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RESEARCH PAPER

Enigmatic fragment possibly marks the first pterosaur record from the Lower Toarcian of Grimmen, NE Germany

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Abstract
Pterosaurs are a well-known component of many Mesozoic fossil ecosystems worldwide. To date, marine and terrestrial faunal elements such as cephalopods, fish, marine reptiles, dinosaurs and insects have been discovered in the Lower Jurassic clay pit near Grimmen (Western Pomerania). A new fragmentary bone is thoroughly described herein and interpreted to represent the first evidence for the presence of pterosaurs in this locality.

Keywords Jurassic · Fossil · Pterosaur · Germany · Lagerstätte · CT

Introduction

In Grimmen, terrestrial vertebrates are described from the *elegantulum* or *capillatum* concretions, respectively (Haubold, 1990; Schade & Ansorge, 2022; Stumpf et al., 2015; Ansorge et al., 2024), but as of yet, no dinosaurs or other terrestrial vertebrates were known from the slightly younger *exaratum* subzone. The small, flat, and well-laminated *exaratum* concretions, intercalated in the grey-green clay of the Lower Toarcian of the Grimmen clay pit, are a valuable source of the marine life in the Northeast German Grimmen Formation (*falciferum* zone) and the terrestrial life, mainly insects, from the Scandinavian mainland and adjacent islands on the Ringkøbing–Fyn–Møn–Rügen High (Ansorge, 2003; Ansorge et al., 2024). Although pterosaurs are known with two dominant genera, *Dorygnathus* and *Campylognathoides*, from many Lower Toarcian localities (Germany Banz, Mistelgau, Franconia: Theodori, 1830, Wild, 1971; Holzmaden, Swabia: Plieninger, 1894, Arthaber, 1919, Broili, 1939, Padian, 2008; Schandelah, Lower Saxony: Wellnhofer & Vahldiek, 1986, Hübner et al., 2020; France Lorraine: Delsate & Wild, 2000, Buffetaut et al., 2010; UK Whitby, Yorkshire: Newton, 1888, O'Sullivan et al., 2013), no pterosaur remains were found in Dobbertin or Grimmen in the NE German Basin. Here, we present the first record of an isolated terrestrial vertebrate bone, tentatively assigned to a pterosaur, from the *exaratum* subzone of the clay pit near Grimmen and discuss its possible affinities.

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This is a contribution to the special issue honouring Professor Ekkehard Herrig on his 90th birthday.

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Materials and methods

J.A. found the new specimen GG 510 in 2022 and subsequently prepared it. The surface of the bone has been steamed with ammonium chloride (NH_4Cl) and moistened with alcohol to enhance visibility of details for some macrophotographs. We scanned the specimen GG 510 to reveal its inner structure and the morphology of the side that is still embedded within the sedimentary matrix, using the microcomputed tomography device MicroXCT-200 (housed in the Imaging Center of the Department of Biology, University of Greifswald). Parameters – voltage: 60 kV, X-ray tube current: 133 µA, exposure time: 2 s, voxel size: 0.0297 mm. The figures showing CT data were produced with the software Amira (6.1), based on tiff files (16 bit). GG 510 is housed in the Geology collections of the Institute of Geography and Geology of the University of Greifswald, Germany.

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Description

The blackish fragment is a long (c. 27 mm) and slender (max. width of 4 mm close to the mid-length and the overhang) element which is broken on both ends but shows a largely intact surface (Figs. 1, 2). The cortical thickness is c. between 0.1 mm and 0.7 mm on the non-bifurcated part (Fig. 2d) and c. 0.25 mm on the large branch of the

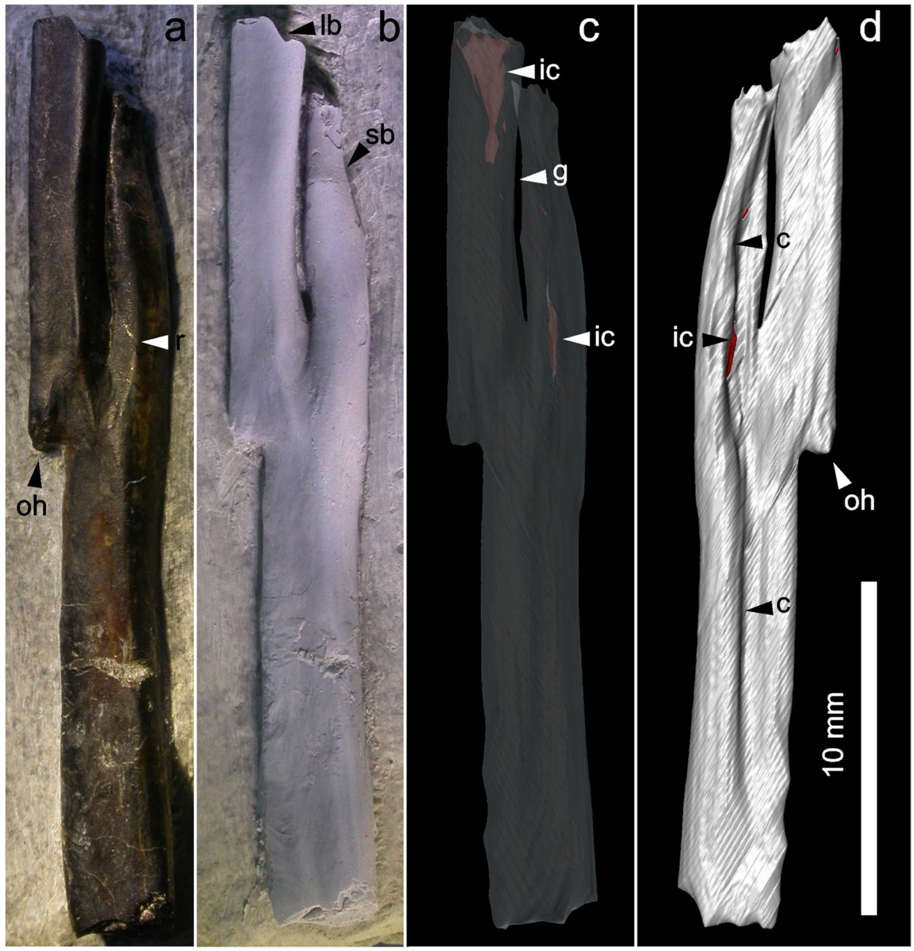

Fig. 1 **a** GG 510, fragmentary tibiofibular (?) of an unknown pterosaur; **b** dusted with ammonium chloride; **c** reconstructed CT model with internal cavities; **d** reconstructed CT model exposing the side of GG 510 that is still embedded in the sedimentary matrix. *c* concavity, *g* gap, *ic* internal cavity, *lb* large branch, *oh* overhang, *r* ridge, *sb* small branch

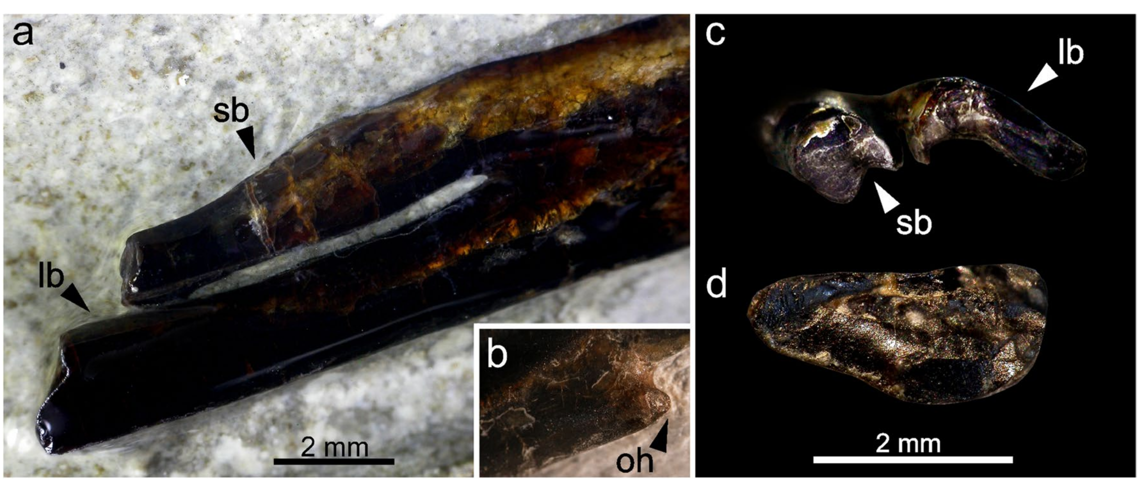

Fig. 2 **a** GG 510, fragmentary tibiofibular (?) of an unknown pterosaur, moistened with alcohol; **b** the overhang; **c**, **d** cross-sections of **c** the potential proximal part and **d** of the potential distal part. Scale bar in **a** applies also to **b**. *lb* large branch, *sb* small branch, *oh* overhang

bifurcated part (Fig. 2c). In contrast to many Jurassic pterosaur bones, GG 510 is not compressed or fractured because it is preserved in a limestone concretion that formed early during diagenesis; hence, taphonomic alterations of the general morphology seem to be absent. There is a bifurcation on its mid-length where the larger, straight branch exhibits an overhang to the border of the element; the overhang is slightly pointed (but seems to have originally been a little longer) and has a very small notch separating it from the margin of the undivided part of the element (Fig. 2b). The other branch is slightly shorter, smaller and somewhat bowed close to the bifurcation, where the narrow gap between the two branches is widest (Figs. 1b, c; 2a). The small branch almost touches the large one in their common further extent. The bifurcation does not only separate the two branches in one dimension (in the direction of the margins in top view) but the small branch also slightly dips into the sedimentary matrix. There is a ridge running from one margin of the one-branched part of the fragment to the bifurcation (Fig. 1a). Here, the ridge bifurcates as well but is more prominent on the inner side of the large branch than on its counterpart; the bifurcated ridge produces a slight depression between the branches. Where the ends of the specimen are broken, the cross-sections of the one-branched end and the large bifurcated one are somewhat sub-oval, whereas the smaller bifurcated end is rather circular (Fig. 2c, d). A cortex is discernible from the medullary realm in the cross-section of the large branch of the bifurcated end and the non-bifurcated end (Fig. 2c, d), however, no trabeculae are identifiable. Additionally, the fossil bone has been mineralogically filled and altered in a way that extinguished any additional bony details. The microCT data suggest that the surface of GG 510 that is still covered in sediment is largely longitudinally concave on the one-branched and the smaller bifurcated part, however, rather flat and even on the larger branch (Fig. 1d). There seems to have been a (now filled) cavity within the large branch, close to its breakage. Additionally, there are minor cavities close to the mid-length of the small branch (Fig. 1c, d).

Discussion

The fragment GG 510 is not associated with other fossil remains, so it can hardly be suggested that it was a part of a regurgitated pellet (regurgitalites; Thies & Hauff, 2013, Hoffmann et al., 2020, Gordon et al., 2020); it may be more likely that it was part of a drifting and decaying carcass. The concavity and the internal cavity pattern described above may be an indication for damage on the aspect of the specimen that is still covered, and the longitudinal depression may actually represent the former medullary cavity. A wide array of fused, bifurcating elements is known in vertebrates. The fused tibia and fibula of the giant insectivore *Deinogalerix koenigswaldi* from the Miocene of Italy may be one arbitrary mammal example here (Freudenthal, 1972; Villier & Carnevale, 2013). Also, uncinate processes of bird ribs (Codd, 2010) and reptilian gastralia of e.g., stem-turtles (Schoch & Sues, 2018), plesiosaurs (Martin et al., 2007; Stumpf et al., 2016) and dinosaurs (Claessens, 2004) may, if fragmented and isolated, resemble the appearance of GG 510. One of the oldest known anurans (Pliensbachian of USA; Shubbin and Jenkins 1995) is preserved with a fused radioulna, and while most extant frog radioulnae are comparably stout, also slender and somewhat undulating morphologies are known (Keeffe & Blackburn, 2022). Additionally, fish remains, e.g., the axonosts of the anal fin, can spot a wide array of morphologies (e.g., Maxwell & Stumpf, 2017). However, for morphological, structural, paleogeographical and distributional reasons, we tentatively opine a pterosaur tibiofibula to be the more likely identity of GG 510. Among others, a fused, bifurcated lower leg is also known from the Early Jurassic (Toarcian) rhamphorhynchid pterosaur *Dorygnathus banthensis* from localities in Germany and France (e.g., Buffetaut et al., 2010; Hübner et al., 2020). In this taxon, Padian (2008) notes that tibia and fibula are usually similar in length and supposedly immature individuals can lack a fusion (see Kellner, 2015 for another report of a missing fusion in a pterosaur tibia and fibula). Most individuals, however, display a condition where the fibula is fused to the tibia along about two-thirds of their common distal course (Padian, 2008). The fibula tapers towards the fusion with the tibia distally and widens proximally, where both contact each other via a lateral trochanter of the tibia (Padian, 2008). A pronounced overhang, as found in GG 510, however, is unknown so far. Usually, tibia and fibula represent straight beams in pterosaurs, whereas at least the small branch of GG 510 is somewhat undulating which in turn produces an irregular gap (interosseous space) in between. Furthermore, whereas the tibia as the larger element commonly describes the axis of the lower leg (while the fibula slightly deviates), this is not clearly the case in GG 510. Whereas in most pterosaurs, the tibia and fibula are oriented sub-parallel to each other and produce a relatively long, regular gap in between, the anurognathid pterosaur *Sinomacrops bondei* (Callovian–Oxfordian of China) seems to bear only a very short gap between the two elements, with a proximal and distal portion where both seem very close but not fused (Wei et al., 2021). In this respect, the lower leg of *Sinomacrops* resembles GG 510, however, anurognathids are known from the late Middle or Late Jurassic onwards (except for *Dimorphodon weintraubi*; see Wei et al., 2021). Additionally, the tibiofibula of other anurognathids seem to show the 'usual' pterosaur features described above (Bennett, 2007; Döderlein, 1923, 1929; Lü et al., 2018). Furthermore, to our knowledge, the exact area in which tibia and fibula separate (or fuse) in pterosaurs is not well exposed and depicted in the literature (with the exception of the pterodactyloid *Balaenognathus maeuseri*; Martill et al., 2023). Instead, the tibia-fibula connection is mostly somewhat covered due to the preserved position and orientation of both, and the fibula just emerges next to the tibia (Buffetaut et al., 2010; Hübner et al., 2020; Augustin et al., 2022). Hence, some sort of overhang may not be unusual or, like the somewhat irregular course of the small branch of GG 510, is possibly due to (pre-diagenetic) preservation or represents a pathologic feature. If the latter option is the case, it is surprising that no obvious irregular (e.g., bulbous) remodelling of the bone is present (see Foth et al., 2015). In case GG 510 represents the tibiofibula of a pterosaur, this fragment was located on around the proximal third of the lower leg and because of the advanced degree of fusion (where large and small branches meet, they are indistinguishably merged with each other; also reported in Buffetaut et al., 2010) may have belonged to a relatively old individual (see Kellner, 2015 for ontogenetic considerations of pterosaur remains).

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Author contributions M.S. designed the project and segmented the CT data. J.A. unearthed GG 510 and prepared the specimen. M.S. and J.A. prepared the figures, interpreted the data and wrote the manuscript.

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Declarations

Conflict of interest The authors declare no conflict of interests.

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