posterior portion of the specimen has been distorted and dorsally displaced (Fig. 1A, B). In dorsal view, there is a large posteriorly directed crack in this area, which is also covered with an array of fossilized oysters. In ventral view (Fig. 1C, D), there is a massive, anteroposteriorly directed crack running through the midline of the rostrum. At approximately the 19th alveolus, a missing section of the palatal surface continues to the end of the specimen.

Premaxillae: As mentioned previously, the majority of the premaxillae are not preserved, so neither the external nares nor any of the premaxillary alveoli can be described. However, the posterior-most portion of the paired premaxillae is robust and horizontally straight in lateral view; these bones would have surrounded the external nares, as in other teleosauroids (e.g. *Indosinosuchus potamosiamensis* Martin *et al.*, 2019, PRC-11; '*Steneosaurus*' *leedsi* Andrews, 1909, NHMUK PV R 3806 and '*Steneosaurus*' *edwardsi* NHMUK PV R 2865). In dorsal view, the premaxilla–maxilla suture is subcircular in shape and moderately interdigitating, most notably at the midline (Fig. 1A, B); in lateral view, it is slightly anteroposteriorly curved; and in ventral view, the posterior area is vertically directed, similar to that found in other teleosauroids (e.g. '*S.*' *leedsi* NHMUK PV R 3806; '*S.*' *edwardsi* NHMUK PV R 2865 and NHMUK PV R 3701). The premaxillae are ornamented with numerous, irregular grooves with varying degrees of depth.

Maxillae: The paired maxillae (Fig. 1) are elongate, anteriorly separate from the premaxillae, transversely narrow and make up the majority of the rostrum. The dorsal surface of the maxillae are ornamented with conspicuous, weakly-to-deeply excavated grooves. In lateral view, one line of small, sparsely spaced neurovascular foramina is present dorsally parallel to the maxillary tooth row. The reception pits are relatively deep in the anterior maxilla, but gradually become much shallower nearer to the posterior part of the rostrum. The anterior maxillae are unornamented in ventral view, and it is near impossible to observe any palatal features posterior to the 11th maxillary alveolus due to poor preservation. There are at least 27 maxillary alveoli per side, which are subcircular, large and well spaced. There is an extensive interalveolar region between each adjacent alveoli, with each being between 9 and 11 mm throughout the entirety of the maxilla (excluding the first two alveoli). Two anterior alveoli (Fig. 1C, D) have partially preserved teeth in the sockets.

Dentition: Only two partial teeth are preserved *in situ* in MNHN.RJN 134c-d (at the third and fourth

left maxillary alveoli), both of which consist of the area near the base (they are both missing the apex and half of the tooth body). The teeth are slightly laterally compressed with numerous, well-developed and pronounced enamel ridges (see Fig. 5A).

DISCUSSION

Comparisons with other teleosauroids

There has been much discussion about whether *Steneosaurus rostromajor* (MNHN.RJN 134c-d) should be classified as a distinct species or if it is referable to another teleosauroid taxon. One of E. Eudes-Deslongchamps' (1867–69) initial suggestions was that *S. rostromajor* was similar to '*Steneosaurus*' *megistorhynchus*. However, the material with which both J. A and E. Eudes-Deslongchamps made this comparison has been lost; as there is no current available rostral material for '*S.*' *megistorhynchus*, it is difficult to assess this statement with confidence. However, '*S.*' *megistorhynchus* is Bathonian in age, whereas *S. rostromajor* (MNHN.RJN 134c-d) is suggested to be Lower Oxfordian, as mentioned previously. Owing to this temporal gap of roughly 10 million years, it is highly unlikely that these represent the same species.

We have also listed several additional teleosauroid taxa (with substantial available skull material) that may hypothetically be equivalent to, and thus referable to, *S. rostromajor*. These are stated here and are used as follows (see Table 1): Hypothesis One: '*Steneosaurus*' *baroni* Newton, 1893; Hypothesis Two: *Mycterosuchus nasutus* Andrews, 1913; Hypothesis Three: '*Steneosaurus*' *leedsi*; Hypothesis Four: *Lemmysuchus obtusidens* (Andrews, 1909; Johnson *et al.*, 2018a); Hypothesis Five: '*Steneosaurus*' *heberti* Morel de Glasville, 1876; and Hypothesis Six: '*Steneosaurus*' *edwardsi* (also considered by J. A. and E. Eudes-Deslongchamps).

Hypothesis One states that *S. rostromajor* (MNHN. RJN 134c d) could be similar to '*Steneosaurus*' *baroni* (NHMUK PV R 1999). However, '*S.*' *baroni* (NHMUK PV R 1999) is Bathonian in age, and is only recorded from a geographically distant locality (north-western Madagascar); as with '*S.*' *megistorhynchus*, it is unlikely that *S. rostromajor* and '*S.*' *baroni* are the same species.

Hypothesis Two: *Mycterosuchus nasutus*. We initially considered that this taxon was a subjective junior synonym of *S. rostromajor* due to both specimens coming from relatively similar stages. However, *S. rostromajor* (MNHN.RJN 134c-d) differs from *Myc. nasutus* (NHMUK PV R 2617) in the following:

1. The dorsal premaxillary–maxillary suture is triangular with no interdigitating in *Myc. nasutus* (NHMUK PV R 2617), whereas in *S. rostromajor* (MNHN.RJN 134c-d) the suture is interdigitating near the midline and subcircular in shape (similar to '*S.*' *edwardsi* NHMUK PV 2865 and '*S.*' *heberti* MNHN.F 1890-13) (Figs 2, 3).
2. In dorsal view, the posterior premaxillae of *Myc. nasutus* (NHMUK PV R 2617; CAMSM J.1420) are strongly mediolaterally constricted at the premaxillae–maxillae suture, whereas there is less constriction in *S. rostromajor* (MNHN.RJN 134c-d) (this is related to the shape of the premaxillary–maxillary suture).
3. *Steneosaurus rostromajor* (MNHN.RJN 134c-d) is significantly less ornamented than *Myc. nasutus* specimens (CAMSM J.1420, NHMUK PV R 2617) (Figs 2, 4).
4. The maxillary reception pits are deep and noticeable throughout the anterior and middle rostrum in *S. rostromajor* (MNHN.RJN 134c-d), whereas in *Myc. nasutus* (CAMSM J.1420, NHMUK PV R 2617) they are relatively shallow (Fig. 4).

Hypothesis Three, similar to Hypothesis Two, focuses on another taxon that is from approximately the same stage: '*Steneosaurus*' *leedsi* (NHMUK PV R 3320, NHMUK PV R 3806). However, as with *Myc. nasutus* (NHMUK PV R 2617), there are some features that differentiate *S. rostromajor* (MNHN.RJN 134c-d) from '*S.*' *leedsi* (NHMUK PV R 3320; NHMUK PV R 3806):

1. The dorsal premaxillary–maxillary suture is anteroposteriorly elongate, subrectangular and extremely interdigitating in '*S.*' *leedsi* (NHMUK PV R3320; NHMUK PV R 3806), whereas in *S. rostromajor* (MNHN.RJN 134c-d) the suture is shorter, relatively interdigitating near the midline and subcircular in shape (Figs 2, 3).
2. There are differences in alveolar size throughout the rostrum of '*S.*' *leedsi* (NHMUK PV R 3320; NHMUK PV R 3806); in *S. rostromajor* (MNHN. RJN 134c-d) all preserved alveoli are relatively the same size.
3. The enamel ridges near the base of the tooth are small and faint in '*S.*' *leedsi* (NHMUK PV R 3320); in *S. rostromajor* they are well pronounced (Fig. 5).
4. The rostrum is relatively more robust and ornamented in *S. rostromajor* (MNHN.RJN 134c-d) than in '*S.*' *leedsi* (NHMUK PV R 3320) (although this may be due to interspecific variation) (Fig. 6).

Hypothesis Four is that *S. rostromajor* could be positioned within the tribe Machimosaurini, or could possibly be referred to the Callovian taxon *Lemmysuchus*

Table 1. Comparison of certain rostral characters as well as age/locality between *Steneosaurus rostromajor*, '*Steneosaurus' baroni*, *Mycterosuchus nasutus*, '*Steneosaurus' leedsi*, *Lemmysuchus obtusidens*, '*Steneosaurus' heberti* and '*Steneosaurus' edwardsi*. HYP refers to the authors' proposed hypotheses (see text)

TAXA	Premaxilla–maxillae suture	Maxilla: reception pits, ornamentation	Posterior premaxilla (in dorsal and lateral view)	Dentition: enamel ridges, tooth base	Age and locality
Steneosaurus rostromajor (MNHN. RJN 134c-d)	Subcircular, moderately interdigitating	Deep anterior reception pits, ridges/grooves	Weakly constricted, horizontally straight	Well pronounced, compressed	Oxfordian, France
HYP:1 '*Steneosaurus' baroni* (NHMUK PV 1999)	Subcircular, moderately interdigitating	Deep anterior reception pits, ridges/grooves	Moderately constricted, horizontally straight	Unknown	Bathonian, Madagascar
HYP 2: *Mycterosuchus nasutus* (NHMUK PV R 2617)	Triangular, no interdigitating	Shallow reception pits, extremely ornamented and rugose	Strongly constricted, horizontally straight	Present but faint, compressed	Callovian, UK
HYP: 3 '*Steneosaurus' leedsi* (NHMUK PV R 3320; NHMUK PV R 3806)	Triangular, extremely interdigitating	Shallow reception pits, ridges/grooves	Moderately constricted, horizontally straight	Present but faint, compressed	Callovian, UK
HYP: 4 *Lemmysuchus obtusidens* (NHMUK PV R 3168; LPP.M.21)	Subcircular, moderately interdigitating	Deep reception pits throughout, ridges/grooves/pits	Moderately constricted, horizontally straight	Well pronounced, no compression	Callovian, UK and France
HYP: 5 '*Steneosaurus' heberti* (MNHN.F 1890-13)	Subcircular, moderately interdigitating	Deep anterior reception pits, ridges/grooves	Strongly constricted, horizontally concave	Present, but faint	Callovian, France
HYP: 6 '*Steneosaurus' edwardsi* (NHMUK PV R 3701; NHMUK PV R 2865)	Subcircular, moderately interdigitating	Deep anterior and middle reception pits, ridges/grooves/pits	Moderately constricted, horizontally straight	Well pronounced	Callovian, UK

Figure 2. Comparative plate displaying the anterior rostrum in dorsal view of: A, *Steneosaurus rostromajor* (MNHN.RJN 134c-d); B, '*Steneosaurus*' *baroni* (NHMUK PV R 1999), *Mycterosuchus nasutus* (C, CAMSM J.1420; D, NHMUK PV R 2617); E, '*Steneosaurus*' *leedsi* (NHMUK PV R 3320); F, '*Steneosaurus*' *heberti* (MNHN.F 1890-13); G, '*Steneosaurus*' *edwardsi* (NHMUK PV R 2865); H, *Lemmysuchus obtusidens* (LPP.M.21). Scale bars: 5 cm.

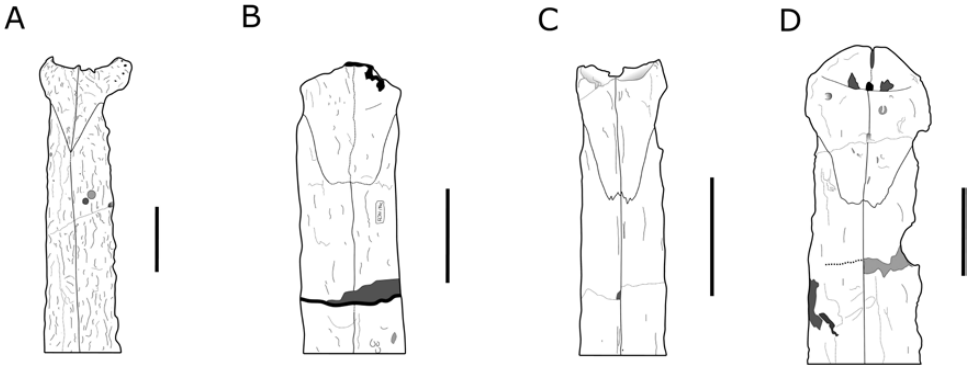

Figure 3. Line drawing highlighting the difference in premaxillae–maxillae suture, in dorsal view. A, *Mycterosuchus nasutus* (NHMUK PV R 2617). B, *Steneosaurus rostromajor* (MNHN.RJN 134c-d). C, '*Steneosaurus*' *leedsi* (NHMUK PV R 3320). D, '*Steneosaurus*' *edwardsi* (NHMUK PV R 2865). Scale bar: 5 cm.

obtusidens [which is one of the two teleosauroids situated at the base of the Machimosaurini, the other being the Bathonian taxon *Yvridiosuchus boutilieri* (Johnson *et al.*, 2019)]. However, as with *Myc. nasutus* (NHMUK PV R 2617) and '*S.*' *leedsi* (NHMUK PV R 3806) in Hypotheses Two and Three, there are some major differences between *S. rostromajor* (MNHN. RJN 134c-d) and *L. obtusidens* (NHMUK PV R 3168). These include:

1. There is one line of smaller neurovascular foramina on the maxilla in *S. rostromajor* (MNHN.RJN 134c-d), whereas in *L. obtusidens* (NHMUK PV R 3168) there are two distinct lines of larger, subcircular foramina (Fig. 7).

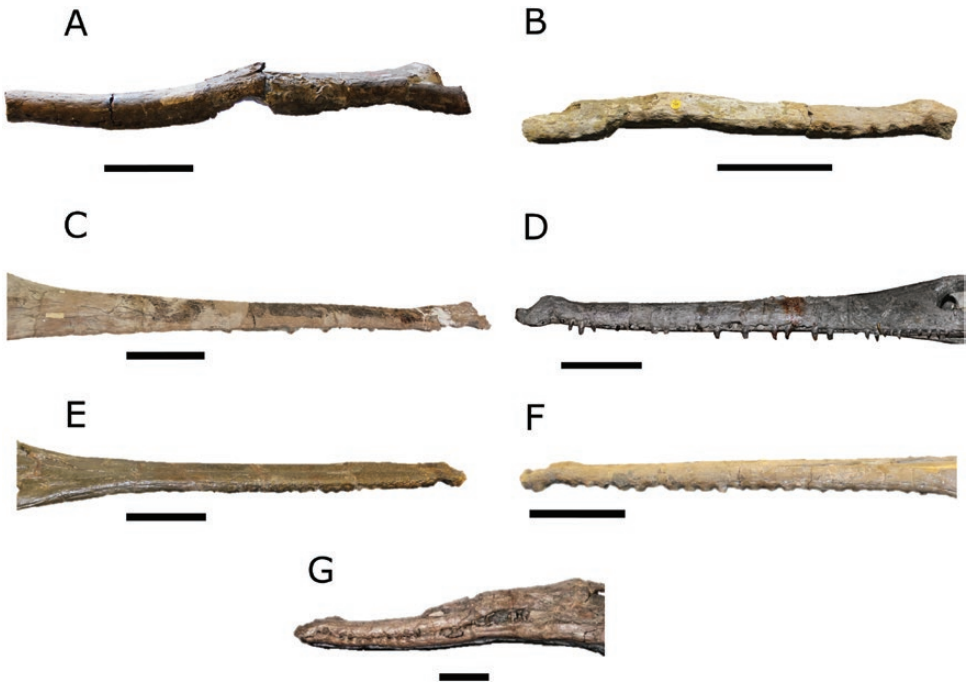

Figure 4. Comparative plate displaying the reception pits of: A, *Steneosaurus rostromajor* (MNHN.RJN 134c-d); B, '*Steneosaurus*' *baroni* (NHMUK PV R 1999); C, *Mycterosuchus nasutus* (CAMSM J.1420); D, '*Steneosaurus*' *heberti* (MNHN.F 1890-13); E, '*Steneosaurus*' *leedsi* (NHMUK PV R 3806); F, '*Steneosaurus*' *edwardsi* (NHMUK PV R 2865); G, *Lemmysuchus obtusidens* (NHMUK PV R 3168). Scale bars: 10 cm (A–F) and 20 cm (G).

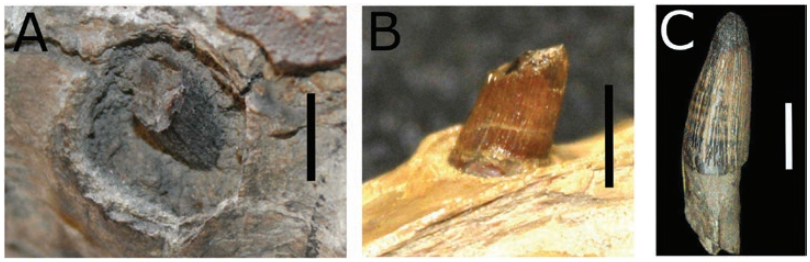

Figure 5. Comparative plate displaying the base enamel ornamentation of the teeth in: A, *Steneosaurus rostromajor* (MNHN.RJN 134c-d); B, '*Steneosaurus*' *leedsi* (NHMUK PV R 3320); C, *Lemmysuchus obtusidens* (NHMUK PV R 3168). Scale bars: 6 mm (A–B) and 2 cm (C).

2. The mid- and posterior-areas of the teeth are slightly compressed in *S. rostromajor* (MNHN.RJN 134c-d), whereas this compression is absent in *L. obtusidens* (NHMUK PV R 3168).
3. The reception pits (for the mandibular dentition) are deep throughout the entirety of the rostrum in *L. obtusidens* (NHMUK PV R 3168), whereas they are only deep anteriorly and mid-maxilla in *S. rostromajor* (MNHN.RJN 134c-d) (Fig. 4).
4. The rostrum is noticeably less ornamented in *S. rostromajor* (MNHN.RJN 134c-d) than in both small and large *L. obtusidens* specimens (NHMUK PV R 3168; NOTNH FS3361) (Fig. 6); in addition, *S. rostromajor* (MNHN.RJN 134c-d) is mainly ornamented with irregular grooves, whereas *L. obtusidens* (NHMUK PV R 3168) has both numerous irregular pits and grooves.

Hypothesis Five is that *S. rostromajor* (MNHN.RJN 134c-d) is a subjective senior synonym to '*Steneosaurus*' *heberti* (MNHN.F 1890-13). These taxa are similar in that (1) the anterior reception pits are relatively deep and gradually disappear posteriorly, (2) '*S.*' *heberti* (MNHN.RJN 1890-13) has an ornamented

Figure 6. Comparative plate displaying the rostral ornamentation of: A, *Steneosaurus rostromajor* (MNHN.RJN 134c-d); B, '*Steneosaurus*' *baroni* (NHMUK PV R 1999); C, *Mycterosuchus nasutus* (NHMUK PV R 2617); D, '*Steneosaurus*' *leedsi* (NHMUK PV R 3806); E, '*Steneosaurus*' *heberti* (MNHN.F 1890-13); F, '*Steneosaurus*' *edwardsi* (NHMUK PV R 2865); G, *Lemmysuchus obtusidens* (NHMUK PV R 3168). Scale bars: 10 cm.

Figure 7. Comparative plate displaying neurovascular foramina of: A, *Steneosaurus rostromajor* (MNHN.RJN 134c-d); B, *Lemmysuchus obtusidens* (LPP.M.21). Note that *S. rostromajor* only has one line of foramina whereas *Lemmysuchus* has two, indicated by arrows. Scale bars: 2 cm.

rostrum comparable to that of *S. rostromajor* (MNHN.RJN 134c-d), and (3) the localities and ages of both specimens are comparable. However, *S. rostromajor* (MNHN.RJN 134c-d) is different from '*S.*' *heberti* (MNHN.F 1890-13) in three key characters:

1. The mediolateral constriction at the posterior premaxilla, parallel to the premaxillary–maxillary suture, is relatively shallow in *S. rostromajor* (MNHN.RJN 134c-d), whereas in '*S.*' *heberti* (MNHN.F 1890-13) the premaxilla is noticeably constricted (Fig. 6).
2. In lateral view, the posterior-most premaxillae of *S. rostromajor* (MNHN.RJN 134c-d) are horizontally straight; in '*S.*' *heberti* (MNHN.F 1890-13), the premaxillae are noticeably convex (it is important to note that neither specimen is dorsoventrally crushed) (Fig. 4).
3. The enamel ridges (situated at the base of the teeth) in *S. rostromajor* (MNHN.RJN 134c-d) are significantly more pronounced than in '*S.*' *heberti* (MNHN.F 1890-13).

COMPARISON WITH '*STENEOSAURUS*' *EDWARDSI* AND THE FATE OF THE GENUS *STENEOSAURUS*

Due to the particular suite of characters in *S. rostromajor* (MNHN.RJN 134c-d) (as stated in the description), it appears not to be synonymous with the aforementioned teleosauroid taxa (Table 1). Therefore, by the process of elimination, the most probable species (which also originates from approximately the same stage) that it could pertain to is '*S.*' *edwardsi* (MNHN.RJN 118; NHMUK PV R 2865; NHMUK PV R 3701). This is our Hypothesis Six. As mentioned before, this was a second species that Eudes-Deslongchamps (1867–69) considered identical to *S. rostromajor*. These two taxa share a combination of features including:

1. A subcircular, moderately interdigitating premaxilla-maxilla suture.
2. Maxillae ornamented with irregular grooves.
3. A shallower mediolateral compression of the posterior maxillae, as opposed to '*S.*' *heberti* (MNHN.F 1890-13).
4. Horizontally flat posterior premaxilla in lateral view.
5. Deep anterior and mid-maxillary reception pits that gradually become shallower towards the posterior maxilla.
6. Subcircular to circular alveoli that remain relatively the same size throughout the maxilla.
7. Teeth with well-pronounced enamel ridges at the base.

However, it is important to note that many of these characters may, in fact, be related to sexual dimorphism, ontogeny and intraspecific variation. In modern crocodylomorphs, many dimorphic and ontogenetic studies revolve around embryonic material and soft tissues (e.g. Larsson, 1998), which is unhelpful when examining fossil specimens. Typical juvenile osteological features include larger orbits and shorter snouts (Monteiro & Soares, 1997; Monteiro *et al.*, 1997; Bustard & Maharana, 1982), but teleosauroids have proportionally larger heads when compared to their total body length (Young *et al.*, 2016) and some hypothesized adult specimens have proportionally larger orbits (e.g. *Indosinosuchus potamosiamensis*, PRC-11) when compared with total skull length, so commonly used osteological and biometric ontogenetic explanations cannot be confidently applied to this group. Sexual dimorphism in modern crocodylians, while well understood in the genera *Alligator* (Frey, 1988) and *Gavialis* (Whitaker & Basu, 1982), usually consists of measuring total body length (Kramer & Medem, 1955; Dodson, 1975; Platt *et al.*, 2009) or skull size (Hall & Portier, 1994; Zeigler *et al.*, 2003) when using skeletal material. While few studies have briefly investigated teleosauroid body sizes (e.g. Young *et al.*, 2016), examining the growth patterns and body size distribution across the entirety of the group has not, as of yet, been attempted. As such, both teleosauroid sexual dimorphism and ontogeny is poorly understood and little studied [only briefly attempted by Vignaud (1995) and Mueller-Töwe (2006)]. There are numerous specimens of varying sizes in the taxa '*Steneosaurus*' *bollensis* von Jäger, 1828, '*S.*' *edwardsi* and '*S.*' *leedsi*, so these types of analyses are possible in the future. Furthermore, there is only one specimen classified as *S. rostromajor* (MNHN.RJN 134c-d), so the sample size for this supposed taxon is extremely limited. Not only that, but there is no current assured way of knowing if this individual is a juvenile or adult, or male or female (based on maxillae measurements comparable to larger '*S.*' *leedsi* and '*S.*' *edwardsi* specimens, it is hypothesized that it is a subadult or adult).

In addition to the sexual dimorphism/ontogeny problem, one of the critical issues about MNHN.RJN 134c-d is that it is poorly preserved. As mentioned previously, both Eudes-Deslongchamps (1867–69) considered this to be one of the determining factors that caused them to question the validity of *S. rostromajor*. MNHN.RJN 134c-d is missing nearly all areas of the skull that display diagnostic characters in teleosauroids, such as the temporal region and premaxillae. The maxillary rostrum itself is relatively undiagnostic; in the majority of longirostrine teleosauroids, the rostrum itself often displays many phenotypically plastic features (e.g. relative elongation of the maxillae, irregular ornamentation, subcircular alveoli), which do little for distinguishing species or examining internal relationships between taxa. Moreover, the preserved material in MNHN.RJN 134c-d is fractured, broken and severely dorsally displaced, with certain sections covered in ironstone oysters, particularly in the posterior areas (see Fig. 1). These factors make it difficult to compare with other taxa. Rather than comparing characters outright, comparison is by process of elimination (or the question of 'what features does this specimen lack?'). This is a slightly inconvenient way of examining specimens, but due to such limited material, it is the only way to attempt comparing MNHN.RJN 134c-d with other teleosauroid taxa.

A third concern is that, in reality, the name *Steneosaurus* is extremely impractical. It was used for many metriorhynchid specimens (e.g. '*Steneosaurus*' *gracilis*, '*Steneosaurus*' *palpebrosus* and '*Steneosaurus*' *manselii*) during much of the 19th century, largely in part due to Cuvier's metriorhynchid skull region (MNHN.RJN 134a-b) being attributed to the teleosauroid rostral section (MNHN.RJN 134c-d). Indeed, the concise, classical definition of '*Steneosaurus*' as we interpret it today was not given until the work of both Eudes-Deslongchampses (1868c, 1867–69), which

labelled it as a 'longirostrine' teleosauroid. Eudes-Deslongchamps (1867–69: 109) understood that Cuvier's assemblage of the teleosauroid rostral and metriorhynchid skull pieces caused great confusion and unavoidable mistakes within teleosauroid nomenclature. They also recognized that the rostrum (MNHN.RJN 134c-d) was '*à la vérité très-mal conserve*' ('in truth very badly preserved') and that it was difficult to base an entire genus on it. Unfortunately, their solution was to create a new type species for their updated definition (either '*S*.' *megistorhynchus* or '*S*.' *edwardsi*, as discussed above), but the current ICZN Code does not allow this; in particular, Article 67.2 (see above). Given that the type species must be either *S. rostromajor* or *S. rostrominor*, we use both position precedence and nomenclatural stability to designate *S. rostromajor* as the type species. After the Eudes-Deslongchampses' treatment, what was left was an undiagnostic, chimeric type specimen for *S. rostromajor* (MNHN.RJN 134) and the genus *Steneosaurus* was redefined using a new type species that was not accepted by some researchers. In addition, since the Eudes-Deslongchampses, there has been no attempt to rectify this taxonomic nightmare; it is almost as if, due largely in part to taxonomic confusion, the existence of *S. rostromajor* was allowed to fade into the background. Since the latter half of the 19th century, '*Steneosaurus*' itself has been crudely regarded as a wastebasket taxon, with note of its multiple taxonomic problems (Jouve *et al.*, 2017) and multiple phylogenetic studies have found to be either paraphyletic or polyphyletic (e.g. Mueller-Töwe, 2006; Foffa *et al.*, 2019; Johnson *et al.*, 2019) (Fig. 6). These problems alone are enough to warrant extreme scepticism on the validity of *Steneosaurus*.

Due to these three significant factors (uncertainty of variable characters, poor preservation and unreasonable name), we have concluded that *S. rostromajor*, and therefore '*Steneosaurus*' (MNHN.RJN 134c-d), cannot be confidently assigned to an existing teleosauroid species. When examining all available characters, the taxon with which it could potentially be synonymous is '*S*.' *edwardsi*, but due to 'weak' or variable characteristics, and with no autapomorphic '*S*.' *edwardsi* features preserved on MNHN.RJN 134c-d, it is premature to assume that they are synonymous. MNHN.RJN 134c-d itself is undiagnostic at the genus and species level; while it retains certain teleosauroid characteristics (e.g. elongated maxillae, a straightened premaxilla–maxilla suture in palatal view), it does not display any autapomorphic features of lower level groups. In addition, MNHN.RJN 134c-d was initially diagnosed based on significant orbital and temporal characteristics (from the metriorhynchid MNHN.RJN 134a-b), along with generic rostral ones. Because the skull material is now known to be from a metriorhynchid, this 'hybrid type specimen' factor adds to the doubtful validity of *Steneosaurus*. According to Article 23.8 of the ICZN Code, 'a species-group name established for an animal later found to be a hybrid (Art. 17) must not be used as the valid name for either of the parental species (even if it is older than all other available names for them)' (this also signifies that the species name *rostromajor* is itself invalid). As such, MNHN.RJN 134c-d serves as an undiagnostic specimen; we, therefore, consider MNHN.RJN 134c-d to be a *nomen dubium* and, as such, *Steneosaurus* is treated as an undiagnostic genus. We believe that establishing teleosauroid taxonomy from the beginning with a series of 'clean' type species/specimens, with every nomenclatural act correctly formulated, is the best course of action, which we will highlight in a forthcoming paper (Johnson, 2019).

CONCLUSION

Steneosaurus is one of the most historically important yet highly controversial genera of Teleosauroidea and of Crocodylomorpha in general. The type specimen ('*S*.' *rostromajor*: MNHN.RJN 134c-d) was initially described and figured by Cuvier in 1800, but was not scientifically named until 1825 by Geoffroy Saint-Hilaire. Due to its complicated and often confusing history, MNHN.RJN 134c-d has been poorly studied and often overlooked when referring to other *Steneosaurus* taxa. In addition, *Steneosaurus* is regularly found to be either paraphyletic or polyphyletic in thalattosuchian phylogenies. This is in part due to the uncertainty of what *Steneosaurus* actually pertains to; only recently has the validity of this genus been scrutinized.

In this paper, we redescribed and revised the type material of *Steneosaurus* (*S. rostromajor*: MNHN.RJN 134c-d), a poorly preserved partial rostrum collected from the Vaches Noires cliff in France. We then compared MNHN.RJN 134c-d to other relevant teleosauroid species, including '*S*.' *baroni*, '*S*.' *heberti*, *Myc. nasutus*, *L. obtusidens*, '*S*.' *leedsi* and '*S*.' *edwardsi*. Through character comparison-and-elimination, the only taxon with which MHNH.RJN 134c-d could hypothetically be referred to is '*S*.' *edwardsi*, but the two do not share any clear autapomorphic characters or a unique combination of characters. Therefore, it is premature to assume that they are synonymous. Thus, due to lack of autapomorphic characters, poor preservation, uncertainty of teleosauroid ontogenetic or sexual dimorphic stages and a generic concept that has changed through time, we agree with de Blainville that *S. rostromajor* is a '*monstre anatomique*' ('anatomical monster'). We find MNHN.RJN 134c-d to be undiagnostic, allocate it as a *nomen dubium*, and consider the genus *Steneosaurus* to be invalid.

We believe that establishing teleosauroid taxonomy from the beginning with a series of 'clean' type species/specimens, with every nomenclatural act correctly formulated, is the best course of action. This will necessitate a revised teleosauroid taxonomy, in which species previously referred to the genus *Steneosaurus* are given new generic names. This work will be published by us in a separate contribution, based on the comprehensive teleosauroid phylogenetic analysis in Johnson's PhD thesis (2019).

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