

An anhanguerian pterodactyloid mandible from the lower Valanginian of Northern Germany, and the German record of Cretaceous pterosaurs

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The record of Cretaceous pterosaur remains from Germany is sparse. The material recovered to date includes the fragmentary holotypes of *Targaryendraco wiedenrothi* and *Ctenochasma roemeri*, as well as a few isolated pterodactyloid teeth and some indeterminate skeletal elements, together with a plaster cast of a large *Purbeckopus* manus imprint. Here, we report the discovery of a pterodactyloid pterosaur mandible from lower Valanginian strata of the Stadthagen Formation in the Lower Saxony Basin of Northern Germany. Based on the size and spacing of its alveoli, this fossil is attributable to the cosmopolitan Early Cretaceous pteranodontoid clade Anhangueria. Moreover, it represents the first and only known pterosaur from the Valanginian of Germany and is one of only a handful Valanginian pterosaur occurrences presently recognized worldwide. In addition to the approximately coeval *Coloborhynchus clavirostris* from the Hastings Bed Group of southern England, the Stadthagen Formation pterosaur mandible is among the stratigraphically oldest identifiable anhanguerians.

Key words: Pterosauria, Pterodactyloidea, Anhangueria, Cretaceous, Stadthagen Formation, Lower Saxony.

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Introduction

Pterosaurs were the first vertebrates to evolve an active volant lifestyle and were globally widespread from the Middle Triassic until their extinction at the end of the Cretaceous (e.g., Butler et al. 2009; Longrich et al. 2018). Among the paraphyletic succession of early pterosaur lineages, only the “short-tailed” pterodactyloids and anurognathids survived beyond the Jurassic–Cretaceous boundary, with pterodactyloids subsequently diverging into the Azhdarchoidea and Pteranodontoidea (Kellner 2003; Hone 2020). One of the most successful of these Cretaceous pterodactyloid clades were the Anhangueria, a cosmopolitan radiation of toothed and often large pteranodontoids, best known from the Aptian–Albian strata of Great Britain and Brazil (Rodrigues and

Kellner 2013), but ranging up into the Turonian elsewhere (Rodrigues and Kellner 2013; Pentland et al. 2019, Frey et al. 2020). To date, the stratigraphically oldest known anhanguerian is *Coloborhynchus clavirostris* Owen, 1874 from the upper Berriasian–lower Valanginian of England (Rodrigues and Kellner 2013; Pentland et al. 2019), which suggests possible origination of the group shortly after the Jurassic–Cretaceous transition.

Here we describe a new fragmentary mandible (RE 551.763.120 A 0333/1) of an anhanguerian pterodactyloid from the lower Valanginian of Northern Germany. This specimen was found by fossil collector and preparator Karl-Heinz Hilpert (formerly at the Geologisch-Paläontologisches Museum Münster) in the abandoned Sachsenhagen clay pit in Lower Saxony, and subsequently donated to the Ruhr

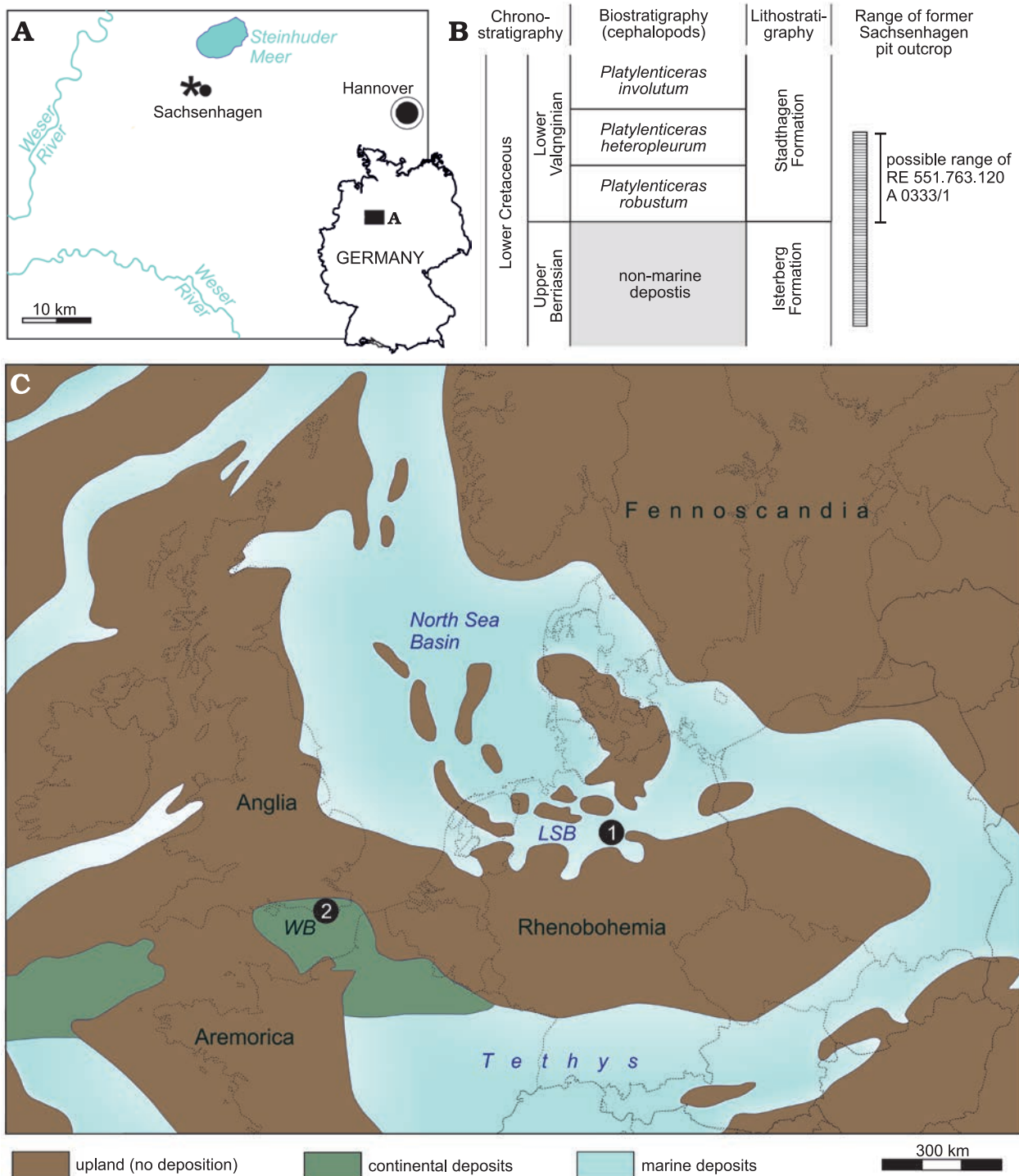


Fig. 1. **A**. Geographic location (asterisk) of the former Sachsenhagen clay-pit. **B**. Stratigraphical framework of the Lower Cretaceous in the former Sachsenhagen clay-pit. Modified after Mutterlose et al. (1997), Mutterlose (2017), and Erbacher et al. (2014a, b). **C**. Palaeogeographic reconstruction of Central Europe during the Valanginian–Hauterivian interval showing the position of Sachsenhagen (1) in the Lower Saxony Basin (LSB) and St. Leonard-on-Sea (2), the locus typicus of the approximately coeval *Coloborhynchus clavirostris*, in the Wessex Basin (WB). Modified after Mutterlose et al. (1997).

Museum Essen in 1998. RE 551.763.120 A 0333/1 is important, because together with *C. clavirostris* it represents one of the oldest known anhanguerian occurrences. In addition, it is one of only very few pterosaur specimens currently identified from the German Cretaceous (von Meyer 1851; Wild 1990; Hornung and Reich 2013; Lanser 2015) and is

also the first documented pterosaur fossil found in Germany that is of Valanginian age.

Institutional abbreviations.—GZG.IF, Ichnofossil collection, Geoscience Centre, University of Göttingen, Göttingen, Germany; LWL, LWL-Museum für Naturkunde, Münster, Germany; RE, Ruhr Museum, Essen, Germany; RPMH,

Römer-Pelizaeus-Museum Hildesheim, Hildesheim, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

Geological setting

The Sachsenhagen clay pit is located approximately 30 km west of Hannover (Fig. 1A) and was operated as brickworks from 1904 to 1986. Most of the quarry area has since been backfilled and used as a waste dump. The exposed profile spans a lithofacially mostly homogenous, pelitic succession of the upper Berriasian upper Isterberg Formation and lower Valanginian lower Stadthagen Formation (Fig. 1B). The transition between these units correlates with a shift from euryhaline to stenohaline conditions following a marine transgression (Kaufmann et al. 1980; Mutterlose 2017). Paleogeographically, the deposits were formed in a shallow gulf that inundated the Lower Saxony Basin as a southward extension of the North Sea Basin (Fig. 1C; see Mutterlose 2017).

Locality information indicates that RE 551.763.120 A 0333/1 derived from the lower Valanginian lower Stadthagen Formation spanning the *Platylenticeras robustum* and *P. heteropleurum* (Mutterlose 1984, 2017) ammonite zones. Zawischa (1992) and Frerichs and Girod (2017) documented a rich vertebrate fossil assemblage, including actinopterygians (Frerichs 2017a), plesiosaurs (Frerichs 2017b), the thalattosuchian crocodylomorph “*Enaliosuchus schroederi*” Kuhn, 1936 (see Schroeder 1923; Sickenberg 1961; Sachs et al. 2020), and additional indeterminate crocodyliform remains (Frerichs 2017b). Most of the material is currently located in private collections.

Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Pteranodontoidea Kellner, 1996

Anhangueria Rodrigues and Kellner, 2013

Anhangueria indet.

Fig. 2.

Material.—RE 551.763.120 A 0333/1, an incomplete mandible from the abandoned Sachsenhagen clay pit, Sachsenhagen, Lower Saxony, Germany (approximate coordinates 52°23'51" N, 09°15'18" E); *Platylenticeras robustum* or *Platylenticeras heteropleurum* ammonite biozones (NW-European ammonite province of the Sub-Boreal Realm: sensu Kemper et al. 1981, Marek and Shulgina 1996), lower Valanginian, Lower Cretaceous, Stadthagen Formation.

Description.—The preserved mandible includes the posterior section of the symphysis and parts of both dentaries and

angulars. The splenials have been disarticulated and are now lost. Thus, the Meckelian groove is exposed on the medial surfaces of both rami (Fig. 2). The mandible has a sub-circular cross-section anterior to the symphyseal contact. There is no evidence of a sagittal crest. The external ventral face of the mandibular rami is shallowly convex. The dorsal side of the symphyseal portion is strongly concave and has an irregular midline suture (Fig. 2A). A conspicuous lateromedial furrow is visible along the length of the rami ventral to the alveolar row. The post-symphyseal space is filled with sediment. However, both rami diverge at an angle of about 23° relative to the longitudinal axis.

The mandible has suffered some diagenetic crushing, resulting in a prominent longitudinal crack on the lateral surface of the left ramus (Fig. 2B). Especially the lateral surface of the right ramus forms two longitudinal bulges, resulting in an undulating surface. The postsymphyseal portions of both rami were previously broken and glued back to the symphysis. Finally, the entire surface area of bone and exposed matrix on RE 551.763.120 A 0333/1 has been varnished and painted at some stage of preparation. This has created a pattern of irregular grooves and ridges along the ventral face of the symphysis. We consider these to be artificial, yet some bulges and rugosities on the median ventral face of the symphysis and posterior parts of the rami could possibly be pathological (Fig. 2C).

Dentary: The dentaries form the mandibular sulcus, alveolar row, and the base of the Meckelian groove. The dorsal trace of the splenial suture is located ventrally adjacent to the alveoli. The ventral suture is not visible. The angular contacts are exposed on the lateral surfaces of the mandibular rami (Fig. 2B, D), however, there is no evidence of the coronoid contacts. On the right ramus, thin ridges extending parallel to the alveolar row and posterodorsally across the lateral surface posterior to the fifth alveolus (Fig. 2D) might border nerve and/or blood vessel channels.

Angular: The angulars form about the ventrolateral third of the external surfaces of the rami, and taper to the level of the posterior-most symphyseal alveoli. Medially, the angu-

Table 1. Linear measurements (in mm) of RE 551.763.120 A 0333/1. Alveoli measured in posterior direction. Asterisks indicate incomplete alveoli and/or alveoli filled with sediment.

Diastemae, ramus	left	14.25	16.84	12.42	12.65		
	right	15.94	16.68	12.76	12.14	13.58	
Alveolar length, ramus	left	4.56*	4.95	4.37*	4.27	4.54	
	right	4.42	4.17	5.20*	4.83	5.31*	5.20
Alveolar width, ramus	left	3.12*	2.99	2.87*	2.70	2.96	
	right	2.86	2.43	2.75	2.58	2.56*	2.81
Maximum preserved length					117.63		
Preserved symphysis, dorsal length					28.27		
Preserved symphysis, ventral length					40.00		
Dentary (left), maximum height					18.73		
Dentary (left), maximum width					5.86		

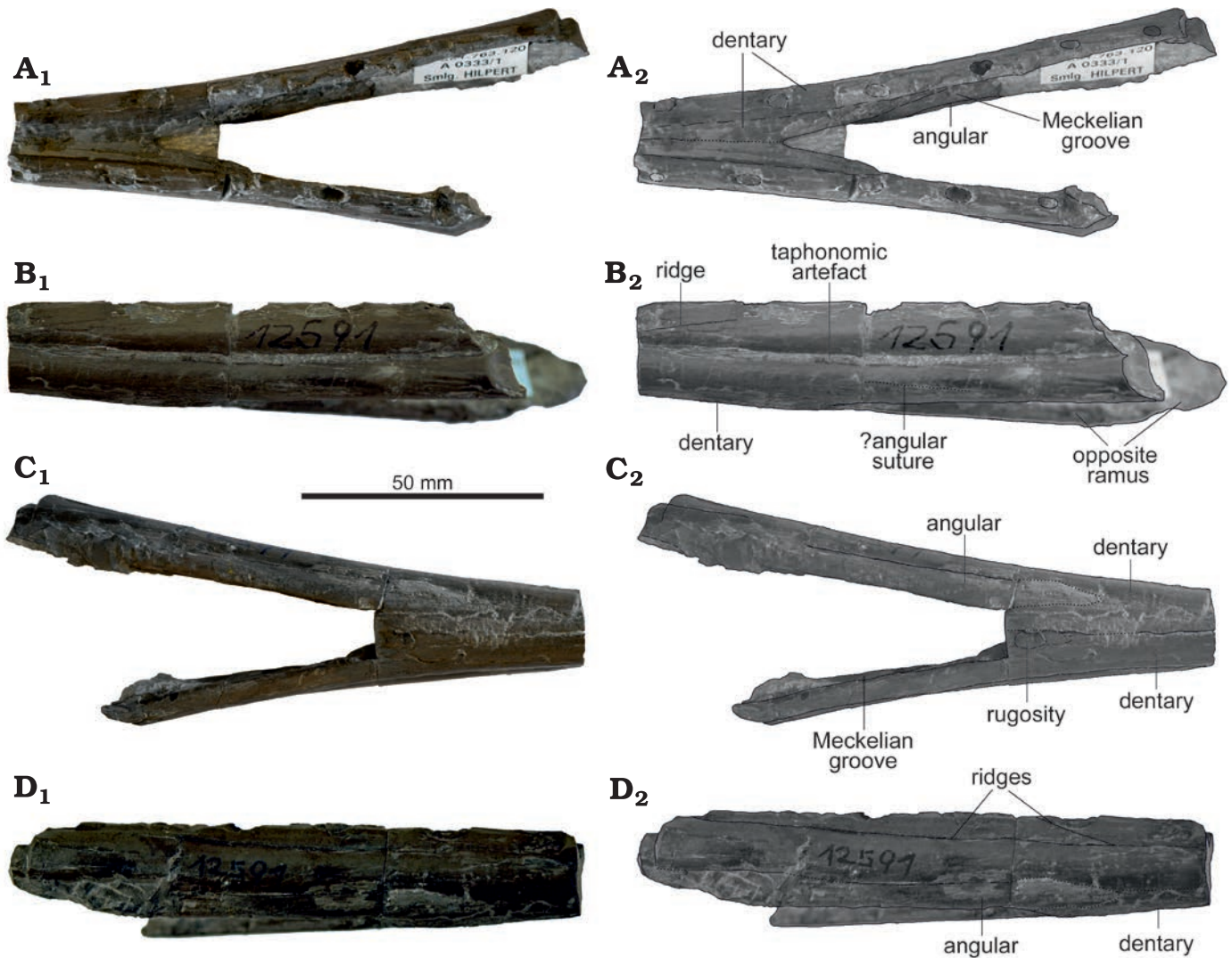


Fig. 2. Mandible of anhanguerian pterosaur RE 551.763.120 A 0333/1 from the lower Valanginian of Sachsenhagen (Northern Germany), in dorsal (A), left lateral (B), ventral (C), and right lateral (D) views. Photographs (A₁–D₁), explanatory drawings (A₂–D₂).

lars border the Meckelian groove and presumably sutured to the splenials dorsally.

Alveoli: Five alveoli are preserved on the left ramus, and six on the right; only two alveoli are placed adjacent to the symphysis on either side. They are about 1.5–1.9 times longer than wide, and each alveolus is slightly anteromedially directed (Table 1). The alveolar margins are flush with the surrounding bone. The interalveolar spaces are 2.5–4 times the length of the alveoli and increase in length posteriorly to the second preserved alveolus, but then decreases again further posteriorly (Table 1).

Discussion

Comparisons and classification.—Among Early Cretaceous toothed pterodactyls, RE 551.763.120 A 0333/1 differs from ctenochasmatids and boreopterids, as these latter possess large numbers of teeth in a “comb-like” arrangement

(Kellner 2003; Lü and Ji 2010; Jiang et al. 2014). *Lonchodraco* Rodrigues and Kellner, 2013 and other putative “lonchodectids”, such as *Lonchodectes compressirostris* Owen, 1851, *Serradraco sagitirostris* Owen, 1874, *Prejanopterus curvirostris* Vidarte and Calvo, 2010, or *Targaryendraco wiedenrothi* Wild, 1990, are distinguished from the specimen described herein by their “lanceolate” jaw outline, inter-alveolar spacing that is sub-equal to the corresponding alveolar length (Wild 1990; Pereda-Suberbiola et al. 2012; Rodrigues and Kellner 2013; Rigal et al. 2017), and alveolar margins raised to a pedestal (Unwin 2001; Rodrigues and Kellner 2013). Likewise, dsungaripterids have closely spaced alveoli, where the dental bone bulges to envelope the base of the tooth crowns (Martill et al. 2000; Witton 2013; Chen et al. 2020). In istiodactyliforms, the alveoli are even more densely packed (Lü et al. 2008; Witton 2013; Kellner et al. 2019).

By contrast, the alveolar morphology of RE 551.763.120 A 0333/1 is very similar to known anhanguerians, which typically have well-spaced alveoli along the mid- and pos-

terior sections of the mandible (e.g., Wellnhofer 1987; Elgin and Frey 2011; Rodrigues and Kellner 2013). A taxonomic assignment of RE 551.763.120 A 0333/1 within Anhangueria, however, proves to be difficult. Especially the taxa of the specimen-rich Cambridge Greensand and other Lower Cretaceous strata of Great Britain are often only based on anterior rostral fragments, prohibiting a direct comparison with RE 551.763.120 A 0333/1 (Rodrigues and Kellner 2013), where these elements are missing. This includes most notably the roughly coeval *Coloborhynchus clavirostris* from the adjacent British Wealden. But even in more completely known mandibles most diagnostic traits are restricted to the anterior part of the symphysis (e.g., Steel et al. 2005).

Nevertheless, RE 551.763.120 A 0333/1 is distinct from *Anhanguera piscator* Kellner and Tomida, 2000, “*Araripesaurus santanae*” Wellnhofer, 1985, *Mythunga* Molnar and Thulburn, 2007, and “*Tropeognathus robustus*” Wellnhofer, 1987, because it lacks inter-alveolar spaces that decrease in length towards the back of the jaw (Wellnhofer 1985, 1987; Veldmeijer 2003; Pentland and Poropat 2019). RE 551.763.120 A 0333/1 further differs from *Brasileodactylus araripensis* Kellner, 1984, *Ferrodraco lentoni* Pentland, Poropat, Tischler, Sloan, R.A. Elliot, H.A. Elliot, J.A. Elliot, and D.A. Elliot, 2019, *Maaradactylus spielbergi* Veldmeijer, 2003, and *Tropeognathus mesembrinus* Wellnhofer, 1987, because these taxa have inter-alveolar spaces that successively increase in length (Wellnhofer 1987; Veldmeijer 2003; Veldmeijer et al. 2009; Pentland et al. 2019). Lastly, unlike *Anhanguera piscator*, “*Araripesaurus santanae*”, and “*Santanadactylus araripensis*” Wellnhofer, 1985, RE 551.763.120 A 0333/1 possesses proportionately large alveoli compared to the transverse width of the mandibular ramus (Wellnhofer 1985; Kellner and Tomida 2000). Besides the alveolar pattern, RE 551.763.120 A 0333/1 differs further from *Maaradactylus spielbergi* by its more pronounced sulcus (Veldmeijer 2003).

The number of symphyseal teeth is variable among anhanguerians, ranging from six in *Cearadactylus atrox* Leonardi and Borgomanero 1985 (Unwin 2002; Vila Nova et al. 2014) or *Tropeognathus mesembrinus* to at least eleven in other far-related species, such as *Maaradactylus spielbergi*, *Brasileodactylus araripensis*, or *Aetodactylus halli* Myers, 2010 (Veldmeijer 2003; Veldmeijer et al. 2009; Myers 2010; Pinheiro and Rodrigues 2017). This makes it impossible to identify the position of the alveoli preserved in our specimen. Nevertheless, in the majority of anhanguerians preserving the mandible, the mandibular rami bear only two to five post-symphyseal teeth (Wellnhofer 1985, 1987; Kellner and Tomida 2000; Veldmeijer 2003; Vila Nova et al. 2014; Pinheiro and Rodrigues 2017), indicating the post-symphyseal alveoli preserved in RE 551.763.120 A 0333/1 may also represent the posterior-most alveoli of the mandible. A notable exception is *Aetodactylus halli*, which has 13 post-symphyseal alveoli (Myers 2010). However, *Aetodactylus halli*, together with the probably closely related *Cimoliopterus cuvieri* Bowerbank, 1851, differ from RE 551.763.120 A 0333/1 and other anhanguerians in their more densely packed teeth

(Myers 2010, 2015). Furthermore, they were found to nest outside Anhangueria by some recent phylogenetic studies (Pêgas et al. 2019).

Unlike RE 551.763.120 A 0333/1 and “*Santanadactylus araripensis*” (Wellnhofer 1985), the angulars in *Cearadactylus atrox* and *Anhanguera piscator* do not extend as far as the posterior end of the tooth row (Leonardi and Borgomanero 1985; Kellner and Tomida 2000). The condition of RE 551.763.120 A 0333/1 is closer to “*Santanadactylus araripensis*”, where the lateral portion of angular reaches almost the level of the posterior-most alveolus, which is in this taxon the fourth post-symphyseal tooth (Wellnhofer 1985). The same author interpreted the angular in “*Araripesaurus santanae*” to extend distinctly beyond the tooth bearing portion of the mandible, reaching at the least the level of the in anterior direction fifth alveolus. However, Kellner and Tomida (2000) argued that the angular may be significantly shorter in both “*Santanadactylus araripensis*” and “*Araripesaurus santanae*” but based this on the assumption of a congeneric relationship with *Anhanguera piscator*. This cannot be confirmed, because “*Santanadactylus araripensis*” and “*Araripesaurus santanae*” are considered to be nomina dubia (Pinheiro and Rodrigues 2017). Irrespectively, the angular of RE 551.763.120 A 0333/1 is most closely comparable to “*Santanadactylus araripensis*” as described by Wellnhofer (1985), although the anterior extremity is less anteriorly tapered in RE 551.763.120 A 0333/1.

Overall, complete mandibles are only barely known in anhanguerians, and often the mandibular bones are fused beyond distinction, suggesting these specimens may represent adult individuals (Kellner and Tomida 2000; Vila Nova et al. 2014). Evidently, RE 551.763.120 A 0333/1 likely derived from an osteologically immature animal.

Cretaceous pterosaurs from Germany.—Germany is world famous for its record of articulated Upper Jurassic pterosaur remains (e.g., Wellnhofer 1970, 1978; Bennett 2002, 2007; Tischlinger 2010; Hone et al. 2013; Tischlinger and Frey 2013). Conversely, pterosaur fossils of Cretaceous age are extremely rare despite the earliest documented occurrences dating back to the 19th century. This is also in stark contrast to other Cretaceous pterosaur-bearing sites in the world with a rich pterosaur diversity like the northeastern Brazilian Santana Group (e.g., Wellnhofer 1985, 1987; Kellner and Tomida 2000; Unwin 2002), or the British Wealden and Cambridge Greensand (e.g., Unwin 2001; Rodrigues and Kellner 2013; Rigal et al. 2017). The German record is currently restricted to the Lower Cretaceous. However, only the Valanginian and Hauterivian pterosaur specimens derive from strata that were deposited in some distance from the paleo-coastline. All other remains originated from non-marine, lagoonal to fully limnic and fluvial environments.

The first Cretaceous pterosaur find described from Germany has been the holotype of *Ctenochasma roemeri* (non-catalogued, von Meyer 1851) from the lower Berriasian Münden Formation of the Deister region of Lower Saxony. It

consisted only of a fragmentary mandible, but unfortunately the original specimen in the collection of Clausthal is not traceable (SS personal observation).

Similarly, Hornung and Reich (2013) described a right manus track (GZG.IF.00102), assignable to the large pterosaur ichnotaxon *Purbeckopus* cf. *pentadactylus* Delair, 1963. This positive plaster cast derived from an imprint found in upper Berriasian silicilastics of the Deister Formation near Bückeburg and was made sometime around 1935. However, the original may have never been collected, and the cast was likely produced in situ.

A fragmentary wing phalanx and jaw elements (GZG.STR.50291, GZG.STR.50292, RPMH “Wd. 025”) from the upper Berriasian Fuhse Formation near Sehnde in Lower Saxony have yet to be described in detail (Hornung 2013). Additional isolated remains have been recovered from upper Valanginian–lower Hauterivian deposits in the Leine Uplands of Lower Saxony and include what was identified as a metacarpal IV and holotype of “*Ornithocheirus hilsensis*” (Koken, 1883). However, a pterosaurian affinity was disputed (e.g., von Meyer 1884; Williston 1885, 1886; but see also Koken 1885, 1886), and the bone has recently been recognized as the pedal phalanx of a theropod dinosaur (Hornung 2020). Today “*O. hilsensis*” is considered a nomen dubium and the whereabouts of the specimen are unknown (Hornung 2020).

The comparatively best-preserved pterosaur from the Cretaceous of Germany is the holotype of *Targaryendraco wiedenrothi* (SMNS 56628) from the lowermost Hauterivian of the Stadthagen Formation near Hannover in Lower Saxony. Wild (1990) initially named it *Ornithocheirus wiedenrothi*, although its assignment to the “wastebasket” genus *Ornithocheirus* Seeley, 1869, is widely debated (Fletcher and Salisbury 2010; Ford 2013; Rodrigues and Kellner 2013; Abel et al. 2019; Pêgas et al. 2019). Fletcher and Salisbury (2010) grouped it in Ornithocheiridae close to *Aussiedraco molnari* Kellner, Rodrigues, and Costa, 2011, and another indeterminate specimen. Ford (2013) considered the species to be a “lonchodectid” and recombined it as *Lonchodectes wiedenrothi*. However, Rodrigues and Kellner (2013) argued against the validity of *Lonchodectes* and an affinity of the specimen as *Ornithocheirus* to be indeterminable, whereas Abel et al. (2019) reiterated a “lonchodectid” affinity. In a subsequent publication, Pêgas et al. (2019) redescribed the material as *Targaryendraco wiedenrothi* and found it to nest outside of Anhangueria, close to *Aussiedraco molnari* and *Barbosania gracilirostris* Elgin and Frey, 2011.

Lastly, Lanser (2015) reported several isolated teeth of putative ornithocheirids from various middle Barremian–lower Aptian karst-fillings in the Sauerland, North Rhine-Westphalia.

RE 551.763.120 A 0333/1 adds to this sparse record as the currently only recognized Valanginian pterosaur. Furthermore, it is one of only a handful Valanginian pterosaur remains in the world (Barrett et al. 2008; Cadena et al. 2020). Of these, only the probable Valanginian *C. clavirostris* can be confidently assigned to Anhangueria, although,

other fragmentary finds may represent anhanguerians as well (Cadena et al. 2020). Finally, RE 551.763.120 A 0333/1 is, next to the teeth described by Lanser (2015), the only clear evidence for anhanguerian pterosaurs found in Germany.

Pterosaurs most frequently occur in limnic, lagoonal, and pelagic paleoenvironments (e.g., Wellnhofer 1970; Wang and Zhonghe 2006; Hone et al. 2018). Given that such depositional settings are typical of the German Cretaceous, the observed scarcity of pterosaur fossils is likely not reflecting their paleoecology, but rather the preservational biases of their fragile bones, and the reduction of Valanginian carbonate platforms in conjunction with a global cooling (Gréselle and Pittet 2010), which might have hindered the formation of Konservatlagerstätten (Butler et al. 2009). This may also explain the globally sparse record of Valanginian pterosaurs. Indeed, sampling is another evident limiting factor relative to other European Early Cretaceous pterosaur assemblages (e.g., the Cambridge Greensand, Unwin 2001; Ford and O’Connor 2004), and suggests that future exploration will likely yield new discoveries.

Conclusions

RE 551.763.120 A 0333/1 is important because it represents the only unambiguous pterosaur fossil of Valanginian age recovered from Germany to date.

RE 551.763.120 A 0333/1 is among only a handful of Valanginian pterosaur occurrences yet identified worldwide.

The British *Coloborhynchus clavirostris* is the only other confidently assigned anhanguerian taxon from the respective time interval, representing together with RE 551.763.120 A 0333/1 the oldest known records of this group.

The sparseness of the German Cretaceous pterosaur record may be best explainable by sampling and preservation biases and does not reflect a paleobiological signal.

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