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Cutting the Gordian knot: a historical and taxonomic revision of the Jurassic crocodylomorph *Metriorhynchus*

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Abstract:	<p>Metriorhynchidae was a clade of extinct crocodylomorphs that adapted to a pelagic lifestyle, becoming a key component of Mesozoic lagoonal and coastal marine ecosystems. The type genus <i>Metriorhynchus</i> is one of the best-known genera of Mesozoic crocodylomorphs, and since the mid 19th Century the 'concept' of <i>Metriorhynchus</i> has become associated with the referred species <i>Me. superciliosus</i> Blainville in Eudes-Deslongchamps, 1852. Historically <i>Metriorhynchus</i> has been the most speciose genus in Metriorhynchidae, with most Middle Jurassic species, and many Late Jurassic species, referred to the genus at some point in their history. However, the type species <i>Me. geoffroyi</i> von Meyer, 1832 has largely been forgotten in the literature. Its type series is a chimera of multiple metriorhynchid species, and a type specimen has never been designated. Moreover, phylogenetic analyses have repeatedly shown that the 19th–20th Century concept of <i>Metriorhynchus</i> is not monophyletic – to the point where only referring every metriorhynchid species, and some basal metriorhynchoids, to the genus would render it monophyletic. Herein we designate a lectotype for <i>Me. geoffroyi</i>, re-described it, and restricted the genus <i>Metriorhynchus</i> to the type species. We also establish the new genus <i>Thalattosuchus</i> for <i>Me. superciliosus</i>, thereby cutting the 'gordian knot' of <i>Metriorhynchus</i> and <i>Th. superciliosus</i>.</p>

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Cutting the Gordian knot: a historical and taxonomic revision of the Jurassic
crocodylomorph *Metriorhynchus*

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RUNNING HEAD: Revision of *Metriorhynchus*

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ABSTRACT

Metriorhynchidae was a clade of extinct crocodylomorphs that adapted to a pelagic lifestyle, becoming a key component of Mesozoic lagoonal and coastal marine ecosystems. The type genus *Metriorhynchus* is one of the best-known genera of Mesozoic crocodylomorphs, and since the mid 19th Century the ‘concept’ of *Metriorhynchus* has become associated with the referred species *Me. superciliosus* ~~Blainville in Eudes-Deslongchamps, 1852~~. Historically *Metriorhynchus* has been the most ~~speciose~~ species-rich genus in Metriorhynchidae, with most Middle Jurassic species; and many Late Jurassic species; referred to the genus at some point in their history. However, the type species *Me. geoffroyii* ~~von Meyer, 1832~~ has largely been ~~forgotten-omitted~~ in the literature. Its type series is a chimera of multiple metriorhynchid species, and a type specimen has never been designated. Moreover, phylogenetic analyses have repeatedly shown that the 19th–20th Century concept of *Metriorhynchus* is not monophyletic – to the point where only referring every metriorhynchid species, and some basal metriorhynchoids, to the genus would render it monophyletic. Herein we designate a lectotype for *Me. geoffroyii*, re-described ~~it~~, and restricted ~~ed~~ the genus *Metriorhynchus* to the type species. We also establish the new genus *Thalattosuchus* for *Me. superciliosus*, thereby cutting the ‘gordian knot’ of *Metriorhynchus* ~~and-with~~ *Th. superciliosus*.

ADDITIONAL KEYWORDS: Crocodylomorpha – Metriorhynchidae – Thalattosuchia –

Taxonomy

INTRODUCTION

Thalattosuchia was a clade of crocodylomorphs that secondarily returned to a marine lifestyle during the Mesozoic Era. However, it was the metriorhynchid subclade that reached the

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zenith of aquatic specialisation, evolving pelagic adaptations such as flipper-like forelimbs, a highly regionalized caudal vertebral column with a hypocercal tail, loss of osteoderms, preorbital salt exocrine glands and compact inner ear semi-circular canals (e.g. Fraas, 1902; von Arthaber, 1906; Andrews, 1913; Fernández & Gasparini, 2000, 2008; Young *et al.*, 2010; Herrera *et al.*, 2013a, 2013b; Sachs *et al.*, 2019a; Schwab *et al.*, 2020). It has also been suggested that metriorhynchids evolved a non-homeothermic mode of endothermy and were viviparous (see Herrera *et al.*, 2015a; Séon *et al.*, 2020).

Arguably, the ~~most~~ historically most important and commonly discussed metriorhynchid genus is *Metriorhynchus* von Meyer, 1832. ~~Originally coined by von Meyer in 1832, it~~ became a ‘wastebasket taxon’ containing a multitude of species named throughout the 19th–20th ~~C~~centuries (e.g. von Meyer, 1832; ~~J.-A. Eudes-Deslongchamps & Blainville, 1852; J.-A. Eudes-Deslongchamps, 1867; E. Eudes-Deslongchamps, 1867–1869; Sauvage, 1874; Woodward, 1885; Lennier, 1887; Schmidt, 1904; Andrews, 1913; Mercier, 1933; Gasparini & Chong, 1977; Gasparini, 1980; Gasparini *et al.*, 2005).~~ ~~In fact, m~~Most Middle Jurassic and many Late Jurassic metriorhynchid species have at some stage been referred to *Metriorhynchus*. Interestingly, the type species *Me. geoffroyii* von Meyer, 1832 has never had a type specimen designated under the International Commission on Zoological Nomenclature (ICZN) Code rules (see below for further details). ~~T~~Worryingly, the type species has been largely ignored in the literature, with the referred species *Me. superciliosus* Blainville in J.-A. Eudes-Deslongchamps, 1852 widely considered as the ‘exemplar’ for *Metriorhynchus*. However, the referral of *Me. superciliosus* to *Metriorhynchus* has never been questioned.

Herein we provide an in-depth historical overview of the genus *Metriorhynchus*, highlighting how the ‘concept of *Metriorhynchus*’ has expanded over time and how metriorhynchid taxonomy has been based on similarity (a phenetic approach) rather than on

shared common ancestry. We act as first reviser designating a lectotype for the type species *Metriorhynchus geoffroyii*, and re-describe ~~the~~ this lectotype specimen. In support of this taxonomic revision we also present a series of phylogenetic analyses based on our revised dataset, and introduce new TNT scripts. These analyses were conducted to determine which of the three hypotheses put forward by Young *et al.* (2020a) on the position of *Me. geoffroyii* within Metriorhynchidae has the best support. These three hypotheses are: 1) sister taxon to *Me. superciliosus*, 2) sister taxon to Rhacheosaurini (with *Maledictosuchus* Parrilla-Bel *et al.*, 2013 being a rhacheosaurin, i.e. *Me. geoffroyii* being basal to *Maledictosuchus*); and 3) sister taxon to Rhacheosaurini (with *Maledictosuchus* not being a rhacheosaurin, i.e. *Me. geoffroyii* being more derived than *Maledictosuchus*). Based on the results of these analyses, hypothesis three is always recovered, but support for discriminating between hypotheses two and three is weak. Finally, we restrict the genus *Metriorhynchus* to only include the type species, and we propose a new genus, ~~*Thalattosuchus*~~, for *Me. superciliosus*, the species most commonly associated with the genus *Metriorhynchus*.

HISTORICAL BACKGROUND

Cuvier (1824) and his “tête à museau plus court”

In the new edition of his seminal work “*Recherches sur les ossemens fossiles*”, George Cuvier (1824: 152–153) formally described two species of fossil ‘gavials’ based on fragmentary cranial and mandibular remains and unassociated vertebrae found “near Honfleur”, Normandy, as well as skull remains from Germany and Burgundy, France and a snout housed in Geneva which was originally from Le Havre, Normandy (for ease of reading we will refer to this specimen as the ‘Havre snout’ throughout). Cuvier (1824: 152) initially mentioned “le cabinet de l’Académie de Genève en possède un que j’y ai dessiné en 1811, et dont M. de Labèche [sic] a publié depuis une lithographie de grandeur naturelle” [“the

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cabinet of the Geneva Academy has one that I have [there] drawn in 1811, and of which M. de la Beche published from a lithograph of natural size”]; and indicated that his drawing of the specimen could be found on plate 10, figures 5–7 of the 1824 monograph. Copies of the original De la Beche lithograph can be found in the Muséum ~~n~~National d’Histoire ~~n~~Naturelle (MNHN) library in Paris, France (the personal copy of Cuvier, presented to him by De la Beche), the Natural History Museum in London, UK (NHMUK); and the Geological Society of London. Cuvier (1824) described and figured both species on the basis of snout length:

1. ‘tête à museau plus allongé’ [(head with a more elongated snout)] (Cuvier, 1824: plate 8, figures 3–4, 8; plate 10, figures 1–4, 8–10).
2. ‘tête à museau plus court’ [(head with a more shortened snout)] (Cuvier, 1824: plate 8, figures 1–2, 5–7; plate 10, figures 5–7).

Cuvier also included in his ‘tête à museau plus allongé’ specimens from the Toarcian of “Altorf” [sic] (Altdorf bei Nürnberg, Germany) (Cuvier, 1824: 151, plate 6, figures 10–15) and from the Tithonian of Burgundy, France (Cuvier, 1824: 153, plate 10, figures 8–10; Gand *et al.*, 2012: fig. 20.1). See Table 1 for an overview of the specimens on plates eight and ten.

The long-snouted species (‘tête à museau plus allongé’) is a chimera of metriorhynchid and teleosauroid material (see Johnson *et al.*, 2020a). Unfortunately, the short-snouted species (‘tête à museau plus court’) is also a chimera. The ‘Havre snout’ (Cuvier, 1824: plate 10, figures 5–7) comes from Kimmeridgian strata of Le Havre, while it has been shown that the “Honfleur” material (Cuvier, 1824: plate 8, figures 1–2, 5–7) is from the Callovian-Oxfordian formations exposed at the base of Vaches Noire Cliffs (Brignon, 2016a, b). It is important to note ~~however~~, that, when describing ‘tête à museau plus court’, Cuvier (1824: 152–153) was describing the ‘Havre snout’ ~~.I~~; it is ~~very~~ clear that he was referring the mandible (plate 8, figures 1–2; Brignon, 2016b: fig. 6) and the premaxilla (plate 8, figures 5–7; Brignon, 2017: fig. 2) from the “Honfleur” area to the same species as the ‘Havre snout’.

Therefore, ‘tête à museau plus court’ is the ‘Havre snout’, and Cuvier (1824) considered these two “Honfleur” specimens to be conspecific. Cuvier (1824: 153) also stated that the Honfleur snout “...est absolument la même que dans le museau de Genève” [“...is absolutely the same as in the muzzle of Geneva”].

This is important, ~~as~~ because all of the various different binomia applied to these specimens are based on differing interpretations of which of Cuvier's specimens were conspecific with the ‘Havre snout’ (see Table 2). It is worth noting that Cuvier (1824) did not mention that the “muzzle of Geneva” (‘Havre snout’) was, in actuality, from Le Havre where Kimmeridgian formations are exposed. In the posthumous fourth edition of Cuvier's (1836: 78, plate 238, figures 5–7) “*Recherches sur les ossements fossiles*”, plate captions were added. For the ‘Havre snout’, the caption reads: “Fragment de mâchoire supérieure d’une seconde espèce de crocodile de Honfleur, dessiné à Genève en 1811” [“fragment of an upper jaw of a second species of crocodile from Honfleur, drawn in Geneva in 1811”]. This indication ~~erroneously~~ wrongly suggested that the specimen came from “Honfleur”, a generic and vague locality name that was generally used to designate the Vaches Noires where late Callovian/early Oxfordian formations are exposed (Brignon, 2016a). This indication did nothing to ease the confusion already introduced by the chimeras described by Cuvier.

Geoffroy Saint-Hilaire (1825 and 1831)

Geoffroy Saint-Hilaire (1825: 146–149) was the first to establish binomials for Cuvier's (1824) ‘gavials de Honfleur’: the name *rostro-major* (no generic name) is first seen on page 147, while the complete binomial (*Steneosaurus rostro-major*); and the binomial *Steneosaurus rostro-minor* both appear on page 149.

Under Article 12 of the ICZN Code, taxonomic names published before 1931 must either be accompanied by: 1) a description or a definition of the taxon it denotes; or 2) an indication

(see Article 12.2). Geoffroy Saint-Hilaire (1825) did not provide a definition, but there was a brief description of *Steneosaurus rostro-major* on page 147. Geoffroy Saint-Hilaire (1825) also provided an indication in footnote (1) on page 147, immediately after “*rostro-major*”:

“Ce qu’on possède en parties crâniennes des gavials de Honfleur, est représenté avec le plus grand soin et d’une manière très-satisfaisante dans les planches de la deuxième partie du cinquième volume des *Ossements fossiles*, savoir: les pièces de l’espèce aux plus longues mâchoires, pl. X, et celles de l’autre espèce, pl. VIII” [“The cranial parts of the Honfleur gavials that we possess are represented with the greatest care and in a ~~very~~-satisfactory manner in the plates of the second part of the fifth volume of the *Ossements fossiles*, namely: the pieces of the species with longer jaws, pl. 10, and those of the other species, pl. 8”].

What we have is an indication that the long-snout species (“l’espèce aux plus longues mâchoires”) was on plate 10 of Cuvier (1824), and that the other species (“l’autre espèce”) was on plate 8. The “espèce aux plus longues mâchoires” is *rostro-major* as indicated by the following: (1) the description matches the name, and (2) the footnote comes immediately after the first instance *rostro-major* in the text, so the “autre espèce” would be *rostro-minor*. This means that Geoffroy Saint-Hilaire (1825) explicitly did not indicate that the ‘Havre snout’ was *Steneosaurus rostro-minor*. The specimens on Cuvier’s (1824) plate 8 are the Honfleur specimens Cuvier referred to the same species as ‘tête à museau plus court’. Moreover, Geoffroy Saint-Hilaire referred to the species as the “gavials de Honfleur” (“gavials of Honfleur”). Therefore, Cuvier’s ‘tête à museau plus court’ and Geoffroy Saint-Hilaire’s *Steneosaurus rostro-minor* are not based on exactly the same group of specimens, as:

‘tête à museau plus court’ = ‘Havre snout’ = Cuvier (1824) plate 10 figures 5–7.

(With two Honfleur specimens referred to that species; Cuvier, 1824: plate 8 figures 1–2, 5–7.)

Steneosaurus rostro-minor = Honfleur specimens (not specifically identified) = Cuvier (1824) plate 8.

On plate 8, Cuvier (1824) figured the lower jaw (figures 1–2) and the premaxilla (figures 5–7) that he referred to as ‘tête à museau plus court’ (Tables 1–2). Thus, these are the only specimens Geoffroy Saint-Hilaire (1825) could have been referring to for his species *St. rostro-minor*. As such, we formally designate the lower jaw (MNHN.F.RJN 116; Cuvier, 1808: plate 11, figures 1–2; Cuvier, 1824: plate 8, figures 1–2) to be the lectotype of *Steneosaurus rostrominor* Geoffroy Saint-Hilaire, 1825. Note that the original spelling of the species name “*rosto-minor*” must be corrected as “*rostrominor*” according to Article 32.5.2.3 of the ICZN Code.

At the ~~very~~ beginning of the 1830s, Geoffroy Saint-Hilaire prepared an important work on crocodiles, of which he published only a few preliminary chapters in the “Mémoires de l’Académie des Sciences” in 1833 (Geoffroy Saint-Hilaire, 1833). Offprints with their own title pages also appeared in 1831. Geoffroy Saint-Hilaire (1831: 41) discussed his new genus *Steneosaurus* saying: “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 furthermore justified by the existence of several species: in Caen, I know two quite distinct ones; in Honfleur, a third one. The fossil crocodile of the Geneva cabinet is yet another species also pertaining to the genus *Steneosaurus*.”]

Based on an unpublished manuscript of Geoffroy Saint-Hilaire’s, Brignon (2013) showed that the two *Steneosaurus* species from the Caen region ~~that~~ Geoffroy Saint-Hilaire intended to introduce were *Steneosaurus quillensis* [~~later~~ named *Steneosaurus megistorhynchus*

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Geoffroy Saint-Hilaire, in Eudes-Deslongchamps, 1866) and *Steneosaurus aubignensis* [(later named *Teleidosaurus calvadosii* (Eudes-Deslongchamps, 1866))].

Concerning the two *Steneosaurus* species from “Honfleur” that he introduced in 1825, it is highly possible that Geoffroy Saint-Hilaire intended to restrict *Steneosaurus rostro-minor* to the Geneva cabinet specimen (‘Havre snout’) and simply assigned all the remaining “Honfleur” material to *Steneosaurus rostro-major* (Tables 2, 3). This would be consistent with the text in Geoffroy Saint-Hilaire (1831: 41), but this is only an assumption and we have to consider what was presented in his 1825 paper: 1) that *Steneosaurus rostro-minor* is ~~the~~ Cuvier’s short muzzle species from Honfleur, and 2) that the species is depicted in plate 8 (Cuvier, 1824), thus excluding the ‘Havre snout’.

Holl (1829)

Holl (1829) followed on from the work of Geoffroy Saint-Hilaire (1825), but instead of using Geoffroy Saint-Hilaire’s species epithets *rostro-major* and *rostro-minor*, Holl (1829: 88) altered them to *longirostris* and *brevirostris*. The nominal authority next to both species was given as “Geoffr.”, and Holl (1829) provided ~~very~~ short diagnoses for both species, which stated where the species were known from and provided an indication ~~to-on~~ on which of Cuvier’s (1824) plates the species were figured ~~on~~ (Table 2). Holl’s (1829) brief description was: “Die Schnauze ist kürzer als bei der vorigen Art und das ganze Thier nur gegen 18 Fuss lange” [“The snout is shorter than in the preceding species (*Steneosaurus longirostris*), and the whole animal just about 18 feet long”]. While Holl (1829) did not refer to specific figures from Cuvier (1824), he did state that *Steneosaurus brevirostris* was: “In der Kreide bei Havre” [“In the chalk from Havre”]. Beside this, Holl (1829: 88) added: “(Cuvier ossem. fossil. Tom. V. p. II. pl. 10.)”, namely, plate 10 of Cuvier (1824). As such, *Steneosaurus*

brevirostris was established specifically for the ‘Havre snout’; and Holl (1829) did not consider the Honfleur specimens as being conspecific.

~~As such,~~ Holl (1829) was thus the first author to specifically refer to the ‘Havre snout’ when establishing a new binomial. Moreover, *Steneosaurus brevirostris* was erected solely for the ‘Havre snout’. Given that Geoffroy Saint-Hilaire (1825) did not establish *Steneosaurus rostro-minor* for the ‘Havre snout’ (see above), Holl’s (1829) work was the first time a binomial was applied to Cuvier’s ‘tête à museau plus court’ (= ‘Havre snout’) that fulfils Article 12 of the ICZN Code. Therefore, the ‘Havre snout’ is the holotype by monotypy of *Steneosaurus brevirostris* Holl, 1829.

Gray (1831)

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* Oppel, 1811. Cuvier’s ‘tête à museau plus court’ and Geoffroy Saint-Hilaire’s *Steneosaurus rostro-minor* were referred to the new taxon ‘*Gavialis Jurinii*’ [sic], named after the Swiss naturalist Louis Jurine, who was ~~the~~ professor of zoology and anatomy at the Geneva Academy when De la Beche and Cuvier saw the ‘Havre snout’. No description was provided, but there ~~was~~ an indication to Cuvier’s (1824) plates (= plate 8 figures 1–2, 6–7; plate 10 figures 5–7) (see Tables 1–2). The species was established for Cuvier’s ‘tête à museau plus court’ and does have an indication that includes the ‘Havre snout’ (plate 10, figure 5–7). -Therefore, we formally designate the ‘Havre snout’ (MHNG V-2232) to be the lectotype of *Gavialis jurinii* Gray, 1831, which is thus. ~~Thus, *Gavialis jurinii* is now~~ established as an objective junior synonym of *Steneosaurus brevirostris*.

Von Meyer (1830, 1832 and 1838)

There has been considerable confusion about which of von Meyer's papers established the name *Metriorhynchus*. The “1830 paper” published in the German journal *Isis* is an overview of a talk given by von Meyer during the Achte Versammlung der Naturforscher und Ärzte [(Eighth meeting of nNaturalists and pPhysicians)], in Heidelberg, September 1829. Von Meyer's talk (number 15) is written on pages 517–519 in the third person by an anonymous secretary (Anonymous, 1830). Here the generic name *Metriorhynchus* appears for the first time with the author name “H. v. Meyer” in a list of several fossil reptile generic names arranged in a classification table. The question marks in parentheses after some names, including *Metriorhynchus* H. v. Meyer, we presume that the author of the talk (i.e. von Meyer) was uncertain about the exact position of some of these genera within his classification. However, the generic name *Metriorhynchus* is given without any description, figure or indication, and therefore must be considered as a *nomen nudum*. Even if *Metriorhynchus* is not valid in this 1830 paper, it did establish that the original author is von Meyer, following the Article 50.2 of the ICZN Code (which addresses the question of the authorship of nomenclatural acts in meeting reports or minutes).

In 1832, von Meyer (1832) separated both of Cuvier's ‘gavials’ on a generic level, establishing the names *Streptospondylus altdorfensis* von Meyer, 1832 gen. et sp. nov. and *Metriorhynchus geoffroyii* von Meyer, 1832 gen. et sp. nov. for what he thought to be Cuvier's ‘tête à museau plus long’ and ‘tête à museau plus court’, respectively. Von Meyer (1832) included additional vertebrae previously documented and described by Cuvier (1808) that were not associated with either of these ‘gavials’ and that had been ignored by Geoffroy Saint-Hilaire (1825) when establishing his two *Steneosaurus* species (Allain, 2001). Von Meyer (1832) referred the biconcave vertebrae that Cuvier (1824) described to his *Metriorhynchus geoffroyii*. The lack of hypapophyses on those cervical and dorsal vertebrae were the main reason von Meyer (1832: 227) did not consider *Me. geoffroyii* to be a

crocodile. The lack of hypapophyses are now known to be apomorphies of Thalattosuchia (see phylogenetic character list in Young *et al.*, 2020a and Supplementary Appendix One herein).

Von Meyer (1832: 106) included the ‘Havre snout’ in the list of specimens he referred to *Metriorhynchus geoffroyii*, along with numerous specimens from the Honfleur area and part of Geoffroy Saint-Hilaire’s *Steneosaurus rostro-minor* (Table 2). Therefore, the type series of *Metriorhynchus geoffroyii* is a chimera of the Kimmeridgian-aged ‘Havre snout’ and Callovian-Oxfordian aged Honfleur material. However, von Meyer (1832) never designated a type specimen for *Me. geoffroyii*. The first time ‘Havre snout’ was considered to be the lectotype was by Vignaud (1995) in his unpublished PhD thesis. Young *et al.* (2010) followed Vignaud (1995) in considering the ‘Havre snout’ as the lectotype of *Me. geoffroyii*. Young *et al.* (2010), stating that MHNG V-2232 was the lectotype of *Me. geoffroyii*, did not constitute a valid designation (under Article 74.7.3 of the Code), as-because they did not contain an express a statement of deliberate designation. As such, we hereby expressly designate MHNG V-2232 to be the lectotype of *Me. geoffroyii*. Based on the type specimen designations herein, *Steneosaurus brevirostris*, *Gavialis jurinii*, and *Metriorhynchus geoffroyii* are now objective synonyms.

Surprisingly, von Meyer assigned the lower jaw MNHN.F.RJN 116, one of Cuvier’s ‘tête à museau plus court’ specimens and the specimen we herein designate as the lectotype of *Steneosaurus rostrominor*, to *Streptospondylus altdorfensis*. Therefore, as far as cranial elements are considered, Cuvier’s ‘tête à museau plus court’ and von Meyer’s *Me. geoffroyii* are not exactly-based on exactly the same group of specimens. In a work published in 1838, von Meyer (1838: 9) changed his mind and stated that this specimen belonged to the genus *Metriorhynchus*. Von Meyer (1838) also considered that the anteriorly convex (opisthocoelous) vertebrae found in the Callovian of Vaches Noires, now recognized as those

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10 of a theropod dinosaur (Allain, 2001), did not belong to his genus *Streptospondylus* contrary
11 to what he previously stated in 1832, but should instead be assigned to *Metriorhynchus*.
12 Furthermore, he resurrected *Steneosaurus* and considered *Streptospondylus* to be invalid:
13 “...appelé autrefois en partie *Streptospondylus*, genre qui doit être rejeté” [“...formerly
14 known in part as *Streptospondylus*, a genus that must be rejected”] (von Meyer, 1838: 9,
15 footnote 1).
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21 **Bronn (1835–1837)**
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23 Bronn (1835–1837) used von Meyer’s (1832) nomenclature retaining the name
24 *Metriorhynchus geoffroyii*. He also re-figured some of Cuvier’s (1824) figures, including
25 those of the ‘Havre snout’. Bronn’s (1835–1837) description of *Me. geoffroyii* has the
26 following characteristics:
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31 1. Skull with a moderately elongate cone-shaped snout (explicitly referenced his re-figuring
32 of the ‘Havre snout’).
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34 2. At the fourth tooth the snout is somewhat constricted, then becomes wider and then
35 towards the tip of the snout smaller again (‘Havre snout’).
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37 3. Lower jaw has approximately 16 teeth either side of the symphyseal suture (explicitly
38 referenced his re-figuring of the Honfleur metriorhynchid lower jaw).
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40 4. Teeth cone-shaped, bicarinate, apicobasally ornamented with a long root.
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42 5. -Vertebral centra connected with neurapophyses by a suture.
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44 6. Vertebral centra anteriorly with a convex and posteriorly with a concave articular face.
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46 7. The articular faces become more planar in the posterior dorsal vertebrae.
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48 8. Axis centrum longer than in *Leptocranius*, having a planar, elongate, quadratic surface on
49 its side. **and**
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9. Thoracic vertebrae with transverse processes have a quadratic pyramidal base, posterior to the surface for the rib head with a deep groove (both missing in modern crocodiles) and ventrally instead of the hypapophysis of crocodiles with two [hemapophyseal] facets.

Because Bronn (1835–1837) described the snout, lower jaw and vertebrae in his description, he considered all the material Cuvier (1824) assigned to ‘tête à museau plus court’ to belong to *Me. geoffroyii*; contrary to von Meyer (1832) who excluded the ‘Honfleur’ lower jaw (lectotype of *Steneosaurus rostrominor*) from this species. Bronn also included in *Me. geoffroyii* the opisthocoelous vertebrae that von Meyer (1832) had placed in *Streptospondylus*.

Owen (1842)

The taxonomy proposed by Owen (1842) for the Honfleur material is somewhat unclear. Owen (1842: 73) differentiated *Steneosaurus* and *Teleosaurus* based on the position of the external nares, being “subterminal” (which he defined as “... a little behind the and above the termination of the upper jaw”) in *Steneosaurus* and “terminal, or at the extremity of the upper jaw” in *Teleosaurus*. The species Owen (1842: 74–80) described as being within *Teleosaurus* included *Te. chapmani* (now ‘*Steneosaurus*’ *bollensis*), *Te. priscus* (now *Aeolodon priscus*) and *Te. cadomensis*. Although, on page 79, Owen (1842) stated that the hindlimb bones of *Teleosaurus* resemble those of “Aëlodon” [sic]. It is unclear how Owen differentiated between the genus *Aeolodon* and its type species *priscus*.

In Owen’s (1842: 82) synonymy list for *Steneosaurus* he included the second ‘gavial d’Honfleur’ and *Steneosaurus rostrominor*. The only species Owen included in the genus *Steneosaurus* was *St. rostrominor*, and in the text he went on to describe a metriorhynchid skull from Shotover, Oxfordshire. Owen (1842) considered specimens with a “subterminal” external naris to be *Steneosaurus*, thus unambiguously using *Steneosaurus* for what we today

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call a metriorhynchid, and was part of a trend of referring metriorhynchids to *Steneosaurus* during the mid 19th Century (see below). Note, Article 69.4 of the ICZN Code expressly excludes “fixation by elimination”, meaning that Owen (1842) did not inadvertently make *rostrominor* the type species of *Steneosaurus*.

In Owen’s (1842: 88) synonymy list for *Streptospondylus*, he included *Steneosaurus rostro-major* and the first ‘gavial d’Honfleur’ – with vertebrae in parentheses afterwards (in reference to the opisthocoelous vertebrae). Owen (1842: 88) appeared to have considered the ‘Havre snout’ referable to *Streptospondylus*: “The very characteristic vertebrae and jaws, of which the singular generic modifications were first described by Cuvier*, were found in the Oxford clay formation at Honfleur, and in the Kimmeridge clay at Havre”. Unfortunately, Owen did not explain how the snout of his *Steneosaurus* and *Streptospondylus* differed, instead focusing on the vertebrae of *Streptospondylus*. Moreover, Owen (1842) never indicated which of the specimens appearing in the plates of Cuvier (1824) he assigned to his concept of *Streptospondylus* and *Steneosaurus*. Thus, we can only conclusively state that Owen considered both genera to be crocodilian, and that he referred the amphicoelous vertebrae to *Steneosaurus* and opisthocoelous vertebrae to *Streptospondylus*.

Pictet (1845)

In the second volume of his “*Traité élémentaire de paléontologie*” [“Elementary treatise of palaeontology”], Pictet (1845) proposed the combination *Streptospondylus rostro-major* for *Steneosaurus rostro-major* and restricted the genus *Steneosaurus* to include only *Steneosaurus rostro-minor*. Pictet noted that: “M. H. v. Meyer a, avec raison, proposé la division du genre de Geoffroy [*Steneosaurus*] en deux, et il a donné le nom de *Métriorynchus* [sic] à l’espèce qui a les vertèbres biconcaves et de *Streptospondylus* à celle qui les a convexo-concaves” [“Mr. H. v. Meyer rightly proposed the division of Geoffroy’s genus

[*Steneosaurus*] into two, naming the species with the biconcave vertebrae *Métriorynchus* [sic] and the species with the convex-concave vertebrae *Streptospondylus*"]. Pictet finally concluded: “Mais la plupart des paléontologistes, considérant que le nom de *sténéosaurus* [sic] a la priorité, l’ont rétabli pour le genre dont il s’agit ici” [“But most palaeontologists, considering that the name *sténéosaurus* has priority, have reinstated it for the genus in question here”]. Thus, Pictet (1845) considered the genus *Metriorhynchus* ~~[sic] von Meyer~~ to be a junior synonym of *Steneosaurus* ~~Geoffroy Saint-Hilaire~~, and that *Metriorhynchus geoffroyi* ~~[sic]~~ was a junior synonym of *Steneosaurus rostro-minor* as well. However, Pictet clearly established these synonymies because he wrongly thought that *Steneosaurus rostro-minor* designated the ‘Havre snout’ as he stated: “Ce reptile est connu par un petit nombre de fragments, parmi lesquels un des principaux est une partie antérieure du museau, qui existe dans le musée d’histoire naturelle de Genève et qui a été figuré pl. 1, fig. 2” [“This reptile is known by a small number of fragments, among which one of the main ones is an anterior part of a snout, which exists in the Natural History Museum of Geneva and has been shown pl. 1, fig. 2 [this figure depicts the ‘Havre snout’]”]. As a consequence, Pictet’s conclusions must be rejected as we know that *Steneosaurus rostro-minor* was erected for only the Callovian-Oxfordian material from the Vaches Noires. This further highlights the confusion surrounding the ‘Havre snout’ described by Cuvier (1824), and Geoffroy Saint-Hilaire’s (1825) intent when establishing *St. rostrominor*.

Blainville in Eudes-Deslongchamps (1852)

In 1848, Jacques-Amand Eudes-Deslongchamps and Henri Marie Ducrotay de Blainville exchanged letters on fossil and living “crocodiles”. After Blainville’s death in 1850, Eudes-Deslongchamps decided to publish this correspondence in the *Mémoires de la Société Linnéenne de Normandie*, appearing in the ninth volume of the journal in 1853 (J.-A. Eudes-

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Deslongchamps & Blainville, 1853). ~~However, s~~Separates comprising the same text, but with their own title page were printed and distributed in 1852 (J.-A. Eudes-Deslongchamps & Blainville, 1852; Brignon, 2018a). According to Article 21.8.1 of the ICZN Code, advance distribution of separates or preprints advances the date of publication. Therefore, the year of publication of the nomenclatural acts contained in this work is 1852, not 1853 as often stated.

In his letter, Blainville did not consider it useful to maintain Geoffroy Saint-Hilaire’s genera *Teleosaurus* and ‘*Sténéosaurus*’ [sic] and assigned ~~throughout~~ all the mentioned thalattosuchian species to the genus *Crocodylus*. He established *Crocodylus superciliosus* “espèce dont les debris sont les plus communs dans les argiles de Dives et des Vaches Noires, dont M. G. Cuvier avait fait ce qu’il nomme si bien un monstre anatomique, et dont M. E. Geoffroy a fait, sans trop dire pourquoi, un genre sous le nom de *Sténéosaurus*” [“species whose debris are the most common in the clays of Dives and the Vaches Noires, of which Mr. G. Cuvier had made what he so aptly named an anatomical monster, and of which Mr. E. Geoffroy [Saint-Hilaire] made, without saying too much why, a genus under the name of *Sténéosaurus*”] (J.-A. Eudes-Deslongchamps & Blainville, 1852: 11–12). Talking about Cuvier, he added: “il a créé plusieurs monstruosités anatomiques, en construisant une espèce avec des pièces de deux autres; ainsi son Crocodile à long museau, avec des mâchoires longues, en effet, réunies au crâne du Crocodile à museau moins long” [“he [Cuvier] created several anatomical monstrosities, by constructing one species with parts of two others; thus his long snout ~~c~~Crocodile, with long jaws, indeed, joined to the skull of the ~~c~~Crocodile with a shorter snout”]. Blainville is thus the first one to note that Cuvier’s “Honfleur crocodile” species were chimeras. Then, he explained: “c’est ce qui m’a déterminé à trancher dans le vif au travers d’une confusion vraiment inextricable, en désignant l’espèce la plus commune dans l’argile de Dives et des Vaches Noires, sous le nom de *Crocodylus superciliosus* que M. Conybeare a donné à un Crocodile fossile d’Angleterre” [“that’s what determined me to cut

through a really inextricable confusion, by designating the most common species in the clay of Dives and the Vaches Noires, under the name of *Crocodilus superciliosus*, which Mr. Conybeare gave to a fossil ~~c~~Crocodile from England”] (J.-A. Eudes-Deslongchamps & Blainville, 1852: 13–14). We learn in this excerpt that the name *Crocodilus superciliosus* was suggested by Conybeare for a “fossil crocodile from England” but was never published before.

Blainville then indicated that “la tête presque entière du Crocodile d’Honfleur à long museau” [“the almost complete head of the ~~c~~Crocodile of Honfleur with long muzzle”] (Cuvier, 1824: plate 10, figure 1–4) was composed of a skull of *Crocodilus superciliosus* attached to a “museau à peu près complet” [“nearly complete muzzle”] belonging to another species closed to the “Crocodile de Quilly” (later named *Steneosaurus megistorhynchus* Geoffroy Saint-Hilaire in J.-A. Eudes-Deslongchamps, 1866). This indication satisfies Article 12.2 and the authorship of the act satisfying the availability of the name is Blainville and not Conybeare despite the name was “invented” by the latter.

In addition, Blainville assigned other specimens to *Crocodilus superciliosus*. Those includes a skull (MNHN.F.RJN 256) and lower jaw (probably MNHN.F.RJN 117) from the Vaches Noires given by Félix de Roissy and a skull from the Callovian of Sannerville, Normandy, in the Vautier collection (Brignon, 2018a). The later specimen was previously described by J.-A. Eudes-Deslongchamps (1844) as stated by Blainville: “*C. Superciliosus* dont vous avez décrit la belle tête de la collection de M Vautier” [“*C. [Crocodilus] Superciliosus* [sic] of which you [J.-A. Eudes-Deslongchamps] have described the nice head in the collection of M. Vautier”]. This is another indication satisfying Article 12.2. Note that the Sannerville skull in the Vautier collection later served as the holotype of *Teleosaurus blainvillei* J.-A. Eudes-Deslongchamps, 1867 then assigned to the genus *Metriorhynchus* in 1869 by Eugène Eudes-Deslongchamps (1867–1869) (Brignon, in press).

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However, Blainville did not formally designate a type specimen. The type series of *Crocodylus superciliosus* included (Brignon, 2018a):

- MNHN.F.RJN 134a–b, skull of the chimera depicted by Cuvier (1824: plate 10, fig. 1–4).
- MNHN.F.RJN 256, skull, Vaches Noires, upper Callovian–lower Oxfordian, de Roissy collection (E. Eudes-Deslongchamps, 1867–1869: plate 20, fig. 2; plate 21, fig. 1).
- Probably MNHN.F.RJN 117, mandible, Vaches Noires. (Note that this lower jaw is not the same as the lower jaw MNHN.F.RJN 116, which we designate as the lectotype of *Steneosaurus rostrominor*.)
- Skull, Sannerville, described by J.-A. Eudes-Deslongchamps (1844) and figured by E. Eudes-Deslongchamps (1867–1869: plate 20, fig. 1a, 1b; plate 21, fig. 2a) under the name *Metriorhynchus blainvillei*.
- Skull, Conybeare’s “fossil crocodile from England”.

In 1869, Eugène Eudes-Deslongchamps (1867–1869: 310) designated the Vaches Noires skull in the Roissy collection (MNHN.F.RJN 256) as the “type” of *Metriorhynchus superciliosus*, thus, it is the lectotype under Article 74.5 of the ICZN Code as shown by Brignon (2018a).

Eugène Eudes-Deslongchamps (1867–1869)

Eugène Eudes-Deslongchamps (1867–1869), the son of Jacques-Amand Eudes-Deslongchamps, emended the diagnosis of *Metriorhynchus*, and included the following characters as distinctive for the genus (Eudes-Deslongchamps, 1867–1869: 132–133):

1. **A**a shortened rostrum with a “*gouttière*” (“depression”) branching back towards the palatines (= palatal grooves).²⁵
2. **V**ery large nasals.²⁵
3. **O**rbits with irregular margins that are poorly visible in dorsal view.²⁵
4. **M**ediolaterally wide frontal with a large anterior region.²⁵
5. **A**nteriorly depressed palatal arch becoming more prominent in the middle and almost ‘streamlined’ posteriorly.²⁵
6. **S**quare temporal pits (= supratemporal fenestrae).²⁵ **and**
7. **P**alatines posteriorly large, with pronounced anterior palatal ‘holes’.

Out of this array of characters, Eudes-Deslongchamps (1867–1869: 133) considered “le plus important est celui du frontal antérieur” [“the most important to be the anterior frontal”]. He also stated that the genus *Metriorhynchus* “[...] est aussi une forme plus rapprochée des crocodiles actuels: il semble être un nouveau type qui s’éloigne des reptiles précédemment créés, et qui tendrait peu à peu à se rapprocher des êtres de la nature actuelle” [“...is also a form closer to current crocodiles [more so than *Teleosaurus*]: it seems to be a new type which differs from the reptiles previously created, and which would gradually tend to approach those of the current nature”] due to the large nasal bones, which “[...] est l’état normal dans le genre *Crocodylus*” [“...is the normal state in the genus *Crocodylus*”] (Eudes-Deslongchamps, 1867–1869: 134). Note, characters (1–5) and (7) are found in all metriorhynchids, and while (6), the shape of the supratemporal fenestrae is variable within Metriorhynchidae, the lectotype of *Me. geoffroyi* lacks the temporal region of the cranium.

Eugène Eudes-Deslongchamps assigned the five following species to the re-diagnosed genus *Metriorhynchus*:

- *Me. blainvillei* (J.-A. Eudes-Deslongchamps, 1867), first species he referred to *Metriorhynchus*, and was originally named *Teleosaurus blainvillei* J.-A. Eudes-

Deslongchamps, 1867. The type specimen is from the Callovian of Sannerville, Normandy (Brignon, in press).

- *Me. superciliosus* (Blainville in J.-A. Eudes-Deslongchamps, 1852), second species he referred to *Metriorhynchus*, which was established as *Crocodilus superciliosus* Blainville in J.-A. Eudes-Deslongchamps, 1852. The type specimen is from the Callovian/Oxfordian of the Vaches Noires, Normandy (Brignon, 2018a).
- *Me. moreli* E. Eudes-Deslongchamps, 1869 (E. Eudes-Deslongchamps, 1867–1869: 320). The type specimen is from the Callovian/Oxfordian of the Vaches Noires.
- *Me. brachyrhynchus* (J.-A. Eudes-Deslongchamps, 1867), the third species referred to *Metriorhynchus*, the original combination was *Teleosaurus brachyrhynchus* J.-A. Eudes-Deslongchamps, 1867. The type specimen is from the Callovian of Mesnil Bavent, Normandy (Morière, 1864; J.-A. Eudes-Deslongchamps, 1864; Vignaud 1995: 223; Brignon, in press).
- *Me. hastifer* (J.-A. Eudes-Deslongchamps, 1867), the fourth species referred to *Metriorhynchus*, and it was introduced with the combination *Teleosaurus hastifer* J.-A. Eudes-Deslongchamps, 1867. The type series is from the Kimmeridgian of Cap de la Hève near Le Havre, Normandy.

Eugène Eudes-Deslongchamps (*in* Lennier 1868: 54) also tentatively assigned to the genus *Metriorhynchus* the species *Me.? incertus* (Eudes-Deslongchamps in Lennier, 1868) that he created based on vertebrae and a single osteoderm. These elements came from the same strata and locality (Cap de la Hève, near Le Havre, Kimmeridgian) as *Me. hastifer*.

Eugène Eudes-Deslongchamps (1867–1869: 118) regarded *Me. superciliosus* as fulfilling the role of type species; ~~however~~, but he noted that “C'est avec certaines pièces appartenant à cette espèce et à d'autres se rapportant soit à la suivante, soit au *Met. hastifer* de La Hève, que

G. Cuvier a fait son Gavial à museau court d'Honfleur" ["It is with certain pieces belonging to this species and to others relating either to the following [*Me. moreli*], or to *Me. hastifer* de La Hève, that G. Cuvier made his Short-nosed Gavial of Honfleur"] (Eudes-Deslongchamps, 1867–1869: 309). Therefore, it is evident that Eudes-Deslongchamps (1867–1869) noted that Cuvier's (1824) 'tête à museau plus court' was a chimera of three metriorhynchid species, and considered it to be a combination of *Me. superciliosus*, *Me. moreli*, both from the Callovian/Oxfordian of the Vaches Noires and *Me. hastifer* from the Kimmeridgian of Le Havre area. He added that "*Metriorhynchus hastifer* ne nous est connu que par des fragments plus ou moins importants, recueillis à de longs intervalles dans les argiles kimméridgiennes du cap La Hève, près le Havre. Cette espèce est une de celles qui a été longtemps désignée sous le nom de Crocodile à museau court de Honfleur, dont nous avons déjà en souvent occasion de parler" ["*Metriorhynchus hastifer* is known to us only by more or less important fragments, collected at long intervals in the Kimmeridgian clays of Cape La Hève, near Le Havre. This species is one of those that has long been known as the sShort-nosed cCrocodile of Honfleur, which we have often spoken of"] (Eudes-Deslongchamps, 1867–1869: 345). However, he attributed the 'Havre snout' to *Me. superciliosus*, mentioning that "Le museau du musée de Genève a été figuré par Cuvier ; c'est bien le même que celui du prétendu gavial à museau court d'Honfleur, par conséquent c'est l'espèce oxfordienne des Vaches Noires, à laquelle de Blainville a donné le nom de *Crocodylus superciliosus*" ["the muzzle of the museum of Geneva was represented by Cuvier; it is indeed the same one as that of the so-called gavial with short muzzle of Honfleur, consequently it is the Oxfordian species of the Vaches Noires to which de Blainville gave the name of *Crocodylus superciliosus*"] (E. Eudes-Deslongchamps, 1867–1869: 117). This clearly means that he did not know that the 'Havre snout' housed in Geneva was from the Kimmeridgian of Le Havre, and was likely misled by the figure caption of the posthumous 4th edition of Cuvier's work where it is written that it

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came from “Honfleur”, a generic and vague locality indication that referred most of the time to the Vaches Noires (Brignon, 2016a).

Hulke (1869 and 1870) and Phillips (1871)

In two papers Hulke (1869, 1870) described material of a large-bodied metriorhynchid from the Kimmeridge Clay Formation of Kimmeridge (Dorset, UK). Note, these specimens were subsequently re-described and collectively referred to the geosaurine *Plesiosuchus manselii* (Hulke, 1870) (see Young *et al.*, 2012). However, during the 1860s there were fewer comparative specimens, and Hulke did not seem to be aware of the work of the Eudes-Deslongchamps’. Thus, Hulke (1869, 1870) used the genus *Steneosaurus* for what today we would call a metriorhynchid. In the first paper, Hulke (1869) described mandibular remains and an associated premaxilla (NHMUK PV OR 40103a), referring them to *Steneosaurus rostro-minor* (largely based on the similarities of the lower jaws). Moreover, based on the similarity in dentition between the Kimmeridge lower jaw and *Dakosaurus*, Hulke (1869: 400) considered “*Dakosaurus* is probably the same as Cuvier’s “deuxieme Gavial de Honfleur, tête à museau plus court””. His comparisons and conclusions are unfortunately due to the small comparative sample size available at the time (e.g. see Hulke, 1869: 398–400).

In the second paper Hulke (1870) described a cranial rostrum (NHMUK PV OR 40103) and used it as the type specimen of his new species *Steneosaurus manselii*. Based on this specimen, Hulke (1870: 170) no longer considered the Kimmeridge material to be referable to *Steneosaurus rostro-minor*. He listed the stoutness of the cranial rostrum, and the number and distribution of the teeth in the lower jaw as reasons for his new species being valid. Hulke (1870: 170) was ~~very~~ clear in his discussion that he considered Cuvier’s ‘tête à museau plus court’ and Geoffroy Saint-Hilaire’s *Steneosaurus rostro-minor* to be synonymous, but continued to refer to the French material as ‘tête à museau plus court’. Moreover, when

Hulke discussed the differences between the cranial rostrum and lower jaw of his *St. manskii* with ‘tête à museau plus court’ he explicitly accepted that the ‘Havre snout’ and the Honfleur material were conspecific (just as he did in the 1869 paper).

Phillips (1871) also used *Steneosaurus* as a metriorhynchid generic name. He described the specimens from the Kimmeridge Clay Formation of Oxfordshire, UK, naming *St. palpebrosus* Phillips, 1871, *St. gracilis* Phillips, 1871 and *St. longirostris* Phillips, 1871. Owen (1842: 82–83) had briefly described the holotype of *St. palpebrosus* (OUMNH J.29823), and referred it to *Steneosaurus*.

The confused use of Geoffroy Saint-Hilaire’s *Steneosaurus* during the 19th Century

After Geoffroy Saint-Hilaire (1825) erected the genus *Steneosaurus*, the usage of this **genus name** during most of the 19th Century was radically different from how *Steneosaurus* is used today. From the 1820s until the 1870s, the genus *Steneosaurus* was used for what today are considered *Metriorhynchus* and/or metriorhynchids in general (see Johnson *et al.*, 2020a). Noticeable examples include: *Steneosaurus gracilis* (= *Cricosaurus gracilis*), *Steneosaurus palpebrosus* (= ‘*Metriorhynchus*’ *palpebrosus*), *Steneosaurus dasyceps* (= subjective junior synonym of *Metriorhynchus superciliosus*), *Steneosaurus* [sic] *elegans* (= *Cricosaurus elegans*) and *Steneosaurus manskii* (= *Plesiosuchus manskii*). Thus, during much of the mid-19th Century the name *Steneosaurus* was applied to specimens that we would today recognise as a metriorhynchid, spanning the Callovian to the Tithonian of western Europe.

In fact, it was not until the seminal work of Eudes-Deslongchamps (1867–1869) that the genus *Metriorhynchus* was thoroughly described and diagnosed. Prior to Eudes-Deslongchamps (1867–1869), the genus *Metriorhynchus* was rarely used. For example, Owen (1842: 82, 88) used von Meyers’ (1832) *Streptospondylus* as the generic name for the

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Geoffroy Saint-Hilaire’s (1825) species *rostromajor*; and *Steneosaurus* as the generic name for *rostrominor*.

In summary, prior to the acceptance of Eudes-Deslongchamps (1867–1869) *Steneosaurus* was used as a generic name for a metriorhynchid (as we understand it today), not for a teleosauroid. However, when Eudes-Deslongchamps (1867–1869) re-diagnosed *Steneosaurus* and *Metriorhynchus* he established new type species for these genera. What he considered the type species of *Steneosaurus* to be is ambiguous (see Johnson *et al.*, 2020a); and he considered *Me. superciliosus* as fulfilling the role of the type species for *Metriorhynchus*. Unfortunately, these actions contravene the ICZN Code (Article 68) – although it must be noted-stressed that the Code did not exist during the 1860s. The correct type species of *Steneosaurus* was finally designated by Johnson *et al.* (2020a), while the correct type species of *Metriorhynchus* is *Me. geoffroyii* (by monotypy). Lydekker (1888) followed Eudes-Deslongchamps in considering *Me. superciliosus* as the type species, although he did advocate the retention of *Me. geoffroyii*. It is worth noting that subsequently, the referral of *Me. superciliosus* to the genus *Metriorhynchus* was never challenged, and it was this better known, Middle Jurassic species, that came to exemplify the genus *Metriorhynchus*, with the Late Jurassic type species being largely forgotten.

Allain (2001)

When Allain (2001) re-validated von Meyer’s (1832) genus *Streptospondylus* as a theropod dinosaur, he also discussed the *Steneosaurus* species of Geoffroy Saint-Hilaire (1825). Allain (2001) stated that the type specimen of *Steneosaurus rostromajor* was the skull figured by Cuvier (1824: plate 8, figures 1–2). He also stated that Geoffroy Saint-Hilaire (1825) named the type specimen of *Steneosaurus rostrominor* as the complete mandible figured by Cuvier (1824: plate 10, figures 1–4).

Again, the figures on Cuvier's plate (1824) are referred to (Table 2), but it appears as though Allain (2001) mixed the two plates around (the skull of *St. rostromajor* is in figures 1–4 on plate 10 not 8; and the lower jaw for *St. rostrominor* is in figures 1–2 on plate 8 not 10). Moreover, the lower jaw on plate 8 is only in figures 1–2, and figures 3–4 are of the anterior portion of the rostrum (anterior part of MNHN.F.RJN 134a–c) of the *Steneosaurus rostromajor* lectotype designated by Johnson *et al.* (2020a). While Allain (2001) stated that the type specimen of *St. rostrominor* is the Honfleur metriorhynchid lower jaw (MNHN.F.RJN 116), he did not formally designate it as a lectotype (simply stating it is the type specimen), thus not fulfilling a role as first reviser.

Metriorhynchus in the late 19th Century

Sauvage (1874: 40) considered that the species *Metriorrhynchus* [sic] *incertus* created by Eugène Eudes-Deslongchamps (*in* Lennier 1868) for vertebrae and a single osteoderm from the Kimmeridgian of Cap de la Hève to be valid. However, he noted that only the vertebrae should be assigned to this species and that the osteoderm should be transferred to the genus *Steneosaurus*. For a portion of snout and a series of vertebrae found in the late Kimmeridgian formations of Boulogne-sur-Mer, Sauvage (1874: 45, pl. 7 figs. 3–4, pl. 8 fig. 1, pl. 9 fig. 6, pl. 10 figs. 5–6) also introduced the new species, *Metriorrhynchus* [sic] *littoreus*. This doubtful species was tentatively assigned to the genus *Steneosaurus* by Roset & Vadet (1986).

In his overview of British fossil Crocodilia, Woodward (1885: 501) stated that: “[nor is] there much definitive information regarding the occurrence of *Metriorhynchus* in this country [the UK]”. Woodward was unaware of the Oxford Clay Formation material that would be described by Hulke (1888), and the plethora of specimens discovered by Alfred Leeds in the Peterborough area that would be described during the early 20th Century. However,

Woodward (1885: 502–503) referred two of Phillips' (1871), *Steneosaurus* species, *St. palpebrosus* and *St. gracilis*, to *Metriorhynchus*. In his taxonomic table, he considered four species of *Metriorhynchus* to valid: ~~*Me. superciliosus*~~, *Me. gracilis*, *Me. hastifer*, *Me. palpebrosus*; and ~~*Me. gracilis*~~, *Me. superciliosus*. He also had a *Metriorhynchus* sp. ind. based on an exceptionally large lower jaw from the Kimmeridge Clay Formation of Dorset; this specimen (NHMUK PV R 1089) was later referred to *Plesiosuchus manselii* by Young *et al.* (2012).

In his “*Description des fossiles du Cap de la Hève*” [“Descriptions of the fossils from the Cap de la Hève”], Lennier (1887) described two new metriorhynchid skulls from the Kimmeridgian of the Le Havre area. The specimens were kept in the Muséum d’Histoire naturelle du Havre where they were destroyed during the Second World War (Cousin & Breton, 1994). ~~He~~ (Lennier, (1887: 80–83, plate 18) assigned the first skull to *Metriorhynchus incertus* Eudes-Deslongchamps in Lennier, 1868, a species based upon an osteoderm and vertebrae. As such, the referral of this skull to *Me. incertus* has to be considered dubious. According to Vignaud (1995: 231), the specimen showed affinities with both *Metriorhynchus* and *Dakosaurus*. Lennier (1887: 84–86, plate 20) also introduced the new species *Metriorhynchus acutus* Lennier, 1887 based upon the second skull. It is characterized by its gracile morphology without external ornamentation.

Hulke (1888) gave a description of post-cranial crocodylomorph elements from the Oxford Clay Formation near Peterborough. The metriorhynchid material was referred to the genus *Metriorhynchus*, while the teleosauroid material was referred to the genus *Steneosaurus*, following the taxonomy of Eudes-Deslongchamps. In a note after the references Hulke (1888: 442) mentions that Richard Lydekker had informed him of *Geosaurus* remains in the collection of what is now called the NHMUK, and that Lydekker

informed him about specimens Mr A. Leeds had collected from the Oxford Clay (“identical with those here described”).

In his *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History)*, Lydekker (1888: 96) cited Eudes-Deslongchamps (1867–1869), footnote 4, and follows his decision regarding the type species of *Metriorhynchus*, stating: “This species [*Metriorhynchus superciliosus*] must apparently be regarded as the type of the genus, since it was on fragments of its skull joined to other genera and species that Cuvier founded both his ‘Gavial à museau allongé’ and ‘Gavial à museau plus court d'Honfleur’⁴; the latter being the *Steneosaurus rostro-minor* of authors, to which Meyer applied the generic name *Metriorhynchus* with the affix *geoffroyi*⁵”. In footnote 5 Lydekker (1888a: 96) wrote: “The writer thinks it might have been advisable to retain this name”. Lydekker (1888a: 95–96, 98) referred *Cricosaurus elegans* to *Metriorhynchus*, and was unsure whether *Gnathosaurus* (then thought to be a thalattosuchian), *Rhacheosaurus* and *Crocodylaemus* were also synonymous with *Metriorhynchus*. Lydekker (1888a: 100) also considered *Steneosaurus palpebrosus* to be within *Metriorhynchus*. However, Lydekker (1888a) did consider *Dakosaurus* to be distinct from *Metriorhynchus*, and he synonymized *Plesiosuchus* with *Dakosaurus*. Note that, at that time Lydekker (1888a: 271–27) considered *Geosaurus* to be a mosasaurid. ~~However, but he~~ after he examined ~~ing~~ the *Geosaurus* material ~~in at~~ the NHMUK, Lydekker (1888b) considered *Geosaurus* to be ‘allied to *Metriorhynchus*’.

Lydekker (1889a: 452) went into more detail on the taxonomy and anatomy of metriorhynchids. He agreed with Wagner that *Geosaurus* was crocodilian and not a mosasaurid, and closely related to *Cricosaurus*. He formally established Geosaurinae, diagnosing its members as having sclerotic rings and lacking external mandibular fenestrae, and stated that it should be placed next to Metriorhynchinae within Teleosauridae. He also considered the skull of *Cricosaurus* to be identical to that of *Metriorhynchus*.

Lydekker (1889b) no longer recognized a distinction between Metriorhynchinae and Geosaurinae, with two key characters listed: “in the collection of Mr. Leeds, as well as from the type of *Geosaurus*, that these Crocodiles have no dermal scutes, but that bony plates were developed in the sclerotic of the eye”. He also cited the “very peculiar” pelvis of *Metriorhynchus* and how they correspond with those in the “slab containing the hinder portion of the type of *Geosaurus*”. Based on the footnote accompanying the comment on the *Metriorhynchus* pelvis, it would seem that the talk Hulke gave before the Zoological Society covered the same material as that described in Hulke (1888). It is worth noting, however, that Lydekker (1889b) still considered *Metriorhynchus* to have external mandibular fenestrae. Lydekker (1889b) also thought that “the genus *Dacosaurus* [sic] must be merged in the earlier *Geosaurus*”, based on their shared lack of cranial ornamentation, dental morphology and the lack of external mandibular fenestrae.

The first metriorhynchid species named from the Oxford Clay Formation was *Suchodus durobrivensis* by Lydekker (1890a). Based on the symphyseal region of a lower jaw with associated tooth crowns (NHMUK PV R 1994) Lydekker (1890a) compared the specimen to known thalattosuchians, including *Machimosaurus mosae*, *Metriorhynchus moreli*, *Me. brachyrhynchus* and *Geosaurus* (= *Dakosaurus*), concluding that it most closely resembled *Mac. mosae*. This was based on the lack of a diastema between the fourth and fifth dentary alveoli, the closely packed alveoli, similarly low alveolar count and how far anteriorly the splenial anterior process proceeded. Note that the specimen Lydekker (1890a) considered to be *Mac. mosae*, is the same very-large jaw from Kimmeridge Bay (NHMUK PV R 1089) that Woodward (1885) considered to be *Metriorhynchus* sp. ind. and which Young *et al.* (2012) referred to *Plesiosuchus manselii*.

In the supplement to his *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History)*, Lydekker (1890b) listed *Geosaurus* as a metriorhynchine (note

that in the taxonomy of Lydekker 1888a, 1890b used Teleosauridae in the same manner as we use Thalattosuchia today, and Metriorhynchinae in the same manner we use Metriorhynchidae today). Lydekker (1890b: 230) synonymized *Dakosaurus* with *Geosaurus*. He also, in part, synonymized *Cricosaurus* with *Geosaurus* and *Metriorhynchus*, and considered *Suchodus* to be distinct from *Metriorhynchus*. He also unjustifiably emended the specific epithet of *Metriorhynchus superciliosus* to the neuter form *superciliosum* (Lydekker 1890b: 232).

Metriorhynchus in the early 20th Century

The concept of *Metriorhynchus* largely took shape with the work of Eudes-Deslongchamps (1867–1869), as mentioned previously. However, other key papers during the early 20th Century were instrumental in the formation of the ‘modern concept’ of *Metriorhynchus*. The first is Fraas (1902). This monographic treatment of the Late Jurassic metriorhynchids *Dakosaurus maximus* and *Geosaurus* (= *Cricosaurus*) *suevicus*, housed in the Staatliches Museum für Naturkunde (SMNS) in Stuttgart, Germany, is another seminal paper in thalattosuchian literature. There, the concept of Thalattosuchia was popularized (first coined by Fraas, 1901), although it had a different definition – instead meaning what we today call Metriorhynchidae. It was the first major paper describing the cranial and post-cranial anatomy of *Dakosaurus*, and it created the ‘*Geosaurus* problem’ (see Young & Andrade, 2009). Moreover, it created a generic-level division within Fraas’ Thalattosuchia (= Metriorhynchidae) that persisted for over 100 years: the species from the Middle Jurassic were retained in the genus *Metriorhynchus* as well as the ‘unspecialized’ Late Jurassic taxa (e.g. *Me. hastifer*, *Me. palpebrosus*), and the more specialized forms from the Late Jurassic were divided into either *Dakosaurus* (large, robust forms with shortened rostra and serrated teeth) or *Geosaurus* (smaller, more gracile forms with elongate rostra and more slender

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teeth). Interestingly, Fraas (1902) used a similarity-based taxonomy rather than one based on shared ancestry. He suggested that *Geosaurus gracilis* (= *Rhacheosaurus gracilis* post-Young & Andrade, 2009) was descended from *Me. superciliosus*, *Ge. suevicus* (= *Cricosaurus suevicus* post-Young & Andrade, 2009) originated from *Me. blainvillei*, *Geosaurus giganteus* was descended from *Me. brachyrhynchus*, and *Dakosaurus maximus* stemmed from *Me. hastifer*. As such, his concept of both *Geosaurus* and *Metriorhynchus* were not monophyletic (in modern terms).

Following Fraas' (1902) seminal work, there was evident interest in metriorhynchids during first decade of the 20th Century, especially among German and Austrian researchers. Based on a specimen (specimen number unknown) from the Oxford Clay Formation in the Berlin museum (MB; now the Museum für Naturkunde Berlin), that comprised of the skull and most of the vertebral column, as well as the pelvis, humerus and femur, Schmidt (1904) described a new species, *Me. jaekeli*. Citing similarities in the morphology of the frontals and prefrontals, he saw a close similarity between his new species and *Me. brachyrhynchus*. He separated the two species based on the more slender proportions of the rostrum in *Me. jaekeli*. Schmidt (1904) rejected the previous concept of classifying the species according to relative rostrum length, arguing that the rostrum shape is strongly affected by fast, and potentially convergent, evolution in response to aquatic locomotion, while the frontals and prefrontals are more conservative in their morphological changes. Accordingly, Schmidt (1904) separated the six species of *Metriorhynchus* into three groups – founded mostly on the shape of the frontal and posteromedial outline of the orbit:

- (1) The *brachyrhynchus* group, including *Me. brachyrhynchus* and *Me. jaekeli*. Schmidt (1904: 98, 101) defined this group as, having the frontal being “the shape of a plane tree leaf”, participating in approximately one-third of the dorsal rim of the orbit.

Prefrontals rounded-to-triangular in shape, strongly projecting laterally above the orbits.

- (2) The *superciliosus* group, including *Me. blainvillei* and *Me. superciliosus* and *Me. blainvillei*. Schmidt (1904) defined this group as having a frontal with a long anteromedial process, elongate prefrontals, and the region of the orbits posterior to the prefrontals being broad and nearly quadrangular.
- (3) The *moreli* group, including *Me. hastifer* and *Me. moreli* and *Me. hastifer*, were defined as having an “anteriorly short” frontal.

Schmidt (1904) went on to describe the available postcranium of his *Me. jaekeli*, focusing on the number of presacral vertebrae in the various sections of the column. Although the series was incomplete, he suggested that *Metriorhynchus* species had ~~six~~6 cervical, 17 thoracic and ~~two~~2 lumbar vertebrae.

Similar to Schmidt, von Arthaber (1906) took the opportunity to describe a newly acquired, but even more complete, specimen from the clay pits of Fletton (Oxford Clay Formation) in the University of Vienna collection. Von Arthaber’s view on *Metriorhynchus* alpha taxonomy contrasted with that of Schmidt, retaining the conservative view that rostral length should be the main diagnostic criterion. He was particularly opposed to a close relationship between *Me. brachyrhynchus* and *Me. jaekeli*, not only because of the substantially shorter rostrum in the former but also because of the separation of the premaxillae from the nasals by the maxillae in *Me. jaekeli*. Von Arthaber considered *Me. brachyrhynchus*, *Me. hastifer* and *Me. moreli* to be well-defined species, while he saw difficulties in separating *Me. superciliosus* from *Me. blainvillei*. Nevertheless, he accepted both *Me. superciliosus* and *Me. blainvillei* as being valid, primarily based on “inflated” nasals projecting ‘more strongly’ above the orbits in *Me. superciliosus* than in *Me. blainvillei*. Von

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Arthaber (1906) emended Schmidt’s species *Me. jaekeli*, and was critical that Schmidt (1904) did not provide a proper diagnosis for the new taxon. Moreover, von Arthaber (1906) pointed out that the holotype had suffered from some damage, especially to the cranium. In the opinion of von Arthaber (1906) the closest relative of *Me. jaekeli* was *Me. blainvillei*, not *Me. brachyrhynchus* (contra Schmidt, 1904). His reasoning was:

- (1) The distance between the premaxillae and the nasals is longer in *Me. blainvillei*, and the “ratio maxillary : nasal along the midline is 1:7.2 (instead of 1:9 in *Me. jaekeli*)” (Note, it is unclear what ratio von Arthaber, 1906 meant here, even Leeds, 1907 expressed some confusion about von Arthaber’s measurements.)
- (2) The nasals are not “inflated” but slightly depressed in *Me. blainvillei*, in contrast to those of *Me. jaekeli*.
- (3) The prefrontals of *Me. blainvillei* have an “oblique quadrangular” outline, in contrast to a triangular outline in *Me. jaekeli*.
- (4) The supratemporal fenestrae are “broadly quadrangular with rounded corners” in *Me. blainvillei*, and “appear” to be more elongate in *Me. jaekeli*, although this is not certain due to deformation.

Based on these differences he referred the Vienna specimen to *Me. jaekeli* and proceeded to describe its postcranial skeleton. In contrast to Schmidt (1904) and von Arthaber (1906), Leeds (1907) had a large number of specimens from the Oxford Clay Formation of the Peterborough area to examine, and considered the differences between *Me. blainvillei*, *Me. jaekeli*, *Me. moreli*, and *Me. superciliosus* to be the result of individual variation. He considered only *Me. superciliosus* as valid, and summarized his view as following: “It would seem that some Continental palaeontologists in their desire to discover new species

forget to take into consideration such trifles as age or sex in relation to size” (Leeds, 1907: 315).

In addition to the material available to Schmidt (1904), von Arthaber (1906) had more of the appendicular skeleton as well as a nearly complete caudal series available. He also included data from other *Metriorhynchus* specimens, namely in Berlin, Stuttgart, and Munich, and attempted a holistic reconstruction of the genus. He corrected the reconstruction of Schmidt by assuming seven⁷ cervical vertebrae, 16 thoracic vertebrae and two² lumbar vertebrae. He reconstructed the caudal series to consist of 44 or 45 vertebrae. In addition, he commented on the ontogeny of the processus odontoides and postulated a phylogenetic trend within crocodylians for a rostral shift of the axis rib onto the atlas. Finally, he observed a stronger reduction of the forelimb compared to the hindlimb, as in the plesiomorphic state.

Abel (1907) criticized some details of von Arthaber’s (1906) reconstruction, as well as his concept of aquatic locomotion types. Von Arthaber (1907a) responded with an updated reconstruction of the entire animal—naming an inadequate artwork in his previous reconstruction as reason for most of the mistakes—but refuted most of Abel’s criticism of his theoretical concepts. Von Arthaber (1907a) was especially critical of Abel’s suggestion that the hindlimb zeugopodium and autopodium formed a “physiological unit”, in the sense that they were united in a single flipper in the living animal. In this regard he was supported by Auer (1907a) who described a new hindlimb skeleton from the Oxford Clay Formation in the Tübingen collection, and pointed out that the tarsal joint is well defined and shows clearly full mobility between the zeugo- and the autopodium. On the other hand, he showed that von Arthaber (1906) misidentified several elements of the forelimb (metatarsal I for the ulna, a scapula for a radius, and a coracoid for a scapula; Auer, 1907a, b). Following a short reply by von Arthaber (1907b), discussing the correct position of the tarsals, Auer (1907b) presented a short, rounded zeugopodial element, which indicated that the forelimb in

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Metriorhynchus (no specific epithets were used in Auer’s work, only referring to the genus itself) was much more strongly derived than previously assessed, similar to that of *Geosaurus* (= *Cricosaurus* post-Young & Andrade, 2009); and supported similar statements by Leeds (1907).

In a revision of the genus *Steneosaurus*, Auer (1909) further added the description of two metriorhynchid skulls from the Oxford Clay Formation in the Tübingen collection, that he referred to *Me. sp.* and *Me. cf. moreli*, respectively. He mentioned the suggestion by Owen (1842: 82) to use *Steneosaurus* as a senior synonym of *Metriorhynchus*, complaining of some confusion created by this proposal, and clarified that the name *Steneosaurus* should only be used in the sense of Geoffroy Saint-Hilaire (1825) and Eudes-Deslongchamps (1867–1869).

The final major publication on *Metriorhynchus* during the first two decades of the 20th Century was Andrews (1913). In his catalogue of the marine reptiles of the British Museum of Natural History (now the NHMUK), Andrews (1913) proposed that the Callovian metriorhynchids could be divided into two groups: 1) a newly discovered morphotype where the dermatocranium lacked conspicuous ornamentation and had over 32 teeth in both the upper and lower jaws (his two new species *Me. laeve* and *Me. leedsi*); and 2) species where the dermatocranium was conspicuously ornamented. Andrews (1913) subdivided the latter group into ‘narrow-skulled’ forms (*Me. superciliosum* [sic] and *Me. moreli*) and ‘broad-skulled’ forms (*Me. brachyrhynchus*, his new species *Me. cultridens* and *Suchodus durobrivensis* – which he referred to as *Metriorhynchus durobrivense* [sic]).

Andrews’ (1913) referral of *Suchodus durobrivensis* to *Metriorhynchus* is curious. He makes two comments on this synonymy: 1) “The skulls range in form from a long slender type to the stout broad type which has been referred to *Suchodus durobrivensis*, but the transition from one form to the other is so gradual that it seems best to retain the same generic name for all” (Andrews, 1913: 144); and 2): “there being no valid generic distinction between

it [*durobrivensis*] and the other short-snouted species of *Metriorhynchus*” (Andrews, 1913: 177). The second statement shows that Andrews (1913) considered there to be no valid distinction between *Suchodus durobrivensis* and the other short/broad-snouted forms. This is unsurprising given that he never mentioned Lydekker’s (1890a, b) defining characteristics of the *Suchodus durobrivensis* holotype (which is the symphyseal region of a lower jaw; NHMUK PV R 1994). From Andrews’ (1913) first statement it is clear he is focusing on the cranium, and as there is a continuum of cranial shape (in dorsal view) he saw no need to subdivide the species into multiple genera. It follows that Andrews’ generic level taxonomy was based on perceived similarity, in particular similarity of cranial shape in dorsal view. In fact, Andrews’ species diagnoses (1913: 180) are largely based on the shape and morphology of the cranium in dorsal view. The exceptions are: maxillary tooth counts, mentioning the tooth crown morphology for his new species *Me. cultridens*, and that his new taxa *Me. laeve* [sic] and *Me. leedsi* have numerous close-set maxillary teeth. This began a century-long tradition of referring Middle Jurassic metriorhynchids to *Metriorhynchus*, and delimiting species based on cranial shape in dorsal view (Adams-Tresman, 1987; Vignaud, 1995; Young, 2006; Pierce *et al.*, 2009).

It is worth noting that, while these key papers presented novel information on the anatomy of the Middle Jurassic metriorhynchids of the Oxford Clay Formation, named new species and expanded the concept of *Metriorhynchus* to include *Suchodus*, not once was the type species mentioned. No doubt was expressed that the Callovian material referred to *Metriorhynchus* was an error. In fact, after these papers the concept of *Metriorhynchus* had largely become synonymous with these descriptions of the Callovian species, in particular *Me. superciliosus*.

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Metriorhynchus taxonomy post-Andrews (divided into specific Jurassic time bins)

Bajocian: The oldest referred specimen to *Metriorhynchus* dates from the lower Bajocian of northern Chile (Gasparini *et al.*, 2000). It is a fragmentary cranium lacking the rostrum, but it is clearly of metriorhynchid affinity (e.g. incipient prefrontal lateral expansion). The phylogenetic analysis of Young & Andrade (2009) found this taxon to be a basal metriorhynchoid, specifically a close sister taxon to Metriorhynchidae (*sensu* Young & Andrade, 2009). Subsequent phylogenetic analyses have also found this specimen to be outside of Metriorhynchidae (e.g. the most recent version of the dataset, Young *et al.*, 2020a). As such, it is no longer referred to *Metriorhynchus*.

Bathonian: Mercier (1933) referred two species from the genus *Teleidosaurus* (*T. bathonicus* and *T. gaudryi*) to *Metriorhynchus*. The incipient expansion of the prefrontals, as well as the enlargement of the nasals and frontal characteristic of metriorhynchids are all evident in these species. These two species were subsequently transferred to the new genus *Eoneustes* by Young *et al.* (2010).

From the upper Bathonian of Argentina, a fragmentary skull was referred to *Metriorhynchus* aff. *Me. brachyrhynchus* (Gasparini *et al.*, 2005). Although this specimen had provisionally been affiliated with the European species *Me. brachyrhynchus*, a previous South American species (*Metriorhynchus* aff. *durobrivense* [sic]) was subsequently recognizsed as a distinct species within a different genus, *Dakosaurus andiniensis* Vignaud & Gasparini, 1996. Based upon the phylogenetic analysis of Young & Andrade (2009) this specimen is not referable to *Me. brachyrhynchus*. Currently this specimen is referred to as Geosaurinae indet. (Young *et al.*, 2010).

Callovian: The taxonomy of *Metriorhynchus* from the Callovian has the greatest confusion. From the Oxford Clay Formation of England and the contemporary fossil beds in ~~n~~Northern France and ~~n~~Northern Chile, twelve species of *Metriorhynchus* have been described over the past 150 years. Eudes-Deslongchamps (1867–1869) considered there to be three long-snouted species (*Me. blainvillei*, *Me. superciliosus*, *Me. moreli* and *Me. superciliosus-Me. blainvillei*) and one short-snouted species (*Me. brachyrhynchus*). However, Andrews (1913) subdivided species into smooth hyperdentate forms (*Me. laeve* and *Me. leedsi*), ornate narrow-skulled forms (*Me. moreli* and *Me. superciliosus* and *Me. moreli*) and ornate broad-skulled forms (*Me. brachyrhynchus*, *Me. cultridens* and *Me. durobrivense* [sic]). Later workers employed morphometric techniques (= similarity-based approach) to quantify the variation in metriorhynchid cranial form and provide stability to their taxonomy (e.g. Adams-Tresman, 1987; Vignaud, 1995; Young, 2006; Pierce *et al.*, 2009).

Perhaps the most widely used classification of the Oxford Clay metriorhynchids in museum collections (MTY pers. obs. 2007–2013) was based on Adams-Tresman (1987), ~~which-who~~ used principal co-ordinates analysis (PCO) on measurements from the skull in dorsal view to morphometrically delineate species. As previously mentioned, there has been a long tradition of grouping *Metriorhynchus* into two cranial morphotypes according to relative rostral length/width (Andrews, 1913; Wenz, 1968; Adams-Tresman, 1987): long, narrow-snouted ('longirostrine') forms and shorter, broad-snouted ('brevirostrine') forms. Adams-Tresman (1987) could not find any distinctive cranial characters to delimit species within either morphotype. Therefore, she regarded the senior synonym as being the species in each group that was described first, in line with the 'Principle of Priority', Article 23 of the ICZN Code. Thus, *Me. laeve*, *Me. leedsi* and *Me. moreli* were considered to be junior subjective synonyms of *Me. superciliosus*; while *Me. cultridens* and *Me. durobrivensis* became junior subjective synonyms of *Me. brachyrhynchus*. Two other 'longirostrine' Anglo-French species

Commented [MC2]: AUTHOR: *Metriorhynchus* is a masculine genus, so the epithet should be corrected to *laevis*, because *laeve* is the neuter form.

erected from Callovian specimens (*Me. jaekeli* and *Me. blainvillei*) were considered junior subjective synonyms of *Me. superciliosus* by Wenz (1968). Wenz (1970) had suggested there could be a single ‘brevirostrine’ species of *Metriorhynchus* in the Callovian of Europe, although she did not propose a synonymy as she had not examined the English Oxford Clay Formation material.

Another Callovian species included by Adams-Tresman (1987) in her synonymy of *Me. brachyrhynchus* was *Metriorhynchus casamiquelai* Gasparini & Chong, 1977, from Chile. Gasparini *et al.* (2000) convincingly cast doubt on this assignment by demonstrating that *Me. casamiquelai* has several autapomorphies not seen in European specimens. In addition, they demonstrated that *Me. westermanni* Gasparini, 1980, the second species described from the Middle Callovian of Chile, is a juvenile specimen, and considered it to be a junior subjective synonym of *Me. casamiquelai*. However, new material of *Me. westermanni* led Gasparini *et al.* (2008) to re-validate the species.

Vignaud (1995, 1997) questioned the synonymy within the longirostrine species of *Metriorhynchus*. Using measurements from the skull in dorsal view, he conducted principal components analyses (PCA). However, he also was unable to morphometrically delimit species within each cranial morphotype, although he argued that the high number of maxillary teeth (the variation in maxilla teeth number between *Me. superciliosus* and *Me. leedsi* is approximately 12 teeth, which is far in excess of any extant species – see Iordansky, 1973) was sufficient to distinguish *Me. leedsi* (with *M. laeve* as a junior subjective synonym) from *M. superciliosus*.

These revisions led to the recognition of five valid species from the Callovian: the Chilean species *Me. casamiquelai* and *Me. westermanni*, and three species from Europe, the ‘longirostrine’ *Me. superciliosus* and *Me. leedsi*, and the ‘brevirostrine’ *Me. brachyrhynchus*. The taxonomy of these species was further complicated by recent series of cladistic analyses

(Young, 2006; Wilkinson *et al.*, 2008; Young & Andrade, 2009). All recovered *Metriorhynchus* as paraphyletic or polyphyletic. The ‘longirostrine’ species *Me. superciliosus* and *Me. leedsi* were more closely related to the genera *Cricosaurus* and *Rhacheosaurus* (these species were previously assigned to *Geosaurus*, see Young & Andrade, 2009 for further details), while the ‘brevirostrine’ species (*Me. brachyrhynchus* and *Me. casamiquelai*) were more closely related to *Dakosaurus*. This led Young *et al.* (2010) to revise the generic taxonomy of the clade, with the European ‘brevirostrine’ *Metriorhynchus* species reverting to *Suchodus*; the South American brevirostrine *Metriorhynchus* species transferred to *Purranisaurus* Rusconi, 1948; with *Metriorhynchus sensu stricto* now being the European species similar in form to *Me. superciliosus*. In addition, they erected the new genus *Gracilineustes* for the hyperdentate European longirostrine forms with smooth cranial bones. Moreover, they accepted the synonymy of *Me. leedsi* and *Me. laeve* meaning only one species of *Gracilineustes* was present in the Oxford Clay Formation.

The diversity of European metriorhynchids from the Callovian has only increased since, with the description of *Maledictosuchus riclaensis* Parrilla-Bel *et al.*, 2013 from Spain, *Tyrannoneustes lythrodictikos* Young *et al.*, 2013 from the UK and *Ieldraan melkshamensis* Foffa *et al.*, 2018a from the UK (Table 4). Following the re-description of the holotype of *Purranisaurus potens* by Herrera *et al.* (2015b), the Callovian species ‘*Me.*’ *casamiquelai* and ‘*Me.*’ *westermanni* are no longer referred to the genus. They will require a new genus after a thorough re-description (see Table 5). ‘*Metriorhynchus*’ *brachyrhynchus* is also no longer considered a member of *Suchodus*, *Su. durobrivensis* is consistently recovered as the basal-most member of Plesiosuchina (e.g. Foffa *et al.*, 2018a; Young *et al.*, 2020a) whereas ‘*Me.*’ *brachyrhynchus* is consistently recovered as a basal geosaurine. Again, a new genus will need to be erected following a thorough re-description (see Table 5).

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Therefore, at present there are six recognized species from the Callovian of Europe (*Metriorhynchus superciliosus*, *Gracilineustes leedsi*, *Maledictosuchus riclaensis*, ‘*Me.*’ *brachyrhynchus*, *Tyrannoneustes lythrodectikos* and *Ieldraan melkshamensis*) and two recognized species from the Callovian of Chile (‘*Me.*’ *casamiquelai* and ‘*Me.*’ *westermanni*).

Oxfordian: There are no exclusively Oxfordian species that have been referred to *Metriorhynchus*. All known specimens are only known from Europe and have been referred to either *Me. superciliosus* or ‘*Me.*’ *brachyrhynchus*. An indeterminate specimen is known from the middle Oxfordian of Burgundy, France (Buffetaut & Thierry, 1977). Given the fragmentary nature of the specimen and its lack of a cranial rostrum, Buffetaut & Thierry (1977) could not determine what cranial morphotype it belonged to. In the upper Oxfordian, a well-preserved skull from Charente-Maritime, France initially believed to be a teleosaurid has subsequently been re-described as belonging to *Me. superciliosus* (Buffetaut, 1977). However, the phylogenetic analysis of Young & Andrade (2009) recovered this specimen as the sister taxon to *Me. hastifer*. From the Oxfordian of England cf. *Metriorhynchus superciliosus* tooth crowns have been found (see Foffa *et al.*, 2018b). All of the Oxfordian material referred to *Metriorhynchus* or Metriorhynchidae need to be re-described.

Kimmeridgian-early Tithonian: During the Kimmeridgian-early Tithonian, five species of ‘*Metriorhynchus*’ have been recorded from Europe. From the early Kimmeridgian of Normandy, France there are *Me. acutus*, *Me. hastifer*, ~~*Me. acutus*~~ and *Me. geoffroyii* (Eudes-Deslongchamps, 1867–1869; Allain, 2001; Lepage *et al.*, 2008). From the late Kimmeridgian of Wiltshire, England there was ‘*Me. superciliosus*’ (Grange & Benton, 1996). The Wiltshire specimen, although tentatively assigned to *Me. superciliosus* (Grange &

Benton, 1996), was named *Dakosaurus carpenteri* by Wilkinson *et al.* (2008). Subsequently, Andrade *et al.* (2010) erected the genus *Torvoneustes* for this species.

Finally, from Shotover Hill, Oxfordshire, England there is *Me. palpebrosus*. Like many historical specimens discovered in the 19th century from Shotover Hill, the holotype of *Me. palpebrosus* lacks precise geological data. This hampers our understanding of many metriorhynchid specimens, including isolated *Dakosaurus* tooth crowns (Young *et al.*, 2015) and isolated *Torvoneustes* tooth crowns (Young *et al.*, 2020b). These specimens are most likely early Tithonian in age, given the age of the rocks that crop out there (Cox, 2001: fig. 2.52).

Of the ‘longirostrine’ Kimmeridgian species, Lydekker (1888a: 100) thought that *Me. palpebrosus* appeared to be “very closely allied to” *Me. hastifer*. While Buffetaut (1982) considered the three species (*Me. acutus*, *Me. hastifer* and *Me. palpebrosus*) to be clearly distinct longirostrine taxa, with *Me. palpebrosus* being similar to *Me. superciliosus*, but with a more elongate snout; *Me. acutus* was gracile, and *Me. hastifer* was a robust species. This is *contra* to Wenz (1968) and previous authors, who placed *Me. hastifer* with the ‘brevirostrine’ species. Unfortunately, during the Second World War the holotype of *Me. acutus* was lost. Young *et al.* (2010) transferred *Me. acutus* to the newly erected *Gracilineustes* based on its described ‘gracile’ nature. New specimens of this species are necessary to confirm this hypothesis.

The validity of the Kimmeridgian-Tithonian *Metriorhynchus* species *Me. geoffroyii*, *Me. hastifer* and *Me. palpebrosus* has never been settled. Vignaud (1995) concluded that *Me. geoffroyii* was distinct from *Me. hastifer*, but the fragmentary nature of *Me. geoffroyii* precluded him from rejecting a synonymy with *Me. palpebrosus*. Young *et al.* (2010; see appendix) concluded that *Me. palpebrosus* and *Me. geoffroyii* were conspecific based on the shape of the external nares. However, after first-hand examination of the *Me. palpebrosus*

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holotype by three of us (LS, MTY and DF), it is clear that the shape is not natural. The region around the third premaxillary alveoli is entirely made of plaster, such that only the anterior and posterior margins of the narial fossa can be confirmed to be real.

Late Tithonian: The youngest species referred to *Metriorhynchus* was the holotype of *Purranisaurus potens* from the late Tithonian or early Berriasian of the Neuquén Basin, Argentina (see Gasparini, 1973). However, with the re-description of this specimen by Herrera *et al.* (2015b) the validity of this species and the distinctiveness of the genus has been demonstrated. As noted above, following Herrera *et al.* (2015b) *Purranisaurus* is a monospecific genus within Geosaurinae.

From this list of specimens, *Metriorhynchus* would have had a temporal range of more than 25 Myr. However, early phylogenetic analyses of Metriorhynchidae (Young, 2006; Wilkinson *et al.* 2008; Young & Andrade, 2009) did not recover *Metriorhynchus* as monophyletic. Following the taxonomic revision of Young *et al.* (2010) *Metriorhynchus* was restricted to a clade of endemic European long-snouted metriorhynchids known from the Callovian, Oxfordian and Kimmeridgian. However, as we will demonstrate herein, *Metriorhynchus* should be restricted to the early Kimmeridgian of France.

Metriorhynchid taxonomy in the 21st Century

Fundamentally, the problems surrounding metriorhynchid taxonomy are based on different philosophies and how they have shifted through time. During the 19th century and early 20th century the taxonomic framework for metriorhynchid genera was based on similarity (i.e. phenetic) rather than common ancestry, and attention to intra-specific variation, or potential intra-specific variation, was minimal (although see Mason, 1869; Fraas, 1902; Leeds, 1907). During the latter half of the 20th century and into the 21st century, intra-specific and

ontogenetic variation was being investigated more rigorously. However, the taxonomic framework for higher level taxa was still based on similarity, while studies looking into potential species synonymy used similarity-based approaches (e.g. morphometrics and cluster analyses, Adams-Tresman, 1987; Vignaud, 1995; Grange, 1996; Young, 2006; Pierce *et al.*, 2009). Unfortunately, the species delineation studies not only used a phenetic paradigm but were focussed on the similarity of metriorhynchid cranial shape in dorsal view. The perceived ‘similarity’ of cranial shape in dorsal view was problematic for three reasons: 1) the vast majority of the Oxford Clay Formation metriorhynchid specimens are taphonomically distorted, with most being dorsoventrally compressed to such a degree that the crania no longer retain their in vivo shape; 2) in using cranial shape (and also suture shape) in dorsal view as the primary criterion for determining ‘similarity’ the broad range of craniomandibular variation was overlooked (not to mention post-cranial variation); and 3) this resulted in a conservative taxonomy (i.e. ‘lumping’) that hid metriorhynchid biodiversity. Recent papers have highlighted the variation in tooth serration morphologies, dental fluting, mandibular geometries, and humerus shape (see Young *et al.*, 2013; Foffa *et al.*, 2018a), thereby demonstrating that the obsession with dorsal view cranial shape similarity has held back metriorhynchid taxonomy for over a century.

More recently, there has been a move to shift the paradigm of metriorhynchid taxonomy away from being based on hypotheses of similarity (e.g. see Fraas, 1902; Andrews, 1913), to being based on hypotheses of common ancestry (monophyly/holophyly) (e.g. see Gasparini *et al.*, 2006; Young & Andrade, 2009; Andrade *et al.*, 2010; Young *et al.* 2010, 2012, 2013; Herrera *et al.* 2013c, 2015b; Foffa *et al.*, 2018a). This paradigm shift is not unique to metriorhynchids or thalattosuchians, and is on-going in other clades as well (e.g. bovid mammals Cotterill *et al.*, 2014 and extant crocodylians, see Brochu & Sumrall, 2020). However, at least for some metriorhynchid genera, there has never been a pretence that they

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were monophyletic (e.g. *Metriorhynchus* and *Geosaurus sensu* Fraas, 1902; e.g. see Fraas, 1902). This creates an anomalous situation in which metriorhynchid taxonomy has been expressly phenetic, choosing ‘similarity’ over shared ancestry, for much of the 20th Century.

Thalattosuchian nomenclature and taxonomy in the 21st Century is undergoing radical change (e.g. see Young & Andrade, 2009; Johnson *et al.*, 2020a). The shift towards incorporating systematics and comparative anatomy to infer common ancestry has clashed with the traditional concept of many genera: as the 20th Century understanding of genera such as *Steneosaurus*, *Metriorhynchus* and *Geosaurus* have been revealed to be paraphyletic or polyphyletic (see Young & Andrade, 2009; Wilberg, 2015a, 2015b; Johnson *et al.*, 2020a; Young *et al.*, 2020a). This has necessitated the creation of multiple new genera, or the resurrection of older ones (e.g. Young & Andrade, 2009; Young *et al.* 2010, 2013; Johnson *et al.*, 2017, 2020b; Sachs *et al.* 2019a, b).

Until now no-one has ‘cut the gordian knot’ and tackled the *Metriorhynchus* problem. Although Young *et al.* (2010) started the process of restricting the genus *Metriorhynchus* to a less inclusive sub-set of taxa, many species are still referred to the genus and the type species needs to be re-described. Herein, we not only designate a lectotype for *Me. brevirostris* **comb. nov.** (the objective senior synonym of *Me. geoffroyii*) but re-describe it. Based on comparative anatomy and our new phylogenetic analyses we restrict the genus *Metriorhynchus* to the type species, and discuss the implications of this decision.

MATERIALS AND METHODS

Abbreviations

Institutional: AMNH, American Museum of Natural History, New York City, USA;
CAMSM, Sedgwick Museum of Earth Sciences, University of Cambridge, Cambridge, UK;

GLAHM, Hunterian Museum, Glasgow, UK; NKMB, Naturkunde-Museum Bamberg, Bamberg, Germany; MGCL, Musée Géologique Cantonal, Lausanne, Switzerland; MHNA, Muséum d'Histoire Naturelle d'Auxerre; MHNG, Muséum d'Histoire naturelle, Genève, Switzerland; MNHN, Museum National d'Histoire Naturelle, Paris, France; NHMUK, Natural History Museum, London, [United KingdomUK](#); NMBE, Naturhistorisches Museum der Burgergemeinde Bern, Switzerland; NMO, Naturmuseum Olten, Olten, Switzerland; OUMNH, Oxford University Museum of Natural History, Oxford, [United KingdomUK](#); PETMG, Peterborough Museum & Art Gallery, Peterborough, UK; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Zurich, Switzerland.

Anatomical: En, external nares; mx, maxilla; na, nasal; nc, nasal cavity; pmx, premaxilla. When discussing the tooth count number in the text, P, premaxilla; M, maxilla. Note, tooth count numbering starts from the anterior-most alveolus (e.g. M4 is the fourth maxillary alveolus).

Datasets and analyses

We conducted a series of phylogenetic analyses to test the position of *Metriorhynchus brevirostris* within Metriorhynchidae. The dataset used herein forms part of the ongoing Crocodylomorph SuperMatrix Project and is continuously being updated. Referred to as the Hastings + Young dataset (or HY dataset), it was first presented in Ristevski *et al.* (2018), and has been subsequently updated (see Ösi *et al.*, 2018, Foffa *et al.*, 2019; Johnson *et al.*, 2020b, in review; Sachs *et al.*, 2019a, 2019b, in review; Abel *et al.*, 2020; Young *et al.*, 2020a). It is one of three datasets that form the core of the Crocodylomorph SuperMatrix Project, the other two also being presented in a modified form in Ösi *et al.* (2018). The HY dataset also forms the phylogenetic framework of the Edinburgh-based CrocTransition

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Project, examining the endocranial evolution of thalattosuchians during the land-to-sea transition.

The previous iteration of this dataset, Young *et al.* (2020a), yielded an interesting result: uncertainty on the position of *Metriorhynchus brevirostris* (MHNG V-2232). They ran several different phylogenetic analyses (unweighted parsimony, weighted parsimony and Bayesian inference), using two different datasets: the first was a morphology-only dataset, and the second was an integrated morphological-molecular dataset. For metriorhynchids addition of the molecular data did not alter their internal relationships. The internal relationships of Metriorhynchidae were identical in the unweighted parsimony analyses, the extended implied weighting analyses, in most of the implied weighted analyses ($k=10$, $k=15$, $k=20$ and $k=50$) for both datasets. In these analyses *Me. brevirostris* was recovered as being more derived than *Maledictosuchus* – i.e. no longer united with *Me. superciliosus*, or any other metriorhynchid species. In the strong homoplasy down-weighting analyses ($k=1$ and $k=3$) from both datasets *Me. brevirostris* and *Me. superciliosus* were recovered as sister taxa, and where the basal-most subclade in Metriorhynchinae. In the Bayesian analyses *Me. brevirostris* was found to be the sister taxon to Rhacheosaurini (i.e. basal to *Maledictosuchus*). Thus, we have three different hypotheses for the position of *Me. brevirostris* within Metriorhynchidae:

- (1) United with *Me. superciliosus*, forming a Callovian-Kimmeridgian subclade of basal metriorhynchines. This hypothesis supports the referral of *Me. superciliosus* to *Metriorhynchus*. All iterations of the Young dataset prior to Young *et al.* (2020a) that have included *Me. brevirostris* supported hypothesis one, as do the strongly down-weighted parsimony results ($k=1$, $k=3$) of Young *et al.* (2020a).
- (2) The sister taxon to Rhacheosaurini, with *Maledictosuchus* being a rhacheosaurin – i.e. *Me. brevirostris* is basal to the clade *Maledictosuchus* + (*Rhacheosaurus* +

Cricosaurus). This hypothesis is based on the Bayesian results from Young *et al.* (2020a). This hypothesis does not support the referral of *Me. superciliosus* to *Metriorhynchus*. It also implies a Callovian-Oxfordian ghost lineage for *Metriorhynchus*, as *Maledictosuchus riclaensis* is known from the middle Callovian.

- (3) The sister taxon to Rhacheosaurini, but *Maledictosuchus* is not a rhacheosaurin – i.e. *Maledictosuchus* is basal to the clade *Me. brevirostris* + (*Rhacheosaurus* + *Cricosaurus*). This hypothesis is based on the unweighted and most of the implied weighted parsimony results (k=10, k=15, k=20 and k=50) from Young *et al.* (2020a). This hypothesis does not support the referral of *Me. superciliosus* to *Metriorhynchus*. It also implies a middle or late Oxfordian ghost lineage for *Metriorhynchus*, as the Cuban rhacheosaurins are known from the middle or late Oxfordian.

In order to test which of these three hypotheses were more likely, we updated the HY dataset. First, we merged the changes made to the HY dataset from the two most-recent iterations: Johnson (2019) (now Johnson *et al.*, in review), and Young *et al.* (2020a). This yielded a new version that contained the sum of changes those studies made. All of the changes made to the dataset are outlined in Supplementary Appendix One.

One new operational taxonomic unit (OTU) was added into the HY dataset, *Almadasuchus figarii* Pol *et al.* (2013). We also revised some braincase scores of *Eopneumatosuchus* based on CT scans of the holotype. Scoring sources are summarized in Supplementary Appendix One. The unstable OTUs identified by Young *et al.* (2020a) were excluded from our analyses. As with previous versions of the HY dataset, reductive coding (Wilkinson, 1995) was used, with character inapplicability scored as '-'. In the supplementary character list, characters that have inapplicable scorings are denoted with (*). Character construction follows Sereno (2007) and Andrade *et al.* (2011), highlighting the ontological dependence between characters. The net changes resulted in a dataset consisting of 179 OTUs

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scored for 574 phenotypic characters (564 osteological characters and 10 soft tissue characters). Forty-five characters are morphoclines, and were treated as ordered (see Supplementary Appendix One). Following Young *et al.* (2020a) *Batrachotomus kupferzellensis* Gower (1999) is the outgroup taxon.

The parsimony analyses were conducted using TNT v1.5 Willi Hennig Society Edition (Goloboff, Farris & Nixon, 2008; Goloboff & Catalano, 2016). Memory settings were increased with General RAM set to 900 Mb. We ran the analyses using newly created TNT scripts (see Supplementary data files; ~~and~~ available upon request from the corresponding author). The seven scripts are used here, of which five are new: seedtest.run, fEIW.run, EIW.run, fEIWTT.run and EIWTT.run. The two non-new scripts are: fourstats.run, an emended version of the stats.run script that comes with TNT (first introduced by Young *et al.*, 2020a); and templetontest.run, a script available freely online that was written by Alexander Schmidt-Lebuhn (<https://www.anbg.gov.au/cpbr/tools/templetontest.tnt>). We created new TNT scripts ~~as because~~ the ones created by Young *et al.* (2020a) do not work on Mac Operating Systems. Moreover, we have decided to shift from running implied weighting analyses to only extended implied weighting analyses (the ImpliedW.run script they created is now redundant).

Of the new scripts, the first, seedtest.run, implements ten equal weights analyses. This is a tester script to check that the data input file is not sensitive to start seed. The script produces six output files:

- 1) .txt log file (includes the descriptive statistics)
- 2) .tre with a random cladogram in parenthetical form

This script runs: an initial ‘new technology’ search (xmult:hits 10 replications 10 rss css xss fuse 5 gfuse 10 ratchet 10 drift 10; sec:drift 10 rounds 10 fuse 3; ratchet:numsubs 40 nogiveup; drift:numsubs 40 nogiveup), then runs a ‘traditional methods’ search (bbreak:TBR)

on the saved cladograms. Next it calculates the descriptive statistics (length, CI, RI, RC and HI) for the randomly selected cladogram. This then loops, so that it is done ten times. The start seed is randomly selected each loop. The log file contains the descriptive statistics from each of the analyses. If they are consistent, then the data input file can be considered insensitive to start seed and further analyses can be conducted.

The script `fEIW.run` is intended to replace `fast.run` from Young *et al.* (2020a). It implements an equal weights analysis and a $k=10$ extended implied weighting analysis (“`xpiwe(*;piwe=10)`”). As its name implies, it is a “fast” version of the `EIW.run` script. It is a tester script to check that the data input file is compatible with the longer-running analysis scripts. It can also be used as a ‘fast’ analysis to check results prior to performing a ‘final’ set of analyses. The script produces eight output files:

- 1) .txt log file (includes the descriptive statistics and the common synapomorphies mapped on a topology)
- 2) .tre file with the resultant cladograms
- 3) .tre file with one randomly selected cladogram
- 4) .svg file of the maximum agreement subtree
- 5) .tre file with the strict consensus topology
- 6) .txt file with the nodal support values
- 7) .svg file of the strict consensus topology
- 8) .svg file of a majority-rule consensus with nodal support values

This script runs: an initial ‘new technology’ search (`xmult:hits 10 replications 10 rss css xss fuse 5 gfuse 10 ratchet 10 drift 10; sec:drift 10 rounds 10 fuse 3; ratchet:numsubs 40 nogiveup; drift:numsubs 40 nogiveup`), then runs a ‘traditional methods’ search (`bbreak:TBR`) on the saved cladograms. Next it calculates the descriptive statistics (length, CI, RI, RC and HI) for one of the randomly selected cladograms (`set feiw_equal_randmpc getrandom [0`

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10 ntrees];tsave* feiw_equal_randmpc.tre;save 'feiw_equal_randmpc';tsave/;keep 0; proc
11 feiw_equal_randmpc.tre;length;run fourstats.run) and the strict consensus topology
12 (tchoose{strict}; length;run fourstats.run). (Note: the latter can be less optimal than the
13 fundamental cladograms.) It also maps all common synapomorphies (proc
14 feiw_equal_trees.tre; apo [;), and saves the maximum agreement subtree as a .svg (proc
15 feiw_equal_trees.tre; prunnelsen +*;ttag=prunnelsen;ttag & feiw_equal_prunnelsen.svg;ttag-
16 ;). After saving the fundamental cladograms (.tre) and strict consensus (.tre) it runs two types
17 of nodal support analyses, heuristic absolute Bremer support analysis (hold 1000;subopt
18 20;bbreak;ttag=;bsupport) and a symmetric resampling analysis (resample=sym replications
19 1000 frequency gc from 0). Finally, it saves two .svg files: 1) strict consensus, and 2) a
20 majority-rule consensus with the nodal support values.
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30 The script EIW.run should be used once the data input file is known to be compatible
31 (see above for using fEIW.run as a tester script). This script implements an equal weights
32 analysis and a series of extended implied weighting analyses (Goloboff, 2014). First, an equal
33 weights analysis is ran (piwe-), which is then followed by seven different extended implied
34 weighting analyses (“xpiwe (*”), varying in their k value (piwe=1, piwe=3, piwe=7,
35 piwe=10, piwe=15, piwe=20 and piwe=50). By using a range of fitting functions, it shows
36 how ~~very~~-strong (k=1 and k=3) to ~~very~~-weak (k=20 and k=50) homoplastic down-weighting
37 impacts the results. Extended implied weighting is recommended for datasets with large
38 amounts of missing data, due to the artificially high implied weights received by OTUs with
39 high proportions of missing data (Goloboff, 2014). Each of the eight different weight
40 analyses produces the eight output files listed above for fEIW.run, meaning that a correctly
41 running EIW.run script will yield 64 files once completed. The procedure EIW.run goes
42 through is identical to fEIW.run, the differences are in the ‘new technology’ analysis settings
43 (xmult:hits 10 replications 100 rss css xss fuse 5 gfuse 10 ratchet 20 drift 20; sec:drift 10
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rounds 10 fuse 3; ratchet:numsubs 40 nogiveup; drift:numsubs 40 nogiveup) and the number of cladograms held per analysis (hold 20000).

Finally, we introduce two scripts for running Templeton Tests (Templeton, 1983). These are: fEIWTT.run and EIWTT.run, designed to be ran with the outputs from fEIW.run and EIW.run respectively. Both of these new scripts use the templetontest.run script to perform the analyses. Both make use of the saved strict consensus .tre files and the randomly saved cladogram .tre files generated by fEIW.run and EIW.run to make a series of Templeton Tests to determine whether the implied weighting topologies are statistically significantly different from the equal weights topology. Both of these two scripts generate two log files, the first comparing the strict consensus and the second log file for the randomly generated cladograms. For either of fEIWTT.run and EIWTT.run to work, they must be in the same folder as the data input file, templetontest.run and the output files from fEIW.run or EIW.run respectively.

Undated Bayesian analyses were performed using MrBayes 3.2.5 (Ronquist *et al.*, 2012) using a Markov (Mk) model (Lewis, 2001), assuming only variable characters were scored (v), and with a gamma distribution (G) to model rate heterogeneity across characters (Mkv + G model). When analysing the dataset, five independent runs, each with ten chains, were ran for ten million generations using 100 cores on the Rocket HPC cluster at Newcastle University. Sampling occurred every 5000 generations, with a burn-in of 40%. Parameters were assessed for stationarity and effective sample sizes in tracer (Rambaut *et al.*, 2018). Consensus trees were plotted and formatted in R (R Development Core Team, 2017) using the 'ggtree' R package (Yu *et al.*, 2017). Note, that as MrBayes does not allow ordered characters to have more than six states, cf. '*C.*' *macrospondylus* was re-scored as state (5) for character 56. State (6) for this character is autapomorphic for cf. '*C.*' *macrospondylus*.

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10 We also ran a series of constraint analyses to test the support for the hypotheses. To
11 do this we reduced the dataset to just Metriorhynchoidea, with *Pelagosaurus typus* acting as
12 the outgroup taxon. For the parsimony analyses, we ran the EIA.run script three times: 1)
13 with *Me. superciliosus* and *Me. brevirostris* constrained to be sister taxa; 2) with
14 *Maledictosuchus* constrained to be a member of Rhacheosaurini, and *Me. geoffroyii* excluded
15 from Rhacheosaurini; and 3) an unconstrained analysis. Bayesian topological hypothesis
16 testing was performed in MrBayes 3.2.5 using the steppingstone method of Xie *et al.* (2011)
17 to estimate the marginal likelihood of trees constrained to have topologies consistent with
18 each hypothesis outlined above. Ten independent steppingstone analyses, each with nine
19 heated chains and one cold chain were run for five million generations with 48 steps
20 following Bergsten *et al.* (2013) and using diagnostic frequencies as outlined in the MrBayes
21 manual. Bayes factors were calculated based on the estimated marginal likelihoods and a
22 $2 \times \log_e(B_{10})$ value greater than ten was taken as strong support for the more likely hypothesis
23 following Kass and Raftery (1995).
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36 SYSTEMATIC PALAEONTOLOGY

37 CROCODYLOMORPHA HAY, 1930 (*SENSU* NESBITT, 2011)

38 THALATTOSUCHIA FRAAS, 1901 (*SENSU* YOUNG & ANDRADE, 2009)

39 METRIORHYNCHIDAE FITZINGER, 1843 (*SENSU* YOUNG & ANDRADE, 2009)

40 METRIORHYNCHINAE FITZINGER, 1843 (*SENSU* YOUNG & ANDRADE, 2009)

41 *METRIORHYNCHUS* VON MEYER, 1832

42 (Figs 1–3)

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49 *Type specimen:*
50 MHNG V-2232, partial cranial rostrum.
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Eugène Eudes-Deslongchamps (1867–1869: 118) attempted to rectify the taxonomic issues associated with *Metriorhynchus*, and designated a new type species for the genus (*Me. superciliosus*). However, the ICZN did not exist during that time, and under Article 68.3 of the Code *M. geoffroyii* is the type species by monotypy. As stated above, von Meyer (1832) never designated a type specimen for *Me. geoffroyii*. The first time MHNG V-2232 was considered to the lectotype was by Vignaud (1995) in his unpublished PhD thesis, which Young *et al.* (2010) followed. However, as noted above, Young *et al.* (2010) merely stated that MHNG V-2232 was the lectotype, they did not designate it so. Thus, until this publication, no-one has ever designated a type specimen for *Metriorhynchus geoffroyii* that fulfils Article 74.7.3 of the ICZN Code. As herein we formally designated MHNG V-2232 to be the lectotype, it ensures that the cranial rostrum description of von Meyer (1832), which was the basis for the generic name, is reflected in the type specimen and ensures taxonomic stability. With the ‘Havre snout’ (MHNG V-2232) being the lectotype of both *Me. geoffroyii* and *Ga. jurinii* it renders them both junior objective synonyms of *Steneosaurus brevirostris* Holl, 1829.

Type species:

Metriorhynchus geoffroyii von Meyer, 1832, a junior objective synonym of *Steneosaurus brevirostris* Holl, 1829 (following Recommendation 67B of the ICZN Code).

Note: we cannot use Article 23.9 to preserve *Me. geoffroyii* as it does not fulfil Article 23.9.1.2. A Google Scholar online search for “*Metriorhynchus geoffroyii*” from 1970–2020 gave 13 results, all are from 2001 onwards and most of the first authors mentioning the species are co-authors on this contribution. We recognize that Google Scholar is not an ideal literature search, especially for historical names, but it does give a general overview of how widespread the usage of a name is.

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Etymology:

~~Latinized from Greek μέτριο, moderate, and ρύγχος, ‘Moderate snout’. *Metrio* is Greek for medium/moderate, while *-rhynchus* is the Latinised form of the Ancient Greek *-rhynchos* which means snout.~~

Diagnosis:

Same as the only species herein regarded to be validly assigned to the genus *Metriorhynchus* (see below).

***METRIORHYNCHUS BREVIROSTRIS* (HOLL, 1829) COMB. NOV.**

(Figs 1–3)

v 1820 Upper jaw of the fossil crocodile from Havre in the Museum of the Academy of Geneva – De la Beche, lithograph

v 1824 Tête à museau plus court [*partim*] – Cuvier, p. 152–153, pl. 10 figures 5–7.

v* 1829 *Steneosaurus brevirostris* sp. nov. – Holl, p. 88.

v* 1831 *Gavialis Jurinii* sp. nov. – Gray, p. 57. [*sic*] [*partim*]

v* 1832 *Metriorhynchus geoffroyii* gen. et sp. nov. – von Meyer, p. 106. [*partim*]

v 1836 Anterior extremity of the upper Jaw of *Steneosaurus* – Buckland, p. 36, pl. 25' figure 3.

v 1837 *Metriorhynchus Geoffroyii* (von Meyer) – Bronn, p. 520, pl. 26 figures 7b,d, 8a,b. [*sic*] [*partim*]

v 1845 *Steneosaurus rostro-minor* [*sic*] Geoffroy Saint-Hilaire – Pictet, p. 46, pl. 1 fig. 2 [*partim*]

v 1853 *Steneosaurus rostro-minor* [*sic*] Geoffroy Saint-Hilaire – Pictet, p. 492–493, pl. 25 fig. 9 [*partim*]

v 1973 *Metriorhynchus geoffroyi* (von Meyer) – Steel., p. 45, figure 18 (10). [*sic*]

v 1987 *Metriorhynchus geoffroyi* (von Meyer) – Adams-Tresman, p. 193. [*sic*]

v 2010 *Metriorhynchus geoffroyii* (von Meyer) – Young *et al.*, p. 803.

Holotype:

MHNG V-2232, partial cranial rostrum.

Casts of holotype:

MGCL 9868, PIMUZ A/III 82 and OUMNH unnumbered.

Type locality and ~~h~~Horizon:

Le Havre, Département de Seine-Maritime, Haute-Normandie, France. Kimmeridgian, Upper Jurassic.

Etymology

: From Latin *brevis*, short, and *rostrum*, snout. The combination with the genus results in ‘The short snouted moderate snout’ (or ‘moderate short snout’), which is ~~A~~perhaps an unfortunate combination.

Diagnosis:

Metriorhynchid crocodylomorph with the following unique combination of characters: premaxilla posterodorsal processes terminate level to the M3 alveoli; the three premaxillary alveoli successively increase in size, with the P1 alveoli being circular in shape, and the P3 alveoli being the most oval of the premaxillary tooth-row; premaxilla is transversely broad level to the narial fossa posterior margin; constriction at the premaxilla-maxilla contact; having at least 13 maxillary alveoli anterior to the palatine anterior processes; maxillary alveoli M1–M13 are irregularly shaped ovals, with the post-M3 alveoli becoming more circular in shape; nasal anterior processes terminate level to the M8 alveoli; lacks a fully ossified internarial bar (thus an undivided external naris); the anterior-margin of the narial

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fossa is posterior to the P1 alveoli and the posterior margin terminates slightly posterior to the premaxillary tooth-row.

Description

The holotype of *Metriorhynchus brevirostris* (MHNG V-2232; Figs 1–3) is the cranial rostrum, preserving the premaxilla, maxilla and the anterior process of the nasals. In palatal view only the premaxilla and maxilla are preserved, and there are no complete tooth crowns. Overall, the snout is long and narrow, with a slightly concave upper margin (Figs 1–2). In dorsal view, widest part of the premaxillae is slightly wider than the anterior portion of the maxillae.

Premaxilla and external nares: In dorsal view, the premaxilla is an anteroposteriorly elongated rhomboid (Fig. 1). The premaxillary posterodorsal processes are not particularly elongated for a metriorhynchid, terminating approximately level to the 3rd (M3) maxillary alveoli. The suture between the premaxilla and maxilla is not entirely clear, but it appears to be almost straight (rather than curved or strongly interdigitating), with the posterodorsal processes convergingly posteriorly. The premaxilla only contacts the maxilla along its posterior margins. In lateral view, the external surfaces are slightly convex (Fig. 2). The ornamentation on the external surfaces is hard to discern due to encrustations.

The external naris aperture is largely circular, undivided, and situated within the larger narial fossa (Figs 1–3). The shape of the narial fossa is unclear, due to the poor preservation of the anterior margin, but it looks to have been oval-shaped. There is no evidence of an ossified narial bar, but the posterior-end of the bar is preserved, slightly overhanging the external naris. The anterior-margin of the narial fossa is posterior to the P1 alveoli, while the posterior-margin of the narial fossa is slightly posterior to the premaxillary tooth-row.

In palatal view, three widely spaced alveoli can be seen (Fig. 1B). The first alveoli (P1) are the smallest and are circular in shape. The P2 alveoli are larger and more oval in shape, while the P3 alveoli are the largest in the premaxilla and are oval in shape. The premaxilla-maxilla contact is an anteriorly directed 'V'-shape created by the maxilla palatal anterior process overlapping the premaxilla. The maxillary palatal process terminates level to the anterior margin of the P3 alveoli. It appears as though the incisive foramen is positioned medial to the P2 alveoli but given the preservation of the rostrum this is not entirely clear. The palatal processes of the premaxilla form the anterior margin of the M1 alveolar margin.

Maxilla: Approximately the anterior half of the maxilla is preserved (Fig. 1). The external surfaces of the maxillae are slightly convex. The ornamentation is difficult to distinguish from the encrustations, ~~however-but~~ along the alveolar margins on the right side, there appears to be natural external surface texture (Fig. 2B). It is composed of well-developed anteroposteriorly aligned ridges, suggesting the rostrum may have been ornamented in life. In *Tyrannoneustes lythrodictikos* (Foffa & Young, 2014) and *Dakosaurus maximus* (Young *et al.*, 2012) there are clear shifts in ornamentation patterns across the maxilla, given the preservation of the holotype we cannot determine if that is true for *Metriorhynchus brevirostris*. In lateral view, the preservation of the specimen precludes us from determining if there were reception pits on the lateral margins of the maxillae (Fig. 2).

In palatal view, 12 alveoli are preserved on the right maxilla (anterior section of the 13th alveolus is visible), while there are 13 complete alveoli on the left maxilla (with the anterior section of the 14th alveolus visible) (Fig. 1). All alveoli are circular to sub-circular in shape. The interalveolar spaces are variable in size. The M1 and M2 alveoli are closely packed, from M2–M7 the interalveolar spaces are wider, between M7–M8 there is the largest preserved gap, M8–M10 has gaps similar in size to those of M2–M7; finally from M10 posteriorly the

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10 intervalveolar spaces become ~~very~~ small. Paired palatal grooves are present on either side of
11 the maxilla midline. The grooves appear to terminate level to the M5 alveoli. In *Ty.*
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13 *lythrodictikos* these grooves terminate level to the M4 alveoli (Foffa & Young, 2014), and in
14 the ‘English rostrum’ from the ‘E-clade’ these grooves continue ~~very~~ anteriorly along maxilla
15 terminating level to the M2 alveoli (Young *et al.*, 2020a).
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20 *Nasals:* ~~Very~~ Little of the nasals are preserved, only the anterior processes. The anterior
21 processes form the characteristic converging triangular shape seen in thalattosuchians (e.g.
22 see Fraas, 1902; Andrews, 1913) (Fig. 1). The nasals are paired, with the anterior processes
23 terminating level to the M8 alveoli. Due to the encrustations the ornamentation is hard to
24 discern, but the external surface has anteroposteriorly aligned grooves.
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31 RESULTS
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35 As our study is focused on the position of *Metriorhynchus brevirostris*, we will only
36 discuss the internal relationships of Metriorhynchidae (the strict consensus topologies with
37 nodal support values, for all eight parsimony analyses are in the Supplementary Appendix
38 Two). The metriorhynchid unweighted parsimony topology is almost identical to the one
39 recovered by Young *et al.* (2020a), the sole exception is the sister group relationship between
40 *Cricosaurus vignaudi* and *C. schroederi* (Fig. 4A, Supplementary Figure). Metriorhynchids
41 are recovered with two large subclades (Metriorhynchinae and Geosaurinae). Within
42 Geosaurinae, the two Chilean ‘*Metriorhynchus*’ species are found to be sister taxa and the
43 basal-most clade. More derived there is a polytomy between *Neptunidraco ammoniticus*,
44 ‘*Metriorhynchus*’ *brachyrhynchus* and Geosaurini. Geosaurini is split into two subclades: one
45 that includes *Tyrannoneustes*, *Purranisaurus*, *Torvoneustes* and the ‘E’-clade taxa. The
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second Geosaurini subclade includes Geosaurina (*Geosaurus* and *Ieldraan*), Plesiosuchina (*Suchodus* and *Plesiosuchus*) and the *Dakosaurus* lineage.

Within Metriorhynchinae are successively: ‘*Metriorhynchus*’ *superciliosus*, *Gracilineustes*, *Maledictosuchus*, *Me. brevirostris* and Rhacheosaurini. Rhacheosaurini is split into two subclades: the first consists of ‘*Me.*’ *palpebrosus*, ‘*Cricosaurus*’ *saltillensis*, the ‘Swiss rhacheosaurin’ re-described by Young *et al.* (2020a) and the diagnostic Early Cretaceous specimen previously referred to *Enaliosuchus macrospondylus* (see Sachs *et al.*, 2020). The second Rhacheosaurini subclade has an indeterminate Cuban specimen as its basal-most member, then a polytomy between *Rhacheosaurus*, *Cricosaurus* and a cf. *Cricosaurus* specimen from Cuba. Within *Cricosaurus* there are two subclades, one consisting of species from the Kimmeridgian-Tithonian of southern Germany; and another consisting of species from the Tithonian of Mexico and Argentina and a Valanginian species from Germany.

In the strong homoplasy down-weighting analyses (k=1, k=3 and k=7) there are three differences compared to the unweighted topology (Fig. 4B, Supplementary Figure): 1) *Geosaurus lapparenti* (Debelmas & Strannoloubsky, 1956) becomes the basal-most member of Geosaurina; 2) the two Chilean metriorhynchids, ‘*Me.*’ *casamiquelai* and ‘*Me.*’ *westermanni*, species form a clade that is recovered as the sister taxon to Metriorhynchidae (i.e. they are no longer recovered as basal geosaurines); and 3) the sister group relationship between *C. vignaudi* and *C. schroederi* is not recovered (the American-Early Cretaceous *Cricosaurus* subclade is a polytomy). This differs from the same analysis performed by Young *et al.* (2020a: Fig 4b) in one notable respect: *Metriorhynchus brevirostris* and ‘*Me.*’ *superciliosus* are not recovered as sister taxa, *Me. brevirostris* is still found to be more derived than *Maledictosuchus*.

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In some moderately down-weighted analyses (k=10) the strict consensus topology differs from that of the unweighted analysis in two ways (Fig. 4C, Supplementary Figure): 1) *Geosaurus lapparenti* is still the basal-most member of Geosaurina, and 2) the American-Early Cretaceous *Cricosaurus* subclade is fully resolved.

In the moderately and weakly down-weighted analyses (k=15 and k=50) the strict consensus topology is almost identical to that of the unweighted analysis, the sole difference is that the American-Early Cretaceous *Cricosaurus* subclade is fully resolved (Fig. 4D, Supplementary Figure). The topology for the k=20 extended implied weighting analysis is unique in resolving *Rhacheosaurus* as the sister taxon to *Cricosaurus* (Fig. 4E, Supplementary Figure). Otherwise, this topology is identical to that of the weakly down-weighted analyses. No statistically significant difference was found between the unweighted topology and any of the extended implied weighting topologies.

Overall the Bayesian results (Fig. 5) are ~~very~~ similar to those found in the moderately and weakly down-weighted analyses (k=15 and k=50). The only differences are that unresolved subclades, such as *Torvoneustes*, the ‘E-clade’ and the German *Cricosaurus* subclade are now fully resolved (although they are ~~very~~ poorly supported nodes).

The constraint analyses show that, while hypothesis three is consistently recovered as the most parsimonious result, it is not a robust one. The parsimony constraint analyses only differ by one or two steps (Supplementary Appendix Three). The unconstrained topologies (which support hypothesis three) are consistently the shortest. When *Maledictosuchus* is forced to be a member of Rhacheosaurini and *Me. brevirostris* excluded (hypothesis two), it only increases step length by one. Finally, forcing ‘*Me.*’ *superciliosus* and *Me. brevirostris* to be sister taxa (hypothesis one) increases the step length by one. Thus, hypothesis three is one step shorter than hypothesis two, and two steps shorter than hypothesis three. This step

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10 difference is consistent across unweighted and weighted analyses (see Supplementary
11 Appendix Three).

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13 Bayesian topological testing strongly supports the conclusion that *Me. brevirostris*
14 and *Me. superciliosus* are not sister taxa (marginal likelihood hypothesis 1 = -2159.734;
15 marginal likelihood hypothesis 2 = -2122.568; $2 \cdot \log_e(B_{12}) = 74.332$) but was unable to
16 differentiate between hypothesis two and hypothesis three (marginal likelihood hypothesis 2
17 = -2122.568; marginal likelihood hypothesis 3 = -2123.047; $2 \cdot \log_e(B_{23}) = 0.958$).
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21 In our phylogenetic analyses, regardless of optimality criterion or parsimony
22 weighting method *Me. brevirostris* was consistently recovered as being more derived than
23 *Maledictosuchus* (Figs 4–5). This supports hypothesis three, which implies that
24 ‘*Metriorhynchus*’ *superciliosus* is not a member of *Metriorhynchus*, and that
25 *Maledictosuchus* is not a member of Rhacheosaurini (as *Me. brevirostris* is one of the
26 external specifiers in the cladogenesis of Rhacheosaurini). That being said, hypothesis two is
27 only one step longer than hypothesis three in the parsimony analyses, and could not
28 statistically differentiated from hypothesis three in the Bayesian topological testing analyses.
29 This is unsurprising given that the *Me. brevirostris* OTU is based solely on a partial cranial
30 rostrum. First-hand re-examination of the metriorhynchid specimens from the Kimmeridgian
31 of Normandy is required to discover more material that can be confidently referred to *Me.*
32 *brevirostris*.
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45 DISCUSSION

46 THE *SUPERCILIOSUS* – *ROSTROMINOR* PROBLEM

47 Where possible herein we have attempted to designate species lectotypes that do not cause
48 nomenclatural problems. However, our designation of MNHN.F RJN 116 as the lectotype of
49 *Steneosaurus rostrominor* impacts the well-known taxon ‘*Metriorhynchus*’ *superciliosus*.
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Following Article 23.9 of the ICZN Code (reversal of precedence), we designate *St. rostrominor* as a *nomen oblitum*. This is done to preserve the prevailing usage of ‘*Me.*’ *superciliosus*. Based on our designated lectotype of *St. rostrominor*, *St. rostrominor* is a subjective senior synonym of ‘*Me.*’ *superciliosus*. This is due to the dental formula of the lower jaw most closely matching that of ‘*Me.*’ *superciliosus* (of the species from the Callovian of Europe; Table 6) and lacking the numerous, small and closely-packed alveoli of *Gracilineustes leedsi* (Andrews, 1913; NHMUK PV R 3014). In order to make *St. rostrominor* a *nomen oblitum* the following two conditions must be met:

- (1) Article 23.9.1.1. the senior synonym or homonym has not been used as a valid name after 1899,
- (2) Article 23.9.1.2. the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years.

Steneosaurus rostrominor fulfils Article 23.9.1.2, as the binomen is rarely mentioned in the literature, and when it is, it is almost always mentioned as being a junior subjective synonym of *Metriorhynchus geoffroyii* (e.g. Steel, 1973). Under Article 23.9.6, these mentions are not to be taken into account when determining Article 23.9.1.1. Allain (2001) mentioned *St. rostrominor* once in his historical overview on the Cuvier (1824) specimens and their complicated history regarding Geoffroy Saint-Hilaire’s (1825) *Steneosaurus* species. Allain (2001) stated that there is a type specimen for *St. rostrominor*, but as discussed above, no type specimen had ever been designated for this species under ICZN Code rules until this paper (note we designated the same specimen as the lectotype that Allain, 2001 mentioned). Allain (2001) went on to indicate that von Meyer (1832) created the

name *Metriorhynchus geoffroyii* for the short snouted species [Cuvier's 'tête à museau plus court'], but Allain did not notice that what he stated to be the type specimen of *St. rostrominor* was assigned to *Streptospondylus altfordensis* by von Meyer. Allain did not comment on the *St. rostrominor* – *Me. geoffroyii* validity. As such, we cannot find a paper after the 19th Century that treated *St. rostrominor* as a valid taxon.

'*Metriorhynchus*' *superciliosus* easily fulfils Article 23.9.1.2, being the most widely cited metriorhynchid species of the past 100 years. In requirement of Article 23.9.1.2 of the ICZN Code, we provide a non-exhaustive list of 50 works in which '*Me.*' *superciliosus* is used as a valid taxon (see references for complete bibliographical details). These works are published by more than 50 authors between 1973 and 2020, thus encompassing a span of much more than 10 years: Adams-Tresman, 1987; Aiglstorfer *et al.*, 2020; Brignon, 2018a, 2018b; Buchy *et al.*, 2013; Buffetaut, 1977, 1979, 1982; Deville, 2004; Foffa *et al.*, 2018a; Foffa & Young, 2014; Gandola *et al.*, 2006; Gasparini *et al.*, 2005, 2006, 2008; Grange & Benton, 1996; Herrera *et al.*, 2013a, 2013b, 2015b; Hua, 1994; Jouve, 2009; Lepage *et al.*, 2008; Massare 1987; Montefeltro *et al.*, 2016; Ōsi *et al.*, 2018; Parrilla-Bel *et al.*, 2013; Pierce *et al.*, 2009; Sachs *et al.*, 2019a, 2020; Steel, 1973; Vignaud, 1997; Waskow *et al.*, 2018; Wilberg, 2015a; Wilkinson *et al.*, 2008; Witmer, 1997; Young & Andrade, 2009; Young *et al.*, 2010, 2011, 2012, 2020a. Therefore, under Article 23.9.2, we consider '*Me.*' *superciliosus* to be *nomen protectum* and *St. rostrominor* to be *nomen oblitum*.

Now that '*Me.*' *superciliosus* is protected, we must establish a new generic name for *superciliosus*. This ensures that the genus *Metriorhynchus* is restricted to Kimmeridgian taxa with at least some posterodorsal retraction of the external nares. This means that 'generalist' long-snouted forms from the Callovian, that retain metriorhynchid symplesiomorphies in narial position, are no longer 'lumped' in with *Metriorhynchus* (see Table 5 for taxa that still require to be re-described and a new generic taxonomy to be established).

SYSTEMATIC PALAEONTOLOGY

METRIORHYNCHIDAE FITZINGER, 1843 (*SENSU* YOUNG & ANDRADE, 2009)

METRIORHYNCHINAE FITZINGER, 1843 (*SENSU* YOUNG & ANDRADE, 2009)

THALATTOSUCHUS GEN. NOV.

(Fig. 6)

Type species

Crocodylus superciliosus Blainville in J.-A. Eudes-Deslongchamps, 1852 (following Recommendation 67B of the ICZN Code) (*nomen protectum*). Now referred to as *Thalattosuchus superciliosus* (Blainville in J.-A. Eudes-Deslongchamps, 1852) comb. nov. Type by designation.

Thalattosuchus superciliosus is a junior subjective synonym of *Steneosaurus rostrominor* Geoffroy Saint-Hilaire, 1825 (*nomen oblitum*).

Etymology

‘Sea crocodile’, given that the species *superciliosus* is perhaps the best known thalattosuchian, it is fitting that the genus be established for this species.

Diagnosis

Same as the only species (see below).

***THALATTOSUCHUS SUPERCILIOSUS* (BLAINVILLE in EUDES-DESLONGCHAMPS, 1852) GEN. ~~ET~~ & COMB. NOV.**

(Fig. 6)

- v 1808 Espèce inconnue de crocodile – Cuvier, p. 90–92, pl. 11, figures 1–2. [*partim*]
- v 1824 Tête à museau plus court – Cuvier, p. 152–153, pl. 8, figures 1–2. [*partim*]
- v 1825 *Steneosaurus rostro-minor* [sic] sp. nov. – Geoffroy Saint-Hilaire, p. 147, 149. [*nomen oblitum*]
- v 1832 *Streptospondylus altfordensis* sp. nov. – von Meyer, p. 106. [*partim*]
- v 1837 *Metriorhynchus geoffroyi* [sic] von Meyer – Bronn, 1835–1837, p. 520, pl. 26, fig. 7b [*partim*]
- v* 1852 *Crocodilus superciliosus* sp. nov. – Blainville in J.-A. Eudes-Deslongchamps, p. 114.
- v 1863 *Teleosaurus superciliosus* (Blainville) comb. nov. – J.-A. Eudes-Deslongchamps, p. 8.
- v 1867 *Teleosaurus superciliosus* (Blainville) – J.-A. Eudes-Deslongchamps, p. 20–21.
- v 1867 *Teleosaurus blainvillei* sp. nov. – J.-A. Eudes-Deslongchamps, p. 19–20.
- v 1869 *Metriorhynchus superciliosus* (Blainville) comb. nov. – E. Eudes-Deslongchamps, 1867–1869, p. 306, pl. 20 fig. 2, pl. 21 fig. 1
- v 1869 *Metriorhynchus blainvillei* (E-Deslongchamps) comb. nov. – Eudes-Deslongchamps, 1867–1869, p. 295, pl. 20 fig. 1, pl. 21 fig. 2–3
- v 1869 *Metriorhynchus moreli* sp. nov. – Eudes-Deslongchamps, 1867–1869, p. 320, pl. 21 fig. 4–5, pl. 22 fig. 1–2.
- v 1869 *Steneosaurus dasyceps* sp. nov. – Seeley, p. 140.
- v 1890b *Metriorhynchus superciliosum* (Blainville) unjust. emend. – Lydekker, p. 232.
- v 1904 *Metriorhynchus jaekeli* sp. nov. – Schmidt, p. 97, pl. 11–12.
- v 1973 *Metriorhynchus superciliosum* [sic] (Blainville) – Steel., p. 45, figures 18 (7, 9), and 19 (7).
- v 1973 *Metriorhynchus blainvillei* (Eudes-Deslongchamps) – Steel., p. 46, figure 19 (2).
- v 1973 *Metriorhynchus moreli* (Eudes-Deslongchamps) – Steel., p. 46, figure 19 (1).
- v 2009 *Metriorhynchus moreli* (Eudes-Deslongchamps) – Young & Andrade, p. 566.
- v 2009 *Metriorhynchus superciliosus* (Blainville) – Young & Andrade, p. 566.
- v 2010 *Metriorhynchus superciliosus* (Blainville) – Young *et al.*, p. 804, fig. 4, 6, 8.
- v 2018 *Metriorhynchus superciliosus* (Blainville) – Brignon, p. 56–61, fig. 11.

Lectotype:

MNHN.F.RJN 256, incomplete skull. (Designation by E. Eudes-Deslongchamps, 1867–1869: 310).

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Note: Young *et al.* (2013) followed Vignaud (1995) in calling MNHN.F.RJN 256 (formerly MNHN 8903) the neotype. As shown by Brignon (2018a) it is in fact the lectotype.

Type locality:

Vaches Noires cliffs, Département du Calvados, Basse-Normandie, France.

Type horizon:

Either the Marnes de Dives Formation or Marnes de Villers Formation. Either upper Callovian or lower Oxfordian, Middle or Upper Jurassic.

Occurrence:

Callovian/Oxfordian of northern France and England (UK).

LSID

Zoobank registration:

Commented [MC3]: Please provide zoobank lsid here for the nomenclatural act of the new genus.

Etymology: The genus is derived from the Greek *θάλαττα*, sea, and *σοῦχος* crocodile [after the Egyptian crocodile god]. The species name derives from Latin, the prefix *Superciliosus* derives from the Latin *super-* for ‘above’, and *-ciliosus*, with eyelashes for ‘eyebrow’, referring to the expanded prefrontals above the orbits.

Diagnosis:

Metriorhynchid crocodylomorph with the following unique combination of characters: conical teeth with little mediolateral compression, crowns have a continuous smooth keel at mesial and distal edges (lacks serrations), enamel on labial and lingual surfaces have conspicuous ornamentation composed of accessory ridges orientated to the apicobasal axis of the crown. Enamel ornamentation is stronger on the lingual face than on the labial face.

Dental formula: 3 premaxillary pairs; 23–27 maxillary pairs, of which 14–15 are anterior to the palatines; 20–22 dentary pairs, of which 16–17 are adjacent to the symphyseal suture and 9–10 are anterior to the splenials. Premaxillary alveoli are consistent in size, with the P1 and P3 being more oval in shape, with the P2 being more sub-circular. The skull is narrow with a mesorostrine snout (*sensu* Young *et al.* 2010). No transverse expansion of the premaxilla (only present in dorsoventrally crushed specimens). Little to no constriction at the premaxilla-maxilla contact. Nasals and premaxillae always separated, in specimens with a basicranial length of 600 mm or more, the distance between the nasals and premaxillae range from 50–132 mm. The nasals terminate anteriorly level to the M9-to-M12 alveoli. Both the frontal and prefrontal bones have a conspicuous pitted ornamentation, although the expression of frontal ornamentation is highly variable. Approximately 90-degree angle formed by the lateral and medial processes of the frontal, with the rostromedial border of the frontoparietal fossa being either rounded or forming a right angle (variability most likely due to taphonomic distortion). A thin sclerotic ring composed of seven ossicles, which do not fill the entire orbit. The deltopectoral crest is moderately developed, with the width of the humerus distal articular head being greater than the width of the deltopectoral crest projecting out from the humerus shaft. (Modified from Young *et al.*, 2013.)

Referred specimens

AMNH FR 997: incomplete skull with mandible, and 23 assorted vertebrae (including cervicals and dorsals); CAMSM J64398: skull (holotype of *Steneosaurus dasyceps*); CAMSM J64900: mid-portion of skull; CAMSM J64918: rostrum; GLAHM V942: skull with mandible from a young individual; GLAHM V963: incomplete skull and mandible, eight dorsal vertebrae, one caudal vertebra, both coracoids, left scapula, right ilium, left ischium and right ischium blade, distal half of the right pubis (from a young individual);

GLAHM V964: skull, mandible, atlas-axis, four cervical vertebrae, cervical and dorsal ribs;
GLAHM V965: skull with right dentary; GLAHM V971: skull in various fragments, atlas-axis, five cervical vertebrae, ten dorsal vertebrae; GLAHM V982: broken skull, mandible, cervical vertebra centrum, atlas left rib; GLAHM V983: broken skull, mandible, sclerotic ring ossicles, dorsal rib; GLAHM V984: broken skull and mandible fragments from two individuals; GLAHM V985: broken skull and mandible fragments, sclerotic ring ossicles; GLAHM V987: broken skull and mandible fragments, sclerotic ring ossicles, rib fragments; GLAHM V988: skull, mandible, atlas-axis, one dorsal vertebra, left ilium, fragment of right pubis, right femur; GLAHM V989: skull with mandible; GLAHM V996: skull with bite marks consistent with that of a *metriorhynchid*; GLAHM V1004: skull and mandible fragments, atlas-axis; GLAHM V1015: incomplete skull, disarticulated mandible, atlas-axis, right atlas rib, both coracoids, right ischium, femora, right tibia and fibula, two coprolites; GLAHM V1027: incomplete skull and mandible, atlas-axis, four cervical vertebrae (from a young individual); GLAHM V1140: broken skull, mandible showing pathological damage, one hyoid, atlas-axis, five cervical vertebrae, 14 dorsal vertebrae, scapulae, both coracoids, humeri, both radii, femora; GLAHM V1142: skull, disarticulated mandible, one hyoid, atlas-axis, right atlas rib, four cervical vertebrae, 19 dorsal vertebrae, two sacral vertebrae, four caudal vertebrae, pubes, ilia, ischia – fused, femora; GLAHM V1143: skull broken in two, mandible, atlas ribs, five cervical vertebrae, four cervical ribs, 17 dorsal vertebrae, right scapula, right coracoid, right humerus (atlas-axis and forelimb lost); MGCL 9959: skull, mandible, associated dorsal and caudal vertebrae, humerus, femur; MGCL 9960: skull, mandible, associated cervical, dorsal and caudal vertebrae, isolated ribs, humerus, pubis, ischium, femur; MNHN.F RJN 116: lower jaw (lectotype of *Steneosaurus rostrominor*, *nomen oblitum*); NHMUK PV R 1530: incomplete skull with mandible, atlas-axis, five cervical vertebrae, 16 dorsal vertebrae, two sacral vertebrae, 35 caudal vertebrae, cervical and

dorsal ribs, coracoid, scapula, humeri, ilia, ischia, pubes, femora, tibiae, fibulae, isolated pes bones, numerous chevrons; NHMUK PV R 1529: skull and mandible (from a young individual); NHMUK PV R 1666: skull and mandible; NHMUK PV R 2030: incomplete skull with mandible; NHMUK PV R 2032: incomplete skull and mandible, atlas-axis, four cervical vertebrae, 17 dorsal vertebrae, two sacral vertebrae, 37 caudal vertebrae, cervical and dorsal ribs, scapula, coracoids, humerus, ilium, ischium, femur; NHMUK PV R 2033: fragmentary skull with mandible, atlas-axis, five cervical vertebrae, 17 dorsal vertebrae, two sacral vertebrae, 29 caudal vertebrae, cervical and dorsal ribs, ilia – fused, ischia – fused, pubes, one tibia, one fibula, two metatarsals; NHMUK PV R 2036: fragments of skull and mandible, one cervical vertebra; NHMUK PV R 2041: incomplete skull; NHMUK PV R 2044: skull and mandible; NHMUK PV R 2049: incomplete skull and mandible, two dorsal vertebrae, one sacral vertebra, ilia, ischia, femora, tibiae, fibulae, isolated bones of the pes; NHMUK PV R 2051: incomplete skull with mandible, atlas-axis, four cervical vertebrae, 15 dorsal vertebrae, two sacral vertebrae, 32 caudal vertebrae, coracoid, scapula, ilia, ischia, pubes, femora, broken tibiae and fibulae, isolated pes bones; NHMUK PV R 2053: incomplete skull; NHMUK PV R 2054: skull, mandible, atlas-axis, four cervical vertebrae, 18 dorsal vertebrae, two sacral vertebrae, 28 caudal vertebrae, cervical and dorsal ribs, ilium, ischium, pubes, tibia, fibula, isolated pes bones, numerous chevrons; NHMUK PV R 2055: incomplete skull; NHMUK PV R 2056: fragments of skull and mandible (from a ~~very~~ young individual); NHMUK PV R 2058: skull with mandibular symphysis; NHMUK PV R 2065: skull fragments (from a young individual); NHMUK PV R 2069: fragments of skull and mandible, atlas-axis, three cervical vertebrae (from a ~~very~~ young individual); NHMUK PV R 3016: incomplete skull, mandible, right coracoid, scapulae, humeri, radius, ulna; NHMUK PV R 6859: skull with disarticulated mandible; NHMUK PV R 6860: skull with disarticulated mandible; PETMG R8: skull lacking rostrum; PETMG R10: incomplete skull;

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PETMG R20: incomplete skull; PETMG R42: incomplete skull; PETMG R180: incomplete skull; SMNS 10115: skull with disarticulated mandible; SMNS 10116: skull with disarticulated mandible.

Note: herein the possibility that *Thalattosuchus superciliosus* is a species-complex and that the epithets *moreli* or *blainvillei* could represent cryptic species is not investigated. That is beyond the scope of this contribution and will be examined in future studies.

COMPARISONS BETWEEN *METRIORHYNCHUS BREVIROSTRIS* AND OTHER
METRIORHYNCHIDS

While the holotype of *Metriorhynchus brevirostris* (MHNG V-2232) lacks autapomorphic characters, it is readily distinguishable from better known metriorhynchid species. It has a unique combination of metriorhynchid symplesiomorphies and a slightly posteriorly retracted narial fossa (see Young *et al.*, 2020a). Furthermore, it lacks the autapomorphies seen in the rostra of the Late Jurassic genera *Dakosaurus*, *Plesiosuchus*, *Torvoneustes*, the ‘E-clade’ taxa, *Cricosaurus* and *Rhacheosaurus* (see Young *et al.* 2012, 2020a; Abel *et al.*, 2020). These include the rostral shortening and resultant reduction in tooth count seen in Geosaurini, the amblygnathous rostrum and lateral plates seen in *Dakosaurus*, the robust triangular rostrum and elongated palatines of *Plesiosuchus*, and the mediolaterally expanded maxillary alveoli seen in the ‘E-clade’ (see Wilkinson *et al.*, 2008; Young *et al.*, 2012, 2020a; Abel *et al.*, 2020). Furthermore, *Me. brevirostris* lacks the ossified internarial bar and more noticeable narial fossa retraction seen in the rhacheosaurin genera *Cricosaurus* and *Rhacheosaurus* (see Young *et al.*, 2020a).

Metriorhynchus brevirostris can be distinguished from all known Middle Jurassic metriorhynchids in that the narial fossa anterior margin is slightly retracted, being level to the

P2 alveoli rather than the P1 alveoli (see Young *et al.*, 2020a). Compared to the Callovian geosaurines, the presence of at least 13 maxillary alveoli anterior to the palatines is higher than the dental formulae of ‘*Metriorhynchus*’ *brachyrhynchus* and *Tyrannoneustes lythrodectikos* (Table 6; Fig. 7). Moreover, the nasal terminates level to the M8 alveoli in *Me. brevirostris* whereas the nasal terminates level to the M6 in ‘*Me.*’ *brachyrhynchus* (NHMUK PV R 3804) and *Ty. lythrodectikos* (PETMG R176) (see Fig. 7). The premaxilla posterodorsal processes terminate level to the M3 alveoli in *Me. brevirostris* also differentiates it from *Ty. lythrodectikos*, where these processes terminate level to the M5 alveoli (PETMG R176, see Fig. 7; Foffa & Young, 2014). *Metriorhynchus brevirostris* can also be distinguished from the Callovian metriorhynchine *Maledictosuchus riclaensis* as it lacks the well-developed reception pits on the lateral margins of the anterior maxilla seen in *Mal. riclaensis* (Parrilla-Bel *et al.*, 2013). *Metriorhynchus brevirostris* is also distinct from *Gracilineustes leedsi* as it lacks: the exceptionally high tooth count, closely packed alveoli, and the poorly developed-to-almost absent maxillary ornamentation of *Gr. leedsi* (Andrews, 1913).

There are notable differences between *Metriorhynchus brevirostris* and *Th. superciliosus*. Although the rostrum of *Me. brevirostris* has encrustations, the maxillary ornamentation is noticeably not as pronounced as it is in *Th. superciliosus* (compare Fig. 1A to 6 and 7C; Andrews, 1913). In dorsal view, there is a constriction at the premaxilla-maxilla contact in *Me. brevirostris*, followed by a noticeable broadening of the premaxilla at approximately the level of the narial fossa posterior margin (Fig. 1A); *Th. superciliosus* lacks both of features, with the posterior premaxilla and anterior maxilla having a largely constant width (PETMG R17 and MNHN.F RJN 256, see Fig 6 and 7C). In *Me. brevirostris* the premaxillary alveoli successively increase in size, with the P1 alveoli being circular in shape, and the P3 alveoli being the most oval of the premaxillary tooth-row (Fig 1B); whereas in *Th. superciliosus* the premaxillary alveoli are largely comparable in size, with the P1 and P3 alveoli being oval in

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shape, and the P2 being the most circular (PETMG R17 and MNHN.F RJN 256, see Fig 6 and 7C). The anterior maxillary alveoli of *Th. superciliosus* are fairly tightly packed, with the interalveolar spaces reduced to thin laminae (especially for the M2–M3 alveoli; PETMG R17 and MNHN.F RJN 256); whereas in *Me. brevirostris* the interalveolar spaces are much broader, even between the M1–M2 and M2–M3 alveoli (Fig. 1). In *Me. brevirostris*, the premaxilla-maxilla suture is almost straight in dorsal view (Fig. 1A), whereas in *Th. superciliosus* it has a more ‘jagged’ interdigitating profile (PETMG R17 and MNHN.F RJN 256, see Fig 6 and 7C). The nasal proceeds slightly further anteriorly in *Me. brevirostris* than in *Th. superciliosus*, with seven maxillary alveoli anterior to the nasals in *Me. brevirostris* (Fig. 1); whereas in *Th. superciliosus* there can be eight (MNHN.F RJN 256, NHMUK PV R 2051), nine (GLAHM V930, NHMUK PV R 2030, PETMG R17) or 10–11 (GLAHM V962).

METRIORHYNCHID PREMAXILLA

One of the characteristic features of thalattosuchians are their long snouts. While there are numerous independent instances of rostral shortening in Thalattosuchia (e.g. *Mystriosaurus* and *Machimosaurini* in Teleosauroidae; *Teleidosaurus*, ‘*Cricosaurus*’ *saltilensis* and Geosaurinae in Metriorhynchoidea; e.g. see Young *et al.*, 2010, 2014; Buchy *et al.*, 2013; Johnson *et al.*, 2017, 2020b; Sachs *et al.*, 2019b), based on their phylogenetic relationships longirostry was the ancestral condition. As discussed by Wilberg (2015b), how thalattosuchians elongated their rostra was different from most other crocodyliform clades. Primary elongation in Thalattosuchia is formed by the maxilla, resulting in the absence of a premaxilla-nasal contact; this contrasts with the elongation of the maxilla and nasals in many other clades, which also retain a premaxilla-nasal contact. The maxilla-only elongation is not unique to Thalattosuchia, it also occurred in the pholidosaurid *Meridiosaurus* (Fortier *et al.*,

2011) and eusuchians such as *Gavialis* (e.g. Martin *et al.*, 2012). What is unique is the combination of an elongated maxilla and a proportionally small premaxilla. First noted and described by Johnson (2019) (see Johnson *et al.*, in review), thalattosuchians sympleiomorphically had a proportionally small premaxilla, contributing less than 25% of total preorbital length. During metriorhynchoid evolution, the premaxilla transitions from a proportionally small bone with four pairs of alveoli (as seen in *Pelagosaurus typus*; Pierce & Benton, 2006) to a proportionally large element with three pairs of alveoli in Metriorhynchidae (Fig. 7). One curiosity of this transition is how the premaxilla goes from being ‘small’ with a variable set of alveoli, three to five pairs in non-metriorhynchids (see Johnson *et al.*, in review), to being proportionally large but restricted to three alveolar pairs in metriorhynchids.

Another peculiarity of premaxillary proportional expansion in Metriorhynchidae is how the premaxilla contacts the maxilla. The phylogenetic dataset of Young *et al.* (2020a) had two characters relating to the premaxillary contact with the first maxillary (M1) alveoli, which herein we merged into a single multi-state character (#359). State (1): “premaxilla does contact the M1 alveoli, but is restricted to the anterior margin in palatal view” was originally scored as a putative apomorphy of *Thalattosuchus superciliosus* and *Me. brevirostris*; however, as can be seen in Fig. 8 this character is actually sympleiomorphic for Metriorhynchidae. Without this character to unite *Th. superciliosus* and *Me. brevirostris* these two species are not found to be sister taxa in any of the unconstrained phylogenetic analyses presented herein.

OTHER METRIORHYNCHIDS FROM THE KIMMERIDGIAN OF NORMANDY

The most recent review of the thalattosuchians from Normandy was by Lepage *et al.* (2008), in which they extensively figured the specimens held in collections in Normandy. In their

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catalogue there were two metriorhynchids from the Kimmeridgian of Normandy. The first was from the Marnes de Bléville Formation (Calcaires à *Harpagodes*; *Rasenia cymodoce* Sub-bBoreal ammonite Zone; lower Kimmeridgian) of Octeville-sur-Mer (Département du Seine-Maritime, Haute-Normandie, France). The specimen is from a large metriorhynchid, estimated to be 5.4 m in length (Young *et al.*, 2011). Lepage *et al.* (2008) provisionally referred the specimen to *Metriorhynchus* cf. *hastifer*, but however the phylogenetic analysis of Abel *et al.* (2020) places this specimen in the unnamed geosaurine ‘E’-clade. Like other members of the ‘E’-clade, the anterior-to-mid maxillary alveoli of this specimen are mediolaterally expanded (Lepage *et al.*, 2008: 51, 53; Abel *et al.*, 2020). Furthermore, the maxillary interalveolar spaces are uniformly ~~very~~ small, being less than half a quarter of the adjacent alveoli. However, ~~the~~ maxillary alveoli of *Metriorhynchus brevirostris* ~~however~~ are circular/sub-circular in shape, and the interalveolar spaces are variable in size (see description above).

The premaxillary alveoli of this ‘E’-clade specimen also differ from that of *Metriorhynchus brevirostris*. In the Lepage *et al.* ‘E’-clade specimen, there is not ~~a great disparity-much difference~~ in size between the P2 and P3 alveoli, and these alveoli are more rounded than the oval-shaped P2 and P3 alveoli of *Me. brevirostris* (Lepage *et al.*, 2008). Finally, the there is no ~~disparity-difference~~ in width between the premaxilla and the anterior region of the maxilla in the Lepage *et al.* (2008) ‘E’-clade specimen. The tightly packed dentition and the similar width of the premaxilla and the anterior region of the maxilla are observed in other members of Geosaurini (e.g. *Dakosaurus maximus* and *Plesiosuchus manselii*, Young *et al.* 2012; *Geosaurus grandis*, Young & Andrade 2009; *Torvoneustes carpenteri*, Grange & Benton, 1996). As such, based on comparative anatomy and the results of our phylogenetic analyses we can preclude a relationship between *Metriorhynchus brevirostris* and the enigmatic ‘E’-clade.

The second Kimmeridgian specimen from Normandy figured by Lepage *et al.* (2008: 137–139) is from Le Havre (Département du Seine-Maritime, Haute-Normandie, France). Lepage *et al.* (2008) referred to this incomplete cranium as *Metriorhynchus* cf. *palpebrosus*. Based on its cranial length, it would have been a medium-sized metriorhynchid, approximately 3.6 m in length (Young *et al.*, 2011). This specimen matches the description of *Metriorhynchus brevirostris* (see above), in the following respects: the three premaxillary alveoli, successively increasing in size, with the P1 alveoli being circular in shape, and the P2–P3 alveoli being oval; lacks a fully ossified internarial bar (thus an undivided external naris); and the anterior-margin of the narial fossa is posterior to the P1 alveoli and the posterior margin terminates slightly posterior to the premaxillary tooth-row. The two specimens also lack all of the rostral autapomorphies observed in the Late Jurassic genera *Dakosaurus*, *Plesiosuchus*, *Torvoneustes*, the ‘E-clade’ taxa, *Cricosaurus* and *Rhacheosaurus* (see the diagnosis above; Wilkinson *et al.*, 2008; Young *et al.* 2012, 2020a; Abel *et al.*, 2020).

The two specimens do differ in some respects. The length of the premaxillary posterodorsal processes in the *Me. brevirostris* holotype terminates level to the M3 alveoli, whereas they terminate level to the M4 alveoli in the Lepage *et al.* (2008) *Me.* cf. *palpebrosus* specimen. It is unclear if the nasal anterior processes terminate level to the M8 alveoli in the Lepage *et al.* (2008) *Me.* cf. *palpebrosus* specimen due to palatal preservation in the region, but it would be either the M8 or M9 alveoli. The shape of the anterior (M1–M3) maxillary alveoli differ between the two specimens with the alveoli being more irregular in shape and more closely-packed in the Lepage *et al.* (2008) *Me.* cf. *palpebrosus* specimen. The variation in tooth count and alveolar shape/spacing could reflect ontogenetic, individual and/or sexual variation. Given the similarities between both specimens, we consider the

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specimen figured in Lepage *et al.* (2008: 137–139) to be better considered as *Metriorhynchus* cf. *brevirostris*.

If the referral of this specimen to *Metriorhynchus* cf. *brevirostris* is correct, then not only did *Me. brevirostris* have an incipiently retracted external nares, but it also had dorsolaterally oriented paroccipital processes, a character diagnostic of Rhacheosaurini (Young *et al.*, 2010; Parrilla-Bel *et al.*, 2013). Lepage *et al.* (2008: 139, figure 8) figured the braincase of the specimen, clearly showing the rhacheosaurin-like paroccipital processes.

CONCLUSIONS

Metriorhynchus is one of the ~~most~~ historically most important genera in Thalattosuchia, and a taxon that is frequently recognized by non-specialist museum colleagues. However, the best-known species is *Me. superciliosus*, a species referred to the genus by E. Eudes-Deslongchamps in the 1860s when he re-diagnosed *Metriorhynchus*. As more, and increasingly complete, *Me. superciliosus* specimens were discovered in England during the late 19th and early 20th Centuries the concept of *Metriorhynchus* became increasingly synonymous with *Me. superciliosus*. ~~As~~ While this happened, the type species (*Me. geoffroyii*) was largely forgotten. ~~At that time in~~ Metriorhynchid taxonomy ~~was used to be~~ entirely phenetic with genera being explicitly based on perceived similarity and not shared ancestry. This resulted in ~~a century of~~ more species being referred to *Metriorhynchus* for a century, based on their superficial how-similarity to ~~they looked to~~ *Me. superciliosus*.

Unfortunately, von Meyer (1832) did not designate a type specimen for *Me. geoffroyii*. ~~As such, We therefore~~ here ~~ein we~~ designated the partial cranial rostrum initially described and figured by Cuvier (1824), MHNG V-2232, as the lectotype. We ~~then~~ re-describe ~~d~~ MHNG V-2232 and demonstrated that it hasd an incipiently retracted narial fossa. Our revised

phylogenetic analyses do not support any named metriorhynchid species being in a clade with MHNG V-2232. Based on our in-depth historical literature review, *Steneosaurus brevirostris* was found to be the senior objective synonym of *Me. geoffroyii*, ~~creating and thus we created~~ the new combination *Metriorhynchus brevirostris*.

Given how integral *Me. superciliosus* has become to *Metriorhynchus* and its ‘popular conception’, we established ~~ed~~ the genus *Thalattosuchus* to contain it. We ~~feel-think~~ it is appropriate that one of the best known thalattosuchian species should be given the generic name *Thalattosuchus*. We also designated ~~d~~ *Th. superciliosus* a *nomen protectum* under Article 23 of the ICZN Code, in order to ~~protect-maintain~~ nomenclatural stability. The lectotype of *Steneosaurus rostrominor* (MNHN.F.RJN 116; designated herein) is most likely from the same species as *Th. superciliosus*, but given the historical confusion surrounding *St. rostrominor* and that it has not been used as a valid name ~~after-since~~ 1899, we designate it a *nomen oblitum*. We now ~~believe-hope that~~ the ‘gordian knot’ ~~that-surrounding~~ is *Metriorhynchus*, *St. rostrominor* and *Th. superciliosus* to have been cut, finally ~~fixing-solving~~ the ‘*Metriorhynchus*’ problem.

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Figure captions

Figure 1. *Metriorhynchus brevirostris* ~~comb. nov.~~ holotype MHNG V-2232. A, dorsal view; B, palatal view. See text for anatomical abbreviations.

Figure 2. *Metriorhynchus brevirostris* ~~comb. nov.~~ holotype MHNG V-2232. A, left lateral view; B, right lateral view. See text for anatomical abbreviations.

Figure 3. *Metriorhynchus brevirostris* ~~comb. nov.~~ holotype MHNG V-2232. A, anterior view; B, posterior view. See text for anatomical abbreviations.

Figure 4. Strict consensus topologies of Metriorhynchinae found in the parsimony analyses. A, unweighted topology; B, strongly down-weighted topology (k=1, k=3 and k=7); C, moderately down-weighted topology (k=10); D, moderate-weak down-weighting topology (k=15 and k=50); E, unique topology (k=20 phenotype dataset). Rhacheosaurini is represented by a large circle.

Figure 5. Phylogram of the phenotypic only dataset Bayesian analysis, focusing on Metriorhynchoidea. Nodes with strong support (posterior probabilities ≥ 0.95) are in red, nodes with low support (posterior probabilities between ≥ 0.90 and < 0.95) are in blue and nodes with poor support (posterior probabilities < 0.90) are unlabelled. Node numbers represent: 1) Metriorhynchidae, 2) Metriorhynchinae, 3) Rhacheosaurini, 4) Geosaurinae, and 5) Geosaurini.

Figure 6. *Thalattosuchus superciliosus* ~~gen. et comb. nov.~~ lectotype MNHN.F RJN 256. A, dorsal view; B, palatal view; C, left lateral view. Scale bar = 10 cm.

Figure 7. Comparative plate of metriorhynchid anterior cranial rostra. A, B, *Metriorhynchus brevirostris* ~~comb. nov.~~, holotype MHNG V-2232 in dorsal and palatal views respectively; C, D *Thalattosuchus superciliosus* ~~gen. et comb. nov.~~, referred specimen PETMG R17 in dorsal and palatal views respectively; E, F, '*Metriorhynchus*' *brachyrhynchus*, referred specimen NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens*) in dorsal and palatal views respectively; G, H, '*Metriorhynchus*' *palpebrosus*, holotype OUMNH J.29823

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10 in dorsal and palatal views respectively; I, J, *Tyrannoneustes lythrodectikos*, referred
11 specimen PETMG R176 in dorsal and palatal views respectively; K, L, *Plesiosuchus*
12 *manselii*, holotype NHMUK PV OR 40103 in dorsal and palatal views respectively. See text
13 for anatomical abbreviations. Scale bar = 5 cm.
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19 **Figure 8.** Comparative plate of metriorhynchid premaxilla-maxilla contact in palatal view. A,
20 *Metriorhynchus brevirostris* ~~comb. nov.~~, holotype MHNG V-2232; B, *Thalattosuchus*
21 *superciliosus* ~~gen. et comb. nov.~~, referred specimen PETMG R17; C, ‘*Metriorhynchus*’
22 *brachyrhynchus*, referred specimen NHMUK PV R 3804 (holotype of ‘*Metriorhynchus*’
23 *cultridens*); D, *Tyrannoneustes lythrodectikos*, referred specimen PETMG R176; E, ‘Swiss
24 rostrum’, NMO 26589; F, ‘English rostrum’, CAMSM J18212; G, ‘Swiss rhacheosaurin’,
25 NMBE 5018135; H, *Cricosaurus bambergensis*, holotype NKMB-P-Watt14/274. See text for
26 anatomical abbreviations. Scale bar = 2 cm.
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Tables

Table 1. The specimens figured in Cuvier’s (1824) plates eight and ten.

Plate	Figures	Material	Specimen number	Taxonomy
8	1–2	Mandible	MNHN.F RJN 116	<i>Steneosaurus rostrominor</i> lectotype (= <i>Thalattosuchus superciliosus</i>)
8	3–4	Snout	MNHN.F RJN 134c	Part of <i>Steneosaurus rostromajor</i> lectotype
8	5–7	premaxilla	MNHN.F RJN 127	Metriorhynchidae

8	8	periorbital region	MNHN.F RJN 124	Metriorhynchidae
8	9–11	atlas-axis	MNHN.F RJN 141	Thalattosuchia indet.
8	12	last cervical and first dorsal vertebrae	MNHN.F.RJN 78	<i>Streptospondylus altdorfensis</i> (Dinosauria)
8	13	Dorsal vertebra	Lost	<i>Streptospondylus altdorfensis</i>
10	1–4	chimera skull	MNHN.F RJN 134c– d (teleosauroid snout) MNHN.F RJN 134a– b (metriorhynchid skull)	Teleosauroid snout (<i>Steneosaurus rostromajor</i> lectotype), and an occipital and periorbital region of a metriorhynchid
10	5–7	snout	MHNG V-2232	<i>Metriorhynchus brevirostris</i> holotype
10	8–10	partial snout	MHNA 70.379	Teleosauroidea

Table 2. List of metriorhynchid species named in reference to Cuvier's (1824) plates.

Author	Species name	Referral to Cuvier's (1824) plates
Cuvier (1824: 152– 153)	'Tête à museau plus court'	Plate 8: figures 1–2, 5–7 Plate 10: figures 5–7
	'Tête à museau plus allongé' [<i>partim</i>]	Plate 10: figures 1–4 (skull only, not the rostrum)
Geoffroy Saint-Hilaire (1825: 147)	<i>Steneosaurus rostro- minor</i>	Plate 8: no figures referred to. Since Geoffroy Saint-Hilaire refers to Cuvier's "short muzzle" species, it

		can be inferred that he designates specimens in figures 1–2, 5–7.
	<i>Steneosaurus rostro-major</i> [partim]	Plate 10: figures 1–4 (skull only, not the rostrum)
Holl (1829: 88)	<i>Steneosaurus brevirostris</i>	Plate 10. In the text, Holl refers to the ‘Havre snout’, thus indicating the specimen in figures 5–7.
Gray (1831: 57)	<i>Gavialis jurinii</i>	Plate 8: figures 1–2, 6–7 Plate 10: figures 5, 7
von Meyer (1832: 106)	<i>Metriorhynchus geoffroyii</i>	Plate 5: figure 10 Plate 8: figures 6–7, 9–11 Plate 9: figures 4–5, 9, 11–12 Plate 10: figures 5–10, 12
	<i>Streptospondylus altfordensis</i> [partim]	Plate 8: figures 1–2 Plate 10: figures 1–4 (skull only, not the rostrum)
Bronn (1835–1837: 520, pl. 26, fig. 7b–d, 8a–b)	<i>Metriorhynchus geoffroyii</i>	Plate 8: figures 1–2, 6–7, 12, 13 Plate 9: figures 3, 6–8, 10 Plate 10: figures 5–7 Re-figures some of Cuvier’s (1824) figures, including plate 10: figures 5–6.
E. Eudes-Deslongchamps (1867–1869: 117, 309)	<i>Metriorhynchus superciliosus</i>	Plate 10: figures 1–4 (skull only, not the rostrum) Plate 10: figures 5–7

	<i>Metriorhynchus moreli</i>	No precise reference to Cuvier's figures.
	<i>Metriorhynchus hastifer</i>	No precise reference to Cuvier's figures.

Table 3. The *Steneosaurus* species of Geoffroy Saint-Hilaire, and the confusion surrounding his 'Honfleur' species according to Brignon (2013).

Geoffroy Saint-Hilaire, 1825	Geoffroy Saint-Hilaire, 1831
'Honfleur' species 1 <i>Steneosaurus rostromajor</i>	'Honfleur' species <i>Steneosaurus rostromajor</i> ?
'Honfleur' species 2 <i>Steneosaurus rostrominor</i>	Geneva cabinet specimen ('Havre snout') <i>Steneosaurus rostrominor</i> ?
	'Caen' species 1: <i>Steneosaurus quillensis</i>
	'Caen' species 2: <i>Steneosaurus aubignensis</i>

Table 4. Sub-division of Callovian-Oxfordian species from England and France previously referred to *Metriorhynchus*.

Reference	Longirostrine species		'Brevirostrine' species
	Well-ornamented skulls	'Smooth' skulls	
E. Eudes-Deslongchamps (1867–1869)	<i>Me. superciliosus</i> <i>Me. moreli</i> <i>Me. blainvillei</i>	-	<i>Me. brachyrhynchus</i>

Andrews (1913)	<i>Me. superciliosus</i>	<i>Me. laeve</i>	<i>Me. brachyrhynchus</i>
	<i>Me. moreli</i>	<i>Me. leedsi</i>	<i>Me. durobrivensis</i>
			<i>Me. cultridens</i>
Adams-Tresman (1987)	<i>Me. superciliosus</i>		<i>Me. brachyrhynchus</i>
Vignaud (1995)	<i>Me. superciliosus</i>	<i>Me. leedsi</i>	<i>Me. brachyrhynchus</i>
Current	<i>Th. superciliosus</i>	<i>Gr. leedsi</i>	' <i>Me.</i> ' <i>brachyrhynchus</i>
			<i>Su. durobrivensis</i>
			<i>Ty. lythrodictikos</i>

Table 5. List of '*Metriorhynchus*' species that require re-description and new generic taxonomy. (Note, some of these species are currently being re-described.)

Species	Age	Locality
' <i>Me.</i> ' <i>brachyrhynchus</i>	Callovian	England, France, Germany
' <i>Me.</i> ' <i>casamiquelai</i>	Callovian	Chile
' <i>Me.</i> ' <i>westermanni</i>	Callovian-?Oxfordian	Chile
' <i>Me.</i> ' <i>hastifer</i>	Kimmeridgian	France
' <i>Me.</i> ' <i>palpebrosus</i>	? early Tithonian	England

Table 6. Dental formulae of metriorhynchid species from the Callovian of Europe.

Species	Specimen	Premaxilla	Maxilla (total)	Maxilla (anterior to palatines)	Dentary (total)	Dentary (adjacent to symphyseal suture)	Dentary (anterior to splenials)
<i>Steneosaurus rostrominor</i>	MNHN.F RJN 116	-	-	-	19 *	12 *	7 *
<i>Thalattosuchus superciliosus</i>	MNHN.F RJN 256	3	~25	16	-	-	-
	NHMUK PV R 2033	3	25	14 or 15	-	-	-
	NHMUK PV R 2044	3	>14	14	>17	14e	9
	NHMUK PV R 2054	?	?	?	21	17	9
	NHMUK PV R 6860	3	23–24	14	?	?	?
	NHMUK PV R 6859	3	27	15	?	?	?
	NHMUK PV OR 46323	?	?	?	>17	17	9
	SMNS 10115	3	24	15	?	?	?
	GLAHM V930	3	25–27	17	~23	17–18	12
	GLAHM V962	3	28	18	21	15–17	~10
	GLAHM V965	3	25	16	>18	NA	NA
	GLAHM V983	3	24	15–16	20–21	>14	NA
	GLAHM V987	3	25e	15–16	21	~17	15
	GLAHM V1004	3	26	-	24	-	-
	PETMG R10	3	25e	-	21–22	15	11
	PETMG R17	3	>18	16	~21	15 or 16	12
	Species range	3	23–28	14–18	20–24	15–18	9–15
<i>Gracilineustes leedsi</i>	NHMUK PV R 2042	3	>28	18e	34e	18e	10
	NHMUK PV R 3014	3	>26	-	34e	19–20e	11–12
	NHMUK PV R 3540	3	>34	20	-	-	-
	Species range	3	>34	20	~34	19–20	10–12
<i>Maledictosuchus riclaensis</i>	Parrilla-Bel <i>et al.</i> (2013)	3	30–33	18	>21	20–21	13 or more
' <i>Metriorhynchus</i> ' <i>brachyrhynchus</i>	NHMUK PV R 3700	3	18	9–10	-	-	-
	NHMUK PV R 3804	3	17	9	17	13	6
	Species range	3	17–18	9–10	17	13	6

<i>Tyrannoneustes lythrodectikos</i>	NHMUK PV R 3939	>1	18e	10	15–16e	>6	~7–8
	PETMG R176	3	18–19	10–11	17–19	14e	8
	<i>Species range</i>	3	18–19	10–11	17–19	14e	8
<i>Suchodus durobrivensis</i>	NHMUK PV R 1994	-	-	-	12–13	10–11	6
	NHMUK PV R 2039	-	-	-	11e	10e	5e
	Lepage <i>et al.</i> (2008)	-	-	-	12	10	6
	<i>Species range</i>	?	?	?	12–13	10–11	5–6

e, Estimate.

* The anterior 4 alveoli of MNHN.F RJN 116 are not preserved.

Figure 1. *Metriorhynchus brevirostris* comb. nov. holotype MHNG V-2232. A, dorsal view; B, palatal view. See text for anatomical abbreviations.

184x227mm (300 x 300 DPI)

Figure 2. *Metriorhynchus brevirostris* comb. nov. holotype MHNG V-2232. A, left lateral view; B, right lateral view. See text for anatomical abbreviations.

184x172mm (600 x 600 DPI)

Figure 3. *Metriorhynchus brevirostris* comb. nov. holotype MHNG V-2232. A, anterior view; B, posterior view. See text for anatomical abbreviations.

92x71mm (300 x 300 DPI)

Figure 4. Strict consensus topologies of Metriorhynchinae found in the parsimony analyses. A, unweighted topology; B, strongly down-weighted topology ($k=1$, $k=3$ and $k=7$); C, moderately down-weighted topology ($k=10$); D, moderate-weak down-weighting topology ($k=15$ and $k=50$); E, unique topology ($k=20$ phenotype dataset). Rhacheosaurini is represented by a large circle.

167x129mm (300 x 300 DPI)

Figure 5. Phylogram of the phenotypic only dataset Bayesian analysis, focusing on Metriorhynchoidea. Nodes with strong support (posterior probabilities ≥ 0.95) are in red, nodes with low support (posterior probabilities between ≥ 0.90 and < 0.95) are in blue and nodes with poor support (posterior probabilities < 0.90) are unlabelled. Node numbers represent: 1) Metriorhynchidae, 2) Metriorhynchinae, 3) Rhacheosaurini, 4) Geosaurinae, and 5) Geosaurini.

208x128mm (300 x 300 DPI)

Figure 6. *Thalattosuchus superciliosus* gen. et comb. nov. lectotype MNHN.F RJN 256. A, dorsal view; B, palatal view; C, left lateral view. Scale bar = 10 cm.

184x153mm (300 x 300 DPI)

Figure 7. Comparative plate of metriorhynchid anterior cranial rostra. A, B, *Metriorhynchus brevirostris* comb. nov., holotype MHNG V-2232 in dorsal and palatal views respectively; C, D *Thalattosuchus superciliosus* gen. et comb. nov, referred specimen PETMG R17 in dorsal and palatal views respectively; E, F, '*Metriorhynchus*' *brachyrhynchus*, referred specimen NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens*) in dorsal and palatal views respectively; G, H, '*Metriorhynchus*' *palpebrosus*, holotype OUMNH J.29823 in dorsal and palatal views respectively; I, J, *Tyrannoneustes lythrodectikos*, referred specimen PETMG R176 in dorsal and palatal views respectively; K, L, *Plesiosuchus manselii*, holotype NHMUK PV OR 40103 in dorsal and palatal views respectively. See text for anatomical abbreviations. Scale bar = 5 cm.

184x110mm (300 x 300 DPI)

Figure 8. Comparative plate of metriorhynchid premaxilla-maxilla contact in palatal view. A, *Metriorhynchus brevirostris* comb. nov., holotype MHNG V-2232; B, *Thalattosuchus superciliosus* gen. et comb. nov., referred specimen PETMG R17; C, '*Metriorhynchus*' *brachyrhynchus*, referred specimen NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens*); D, *Tyrannoneustes lythrodectikos*, referred specimen PETMG R176; E, 'Swiss rostrum', NMO 26589; F, 'English rostrum', CAMSM J18212; G, 'Swiss rhacheosaurin', NMBE 5018135; H, *Cricosaurus bambergensis*, holotype NKMB-P-Watt14/274. See text for anatomical abbreviations. Scale bar = 2 cm.

92x99mm (300 x 300 DPI)