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The enigma of Enaliosuchus, and a reassessment of the Lower Cretaceous fossil record of Metriorhynchidae

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Abstract

Enaliosuchus macrospondylus Koken, 1883 was one of the first thalattosuchian taxa from the Cretaceous to be described. The type series includes an atlas-axis complex, remnants of three post-axial cervical vertebrae, several dorsal vertebrae, a caudal vertebra, an incomplete femur and a fragmentary sacral rib from the upper Valanginian of northern Germany. Additionally, two isolated, non-thalattosuchian, tooth crowns from the uppermost Valanginian to lowermost Hauterivian of different localities in northern Germany were tentatively assigned to E. macrospondylus by Koken. The taxon was established for the distinctive the atlas-axis morphology, in particular the apparent lack of an axis parapophysis. Enaliosuchus macrospondylus has been considered a valid taxon in recent studies, based upon a largely complete metriorhynchid specimen from the Valanginian of France that had been referred to this taxon, an assignment that has never been questioned. Here we provide a detailed re-description of the E. macrospondylus holotype specimen and determine whether it is diagnostic, and if a referral of the French specimen to E. macrospondylus is justified. We also discuss whether E. macrospondylus and another metriorhynchid specimen from the Valanginian of northern Germany, described as Enaliosuchus schroederi, are conspecific. Finally, we provide an overview of the current knowledge of metriorhynchid diversity during the Cretaceous.

Keywords	Crocodylomorpha; Thalattosuchia; Metriorhynchidae; Lower Cretaceous; Germany
Taxonomy	Systematic Paleontology, Vertebrate Paleontology

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28.02.2020

Dear Eduardo,

we are grateful for the comments on our manuscript “The enigma of *Enaliosuchus*, and a reassessment of the Lower Cretaceous fossil record of Metriorhynchidae” are we are pleased to resubmit a revised version. We incorporated most of the suggested changes and provide a detailed response in a separate file. Both reviews were very fair and helped to improve the quality of our paper.

We hope you will find our revised manuscript suitable for publication in *Cretaceous Research*.

Best wishes,

Sven Sachs

The enigma of *Enaliosuchus*, and a reassessment of the Lower Cretaceous fossil record of Metriorhynchidae

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ABSTRACT

Enaliosuchus macrospondylus Koken, 1883 was one of the first thalattosuchian taxa from the Cretaceous to be described. The type series includes an atlas-axis complex, remnants of three post-axial cervical vertebrae, several dorsal vertebrae, a caudal vertebra, an incomplete femur and a fragmentary sacral rib from the upper Valanginian of northern Germany. Additionally, two isolated, non-thalattosuchian, tooth crowns from the uppermost Valanginian to lowermost Hauterivian of different localities in northern Germany were tentatively assigned to *E. macrospondylus* by Koken. The taxon was established for the distinctive the atlas-axis morphology, in particular the apparent lack of an axis parapophysis. *Enaliosuchus macrospondylus* has been considered a valid taxon in recent studies, based upon a largely complete metriorhynchid specimen from the Valanginian of France that had been referred to this taxon, an assignment that has never been questioned. Here we provide a detailed re-description of the *E. macrospondylus* holotype specimen and determine whether it is diagnostic, and if a referral of the French specimen to *E. macrospondylus* is justified. We also discuss whether *E. macrospondylus* and another metriorhynchid specimen from the Valanginian of northern

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Keywords:
Crocodylomorpha
Thalattosuchia
Metriorhynchidae
Lower Cretaceous
Germany

1. Introduction

Thalattosuchian crocodylomorphs are considered to be rare in Lower Cretaceous strata. These specimens include the youngest recorded examples of the group, which so far is documented to the lowermost Aptian (see discussion below). In Germany, the first Cretaceous thalattosuchian remains were described by Ernst Koken from the Valanginian of Lower Saxony as a new genus and species, *Enaliosuchus macrospondylus* Koken, 1883. The holotype material comprises a number of cervical, dorsal and caudal vertebrae, along with limb and rib elements. Additionally, Koken (1883) tentatively referred two isolated teeth from two separate localities to his new taxon. Due to its geological age and the well preserved atlas-axis complex, the type specimen of *E. macrospondylus* sparked controversy and curiosity into the diversity and taxonomy of Cretaceous thalattosuchians (e.g. Schroeder 1921; Kuhn 1936; Hua *et al*., 2000; Karl *et al*., 2006), and also the diversity of cervical osteology in crocodylomorphs (e.g. Koken 1883, 1887; Baur 1886; Jaekel 1904; Boschma 1922). However, the *E. macrospondylus* holotype has never received an in-depth reappraisal, and its purported relationships with other thalattosuchian specimens (Kuhn 1936; Hua *et al*., 2000; Karl *et al*., 2006) have largely been based upon Koken's (1883) description. This original description was extensive, but it was limited by a lack of comparative metriorhynchid specimens during the late 19th

Century. Here we redescribe the holotype of *E. macrospondylus*, and assess the impact this has for the taxonomy of Early Cretaceous metriorhynchids.

1.1 Historical overview

Koken (1883) established *Enaliosuchus macrospondylus* as a new genus and species because of the seemingly novel morphology of the atlas-axis complex. In particular, the presence of atlas rib facets being placed anteroventrally on the atlas centrum was listed as a peculiar feature for *Enaliosuchus* (Koken 1883: 799). Koken (1883) compared the atlas-axis complex to those of modern crocodylians, teleosauroids and the basal metriorhynchoid *Pelagosaurus typus* Bronn, 1841 (see Koken 1883: 809, table therein); but not with metriorhynchids.

A second specimen, comprising an incomplete cranium and lower jaw, with the atlas-axis and first post-axial cervical vertebra from the lower to middle Valanginian Stadthagen Formation of north-western Germany was referred to *Enaliosuchus* by Schroeder (1921). The basis for this referral was that the atlas-axis complex had similar atlas rib placement as that described by Koken (1883) for *Enaliosuchus macrospondylus* (see Schroeder 1921: 364). Interestingly, Schroeder (1921) neither explicitly referred the new specimen to *E. macrospondylus*, nor did he erect a new species for it. This was carried out later by Kuhn (1936) who named the specimen *E. schröderi* Kuhn, 1936. Note, that the use of the umlaut in the specific epithet by Kuhn (1936) was a hypercorrection, as the correct spelling of Schroeder's name is with the *oe*. Furthermore, usage of diacritic marks is not acceptable in a scientific name, in accordance with Article 27 of the ICZN Code. Thus, the correct spelling is *E. schroederi*.

The acceptance of *E. schroederi* as a distinct species has been disputed. While some papers have accepted both species as being valid (e.g. Steel 1973; Young & Andrade, 2009), they did not base their opinions on a detailed comparison of the holotypes. Sickenberg (1961) was the first to ask whether *E. schroederi* was distinct from *E. macrospondylus*, principally because Schroeder

(1921) was unsure in his original description whether the two specimens were conspecific (due to the limited overlap between them) and only assigned the specimen to the genus *Enaliosuchus*, leaving the species open. Hua *et al*. (2000) were the first to formally considered *E. schroederi* to be a subjective junior synonym of *E. macrospondylus*, rendering *Enaliosuchus* a monospecific genus. Jouve (2009) followed the taxonomy of Hua *et al.* (2000). Karl *et al*. (2006: 56) considered the establishment of *E. schroederi* to be "completely unnecessary", and could not preclude that the two species were conspecific.

A third putative *Enaliosuchus* specimen, an incomplete skeleton from the lower Valanginian (*Busnardoites campylotoxus* ammonite Zone) of south-eastern France, was referred to *E. macrospondylus* by Hua *et al*. (2000). This specimen (catalogue number 990201 from the collection of the Clément, Réserve Naturelle Géologique de Haute Provence in Digne les Bains – here later referred to as RNGD 990201) comprises most of the cranium and mandible, an incomplete atlas-axis complex, as well as five post-axial cervical and 15 dorsal vertebrae. While there is only minor overlap with the *Enaliosuchus macrospondylus* holotype material, this referral was accepted without comment in subsequent publications (e.g. Young & Andrade, 2009; Parrilla-Bel & Canudo, 2015; Sachs *et al.*, 2019). The cranial rostrum of RNGD 990201 is highly distinctive with its posterodorsally retracted external nares, and Hua *et al*. (2000) used this specimen to emend the diagnosis of *E. macrospondylus*. For the first time *Enaliosuchus* was clearly defined, and shown to be distinct from other metriorhynchid taxa.

Enaliosuchus has been considered to be a poorly known metriorhynchid (von Huene 1956; Steel 1973). Note, Young & Andrade (2009) altered the generic composition of *Geosaurus*, which from 1901 – 2008 was considered to be a Late Jurassic longirostrine form, and moved several species from *Geosaurus* to *Cricosaurus* and *Rhacheosaurus*. This unfortunately complicates the next two paragraphs and their discussion on previous hypotheses on the position of *Enaliosuchus* in Metriorhynchdae. Buffetaut (1982: 26) considered the *E. schroederi* holotype to be very similar to

104 *Geosaurus* Cuvier, 1824 (*Cricosaurus* Wagner, 1858 and *Rhacheosaurus* von Meyer, 1831 sensu
105 Young & Andrade, 2009), and based on the *E. schroederi* holotype, Buffetaut (1982) concluded that
106 the genus was distinct and valid. In Vignaud's (1995) unpublished PhD thesis, he considered
107 *Enaliosuchus* to be similar to *Geosaurus gracilis* (von Meyer, 1831) (*Rhacheosaurus* sensu Young
108 & Andrade, 2009), although he noted that the *E. schroederi* holotype and '*G.*' *gracilis* can be
109 differentiated on prefrontal and tooth enamel ornamentation characters. Vignaud (1995) therefore
110 provisionally retained *Enaliosuchus* as a valid genus. Neither Buffetaut (1982) nor Vignaud (1995)
111 examined a potential synonymy between *E. macrospondylus* and *E. schroederi*, although Vignaud
112 (1995) did state that Kuhn (1936) did not provide a diagnosis for *E. schroederi*. Moreover, it is clear
113 that the retention of *Enaliosuchus* as a valid genus by both Buffetaut (1982) and Vignaud (1995)
114 was based on the anatomy of the *E. schroederi* holotype, not the *E. macrospondylus* holotype.

115 The evolutionary relationships of *Enaliosuchus* have been further discussed since the
116 description of the French specimen by Hua *et al*. (2000) who considered *Enaliosuchus* to be closely
117 related to *Geosaurus* (*Cricosaurus* and *Rhacheosaurus* sensu Young & Andrade, 2009). The
118 evolutionary relationships of *Enaliosuchus* was first tested by Wilkinson *et al*. (2008), who found *E.*
119 *macrospondylus* (scoring based on the *E. macrospondylus* holotype and the French specimen) to be
120 within a clade formed by *Geosaurus* species (pre-Young & Andrade, 2009 metriorhynchid
121 taxonomy). Jouve (2009) however recovered *Enaliosuchus macrospondylus* (scoring based on the
122 *E. schroederi* holotype and the French specimen) as the sister taxon to *Dakosaurus* Quenstedt,
123 1856. It is unclear whether the different specimen scoring sources, and/or the different character and
124 taxon sets, are responsible for these differences.

125 The validity of the genus *Enaliosuchus* has been questioned, in different ways, by Karl *et al*.
126 (2006) and Young & Andrade (2009). Karl *et al*. (2006) referred both *E. macrospondylus* and *E.*
127 *schroederi* to the genus *Metriorhynchus* von Meyer, 1832, but did not retain either species as valid.
128 Whereas, based on their phylogenetic analysis, Young & Andrade (2009) considered *Enaliosuchus*

to be a subjective junior synonym of *Cricosaurus*, as *E. macrospondylus* and *E. schroederi* were recovered as a subclade within their *Cricosaurus* clade. Young & Andrade (2009) chose not to retain *Enaliosuchus*, as under their evolutionary hypothesis it would render *Cricosaurus* paraphyletic, or demand the creation of multiple new genera. Note however, that they followed the emended diagnosis of *Enaliosuchus* from Hua *et al*. (2000) without comment; and that the *E. macrospondylus* operational taxonomic unit (OTU) scored by Young & Andrade (2009) was based on the referred French specimen and the holotype. Interestingly, further iterations of the phylogenetic dataset used by Young & Andrade (2009) have found *E. macrospondylus* and *E. schroederi* to be distantly related, albeit both within Rhacheosaurini (datasets starting from Young *et al*., 2017).

In sum, *Enaliosuchus* is one of the most poorly understood metriorhynchid genera. Previous studies have questioned the validity of the genus, and the validity of the second species assigned to the genus (*E. schroederi*). Some studies that accept the validity of *Enaliosuchus* have done so based on the anatomy of the *E. schroederi* holotype, not the *E. macrospondylus* holotype. The referral of the highly diagnostic French specimen to *E. macrospondylus* was used to emended the specific diagnosis, and for the first time clearly define *Enaliosuchus* and show it to be distinct from other metriorhynchid taxa. Therefore, the following questions need to be addressed, and will be herein: (1) is the *E. macrospondylus* holotype diagnostic; (2) do the holotypes of *E. macrospondylus* and *E. schroederi* share synapomorphies that would justify assigning them to the same species (i.e. the monospecific hypothesis of Hua *et al*. (2000)); and (3) was the referral of the highly diagnostic French specimen to *E. macrospondylus* justified?

1.2. Institutional Abbreviations

MB – Museum für Naturkunde, Berlin, Germany; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK – Natural History Museum, London, UK; RMH – Roemer und Pelizaeus

Museum, Hildesheim, Germany; RNGD – Réserve Naturelle Géologique de Haute Provence, Digne les Bains, France; MM – Mindener Museum, Minden, Germany.

2. Geological settings

The material that constitutes the holotype of *Enaliosuchus macrospondylus* and the referred teeth were found in two different locations in southern Lower Saxony, Germany and are actually separated by a significant stratigraphical gap. With regard to the holotype, Koken (1883: 792) specified the "Hils [strata] of the Osterwald" as the locality, and the horizon as "level of *Ammonites (Olcostephanus) marginatus*". Unfortunately, this information is somewhat ambiguous by present-day concepts and need to be further elucidated. Geographically, the term "Osterwald" describes a small mountainous region, ca. 30 km south-southwest of Hannover; as well as to the town of Osterwald, which is located in the southern margin of those hills (Fig. 1A-B). The grammatical form used by Koken ("des Osterwaldes") indicates that he referred to the mountains rather than to the settlement proper. Most of the Osterwald mountain range is formed by strata from the Jurassic and the non-marine Berriasian – the marine Lower Cretaceous is exposed only in a small area in the southeastern part due to a southeasterly dip of the succession (Albrecht 1913). While there are numerous fossils from the marine Lower Cretaceous with the label "Osterwald" in museum collections, as well as mentioned in the literature, details of the exact nature of this or these outcrop(s) are rarely given. Von Koenen (1902) mentioned two important sources of such material from Osterwald:

(1) the now abandoned brickworks clay-pit of the town of Osterwald, located c. 0.5 km to the east of the settlement. It exposed upper Hauterivian clay- and marlstones with an abundancy of the heteromorph ammonite *Aegocrioceras capricornu* (Roemer 1841), preserved in calcareous concretions (see also Stolley 1908).

(2) The Osterwald Tiefbauschacht, an abandoned mine shaft, c. 1.3 km east of the town of Osterwald, that penetrated Valanginian marine strata to reach the Berriasian coal seams below (Albrecht 1913). The mine shaft was constructed between 1879 and 1890 (Grimme, 2010).

The lithostratigraphic term "Hils [Formation]", used by Koken, that denotes marine, mostly pelitic deposits of Valanginian through Albian age in northern Germany, is currently superseded by the Minden Braunschweig Group (Erbacher *et al*., 2014a). In the Osterwald region, it can include beds of Valanginian through Hauterivian age.

Unfortunately, the sedimentary matrix of the type specimen, consisting of a reddish sideritic claystone ("rothbrauner Thoneisenstein" in the terminology of Koken) is not conclusive, as this lithotype may occur in the Valanginian as well as in the Hauterivian of the region (e.g. Mutterlose 1984). The biostratigraphic information provided by Koken for the stratum typicum is problematic as well. His "*Ammonites (Olcostephanus) marginatus*" obviously refers to the occurrence of the ammonite species described by Neumayr & Uhlig (1881: 157) as "*Olcostephanus marginatus* (Phill?) Römer" from Osterwald. These authors – following Roemer (1841) - redefined the species *Ammonites marginatus* Phillips, 1829, based on a poorly figured and described juvenile individual from England, to include some specimens from Lower Saxony. However, von Koenen (1902, 1909) separated the Lower Saxonian material as *Polyptychites marginatus* (Neumayr & Uhlig, 1881) from the English *Ammonites marginatus* Phillips, 1829. The latter was revised as *Simbirskites marginatus* (Phillips, 1829), a zone index fossil from the upper Hauterivian, by Rawson (1971).

The referred material of "*Polyptychites marginatus*" sensu Neumayr & Uhlig (1881), figured and discussed by von Koenen (1902, 1909), was subsequently partly reassigned to *Polyptychites keyserlingi* (Neumayr & Uhlig, 1881) by Jeletzky & Kemper (1988), and partly to *Polyptychites polyptychus* (von Keyserling, 1846) by Bogomolov (1989). *Polyptychites keyserlingi* is clearly a middle lower Valanginian taxon, while *P. polyptychus* was reported from the lowermost

upper Valanginian (Jeletzky and Kemper 1988). With regard to the original material of "*Olcostephanus*" *marginatus* from Neumayr & Uhlig (1881), Jeletzky & Kemper (1988: 29) noticed some doubts about the source stratum, suggesting that it may be "misplaced" from the Jurassic.

Nevertheless, Koken (1883) also clearly associated the horizon of "*Ammonites (Olcostephanus) marginatus*" with the "Hils Formation", and the matrix lithology supports a Lower Cretaceous origin of the *Enaliosuchus macrospondylus* postcranial material. Considering that the taxa currently comprising von Koenen's (1902, 1909) concept of his Lower Cretaceous "*Polyptychites marginatus*" (that was in turn based on Neumayr & Uhlig 1881) range from the middle lower to lowermost upper Valanginian (Jeletzky & Kemper 1988, Bogomolov 1989), it is the most plausible assumption that the holotype of *Enaliosuchus macrospondylus* originates from this chronostratigraphic interval of the lower Stadthagen Formation in the Minden Braunschweig Group (sensu Erbacher *et al*. 2014a). The locality was possibly the Tiefbauschacht Osterwald mine shaft near the town of Osterwald. This localization is also in concordance with the information in von Koenen (1902) for the ammonite material from "Osterwald". It remains unclear, on what basis Karl *et al*. (2006) correlated the stratum typicum with the "Astierienschichten". The "Astierienschichten" ("Astierien beds", an obsolete lithostratigaphic term) are lowermost Hauterivian in age according to Mutterlose (1992a).

The first isolated tooth referred to *E. macrospondylus* by Koken (1883: 824; MB.R.3636) was found at the Elligser Brink, a hill ca. 0.6 km south of the town of Delligsen in the Hils Mountains, about 50 km south of Hannover. Koken (1883) noted that it originates from the collection of Friedrich Koch. Koch & Dunker (1837) described an assortment of vertebrate remains in the marine Lower Cretaceous strata of this locality, that became known as the "Elligserbrink bed". As Koken (1883) did not mention otherwise, it is plausible that the tooth came from the same horizon. This is corroborated by the fact that Koken referred also to this collection, stratum, and

locality, when describing the disputed pterosaur "*Ornithocheirus*" *hilsensis* in the same work (Koken 1883: 824f.). According to Burri (1956), the "Elligserbrink bed" dates to the uppermost Valanginian or lowermost Hauterivian (Stadthagen Formation, Minden-Braunschweig-Group).

The second isolated tooth Koken (1883) referred to *E. macrospondylus* (RMH uncatalogued [2]) originates from the "Hils conglomerate of the Osterwald". According to Erbacher *et al*. (2014b) the lithostratigraphic name "Hils Conglomerate" in its classic sense (Roemer 1841) is obsolete and defines various homonymous units, ranging from the Berriasian to the Cenomanian. However, in a more strict and regional sense it is synonymous to the Grenzlerburg Member of the Salzgitter Formation (uppermost Valanginian through lower Hauterivian, Erbacher *et al*. 2014b).

From a palaeoenvironmental point of view, all localities were situated in an open marine, euhaline, oxygenated shallow-water setting with fine-grained sedimentation and low background sedimentation rates. The Grenzlerburg Member represents partly a transgressive carbonatic conglomerate in a marginal setting with abundant fauna (e.g. Mutterlose 1984, 1992a, b; Mutterlose & Bornemann, 2000; Fig. 1C)

3. Description of Koken's hypodigm of *Enaliosuchus macrospondylus*

3.1. Status of the type material

Koken (1883: 792) described the majority of his material as if it came from a single individual, although it was in a largely disarticulated and dissociated state when he studied it. He based his assumption on the fact that it derived from a single locality and stratum, the fitting proportions and the lack of duplicate skeletal elements. Consequently, the remains received one accession MB.R.1943 (with 16 subnumbers MB.R.1943.1-16) and are considered the holotype of *Enaliosuchus macrospondylus*. Koken (1883) mentioned that the material was initially part of the Henne collection, but the exact whereabouts of the discovery remain unknown. It is also unknown if all parts of the axial skeleton where found in association (Koken 1883 p. 792 only mentioned that

some ribs and limb elements were found separately). Therefore we cannot be certain the elements found at the type locality all come from the same individual.

Additionally, Koken (1883) referred an isolated dorsal vertebra (RMH uncatalogued (1)) from another collection but the same locality and stratum, and two isolated tooth crowns (RMH uncatalogued (2) and MB.R.3636) to his new taxon. The latter were added by Koken for being identified as "crocodilian" and originating from marine strata of similar age and region. A fragmentary phalanx (MB.R.1939), likewise from the Henne collection and from the same locality and stratum, is present in MB collection, but was not described by Koken (1883). These four specimens need to be excluded from the type material, as is described in the Systematic Synopsis below.

Below the material is described as it was summarised by Koken (1883).

3.2. Teeth

Koken (1883) assigned two teeth to the *Enaliosuchus macrospondylus* hypodigm, one from the MB collection and one from the RHM collection (Fig. 2). Both teeth were found separately from the remainder of the skeleton (see the geological history section above) and the referral to *Enaliosuchus* was not justified. Curiously, the RHM houses two teeth which are labelled *Enaliosuchus macrospondylus*, but following Koken's (1883) description of the tooth crown being incomplete, the right specimen in Fig. 2C appears to be the correct referred specimen.

The tooth crown MB.R.3636 (Fig. 2A, B) is conical, slightly lingually curved and bears pronounced apicobasally aligned enamel ridges that are contiguous from the base of the crown to the apex. Such enamel ridges are rare in Thalattosuchia, as most ridged teeth have both long ridges and shorter ridges, generally closely packed, but the ridges rarely are contiguous along the entirety of the crown (see the tooth close-up photographs in Young *et al*. 2013, 2014a). The enamel ridges in MB.R.3636 become closer to one another apically. The apex itself is not present, as the crown is

extensively worn in that region. Whether it is taphonomic or biological in origin is unclear without scanning electron microscopy. Carinae are formed mesially and distally, bearing fine denticles. The basal enamel ornamentation is reminiscent of *Anteophthalmosuchus* Salisbury & Naish, 2011 (see Ristevski *et al*. 2018); however, given the lack of a complete tooth crown, and the lack of an in-depth study into the dental variation within Goniopholididae, this specimen can only be referred to as ?Goniopholididae. The RMH (uncatalogued (2)) tooth crown (Fig. 2C) is largely damaged and bears more enamel ridges that are place closer to one another.

As these remains cannot be demonstrated to belong to the holotype or *Enaliosuchus macrospondylus* at all, they have to be excluded from the type material. In consequence no cranial material is known from *Enaliosuchus macrospondylus*.

3.3. Atlas-axis complex

The atlas-axis complex (MR.R.1943.2) comprises the atlas intercentrum, the atlas and axis centra, parts of the atlas and axis neural arches, as well as the axis neural spine (Fig. 3). A fragmentary left atlas rib is also preserved. The atlas intercentrum forms the ventral part of the atlas cup (Fig. 3A). It is semicircular in anterior view, and slightly displaced from its original position. Dorsally the atlas intercentrum reaches to about mid-height of the atlas centrum, where it meets the atlas neural arches (Fig. 3A, B, E). Posteriorly and ventrally the atlas intercentrum contacts the atlas centrum. Posteroventrally, the slightly convex ventral side of the atlas intercentrum meets the anterior surface of the axis centrum (Fig. 3F). Laterally the atlas intercentrum forms the anterior part of the atlas rib facet, of which the remainder is formed by the atlas centrum (Fig. 3B, E). The anterior fragment of the left atlas rib is still attached to the rib facet. The atlas rib is slightly posterolaterally inclined and becomes transversely narrower posteriorly (Fig. 3B).

The atlas centrum has a sub-triangular shape in right lateral aspect. Anteriorly the atlas centrum bears a flat surface that forms the posterior demarcation of the atlas cup (Fig. 3A). The

ventral side of the atlas centrum is contacted by the atlas intercentrum and dorsally the atlas neural arches are attached. The posterior side of the atlas centrum is fused to the axis centrum but keeps an open, in lateral view slightly oblique running suture (Fig. 3B, E). On the right side, the anteroventral region on both sides of the suture, is strongly rugose, passing indistinctly into the parapophyseal facet ventrally. On the left side, the same region is much smoother. The rugosities may be pathological in origin.

The atlas neural arches form the dorsal part of the atlas cup. Their concave anteromedial sides bear a sharp anterior margin (Fig. 3A). Dorsally, at the base of the neural canal, there is a gap between the left and right atlas neural arch (Fig. 3A). Posteriorly the atlas neural arches contact the atlas centrum. The posterodorsally inclined atlas postzygapophysis (Fig. 3E) is present in its original position on the right side, whereas the left one is preserved isolated. The atlas postzygapophysis narrows posteriorly, contacts the axis prezygapophysis and frames an oval foramen (Fig. 3E).

The axis centrum has a quadratic shape in lateral view (Fig. 3B, E). Anteriorly the axis centrum sutures to the atlas centrum and anteroventrally a short contact with the atlas intercentrum is established. The posterior side of the axis centrum bears a high-oval articular surface that is largely filled with matrix (Fig. 3D). Ventrally an anteriorly damaged midline ridge is formed. In ventral aspect, the axis centrum is expanded anteriorly and posteriorly, and is constricted in the middle (Fig. 3F). On both sides of the axis the diapophyses are preserved as robust transversal projections of dorsoventrally compressed, rhomboidal cross-section, that originate immediately below the neural arch. The articular facets are not preserved. The fragment of an axis rib that was described and figured by Koken (1883: pl. XXIV, fig. 5) in articulation with the left diapophysis, is missing in the material as preserved. The parapophysis is a small, anteroposteriorly elongate, tuberosity located anteroventrally on the axis centrum, adjacent to the atlas centrum (Fig. 3B). The

328 shallow parapophyseal facet extends for a small portion anteriorly onto the posteroventral region of
329 the atlas centrum. It is therefore divided by the suture between the atlas and axis centra.
330 The axis neural arches originate somewhat anterior to the dorsal rim of the articular face of
331 the axis centrum (Fig. 3B, E). The axis prezygapophyses is obscured by the atlas postzygapophysis
332 on the right side of the specimen (Fig. 3E). Laterally the ventrally protruding neural arches extend
333 to about mid-height of the axis centrum. This protruding lateral portion bears the diapophyses for
334 the axis ribs which are damaged on both sides. The axis neural spine is largely broken off and only
335 the transversely thin bases are still preserved (Fig. 3C, E).
336
337 *3.4. Postaxial cervical vertebra*
338 Parts of three postaxial cervical vertebrae are preserved; an isolated centrum (MR.R.1943.3, Fig.
339 4A-E) with attached neurapophyses, and a nearly complete vertebra, embedded in matrix with part
340 of the neurapophysis of the preceding vertebra attached to it (MR.R.1943.1, Fig. 4F, G). The centra
341 of MR.R.1943.1 and MR.R.1943.3 are longer than wide/high. The articular faces of MR.R.1943.3
342 are oval (Fig. 4B, D), whereas those of MR.R.1943.1 are more circular (Fig. 4F). In both specimens
343 the slightly indented articular faces are surrounded by thickened rims. Only the left diapophysis of
344 MR.R.1943.3 is well preserved, the other diapophyses are either damaged, broken off or embedded
345 in matrix. The complete diapophysis is ventrally and slightly posteriorly inclined and reaches to a
346 point dorsal to the dorsoventral midsection of the centrum (Fig. 4A). It bears a long-oval and
347 slightly indented rib facet. The parapophyses are both broken off in the isolated centrum. Their
348 bases indicate that they were about equally large and slightly more anteriorly placed than the
349 diapophyses, which indicates a placement in the anterior part of the neck. In MR.R.1943.1 the right
350 parapophysis is preserved, which has a circular shape and a slightly indented surface (Fig. 4G). It is
351 considerably smaller than the base of the diapophysis and placed anteroventral to the latter. This
352 indicates a placement in the posterior part of the neck. The ventral side of the centrum is well

353 preserved in MR.R.1943.3 and bears a pronounced and rounded midline keel adjacent to which the
354 centrum is dished (Fig. 4E). The anterior and posterior sections of the ventral side of the centrum
355 are thickened and the anterior one also protrudes slightly ventrally (Fig. 4A). Dorsally remnants of
356 the zygapophyses are preserved in the isolated vertebra. Here the right prezygapophysis is more
357 complete and terminates approximately in line with the lateral margin of the centrum (Fig. 4B). The
358 left prezygapophysis is also preserved in MR.R.1943.1 and still articulated with the
359 postzygapophysis of the preceding cervical (Fig. 4G). The postzygapophyses are otherwise largely
360 broken off in both specimens.

361 The neural spine is preserved in MR.R.1943.1. It is considerably higher than the centrum
362 and slightly posteriorly inclined. It bears an almost straight anterior edge and a slightly convex
363 dorsal side. The posterior edge of this neural spine is damaged. The second neural spine adjacent to
364 the afore described, is incomplete but appears shorter (Fig. 4G).

365

366 *3.5. Dorsal vertebrae*

367 Remnants of seven dorsal vertebrae (MB.R.1943.4-10) are preserved in the holotype material (Fig.
368 5A-H). An additional dorsal centrum (Fig. 5J-N) was assigned to the same individual by Koken
369 (1883) and is kept in the collection of the Roemer- und Pelizaeus-Museum (RMH uncatalogued
370 (1)). It is herein excluded from the type material of *Enaliosuchus macrospondylus* and referred to an
371 indeterminate thalattosuchian.

372 All centra are elongate and bear oval and slightly indented articular faces which are
373 surrounded by a thin rim. Laterally, adjacent to the articular faces, some longitudinal rugosities are
374 present. The lateral sides of the centra, showing open neurocentral sutures, are gently concave and
375 so are their ventral sides. The transverse processes are elongate, thin, have a subtriangular cross-
376 section and gradually narrow laterally, which indicates a placement in the anterior part of the dorsal
377 vertebral column. The laterally placed diapophysis is sub-circular and well preserved in

MB.R.1943.4 (Fig. 5A). In dorsal view the posterior sides of the transverse processes of MB.R.1943.4 and MB.R.1943.5 are almost straight, while the anterior ones curve from the diapophysis slightly anteromedially to meet the parapophysis (Fig. 5C). In the RMH specimen (Fig. 5J-N) part of the right transverse process is preserved which extends straight lateromedially and is wider than the transverse processes in the aforementioned vertebrae. A similar pattern is indicated by the broken off bases of the transverse processes in another dorsal centrum (MB.R.1943.6, Fig. 5E, F). These vertebrae seem to have had a more posterior placement in the dorsal vertebral column.

The parapophyses are preserved in the isolated neuropophyseal fragment (MB.R.1943.7, Fig. 5G, H) and in the anterior dorsal vertebra (MB.R.1943.4, Fig. 5A-D). In both specimens they are slightly anteriorly inclined, placed at the anterior end of the neural arch, and are surrounded by a thin edge. The zygapophyses are broken off and the neural canal is filled with matrix in all of the dorsal vertebrae. The transversely thin neural spine is preserved in the neuropophyseal fragment (MB.R.1943.7, Fig. 5G, H). It has a high rectangular appearance with an almost straight anterior margin, a slightly convex dorsal side and bears a gently concave posterior side.

3.6. Dorsal ribs

A largely complete, lateroventrally curved dorsal rib is present in the block that contains the almost complete cervical vertebra (MB.R.1943.1, Fig. 5I). Several rib fragments are preserved (MB.R.1943.9, 12, 13) which show subcircular cross-sections. Additional rib fragments are present in the RHM collections.

3.7. Caudal vertebra

An isolated caudal centrum (MB.R.1943.11, Fig. 5O-S) is preserved. The elongate centrum bears oval and slightly concave articular faces (Fig. 5P, R) of which the posterior one extends further

ventrally than the anterior articular face (Fig. 5O). The ventral side of the centrum is deeply concave. Two semi-circular hemapophyseal facets are present posteroventrally (Fig. 5Q). Dorsolaterally remnants of the broken off transverse processes are preserved. There large size indicates that the vertebra derives from the proximal part of the tail. Ventral to the transverse processes the lateral sides of centrum are concave, giving it an hourglass-like shape in ventral view (Fig. 5Q). Dorsally, in the mid-section of the centrum, the bases of the broken off neural arches are preserved. They start adjacent to the centrums posterior articular face but terminate approximately 1 cm posterior to the anterior articular face. The preserved portion of the neural canal was narrowest at about midlength of the neural arch.

3.8. Femur

An incomplete, possibly left, femur is preserved (MR.R.1943.15.1+2, Fig. 6A-D). Koken (1883) initially identified the two fragments as one tibia broken apart in the middle, the uniform morphology indicates that these are indeed parts of one element, but given its size and curvature the element is in fact a femur. The element has an oval cross-section, with the distal end being more strongly compressed mediolaterally (Fig. 6A, D) and the shaft, as preserved, is gently curved. The proximal (Fig. 6A) and distal ends (Fig. 6B) are irregular, lacking well defined epiphyses. While all metriorhynchids characteristically lack well defined distal epiphyses (e.g. see Andrews 1913), this is one of the few metriorhynchids found where the proximal epiphyses also look to be poorly defined. Given that proximal end appears to be either damaged and/or has some sort of pathology, we cannot ascertain whether this feature is an artefactual or represents a more cartilaginous hip articulation.

3.9. Additional elements

Koken (1883: 818) mentioned and briefly described a proximal end of a metatarsal. This specimen (MB.R.1943.16, Fig. 7A, B) is slightly curved and bears a shallow furrow on the supposed ventral side. It resembles the sacral ribs of the second sacral vertebra (see e.g. Andrews 1913, fig. 64). Another specimen from the Henne collection (MB.R.1939, Fig. 6C, D) that derives from the same locality as the reminder of the material was catalogued as proximal fragment of a metapodial element of *E. macrospondylus*. This element of which the original hour-glass like shape is still indicated, nicely resembles a phalanx from the hind limb.

4. Discussion

4.1. The Koken (1883) character set

Koken (1883) faced difficulties in defining his new genus *Enaliosuchus*, partly due to the incompleteness of the material available to him, and partly from a lack of comparative material and descriptions. He never stated an autapomorphy-based diagnosis, but presented what can be considered by modern standards a comparative diagnosis. He focused on the atlas-axis complex and compared a total of nine characters with a range of extant and fossil crocodylians, and thalattosuchians. These include:

(1) the contact of the proatlas with the atlas neurapophyses: with the proatlas sitting atop, or in an excavation of the atlas neurapophyses;

(2) complete fusion of atlas centrum to the axis centrum;

(3) medial contact of the atlas neurapophyses;

(4) presence of an atlas intercentrum (atlas hypapophysis *sensu* Koken 1883);

(5) presence of a diapophysis on the axis;

(6) presence of a parapophysis on the axis;

(7) morphology of the ventral surface of the axis centrum;

(8) position of the atlas rib articulation: on the atlas intercentrum, on the atlas centrum, or between both;

(9) position and morphology of the axial ribs: single-headed or double-headed, articulating solely with the axis centrum, or with the axis and (fused) atlas centrum.

His comparative taxa included the crocodylid *Osteolaemus tetraspis* Cope, 1861 ("*Crocodilus frontatus*" *sensu* Koken, 1883), the alligatorids *Alligator mississippiensis* (Daudin, 1802), and *Diplocynodon darwini* (Ludwig, 1877) ("*Crocodilus ebertsi*" and "*Alligator darwini*" *sensu* Koken 1883), as well as the thalattosuchians *Machimosaurus mosae* Sauvage & Lienard, 1879, *Teleosaurus cadomensis* Lamouroux, 1820, *Steneosaurus bollensis* (Jaeger, 1828) ("*Mystriosaurus tiedemanni*", "*Mystriosaurus longipes*", and "*Mystriosaurus mandelslohi*" in Koken, 1883), and *Pelagosaurus typus* (including "*Teleosaurus temporalis*" *sensu* Koken 1883). As a consequence, from his original list of 11 taxa, only 7 are considered valid today, while 4 are actually subjective junior synonyms of other species on the list.

From his characters, (1) is unknown due to preservation in many fossil taxa; (2) is undiagnostic, because it is controlled ontogenetically in many crocodyliform taxa (e.g. Vieria *et al.* 2018), (3) is common in Thalattosuchia (e.g. *Metriorhynchus superciliosus, 'M.' brachrhynchus, Gracilineustes leedsi*; Arthaber 1906, Andrews 1913), (4) is ubiquitous in crocodyliform taxa (Romer 1956); (5) and (6) are not diagnostic on less inclusive systematic levels; (7) may have some significance but the character distribution is not clear, and this area is not well preserved in the *E. macrospondylus* holotype; (8) and (9) may have a more differentiated taxonomic significance, but - as will be discussed below – Koken's (1883) interpretation of these characters are fraught with some misinterpretations.

From his overall comparisons Koken (1883: 807) concluded that the genus "*Teleosaurus*" may be the closest relative of his new species. However, it must be noted that only one of the two

477 species in his "*Teleosaurus*" is still included in this genus, the type species *T. cadomensis*. His
478 second species, "*T. temporalis*", is a subjective junior synonym of *Pelagosaurus typus*. From
479 context it appears that he mostly referred to the latter, as the atlas-axis-complex was discussed
480 extensively by Eudes-Deslongchamps (1864), while it was only incompletely known in *T.*
481 *cadomensis*.

482 According to Koken (1883), "*Teleosaurus*" shares with *E. macrospondylus* the following
483 characters:

484 (1) the proatlas is nested within an anterior excavation of the atlas neurapophyses [the element
485 questionably identified as proatlas in *E. macrospondylus* by Koken 1883 is herein identified as atlas
486 postzygapophysis];

487 (2) well developed diapophyses and inconspicuous parapophyses ("tuberosities") on the axis
488 centrum;

489 (3) the presence of a groove on the ventral side of the axis centrum;

490 (4) the "general morphology" of the atlas neurapophyses.

491

492 In contrast Koken (1883) listed the following characteristics that *Enaliosuchus* had, but
493 "*Teleosaurus*" lacked:

494 (5) the broad head of the atlas ribs covers the axis parapophyses (which are reduced to mere
495 tuberosities) in lateral view;

496 (6) the atlas centrum contacts the atlas ribs, the rib facet is jointly formed by the atlas intercentrum
497 and atlas centrum;

498 (7) the axis centrum bears single-headed ribs that articulate with the diapophysis and points straight
499 ventrally;

500 (8) the contact between the atlas intercentrum and the atlas neurapophyses is short;

501 (9) the atlas intercentrum bears a strongly concave morphology;

(10) the atlas neurapophyses are separated from each other along their whole anteroposterior length; (11) the axis centrum is fused to the atlas centrum, but separated by a visible, oblique suture.

Of these characters, (1) cannot be proven, as the small fragment, questionably identified by Koken (1883) as the proatlas in *E. macrospondylus* is considered here as the atlas postzygapophysis, (2) occurs in other metriorhynchids. Koken (1883) described the axis parapophyses as "tuberosities" and doubted that they articulated with the axis rib, speculating that they may have contacted the atlas rib. Jaekel (1904) supported this interpretation but stated that similar "tuberosities" were present in *Metriorhynchus superciliosus* (=*M. jaekeli* in Jaekel 1904). In contrast Baur (1886) already interpreted these "tuberosities" correctly as parapophyses, which was confirmed by von Arthaber (1906). The latter clearly figured that in *Metriorhynchus superciliosus* the parapophyseal facet extends across the suture of the atlas and axis centra. Boschma (1922, based on the figure in Jaekel 1907) located the parapophyseal facet in *Enaliosuchus macrospondylus* solely on the axis centrum and found this an important contrast to *Metriorhynchus superciliosus* in which the parapophyseal facet is located on the axis as well as on the axis centrum. However, the latter condition actually also occurs in *Enaliosuchus macrospondylus* (Fig. 3). (3) is inconclusive, as the type material of *E. macrospondylus* is damaged in this region. The absence of a sharp keel is widespread among crocodyliforms and thalattosuchians. (4) is unspecific. (5) and (7) result from a misinterpretation due to a lack of preservation. As shown by von Arthaber (1906), the parapophyses in metriorhynchids are in the same position and similarly inconspicuous. However, they articulate with the capitulum of a flat, bicapitate rib that forms almost a right angle with the tuberculum. The "straight, ventrally pointing" axis rib of Koken (1883: 806 and pl, XXIV, fig. 5) is therefore only the shaft of the tuberculum that tapered strongly distally. However, Koken (1883: 806) himself wrote that this rib fragment was originally embedded "closely" to the diapophysis and was removed during preparation. In lateral view, the axis rib capitulum (if it would have been preserved) is

hidden by the head of the atlas rib, which has been discussed and clarified for *Enaliosuchus macrospondylus* by Baur (1886).

(6) and (8) through (11) are shared by metriorhynchids (von Arthaber 1906, Andrews 1913).

Although Koken (1883) made detailed observations and tried to make a comprehensive comparison, he entirely omitted metriorhynchid material or references. This is understandable, as detailed studies of the corresponding anatomy in this group were not available before the 20th Century. It also explains the peculiarities that he observed in his material, and his conclusion that it represents a new taxon. Unfortunately, a synoptic view of metriorhynchid morphology results in the conclusion that the characters he found distinguishing are more widely distributed in this group.

The other metriorhynchid elements described for *Enaliosuchus macrospondylus* by Koken (1883) show the general morphology seen in various taxa and are of no diagnostic value.

4.2. The Schroeder (1921) character

Schroeder (1921) referred a new metriorhynchid specimen from the Lower Cretaceous of northern Germany to *Enaliosuchus* based on the morphology of the axis ribs (this is the specimen Kuhn 1936 establish as the *Enaliosuchus schroederi* holotype). His new specimen preserved axis ribs in which the capitulum and tuberculum remained unfused, effectively resulting in two axis ribs on each side. Schroeder (1921: 364) claimed the same condition to be present in the *E. macrospondylus* holotype. However, this cannot be substantiated as the axis ribs are no longer preserved in the *E. macrospondylus* holotype, and the fragment that was described by Koken (1883) is not unambiguous in interpretation (see above).

4.3. The Hua et al. (2000) character set

The *Enaliosuchus* taxonomy of Hua *et al*. (2000) is a monospecific hypothesis, with all three specimens included in *E. macrospondylus*. However, the only elements shared by all three

552 specimens are the atlas-axis complex and one post-axial cervical vertebra. The emended diagnosis
553 of *Enaliosuchus* by Hua *et al*. (2000: 472) focussed largely on cranial characters, which thus cannot
554 be applied for the holotype specimen (MB.R.1943.1-16). However, Hua *et al*. (2000) considered
555 five characters in the atlas-axis complex to be diagnostic for *Enaliosuchus*: (1) a massive atlas
556 centrum that is sub-quadrangular in lateral view, (2) the atlas ribs inserted on both the atlas
557 intercentrum and axis centrum, (3) the diapophyses are placed on the axis neural arches, (4)
558 presence of a ventral midline keel on the axis centrum, and (5) the axis neural spine is curved and
559 anteriorly inclined. Unfortunately, these five characters do not unite these three specimens to the
560 exclusion of other metriorhynchids:

561 (1) In the *Enaliosuchus macrospondylus* holotype specimen (MB.R.1943.2), the atlas
562 centrum is partly obscured by the atlas neural arches and the atlas intercentrum, but the morphology
563 is clearly more triangular than quadrangular in lateral view (Figs. 3, 6A), similar to the condition
564 present in *Metriorhynchus superciliosus* de Blainville, 1853 (Fig. 7D). The shape of the atlas
565 centrum in *E. schroederi* cannot be seen because the atlas intercentrum, atlas neural arches and atlas
566 ribs obscure most of the element (Fig. 7B).

567 (2) The atlas rib facets in MB.R.1943.2 are largely formed by the atlas intercentrum and
568 atlas centrum (Figs. 3, 6A). In other metriorhynchids such as *Cricosaurus vignaudi* (Frey, Buchy,
569 Stinnesbeck & López-Oliva, 2002) (see Frey *et al.* 2002: fig. 6), '*Metriorhynchus*' *brachyrhynchus*
570 Eudes-Deslongchamps, 1868 (Fig. 7E) and *Gracilineustes leedsi* (Andrews, 1913) (Fig. 7F) they
571 are mainly borne by the atlas centrum. The participation of the atlas intercentrum in the formation
572 of the rib facet was described for *Metriorhynchus jaekeli* Schmidt, 1904 (see Jaekel 1904: fig. 1)
573 and is figured for *M. superciliosus* (see Andrews 1913: fig. 61). In *E. schroederi* the atlas ribs
574 obscure the rib facets on both sides (Fig. 7B, I), but it appears that the atlas intercentrum might have
575 participated in the atlas rib facet. In the referred specimen of *E. macrospondylus* (RNGD 990201)

576 the rib facet is borne on the atlas centrum (Fig. 7C). Whether or not the atlas intercentrum took part
577 in the formation of the atlas rib facet is unclear as this element is not preserved in RNGD 990201.

578 (3) The diapophyses are present on the axis neural arches in all examined metriorhynchid
579 taxa, such as *M. superciliosus* (Fig. 7D), '*M.*' *brachyrhynchus* (Fig. 7E) and *Cricosaurus vignaudi*
580 (see Frey *et al*. 2002: fig. 6), and thus this character is of no diagnostic value.

581 (4) A ventral ridge on the axis centrum is present on MB.R.1943.2, although its anterior
582 portion is damaged (Fig. 3E). This ridge is very indistinct in *E. schroederi* (Fig. 7I), especially
583 when compared with the pronounced ridges that occur in other metriorhynchids such as *G. leedsi*
584 (Fig. 7G) and *M. superciliosus* (Fig. 7H).

585 (5) The shape of the axis neural spine cannot be compared between RNGD 990201 and the
586 *E. macrospondylus* and *E. schroederi* holotypes as it is incomplete in the German specimens (Fig.
587 7A, B). A similar shape of the RNGD 990201 axis neural spine is, however, present in *M.*
588 *superciliosus* (Fig. 7D).

589 Therefore, based upon the five characters listed by Hua *et al*. (2000), the referral of the
590 French material to *Enaliosuchus macrospondylus* cannot be supported. The shape of the atlas
591 centrum differs between the specimens. It was described as sub-quadrangular in RNGD 990201,
592 whereas it is triangular in MB.R.1943.2. The atlas rib facet is borne by the atlas intercentrum and
593 atlas centrum in MB.R.1943.2, whereas the atlas intercentrum is missing in RNGD 990201 but a
594 large rib facet is evident at the atlas centrum. The diapophyses are consistently placed on the axis
595 neural arches in metriorhynchids, and a ventral keel on the axis centrum is not unique. Finally, the
596 shape of the axis neural spine is largely damaged in MB.R.1943.2 and cannot be compared.
597 Moreover, the length-to-height ratio of the axis centrum likewise differs between MB.R.1943.2
598 (1:1) and RNGD 990201 (1:0.7). Although, in the latter the transverse compression may impact this
599 ratio. A longer ratio also occurs in *Metriorhynchus superciliosus* (NHMUK PV R 2051, 1:1.16),

Gracilineustes leedsi (NHMUK PV R 3014, 1:1.16) and '*M.*' *brachyrhynchus* (NHMUK PV R 2039, 1:1.08 and NHMUK PV R 3804, 1:1.11).

The referral of the *Enaliosuchus schroederi* holotype by Hua *et al.* (2000) to the *Enaliosuchus macrospondylus* hypodigm is also questionable. Several elements in the atlas-axis complex of this specimen differ from MB.R.1943.2, such as the atlas intercentrum that extends more dorsally, and the atlas neural arches which have a carved anteroventral portion for the articulation with the atlas intercentrum (Fig. 7B). A re-description of the *E. schroederi* holotype is forthcoming, which will discuss the atlas-axis in more detail.

4.4. The Karl et al. (2006) taxonomy

Curiously, Karl *et al.* (2006) assigned the holotypes of both *E. macrospondylus* and *E. schroederi* to the genus *Metriorhynchus*, as *Metriorhynchus* sp.. The arguments in Karl *et al.* (2006) are very superficial, no detailed comparisons were made, and their phylogenetic analysis had an odd sample-set for testing the internal position of *Enaliosuchus* within Metriorhynchidae. *Enaliosuchus schroederi* can be distinguished from *Metriorhynchus* spp. with the same atlas-axis characters by which it differs from *E. macrospondylus*, whereas several characters present in *E. macrospondylus* do indeed occur in *M. superciliosus* (Fig. 7D) and '*M.*' *brachyrhynchus* (Fig. 7E) (see discussion above). However, given that the atlas-axis complex is only known and well-described in a limited number of metriorhynchid taxa, and that most characters listed by Koken (1883), Hua *et al.* (2000), and Karl *et al.* (2006) have a widespread distribution in Metriorhynchidae (see discussion above), we cannot agree with the unambiguous referral of the *E. macrospondylus* and *E. schroederi* holotypes to the genus *Metriorhynchus* as proposed by Karl *et al.* (2006).

Oddly, the cranial morphology of the *E. schroederi* holotype alone is enough to readily distinguish it from *Metriorhynchus* (e.g. smooth dermatocranium, very large sclerotic rings, jugal excluded from the preorbital fenestrae). As stated above, the phylogenetic analysis of Young &

Andrade (2009) recovered *E. schroederi* and the French specimen referred to *E. macrospondylus* as derived metriorhynchines, thus supporting its distinction from *Metriorhynchus*. The phylogenetic analysis of Jouve (2009) recovering *Enaliosuchus* as the sister taxon to *Dakosaurus* similarly falsifies the *Metriorhynchus* subjective synonymy hypothesis. This contrasts with the strange taxon and character sample set in the phylogenetic analysis of Karl *et al*. (2006), which had a single metriorhynchid OTU, referred to as "*Enaliosuchus*/*Metriorhynchus*". The remaining OTUs were four crocodylians, three teleosauroids and the basal metriorhynchoid *Pelagosaurus typus* (the same taxon-sample as Koken 1883). The specimens that were the basis for scoring their OTUs is not given. Only ten characters were included, three cranial characters, and seven out of the nine atlas-axis characters from Koken (1883). While the Karl *et al*. (2006) phylogenetic analysis does show that most of the atlas-axis characters used by Koken (1883) to establish *E. macrospondylus* has a wide distribution in crocodyliforms, it does not support their contention that *Enaliosuchus* is a subjective junior synonym of *Metriorhynchus*. Principally because they never tested it. It is not clear why Karl *et al*. (2006) used a phylogenetic analysis to highlight the distribution of atlas-axis characters rather than a comparative plate figuring the characters.

Moreover, in using a sub-sample of Koken's (1883) atlas-axis character set, and the same limited taxon set as Koken (1883), Karl *et al*. (2006) compound the original issue Koken had: the lack of comparative data with metriorhynchids. The difference being, the lack of comparative material is understandable in Koken (1883). Finally, Karl *et al*. (2006) did not mention the Hua *et al*. (2000) study. It appears they were unaware of the third putative *Enaliosuchus* specimen, and the new atlas-axis characters proposed by Hua *et al*. (2000).

5. Cretaceous metriorhynchids

650 The fossil record of Metriorhynchidae is poorer in the Cretaceous than in the Jurassic. Early
651 overviews of metriorhynchid evolution and species diversity found metriorhynchid biodiversity was
652 affected by an extinction at the Jurassic-Cretaceous boundary (Pierce *et al*. 2009; Young *et al*.
653 2010), with Cretaceous metriorhynchids characterised as a "dead clade walking" (Young *et al*.
654 2010). However, over the past decade the two-phase extinction hypothesis (end-Tithonian
655 biodiversity crash and Valanginian-Hauterivian boundary final extinction) posited by Young *et al*.
656 (2010) has been falsified. Re-examination of Cretaceous fossils found that at least four
657 metriorhynchid lineages are known to survived into the Cretaceous (Young *et al*. 2014b). It is
658 unclear whether some of the metriorhynchid specimens from the Vaca Muerta Formation of
659 Argentina, such as the *Purranisaurus potens* Rusconi 1948 holotype and those referred to
660 *Cricosaurus* sp. and *Dakosaurus andiniensis* Vignaud & Gasparini, 1996 are uppermost Tithonian
661 or lowermost Berriasian in age (Herrera *et al*. 2015; Fernández *et al*. 2019; Herrera pers. comm.
662 2019). Thus, potentially six metriorhynchid lineages crossed the Jurassic–Cretaceous boundary. An
663 incomplete metriorhynchid skull from Berriasian strata of the Neuquén basin is known (Fernández
664 *et al*. 2019). The specimens from the uppermost Tithonian or lowermost Berriasian of Russia are
665 taxonomically indeterminate (Ochev 1981).

666 From the Valanginian of France and Germany four different lineages of metriorhynchid are
667 known: Geosaurina, Plesiosuchina and two lineages of Rhacheosaurini (Table 1). These include the
668 holotype of the nomen dubium *Neustosaurus gigondarum* Raspail, 1842, the holotype of
669 *Enaliosuchus macrospondylus*, the holotype of *Enaliosuchus schroederi*, the holotype of *Geosaurus*
670 *lapparenti* (Debelmas & Strannoloubsky, 1957), the French specimen referred to *Enaliosuchus*
671 *macrospondylus*, a specimen referred to as cf. *Geosaurus lapparenti* and an indeterminate
672 Plesiosuchina specimen (Raspail 1842; Debelmas & Stannoloubsky 1956; Debelmas 1958; Hua *et*
673 *al*. 2000; Karl *et al*. 2006; Young *et al*. 2014b). A skull from the Valanginian of Colombia has been
674 referred to cf. *Cricosaurus* (Larsson *et al*. 2012).

From the upper Valanginian or lower Hauterivian of France an indeterminate metriorhynchid is known (Debelmas & Demians D'Archimbaud 1956), and from the lower Hauterivian of France an incomplete skeleton has been referred to *Geosaurus lapparenti* (Debelmas, 1952).

Post-Hauterivian metriorhynchids are exceptionally rare. A poorly preserved incomplete skull from the Barremian of Spain had been considered to be a possible metriorhynchid (Parrilla-Bel *et al*., 2012), although this seems less likely now (Parrilla-Bel pers. comm. 2017). Chiarenza *et al*. (2015) referred an isolated tooth crown from the lowermost Aptian of Sicily to Plesiosuchina based on a series of apomorphies. This tooth significantly increased the known geological range of Metriorhynchidae. Curiously, Fischer *et al*. (2015) raised the issue that the Sicilian tooth could in fact be a brachauchenine pliosaurid, like *Makhaira rossica* Fischer, Arkhangelsky, Stenshin, Uspensky, Zverkov & Benson, 2015. However, they did not address the list of apomorphies Chiarenza *et al*. (2015) gave when they referred the tooth to Plesiosuchina (such as the presence of contiguous microdenticles, the denticles being rectangular in shape, and the presence of 'weak' carina flanges). The convergences between the Sicilian tooth and *Makhaira rossica* are interesting, but it is based on superficial similarities and not on apomorphies. In fact, *Makhaira rossica* lacks all of the plesiosuchin apomorphies observable in the Sicilian tooth. As such, Fischer *et al*. (2015) inadvertently strengthened the referral of the Sicilian tooth to Plesiosuchina (as Cretaceous pliosaurids did not seem to evolve the apomorphies seen in metriorhynchids), not the reverse. Although, in the absence of more complete material, the specimen still needs to be considered cf. Plesiosuchina. Post-Hauterivian survival of Metriorhynchidae needs confirmation with more complete material. However, with the description of a Barremian teleosauroid specimen (see Cortés *et al*., 2019), it does seem that thalattosuchians persisted for longer than previously realised closer to the equator. Their continued presence could have acted as a barrier to large-bodied neosuchians colonising Lower Cretaceous marine ecosystems.

6. Are *Enaliosuchus* and *Neustosaurus* congeneric?

The poorly ossified proximal femoral epiphyses seen in *Enaliosuchus macrospondylus* Koken, 1883 (Fig. 6), as mentioned above, are either artefactual, pathological, or evidence of a shift in femoral morphology during the Cretaceous. The holotype of *Neustosaurus gigondarum* Raspail, 1842 is a largely complete post-dorsal postcranial skeleton from the Valanginian of France. Considered to be a nomen dubium by Young & Andrade (2009), the whereabouts of the holotype has never been ascertained (although a cast of a very small portion of the skeleton is on display in the MNHN). Raspail (1842) figured both femora, and they look strikingly similar to our reconstruction of the femur in *Enaliosuchus macrospondylus* (Fig. 6).

That being said, the obvious problems are: (1) the *E. macrospondylus* femur is incomplete, and (2) the *N. gigondarum* femora cannot be checked first-hand. With these caveats in mind, the peculiar sigmoidal shape and the oddly flat proximal epiphyses are unique to these two specimens. Should both of these features prove to be genuine (which we cannot be certain of), it hints a possible relationship between these two genera. New discoveries of Valanginian metriorhynchids are needed to elucidate femoral morphotypes, thus it is premature to posit *Enaliosuchus* as a subjective junior synonym of *Neustosaurus*. But this is a hypothesis that should be tested when more data becomes available.

7. Conclusions

In conclusion, the holotype specimen of *Enaliosuchus macrospondylus* (MB.R.1943.1-16) lacks unique anatomical traits (although see our discussion on the femur above), and preserved axial skeleton largely resembles the morphology present in other metriorhynchids such as *Metriorhynchus superciliosus*, *'M.' brachyrhynchus* and *Gracilineustes leedsi*. The atlas-axis complex preserved with the *E. schroederi* holotype shows several symplesiomorphic

metriorhynchid traits, but the *E. macrospondylus* holotype lacks the peculiar morphology of the atlas intercentrum and atlas neural spine, which indicates that they are distinct taxa. The French specimen (RNGD 990201) referred to *Enaliosuchus macrospondylus* by Hua *et al*. (2000) is distinct from MB.R.1943.1-16 in the shape of the atlas centrum, and possibly in the placement of the atlas rib facet and the proportions of the axis centrum.

Given these morphological differences, the monospecific hypothesis of Hua *et al*. (2000) (with the *Enaliosuchus macrospondylus* and *E. schroederi* holotypes and the French specimen RNGD 990201 all referred to the same species) is not justifiable. With the lack of evidence to refer other specimens to this taxon, only the holotype specimen (MB.R.1943.1-16) can be referred to as *Enaliosuchus macrospondylus*. While the femur is incomplete, it shows a striking resemblance to those of *Neustosaurus gigondarum* (a species known from a single specimen, which unfortunately cannot be examined first-hand). Due to the lack of verifiable autapomorphies, *E. macrospondylus* is here considered a nomen dubium that is best classified as Metriorhynchidae gen. et sp. indet. As the Cretaceous fossil record of Metriorhynchidae improves, new discoveries could resurrect *E. macrospondylus*, and test a possible synonymy between *Enaliosuchus* and *Neustosaurus*. Until then, we consider *E. macrospondylus* to be a nomen dubium, '*E.*' *schroederi* to be a valid taxon, and the French specimen an unnamed distinct species. As the location of the *Neustosaurus gigondarum* holotype is still unknown, we follow Young &Andrade (2009) in considering it to be a nomen dubium.

8. Systematic synopsis

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

Crocodylomorpha gen. et sp. indet.

Material: RMH uncatalogued (2), an isolated tooth crown (Fig. 2C).

Locality: “Osterwald [Mountains]” (Koken 1883), southern Lower Saxony, northern Germany.

Stratigraphy: “Hils-Conglomerat” (Koken 1883); i.e. Grenzlerburg Member, Salzgitter Formation, Minden Braunschweig Group, uppermost Valanginian to lowermost Hauterivian, Lower Cretaceous.

Goniopholididae Cope, 1875

?Goniopholididae gen. et. sp. indet.

Material: MB.R.3636, an isolated tooth crown (Fig. 2A,B).

Locality: Elligser Brink near Delligsen, southern Lower Saxony, northern Germany (Koken 1883).

Stratigraphy: “Elligserbrink-Schicht”, Stadthagen Formation, Minden Braunschweig Group, uppermost Valanginian to lowermost Hauterivian.

Metriorhynchidae Fitzinger, 1843 (*sensu* Young & Andrade, 2009)

?Metriorhynchidae gen. et sp. indet.

Material: MB.R.1939. Fragmentary phalanx. RMH uncatalogued (1). Dorsal vertebra (Fig. 4Q-U).

Locality: “Osterwald [Mountains]” (Koken 1883), probably the former Osterwald Tiefbauschacht mine shaft, c. 1.3 km east of the town of Osterwald, southern Lower Saxony, northern Germany (approx. 52°06’34’’N, 9°38’37’’E).

Stratigraphy: Lower part of Stadthagen Formation, Minden Braunschweig Group. Most probably middle lower to lowermost upper Valanginian, Lower Cretaceous.

Metriorhynchidae Fitzinger, 1843 (*sensu* Young & Andrade, 2009)

Metriorhynchidae gen. et sp. indet.

Enaliosuchus macrospondylus Koken, 1883

(nomen dubium)

Figs. 3-6

Holotype: MB.R.1943.1-16. Atlas-axis complex, remnants of three post-axial cervical vertebrae, eight dorsal vertebrae, several fragmentary dorsal ribs, one caudal vertebra, an incomplete femur, fragment of a sacral rib.

Type locality: “Osterwald [Mountains]” (Koken 1883), probably the former Osterwald Tiefbauschacht mine shaft, c. 1.3 km east of the town of Osterwald, southern Lower Saxony, northern Germany (approx. 52°06’34’’N, 9°38’37’’E).

Stratigraphy: Lower part of Stadthagen Formation, Minden Braunschweig Group, most probably middle lower to lowermost upper Valanginian, Lower Cretaceous.

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Figure captions

Figure 1: Geographic, palaeogeographic and geological situation of the *Enaliosuchus macrospondylus* material. A) General location map, B) Geological situation in the vicinity of the Osterwald Mountains, with location of the potential type localities Osterwald clay-pit (1) and Tiefbauschacht Osterwald mine shaft (2). Geological data from Landesamt für Bergbau, Energie und Geologie (NIBIS® Kartenserver, 2014), C) Palaeogeographical sketch map for the Valanginian, showing the location of Osterwald and Elligser Brink. Note that during the earliest Hauterivian the shoreline shifted further landward due to transgression. After Mutterlose (1984), modified.
[Intended for page width]

Figure 2. Teeth initially referred to *Enaliosuchus macrospondylus*. ?Goniopholidae gen. et sp. indet. (MB.R.3636), uppermost Valanginian to lowermost Hauterivian of Elligser Brink near Delligsen in (A) distal and (B) labial views. (C) Crocodylomorpha gen. et. sp. indet. (RMH uncatalogued), uppermost Valanginian to lowermost Hauterivian of the Osterwald Mountains. Note that only the tooth on the right side, shown in labial view, is mentioned in Koken (1883). Scale bar equals 1 cm.
[Intended for page width]

Figure 3. Atlas-axis complex (MB.R.1943.2) of the *Enaliosuchus macrospondylus* holotype specimen, middle to upper Valanginian of the Osterwald Mountains in (A) anterior, (B) left lateral, (C) dorsal, (D) posterior, (E) right lateral and (F) ventral view. Scale bar equals 5 cm. Abbreviations: apo, atlas postzygapophysis; apr, axis prezygapophysis; atc, atlas centrum; atic, atlas intercentrum; atn, atlas neural arch; atr, atlas rib; ap, axis parapophysis; axc, axis centrum; axn, axis neural arch; dia, axis diapophysis.

[Intended for page width]

Figure 4. Postaxial cervical vertebrae of the *Enaliosuchus macrospondylus* holotype from the middle to upper Valanginian of the Osterwald Mountains. Cervical vertebra (MB.R.1943.3) in (A) lateral, (B) anterior, (C) posterior, (D) dorsal and (E) ventral view. Posterior cervical vertebra (MB.R.1943.1) in (F) posterior and (G) lateral view. Scale bars equal 5 cm. Abbreviations: dia, diapophysis; mk, midline keel; ns, neural spine; pap, parapophysis; prz, prezygapophysis.

[Intended for page width]

Figure 5. Additional postaxial vertebrae and ribs of the *Enaliosuchus macrospondylus* hypodigm from the lowermost upper Valanginian of the Osterwald [Mountains]. Dorsal vertebra (MB.R.1943.4) in (A) lateral, (B) posterior, (C) dorsal and (D) anterior view. Dorsal centrum (MB.R.1943.6) in (E) anterior and (F) lateral view. Neurapophysis of a dorsal vertebra (MB.R.1943.7) in (G) lateral and (H) anterior view. (I) Rib fragments (MB.R.1943.9). RMH uncatalogued. Dorsal vertebra referred to *Enaliosuchus macrospondylus* by Koken (1883) in (J) lateral, (K) anterior, (L) ventral, (M) posterior and (N) dorsal view. Caudal vertebra (MB.R.1943.11) in (O) lateral, (P) anterior, (Q) ventral, (R) posterior and (S) dorsal view. Scale bars equal 5 cm. Abbreviations: bn, base of neural arch; hf, hemapophyseal facet; ns, neural spine; pap, parapophysis; tp, transverse process.

[Intended for page width]

Figure 6. Incomplete, possibly left, femur (MB.R.1943.15.1+2) of the *Enaliosuchus macrospondylus* holotype specimen from the lowermost upper Valanginian of the Osterwald [Mountains] with the missing part of the shaft being based upon *Neustosaurus gigondarum*. (A) proximal, (B) medial, (C) lateral and (D) proximal view. Scale bar equals 5 cm.

[Intended for ½ page width]

Figure 7. Additional elements of the *Enaliosuchus macrospondylus* hypodigm from the lowermost upper Valanginian of the Osterwald [Mountains]. (A, B) supposed proximal portion of a sacral rib (MB.R.1943.16), (C, D) fragmentary phalanx (MB.R.1939). Scale bars equal 1 cm.

[Intended for ½ page width]

Figure 8. Comparison of metriorhynchid atlas-axis components of (A) *Enaliosuchus macrospondylus* holotype (MB.R.1943.1-16) in lateral view, (B) *Enaliosuchus schroederi* holotype (MM uncatalogued) in lateral view, (C) referred specimen of *Enaliosuchus macrospondylus* (RNGD 990201) in lateral view, (D) *Metriorhynchus superciliosus* (NHMUK PV R 2051) in lateral view, (E) ‘*Metriorhynchus*‘ *brachyrhynchus* (NHMUK PV R 3804) in lateral view, (F) *Gracilineustes leedsi* (NHMUK PV R 3015) in lateral view, (G) *Gracilineustes leedsi* (NHMUK PV R 3014) in ventral view, (H) *Metriorhynchus superciliosus* (NHMUK PV R 2051) in ventral view, (I) *Enaliosuchus schroederi* holotype (MM uncatalogued) in ventral view. Abbreviations: arf, atlas rib facet; atc, atlas centrum; atic, atlas intercentrum; atr, atlas rib; axc, axis centrum; axp, axis parapophysis; dia, diapophysis; vk, ventral keel. Scale bars equal 1 cm.

[Intended for page width]

Table 1. Table of all published thalattosuchian specimens from the Cretaceous. Note that all the French Cretaceous metriorhynchids are from the Région Provence-Alpes-Côte d'Azur, and the German Cretaceous metriorhynchids are from Lower Saxony. Furthermore, the age of the Russian material is either uppermost Jurassic or lowermost Cretaceous.

	Specimen	**Age**	**Locality**	**Reference**
1	*Dakosaurus andiniensis* referred specimen	Upper Tithonian or Lower Berriasian	Yesera del Tromen-Pampa Tril area, Neuquén Province, Argentina	Herrera *et al*. 2015; Fernández *et al*. 2019
2	*Purranisaurus potens* holotype	Upper Tithonian or Lower Berriasian	Malargüe Department, Mendoza Province, Argentina	Herrera *et al*. 2015; Fernández *et al*. 2019
3	*Cricosaurus* sp.	Upper Tithonian or Lower Berriasian	Arroyo Durazno, Mendoza Province, Argentina	Fernández *et al*. 2019
4	Metriorhynchidae indeterminate	Upper Tithonian or Lower Berriasian	Arroyo Paulino, Mendoza Province, Argentina	Fernández *et al*. 2019
5	Metriorhynchidae indeterminate	Upper Tithonian or Lower Berriasian	Khoroshevskii Island, Volga Region, Russia	Ochev 1981
6	Metriorhynchidae indeterminate	Lower Berriasian	Arroyo Paulino, Mendoza Province, Argentina	Fernández *et al*. 2019
7	*Neustosaurus gigondarum* holotype	Lower Valanginian	Département du Vaucluse, France	Raspail 1842
8	'*Cricosaurus*' *macrospondylus* referred specimen	Lower Valanginian	Département des Hautes-Alpes, France	Hua *et al*. 2000
9	*Cricosaurus schroederi* holotype	Lower Valanginian	Landkreis Schaumburg, Germany	Karl *et al*. 2006
10	cf. *Geosaurus lapparenti*	Lower Valanginian	Département du Vaucluse, France	Debelmas 1958
12	*Enaliosuchus macrospondylus* holotype	Lower upper Valanginian	Landkreis Hamelin-Pyrmont, Germany	Koken 1883
13	cf. *Cricosaurus*	Upper Valanginian	Colombia	Larsson *et al*. 2012
14	Plesiosuchina indeterminate	LowerUpper Valanginian	Département des Bouches-du-Rhône, France	Young *et al*. 2014b
15	*Geosaurus lapparenti* holotype	Upper Valanginian	Département du Var, France	Debelmas & Stannoloubsky 1957
16	Metriorhynchidae indeterminate	Upper Valanginian or Lower Hauterivian	Département du Vaucluse, France	Debelmas & Demains D'Archimbaud 1956

17	*Machimosaurus rex* holotype	Hauterivian? (Upper Jurassic–Lower Cretaceous)	Touil el Mhahir, Tataouine Governorate, Tunisia	Fanti *et al*. 2016 (but see Cortés *et al*., 2019)
18	*Geosaurus lapparenti* referred specimen	Lower Hauterivian	Département du Var, France	Debelmas 1952
19	Teleosauroidea gen. et sp. indet.	Upper Barremian	Loma La Cabrera, Colombia	Cortés *et al*., 2019
20	cf. Plesiosuchina	Lowermost Aptian	Montagna Grande area, Sicily	Chiarenza *et al*. 2015

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Response to comments of reviewers and editor

Please ensure the text of your paper is double-spaced and has consecutive line numbering – this is an essential peer review requirement

This has been done

- Chronostratigraphy versus geochronology - When referring to rocks (formations, deposits, strata, …) refer to the chronostratigraphic attributes upper/lower (Stages), when dealing with time (geochronology) to late/early (Ages).

In addition, when referring to fossil specimens, use the chronostratigraphic notation Lower/Upper (see Owen, 2009. Stratigraphy, vol. 6, no. 2, p. 110:“In discussing the age relationships of fossils, the clearest terminology would be to refer to fossils as lower, middle, and upper as in Upper Cretaceous fossils. In discussing the living organisms that later became fossils, the clearest terminology would be early, middle, and late, as in Late Cretaceous dinosaur behavior.”

For instance,

Title: change FROM "Early Cretaceous fossil record" TO "Lower Cretaceous fossil record"

Please check and correct the usage in the manuscript.

We carefully checked this and altered the text accordingly

- Scale bars have to be provided to all figured specimens and details.

Figure 6: Though it is mentioned that "No scale intended.", if possible please add scale bars
Scale bars have been added

Order of Figures: All figures must to be presented in the same sequence that have their first citations in the manuscript text. Please check and correct carefully the order of figures in the manuscript and their corresponding first citations. Delete out-of order citations and/or rearrange them if necessary. Check also for missing citations.

This has been done

ACKNOWLEDGEMENTS: Though it is not mandatory, it is always very much appreciated when authors thank the reviewers in the Acknowledgments, by name if his/her identity has been revealed, or as "anonymous reviewers" if you do not know their names.

This has been done

-**Reviewer 1**

1) I think that the portions of the tibiae are the proximal and distal ends of the left femur (see picture attached in the pdf). Also, I think that the metacarpal is the distal end of a sacral rib. I have pictures of the material that the authors mentioned that were not found in the collection of MB or RHM. I can share the files.

We are grateful for this comment and agree that this is the left femur. The description and figure has been modified accordingly.

2) The authors have to ask for a new collection number for the ?Goniopholididae gen. et. sp. indet. or for Metriorhynchidae gen. et sp. indet. Currently, both have the same collection number.

This has been done

There is not any mention of the neurocentral suture that is open in most of these dorsal vertebrae
Thanks for the comment. We added it to the description.

I was working on the collection of the MB (December 2015), and the material was at the collection. If the authors need, I can share the pictures
We are grateful for this comment. We added the supposed missing elements to the description and compiled new figures showing the material.

The same collection number than ?Goniopholididae gen. et. sp. indet. One of these specimens requires a new collection number
This has been fixed. The tooth has a different collection number.

-**Reviewer 2**

- Sachs et al. redescribe the holotype material of Enaliosuchus macrospondylus in light of current understanding of metriorhynchid diversity and morphology. They compare it with overlapping material from the referred French specimen and E. schroederi (as well as other metrhorhynchids). They find E. macrospondylus to be a nomen dubuim as the holotype material lacks autapomorphies. This is a much-needed revision of this taxon and is clearly written. I appreciate the detailed comparisons with other material. I do not have any major suggestions for revision. I have made a number of minor comments throughout the annotated pdf copy of the manuscript. The figures could be improved with some relatively minor modifications detailed below.

We are grateful for this comment

Comments on Figures:

Figure 3 – There are some fairly heavy shadows in these images that make interpretation of some of the morphology a little difficult. The figure may be more informative if the authors were to draw lines over the sutures and facets discussed in the text. Additionally, some of the lines for the labels are difficult to trace across the dark parts of the photographs; the addition of a white line (or shadow) immediately adjacent to the black would make it easier to follow across changing colors. Additionally, it might be helpful to label the facet for the atlas rib (on the right side).

A new figure with new photos has been compiled that is more informative than the original one.

Figure 3 caption – "axc" is missing

Thank you. It has now been added.

Figure 5 – Presumably this figure shows both tibiae? A & B appear to be the same bone from different angles, but C (labeled as "medial view") looks like a different bone (and I can't tell if D is the distal end of B or C). These should be more clearly labeled.

This has been changed and is clarified in the text.

Figure 6 – The text labels on part C are very difficult to read against the dark background. I see that the authors added a thin white outline to the text in an effort to make it stand out, but at print size, this is barely perceptible. Perhaps making this white border thicker would help the letters stand out better? Or maybe lightening the surrounding matrix in photoshop so the black labels are legible (which would have the added bonus of making the bone stand out better too). As in Figure 3, some of the black lines indicating labeled features are difficult to follow across dark portions of the photographs and white shadow lines would be helpful (as in part C). Finally, maybe outlining (or placing a translucent polygon over) the atlas rib facet would be helpful as its borders are not particularly obvious on some of the specimens.

This figure has been modified so that all lines in darker parts are nicely visible. Also the labels in part C have also been enhanced. The position of the atlas ribs are well visible in all images (image A has been renewed and an interpretation is available in figure 3).

(2) the atlas ribs inserted on both the atlas intercentrum and axis centrum,
The reviewer notes that it should be the axis centrum and he is correct. But this text is a translation of the original text of Hua et al. (2000) and these authors indeed (and incorrectly) refer to the axis and not the atlas centrum. We, however, discussed this in the text.

The enigma of *Enaliosuchus*, and a reassessment of the Lower Cretaceous fossil record of Metriorhynchidae

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ABSTRACT

Enaliosuchus macrospondylus Koken, 1883 was one of the first thalattosuchian taxa from the Cretaceous to be described. The type series includes an atlas-axis complex, remnants of three post-axial cervical vertebrae, several dorsal vertebrae, a caudal vertebra, an incomplete femur and a fragmentary sacral rib from the upper Valanginian of northern Germany. Additionally, two isolated, non-thalattosuchian, tooth crowns from the uppermost Valanginian to lowermost Hauterivian of different localities in northern Germany were tentatively assigned to *E. macrospondylus* by Koken. The taxon was established for the distinctive the atlas-axis morphology, in particular the apparent lack of an axis parapophysis. *Enaliosuchus macrospondylus* has been considered a valid taxon in recent studies, based upon a largely complete metriorhynchid specimen from the Valanginian of France that had been referred to this taxon, an assignment that has never been questioned. Here we provide a detailed re-description of the *E. macrospondylus* holotype specimen and determine whether it is diagnostic, and if a referral of the French specimen to *E. macrospondylus* is justified. We also discuss whether *E. macrospondylus* and another metriorhynchid specimen from the Valanginian of northern

Germany, described as *Enaliosuchus schroederi*, are conspecific. Finally, we provide an overview of the current knowledge of metriorhynchid diversity during the Cretaceous.

Keywords:
Crocodylomorpha
Thalattosuchia
Metriorhynchidae
Lower Cretaceous
Germany

1. Introduction

Thalattosuchian crocodylomorphs are considered to be rare in Lower Cretaceous strata. These specimens include the youngest recorded examples of the group, which so far is documented to the lowermost Aptian (see discussion below). In Germany, the first Cretaceous thalattosuchian remains were described by Ernst Koken from the Valanginian of Lower Saxony as a new genus and species, *Enaliosuchus macrospondylus* Koken, 1883. The holotype material comprises a number of cervical, dorsal and caudal vertebrae, along with limb and rib elements. Additionally, Koken (1883) tentatively referred two isolated teeth from two separate localities to his new taxon. Due to its geological age and the well preserved atlas-axis complex, the type specimen of *E. macrospondylus* sparked controversy and curiosity into the diversity and taxonomy of Cretaceous thalattosuchians (e.g. Schroeder 1921; Kuhn 1936; Hua *et al*., 2000; Karl *et al*., 2006), and also the diversity of cervical osteology in crocodylomorphs (e.g. Koken 1883, 1887; Baur 1886; Jaekel 1904; Boschma 1922). However, the *E. macrospondylus* holotype has never received an in-depth reappraisal, and its purported relationships with other thalattosuchian specimens (Kuhn 1936; Hua *et al*., 2000; Karl *et al*., 2006) have largely been based upon Koken's (1883) description. This original description was extensive, but it was limited by a lack of comparative metriorhynchid specimens during the late 19th

Century. Here we redescribe the holotype of *E. macrospondylus*, and assess the impact this has for the taxonomy of Early Cretaceous metriorhynchids.

1.1 Historical overview

Koken (1883) established *Enaliosuchus macrospondylus* as a new genus and species because of the seemingly novel morphology of the atlas-axis complex. In particular, the presence of atlas rib facets being placed anteroventrally on the atlas centrum was listed as a peculiar feature for *Enaliosuchus* (Koken 1883: 799). Koken (1883) compared the atlas-axis complex to those of modern crocodylians, teleosauroids and the basal metriorhynchoid *Pelagosaurus typus* Bronn, 1841 (see Koken 1883: 809, table therein); but not with metriorhynchids.

A second specimen, comprising an incomplete cranium and lower jaw, with the atlas-axis and first post-axial cervical vertebra from the lower to middle Valanginian Stadthagen Formation of north-western Germany was referred to *Enaliosuchus* by Schroeder (1921). The basis for this referral was that the atlas-axis complex had similar atlas rib placement as that described by Koken (1883) for *Enaliosuchus macrospondylus* (see Schroeder 1921: 364). Interestingly, Schroeder (1921) neither explicitly referred the new specimen to *E. macrospondylus*, nor did he erect a new species for it. This was carried out later by Kuhn (1936) who named the specimen *E. schröderi* Kuhn, 1936. Note, that the use of the umlaut in the specific epithet by Kuhn (1936) was a hypercorrection, as the correct spelling of Schroeder's name is with the *oe*. Furthermore, usage of diacritic marks is not acceptable in a scientific name, in accordance with Article 27 of the ICZN Code. Thus, the correct spelling is *E. schroederi*.

The acceptance of *E. schroederi* as a distinct species has been disputed. While some papers have accepted both species as being valid (e.g. Steel 1973; Young & Andrade, 2009), they did not base their opinions on a detailed comparison of the holotypes. Sickenberg (1961) was the first to ask whether *E. schroederi* was distinct from *E. macrospondylus*, principally because Schroeder

(1921) was unsure in his original description whether the two specimens were conspecific (due to the limited overlap between them) and only assigned the specimen to the genus *Enaliosuchus*, leaving the species open. Hua *et al*. (2000) were the first to formally considered *E. schroederi* to be a subjective junior synonym of *E. macrospondylus*, rendering *Enaliosuchus* a monospecific genus. Jouve (2009) followed the taxonomy of Hua *et al.* (2000). Karl *et al*. (2006: 56) considered the establishment of *E. schroederi* to be "completely unnecessary", and could not preclude that the two species were conspecific.

A third putative *Enaliosuchus* specimen, an incomplete skeleton from the lower Valanginian (*Busnardoites campylotoxus* ammonite Zone) of south-eastern France, was referred to *E. macrospondylus* by Hua *et al*. (2000). This specimen (catalogue number 990201 from the collection of the Clément, Réserve Naturelle Géologique de Haute Provence in Digne les Bains – here later referred to as RNGD 990201) comprises most of the cranium and mandible, an incomplete atlas-axis complex, as well as five post-axial cervical and 15 dorsal vertebrae. While there is only minor overlap with the *Enaliosuchus macrospondylus* holotype material, this referral was accepted without comment in subsequent publications (e.g. Young & Andrade, 2009; Parrilla-Bel & Canudo, 2015; Sachs *et al.*, 2019). The cranial rostrum of RNGD 990201 is highly distinctive with its posterodorsally retracted external nares, and Hua *et al*. (2000) used this specimen to emend the diagnosis of *E. macrospondylus*. For the first time *Enaliosuchus* was clearly defined, and shown to be distinct from other metriorhynchid taxa.

Enaliosuchus has been considered to be a poorly known metriorhynchid (von Huene 1956; Steel 1973). Note, Young & Andrade (2009) altered the generic composition of *Geosaurus*, which from 1901 – 2008 was considered to be a Late Jurassic longirostrine form, and moved several species from *Geosaurus* to *Cricosaurus* and *Rhacheosaurus*. This unfortunately complicates the next two paragraphs and their discussion on previous hypotheses on the position of *Enaliosuchus* in Metriorhynchdae. Buffetaut (1982: 26) considered the *E. schroederi* holotype to be very similar to

Geosaurus Cuvier, 1824 (*Cricosaurus* Wagner, 1858 and *Rhacheosaurus* von Meyer, 1831 sensu Young & Andrade, 2009), and based on the *E. schroederi* holotype, Buffetaut (1982) concluded that the genus was distinct and valid. In Vignaud's (1995) unpublished PhD thesis, he considered *Enaliosuchus* to be similar to *Geosaurus gracilis* (von Meyer, 1831) (*Rhacheosaurus* sensu Young & Andrade, 2009), although he noted that the *E. schroederi* holotype and '*G.*' *gracilis* can be differentiated on prefrontal and tooth enamel ornamentation characters. Vignaud (1995) therefore provisionally retained *Enaliosuchus* as a valid genus. Neither Buffetaut (1982) nor Vignaud (1995) examined a potential synonymy between *E. macrospondylus* and *E. schroederi*, although Vignaud (1995) did state that Kuhn (1936) did not provide a diagnosis for *E. schroederi*. Moreover, it is clear that the retention of *Enaliosuchus* as a valid genus by both Buffetaut (1982) and Vignaud (1995) was based on the anatomy of the *E. schroederi* holotype, not the *E. macrospondylus* holotype.

The evolutionary relationships of *Enaliosuchus* have been further discussed since the description of the French specimen by Hua *et al*. (2000) who considered *Enaliosuchus* to be closely related to *Geosaurus* (*Cricosaurus* and *Rhacheosaurus* sensu Young & Andrade, 2009). The evolutionary relationships of *Enaliosuchus* was first tested by Wilkinson *et al*. (2008), who found *E. macrospondylus* (scoring based on the *E. macrospondylus* holotype and the French specimen) to be within a clade formed by *Geosaurus* species (pre-Young & Andrade, 2009 metriorhynchid taxonomy). Jouve (2009) however recovered *Enaliosuchus macrospondylus* (scoring based on the *E. schroederi* holotype and the French specimen) as the sister taxon to *Dakosaurus* Quenstedt, 1856. It is unclear whether the different specimen scoring sources, and/or the different character and taxon sets, are responsible for these differences.

The validity of the genus *Enaliosuchus* has been questioned, in different ways, by Karl *et al*. (2006) and Young & Andrade (2009). Karl *et al*. (2006) referred both *E. macrospondylus* and *E. schroederi* to the genus *Metriorhynchus* von Meyer, 1832, but did not retain either species as valid. Whereas, based on their phylogenetic analysis, Young & Andrade (2009) considered *Enaliosuchus*

to be a subjective junior synonym of *Cricosaurus*, as *E. macrospondylus* and *E. schroederi* were recovered as a subclade within their *Cricosaurus* clade. Young & Andrade (2009) chose not to retain *Enaliosuchus*, as under their evolutionary hypothesis it would render *Cricosaurus* paraphyletic, or demand the creation of multiple new genera. Note however, that they followed the emended diagnosis of *Enaliosuchus* from Hua *et al*. (2000) without comment; and that the *E. macrospondylus* operational taxonomic unit (OTU) scored by Young & Andrade (2009) was based on the referred French specimen and the holotype. Interestingly, further iterations of the phylogenetic dataset used by Young & Andrade (2009) have found *E. macrospondylus* and *E. schroederi* to be distantly related, albeit both within Rhacheosaurini (datasets starting from Young *et al*., 2017).

In sum, *Enaliosuchus* is one of the most poorly understood metriorhynchid genera. Previous studies have questioned the validity of the genus, and the validity of the second species assigned to the genus (*E. schroederi*). Some studies that accept the validity of *Enaliosuchus* have done so based on the anatomy of the *E. schroederi* holotype, not the *E. macrospondylus* holotype. The referral of the highly diagnostic French specimen to *E. macrospondylus* was used to emended the specific diagnosis, and for the first time clearly define *Enaliosuchus* and show it to be distinct from other metriorhynchid taxa. Therefore, the following questions need to be addressed, and will be herein: (1) is the *E. macrospondylus* holotype diagnostic; (2) do the holotypes of *E. macrospondylus* and *E. schroederi* share synapomorphies that would justify assigning them to the same species (i.e. the monospecific hypothesis of Hua *et al*. (2000)); and (3) was the referral of the highly diagnostic French specimen to *E. macrospondylus* justified?

1.2. Institutional Abbreviations

MB – Museum für Naturkunde, Berlin, Germany; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK – Natural History Museum, London, UK; RMH – Roemer und Pelizaeus

Museum, Hildesheim, Germany; RNGD – Réserve Naturelle Géologique de Haute Provence, Digne les Bains, France; MM – Mindener Museum, Minden, Germany.

2. Geological settings

The material that constitutes the holotype of *Enaliosuchus macrospondylus* and the referred teeth were found in two different locations in southern Lower Saxony, Germany and are actually separated by a significant stratigraphical gap. With regard to the holotype, Koken (1883: 792) specified the "Hils [strata] of the Osterwald" as the locality, and the horizon as "level of *Ammonites (Olcostephanus) marginatus*". Unfortunately, this information is somewhat ambiguous by present-day concepts and need to be further elucidated. Geographically, the term "Osterwald" describes a small mountainous region, ca. 30 km south-southwest of Hannover; as well as to the town of Osterwald, which is located in the southern margin of those hills (Fig. 1A-B). The grammatical form used by Koken ("des Osterwaldes") indicates that he referred to the mountains rather than to the settlement proper. Most of the Osterwald mountain range is formed by strata from the Jurassic and the non-marine Berriasian – the marine Lower Cretaceous is exposed only in a small area in the southeastern part due to a southeasterly dip of the succession (Albrecht 1913). While there are numerous fossils from the marine Lower Cretaceous with the label "Osterwald" in museum collections, as well as mentioned in the literature, details of the exact nature of this or these outcrop(s) are rarely given. Von Koenen (1902) mentioned two important sources of such material from Osterwald:

(1) the now abandoned brickworks clay-pit of the town of Osterwald, located c. 0.5 km to the east of the settlement. It exposed upper Hauterivian clay- and marlstones with an abundancy of the heteromorph ammonite *Aegocrioceras capricornu* (Roemer 1841), preserved in calcareous concretions (see also Stolley 1908).

(2) The Osterwald Tiefbauschacht, an abandoned mine shaft, c. 1.3 km east of the town of Osterwald, that penetrated Valanginian marine strata to reach the Berriasian coal seams below (Albrecht 1913). The mine shaft was constructed between 1879 and 1890 (Grimme, 2010).

The lithostratigraphic term "Hils [Formation]", used by Koken, that denotes marine, mostly pelitic deposits of Valanginian through Albian age in northern Germany, is currently superseded by the Minden Braunschweig Group (Erbacher *et al*., 2014a). In the Osterwald region, it can include beds of Valanginian through Hauterivian age.

Unfortunately, the sedimentary matrix of the type specimen, consisting of a reddish sideritic claystone ("rothbrauner Thoneisenstein" in the terminology of Koken) is not conclusive, as this lithotype may occur in the Valanginian as well as in the Hauterivian of the region (e.g. Mutterlose 1984). The biostratigraphic information provided by Koken for the stratum typicum is problematic as well. His "*Ammonites (Olcostephanus) marginatus*" obviously refers to the occurrence of the ammonite species described by Neumayr & Uhlig (1881: 157) as "*Olcostephanus marginatus* (Phill?) Römer" from Osterwald. These authors – following Roemer (1841) - redefined the species *Ammonites marginatus* Phillips, 1829, based on a poorly figured and described juvenile individual from England, to include some specimens from Lower Saxony. However, von Koenen (1902, 1909) separated the Lower Saxonian material as *Polyptychites marginatus* (Neumayr & Uhlig, 1881) from the English *Ammonites marginatus* Phillips, 1829. The latter was revised as *Simbirskites marginatus* (Phillips, 1829), a zone index fossil from the upper Hauterivian, by Rawson (1971).

The referred material of "*Polyptychites marginatus*" sensu Neumayr & Uhlig (1881), figured and discussed by von Koenen (1902, 1909), was subsequently partly reassigned to *Polyptychites keyserlingi* (Neumayr & Uhlig, 1881) by Jeletzky & Kemper (1988), and partly to *Polyptychites polyptychus* (von Keyserling, 1846) by Bogomolov (1989). *Polyptychites keyserlingi* is clearly a middle lower Valanginian taxon, while *P. polyptychus* was reported from the lowermost

upper Valanginian (Jeletzky and Kemper 1988). With regard to the original material of "*Olcostephanus*" *marginatus* from Neumayr & Uhlig (1881), Jeletzky & Kemper (1988: 29) noticed some doubts about the source stratum, suggesting that it may be "misplaced" from the Jurassic.

Nevertheless, Koken (1883) also clearly associated the horizon of "*Ammonites (Olcostephanus) marginatus*" with the "Hils Formation", and the matrix lithology supports a Lower Cretaceous origin of the *Enaliosuchus macrospondylus* postcranial material. Considering that the taxa currently comprising von Koenen's (1902, 1909) concept of his Lower Cretaceous "*Polyptychites marginatus*" (that was in turn based on Neumayr & Uhlig 1881) range from the middle lower to lowermost upper Valanginian (Jeletzky & Kemper 1988, Bogomolov 1989), it is the most plausible assumption that the holotype of *Enaliosuchus macrospondylus* originates from this chronostratigraphic interval of the lower Stadthagen Formation in the Minden Braunschweig Group (sensu Erbacher *et al*. 2014a). The locality was possibly the Tiefbauschacht Osterwald mine shaft near the town of Osterwald. This localization is also in concordance with the information in von Koenen (1902) for the ammonite material from "Osterwald". It remains unclear, on what basis Karl *et al*. (2006) correlated the stratum typicum with the "Astierienschichten". The "Astierienschichten" ("Astierien beds", an obsolete lithostratigaphic term) are lowermost Hauterivian in age according to Mutterlose (1992a).

The first isolated tooth referred to *E. macrospondylus* by Koken (1883: 824; MB.R.3636) was found at the Elligser Brink, a hill ca. 0.6 km south of the town of Delligsen in the Hils Mountains, about 50 km south of Hannover. Koken (1883) noted that it originates from the collection of Friedrich Koch. Koch & Dunker (1837) described an assortment of vertebrate remains in the marine Lower Cretaceous strata of this locality, that became known as the "Elligserbrink bed". As Koken (1883) did not mention otherwise, it is plausible that the tooth came from the same horizon. This is corroborated by the fact that Koken referred also to this collection, stratum, and

locality, when describing the disputed pterosaur "*Ornithocheirus*" *hilsensis* in the same work (Koken 1883: 824f.). According to Burri (1956), the "Elligserbrink bed" dates to the uppermost Valanginian or lowermost Hauterivian (Stadthagen Formation, Minden-Braunschweig-Group).

The second isolated tooth Koken (1883) referred to *E. macrospondylus* (RMH uncatalogued [2]) originates from the "Hils conglomerate of the Osterwald". According to Erbacher *et al*. (2014b) the lithostratigraphic name "Hils Conglomerate" in its classic sense (Roemer 1841) is obsolete and defines various homonymous units, ranging from the Berriasian to the Cenomanian. However, in a more strict and regional sense it is synonymous to the Grenzlerburg Member of the Salzgitter Formation (uppermost Valanginian through lower Hauterivian, Erbacher *et al*. 2014b).

From a palaeoenvironmental point of view, all localities were situated in an open marine, euhaline, oxygenated shallow-water setting with fine-grained sedimentation and low background sedimentation rates. The Grenzlerburg Member represents partly a transgressive carbonatic conglomerate in a marginal setting with abundant fauna (e.g. Mutterlose 1984, 1992a, b; Mutterlose & Bornemann, 2000; Fig. 1C)

3. Description of Koken's hypodigm of *Enaliosuchus macrospondylus*

3.1. Status of the type material

Koken (1883: 792) described the majority of his material as if it came from a single individual, although it was in a largely disarticulated and dissociated state when he studied it. He based his assumption on the fact that it derived from a single locality and stratum, the fitting proportions and the lack of duplicate skeletal elements. Consequently, the remains received one accession MB.R.1943 (with 16 subnumbers MB.R.1943.1-16) and are considered the holotype of *Enaliosuchus macrospondylus*. Koken (1883) mentioned that the material was initially part of the Henne collection, but the exact whereabouts of the discovery remain unknown. It is also unknown if all parts of the axial skeleton where found in association (Koken 1883 p. 792 only mentioned that

some ribs and limb elements were found separately). Therefore we cannot be certain the elements found at the type locality all come from the same individual.

Additionally, Koken (1883) referred an isolated dorsal vertebra (RMH uncatalogued (1)) from another collection but the same locality and stratum, and two isolated tooth crowns (RMH uncatalogued (2) and MB.R.3636) to his new taxon. The latter were added by Koken for being identified as “crocodilian” and originating from marine strata of similar age and region. A fragmentary phalanx (MB.R.1939), likewise from the Henne collection and from the same locality and stratum, is present in MB collection, but was not described by Koken (1883). These four specimens need to be excluded from the type material, as is described in the Systematic Synopsis below.

Below the material is described as it was summarised by Koken (1883).

3.2. Teeth

Koken (1883) assigned two teeth to the *Enaliosuchus macrospondylus* hypodigm, one from the MB collection and one from the RHM collection (Fig. 2). Both teeth were found separately from the remainder of the skeleton (see the geological history section above) and the referral to *Enaliosuchus* was not justified. Curiously, the RHM houses two teeth which are labelled *Enaliosuchus macrospondylus*, but following Koken’s (1883) description of the tooth crown being incomplete, the right specimen in Fig. 2C appears to be the correct referred specimen.

The tooth crown MB.R.3636 (Fig. 2A, B) is conical, slightly lingually curved and bears pronounced apicobasally aligned enamel ridges that are contiguous from the base of the crown to the apex. Such enamel ridges are rare in Thalattosuchia, as most ridged teeth have both long ridges and shorter ridges, generally closely packed, but the ridges rarely are contiguous along the entirety of the crown (see the tooth close-up photographs in Young *et al*. 2013, 2014a). The enamel ridges in MB.R.3636 become closer to one another apically. The apex itself is not present, as the crown is

extensively worn in that region. Whether it is taphonomic or biological in origin is unclear without scanning electron microscopy. Carinae are formed mesially and distally, bearing fine denticles. The basal enamel ornamentation is reminiscent of *Anteophthalmosuchus* Salisbury & Naish, 2011 (see Ristevski *et al*. 2018); however, given the lack of a complete tooth crown, and the lack of an in-depth study into the dental variation within Goniopholididae, this specimen can only be referred to as ?Goniopholididae. The RMH (uncatalogued (2)) tooth crown (Fig. 2C) is largely damaged and bears more enamel ridges that are place closer to one another.

As these remains cannot be demonstrated to belong to the holotype or *Enaliosuchus macrospondylus* at all, they have to be excluded from the type material. In consequence no cranial material is known from *Enaliosuchus macrospondylus*.

3.3. Atlas-axis complex

The atlas-axis complex (MR.R.1943.2) comprises the atlas intercentrum, the atlas and axis centra, parts of the atlas and axis neural arches, as well as the axis neural spine (Fig. 3). A fragmentary left atlas rib is also preserved. The atlas intercentrum forms the ventral part of the atlas cup (Fig. 3A). It is semicircular in anterior view, and slightly displaced from its original position. Dorsally the atlas intercentrum reaches to about mid-height of the atlas centrum, where it meets the atlas neural arches (Fig. 3A, B, E). Posteriorly and ventrally the atlas intercentrum contacts the atlas centrum. Posteroventrally, the slightly convex ventral side of the atlas intercentrum meets the anterior surface of the axis centrum (Fig. 3F). Laterally the atlas intercentrum forms the anterior part of the atlas rib facet, of which the remainder is formed by the atlas centrum (Fig. 3B, E). The anterior fragment of the left atlas rib is still attached to the rib facet. The atlas rib is slightly posterolaterally inclined and becomes transversely narrower posteriorly (Fig. 3B).

The atlas centrum has a sub-triangular shape in right lateral aspect. Anteriorly the atlas centrum bears a flat surface that forms the posterior demarcation of the atlas cup (Fig. 3A). The

ventral side of the atlas centrum is contacted by the atlas intercentrum and dorsally the atlas neural arches are attached. The posterior side of the atlas centrum is fused to the axis centrum but keeps an open, in lateral view slightly oblique running suture (Fig. 3B, E). On the right side, the anteroventral region on both sides of the suture, is strongly rugose, passing indistinctly into the parapophyseal facet ventrally. On the left side, the same region is much smoother. The rugosities may be pathological in origin.

The atlas neural arches form the dorsal part of the atlas cup. Their concave anteromedial sides bear a sharp anterior margin (Fig. 3A). Dorsally, at the base of the neural canal, there is a gap between the left and right atlas neural arch (Fig. 3A). Posteriorly the atlas neural arches contact the atlas centrum. The posterodorsally inclined atlas postzygapophysis (Fig. 3E) is present in its original position on the right side, whereas the left one is preserved isolated. The atlas postzygapophysis narrows posteriorly, contacts the axis prezygapophysis and frames an oval foramen (Fig. 3E).

The axis centrum has a quadratic shape in lateral view (Fig. 3B, E). Anteriorly the axis centrum sutures to the atlas centrum and anteroventrally a short contact with the atlas intercentrum is established. The posterior side of the axis centrum bears a high-oval articular surface that is largely filled with matrix (Fig. 3D). Ventrally an anteriorly damaged midline ridge is formed. In ventral aspect, the axis centrum is expanded anteriorly and posteriorly, and is constricted in the middle (Fig. 3F). On both sides of the axis the diapophyses are preserved as robust transversal projections of dorsoventrally compressed, rhomboidal cross-section, that originate immediately below the neural arch. The articular facets are not preserved. The fragment of an axis rib that was described and figured by Koken (1883: pl. XXIV, fig. 5) in articulation with the left diapophysis, is missing in the material as preserved. The parapophysis is a small, anteroposteriorly elongate, tuberosity located anteroventrally on the axis centrum, adjacent to the atlas centrum (Fig. 3B). The

shallow parapophyseal facet extends for a small portion anteriorly onto the posteroventral region of the atlas centrum. It is therefore divided by the suture between the atlas and axis centra.

The axis neural arches originate somewhat anterior to the dorsal rim of the articular face of the axis centrum (Fig. 3B, E). The axis prezygapophyses is obscured by the atlas postzygapophysis on the right side of the specimen (Fig. 3E). Laterally the ventrally protruding neural arches extend to about mid-height of the axis centrum. This protruding lateral portion bears the diapophyses for the axis ribs which are damaged on both sides. The axis neural spine is largely broken off and only the transversely thin bases are still preserved (Fig. 3C, E).

3.4. Postaxial cervical vertebra

Parts of three postaxial cervical vertebrae are preserved; an isolated centrum (MR.R.1943.3, Fig. 4A-E) with attached neurapophyses, and a nearly complete vertebra, embedded in matrix with part of the neurapophysis of the preceding vertebra attached to it (MR.R.1943.1, Fig. 4F, G). The centra of MR.R.1943.1 and MR.R.1943.3 are longer than wide/high. The articular faces of MR.R.1943.3 are oval (Fig. 4B, D), whereas those of MR.R.1943.1 are more circular (Fig. 4F). In both specimens the slightly indented articular faces are surrounded by thickened rims. Only the left diapophysis of MR.R.1943.3 is well preserved, the other diapophyses are either damaged, broken off or embedded in matrix. The complete diapophysis is ventrally and slightly posteriorly inclined and reaches to a point dorsal to the dorsoventral midsection of the centrum (Fig. 4A). It bears a long-oval and slightly indented rib facet. The parapophyses are both broken off in the isolated centrum. Their bases indicate that they were about equally large and slightly more anteriorly placed than the diapophyses, which indicates a placement in the anterior part of the neck. In MR.R.1943.1 the right parapophysis is preserved, which has a circular shape and a slightly indented surface (Fig. 4G). It is considerably smaller than the base of the diapophysis and placed anteroventral to the latter. This indicates a placement in the posterior part of the neck. The ventral side of the centrum is well

353 preserved in MR.R.1943.3 and bears a pronounced and rounded midline keel adjacent to which the
354 centrum is dished (Fig. 4E). The anterior and posterior sections of the ventral side of the centrum
355 are thickened and the anterior one also protrudes slightly ventrally (Fig. 4A). Dorsally remnants of
356 the zygapophyses are preserved in the isolated vertebra. Here the right prezygapophysis is more
357 complete and terminates approximately in line with the lateral margin of the centrum (Fig. 4B). The
358 left prezygapophysis is also preserved in MR.R.1943.1 and still articulated with the
359 postzygapophysis of the preceding cervical (Fig. 4G). The postzygapophyses are otherwise largely
360 broken off in both specimens.

361 The neural spine is preserved in MR.R.1943.1. It is considerably higher than the centrum
362 and slightly posteriorly inclined. It bears an almost straight anterior edge and a slightly convex
363 dorsal side. The posterior edge of this neural spine is damaged. The second neural spine adjacent to
364 the afore described, is incomplete but appears shorter (Fig. 4G).

365

366 *3.5. Dorsal vertebrae*

367 Remnants of seven dorsal vertebrae (MB.R.1943.4-10) are preserved in the holotype material (Fig.
368 5A-H). An additional dorsal centrum (Fig. 5J-N) was assigned to the same individual by Koken
369 (1883) and is kept in the collection of the Roemer- und Pelizaeus-Museum (RMH uncatalogued
370 (1)). It is herein excluded from the type material of *Enaliosuchus macrospondylus* and referred to an
371 indeterminate thalattosuchian.

372 All centra are elongate and bear oval and slightly indented articular faces which are
373 surrounded by a thin rim. Laterally, adjacent to the articular faces, some longitudinal rugosities are
374 present. The lateral sides of the centra, showing open neurocentral sutures, are gently concave and
375 so are their ventral sides. The transverse processes are elongate, thin, have a subtriangular cross-
376 section and gradually narrow laterally, which indicates a placement in the anterior part of the dorsal
377 vertebral column. The laterally placed diapophysis is sub-circular and well preserved in

MB.R.1943.4 (Fig. 5A). In dorsal view the posterior sides of the transverse processes of MB.R.1943.4 and MB.R.1943.5 are almost straight, while the anterior ones curve from the diapophysis slightly anteromedially to meet the parapophysis (Fig. 5C). In the RMH specimen (Fig. 5J-N) part of the right transverse process is preserved which extends straight lateromedially and is wider than the transverse processes in the aforementioned vertebrae. A similar pattern is indicated by the broken off bases of the transverse processes in another dorsal centrum (MB.R.1943.6, Fig. 5E, F). These vertebrae seem to have had a more posterior placement in the dorsal vertebral column.

The parapophyses are preserved in the isolated neuropophyseal fragment (MB.R.1943.7, Fig. 5G, H) and in the anterior dorsal vertebra (MB.R.1943.4, Fig. 5A-D). In both specimens they are slightly anteriorly inclined, placed at the anterior end of the neural arch, and are surrounded by a thin edge. The zygapophyses are broken off and the neural canal is filled with matrix in all of the dorsal vertebrae. The transversely thin neural spine is preserved in the neuropophyseal fragment (MB.R.1943.7, Fig. 5G, H). It has a high rectangular appearance with an almost straight anterior margin, a slightly convex dorsal side and bears a gently concave posterior side.

3.6. Dorsal ribs

A largely complete, lateroventrally curved dorsal rib is present in the block that contains the almost complete cervical vertebra (MB.R.1943.1, Fig. 5I). Several rib fragments are preserved (MB.R.1943.9, 12, 13) which show subcircular cross-sections. Additional rib fragments are present in the RHM collections.

3.7. Caudal vertebra

An isolated caudal centrum (MB.R.1943.11, Fig. 5O-S) is preserved. The elongate centrum bears oval and slightly concave articular faces (Fig. 5P, R) of which the posterior one extends further

ventrally than the anterior articular face (Fig. 5O). The ventral side of the centrum is deeply concave. Two semi-circular hemapophyseal facets are present posteroventrally (Fig. 5Q). Dorsolaterally remnants of the broken off transverse processes are preserved. There large size indicates that the vertebra derives from the proximal part of the tail. Ventral to the transverse processes the lateral sides of centrum are concave, giving it an hourglass-like shape in ventral view (Fig. 5Q). Dorsally, in the mid-section of the centrum, the bases of the broken off neural arches are preserved. They start adjacent to the centrums posterior articular face but terminate approximately 1 cm posterior to the anterior articular face. The preserved portion of the neural canal was narrowest at about midlength of the neural arch.

3.8. Femur

An incomplete, possibly left, femur is preserved (MR.R.1943.15.1+2, Fig. 6A-D). Koken (1883) initially identified the two fragments as one tibia broken apart in the middle, the uniform morphology indicates that these are indeed parts of one element, but given its size and curvature the element is in fact a femur. The element has an oval cross-section, with the distal end being more strongly compressed mediolaterally (Fig. 6A, D) and the shaft, as preserved, is gently curved. The proximal (Fig. 6A) and distal ends (Fig. 6B) are irregular, lacking well defined epiphyses. While all metriorhynchids characteristically lack well defined distal epiphyses (e.g. see Andrews 1913), this is one of the few metriorhynchids found where the proximal epiphyses also look to be poorly defined. Given that proximal end appears to be either damaged and/or has some sort of pathology, we cannot ascertain whether this feature is an artefactual or represents a more cartilaginous hip articulation.

3.9. Additional elements

Koken (1883: 818) mentioned and briefly described a proximal end of a metatarsal. This specimen (MB.R.1943.16, Fig. 7A, B) is slightly curved and bears a shallow furrow on the supposed ventral side. It resembles the sacral ribs of the second sacral vertebra (see e.g. Andrews 1913, fig. 64). Another specimen from the Henne collection (MB.R.1939, Fig. 6C, D) that derives from the same locality as the reminder of the material was catalogued as proximal fragment of a metapodial element of *E. macrospondylus*. This element of which the original hour-glass like shape is still indicated, nicely resembles a phalanx from the hind limb.

4. Discussion

4.1. The Koken (1883) character set

Koken (1883) faced difficulties in defining his new genus *Enaliosuchus*, partly due to the incompleteness of the material available to him, and partly from a lack of comparative material and descriptions. He never stated an autapomorphy-based diagnosis, but presented what can be considered by modern standards a comparative diagnosis. He focused on the atlas-axis complex and compared a total of nine characters with a range of extant and fossil crocodylians, and thalattosuchians. These include:

(1) the contact of the proatlas with the atlas neurapophyses: with the proatlas sitting atop, or in an excavation of the atlas neurapophyses;
(2) complete fusion of atlas centrum to the axis centrum;
(3) medial contact of the atlas neurapophyses;
(4) presence of an atlas intercentrum (atlas hypapophysis *sensu* Koken 1883);
(5) presence of a diapophysis on the axis;
(6) presence of a parapophysis on the axis;
(7) morphology of the ventral surface of the axis centrum;

(8) position of the atlas rib articulation: on the atlas intercentrum, on the atlas centrum, or between both;

(9) position and morphology of the axial ribs: single-headed or double-headed, articulating solely with the axis centrum, or with the axis and (fused) atlas centrum.

His comparative taxa included the crocodylid *Osteolaemus tetraspis* Cope, 1861 ("*Crocodilus frontatus*" *sensu* Koken, 1883), the alligatorids *Alligator mississippiensis* (Daudin, 1802), and *Diplocynodon darwini* (Ludwig, 1877) ("*Crocodilus ebertsi*" and "*Alligator darwini*" *sensu* Koken 1883), as well as the thalattosuchians *Machimosaurus mosae* Sauvage & Lienard, 1879, *Teleosaurus cadomensis* Lamouroux, 1820, *Steneosaurus bollensis* (Jaeger, 1828) ("*Mystriosaurus tiedemanni*", "*Mystriosaurus longipes*", and "*Mystriosaurus mandelslohi*" in Koken, 1883), and *Pelagosaurus typus* (including "*Teleosaurus temporalis*" *sensu* Koken 1883). As a consequence, from his original list of 11 taxa, only 7 are considered valid today, while 4 are actually subjective junior synonyms of other species on the list.

From his characters, (1) is unknown due to preservation in many fossil taxa; (2) is undiagnostic, because it is controlled ontogenetically in many crocodyliform taxa (e.g. Vieria *et al.* 2018), (3) is common in Thalattosuchia (e.g. *Metriorhynchus superciliosus, 'M.' brachrhynchus, Gracilineustes leedsi*; Arthaber 1906, Andrews 1913), (4) is ubiquitous in crocodyliform taxa (Romer 1956); (5) and (6) are not diagnostic on less inclusive systematic levels; (7) may have some significance but the character distribution is not clear, and this area is not well preserved in the *E. macrospondylus* holotype; (8) and (9) may have a more differentiated taxonomic significance, but - as will be discussed below – Koken's (1883) interpretation of these characters are fraught with some misinterpretations.

From his overall comparisons Koken (1883: 807) concluded that the genus "*Teleosaurus*" may be the closest relative of his new species. However, it must be noted that only one of the two

species in his "*Teleosaurus*" is still included in this genus, the type species *T. cadomensis*. His second species, "*T. temporalis*", is a subjective junior synonym of *Pelagosaurus typus*. From context it appears that he mostly referred to the latter, as the atlas-axis-complex was discussed extensively by Eudes-Deslongchamps (1864), while it was only incompletely known in *T. cadomensis*.

According to Koken (1883), "*Teleosaurus*" shares with *E. macrospondylus* the following characters:

(1) the proatlas is nested within an anterior excavation of the atlas neurapophyses [the element questionably identified as proatlas in *E. macrospondylus* by Koken 1883 is herein identified as atlas postzygapophysis];

(2) well developed diapophyses and inconspicuous parapophyses ("tuberosities") on the axis centrum;

(3) the presence of a groove on the ventral side of the axis centrum;

(4) the "general morphology" of the atlas neurapophyses.

In contrast Koken (1883) listed the following characteristics that *Enaliosuchus* had, but "*Teleosaurus*" lacked:

(5) the broad head of the atlas ribs covers the axis parapophyses (which are reduced to mere tuberosities) in lateral view;

(6) the atlas centrum contacts the atlas ribs, the rib facet is jointly formed by the atlas intercentrum and atlas centrum;

(7) the axis centrum bears single-headed ribs that articulate with the diapophysis and points straight ventrally;

(8) the contact between the atlas intercentrum and the atlas neurapophyses is short;

(9) the atlas intercentrum bears a strongly concave morphology;

(10) the atlas neurapophyses are separated from each other along their whole anteroposterior length; (11) the axis centrum is fused to the atlas centrum, but separated by a visible, oblique suture.

Of these characters, (1) cannot be proven, as the small fragment, questionably identified by Koken (1883) as the proatlas in *E. macrospondylus* is considered here as the atlas postzygapophysis, (2) occurs in other metriorhynchids. Koken (1883) described the axis parapophyses as “tuberosities” and doubted that they articulated with the axis rib, speculating that they may have contacted the atlas rib. Jaekel (1904) supported this interpretation but stated that similar “tuberosities” were present in *Metriorhynchus superciliosus* (=*M. jaekeli* in Jaekel 1904). In contrast Baur (1886) already interpreted these “tuberosities” correctly as parapophyses, which was confirmed by von Arthaber (1906). The latter clearly figured that in *Metriorhynchus superciliosus* the parapophyseal facet extends across the suture of the atlas and axis centra. Boschma (1922, based on the figure in Jaekel 1907) located the parapophyseal facet in *Enaliosuchus macrospondylus* solely on the axis centrum and found this an important contrast to *Metriorhynchus superciliosus* in which the parapophyseal facet is located on the axis as well as on the axis centrum. However, the latter condition actually also occurs in *Enaliosuchus macrospondylus* (Fig. 3). (3) is inconclusive, as the type material of *E. macrospondylus* is damaged in this region. The absence of a sharp keel is widespread among crocodyliforms and thalattosuchians. (4) is unspecific. (5) and (7) result from a misinterpretation due to a lack of preservation. As shown by von Arthaber (1906), the parapophyses in metriorhynchids are in the same position and similarly inconspicuous. However, they articulate with the capitulum of a flat, bicapitate rib that forms almost a right angle with the tuberculum. The “straight, ventrally pointing” axis rib of Koken (1883: 806 and pl, XXIV, fig. 5) is therefore only the shaft of the tuberculum that tapered strongly distally. However, Koken (1883: 806) himself wrote that this rib fragment was originally embedded “closely” to the diapophysis and was removed during preparation. In lateral view, the axis rib capitulum (if it would have been preserved) is

hidden by the head of the atlas rib, which has been discussed and clarified for *Enaliosuchus macrospondylus* by Baur (1886).

(6) and (8) through (11) are shared by metriorhynchids (von Arthaber 1906, Andrews 1913).

Although Koken (1883) made detailed observations and tried to make a comprehensive comparison, he entirely omitted metriorhynchid material or references. This is understandable, as detailed studies of the corresponding anatomy in this group were not available before the 20th Century. It also explains the peculiarities that he observed in his material, and his conclusion that it represents a new taxon. Unfortunately, a synoptic view of metriorhynchid morphology results in the conclusion that the characters he found distinguishing are more widely distributed in this group.

The other metriorhynchid elements described for *Enaliosuchus macrospondylus* by Koken (1883) show the general morphology seen in various taxa and are of no diagnostic value.

4.2. The Schroeder (1921) character

Schroeder (1921) referred a new metriorhynchid specimen from the Lower Cretaceous of northern Germany to *Enaliosuchus* based on the morphology of the axis ribs (this is the specimen Kuhn 1936 establish as the *Enaliosuchus schroederi* holotype). His new specimen preserved axis ribs in which the capitulum and tuberculum remained unfused, effectively resulting in two axis ribs on each side. Schroeder (1921: 364) claimed the same condition to be present in the *E. macrospondylus* holotype. However, this cannot be substantiated as the axis ribs are no longer preserved in the *E. macrospondylus* holotype, and the fragment that was described by Koken (1883) is not unambiguous in interpretation (see above).

4.3. The Hua et al. (2000) character set

The *Enaliosuchus* taxonomy of Hua *et al*. (2000) is a monospecific hypothesis, with all three specimens included in *E. macrospondylus*. However, the only elements shared by all three

552 specimens are the atlas-axis complex and one post-axial cervical vertebra. The emended diagnosis
553 of *Enaliosuchus* by Hua *et al*. (2000: 472) focussed largely on cranial characters, which thus cannot
554 be applied for the holotype specimen (MB.R.1943.1-16). However, Hua *et al*. (2000) considered
555 five characters in the atlas-axis complex to be diagnostic for *Enaliosuchus*: (1) a massive atlas
556 centrum that is sub-quadrangular in lateral view, (2) the atlas ribs inserted on both the atlas
557 intercentrum and axis centrum, (3) the diapophyses are placed on the axis neural arches, (4)
558 presence of a ventral midline keel on the axis centrum, and (5) the axis neural spine is curved and
559 anteriorly inclined. Unfortunately, these five characters do not unite these three specimens to the
560 exclusion of other metriorhynchids:

561 (1) In the *Enaliosuchus macrospondylus* holotype specimen (MB.R.1943.2), the atlas
562 centrum is partly obscured by the atlas neural arches and the atlas intercentrum, but the morphology
563 is clearly more triangular than quadrangular in lateral view (Figs. 3, 6A), similar to the condition
564 present in *Metriorhynchus superciliosus* de Blainville, 1853 (Fig. 7D). The shape of the atlas
565 centrum in *E. schroederi* cannot be seen because the atlas intercentrum, atlas neural arches and atlas
566 ribs obscure most of the element (Fig. 7B).

567 (2) The atlas rib facets in MB.R.1943.2 are largely formed by the atlas intercentrum and
568 atlas centrum (Figs. 3, 6A). In other metriorhynchids such as *Cricosaurus vignaudi* (Frey, Buchy,
569 Stinnesbeck & López-Oliva, 2002) (see Frey *et al.* 2002: fig. 6), '*Metriorhynchus*' *brachyrhynchus*
570 Eudes-Deslongchamps, 1868 (Fig. 7E) and *Gracilineustes leedsi* (Andrews, 1913) (Fig. 7F) they
571 are mainly borne by the atlas centrum. The participation of the atlas intercentrum in the formation
572 of the rib facet was described for *Metriorhynchus jaekeli* Schmidt, 1904 (see Jaekel 1904: fig. 1)
573 and is figured for *M. superciliosus* (see Andrews 1913: fig. 61). In *E. schroederi* the atlas ribs
574 obscure the rib facets on both sides (Fig. 7B, I), but it appears that the atlas intercentrum might have
575 participated in the atlas rib facet. In the referred specimen of *E. macrospondylus* (RNGD 990201)

the rib facet is borne on the atlas centrum (Fig. 7C). Whether or not the atlas intercentrum took part in the formation of the atlas rib facet is unclear as this element is not preserved in RNGD 990201.

(3) The diapophyses are present on the axis neural arches in all examined metriorhynchid taxa, such as *M. superciliosus* (Fig. 7D), '*M.*' *brachyrhynchus* (Fig. 7E) and *Cricosaurus vignaudi* (see Frey *et al*. 2002: fig. 6), and thus this character is of no diagnostic value.

(4) A ventral ridge on the axis centrum is present on MB.R.1943.2, although its anterior portion is damaged (Fig. 3E). This ridge is very indistinct in *E. schroederi* (Fig. 7I), especially when compared with the pronounced ridges that occur in other metriorhynchids such as *G. leedsi* (Fig. 7G) and *M. superciliosus* (Fig. 7H).

(5) The shape of the axis neural spine cannot be compared between RNGD 990201 and the *E. macrospondylus* and *E. schroederi* holotypes as it is incomplete in the German specimens (Fig. 7A, B). A similar shape of the RNGD 990201 axis neural spine is, however, present in *M. superciliosus* (Fig. 7D).

Therefore, based upon the five characters listed by Hua *et al*. (2000), the referral of the French material to *Enaliosuchus macrospondylus* cannot be supported. The shape of the atlas centrum differs between the specimens. It was described as sub-quadrangular in RNGD 990201, whereas it is triangular in MB.R.1943.2. The atlas rib facet is borne by the atlas intercentrum and atlas centrum in MB.R.1943.2, whereas the atlas intercentrum is missing in RNGD 990201 but a large rib facet is evident at the atlas centrum. The diapophyses are consistently placed on the axis neural arches in metriorhynchids, and a ventral keel on the axis centrum is not unique. Finally, the shape of the axis neural spine is largely damaged in MB.R.1943.2 and cannot be compared. Moreover, the length-to-height ratio of the axis centrum likewise differs between MB.R.1943.2 (1:1) and RNGD 990201 (1:0.7). Although, in the latter the transverse compression may impact this ratio. A longer ratio also occurs in *Metriorhynchus superciliosus* (NHMUK PV R 2051, 1:1.16),

Gracilineustes leedsi (NHMUK PV R 3014, 1:1.16) and '*M.*' *brachyrhynchus* (NHMUK PV R 2039, 1:1.08 and NHMUK PV R 3804, 1:1.11).

The referral of the *Enaliosuchus schroederi* holotype by Hua *et al.* (2000) to the *Enaliosuchus macrospondylus* hypodigm is also questionable. Several elements in the atlas-axis complex of this specimen differ from MB.R.1943.2, such as the atlas intercentrum that extends more dorsally, and the atlas neural arches which have a carved anteroventral portion for the articulation with the atlas intercentrum (Fig. 7B). A re-description of the *E. schroederi* holotype is forthcoming, which will discuss the atlas-axis in more detail.

4.4. The Karl et al. (2006) taxonomy

Curiously, Karl *et al*. (2006) assigned the holotypes of both *E. macrospondylus* and *E. schroederi* to the genus *Metriorhynchus*, as *Metriorhynchus* sp.. The arguments in Karl *et al*. (2006) are very superficial, no detailed comparisons were made, and their phylogenetic analysis had an odd sample-set for testing the internal position of *Enaliosuchus* within Metriorhynchidae. *Enaliosuchus schroederi* can be distinguished from *Metriorhynchus* spp. with the same atlas-axis characters by which it differs from *E. macrospondylus*, whereas several characters present in *E. macrospondylus* do indeed occur in *M. superciliosus* (Fig. 7D) and '*M.*' *brachyrhynchus* (Fig. 7E) (see discussion above). However, given that the atlas-axis complex is only known and well-described in a limited number of metriorhynchid taxa, and that most characters listed by Koken (1883), Hua *et al*. (2000), and Karl *et al*. (2006) have a widespread distribution in Metriorhynchidae (see discussion above), we cannot agree with the unambiguous referral of the *E. macrospondylus* and *E. schroederi* holotypes to the genus *Metriorhynchus* as proposed by Karl *et al*. (2006).

Oddly, the cranial morphology of the *E. schroederi* holotype alone is enough to readily distinguish it from *Metriorhynchus* (e.g. smooth dermatocranium, very large sclerotic rings, jugal excluded from the preorbital fenestrae). As stated above, the phylogenetic analysis of Young &

Andrade (2009) recovered *E. schroederi* and the French specimen referred to *E. macrospondylus* as derived metriorhynchines, thus supporting its distinction from *Metriorhynchus*. The phylogenetic analysis of Jouve (2009) recovering *Enaliosuchus* as the sister taxon to *Dakosaurus* similarly falsifies the *Metriorhynchus* subjective synonymy hypothesis. This contrasts with the strange taxon and character sample set in the phylogenetic analysis of Karl *et al*. (2006), which had a single metriorhynchid OTU, referred to as "*Enaliosuchus*/*Metriorhynchus*". The remaining OTUs were four crocodylians, three teleosauroids and the basal metriorhynchoid *Pelagosaurus typus* (the same taxon-sample as Koken 1883). The specimens that were the basis for scoring their OTUs is not given. Only ten characters were included, three cranial characters, and seven out of the nine atlas-axis characters from Koken (1883). While the Karl *et al*. (2006) phylogenetic analysis does show that most of the atlas-axis characters used by Koken (1883) to establish *E. macrospondylus* has a wide distribution in crocodyliforms, it does not support their contention that *Enaliosuchus* is a subjective junior synonym of *Metriorhynchus*. Principally because they never tested it. It is not clear why Karl *et al*. (2006) used a phylogenetic analysis to highlight the distribution of atlas-axis characters rather than a comparative plate figuring the characters.

Moreover, in using a sub-sample of Koken's (1883) atlas-axis character set, and the same limited taxon set as Koken (1883), Karl *et al*. (2006) compound the original issue Koken had: the lack of comparative data with metriorhynchids. The difference being, the lack of comparative material is understandable in Koken (1883). Finally, Karl *et al*. (2006) did not mention the Hua *et al*. (2000) study. It appears they were unaware of the third putative *Enaliosuchus* specimen, and the new atlas-axis characters proposed by Hua *et al*. (2000).

5. Cretaceous metriorhynchids

The fossil record of Metriorhynchidae is poorer in the Cretaceous than in the Jurassic. Early overviews of metriorhynchid evolution and species diversity found metriorhynchid biodiversity was affected by an extinction at the Jurassic-Cretaceous boundary (Pierce *et al*. 2009; Young *et al*. 2010), with Cretaceous metriorhynchids characterised as a "dead clade walking" (Young *et al*. 2010). However, over the past decade the two-phase extinction hypothesis (end-Tithonian biodiversity crash and Valanginian-Hauterivian boundary final extinction) posited by Young *et al*. (2010) has been falsified. Re-examination of Cretaceous fossils found that at least four metriorhynchid lineages are known to survived into the Cretaceous (Young *et al*. 2014b). It is unclear whether some of the metriorhynchid specimens from the Vaca Muerta Formation of Argentina, such as the *Purranisaurus potens* Rusconi 1948 holotype and those referred to *Cricosaurus* sp. and *Dakosaurus andiniensis* Vignaud & Gasparini, 1996 are uppermost Tithonian or lowermost Berriasian in age (Herrera *et al*. 2015; Fernández *et al*. 2019; Herrera pers. comm. 2019). Thus, potentially six metriorhynchid lineages crossed the Jurassic–Cretaceous boundary. An incomplete metriorhynchid skull from Berriasian strata of the Neuquén basin is known (Fernández *et al*. 2019). The specimens from the uppermost Tithonian or lowermost Berriasian of Russia are taxonomically indeterminate (Ochev 1981).

From the Valanginian of France and Germany four different lineages of metriorhynchid are known: Geosaurina, Plesiosuchina and two lineages of Rhacheosaurini (Table 1). These include the holotype of the nomen dubium *Neustosaurus gigondarum* Raspail, 1842, the holotype of *Enaliosuchus macrospondylus*, the holotype of *Enaliosuchus schroederi*, the holotype of *Geosaurus lapparenti* (Debelmas & Strannoloubsky, 1957), the French specimen referred to *Enaliosuchus macrospondylus*, a specimen referred to as cf. *Geosaurus lapparenti* and an indeterminate Plesiosuchina specimen (Raspail 1842; Debelmas & Stannoloubsky 1956; Debelmas 1958; Hua *et al*. 2000; Karl *et al*. 2006; Young *et al*. 2014b). A skull from the Valanginian of Colombia has been referred to cf. *Cricosaurus* (Larsson *et al*. 2012).

From the upper Valanginian or lower Hauterivian of France an indeterminate metriorhynchid is known (Debelmas & Demians D'Archimbaud 1956), and from the lower Hauterivian of France an incomplete skeleton has been referred to *Geosaurus lapparenti* (Debelmas, 1952).

Post-Hauterivian metriorhynchids are exceptionally rare. A poorly preserved incomplete skull from the Barremian of Spain had been considered to be a possible metriorhynchid (Parrilla-Bel *et al*., 2012), although this seems less likely now (Parrilla-Bel pers. comm. 2017). Chiarenza *et al*. (2015) referred an isolated tooth crown from the lowermost Aptian of Sicily to Plesiosuchina based on a series of apomorphies. This tooth significantly increased the known geological range of Metriorhynchidae. Curiously, Fischer *et al*. (2015) raised the issue that the Sicilian tooth could in fact be a brachauchenine pliosaurid, like *Makhaira rossica* Fischer, Arkhangelsky, Stenshin, Uspensky, Zverkov & Benson, 2015. However, they did not address the list of apomorphies Chiarenza *et al*. (2015) gave when they referred the tooth to Plesiosuchina (such as the presence of contiguous microdenticles, the denticles being rectangular in shape, and the presence of ‘weak’ carina flanges). The convergences between the Sicilian tooth and *Makhaira rossica* are interesting, but it is based on superficial similarities and not on apomorphies. In fact, *Makhaira rossica* lacks all of the plesiosuchin apomorphies observable in the Sicilian tooth. As such, Fischer *et al*. (2015) inadvertently strengthened the referral of the Sicilian tooth to Plesiosuchina (as Cretaceous pliosaurids did not seem to evolve the apomorphies seen in metriorhynchids), not the reverse. Although, in the absence of more complete material, the specimen still needs to be considered cf. Plesiosuchina. Post-Hauterivian survival of Metriorhynchidae needs confirmation with more complete material. However, with the description of a Barremian teleosauroid specimen (see Cortés *et al*., 2019), it does seem that thalattosuchians persisted for longer than previously realised closer to the equator. Their continued presence could have acted as a barrier to large-bodied neosuchians colonising Lower Cretaceous marine ecosystems.

6. Are *Enaliosuchus* and *Neustosaurus* congeneric?

The poorly ossified proximal femoral epiphyses seen in *Enaliosuchus macrospondylus* Koken, 1883 (Fig. 6), as mentioned above, are either artefactual, pathological, or evidence of a shift in femoral morphology during the Cretaceous. The holotype of *Neustosaurus gigondarum* Raspail, 1842 is a largely complete post-dorsal postcranial skeleton from the Valanginian of France. Considered to be a nomen dubium by Young & Andrade (2009), the whereabouts of the holotype has never been ascertained (although a cast of a very small portion of the skeleton is on display in the MNHN). Raspail (1842) figured both femora, and they look strikingly similar to our reconstruction of the femur in *Enaliosuchus macrospondylus* (Fig. 6).

That being said, the obvious problems are: (1) the *E. macrospondylus* femur is incomplete, and (2) the *N. gigondarum* femora cannot be checked first-hand. With these caveats in mind, the peculiar sigmoidal shape and the oddly flat proximal epiphyses are unique to these two specimens. Should both of these features prove to be genuine (which we cannot be certain of), it hints a possible relationship between these two genera. New discoveries of Valanginian metriorhynchids are needed to elucidate femoral morphotypes, thus it is premature to posit *Enaliosuchus* as a subjective junior synonym of *Neustosaurus*. But this is a hypothesis that should be tested when more data becomes available.

7. Conclusions

In conclusion, the holotype specimen of *Enaliosuchus macrospondylus* (MB.R.1943.1-16) lacks unique anatomical traits (although see our discussion on the femur above), and preserved axial skeleton largely resembles the morphology present in other metriorhynchids such as *Metriorhynchus superciliosus*, *'M.' brachyrhynchus* and *Gracilineustes leedsi*. The atlas-axis complex preserved with the *E. schroederi* holotype shows several symplesiomorphic

metriorhynchid traits, but the *E. macrospondylus* holotype lacks the peculiar morphology of the atlas intercentrum and atlas neural spine, which indicates that they are distinct taxa. The French specimen (RNGD 990201) referred to *Enaliosuchus macrospondylus* by Hua *et al*. (2000) is distinct from MB.R.1943.1-16 in the shape of the atlas centrum, and possibly in the placement of the atlas rib facet and the proportions of the axis centrum.

Given these morphological differences, the monospecific hypothesis of Hua *et al*. (2000) (with the *Enaliosuchus macrospondylus* and *E. schroederi* holotypes and the French specimen RNGD 990201 all referred to the same species) is not justifiable. With the lack of evidence to refer other specimens to this taxon, only the holotype specimen (MB.R.1943.1-16) can be referred to as *Enaliosuchus macrospondylus*. While the femur is incomplete, it shows a striking resemblance to those of *Neustosaurus gigondarum* (a species known from a single specimen, which unfortunately cannot be examined first-hand). Due to the lack of verifiable autapomorphies, *E. macrospondylus* is here considered a nomen dubium that is best classified as Metriorhynchidae gen. et sp. indet. As the Cretaceous fossil record of Metriorhynchidae improves, new discoveries could resurrect *E. macrospondylus*, and test a possible synonymy between *Enaliosuchus* and *Neustosaurus*. Until then, we consider *E. macrospondylus* to be a nomen dubium, '*E.*' *schroederi* to be a valid taxon, and the French specimen an unnamed distinct species. As the location of the *Neustosaurus gigondarum* holotype is still unknown, we follow Young &Andrade (2009) in considering it to be a nomen dubium.

8. Systematic synopsis

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

Crocodylomorpha gen. et sp. indet.

Material: RMH uncatalogued (2), an isolated tooth crown (Fig. 2C).

Locality: “Osterwald [Mountains]” (Koken 1883), southern Lower Saxony, northern Germany.

Stratigraphy: “Hils-Conglomerat” (Koken 1883); i.e. Grenzlerburg Member, Salzgitter Formation, Minden Braunschweig Group, uppermost Valanginian to lowermost Hauterivian, Lower Cretaceous.

Goniopholididae Cope, 1875

?Goniopholididae gen. et. sp. indet.

Material: MB.R.3636, an isolated tooth crown (Fig. 2A,B).

Locality: Elligser Brink near Delligsen, southern Lower Saxony, northern Germany (Koken 1883).

Stratigraphy: “Elligserbrink-Schicht”, Stadthagen Formation, Minden Braunschweig Group, uppermost Valanginian to lowermost Hauterivian.

Metriorhynchidae Fitzinger, 1843 (*sensu* Young & Andrade, 2009)

?Metriorhynchidae gen. et sp. indet.

Material: MB.R.1939. Fragmentary phalanx. RMH uncatalogued (1). Dorsal vertebra (Fig. 4Q-U).

Locality: “Osterwald [Mountains]” (Koken 1883), probably the former Osterwald Tiefbauschacht mine shaft, c. 1.3 km east of the town of Osterwald, southern Lower Saxony, northern Germany (approx. 52°06’34’’N, 9°38’37’’E).

Stratigraphy: Lower part of Stadthagen Formation, Minden Braunschweig Group. Most probably middle lower to lowermost upper Valanginian, Lower Cretaceous.

Metriorhynchidae Fitzinger, 1843 (*sensu* Young & Andrade, 2009)

Metriorhynchidae gen. et sp. indet.

Enaliosuchus macrospondylus Koken, 1883

(nomen dubium)

Figs. 3-6

Holotype: MB.R.1943.1-16. Atlas-axis complex, remnants of three post-axial cervical vertebrae, eight dorsal vertebrae, several fragmentary dorsal ribs, one caudal vertebra, an incomplete femur, fragment of a sacral rib.

Type locality: “Osterwald [Mountains]” (Koken 1883), probably the former Osterwald Tiefbauschacht mine shaft, c. 1.3 km east of the town of Osterwald, southern Lower Saxony, northern Germany (approx. 52°06’34’’N, 9°38’37’’E).

Stratigraphy: Lower part of Stadthagen Formation, Minden Braunschweig Group, most probably middle lower to lowermost upper Valanginian, Lower Cretaceous.

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Figure captions

Figure 1: Geographic, palaeogeographic and geological situation of the *Enaliosuchus macrospondylus* material. A) General location map, B) Geological situation in the vicinity of the Osterwald Mountains, with location of the potential type localities Osterwald clay-pit (1) and Tiefbauschacht Osterwald mine shaft (2). Geological data from Landesamt für Bergbau, Energie und Geologie (NIBIS® Kartenserver, 2014), C) Palaeogeographical sketch map for the Valanginian, showing the location of Osterwald and Elligser Brink. Note that during the earliest Hauterivian the shoreline shifted further landward due to transgression. After Mutterlose (1984), modified.
[Intended for page width]

Figure 2. Teeth initially referred to *Enaliosuchus macrospondylus*. ?Goniopholidae gen. et sp. indet. (MB.R.3636), uppermost Valanginian to lowermost Hauterivian of Elligser Brink near Delligsen in (A) distal and (B) labial views. (C) Crocodylomorpha gen. et. sp. indet. (RMH uncatalogued), uppermost Valanginian to lowermost Hauterivian of the Osterwald Mountains. Note that only the tooth on the right side, shown in labial view, is mentioned in Koken (1883). Scale bar equals 1 cm.
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Figure 3. Atlas-axis complex (MB.R.1943.2) of the *Enaliosuchus macrospondylus* holotype specimen, middle to upper Valanginian of the Osterwald Mountains in (A) anterior, (B) left lateral, (C) dorsal, (D) posterior, (E) right lateral and (F) ventral view. Scale bar equals 5 cm. Abbreviations: apo, atlas postzygapophysis; apr, axis prezygapophysis; atc, atlas centrum; atic, atlas intercentrum; atn, atlas neural arch; atr, atlas rib; ap, axis parapophysis; axc, axis centrum; axn, axis neural arch; dia, axis diapophysis.

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Figure 4. Postaxial cervical vertebrae of the *Enaliosuchus macrospondylus* holotype from the middle to upper Valanginian of the Osterwald Mountains. Cervical vertebra (MB.R.1943.3) in (A) lateral, (B) anterior, (C) posterior, (D) dorsal and (E) ventral view. Posterior cervical vertebra (MB.R.1943.1) in (F) posterior and (G) lateral view. Scale bars equal 5 cm. Abbreviations: dia, diapophysis; mk, midline keel; ns, neural spine; pap, parapophysis; prz, prezygapophysis.

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Figure 5. Additional postaxial vertebrae and ribs of the *Enaliosuchus macrospondylus* hypodigm from the lowermost upper Valanginian of the Osterwald [Mountains]. Dorsal vertebra (MB.R.1943.4) in (A) lateral, (B) posterior, (C) dorsal and (D) anterior view. Dorsal centrum (MB.R.1943.6) in (E) anterior and (F) lateral view. Neurapophysis of a dorsal vertebra (MB.R.1943.7) in (G) lateral and (H) anterior view. (I) Rib fragments (MB.R.1943.9). RMH uncatalogued. Dorsal vertebra referred to *Enaliosuchus macrospondylus* by Koken (1883) in (J) lateral, (K) anterior, (L) ventral, (M) posterior and (N) dorsal view. Caudal vertebra (MB.R.1943.11) in (O) lateral, (P) anterior, (Q) ventral, (R) posterior and (S) dorsal view. Scale bars equal 5 cm. Abbreviations: bn, base of neural arch; hf, hemapophyseal facet; ns, neural spine; pap, parapophysis; tp, transverse process.

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Figure 6. Incomplete, possibly left, femur (MB.R.1943.15.1+2) of the *Enaliosuchus macrospondylus* holotype specimen from the lowermost upper Valanginian of the Osterwald [Mountains] with the missing part of the shaft being based upon *Neustosaurus gigondarum*. (A) proximal, (B) medial, (C) lateral and (D) proximal view. Scale bar equals 5 cm.

[Intended for ½ page width]

Figure 7. Additional elements of the *Enaliosuchus macrospondylus* hypodigm from the lowermost upper Valanginian of the Osterwald [Mountains]. (A, B) supposed proximal portion of a sacral rib (MB.R.1943.16), (C, D) fragmentary phalanx (MB.R.1939). Scale bars equal 1 cm.

[Intended for ½ page width]

Figure 8. Comparison of metriorhynchid atlas-axis components of (A) *Enaliosuchus macrospondylus* holotype (MB.R.1943.1-16) in lateral view, (B) *Enaliosuchus schroederi* holotype (MM uncatalogued) in lateral view, (C) referred specimen of *Enaliosuchus macrospondylus* (RNGD 990201) in lateral view, (D) *Metriorhynchus superciliosus* (NHMUK PV R 2051) in lateral view, (E) ‘*Metriorhynchus*‘ *brachyrhynchus* (NHMUK PV R 3804) in lateral view, (F) *Gracilineustes leedsi* (NHMUK PV R 3015) in lateral view, (G) *Gracilineustes leedsi* (NHMUK PV R 3014) in ventral view, (H) *Metriorhynchus superciliosus* (NHMUK PV R 2051) in ventral view, (I) *Enaliosuchus schroederi* holotype (MM uncatalogued) in ventral view. Abbreviations: arf, atlas rib facet; atc, atlas centrum; atic, atlas intercentrum; atr, atlas rib; axc, axis centrum; axp, axis parapophysis; dia, diapophysis; vk, ventral keel. Scale bars equal 1 cm.

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1088 Table 1. Table of all published thalattosuchian specimens from the Cretaceous. Note that all the French Cretaceous metriorhynchids are from the
1089 Région Provence-Alpes-Côte d'Azur, and the German Cretaceous metriorhynchids are from Lower Saxony. Furthermore, the age of the Russian
1090 material is either uppermost Jurassic or lowermost Cretaceous.

	Specimen	**Age**	**Locality**	**Reference**
1	*Dakosaurus andiniensis* referred specimen	Upper Tithonian or Lower Berriasian	Yesera del Tromen-Pampa Tril area, Neuquén Province, Argentina	Herrera *et al*. 2015; Fernández *et al*. 2019
2	*Purranisaurus potens* holotype	Upper Tithonian or Lower Berriasian	Malargüe Department, Mendoza Province, Argentina	Herrera *et al*. 2015; Fernández *et al*. 2019
3	*Cricosaurus* sp.	Upper Tithonian or Lower Berriasian	Arroyo Durazno, Mendoza Province, Argentina	Fernández *et al*. 2019
4	Metriorhynchidae indeterminate	Upper Tithonian or Lower Berriasian	Arroyo Paulino, Mendoza Province, Argentina	Fernández *et al*. 2019
5	Metriorhynchidae indeterminate	Upper Tithonian or Lower Berriasian	Khoroshevskii Island, Volga Region, Russia	Ochev 1981
6	Metriorhynchidae indeterminate	Lower Berriasian	Arroyo Paulino, Mendoza Province, Argentina	Fernández *et al*. 2019
7	*Neustosaurus gigondarum* holotype	Lower Valanginian	Département du Vaucluse, France	Raspail 1842
8	'*Cricosaurus*' *macrospondylus* referred specimen	Lower Valanginian	Département des Hautes-Alpes, France	Hua *et al*. 2000
9	*Cricosaurus schroederi* holotype	Lower Valanginian	Landkreis Schaumburg, Germany	Karl *et al*. 2006
10	cf. *Geosaurus lapparenti*	Lower Valanginian	Département du Vaucluse, France	Debelmas 1958
12	*Enaliosuchus macrospondylus* holotype	Lower upper Valanginian	Landkreis Hamelin-Pyrmont, Germany	Koken 1883
13	cf. *Cricosaurus*	Upper Valanginian	Colombia	Larsson *et al*. 2012
14	Plesiosuchina indeterminate	LowerUpper Valanginian	Département des Bouches-du-Rhône, France	Young *et al*. 2014b
15	*Geosaurus lapparenti* holotype	Upper Valanginian	Département du Var, France	Debelmas & Stannoloubsky 1957
16	Metriorhynchidae indeterminate	Upper Valanginian or Lower Hauterivian	Département du Vaucluse, France	Debelmas & Demains D'Archimbaud 1956

17	*Machimosaurus rex* holotype	Hauterivian? (Upper Jurassic–Lower Cretaceous)	Touil el Mhahir, Tataouine Governorate, Tunisia	Fanti *et al*. 2016 (but see Cortés *et al*., 2019)
18	*Geosaurus lapparenti* referred specimen	Lower Hauterivian	Département du Var, France	Debelmas 1952
19	Teleosauroidea gen. et sp. indet.	Upper Barremian	Loma La Cabrera, Colombia	Cortés *et al.*, 2019
20	cf. Plesiosuchina	Lowermost Aptian	Montagna Grande area, Sicily	Chiarenza *et al*. 2015

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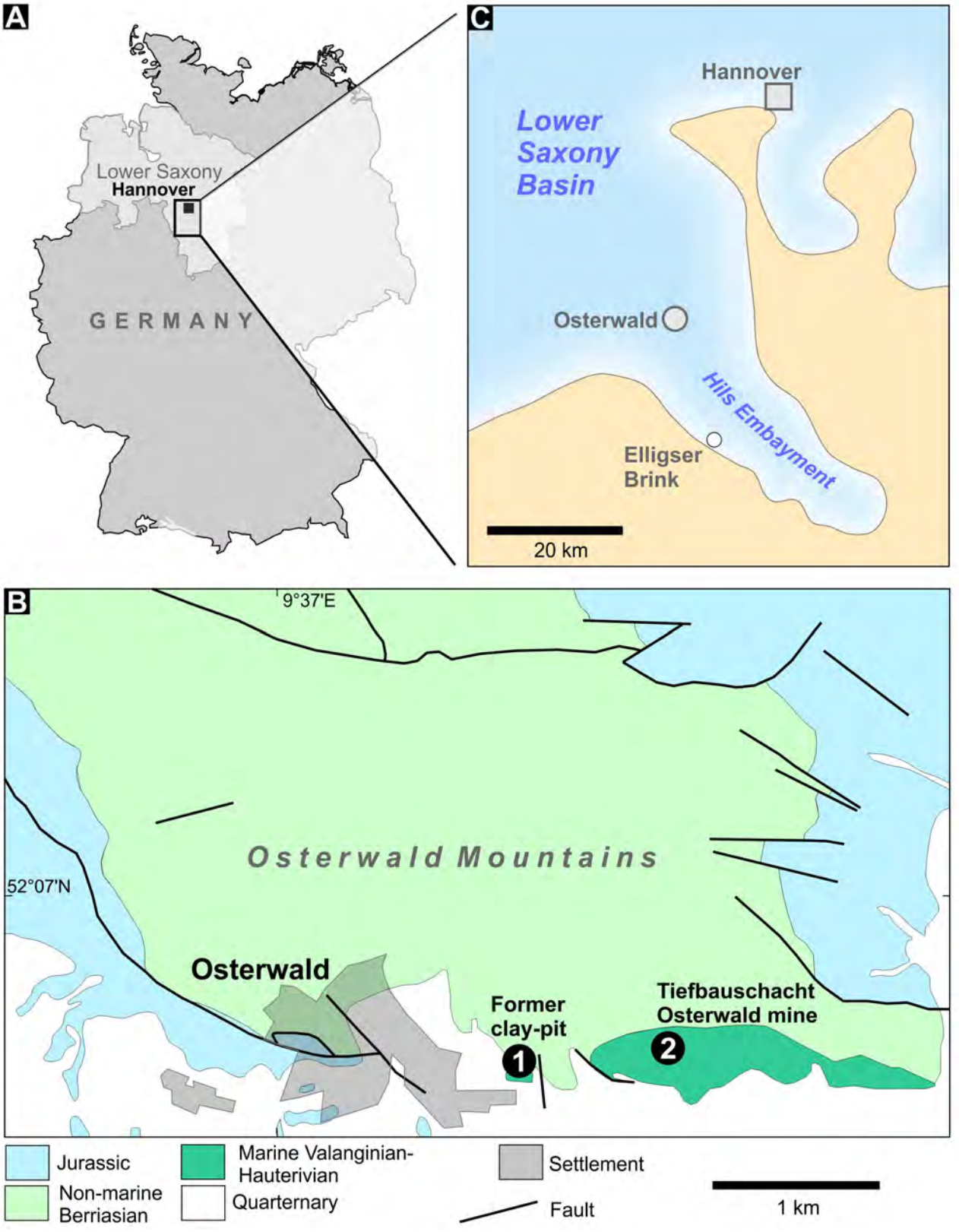
A
Lower Saxony
Hannover
GERMANY
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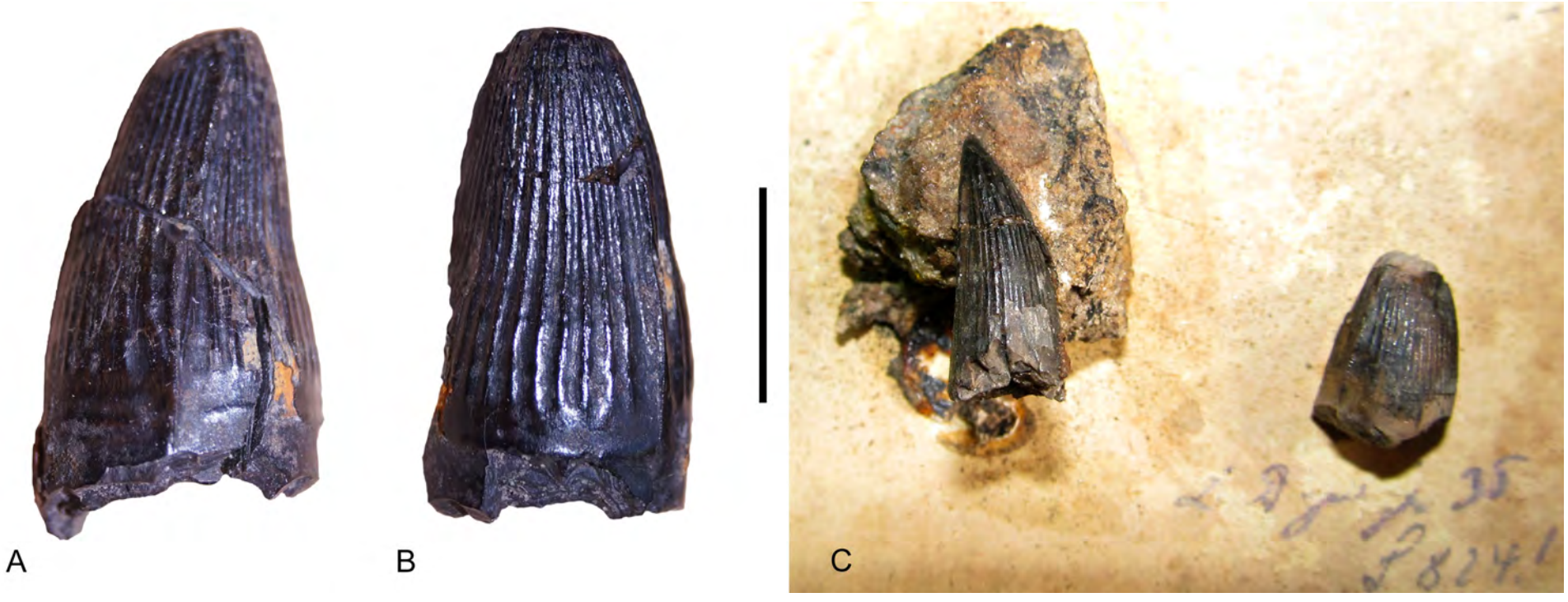
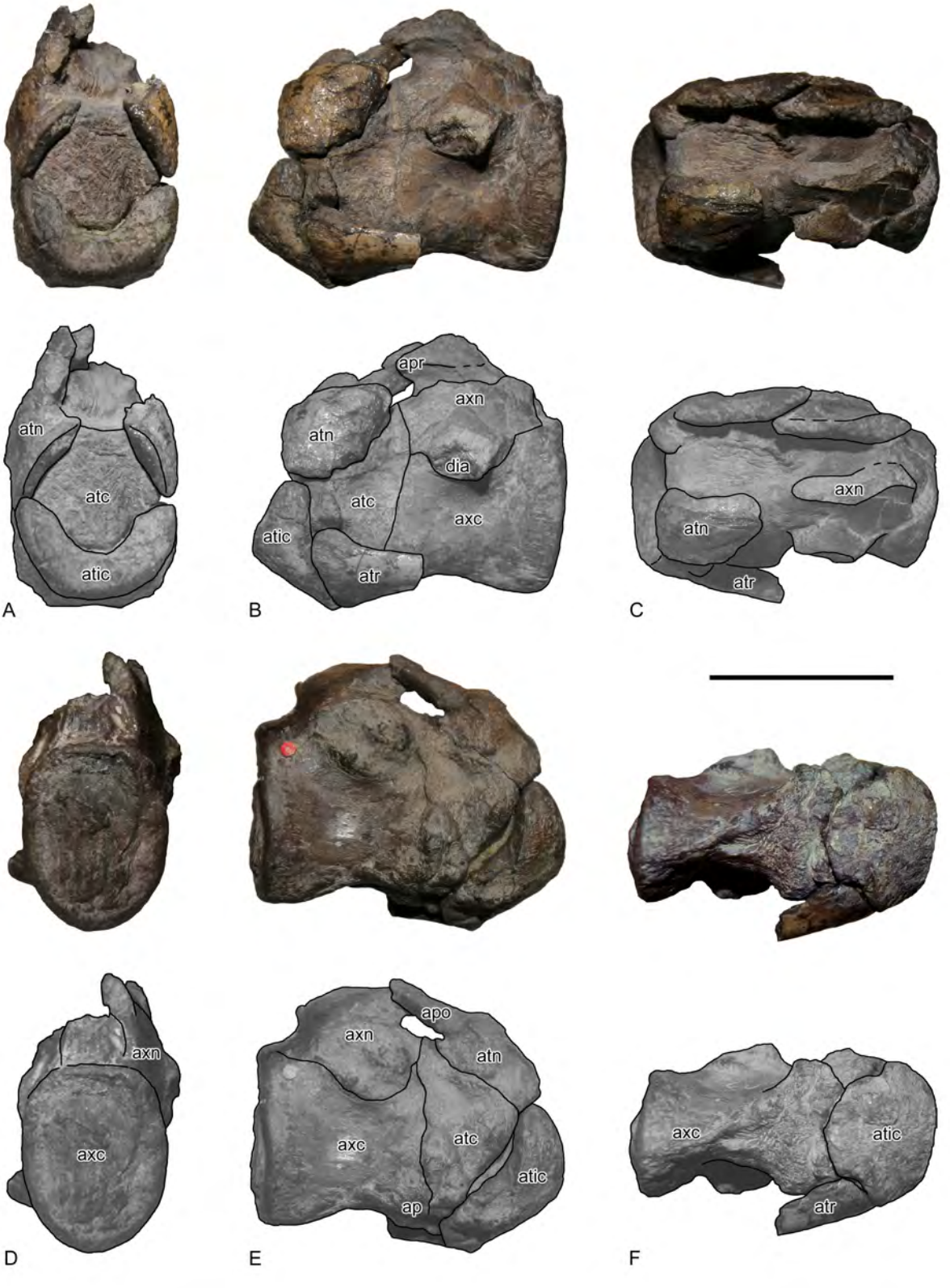
Hannover
Lower Saxony Basin
Osterwald
Hils Embayment
Elligser Brink
20 km
B
9°37'E
52°07'N
Osterwald Mountains
Osterwald
Former clay-pit
1
Tiefbauschacht Osterwald mine
2
Jurassic
Non-marine Berriasian
Marine Valanginian-Hauterivian
Quarternary
Settlement
Fault
1 km


A
B
C


atn
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atic
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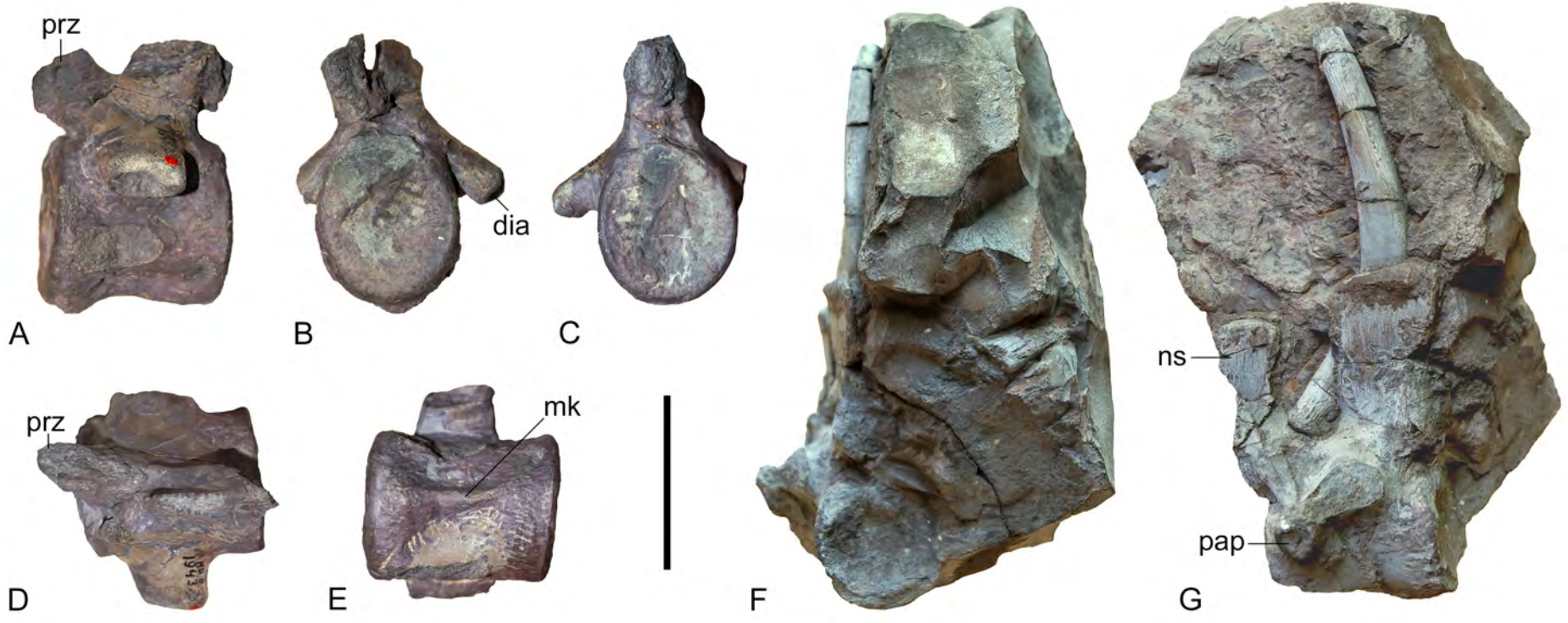
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pap
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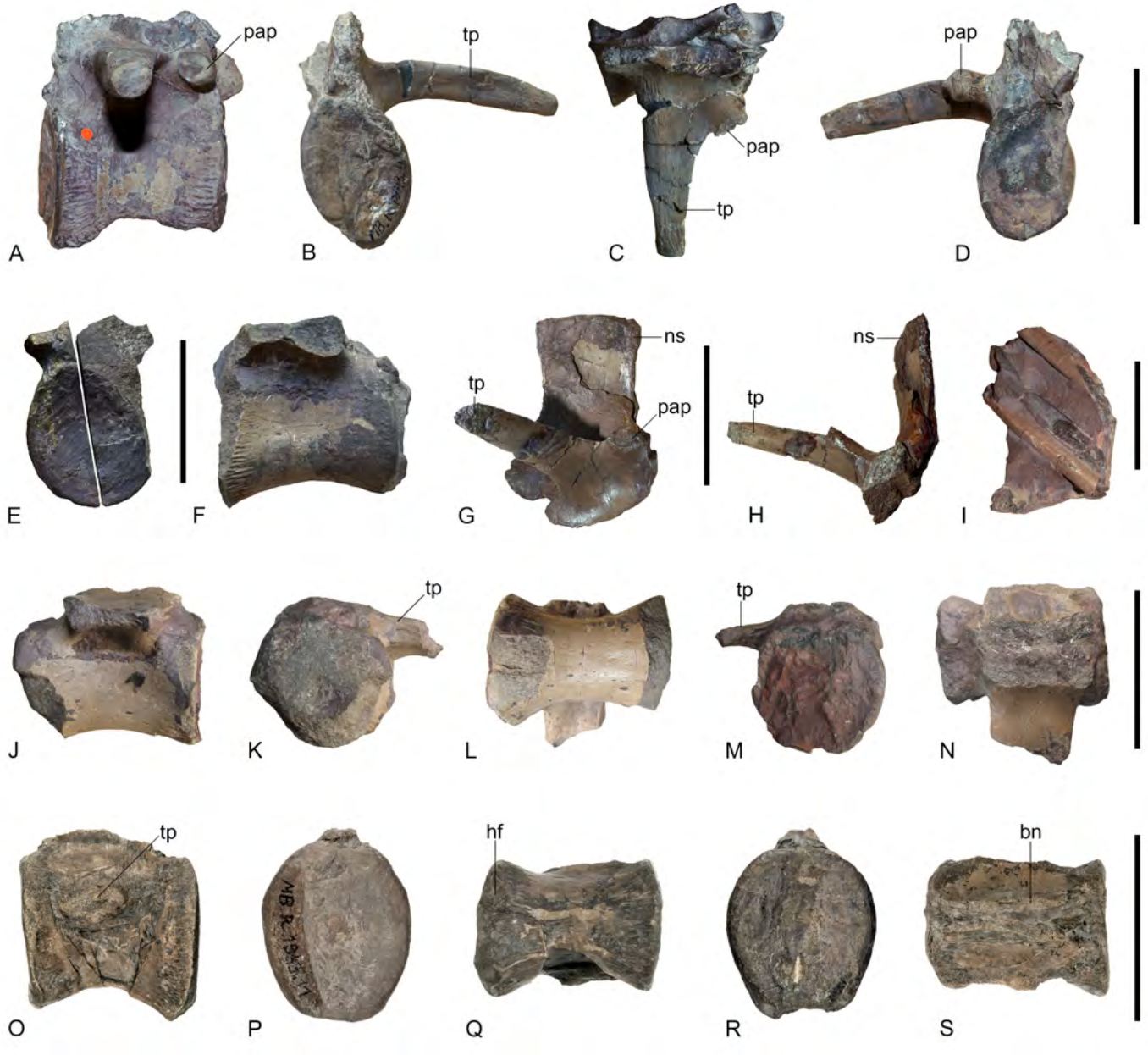
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tp
K
L
tp
M
N
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O
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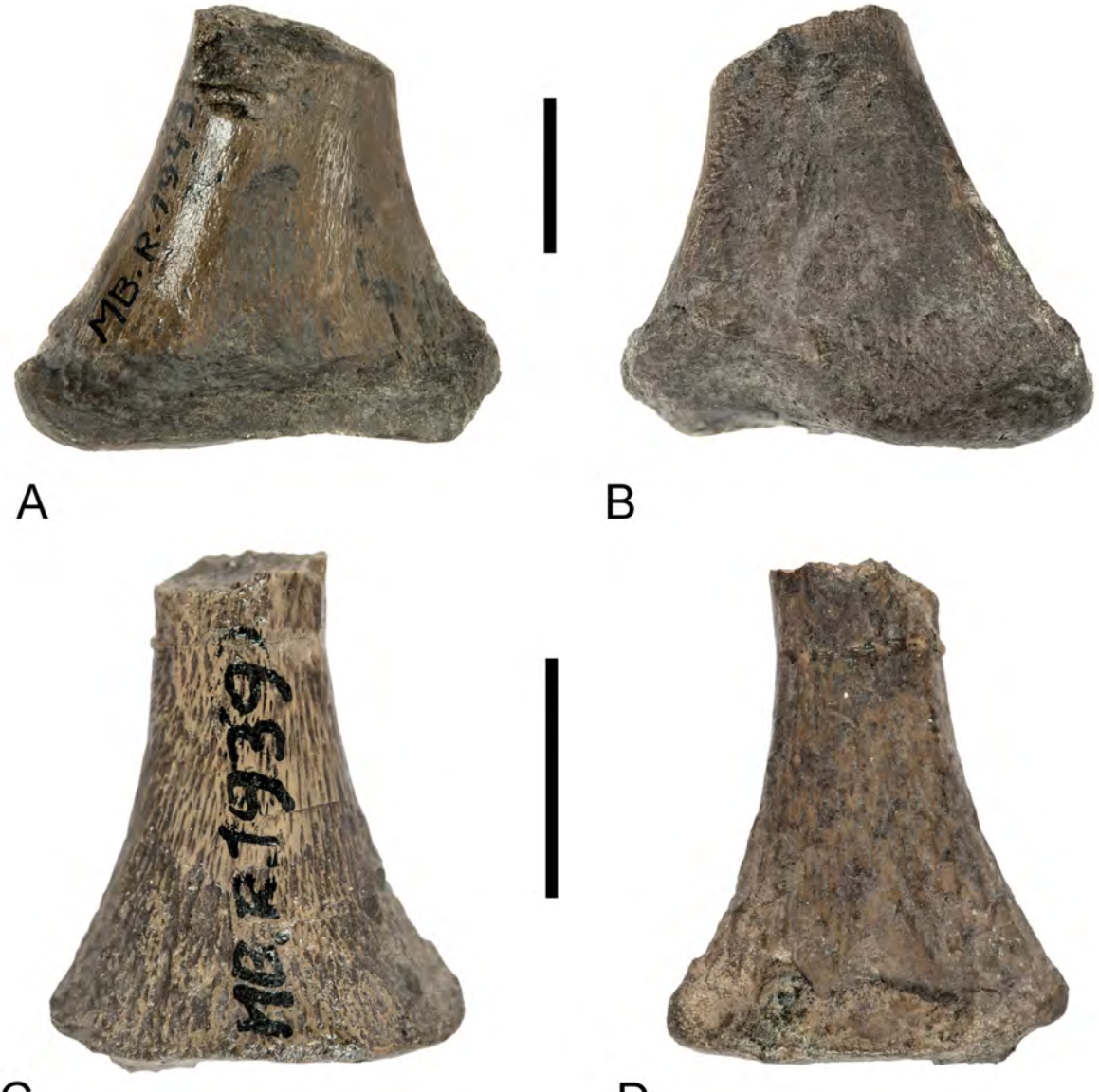
Q
R
bn
S

A
B
MB.R.1943.15.1
Ostenwald
C
MB.R.1943.15.2
D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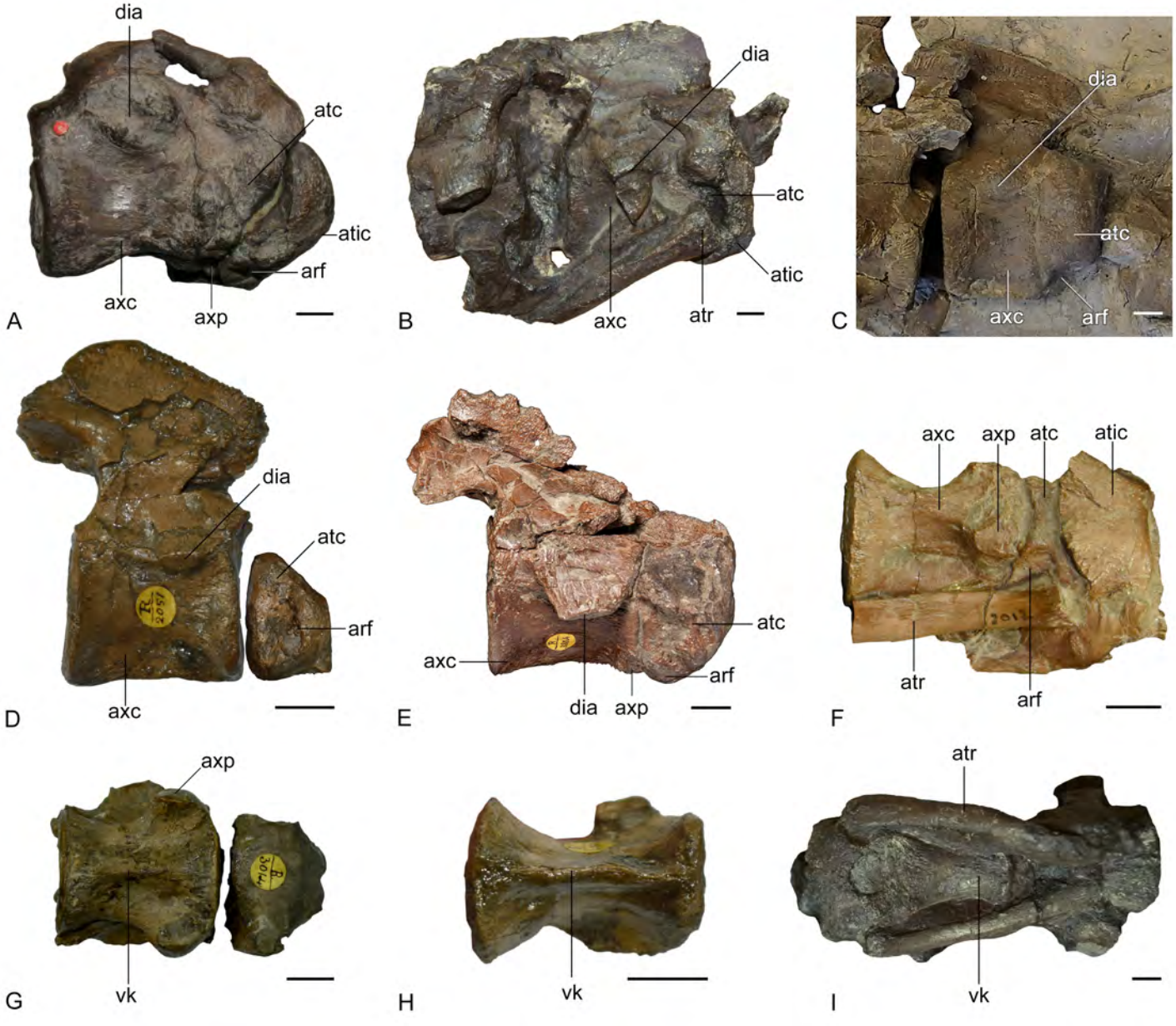
MB.R.1959
C
D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dia
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arf
E
axc
axp
atc
atic
atr
arf
F
axp
vk
G
vk
H
atr
vk
I

There are no conflicts of interest

All authors

Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing - Original Draft, Writing, Review & Editing